

The seasonality of reproduction in photoperiod responsive and nonresponsive northern red-backed voles (*Myodes rutilus*) in Alaska

K.T. Stevenson, I.G. van Tets, and L.A.I. Nay

Abstract: High-latitude arvicoline rodents usually reproduce in warmer months, but winter breeding has been documented in several species, including the northern red-backed vole (*Myodes rutilus* (Pallas, 1779) Wilson and Reeder, 2005; formerly *Clethrionomys rutilus* (Pallas, 1779)). We tested whether the reproductive condition of the species is linked to changes in environmental parameters or its body condition, and we tested the frequencies at which different reproductive phenotypes are exhibited under field and laboratory conditions. Free-living voles in south-central Alaska reached peak reproductive organ masses in spring (females) and early summer (males). Between-subject comparisons showed an effect of body mass, photoperiod, percent fat, temperature, and snow depth on reproductive organ masses, depending on the sex and breeding period ($p < 0.05$). One instance of late-summer photoperiod nonresponsiveness was observed, but we detected no winter breeding. Captive male voles given food ad libitum and housed at room temperature exhibited strong phenotypic variation in testis mass in response to short photoperiods. The percentage of nonresponders was 28.2% and was within the known range of nonresponsiveness for lower latitude species (20%–40%). Thus, photoperiod nonresponsive morphs are conserved in at least one arctic and subarctic species at frequencies comparable to lower latitude voles despite no observance of winter breeding in the field. Voles exhibit reproductive elasticity and may breed in winter if environmental conditions enable them.

Résumé : Les rongeurs arvicolinés des hautes latitudes se reproduisent généralement durant les mois plus chauds, mais on a signalé des cas de reproduction hivernale chez plusieurs espèces, en particulier chez le campagnol boréal (*Myodes rutilus* (Pallas, 1779) Wilson and Reeder, 2005; antérieurement *Clethrionomys rutilus* (Pallas, 1779)). Vous avons testé si la condition reproductive chez cette espèce est reliée aux changements des variables environnementales ou à sa condition corporelle et avons vérifié les fréquences auxquelles les divers phénotypes reproductifs se présentent dans des conditions de terrain et de laboratoire. Chez les campagnols libres en nature dans le centre-sud de l'Alaska, la masse des organes reproducteurs atteint son maximum au printemps (femelles) et au début de l'été (mâles). Des comparaisons entre individus révèlent un effet de la masse corporelle, de la photopériode, du pourcentage de graisses, de la température et de la profondeur de la neige sur la masse des organes reproducteurs en fonction du sexe et de la période de reproduction ($p < 0,05$). Nous avons observé un cas d'absence de réaction à la photopériode en fin d'été, mais détecté aucune reproduction hivernale. Des campagnols mâles en captivité, nourris ad libitum et maintenus à la température de la pièce, montrent une importante variation phénotypique dans leur masse testiculaire en réaction aux photopériodes courtes. Le pourcentage d'individus sans réaction était de 28,2 %, ce qui est dans la gamme connue d'absence de réaction chez les espèces de latitudes plus basses (20 % – 40 %). Ainsi, les formes qui ne réagissent pas à la photopériode sont conservées chez au moins une espèce arctique et subarctique à des fréquences comparables à celles trouvées chez les campagnols de latitudes plus basses, même si aucune reproduction hivernale n'a été observée en nature. Les campagnols possèdent une plasticité reproductrice et peuvent se reproduire en hiver si les conditions du milieu le permettent.

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Introduction

Arvicoline rodents (voles and lemmings) are small mammals that strongly influence plant growth and distribution in northern ecosystems (Pitelka 1964; Schultz 1964; Howe and Brown 1999) and that form a major prey resource for pred-

tory birds and mammals (Wilson and Bromley 2001; Gilg et al. 2003). In nontropical species, reproduction is usually triggered by day length and is linked to other environmental variables. The high energy costs of winter thermoregulation and summer reproduction create an energetic bottleneck that shapes the seasonality of breeding (Levins 1968; Nelson et

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al. 1998). Reproduction usually occurs during warmer months and longer day lengths in most temperate-zoned and high-latitude arvicoline rodents (Sealander 1967; Batzli and Pitelka 1971; Nelson 1985b; Hasbrouck et al. 1986; Negus and Berger 1998; Wallen and Schneider 2000; McNabb 2002). It ceases prior to winter and is usually characterized by regression of reproductive organs. Yet, some are able to overcome these reproductive challenges and constraints to successfully breed out of season. Amazingly, almost every species studied has been documented to have bred in winter (Nelson 1987; Bronson 1989; Bronson and Heideman 1994; Nelson et al. 1998; Gockel and Ruf 2001) — even arctic and subarctic voles and lemmings (Mullen 1968; Whitney 1976; Eriksson 1984; Hansson 1984; Millar 2001). Winter breeding is very rare, however, and does not occur in all individuals or all years, suggesting an environmental or nutritional influence upon its frequency. Photoperiod nonresponsive morphs are unique individuals within small-mammal populations that possess the genetic capability to maintain the size and function of their reproductive structures under short day lengths (Nelson 1987; Kriegsfeld et al. 2000a). In lower latitude vole colonies, approximately 20%–40% of individuals housed at room temperature and given food and water ad libitum exhibit the nonresponsive phenotype when exposed to short days (Nelson 1987; Kriegsfeld et al. 2000a). Nonresponsiveness has not been examined closely in arctic and subarctic species.

Frequencies of winter breeding have not been compared across a latitudinal gradient, but it seems plausible that there could be selection against the photoperiod nonresponsive trait (i.e., winter-breeding ability) in high-latitude regions which might contribute to a decrease in its frequency. Winters are harsher, and individuals that attempt to breed in winter could be less likely to survive and (or) have their offspring survive. This might cause a decrease in the frequency of nonresponsive morphs in small-mammal populations at high latitudes.

Reproduction is an expensive process for arvicoline rodents, and the timing of breeding is critical for maximizing reproductive fitness. The costs of gestation and lactation can more than double total energy requirements in voles (Kacmarski 1966; Migula 1969; Millar 1977; Innes and Millar 1981), and they can triple or quadruple energetic costs in other mammalian taxa (Bronson 1989; Clutton-Brock 1991). Both male and female arvicoline rodents live a much faster pace of life in spring and summer through increases in mating interactions, activity, foraging, and growth rates (Stebbins 1974; Batzli and Esseks 1992; Zuercher et al. 1999; Getz et al. 2005; Stevenson et al. 2009). In fact, voles born in spring have been known to reach maturity and produce litters by the end of summer in the same year (Whitaker 1996).

In winter, voles do not migrate or hibernate but remain active under the snow (Sealander 1967; Stebbins 1974; West 1977). They occupy the subnivean space and employ changes in their body mass, overall physiology, social structure, and activity to save energy (Sealander 1967, 1972; Stebbins 1974; West 1977; Wolff and Lidicker 1981). Despite these seasonal changes in physiology and behavior, voles and lemmings must still use large amounts of energy to maintain a relatively constant body temperature via shiv-

ering and nonshivering thermogenesis. Voles that maintain reproductive structures to breed in winter are also likely to maintain body conditions conducive to fueling and (or) maintaining excess reproductive tissues, mating interactions, and offspring.

Nonphotoperiodic cues, such as temperature, precipitation, food availability, and the ingestion of plant secondary compounds in green vegetation have been proposed and (or) affirmed as alternate signals cuing for reproduction in species inhabiting seasonal environments (Negus and Berger 1977; Negus and Berger 1998; McNabb 2002), but photoperiod has been regarded as the dominant cue (Nelson 1987; Kriegsfeld and Nelson 1999; Wallen and Schneider 2000; McNabb 2002). It has been clearly established that males respond to changes in photoperiod (Sealander 1967; Batzli and Pitelka 1971; Whitney 1976; Nelson 1985a), but the cause of female readiness in the wild is less well known and may be species-specific. Females may be responsive to one or more environmental variables (Meek and Lee 1994), but they are more commonly thought to respond to stimulation from a reproductive male (e.g., copulation or some olfactory cue; Breed 1972; Odberg 1984; Clulow and Mallory 1970).

The effect of body condition or nutritional state on the reproductive timing and condition of arvicoline rodents is also not entirely known. Previous studies have shown an influence of nutrition and food availability on reproductive state (Cengel et al. 1978; Hasbrouck et al. 1986), but body-fat levels do not necessarily correlate to reproductive condition (Batzli and Esseks 1992) and may or may not change seasonally (Cengel et al. 1978; Batzli and Esseks 1992; Zuercher et al. 1999). We suggest Bronson (1989) for a thorough review on the effects of diet, food restriction, temperature, and other environmental parameters on the reproductive systems of small mammals.

The primary aim of this study was to determine the timing of reproduction, the pattern of organ-mass change, the factors affecting timing and seasonal change, and the frequency of photoperiod nonresponsiveness in the northern red-backed vole, *Myodes rutilus* (Pallas, 1779) (Wilson and Reader 2005; formerly *Clethrionomys rutilus* (Pallas, 1779)), an arvicoline rodent that inhabits both subarctic and arctic climates and is known to have bred in winter (Khlebnikov 1970; Whitney 1976, 1977; Hansson 1984). Maximum organ size is often correlated with peak reproductive activity in small mammals (Brown 1997), while decreases in reproductive organ masses correspond to declines in breeding (Benton 1955). Therefore, we trapped voles at regular intervals over multiple seasons in south-central Alaska and dissected them to test for correlations between reproductive organ masses and environmental and body-condition parameters. In the aforementioned studies that report reproductive data for *M. rutilus*, occurrences of winter breeding were moderate at a lower latitude site in the Western Sayan Mountains near the Russian–Mongolian border (Khlebnikov 1970), but very rare at higher latitude sites in interior Alaska (Sealander 1967; Whitney 1976, 1977; Hansson 1984). We predicted that out-of-season breeding would be more frequent in coastal south-central Alaska (61°N) than in interior Alaska because of longer winter day lengths, relatively milder temperatures, more abundant ground-level vegetation, and generally higher levels of snowfall. Finally, we used a

controlled, captive experiment to test whether the frequency of nonresponsive morphs in this high-latitude species is conserved relative to temperate-zoned species, and we tested our hypothesis that a relationship exists between reproductive phenotype and body mass.

Materials and methods

Field study

Myodes rutilus were collected from trapping grids around Chugach State Park, Alaska (61°N), between November 2004 and August 2006. Animals were captured and treated following procedures approved by the University of Alaska Anchorage Institutional Animal Care and Use Committee (IACUC protocol no. 2005vanT1). The breeding condition of voles was first assessed externally by the presence of descended testes in males and by palpation, occurrence of lactation, or presence of open pubic symphases in females (Batzli and Pitelka 1971). We dissected and weighed the testes, epididymides, and seminal vesicles of males and the ovaries and uterus of nonpregnant females. Seven of the females trapped during the study were in varying stages of pregnancy. Their paired ovary masses were included in the analyses, but their uterine masses were excluded. The testes of males were examined histologically to confirm the reproductive and nonreproductive state of these animals.

We used mass thresholds to distinguish age classes in *M. rutilus* in early- and late-summer seasons (Sealander 1967; Whitney 1976; Zuercher et al. 1999). In summer (June through September), voles weighing <13 g were considered immature juveniles, those ranging from 13 to 17.5 g were classified as adolescents, and those >17.5 g were determined to be of adult age (Zuercher et al. 1999). In the remaining seasons, all animals were classified as adults.

The compiled reproductive organ mass data set was bimodal owing to the short transition period between nonreproductive and reproductive periods. Therefore, we divided the compiled reproductive organ mass data into two subsets corresponding to a general breeding period (1 April to 25 August) and a general nonbreeding period (26 August to 31 March). The reproductive data in each of the resulting subsets were log-transformed to achieve normality. Fat mass was determined by scanning each animal with a dual-energy X-ray absorptiometry (DXA) apparatus (Lunar/GE PIXI Mus2) that was previously validated for use in *M. rutilus* to assess body composition (Stevenson and van Tets 2008). The equation for fat mass in free-living voles from this validation was used to obtain actual fat-mass values.

Photoperiod (hours of day light) was recorded on each capture date. Mean ambient temperature (T_a) was recorded every hour by data loggers (Hobo, Inc.) that were placed at a height of 2 m near our trapping sites. We used data from National Resources Conservation Services (NRCS) SNOTEL sites in Chugach State Park, Alaska (Anchorage Hillside), and Moraine, Alaska, to confirm ambient temperature measurements and obtain levels of snow depth and precipitation. SPSS version 14.0 (SPSS Inc., Chicago, Illinois) was used for all statistical analyses. We used analysis of covariance (ANCOVA) to determine between-subject effects of body condition and environmental variables on reproductive organ masses, and we used simple regressions to character-

ize the relationship between photoperiod and body condition.

Laboratory study

From 2006 to 2007 we bred and raised captive *M. rutilus* from a pre-existing captive colony in animal quarters at the University of Alaska Fairbanks campus (IACUC protocol no. 06-53). The colony consisted of animals trapped in different locations around interior Alaska in 1999 and 2004, and was diverse in age and activity pattern (Tavernier et al. 2004). We selected a homogenous subset of captive male voles that had been raised and maintained on long photoperiods (16 h light (L) : 8 h dark (D)). These voles were then age-matched and categorized into three groups: pre-study control ("PRE", 16 h L : 8 h D, $n = 20$), continued long-day treatment ("LD", 16 h L : 8 h D, $n = 18$), and short-day treatment ("SD", 8 h L : 16 h D, $n = 78$). Based on earlier work, we elected to place substantially more animals in the SD group to increase the chances of detecting non-responsive morphs in the event that the percentage of this morph was low and to assess the frequency of all three morphs with strong confidence (Kriegsfeld et al. 2000a; Kriegsfeld et al. 2000b). Approximately 30 days prior to the study, our male subjects were separated from the colony and placed in individual cages. LD and PRE cages were kept on racks in a photoperiod-controlled room, while SD cages were kept in photoperiod-controlled chambers (up to 12 animals per chamber). All subjects remained on long photoperiods (25 °C) at room temperature during this time and were given food and water ad libitum.

Prior to the start of the study while all animals were on long days, we measured the external testis volume and body mass of each animal. We anesthetized voles using an isoflurane vaporizer interfaced with a plastic holding container and a re-breathe bag. We weighed each animal, shaved the left side of the scrotum, and obtained a left testis length and width (to the nearest 0.01 mm) using digital calipers. Testis volume was measured every 2 weeks, at which time a retro-orbital blood sample was collected from a subset of only 10 animals for use in a different study. The technique is a standard laboratory procedure (Halpern and Pacaud 1951; Hoff 2000) and caused no harm, as voles were already anesthetized to obtain measurements of testis size. Blood samples were taken within 2 min of initial handling and did not add additional stress to the animals. Because of our large sample size, not every animal was bled during the 12-week study, and no animal was bled more than once.

At the start of the experiment, all PRE animals were euthanized for comparisons with the other groups at the end of the experiment, and served as a control group with respect to LD animals. An overdose of sodium pentobarbital (50–75 mg/kg) was injected interperitoneally, and a toe-pinch reflex test was used to ensure that animals were unconscious. This allowed the heart to continue beating for several minutes while blood was drawn by cardiac puncture. Voles were then perfused with a wash solution and a paraformaldehyde solution. Testes were removed, along with blood and other tissues for use in a separate study. We determined paired testis mass and actual testis volume of each subject. A strong correlation existed between perfused testis mass and both the perfused testis volume and the estimated exter-

nal testis volumes at week 10, ensuring that perfusion did affect the integrity of the testis mass data.

The 12-week photoperiod treatment then commenced for the remaining two groups. LD animals remained on long photoperiods, while SD animals were switched to short photoperiods. All animals remained on ad libitum food and water at room temperature. After 12 weeks, LD and SD animals were euthanized in the same manner as the PRE animals.

Based on final testes mass of PRE and LD animals, the 12 additional weeks of long-day photoperiod treatment did not cause LD animals to become photorefractory (a regression of the testes owing to overexposure of long days) relative to PRE animals that were euthanized 12 weeks earlier (Student's *t* test, $p < 0.05$). Only one LD animal had regressed testes, but this did not cause any significant difference between the groups. Therefore, these two groups were combined into one large group ("LD*", $n = 37$) for testis-mass comparisons with SD animals.

Means and standard deviations of LD* paired testis masses were calculated to determine the different photoperiodic morphs within SD animals (Nelson et al. 1989; Kriegsfeld and Nelson 1999). Any SD animal having a perfused paired testis mass within 1 standard deviation of the LD* mean was categorized as a photoperiod nonresponsive morph (NR). Those falling between 1 and 2 standard deviations below the LD* mean were classified as intermediately responsive morphs (IR), while those having a testis mass below 2 standard deviations of the LD* mean were photoperiod responsive morphs (R). We used a Student's *t* test to assess differences between LD and SD animals, and we used analysis of variance (ANOVA) with Tukey's HSD tests to determine body-mass differences between LD, NR, IR, and R groups.

Results

Field study

Although trapping was conducted on a consistent basis at different locations throughout Chugach State Park, animal capture was not always consistent. Summer trapping success typically ranged from 10% to 40%, while winter trapping success was usually <5%. Our most complete and consistent data set was from May 2005 to September 2006. Locating voles in winter was challenging, even when subnivean nest boxes were used. Animals trapped in fall and winter were often found in pairs or groups (West 1977; Stevenson et al. 2009), suggesting communal nesting.

Males in our study typically became reproductive and had descended testes in early spring (April). In spring of both 2005 and 2006, male voles showed increases in testis mass while snow still covered the ground and no grasses had emerged. In April 2006, we observed males becoming active through a steady increase in reproductive organ mass from mid- to late April. Voles were inactive through the end of March, but began to transition within the first 10 days of April. At this time, we also observed an external anatomical change in the female vole reproductive anatomy prior to any copulation with males. Females trapped during the same time as these males with increasing testis masses did not yet have open pubic symphesises. However, the presence of a

small, thin line running laterally across the closed (unpenetrated) pubic symphesis of females was observed in mid-April. We did not detect this in voles trapped during the preceding winter, and we suspect that it is an external indicator of an internal physiological change towards reproductive readiness. We detected evidence of copulation in females approximately 10 days after discovering this feature.

In spring and summer seasons, reproductively active males had large testes with expanded seminiferous tubules that contained a well-defined lumen and maturing (pinched) spermatids and spermatozoa. Inactive males had small testes with seminiferous tubules that lacked lumina, with no evidence of maturing spermatids or spermatozoa. In general, adult reproductive structures of males and females were largest in spring and early-summer months. Organ masses declined at the end of summer and stayed low until the end of winter (Fig. 1). Litter size ranged from 4 to 7 pups and averaged 5.7 ± 0.4 pups per litter. No winter breeding was detected in the free-living populations studied.

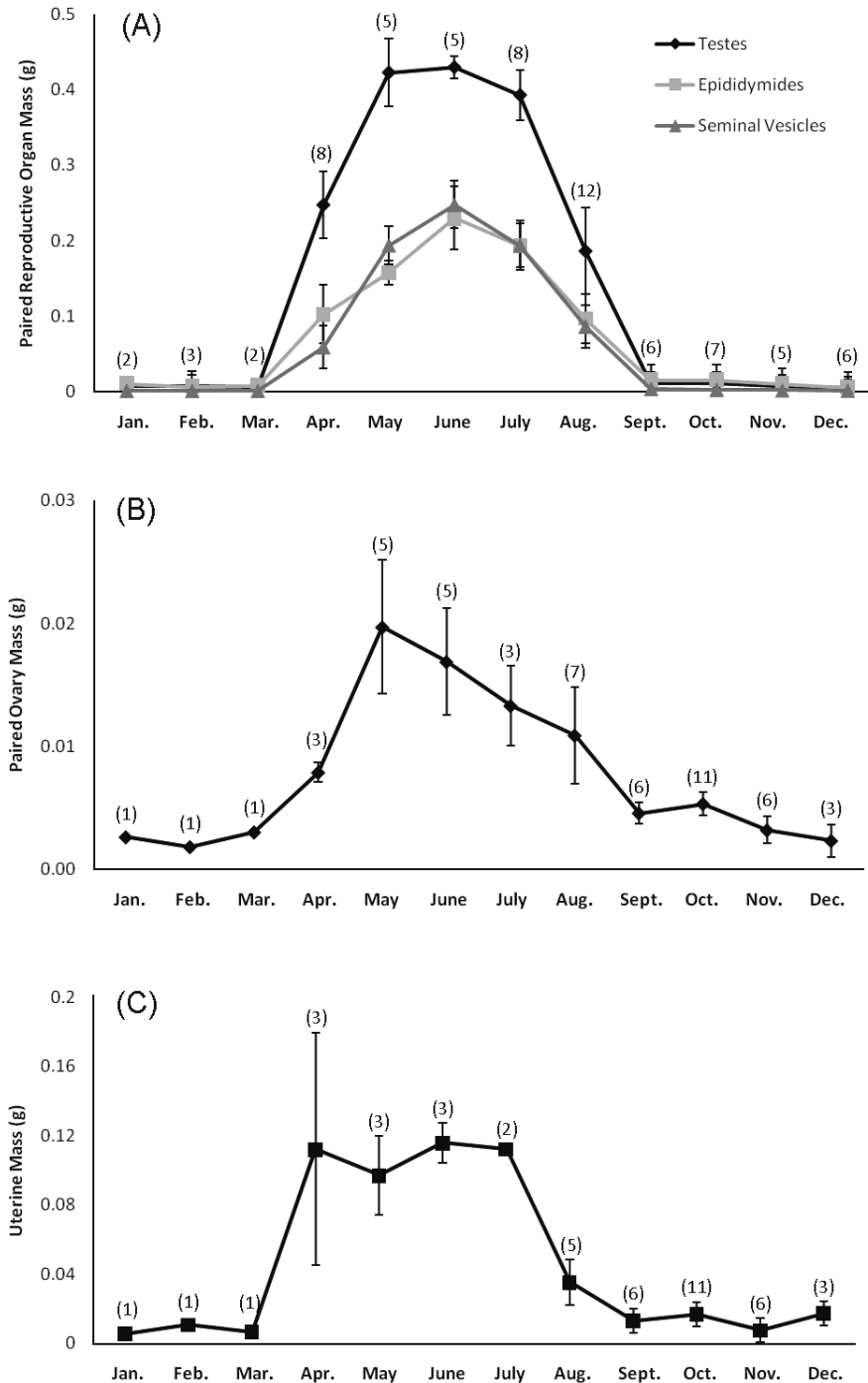
Of the 13 adult male voles collected between 22 August and 14 September 2005, 9 were inactive and had regressed testes (69.2%), 3 appeared to be regressing towards inactivity (23.1%), and 1 remained active (7.7%). Thus, 12 were responsive or intermediately responsive to photoperiod, while only 1 was found to be nonresponsive and fully reproductive during this time (Table 1). The nonresponsive animal had the largest body mass, the second largest amount of total body fat, and the largest value for testis : body mass index (Table 1). No reproductive males were observed later than this, and lactating females were not observed past October.

The ANCOVAs detected a significant effect of body mass, photoperiod, and temperature upon male reproductive organ masses during both the breeding and nonbreeding periods ($p < 0.05$; Table 2A). In females, body mass, percent fat, photoperiod, and snow depth all had a significant effect upon female reproductive organ masses during the nonbreeding season only (Table 2B). Both body mass and total fat mass were both positively correlated with photoperiod, but percent fat remained low year-round and did not change seasonally (Fig. 2).

Laboratory study

We observed a high degree of intraspecific variability in testis mass within the SD treatment group after the 12-week photoperiod treatment (Fig. 3). All three reproductive phenotypes were exhibited, and in the following proportions (mean \pm SE paired perfused testis masses are in parentheses): 28.2% NR (0.5457 ± 0.0137 , $n = 22$), 20.5% IR (0.4135 ± 0.0095 , $n = 16$), and 51.3% R (0.1397 ± 0.0145 , $n = 40$). Older and younger aged animals were well represented in each reproductive grouping. Overall, SD animals exhibited a negative change in body mass over 12 weeks, while LD animals exhibited a slight mass increase (Fig. 4A), and the difference between the two groups was significantly different (Student's *t* test, $p < 0.001$). The mean change in body mass of over the course of the study was highest in the LD group (2.917 ± 0.675), but this was not significantly different from the mass change in the NR group (0.650 ± 0.612 , ANOVA multiple comparisons, $p =$

Fig. 1. Monthly variation in reproductive organ masses of male and female northern red-backed voles (*Myodes rutilus*) in Chugach State Park, Alaska. Means and SE are shown with sample sizes in parentheses. (A) Male testes, epididymides, and seminal vesicles of males increased early in spring, peaked in early summer, and declined in late summer. (B) Ovarian mass also reached peak values in spring and decreased gradually to their lowest levels in winter. (C) Nonpregnant female uterine masses reached peak values in spring and decreased during late summer. Only nonpregnant uterine masses were used in summer months, and this is reflected in the lower sample sizes for these months relative to Fig. 1B.



0.283; Fig. 4B). However, the overall change in body mass was significantly higher in the LD group than both the IR group (-0.631 ± 0.672 , $p < 0.001$) and the R group (-4.688 ± 0.812 , $p < 0.001$), a trend that mirrored changes in testis mass (Fig. 3).

Discussion

Arctic and subarctic voles are not frequent winter breeders in the wild but do maintain the ability to breed out of season. This is achieved through the presence of non-

Table 1. Reproductive status of adult (>17.5 g) male northern red-backed voles (*Myodes rutilus*) trapped from 29 August to 14 September in 2005.

Trap date	Body mass (g)	Fat mass (g)	Percent fat (%)	Paired testis mass (g)	Testes : body mass index	Reproductive state
29 August 2005	18.8	0.88	4.7	67	4	Inactive
	18.7	0.76	4.1	64	3	Inactive
30 August 2005	19.9	1.50	7.5	70	4	Inactive
	20.4	0.80	3.9	51	3	Inactive
	18.4	0.94	5.1	70	4	Inactive
	18.6	0.77	4.1	165	9	Regressing
	26.6	1.08	4.1	4563	172	Active
5 September 2005	19.3	0.93	4.9	108	6	Regressing
7 September 2005	17.6	0.61	3.6	51	3	Inactive
14 September 2005	18.4	0.82	4.5	60	3	Inactive
	19.1	0.99	5.2	83	4	Inactive
	19.4	0.70	3.6	284	15	Regressing
	19.4	0.81	4.2	69	4	Inactive

Note: Of the 13 animals collected, 9 were reproductively inactive, 3 appeared to be transitioning, and 1 was reproductively active. This single active animal had a larger body size and a larger testes : body mass index. Data on female ovaries and uteri are not listed because voles cycle through pregnancy and lactation, giving birth to multiple litters in a single summer. Most males, however, are able to continue copulating during the entire breeding season and are not likely to undergo testicular regression or body-mass reduction until decreasing day lengths reach a critical value and trigger the physiological response.

responsive morphs within their populations. The frequency of nonresponsive morphs in captive *M. rutilus* fell within the known range for lower latitude voles, suggesting no selection against the morph at high latitudes. Nonresponsive animals were typically in better condition (larger body mass, more total body fat, larger testis : body mass index) than responders, as observed in our field and laboratory studies. Reproductive organ masses of males and females were linked to environmental variables and body mass, but not to percent body fat.

The reproductive organ masses of *M. rutilus* in south-central Alaska showed dramatic seasonal changes similar to those recorded for voles in interior Alaska (Sealander 1967; Whitney 1976; Fig. 1). The longer winter photoperiod, milder coastal climate, abundance of low-level vegetation, and heavier snowfall characteristic of south-central Alaska did not contribute to higher levels of photoperiod nonresponsiveness or winter breeding relative to these earlier studies in the Interior. Although south-central Alaska experiences higher levels of snowfall, it can be susceptible to unpredictable freeze-thaw cycles in fall, winter, and spring. We observed such events in each nonreproductive season in every year of our study. These freeze-thaw cycles are likely to negatively affect vole survival and inhibit winter breeding. In higher latitude and noncoastal regions where freezing and thawing are usually predictable and relatively isolated seasonal events, survival and reproduction of arvicoline rodents appear to be less affected by extremely low winter temperatures and low snowfall, but more negatively affected by first snowfall and spring melt (Whitney 1976; Millar 2001). This is probably due to the presence of low-temperature water (freezing rain, sleet, melted snow) that accumulates and can increase the rate of heat loss from voles through conduction. Water that refreezes into sheets of ice may also inhibit foraging and energy intake at this time, further reducing chances for survival and reproduction. However, Holleman et al. (1982) found that field metabolic rates of free-living in

M. rutilus in interior Alaska were higher in winter and summer than in spring, suggesting that extremely low temperatures and extremely high temperatures might adversely affect vole survival more than spring melt in that region.

Both male and female voles became reproductive at the beginning of April under an increasing photoperiod of ~13 h of daylight and began to regress at the end of August under a decreasing photoperiod of ~14.5 h of daylight (Figs. 1A–1C). In consecutive years, voles became reproductive in April while snow still covered the ground and grasses had not yet emerged. This indicates that voles in this region do not typically time reproduction through plant secondary compounds (see Negus and Berger 1977; Berger et al. 1981; Negus and Berger 1998) because they begin their reproductive change well before there are any freshly sprouted monocots available for them to ingest. Body mass and bone-mineral density in this species begin to increase at the end of late winter and rapidly increased in early spring (Stevenson et al. 2009; Figs. 2A–2C). The presence of hypogeous fungi in the stomachs of voles and on the roots of birch and other trees in different seasons suggest that this could be a primary food source which helps to fuel the increases in body mass and reproductive organ masses in spring. Thus, a readily available food source may be present to fuel winter breeding, but access to it may be limited to the extent that any autumnal or late winter freeze-thaw cycles can generate ice sheets.

The voles that we studied did not show seasonal changes in percent body fat (Fig. 2C), but instead underwent increases in total body fat (Fig. 2B) and total body mass (Fig. 2A) during the reproductive season (similar to Zuercher et al. 1999). Although percent fat remained low year-round, more total fat was available in spring and summer for breeding activity, territory guarding, and (or) gestation and lactation (Fig. 2B). It appears to be immediately replenishable by the high availability of preferred foods in the surrounding environment during the breeding season. The ability of nonresponsive morphs in *M. rutilus*

Table 2. Analysis of covariance (ANCOVA) of reproductive organ masses of adult northern red-backed voles (*Myodes rutilus*) during breeding (A) and nonbreeding (B) periods.

	Male						Female			
	Log(testes mass)		Log(epididymides mass)		Log(seminal vesicles mass)		Log(ovaries mass)		Log(uterus mass)	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
(A) Breeding period										
Corrected model	5.656	<0.001	16.764	<0.001	7.540	<0.001	0.828	0.587	0.260	0.935
Intercept	0.376	0.546	3.404	0.079	1.973	0.174	1.173	0.304	0.958	0.400
Fixed factors										
Year	2.588	0.122	0.205	0.655	0.042	0.840	0.121	0.735	0.653	0.478
Covariates										
Log(mass)	8.465	0.008	59.916	<0.001	13.281	0.001	1.447	0.257	0.006	0.944
Percent fat	2.310	0.143	0.002	0.963	0.064	0.802	2.097	0.178	0.754	0.449
Photoperiod	0.851	0.366	5.534	0.028	0.028	0.869	0.006	0.938	0.988	0.394
Snow depth	0.635	0.434	1.118	0.302	0.648	0.429	0.364	0.560	0.472	0.541
Precipitation	0.374	0.547	2.914	0.102	0.220	0.643	0.066	0.803	0.843	0.426
Temperature	5.555	0.028	14.408	<0.001	0.715	0.407	0.570	0.468	0.813	0.434
(B) Nonbreeding period										
Corrected model	2.579	0.036	3.420	0.010	2.584	0.035	1.262	0.322	5.003	0.003
Intercept	12.026	0.002	13.851	0.001	12.148	0.002	2.468	0.134	7.833	0.012
Fixed factors										
Year	0.203	0.140	0.280	0.079	0.158	0.147	0.350	0.562	3.914	0.063
Covariates										
Log(mass)	14.842	0.001	18.306	<0.001	14.937	0.001	5.530	0.030	21.718	<0.001
Percent fat	1.603	0.216	2.734	0.110	1.614	0.215	0.748	0.399	6.279	0.022
Photoperiod	7.096	0.013	8.720	0.006	7.451	0.011	0.202	0.658	5.082	0.037
Snow depth	0.401	0.532	0.166	0.687	0.438	0.514	1.404	0.252	12.489	0.002
Precipitation	1.519	0.228	1.839	0.186	1.634	0.212	0.195	0.664	0.032	0.860
Temperature	4.401	0.045	5.673	0.025	4.603	0.041	0.120	0.733	1.544	0.230

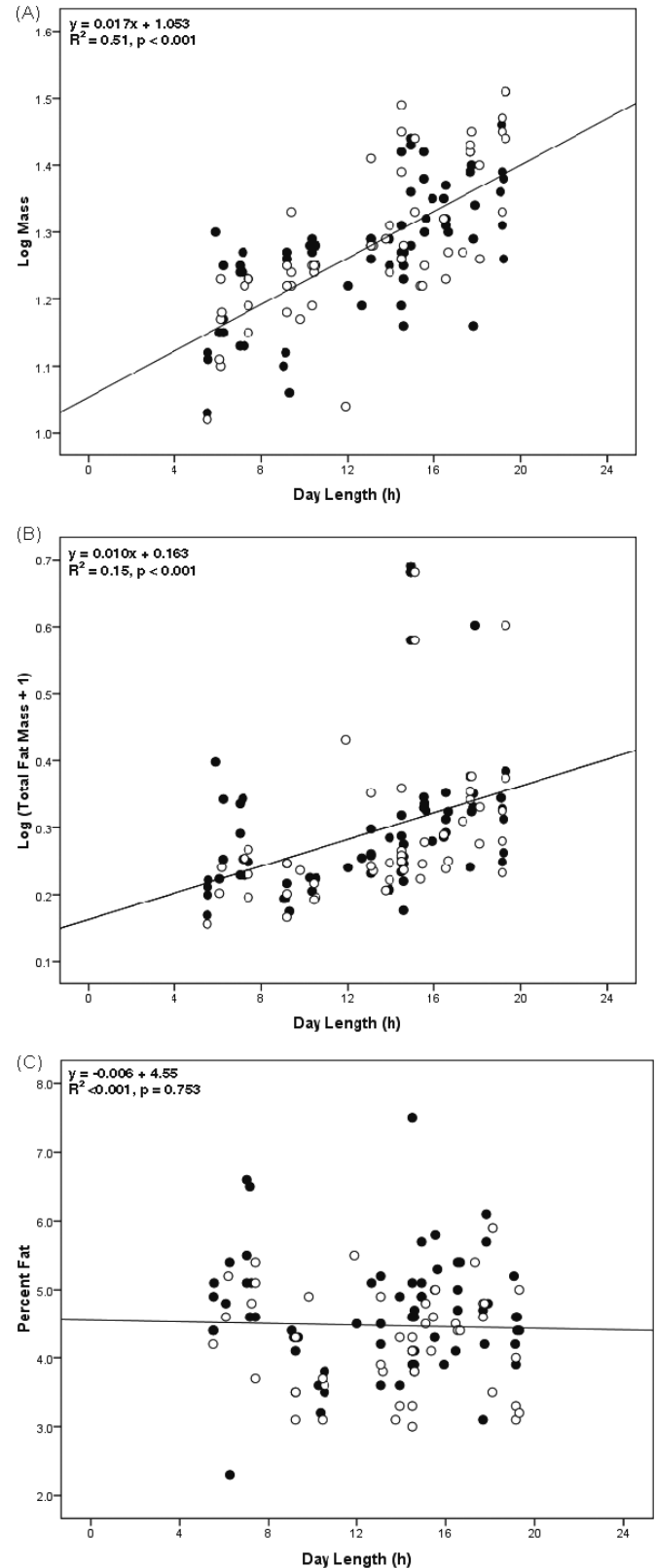
Note: *P* < 0.05 are in boldface type. Uteri containing pups were excluded from the analyses. Sample size (*n*) for breeding period: males = 30; females = 11 and 18 for ovarian and uterine masses, respectively. Sample size for nonbreeding period: males = 35; females = 26.

Fig. 2. The relationship between photoperiod, body mass, and body fat in free-living northern red-backed voles (*Myodes rutilus*) trapped between November 2004 and August 2006. (A) Body mass vs. day length. Solid circles correspond to males and open circles correspond to females. Mass was directly proportional to day length and increases with increasing photoperiod ($y = 0.017x + 1.053$, $R^2 = 0.51$, $p < 0.001$). (B) Total fat mass vs. day length. Total body fat was directly proportional to day length and increased with increasing photoperiod ($y = 0.010x + 0.163$, $R^2 = 0.15$, $p < 0.001$). (C) Percent body fat vs. day length. Percent body fat was static and did not vary seasonally ($y = -0.006x + 4.55$, $R^2 < 0.001$, $p = 0.753$).

and other arvicoline rodent populations to maintain, or even increase percent body fat in a given winter (Anderson and Rauch 1984; Batzli and Esseks 1992; Zuercher et al. 1999), may determine their ability to breed during that season.

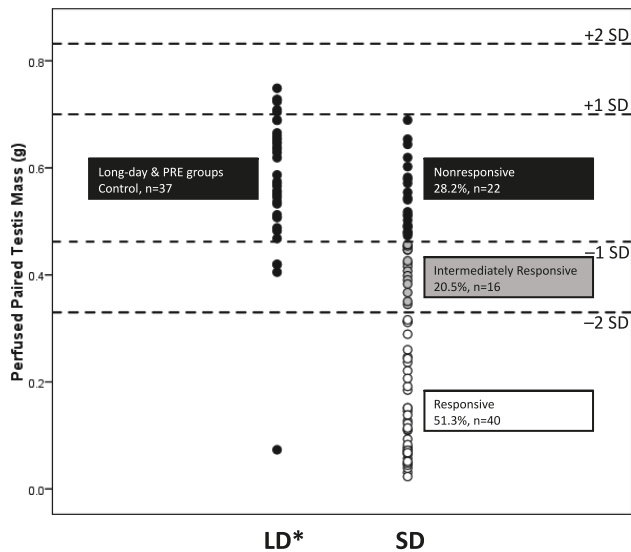
The level of diversity in the reproductive response of this high-latitude species to photoperiod is profound in that it is likely to allow for continued breeding during reduced photoperiods when environmental or nutritional conditions are favorable. Whether nonresponsive morphs exhibit the nonresponsive phenotype and attempt to breed in winter during a given year may ultimately be related to energy availability and expenditure. Specifically, there is likely to be an effect of food availability, food quality, or temperature on photoperiod nonresponsiveness. For instance, almost all male prairie voles (*Microtus ochrogaster* (Wagner, 1842)) housed at 8 °C undergo testicular regression in response to short photoperiods, while those housed at 20 °C on identical day lengths exhibit the normal 20%–40% frequency of nonresponsiveness (Kriegsfeld et al. 2000a). Food supplementation and photoperiod have been shown to interact to influence the reproductive condition of pine voles (*Microtus pinetorum* (LeConte, 1830)) and other small mammals, suggesting a strong nutritional affect (Cengel et al. 1978; Hasbrouck et al. 1986; Bronson 1989).

It seems logical that winter breeding would usually occur by an extension of the late-summer breeding season (as shown by the one nonresponsive adult male in our study that showed no regression of testes during late summer). However, it is possible that some other factor (e.g., warm temperatures or acute food availability) could cause the spontaneous growth of reproductive structures in fall or mid-winter, and subsequent out-of-season breeding would commence. Two studies on record support the idea that spontaneous mid-winter recrudescence of reproductive structures is possible. Kaikusalo and Tast (1984) observed a population of root voles in Kilpisjärvi, Finnish Lapland (69°N), in which none of the trapped subjects were reproductively active in October. When the same population was retrapped in February, however, 80% were found to be breeding. Similarly, Whitney (1976) found no early-winter breeding in *M. rutilus*, yet he found one individual in late winter (March) that was in reproductive condition. An alternate explanation for these occurrences is that there may be some natural selection occurring for an early entry into reproductive condition based on a day-length cue that is shorter than the normal critical day length which typically triggers reproductive activity for each species (both occurrences were between the winter solstice and spring equinox when days were getting progressively longer). Each of these studies oc-



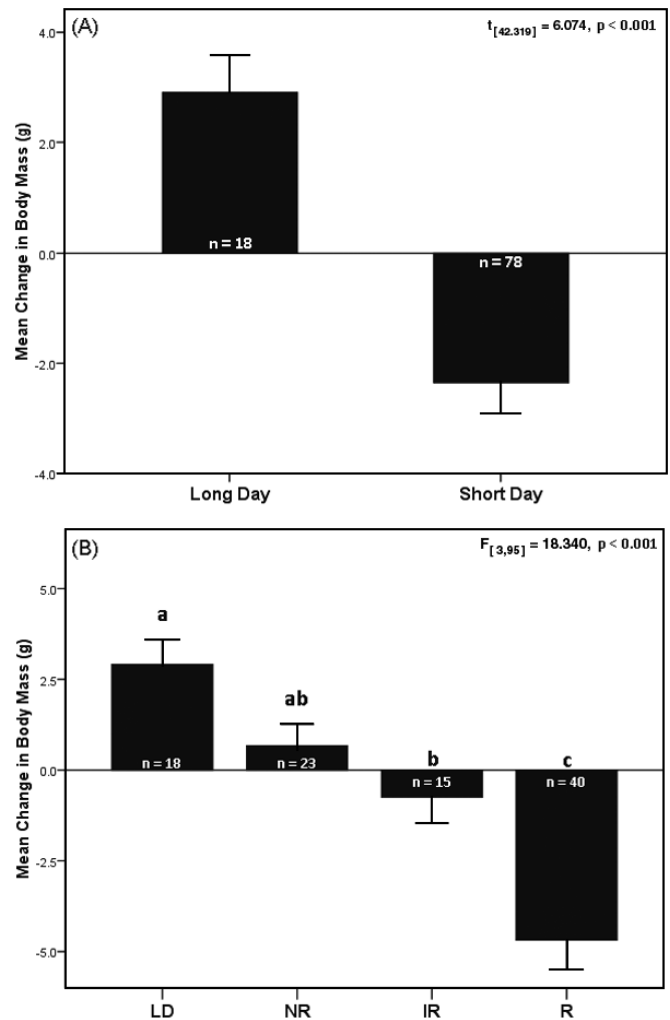
curred at latitudes higher than 64°N where February and March temperatures often reach below -40 °C. However, unseasonably high temperatures or a particularly snowy winter generating a thick insulative snowpack could lower overall costs of thermoregulation.

Fig. 3. Intraspecies variation in reproductive response to short photoperiod in an arctic and subarctic arvicoline rodent species, the northern red-backed vole (*Myodes rutilus*). Photoperiod nonresponsive voles had perfused paired testis masses within 1 standard deviation (SD) of the mean of LD* animals. The percentage of voles not responsive to photoperiod (28.2%, $n = 22$) fell within the 20%–40% range known for lower latitude species. Intermediate responders (20.5%, $n = 16$) had paired testis masses between -1 SD and -2 SD of the mean of LD* animals, while photoperiod responsive voles (51.3%, $n = 40$) had testis masses at least 2 SD below the LD* mean. LD* on x axis represents the combined long-day and PRE group animals, while SD on x axis represents the short-day animals.



Whether the rare occurrences of winter breeding in small mammals are attributed to an extension of the normal breeding season or to spontaneous mid-winter recrudescence of reproductive structures, an acute energy source is likely to be beneficial for males, females, and offspring. Moose and other large animals often starve, fall ill, or are killed by other animals or humans prior to or during winter. If the whole or partial carcass of such an animal became buried by snowfall, it could provide a protected, long-term, nutritious, subnivean food source for a local population of voles or lemmings that might, thereby, enable nonresponsive morphs to maintain or re-enter a reproductively active condition and breed successfully. *Myodes rutilus* may be primarily herbivorous, but it will feed on animal remains in winter. Snap-trapped voles in our study site were sometimes cannibalized by other voles, and hair from various mammal species was found in the feces and stomach contents of winter-trapped *M. rutilus* (K.T. Stevenson and I.G. van Tets, personal observation). We found anecdotal support of this “fallen moose hypothesis” in the form of a communal vole nesting area detected near a moose carcass we discovered northeast of Fairbanks, Alaska, along the Chatanika River during the spring melt of 2007. The carcass was surrounded and partially covered by tens of thousands of fecal pellets of a size and shape characteristic of *M. rutilus* (K.T. Stevenson, personal observation). A moose or caribou that starves in winter and is covered by snow will not begin to decompose until spring. If 20%–40% of a nearby vole popu-

Fig 4. The relationship between photoperiod, body mass, and reproductive grouping in captive northern red-backed voles (*Myodes rutilus*). (A) Captive voles that remained on long days increased in mass, while those switched from long to short days lost mass after 12 weeks. The overall change in body mass during the controlled study was significantly greater in the long-day than in the short-day groups (independent samples Student’s t test, equal variances not assumed, $t_{[42,319]} = 6.074$, $p < 0.001$). (B) Comparison of the overall change in body mass over 12 weeks for captive voles in four reproductive groupings: long day (LD), short day nonresponsive (NR), short day intermediately responsive (IR), and short day responsive (R) (ANOVA, $F_{[3,95]} = 18.340$, $p < 0.001$). Voles in LD and NR groups both maintained large testes and gained body mass. Intermediately responsive and responsive voles reduced in body mass. The body size of voles appears to change in proportion to testis size.



lation is genotypically nonresponsive, a high rate of local winter breeding could result.

Captive *M. rutilus* showed a high degree of intraspecies variation in their response to short photoperiod (Fig. 3). Previous studies on lower latitude small-mammal species have listed the percentage of nonresponsive morphs in a population as either 20%–30% (Eskes and Zucker 1978; Zucker et al. 1980; Beasley et al. 1981; Nelson and Zucker 1981; Desjardins and Lopez 1983) or as 20%–40% (Nelson 1987;

Kriegsfeld et al. 2000a). The percentage of nonresponsive individuals in our captive population of a high-latitude vole was 28.2%, within the expected range of frequency for captive lower latitude small-mammal populations. This validates the sporadic observance of winter breeding that has been detected in many high-latitude species. Despite the fact that winter breeding is rare in the arctic and does not occur in all individuals or all years, the frequency of non-responsive morphs in the colony appears undiminished.

Long-term, established captive rodent colonies have sometimes selected for NR individuals, increasing the percentages of nonresponders relative to those present in the wild (Nelson 1985b; Gorman and Zucker 1997). Such confusion is unlikely in this case, as we used only reproductively mature animals from a relatively young colony (started 9 years ago, with free-living additions as recently as 5 years ago) that has only ever been bred, weaned, and raised to age of reproduction on long photoperiods. Selection in at least one documented case was the result of breeding, weaning, and juvenile development under short photoperiods (Nelson 1985b). The scale of nonresponsiveness that we observed was also within the typical range for lower latitude rodents (20%–40%; Nelson 1987; Kriegsfeld et al. 2000a).

The mechanisms underpinning winter breeding have still not been entirely identified. However, body mass (but not necessarily percent body fat) was correlated with reproductive state in both our field (Figs. 2A–C) and captive studies (Figs. 4A–4B), regardless of photoperiod. Gonadectomy is known to enhance body-mass changes in other vole species (Kriegsfeld and Nelson 1996), and the two parameters appear to be linked in *M. rutilus* (Figs. 3, 4B). In our captive study, the direction and degree of change in gonadal mass and body mass were similar within each photoperiodic group. However, decreasing day lengths can arrest both somatic and reproductive development, and it is not impossible that photoperiod variably altered body mass, resulting in some effect upon reproductive condition.

The uncoupling of photoperiodic processing and reproductive function has been studied in other small mammals. House mice (*Mus musculus* L., 1758) process photoperiodic information, discriminating short from long days. While this is normally uncoupled from reproduction, the interaction of bulbectomy or testosterone injections with short days causes testicular regression (Nelson 1990). Interestingly, body mass is not affected by day length in such cases, as it was for *M. rutilus* in our study. In *Peromyscus leucopus* (Rafinesque, 1818), the daily rhythm of melatonin antigonadal action appears to be linked to changes in responsiveness of melatonin target neurons in the suprachiasmatic nucleus (SCN) (Glass and Lynch 1982). As in many rodent species, an endogenous timing mechanism sustains reproductive inhibition in *P. leucopus* under short day lengths until photorefractoriness occurs, resulting in spontaneous testicular recrudescence.

Photoperiodic sensitivity and insensitivity in Syrian hamsters (*Mesocricetus auratus* (Waterhouse, 1839)) has also been attributed to effects of melatonin produced in the pineal gland. Syrian hamsters measure day length by determining whether light impinges on an endogenous circadian rhythm of sensitivity to light. Reproductive stimulation oc-

curs when day length is long enough to overlap with the sensitive phase of this endogenous rhythm (Elliot 1981; Elliot and Goldman 1981; Bronson 1989). Conversely, reproductive inhibition occurs when day lengths are not long enough to achieve this. Strains of this species have been shown to vary drastically in their reproductive response to shortened photoperiods, and the length of short photoperiod exposure is known to have an effect on the degree of testicular regression (Vitaterna and Turek 1993). Yet, genetic differences in reproductive response to photoperiod do not appear to be linked to circadian rhythmicity for this species (Vitaterna and Turek 1993).

The extent to which circadian rhythm and reproductive state are linked in voles is unknown. Differences may exist in melatonin production in the pineal gland or in the SCN, but it is quite possible that individuals first begin displaying differences farther downstream at some point along the hypothalamic–pituitary–gonad axis, e.g., expression of GnRH or GnIH neuropeptides in the hypothalamus, LH or FSH in the pituitary, or gonadal testosterone production.

The link between reproductive organ mass and body mass observed in our captive study (Fig. 4) sheds new light upon our field data (Table 2, Fig. 2A). It is likely that in free-living populations, many older animals die off prior to or during winter because a larger body size is not typically conducive to survival in these seasons. The energetic costs of maintaining reproductive organ masses and continued breeding into the fall and winter seasons could negatively affect immune function and overall survival (Nelson and Demas 1996), and a large body size could intensify or accelerate these negative effects in certain seasons. Perhaps this is why most overwintering animals are found with smaller body sizes and most larger animals die off. Although a larger body size may, by virtue of its lower surface area : volume ratio, resist heat loss more effectively than a smaller one, the benefit of lower total-tissue maintenance appears more important to winter survival in some arvicoline rodents. Nonresponsive voles may, however, be able to take advantage of both a large body size and lower individual maintenance costs in winter through communal nesting (West 1977; Wolff and Lidicker 1981; West and Dublin 1984; Stevenson et al. 2009). Voles huddle together and become one larger “vole unit” to resist heat loss, separating only to forage. Such communal nesting should improve the success of winter breeding through the close proximity of males and females during a very long and perhaps otherwise uneventful season. Since most small rodents have life spans of <1 year in the wild, the process of winter breeding could significantly increase the fitness of nonresponsive morphs. More data is needed to investigate cues and responses of female voles. Our field results suggest an effect of photoperiod on reproductive structures, but ovulation may ultimately be induced by males. It is possible that females also exhibit an intraspecific variation in their reproductive response to short photoperiods, and this should be tested further in more species (especially high-latitude ones).

We conclude that the combined data on reproductive timing and intraspecific variation in response to photoperiod portray this species as reproductively elastic. Therefore, if climate changes in this region in ways that reduce the ener-

getic demands on voles during fall and winter, they are likely to be able to breed for longer lengths of time, regardless of shortened photoperiod. Conversely, if climate changes in ways that are more conducive to unpredictable freeze-thaw events and a reduced insulative snowpack, breeding is likely to be restricted to the summer period. Change in either direction in a vole or lemming population is likely to affect the abundance of predators that rely heavily on rodents and the secondary prey species subject to increased predation when voles are scarce (Sittler et al. 2000; Wilson and Bromley 2001).

Conclusion

Free-living male and female *M. rutilus* exhibit dramatic seasonal changes in their reproductive organ masses as a result of a photoperiodic threshold. Body mass changes proportionally to testis mass in male voles, and testis mass exhibits considerable variation in its reproductive response to short photoperiods in the laboratory. Highly seasonal environments inhibit the ability of most arvicoline rodents to breed in winter, but the apparently rare occurrence of winter reproduction has not resulted in a lower proportion of photoperiod nonresponsive morphs relative to lower latitude vole species. The diverse phenotypic reproductive response of *M. rutilus* to short day lengths under laboratory conditions confirms that reproductive timing is fairly elastic in voles. *Myodes rutilus* are able to breed successfully when good summer conditions are prolonged or when winter conditions and (or) food availability become more favorable. A long-term warming trend in northern latitudes could affect the frequency and timing of breeding of this and related species, and thus also the success of predator and prey species that are influenced by them. Whether the affect of such a potential trend is positive or negative is likely to depend on its affect on the thickness of the insulatory winter snowpack and on climactic conditions in spring and fall.

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