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Small mammals in boreal forest ecosystems fluctuate dramatically in abundance and 1 possible mechanism to explain these changes is the bottom-up hypothesis of variation in food supplies. Here we ask if variation in berry crops produced by 6 major species of dwarf shrubs and herbs, epigeous mushroom crops, and white spruce seeds allow us to predict changes in the abundance of the red-backed vole (*Myodes* [= *Clethrionomys*] *rutilus*), the deer mouse (*Peromyscus maniculatus*), and field voles (*Microtus oeconomus* and *M. pennsylvanicus* combined) over 13 years (1997–2009) in the Kluane Lake region of the southwestern Yukon, Canada. *M. rutilus* is the dominant rodent in these forests, comprising 64% of the catch. Overwinter survival is a key demographic variable in all these rodents, and the winter food supply—principally berries produced the previous summer— may be 1 key to overwinter survival. We predicted that berry, mushroom, and tree seed crops in year *t* would produce changes in rodent density in year *t* + 1. We could explain statistically 78–98% of the variation in May and August abundance of all 3 rodent species with indices of berry crops and mushrooms in the previous summer. For *M. rutilus* the critical predictor was berry crops of *Empetrum nigrum*. For *P. maniculatus*, the critical species were *Arctostaphylos uva-ursi*, *A. rubra*, and mushrooms. Spruce seed crops were not significantly correlated with rodent densities or changes in density. A large fraction of the variation in rodent numbers in this ecosystem is explained by a simple bottom-up model of population limitation. DOI: 10.1644/09-MAMM-A-005.1.

Key words: berry production, bottom-up control, *Microtus*, mushrooms, *Myodes rutilus*, *Peromyscus maniculatus*, population limitation, white spruce seed, Yukon

Population fluctuations in the small mammals of boreal forest ecosystems have been studied for many years with wildly conflicting views about the mechanisms behind these population changes (Boonstra and Krebs 2006; Korpimäki et al. 2004; Lambin et al. 2002; Norrdahl 1995). The 3 basic models that are used to explain small mammal population fluctuations are the bottom-up model, in which food supplies are paramount (Hansson 1979); the top-down model, in which predation, parasites, or disease dominate (Korpimäki et al. 2002); and the social behavior model, in which social interactions involving territoriality or infanticide are key (Krebs et al. 2007). We explore here a test of the 1st hypothesis for population fluctuations of small rodents in the southern Yukon, Canada.

Testing the bottom-up model for small rodents has relied on 2 approaches. Direct feeding experiments can be carried out to determine if food supplies are limiting rodent numbers. We did this type of experiment with sunflower seeds in the Kluane area with a strong positive result for *Myodes rutilus* and

Peromyscus maniculatus (Gilbert and Krebs 1981). These experiments suffer from 2 shortcomings—a pantry effect so that changes in numbers are driven largely by immigration, and a type-of-food effect because the types of food used in a feeding experiment are not the natural food items for the rodent species involved. The 2nd approach is to measure the abundance of the food items actually used by the species and then correlate changes in abundance of the food items to changes in rodent density. This approach has been used successfully with rodents that feed on seed mast from deciduous trees (e.g., Falls et al. 2007; Ostfeld et al. 1996) and is the approach taken here.

The small mammal community of the boreal forest of the Kluane Region of the Yukon is dominated by the northern red backed vole (*Myodes* [= *Clethrionomys*] *rutilus*). From 1997 to 2008 *M. rutilus* comprised 64% of the catch and *P.*

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maniculatus 13%, with the remaining 23% being *Microtus* spp. (C. J. Krebs, pers. obs.). Hereafter, for brevity we use *Myodes* for *M. rutilus* and *Peromyscus* for *P. maniculatus*.

The key variable that affects population trends in these Yukon small rodents is overwinter survival (Gilbert and Krebs 1991), and this led Boonstra et al. (2001) to postulate a bottom-up model in which food supplies provided by the berry crop could permit good overwinter survival and good summer reproduction. The hypothesis that berry crops are a critical factor in small rodent population dynamics was suggested earlier by Dyke (1971) and West (1982). In this paper we use the 2nd, correlative approach to address the bottom-up model because previous work on these rodents has shown that predator abundance is not associated with rodent population changes in this ecosystem (Boonstra et al. 2001). The food habits of these 4 species differ dramatically (Bergman and Krebs 1993; Dyke 1971; Martell and Macaulay 1981; Reich 1981; West 1982), and this is associated with their different habitat preferences. *Microtus oeconomus* and *M. pennsylvanicus* prefer grassland habitats, and *Myodes* and *Peromyscus* prefer forested areas; niche overlap between *Microtus* spp. and the 2 dominant rodents is low (Krebs and Wingate 1976). In this part of the Yukon it is difficult in livetrapping studies to distinguish *M. pennsylvanicus* and *M. oeconomus*. Therefore, we have grouped these 2 *Microtus* into a single taxon that we assume to be functional equivalents and we refer to as *Microtus* spp. Given the observed habitat segregation (Krebs and Wingate 1976), no suggestion of competition between the *Microtus* spp. and the 2 dominants, *Myodes* and *Peromyscus*, is considered nor can we see any obvious sign of competition between the 2 dominant species. When *Peromyscus* disappeared for 6 years in the early 1990s we saw no sign of a competitive release of *Myodes*, and no sign of any effect on abundance of *Myodes* in the late 1990s when *Peromyscus* reappeared (Fig. 1). Our only experimental analysis of competition between 2 *Microtus* species in alpine tundra showed no sign of competitive release after species removals (Galindo and Krebs 1985). In the absence of predator limitation and a lack of interspecific competition, only 4 mechanisms remain that can drive population changes—weather, food supplies, parasitism and disease, and social interactions. Here we investigate 1 important part of overwinter food supplies, berry crops, and test the hypothesis that berry crops in one year affect rodent numbers in the subsequent year. The expectation was that there must be a time lag in this potential mechanism. Berry production in the summer of year *t* should affect overwinter survival of rodent numbers, so that rodent numbers in May and August of year *t* + 1 will be higher. High berry production could increase August rodent numbers in the same year, but this was unlikely because the berries do not ripen until August. The most significant variable predicting August rodent numbers was May numbers in the same year (Gilbert and Krebs 1991).

We began measuring berry production by dwarf shrubs in the Kluane region in 1997 and this paper reports on the data on rodent population changes and berry production for the
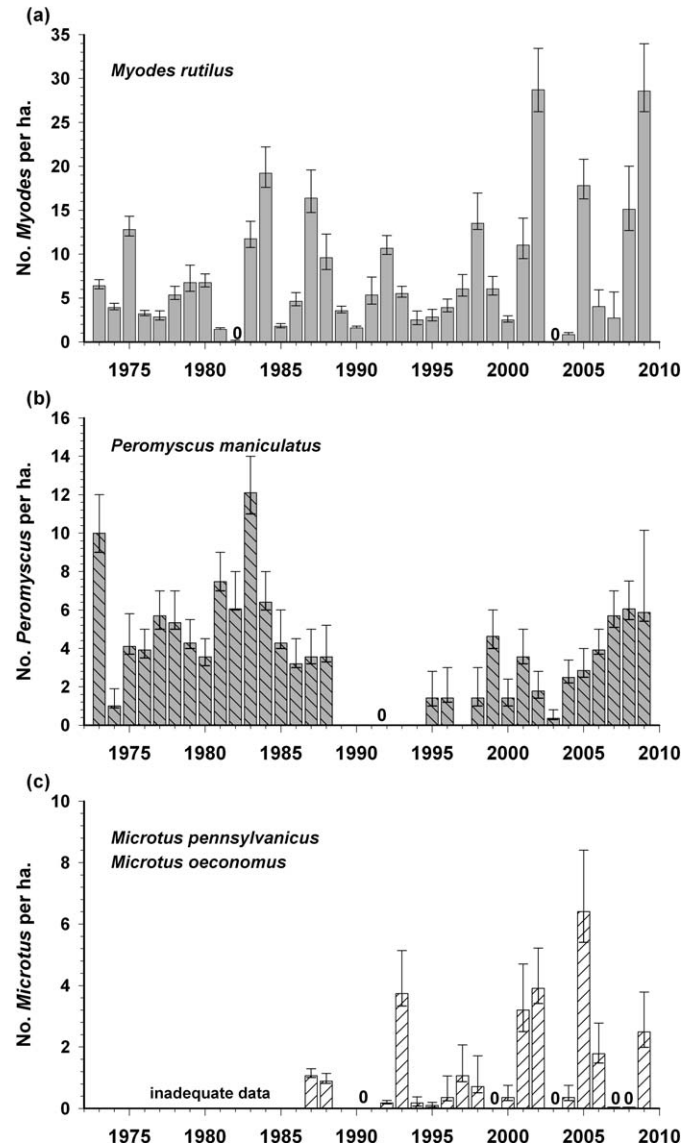

FIG. 1.—Small mammal population trends in August in the Kluane region of the Yukon, Canada, from 1973 to 2009 for a) *Myodes rutilus*, b) *Peromyscus maniculatus*, and c) *Microtus* spp. No *Peromyscus* were caught for 6 years in the early 1990s. Habitats of *Microtus* were poorly sampled before 1987. Data for 1973–1989 are from Gilbert and Krebs (1991). Only 1997–2009 data are analyzed. Scales of the y-axes differ. Error bars are 95% confidence intervals.

interval 1997–2009. We tested the general hypothesis that changes in rodent numbers can be associated with the size of berry crops. In particular, we tested the specific hypothesis that berry crops in one year determine rodent numbers in the following year. We have previously tested and rejected 1 alternative bottom-up hypothesis that rodent population changes are associated with seed crops of white spruce (*Picea glauca*—Boonstra et al. 2001). We reconsider this alternative hypothesis with an additional 12 years of data on spruce seed crops. In addition to berry crops and spruce seeds, we have data on epigeous mushroom production, another highly variable food source for small rodents, and we attempt to pinpoint which of these fluctuating food sources might be

associated with changes in rodent numbers in the boreal forests of the southwestern Yukon.

MATERIALS AND METHODS

Study area.—The study site was located in the southwestern Yukon near Kluane Lake by the Alaska Highway within the Shakwak Trench system (61°01′N, 138°24′W), and lies within the rain shadow of the St. Elias Mountains. Mean annual precipitation is approximately 280 mm and includes an average annual snowfall of approximately 100 cm (Environment Canada; http://www.climate.weatheroffice.gc.ca/Welcome_e.html). The tree community is dominated by white spruce (*P. glauca*) interspersed with trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The upper shrub layer is composed of willow (*Salix* spp.), soapberry (*Shepherdia canadensis*), and dwarf birch (*Betula glandulosa*), whereas the ground layers are composed of dwarf shrubs and herbaceous plants such as bearberries (*Arctostaphylos rubra* and *A. uva-ursi*), crowberry (*Empetrum nigrum*), cranberry (*Vaccinium vitis-idaea* ssp. *minus*), toadflax (*Geocaulon lividum*), arctic lupine (*Lupinus arcticus*), and other forbs (Turkington et al. 2002). An aerial photo and Landsat vegetation classification of the Kluane region showed that grassland occupied about 8–9% of the forested zone, and about two-thirds of the valley was spruce forest, the remainder being willow and birch shrubland (Krebs and Boonstra 2001).

Trapping methods.—Small rodents were livetrapped on 4 unmanipulated sites spaced along a 25-km section of the Alaska Highway just south of Kluane Lake. Trapping grids were separated by a minimum of 2 km to a maximum of 24 km in continuous boreal forest, with scattered small patches of grassland. Each grid had 100 stations 15 m apart in a 10 × 10 array with 50 Longworth traps in alternate rows (i.e., A1, B2, A3, etc.). When rodent numbers were high and the possibility of trap saturation existed we used 100 traps, 1 at every station. Traps were prebaited with seed oats for a week before trapping, and where necessary, traps were placed inside mesh cages to prevent squirrels from triggering the trap. Traps (locked open) were left in place all year. Trapping sessions were conducted over 3 days in May and August each year, and small mammals captured were tagged on the right ear with numbered fingerling fish tags (see Gilbert and Krebs [1981] for more details on methods). In this part of the Yukon *M. pennsylvanicus* and *M. oeconomus* are nearly impossible to tell apart when alive, and we have grouped them together in the analysis. In snap-trap collections in this region *M. pennsylvanicus* has been the more abundant of these 2 in a ratio of about 3:1 (Krebs and Wingate 1985).

Mark–recapture population estimates for all small mammals were calculated from program CAPTURE using the Jackknife model except when <7 individuals were caught, when we used the minimum number known alive with Poisson confidence limits. These population estimates were adjusted to an effective grid size using program DENSITY 4.3 (Efford 2004) to provide absolute density estimates for each capture session with a boundary strip calculated from a maximum-likelihood analysis of recapture distances. We have studied the detailed summer dynamics of these Kluane rodent species for >10 years (Gilbert and Krebs 1991), and we have found that we can capture population changes by a trapping session in May and a trapping session in August. All of these rodents have a very high trappability in the Kluane region (trappability $\bar{X} = 92\% \pm 3\%$ *SE*; documented in Boonstra and Krebs [2006]). Some breeding continues into September so that the late summer density estimates are not peak densities but provide an index of the rate of increase in summer populations. We have found no evidence of winter breeding in these 3 species at Kluane. Two trapping sessions per year does not permit specific survival or detailed reproductive analyses of these populations because this would require biweekly trapping or radiocollaring that was beyond the scope of this study. To partially compensate, we have calculated 2 indices of population change. An overwintering index was calculated for each year by dividing the population density in May of year $t + 1$ by the August density of year t and taking the $\log_{10}$ of this ratio. A summer population growth index was similarly calculated by dividing the August density estimate by the May density estimate of the same year and taking the $\log_{10}$ of this ratio. Logs to the base 10 were used for convenience.

We used August rodent population densities in all our statistical analyses because fewer very low or zero catches were obtained compared with May densities. All the results reported here were nearly identical when we used May numbers in the analyses, so the results are robust to whichever season is used because May and August numbers are highly correlated (Pearson $r > 0.82$ for all species). A log transformation of May and August densities did not show any improvement in predictability over the raw data, so we used the raw density data in all analyses.

All livetrapping of rodents was carried out in accord with the animal care principles of the American Society of Mammalogists (Gannon et al. 2007), and all our protocols were approved by the University of British Columbia Animal Care Committee.

Berry production indices.—We measured indices of berry production at 10 locations along 210 km of the Alaska Highway and the Haines Road, stretching from St. Elias Lake (60.333°N, 137.049°W) to the Donjek River (61.684°N, 139.774°W). For *A. rubra*, *A. uva-ursi*, *E. nigrum*, *V. vitis-idaea*, and *G. lividum* berry quadrats were 0.8 × 0.4 m in size and consisted of two 0.4 × 0.4-m quadrats laid side by side, for a total of 50–100 quadrats (25–50 plots × 2 quadrats each) at each of the 10 locations. We counted on average 696 quadrats each year (Krebs et al. 2009). Not all areas had the same number of suitable berry sites to sample. Sampling plots were placed systematically at 100-m intervals on snowshoe hare trapping grids at grid points that had adequate plant coverage. The same quadrats were counted each year (except for 2–5% of the plots, which were destroyed by animal digging or by tree falls and had to be replaced). The quadrats

are meant to provide an index of berry production to measure year to year changes in berry counts. All these plants have berries of approximately the same size. Plant cover was estimated for all species, and all ground berries within the plots were counted while still green, typically in early to mid-July, to minimize the number lost to mammals and birds. Because berry counts within each subplot are higher when cover is higher, we adjusted each berry count for all species to a standard 50% cover for each species. We tested each species to determine if the regression of berry counts on cover values had a slope of 1.0, and thus validated the adjustment of counts to a standard of 50% cover. Species with <5% cover in a quadrat were not included in the data analysis. Not all berry species occurred in each plot. The experimental design was of subplots (40 × 40 cm) nested within plots (40 × 80 cm) nested within locations (10) nested within years. We were not interested in the variance structure of the nested design, and the mean berry index for each of the 12 years was the variable used in the statistical analysis. A general tendency exists for all locations within the study area to be in phase for berry production (Cronbach's alpha = 0.60–0.85 for the 6 berry species—Cronbach 1951), so it is legitimate to use a single area-wide average for berry production in a given year.

At each of 14 sites along this same stretch of highway soapberry (*S. canadensis*) berries were counted on 2 stems on each of 10 plants. The same 2 marked stems per bush were counted every year in July while the berries were still green. Stem diameter in millimeters was measured at the base. Soapberry counts were adjusted to a standard 10-mm-diameter stem by the use of the least-squares estimate of slope (0.7105) for the regression of soapberry numbers on stem diameter for all sites:

adjusted no. soapberries =

$$\left\{\sqrt{(\text{observed no. berries})} + [(10 - \text{observed diameter}) \times 0.7105]\right\}^2.$$

The resultant standardized numbers of soapberries are meant as an index of soapberry production and not as an absolute estimate per unit area. All 14 sites were highly correlated in their soapberry production (Cronbach's alpha = 0.92).

Berry records are available from 1997 onward (Krebs et al. 2009). Thus statistical analysis is limited to a 13-year period from 1997 to 2009. All statistical analyses were done in NCSS (Number Crunching Statistical System, Kay, Utah; www.ncss. com). To relate rodent numbers to berry crops, stepwise multiple regression was used to select the best berry variables, followed by robust multiple regression using Huber's method ($C = 1.345$, with C being the tuning constant for Huber's method of robust regression) to estimate parameters for the multiple regression. In all cases where competing models gave similar high R^2 values we used Akaike's information criterion corrected for small sample size (AIC_C) to determine the best model ($\Delta AIC \leq 2$) following the recommendations of Anderson (2008). We tested all multiple regressions for multicollinearity and found

no evidence of this problem in our data. We used berry production in one year to predict rodent abundance in the following year. A preliminary analysis showed no significant relationships of rodent numbers with berry production either in the current year or in 2 years previous. Confidence limits for all berry estimates were estimated by bootstrapping 10,000 samples.

Mushroom production and spruce seed indices.—We have described in detail the methods used to measure aboveground mushroom production in the Kluane region in Krebs et al. (2008). Mushroom biomass was measured on an average of 668 plots of 28.3 m^2 each year. Spruce seed production was estimated both by white spruce cone counts ($n = 440$ trees each year) and by 160 seed collection trays each year. Methods are described in Dale et al. (2001).

RESULTS

Changes in small mammal numbers.—Rodent numbers were estimated for the Kluane area for the late-summer period from 1973 to 2009 (Fig. 1). Over the time period of this study (1997–2009) *Myodes* averaged 9.0 individuals/ha (coefficient of variation [CV] = 104%), *Peromyscus* 1.5 individuals/ha ($CV = 83\%$), and *M. oeconomus* and *M. pennsylvanicus* 1.4 individuals/ha ($CV = 152\%$). During 1997–2008 peak numbers of *Myodes* occurred in 1998, 2002, 2005, and 2008; deer mice were most abundant in 1999 and 2007–2008; and *Microtus* spp. reached relatively high numbers in 2002 and 2005. The net result is no significant correlation between the August densities of *Myodes* and *Peromyscus* ($r = 0.21$, $n = 12$ years), but a significant correlation existed between densities of *Myodes* and *Microtus* spp. for 1997–2008 because of their simultaneous peaks in 2002 and 2005 ($r = 0.68$, $n = 12$, $P = 0.01$). The 1993 peak in *Microtus* spp. did not coincide exactly with the peak in *Myodes* of 1992.

Changes in berry production.—Berry production fluctuated dramatically over the time period 1997–2009 (Fig. 2). Some correlation existed between the yearly indices of the 6 berry species. Four (*A. uva-ursi* versus *V. vitis-idaea*, $r = 0.59$, $n = 13$; *A. uva-ursi* versus *A. rubra*, $r = 0.59$; *A. rubra* versus *Empetrum*, $r = 0.65$; and *Empetrum* versus *Geocaulon*, $r = -0.59$) of the 15 possible correlations were statistically significant ($P < 0.05$). None of these correlations were very strong, but they indicate some tendency for covariation in berry crops. The most productive plant for the number of berries per unit area was *E. nigrum*, which was 1.9–5.0 times more productive of berries than the other species sampled in quadrats (Table 1).

We do not have any proper measure of the regional abundance of these berry-producing plants in the boreal forests around Kluane. The 2 *Arctostaphylos* species are the most common berry-producing plants in the Kluane region (Table 1), which agrees with our natural history observations from many years of working in these plant communities. Sample sizes do not accurately reflect the relative abundance of these 5 berry species in the Kluane region because these
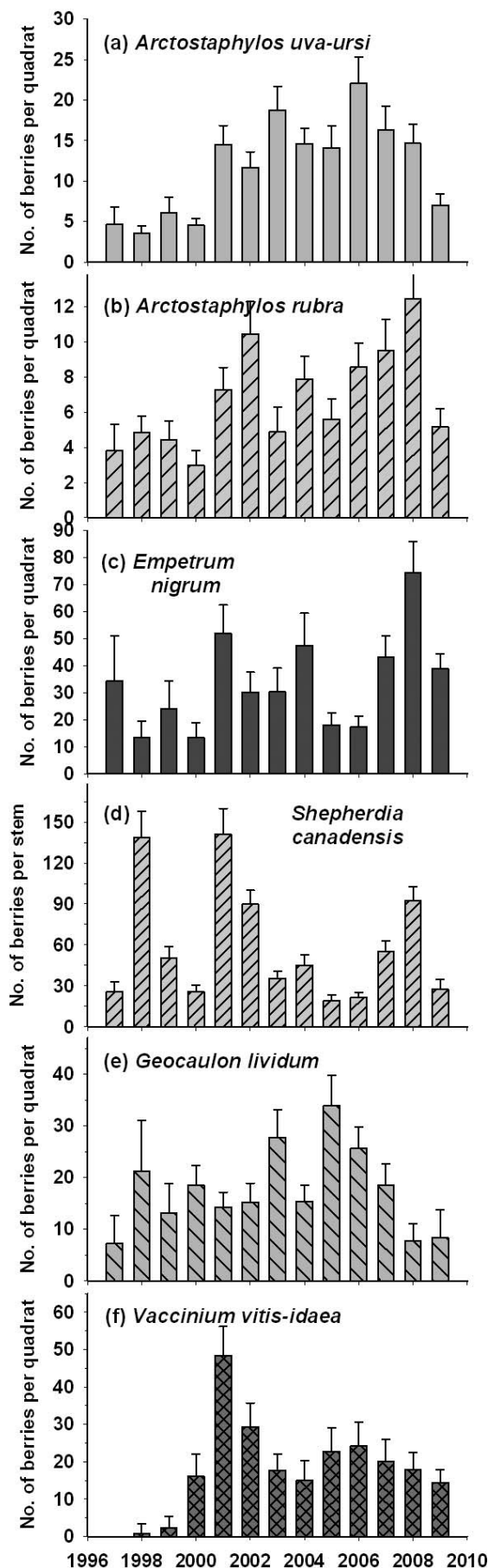
FIG. 2.—Indices of berry production of 6 plant species from 1997 to 2009 from the Kluane region of southwestern Yukon, Canada. Error bars are upper 95% confidence limits.

TABLE 1.—Mean annual counts of berries in 40×40-cm quadrats for the entire 13-year sampling period for 5 species, along with the coefficient of variation among years. All berry counts for each species are adjusted to 50% cover values. Sample size is the number of quadrats counted with that species present with >5% cover over the 13 years.

Species	Mean no. berries/year	*SD*	*CV* (%)	Sample size
Arctostaphylos uva-ursi	11.0	5.95	54	3,701
Arctostaphylos rubra	6.7	2.86	42	4,262
Empetrum nigrum	33.6	17.66	53	1,651
Vaccinium vitis-idaea	17.6	12.94	74	1,853
Geocaulon lividum	17.5	8.06	46	1,646

quadrats were not chosen randomly, and we have deliberately chosen sites to provide adequate sample sizes of the less-common berry plants.

Berry production and small mammal numbers.—For the 1997–2009 data the correlation between May and August population densities was $r = 0.94$ ($P < 0.001$) for *Myodes* and $r = 0.78$ for *Peromyscus* ($P < 0.01$, $n = 14$). For *Myodes* a linear regression using the production of *E. nigrum* from the previous summer was significant ($P < 0.001$) for both May numbers ($R^2 = 0.78$) and for August numbers ($R^2 = 0.85$; Table 2). None of the other berry-producing plants showed any statistically significant relationship to May or August numbers of *Myodes* over the 13 years of study. Neither mushroom abundance nor white spruce seed production of the previous year was related to numbers of *Myodes*. In contrast to the successful prediction of numbers of *Myodes*, we could not predict the ($\log_{10}$) overwinter index for *Myodes*. The ($\log_{10}$) summer population growth index for *Myodes* could be predicted from berry crop of the current year ($R^2 = 0.48$; Table 2). We tested whether including a density-dependent covariate with berry data would allow us to predict the summer index and the winter index, but we did not find a density-dependent correlation in our data of *Myodes* that would help to explain variation in these 2 indices.

For May numbers of *Peromyscus* a multiple regression using the production of *A. rubra* and epigeous mushrooms was significant ($P < 0.001$, $R^2 = 0.89$; Table 2). None of the other berry producing plants showed any statistically significant relationship to May numbers of *Peromyscus*, although the correlation with *A. uva-ursi* ($r = 0.53$, $n = 14$, $P = 0.051$) was suggestive. The prediction of August numbers of *Peromyscus* picked *A. uva-ursi* and *A. rubra* as predictors with a similar R^2 of 0.82 ($P < 0.001$). The multiple regression prediction of the summer population growth index of *Peromyscus* ($\log_{10}$) from

TABLE 2.—Multiple regressions to predict small rodent population density in year $t + 1$ from berry counts in year t. Only significant regressions are given. D = density, E = *Empetrum nigrum*, R = *Arctostaphylos rubra*, U = *Arctostaphylos uva-ursi*, V = *Vaccinium vitis-idaea*, SH = *Shepherdia canadensis*, G = *Geocaulon lividum*, M = wet biomass of epigeous mushrooms per 10 m². Summer rate of change of *Microtus* is predicted from counts of *Shepherdia* of the same year.

Species	Season	Multiple regression	R^2	$F_{d.f.}$	P
Myodes rutilus	May density	D = 0.0970E	0.78	$40.1_{1,11}$	0.000
	August density	D = 0.3612E	0.85	$60.3_{1,11}$	0.000
	Summer rate of change	Log_{10}(summer ratio) = 0.5046 + 0.0128V − 0.0236U	0.48	$4.62_{2,10}$	0.034
Peromyscus maniculatus	May density	D = 0.1563R + 0.0099M	0.89	$42.1_{2,10}$	0.000
	August density	D = 0.1180R + 0.0781U	0.82	$23.1_{2,10}$	0.000
Microtus spp.	May density	D = 0.1460V − 0.1346U	0.86	$30.2_{2,10}$	0.000
	August density	D = 0.1077V + 0.0970E − 0.5027R	0.98	$162.8_{3,9}$	0.000
	Summer rate of change	Log_{10}(summer ratio) = 0.0072SH of same year	0.55	$14.61_{1,12}$	0.002
	Winter rate of change	Log_{10}(winter ratio) = −1.4764 + 0.0353E	0.49	$9.52_{1,10}$	0.011

berry crops of the current year was not significant ($P = 0.09$). We found no density-dependent relation of higher spring densities leading to lower summer population growth in *Peromyscus* ($r = 0.00$, $n = 14$, $P > 0.05$). The prediction of the (log_{10}) overwinter survival index for *Peromyscus* was nonsignificant ($P = 0.12$), and the highest correlation was with berry counts of *Shepherdia* of the previous year ($r = 0.47$, $n = 11$, $P = 0.16$).

For May numbers of *Microtus* spp. a multiple regression using the production of *A. uva-ursi* and *V. vitis-idaea* was significant ($P < 0.001$, $R^2 = 0.86$; Table 2). None of the other berry-producing plants showed any relationship to May number of *Microtus*. The prediction of August numbers of *Microtus* picked *V. vitis-idaea*, *E. nigrum*, and *A. rubra* with a higher R^2 of 0.98 ($P < 0.001$). The corresponding multiple regression prediction of the (log_{10}) overwinter index for *Microtus* was significant ($P = 0.04$), and the highest correlation was with berry counts of *E. nigrum* of the previous summer ($r = 0.70$, $n = 12$, $P < 0.05$). The prediction of the summer population growth index for *Microtus* was significant ($P = 0.006$), and the highest correlation was with berry counts

of *S. canadensis* of the current year ($r = 0.59$, $n = 13$, $P = 0.03$). Introducing density-dependent terms into the multiple regressions for the 2 indices for *Microtus* did not add any statistical value to the predictions.

With respect to the plant species most strongly related to rodent population changes, the most useful predictor was *E. nigrum* (Table 3). *G. lividum* was never chosen as a useful predictor of rodent population densities. Seed production of white spruce also was never correlated with any of the rodent density parameters for any of the rodent species. *S. canadensis* was a significant predictor only for summer rates of change in *Microtus*.

The multiple regressions given in Table 2 provide predictive models for rodent densities in the boreal forests of the Yukon (Fig. 3). In most cases the explanatory ability of these statistical models was based on a few high-density years that coincide with an appropriate high production of berries of one species or another. Most of these relationships showed considerable scatter at low rodent densities. Predictions in all of our multiple regressions are precise, and this will facilitate future testing of these relationships.

TABLE 3.—Plant species chosen by multiple regressions as the best statistical predictors of rodent population indices for the 3 main rodent species. Pearson simple correlation coefficients (r) are given. May and August density and overwinter indices were predicted from the previous year's berry crop, and the summer population growth index was predicted from the current year's berry crop. Boldface type indicates predictive variables, all with $P < 0.05$.

Species	Parameter	*Arctostaphylos uva-ursi*	*Arctostaphylos rubra*	*Empetrum nigrum*	*Shepherdia canadensis*	*Vaccinium vitis-idaea*	*Geocaulon lividum*	Mushrooms
Myodes rutilus	May density			**0.71**				
	August density			**0.82**				
	Overwinter index							
	Summer population growth index	−0.20				0.41		
Peromyscus maniculatus	May density	0.53[a]	**0.65**	**0.62**				0.46
	August density	**0.67**	0.57[a]					0.40
	Overwinter index							
	Summer population growth index						0.50[a]	
Microtus spp.	May density	0.24				**0.80**		
	August density		0.18	0.57[a]		**0.62**		
	Overwinter index				**0.70**			
	Summer population growth index				**0.74**			

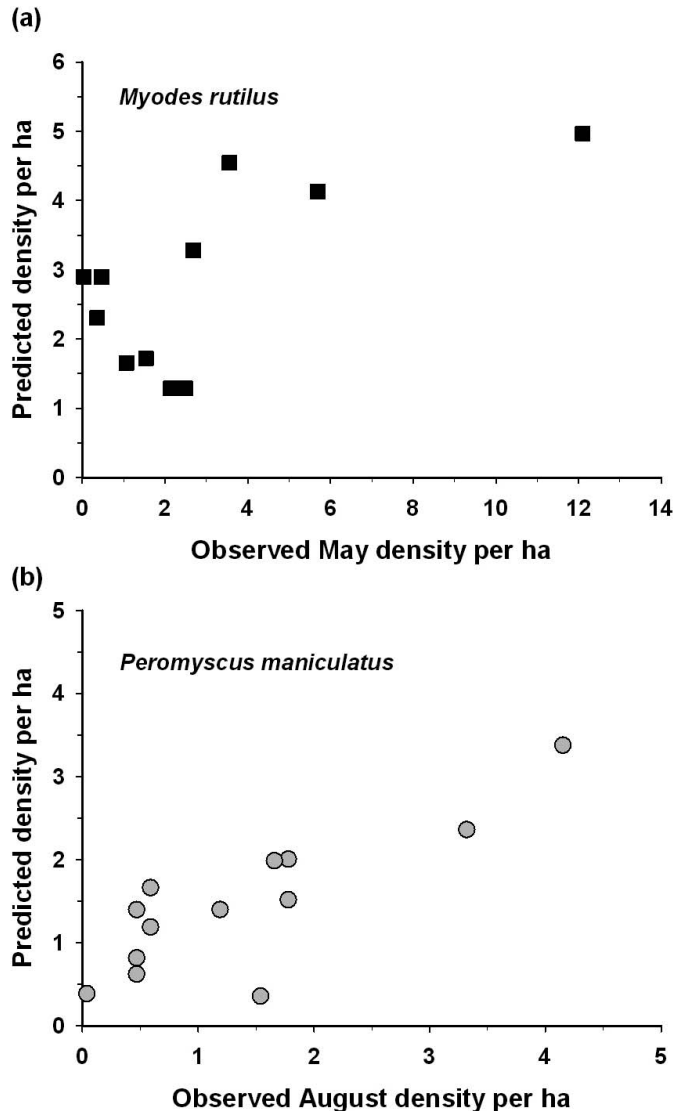[a] $0.05 < P < 0.10$.

(a)

(b)

Fig. 3.—Relationship between observed and predicted densities of a) *Myodes rutilus* in May 1998–2009, from the abundance of berries of *Empetrum nigrum* of the previous summer; and b) *Peromyscus maniculatus* in August, 1996–2009, from the abundance of *Arctostaphylos rubra* and mushroom production in the previous summer. Predictive equations are given in Table 2.

DISCUSSION

Berries, with their high-caloric seeds, provide an excellent source of food for *M. rutilus*, which relies more on berries than other small mammals such as *M. oeconomus* (Hansson 1985; West 1982). West (1982) discovered that berries and seeds comprised 62–92% of the summer and fall diet in *M. rutilus*, and voles trapped from under 1 m of snow had primarily berries in their stomachs. Merritt and Merritt (1978) reported that seeds made up 75% of the diet of *Myodes gapperi* in winter. *M. gapperi* may specialize on different foods than *M. rutilus*, but seeds and fruits seem to be an important part of the diets of both (Hansson 1971, 1985).

Peromyscus maniculatus is a generalist feeder, and dietary studies of various species of *Peromyscus* in other parts of their

geographic range give seeds a high ranking in their diet (Hanley and Barnard 1999; Martell and Macauley 1981; Reese et al. 1997). *Microtus* species in general are leaf-eaters, but they also consume many seeds in some environments and particularly during the winter months (Batzli 1985). Unfortunately, we do not have detailed dietary data for either *Peromyscus* or *Microtus* from the Kluane region of the Yukon.

We suggest here that the abundance of berries can affect the abundance of these small mammals by providing time-delayed positive feedback. However, the abundance of berries appears to be driven by climate (Krebs et al. 2009), and no possibility exists of a short-term feedback loop from rodents to the abundance of these northern berry plants, which are long-lived perennials subject to disturbance only by forest fires and the resulting succession processes. This system is similar to what Caughley (1976) defined as a noninteractive grazing system that is reactive to plant production because winter survival depends on berry production.

Several constraints characterize our study design. The measurement of berry production was carried out by indices, and we pooled all the data from the 10 locations because general synchrony existed among sites—good berry years were good across the boreal forest area of Kluane. We did not have measures of the absolute abundance of berries per hectare, only indices of year-to-year changes. The problem this raises is that some of our study sites did not have stands of some of the berry species. As an example, 2 of our long-term rodent trapping areas (Sulphur Lake and Silver) had little or no *E. nigrum*, yet both areas contain normal populations of *M. rutilus*. We did not have enough microsite-specific data to test if changes in rodent numbers on a particular small area responded to the berry species present only on that particular site.

The measurement of rodent numbers was limited to 2 sessions each summer, May and August. All of these rodents can breed into September and possibly October in some years, and consequently, the August data point cannot be assumed to be the maximum population for autumn. A consequence is that the overwinter index may be >1.0 (log(index) > 0) in some winters at a time when the population should only be decreasing. We do not know why we could not predict the index of overwinter survival for *Myodes* and *Peromyscus*. We are convinced from our natural history observations that berry production in year t determines overwinter survival in winter t to $t + 1$, but the data we present here do not support this belief. Our explanation of this serious discrepancy is that the August density data do not accurately reflect the number of rodents going into the winter period, so the overwinter index is a poor measure of overwinter survival. This was not due to poor trapping efficiency. The population estimates for each data point were precise because these species are easily trapped, and minimum-number-alive counts were virtually always within a few percent of the program CAPTURE estimates. We caught and marked almost the entire population on our sample sites. We accept this negative evidence as pointing to a need for further research on overwinter loss rates with more intensive livetrapping and radiotelemetry.

Finally, we acknowledge that multiple regression is a crude method for testing ecological relationships. In this case we have no alternative. Clearly a preferred method would be to manipulate berry numbers experimentally, but we are limited in not yet being able to manipulate berry crops on a spatial scale that would allow us to test hypotheses more exactly. The question of what factors cause berry crops to vary annually is addressed elsewhere (Krebs et al. 2009); climatic variables provide a strong prediction of year-to-year variation in berry production. In this type of climatically driven ecological system, a mensurative experiment may be the only way to test specific hypotheses. We attempted to increase berry production experimentally by adding trace amounts of nitrogen fertilizer to plots, but these treatments over 2 years failed to change berry production (Cowcill 2006; C. J. Krebs, pers. obs.).

All studies of food habits in *M. pennsylvanicus* and *M. oeconomus* show that berries are not part of the diet of these grass, root, and monocot seed eaters (Batzli 1985). This casts doubt on the conclusion that we can predict changes in numbers of *Microtus* from berry crops. Two possible alternatives flow from this. First, it may be that the multiple regressions we have developed are giving us ecological nonsense, and hence they should be rejected; or 2nd, good berry crops, because they are driven by climate, may correlate with the production of grass and monocot and dicot vegetative growth in these ecosystems. We have no measures of grass growth or seed production of grasses for this system, but we have an independent measure of general plant production in the growth rates of willow shrubs (*Salix glauca*). We measured each year a relative index of growth shown by the terminal twigs of willows, as described in Krebs et al. (2001). The canonical correlation of the 5 ground berry species with willow growth (0.92, $n = 11$, $P = 0.05$) suggests that ground berries might be an indicator of general plant production in this ecosystem. We thus prefer to interpret the correlations for *Microtus* as the 2nd alternative of correlated plant growth, but we have no herb and grass data to test this inference directly at present.

Two major surprises arose from these data. First, the most common dwarf shrub in the Kluane area, *A. uva-ursi*, showed little or no relationship to changes in numbers of the dominant vole *Myodes*, although it was a significant predictor for both *Peromyscus* and *Microtus*. We do not understand why this is the case. The habitat of *Myodes* is restricted largely to boreal forests dominated by black and white spruce (*Picea mariana* and *P. glauca*) and to those areas recovering from forest fires (Fuller 1969; Whitney 1976). In the southern Yukon we virtually never caught *Myodes* in grassland habitat (Boonstra and Krebs 2006). *Myodes* eats a wide variety of foods (Dyke 1971; Grodzinski 1971; West 1982), including seeds of dwarf shrubs (*Arctostaphylos* spp., *E. nigrum*, and *Vaccinium* spp.); leaves of herbs, shrubs, and trees; lichens; epigeous and hypogeous fungi; and occasionally mosses and arthropods. The fungi are eaten only in summer and, although *Myodes* will eat spruce seeds, it cannot survive on them (Grodzinski 1971),

nor do populations increase in spruce mast years (Boonstra and Krebs 2006). Seeds from the dwarf shrubs appear to be key to overwinter survival and population growth of *Myodes*, but *A. uva-ursi* does not appear to be a key species in our region. It is possible that some of the reported correlations here represent ghost correlations with other plant species that supply critical food items, but it is not obvious to us what these species might be. Insects could possibly form some important food items, especially because insect production also could be positively related to berry or overall plant production, but we have no data on that component.

A 2nd surprise was that the large seed crops of white spruce did not show any significant correlation with any of the rodent population changes. There are good data from southern populations of *Peromyscus* showing a strong response to mast years of oak trees (Elias et al. 2004; Ostfeld et al. 1996) and of sugar maples (Falls et al. 2007). *Myodes glareolus* in Europe responds to deciduous tree mast years with outbreaks, but good mast years do not affect overwinter survival (Pucek et al. 1993). In the Yukon boreal forest white spruce seeds appear to have little demographic impact on any of the rodent species, although they are critical for good survival and reproduction of red squirrels (*Tamiasciurus hudsonicus*—Boutin et al. 2006).

We can explain statistically a large part of the densities of these northern rodents from a bottom-up perspective with estimates of berry production from the previous year, but in general, about 10–20% of the variation remains to be explained by other factors that affect population density. Some of this variance could arise from taking regional means of the variables. Top-down processes via predation do not play a strong role in this ecosystem because predators of small mammals are rare (Boonstra et al. 2001). Social interactions in *Myodes* are known to have an effect on changes in density, and this could explain some of the missing variation (Gilbert et al. 1986). Winter weather is another possible confounding variable, but to date we have been unable to see any clear correlations of changes in rodent numbers with measures of winter severity.

We suggest that future efforts focus on detailed study of small study sites in which the absolute abundance, reproductive rates, and survival rates of the rodents are measured and the local berry production per unit area is quantified. On the same sites detailed data on climatic and soil variables should be recorded to determine if variation in berry numbers is driven by variations in summer or winter weather patterns. Finally, we need detailed dietary data on these rodents in the Kluane region to test the generality of diet studies that have been published for other plant communities.

ACKNOWLEDGMENTS

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