

Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck

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Abstract: We undertook a large-scale survey of the distribution of northern, *Glaucomys sabrinus* (Shaw, 1801), and southern, *Glaucomys volans* (L., 1758), flying squirrels in Ontario, Canada. Livetrapping was conducted along a north-south transect spanning about 500 km, from 42.5°N to 47.2°N. During 2002–2004, we conducted 42 971 trap-nights at 26 sites and captured 232 northern and 538 southern flying squirrels. During 2002 and 2003, southern flying squirrels occurred >200 km farther north than we expected. However, the range of this species appeared to contract to the south by about 240 km after the winter of 2004. Weather and food data suggested that cold temperatures during January and February 2004 combined with a failed mast crop in the autumn of 2003 resulted in an energetic bottleneck and subsequent population crash. We speculate that prior to 2004 southern flying squirrels had expanded their geographic range in response to recent climate warming. In particular, the nine winters between 1994 and 2004 were relatively warm. By measuring the range expansion over this warm interval, we were able to estimate a rate of spread of 22 km per year, and a diffusion coefficient of 6.9×10^7 m² per generation.

Résumé : Nous avons fait un inventaire à grande échelle de la répartition des écureuils volants du nord, *Glaucomys sabrinus* (Shaw, 1801), et du sud, *Glaucomys volans* (L., 1758), en Ontario, Canada. Nous avons piégé des animaux vivants le long d'une ligne-échantillon nord-sud d'environ 500 km, de 42,5°N à 47,2°N. De 2002 à 2004, nous avons fait 42 971 pièges-nuits de trappage à 26 sites et capturé 232 écureuils volants du nord et 538 écureuils volants du sud. En 2002 et 2003, les écureuils volants du sud se retrouvait >200 km plus au nord que nous le prévoyions. Cependant, l'aire de répartition de l'espèce semble s'être contractée vers le sud d'environ 240 km après l'hiver 2004. Les données de nourriture et de climat laissent croire que les températures froides en janvier et en février 2004 combinées à l'insuccès de la glandée à l'automne 2003 ont eu comme conséquence un goulot d'étranglement énergétique et une chute subséquente de la population. Nous spéculons qu'avant 2004 les écureuils volants du sud avait agrandi son aire de répartition grâce au réchauffement climatique récent. En particulier, les neuf hivers de 1994 à 2004 ont été relativement chauds. D'après la mesure de l'extension d'aire durant cet intervalle plus chaud, nous pouvons estimer un taux d'étalement de la population de 22 km par année et un coefficient de diffusion de $6,9 \times 10^7$ m² par génération.

[Traduit par la Rédaction]

Introduction

Range boundary limits can be caused either by biotic factors such as competition, predation, and parasitism, or by abiotic factors such as the availability of nesting substrates or climate. It has been suggested that in the temperate zone biotic factors will tend to limit ranges to the south, whereas abiotic factors will limit them to the north (MacArthur 1972; Brown 1995). For many species, a likely abiotic limit in the north is a seasonal energetic bottleneck (Humphries et al. 2004).

Seasonal energetic bottlenecks result from seasonal periods

of negative energy balance. Where this occurs, the range limit should be determined by a trade-off between the size of accumulated energy reserves, the rate at which reserves are depleted during the period of negative balance, and the length of the period of negative balance (Humphries et al. 2004). Where the size of the reserve does not meet or exceed the demands on the reserve, individuals will perish. At a population level, this can result in a failure to persist.

In North America, such energetic bottlenecks are thought to be especially important in winter. For example, Brocke (1970) demonstrated a physiological relationship between

Received 30 March 2005. Accepted 21 September 2005. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 11 November 2005.

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winter temperature, snow depth, and opossum (*Didelphis virginiana* Kerr, 1792) mortality. Similarly, a combination of winter length and hibernaculum temperature is correlated with northern range limits of little brown bats, *Myotis lucifugus* (Le Conte, 1831) (Humphries et al. 2002).

The southern flying squirrel, *Glaucomys volans* (L., 1758), is a small, nocturnal, gliding squirrel common to the temperate forests of eastern North America. These squirrels are active during winter, and they apparently have developed a number of strategies for dealing with possible energetic bottlenecks. One is to cache hard mast (e.g., Thomas and Weigl 1998) that is collected in the summer and fall to provide a winter food supply. Another is to form aggregations in winter, huddling in tree cavities to decrease resting metabolic costs (Stapp et al. 1991). Finally, the species exhibits seasonal thermogenesis (Merritt et al. 2001). Muul (1968), Stapp et al. (1991), and Merritt et al. (2001) studied the winter energy constraints of southern flying squirrels and suggested that energetic bottlenecks should occur in northern environments.

Southern flying squirrels have been identified by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as a species of special concern (Stabb 1988). This status is due both (i) to the species reaching its northern range limit in southern Canada and (ii) to its Canadian range being largely coincident with areas of high forest loss. Stabb (1988) conducted surveys in Ontario and found that the northern range boundary occurred at about 45°N latitude. This range limit coincided with the -12 °C isotherm of average daily January temperature, leading Stabb (1988) to suggest that this isotherm represents a likely energetic limit for southern flying squirrels.

We used field surveys to update the distribution and status of both southern and northern (*Glaucomys sabrinus* (Shaw, 1801)) flying squirrels in Ontario and to test whether the southern species has expanded its geographic range in response to recent climate warming (Intergovernmental Panel on Climate Change 2001). We also used a natural experiment created by food and weather patterns to test the hypothesis that southern flying squirrels are limited at the northern edge of their range by a seasonal energetic bottleneck.

Materials and methods

Flying squirrel sampling

In 2002, we began what was originally a study of northern flying squirrel population genetics and habitat use in Ontario. Livetrapping surveys for flying squirrels were conducted at 5 sites in central Ontario (Appendix Table A1). We were surprised to find that the southern flying squirrel was abundant at all of these sites, despite the fact that the sites in some cases were well beyond the northern limit of the species range as mapped by Stabb (1988). Indeed, prior to our trapping in 2002, Strickland and Rutter (1994) did not consider southern flying squirrels to be residents of Algonquin Provincial Park, and there were only three records from the park (e.g., Dobbyn 1994), despite >50 years of small-mammal trapping.

Our findings led us to suspect that southern flying squirrels had expanded their range relatively recently. Accord-

ingly, we undertook larger scale sampling in 2003 and 2004 along an approximate north-south transect, running from the north shore of Lake Erie (42.52°N latitude) to a site north of Temagami (47.29°N latitude). With some exceptions, sites along this transect were selected based on the occurrence of what we perceived to be good southern flying squirrel habitat; namely, mature tolerant hardwood forest, with abundant oak (species of *Quercus* L.) and (or) beech (*Fagus grandifolia* Ehrh.) in the overstory (Weigl 1978; Fridell and Litvaitis 1991). We deviated from an actual linear transect in many places to take advantage of partnering with ongoing studies and to sample some sites of particular interest (e.g., protected areas). In total, 26 different sites were visited during 2002–2004, with some sites being sampled in all years and others in only 1 or 2 years (Appendix Table A1).

Because we took advantage of ongoing studies where possible, trapping methods varied somewhat among sites. In general, we established one or more line transects at a site, spacing live traps placed 1.5–2.0 m high on tree trunks at intervals of 20–40 m along each transect. Traps were placed either on a wooden platform on a shelf bracket or on a platform of two large nails and secured with an elastic cord. Traps were either Tomahawk model 102 (Tomahawk Live Traps, Tomahawk, Wisconsin), Sherman model LFAHD (H.B. Sherman Traps, Tallahassee, Florida), or Sherman model 5515AHD. Traps at most sites were baited with a mixture of oats, molasses, and peanut butter. At some sites we used sunflower seeds, green apples, and small quantities of peanut butter to minimize trap disturbance by black bears (*Ursus americanus* Pallas, 1780). A minority of sites were prebaited for up to 1 week. All trapping was done between May and October in each of the 3 years. Time spent at any particular site varied between 3 days and several months.

All captured squirrels were weighed, sexed, ear-tagged (National Band and Tag Co., Newport, Kentucky), and assigned an age class (adult or juvenile). The two flying squirrel species were distinguished using a suite of morphological characteristics, including the tail and hind-foot length, tail colouration, and basal colour of fur on the venter (Peterson 1966; Woods 1980; Banfield 1987). Hairs (with roots intact) were sampled from most individuals for an ongoing study of population genetics. Some squirrels were radio-collared as part of ancillary, ongoing studies (J. Bowman, in preparation; G.L. Holloway and J.R. Malcolm, in preparation). All animal handling procedures were approved by Animal Care Committees of the Ontario Ministry of Natural Resources or the University of Toronto.

Temperature and mast data

Numerous studies seeking to characterize severe winter temperatures have used average daily minimum temperature in January as an index of winter severity (e.g., Root 1988; Stabb 1988; Stapp et al. 1991). Because we wished a measure that would better reflect the duration of extreme temperatures, which is potentially important in defining an energetic bottleneck (Humphries et al. 2004), we used the average daily minimum temperature of the two coldest months, January and February.

We obtained daily winter temperatures for 1900–2004 for all weather stations in Ontario from the Meteorological Service of Canada (Environment Canada). We stratified our

analysis of temperature in the study region into three 1° latitudinal bands. Specifically, these consisted of a southernmost band (44°N–45°N) that was within the area traditionally considered to be occupied by southern flying squirrels; a middle band (45°N–46°N) that was considered to be the proximate range expansion zone; and a northernmost band (46°N–47°N) that was considered to be the distal range expansion zone. All weather stations that fell within the bands were used in our analyses, including those with some missing or unreported data. For each band, we plotted the relationship between average daily minimum temperature in January and February and year for the period 1900–2004, and assessed the relationship with a linear regression.

We assessed potential food crops for southern flying squirrels during the period of our survey by using data from annual wildlife food surveys undertaken by the Ontario Ministry of Natural Resources (OMNR, unpublished data). Within our study area, several OMNR administrative districts each collected information on a range of wildlife foods using annually surveyed routes. Surveys were used from all OMNR offices reporting for any given year within the Peterborough, Parry Sound, Pembroke, North Bay, Sudbury, and Sault Ste. Marie districts. Surveys across this region have been undertaken every year since 1998, but not every office completed a survey every year.

The production of food crops in these surveys was ranked using a scale from 0 (absent) to 4 (bumper crop). The two main mast crops for southern flying squirrels in Ontario are beech nuts and acorns (Stabb 1988), so we used data for these two species in our analyses. Acorns within the study area were predominantly red oak, *Quercus rubra* L., which extends farther north in Ontario than white oak, *Quercus alba* L. (Farrar 1995). We were mostly interested in year-to-year variation, so for each mast species we averaged surveys across the region for each year of interest.

Southern flying squirrels cache food to provide the accumulated energy reserves that they require to survive during winter, when temperatures are cold and food is scarce (Stapp et al. 1991). The size of these stored reserves is thought to be directly related to a squirrel's ability to survive. According to this line of reasoning, the size of food crops in the autumn will thus affect overwinter survival and hence the size of the squirrel populations the following spring and summer. This should produce a lag of nearly a year in the relationship between food crop abundance and southern flying squirrel abundance. Therefore, we compared flying squirrel abundances from our surveys to food crop abundances assessed the previous year.

Historical small-mammal data from Algonquin Provincial Park

As mentioned, in 2002 we obtained an unusually large number of observations of southern flying squirrels in Algonquin Provincial Park. The park has been the site of a long-term small-mammal livetrapping program initiated by J.B. Falls in 1952 (e.g., Fryxell et al. 1998). It appears that prior to our work, few records of southern flying squirrels had been obtained by this program. A southern flying squirrel

was collected in Algonquin Park by J.B. Falls in 1984 and donated to the Royal Ontario Museum (ROM catalogue No. 90715), and two other records are documented from the park: one in 1985 and one in 1987 (Dobbyn 1994). However, small numbers of northern flying squirrels were regularly captured by the small-mammal trapping program in Algonquin Park. Because there is some potential to misidentify these species (especially given that the southern species was not expected), we assessed the Algonquin Park capture data for unusual trends that might suggest periods of range expansion by southern flying squirrels. Our trapping data revealed that in some localities, southern flying squirrels occurred at higher densities than the northern species; hence, we felt that their incursion into the park might be noticeable in the squirrel time series. Furthermore, squirrel masses prior to the appearance of young of the year (i.e., late June) should serve to distinguish the smaller southern flying squirrels from the northern flying squirrels. Therefore, we examined squirrel masses to identify potential southern flying squirrels. Our objective in assessing these Algonquin trapping records was to obtain additional evidence about the presence and timing of a range expansion by southern flying squirrels. Capture data were obtained from annual reports provided to OMNR (e.g., Alkins et al. 2004)² and mass data were from R.J. Brooks, University of Guelph (unpublished data).

Results

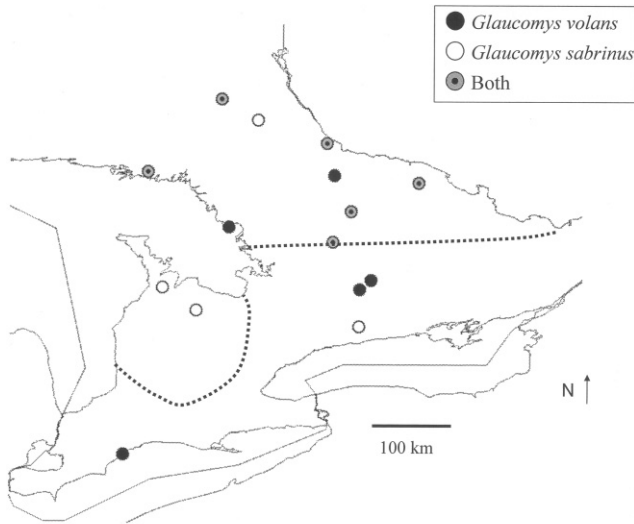
Flying squirrel distributions

During 2002, we surveyed five sites in central Ontario for flying squirrels, ranging in latitude from 44.57°N to 45.95°N. To our surprise, southern flying squirrels were present at each site (Appendix Table A1). This was the first evidence that southern flying squirrels had a more extensive range in Ontario than was identified by Stabb (1988). This difference was due either to a recent range expansion or to historical under-detection. We captured northern flying squirrels at all but one of our sites that year. At every site we obtained a lower rate of capture for the northern than the southern species (Appendix Table A1). In all, we conducted 8542 trap-nights during 2002 and recorded 116 captures of 76 southern flying squirrels and 40 captures of 21 northern flying squirrels.

During the expanded surveys of 2003, we captured southern flying squirrels as far north as we searched, even at a latitude of 46.95°N (Appendix Table A1; Fig. 1). Our farthest north captures were just over 200 km farther north than the northern range limit suggested by Stabb (1988). We trapped at eight sites north of Stabb's proposed limit during 2003 and detected southern flying squirrel populations at seven of these eight sites. At many of these northern sites, southern flying squirrels were quite abundant. For example, in the hardwood forests north of Mattawa (around 46.4°N), 58 captures of 50 individuals were made in 315 trap-nights (18.4 captures per 100 trap-nights; Appendix Table A1). A total of 15 sites were surveyed during 2003; southern flying squirrels were detected at 11 of these sites and northern flying squirrels were detected at 10 sites. Overall in 2003, there

²T. Alkins, P. Tran, and R.J. Brooks. 2004. Populations of small mammals in Algonquin Provincial Park, 2003. Unpublished report to the Ontario Ministry of Natural Resources.

Fig. 1. Distribution of northern (*Glaucomys sabrinus*) and southern (*Glaucomys volans*) flying squirrels livetrapped at sites during 2003 in Ontario, Canada. The dotted line indicates the northern limit of southern flying squirrels established by Stabb (1988). Circles mark centroids of area sampled at each site.



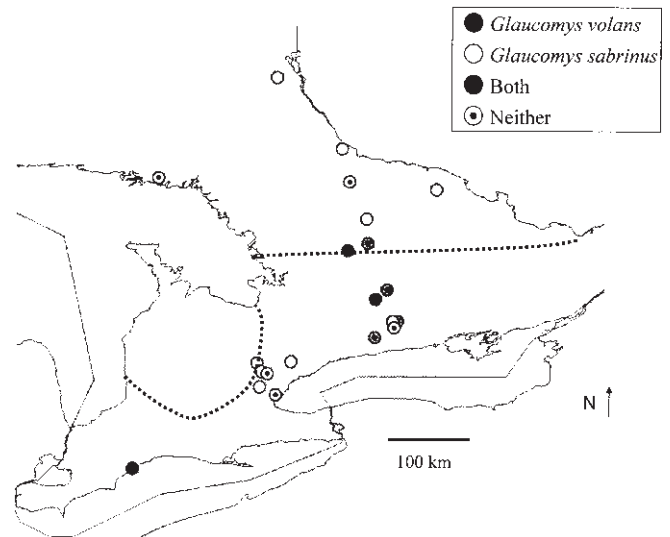
were 16 597 trap-nights, 672 captures of 430 southern flying squirrels and 158 captures of 109 northern flying squirrels (Appendix Table A1).

The distribution of southern flying squirrels was very different in 2004 (Appendix Table A1; Fig. 2). Despite additional trapping at many of the sites visited in 2003, our farthest north capture was at a latitude of 45.35°N, some 240 km south of the farthest north captures from the previous year. Remarkably, 13 259 trap-nights north of 45.35°N during 2004 caught no southern flying squirrels, whereas a similar effort north of that latitude in 2003 (13 912 trap-nights) yielded 492 captures. There were five sites trapped north of 45.35°N in both 2003 and 2004. In 2003, these five sites yielded 485 captures of 309 squirrels in 13 397 trap-nights, whereas there were no captures at these sites in 12 945 trap-nights during 2004. In total, 20 sites were surveyed in 2004; southern flying squirrels were detected at 6 of these sites and northern flying squirrels were detected at 11 of these sites. There were 17 832 trap-nights conducted across the study area, resulting in 178 captures of 102 northern flying squirrels and 39 captures of 32 southern flying squirrels (Appendix Table A1). A Wilcoxon's signed-rank test of 10 sites from across the transect that were sampled in both 2003 and 2004 demonstrated a decrease in southern flying squirrel abundance in 2004 ($z = 1.99$, $P = 0.047$).

Temperature trends

The average daily minimum temperature in January and February has increased since 1900 (Fig. 3). A linear regression demonstrated positive relationships between temperature and time for stations within the 44°N–45°N latitudinal band ($F_{[1,103]} = 8.10$, $P = 0.0053$, $R^2 = 0.07$; Fig. 3), within the 45°N–46°N latitudinal band ($F_{[1,103]} = 4.14$, $P = 0.0387$, $R^2 = 0.04$; Fig. 3), and within the 46°N–47°N latitudinal band ($F_{[1,103]} = 13.18$, $P = 0.0004$, $R^2 = 0.11$, Fig. 3). Both 2003 and 2004 were cold winters relative to the line of best

Fig. 2. Distribution of northern and southern flying squirrels livetrapped at sites during 2004 in Ontario, Canada. The dotted line indicates the northern limit of southern flying squirrels established by Stabb (1988). Circles mark centroids of area sampled at each site.



fit (Fig. 3), and 2003 was colder than 2004. Prior to 2003, there were several consecutive warm years, and notably, an extremely cold year in 1994.

Mast

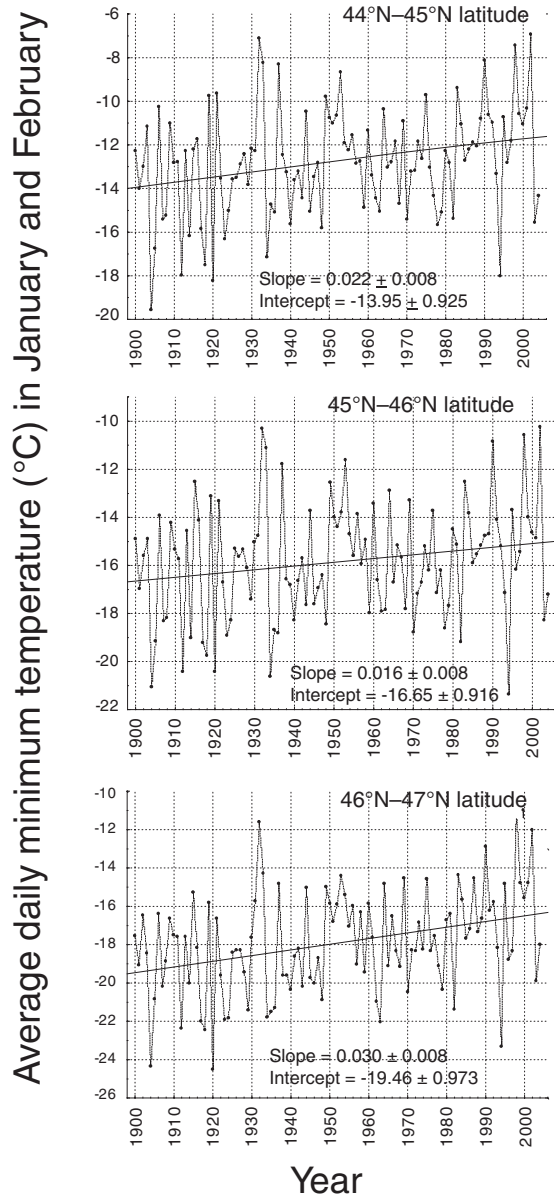
Indices of oak and beech mast abundance were synchronous across years during 1998–2003, with peaks in 1998, 2000, and 2002 (Fig. 4). In the context of our flying squirrel surveys, it is notable that mast abundance was at low to moderate levels in 2001, increased to a peak in 2002, and subsequently declined in 2003 (Fig. 5). This temporal pattern mirrored the 1 year lagged changes in southern flying squirrel abundances at three sites where the species was trapped in each year of the study (Fig. 5). In other words, mast available in the autumn of a year varied in the same way as squirrel abundance did the following summer.

Algonquin Provincial Park small-mammal data

Flying squirrels were rarely captured during the Algonquin Provincial Park small-mammal surveys, which is not surprising given that only ground traps were set. The mean annual flying squirrel capture success over the whole period 1952–2003 was 0.0010 captures per 100 trap-nights (0.0006–0.0013; 95% confidence interval). Prior to 1999, the maximum capture success was 0.0025 northern flying squirrels per 100 trap-nights and captures fluctuated around a mean of 0.0007 per 100 trap-nights (0.0005–0.0009). In 1999, there was a 10-fold increase from the mean, with 0.0067 captures per 100 trap-nights, and since that year, the mean number of northern flying squirrel captures has been 0.0038 per 100 trap-nights (0.0013–0.0063) (Fig. 6). The 1999 increase in flying squirrel captures occurred 1 year after a peak mast year (1998; Fig. 4).

Assessment of flying squirrel spring masses from the Algonquin Park small-mammal survey lines could only be done using data from 1999 or later (prior to that time, flying

Fig. 3. The relationship between average daily minimum temperature during January and February for the period 1900–2004 in three 1° latitude bands in Ontario, Canada. Linear regressions were significantly positive at the 44°N–45°N latitude band ($R^2 = 0.073$, $P = 0.0053$), at the 45°N–46°N latitude band ($R^2 = 0.038$, $P = 0.0004$), and at the 46°N–47°N latitude band ($R^2 = 0.113$, $P = 0.0004$).



squirrel masses were not available). Most trap-nights from the small-mammal program were carried out after the beginning of June, which is too late in the season to have confidence that the small flying squirrels were southern flying squirrels and not immature northern flying squirrels, since parturition in northern flying squirrels may occur before the end of June (Villa et al. 1999). However, some capture records were suggestive of southern flying squirrels. For example, in 1999, a pregnant female weighing 88 g (ear tag No. 365) was captured on 23 May. Similarly, a 65 g female (ear tag No. 1631) was captured on 22 June 1999. The maximum female southern flying squirrel mass from our recent

Fig. 4. Change in indices of beech (*Fagus grandifolia*; ●) and oak (*Quercus* spp.; ■) mast crop abundance during 1998–2003 in Ontario, Canada. Indices were calculated from Ontario Ministry of Natural Resources surveys (6–19 (beech) and 15–23 (oak) surveys, depending on the year) and are reported as index \pm SE. The thick line depicts the annual average beech and oak mast.

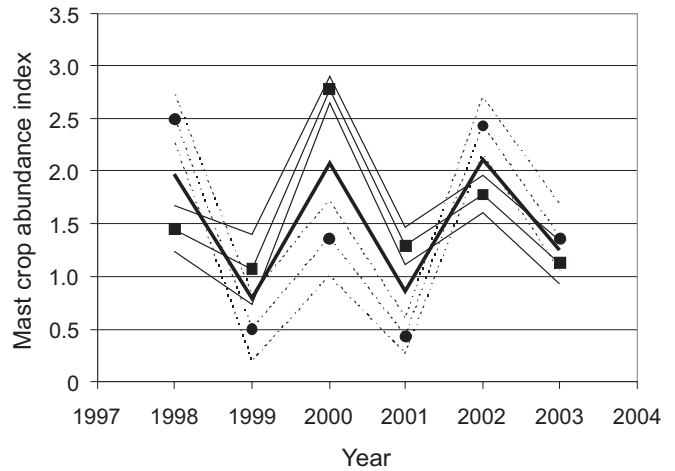
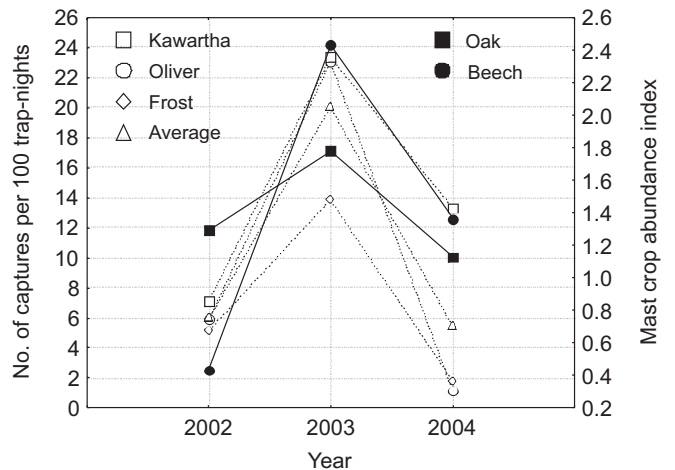


Fig. 5. Abundance of southern flying squirrels at three sites in central Ontario, Canada, during July and August 2002–2004, and average beech and oak mast crop abundance measures for the previous year (i.e., mast crop indices are lagged by 1 year). Open symbols depict squirrel abundances and solid symbols depict mast crop abundances. Flying squirrel abundances from each of the Kawartha Highlands, Oliver Property, and Leslie M. Frost sites are depicted, as well as the annual average abundance at these three sites.

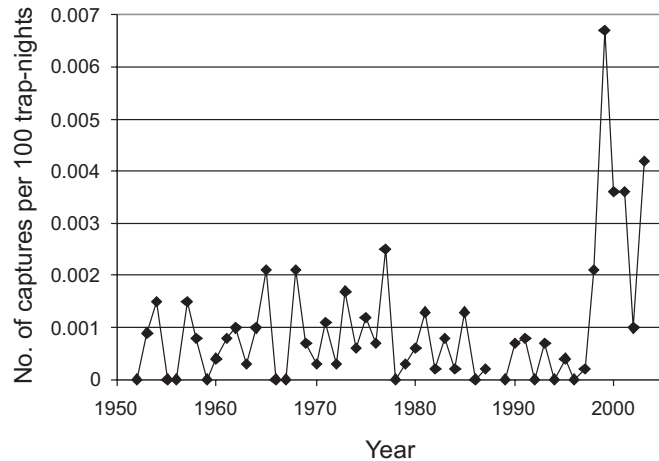


surveys in Algonquin Park was 97 g, whereas the minimum adult female northern flying squirrel mass was 85 g (G.L. Holloway and J.R. Malcolm, in preparation).

Discussion

Our data support the hypothesis that the range contraction of southern flying squirrels during 2004 was due to an energetic bottleneck that occurs during some winters, when cold temperatures and lack of food combine to produce an ener-

Fig. 6. Number of flying squirrel captures per 100 trap-nights in Algonquin Provincial Park, Ontario, Canada, from long-term small-mammal surveys.



getic deficit that results in large-scale squirrel mortality. According to this idea, failed mast crops during 2003 meant that beyond a certain latitude squirrels did not have adequate caches of food to withstand the period of negative energy balance produced by cold temperatures. That is, there is a latitude threshold produced by the north–south gradients in both temperature and mast-crop density that defines the presence and location of the energetic bottleneck.

Our results underscore the importance of both food and temperature in concert. Winter temperatures alone were unable to explain the remarkable population crash in 2004: the winter of 2004 was actually slightly warmer than that of 2003, and the cold winter of 2003 preceded the southern flying squirrel population peak. The critical difference appears to have been mast supply: although the 2003 peak squirrel population was preceded by a cold winter, it also was preceded by peak mast crops. The 2004 population crash was preceded both by cold temperatures and by a failed mast crop. Food crops during 2001 were nearly as poor as those during 2003, but in 2002, winter temperatures were warm, and the squirrels remained in northern sites such as Algonquin Park. Only when both temperatures and mast abundances were low did we observe range contraction. Given the natural experiment provided by these food and weather combinations, we consider it unlikely that the range contraction was caused by other processes, such as competition, predation, or parasitism. An energetic bottleneck is the most parsimonious explanation.

During the last century, temperatures around the globe have risen, and this trend is expected to continue for the next 50–100 years (Intergovernmental Panel on Climate Change 2001). Average daily minimum temperatures during January and February in our study area also warmed significantly during 1900–2004 (Fig. 3). Such climate warming can have widespread effects on species, such as changes in reproductive biology, phenology, and geographical and altitudinal range limits (Parmesan and Yohe 2003; Root et al. 2003).

Expansion of northern range limits owing to climate warming should be particularly evident for species that exhibit energetic bottlenecks during winter (Humphries et al. 2004). It would appear from our study that southern flying

squirrels expanded their northern range boundary in Ontario by about 200 km between mid-1980s and 2003.

It is possible that their range was underestimated in the 1980s; however, we view this as unlikely given the contraction of the range in 2004 to approximately the 1980s position. This presumptive northward expansion is consistent with recent northward range boundary shifts in numerous species, including raccoons, *Procyon lotor* (L., 1758) (Voigt et al. 2000), red foxes, *Vulpes vulpes* (L., 1758) (Hersteinsson and Macdonald 1992), little brown bats (Humphries et al. 2002), and numerous bird and butterfly species (Parmesan et al. 1999; Thomas and Lennon 1999; Parmesan and Yohe 2003; Root et al. 2003; Crozier 2004). The recent increase in flying squirrel captures in the Algonquin park small-mammal surveys (Fig. 6) also is consistent with a recent range expansion by southern flying squirrels.

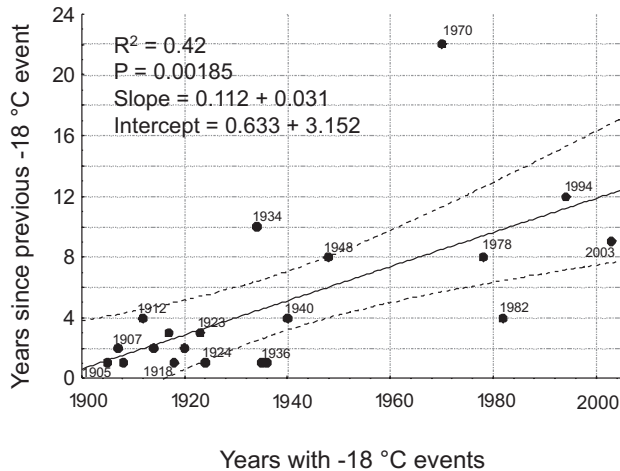
Range expansion often is depicted as a monotonic spread, whereas our study demonstrated the dynamism of the boundary. Particularly dramatic was the contraction of the northern range limit of southern flying squirrels by about 240 km during the winter of 2004 to a new range limit that was very close to the one identified by Stabb (1988). This suggests a process of interannual variability in rates of colonization and extinction at the range boundary that produces fluctuation in the boundary's location. Similar dynamic boundaries have been observed for passerines by Mehlman (1997).

Although minimum winter temperatures are increasing, potentially leading to range expansions, they are variable among years, and relatively cold years still occur. An important question in understanding range expansions is to determine how the frequency of the occurrence of cold years has changed. To investigate this, we assumed that an average daily minimum temperature in January and February of -18°C was a reasonable proxy for a “cold year” (i.e., one that would produce an energetic bottleneck for southern flying squirrels under typical food conditions). For the 45°N – 46°N latitudinal band, the interval (number of years) between -18°C events was regressed against the year of the event (Fig. 7). This analysis demonstrated that cold years are becoming less frequent (i.e., the warm intervals between the cold years are getting longer). Southern flying squirrels, therefore, will have more opportunities to expand their range farther during these warm intervals before their range is contracted owing to an energetic bottleneck. The corollary of this idea is that there is potential for contractions to be large when they do happen, since squirrel populations have the opportunity during long warm intervals to expand northward relatively far.

We can use this concept of warm intervals to speculate upon the rate of spread that southern flying squirrel populations exhibited during the recent range expansion. The winter of 1994 was the coldest in many decades, with an average daily minimum temperature of less than -21°C at the 45°N – 46°N latitudinal band (Fig. 3). We think that it is reasonable (and conservative) to assume that southern flying squirrels would have been no farther north than the limit suggested by Stabb (1988) after the 1994 winter. Under this assumption, the squirrels would have had to have spread north by 200 km in 9 years; that is, at a rate of spread of just over 22 km per year.

Such a rate of spread can be put into a comparative ecological context using a diffusion model. Andow et al. (1990)

Fig. 7. Change in duration of warm intervals during 1900–2004 at the 45°N–46°N latitude band in Ontario, Canada. Cold winters were considered to be those with an average daily minimum temperature in January and February of less than -18°C . Each cold winter is depicted in relation to the years passed since the previous cold winter.



showed that rate of spread is related to the intrinsic rate of increase (r_{\max}) and a diffusion coefficient (D) according to

$$[1] \text{ Rate of spread}^2 = 4r_{\max}D$$

If we use Blueweiss et al. (1978) to estimate that $r_{\max} = 3$ for southern flying squirrels, using a rate of spread of 22 km per year (where year = 1 generation), we find $D = 6.9 \times 10^7 \text{ m}^2$ per generation. Using a generation of 1 year assumes that no spring-born squirrels will reproduce during the late summer of their first year. Although this may occur, it is considered rare (e.g., Lee and Zucker 1990). Turchin (1998) estimated diffusion coefficients for a range of mammal species (Table 7.2, p. 261). In his analysis, D for small-bodied rodents was between 3.2×10^1 and $2.0 \times 10^6 \text{ m}^2$ per generation for meadow voles (*Microtus pennsylvanicus* (Ord, 1815)) and Columbian ground squirrels (*Spermophilus columbianus* (Ord, 1815)), respectively. Our estimate for southern flying squirrels is at least an order of magnitude above these, similar to Turchin's (1998) estimates of 1.3×10^7 to $3.6 \times 10^7 \text{ m}^2$ per generation for black-tailed deer (*Odocoileus hemionus* (Rafinesque, 1817)). At least two alternative explanations for the apparently large value of D in southern flying squirrels seem plausible. Either long-distance dispersal events inconsistent with diffusion actually governed the rate of spread for southern flying squirrels (e.g., the "fat tails" of Clark 1998) or some relictual populations persisted during the previous range contractions and contributed to the rapid expansion of the population front (see Clark 1998). Both possibilities warrant further study.

An additional surprising finding of our field surveys was that southern flying squirrels were either rare or absent in a number of sites in southern or southwestern Ontario, including Grey and Bruce counties, all sites in the Aurora District, the Ganaraska forest, and the woodlots around Peterborough (Figs. 1, 2; Appendix Table A1). In general, these sites were similar in that they were all forest remnants surrounded by developed and agricultural land. The majority of such forest

remnants that we surveyed contained northern, but not southern, flying squirrels. A possibility is that southern flying squirrels have expanded their range through the contiguous forests of central Ontario and Quebec, but not through the fragmented forests of the southwest. Expansion for this volant species may have been blocked by the lack of connectivity in the agricultural landscapes of southwestern Ontario, a possibility that suggests an interesting example of the interaction between fragmentation and climate-warming effects (e.g., Opdam and Wascher 2004).

Northern flying squirrels were distributed throughout our sampling area and were sympatric with southern flying squirrels at many sites. However, the northern flying squirrels were most abundant at sites where the southern species was either rare or absent (Appendix Table A1). Muul (1968) suggested that northern flying squirrels should be limited at the southern edge of their range by competition for nest spaces with the more aggressive southern flying squirrels. Alternatively, Weigl (1969) and Price et al. (1988) have suggested that northern flying squirrels might be limited through parasite-mediated competition with southern flying squirrels, which can carry an intestinal parasite (*Strongyloides robustus* Chandler, 1942) that may be deleterious to the northern flying squirrel. Our study was not designed to test for competition between these two squirrel species. However, our surveys do provide a baseline for a future test of the hypothesis of competition. If northern flying squirrel populations are limited by competition with their southern congeners, then we should observe future range contractions of the northern flying squirrel in response to southern flying squirrel range expansions. Areas that are not exposed to the expanding southern flying squirrel population front (e.g., unconnected forest remnants in agricultural matrix) should not contract.

A final issue concerns the status of the southern flying squirrel, which is listed as a species of special concern by COSEWIC. The northward expansion of the species' range in Ontario opens up the large areas of hardwood forest habitat on the southern Canadian Shield, thus potentially increasing habitat availability and the population size in the province. Future continued range expansions are likely under continued global warming, although we expect that these expansions will be limited by the distribution of masting tree species.

Acknowledgements

This study received financial support from the Natural Sciences and Engineering Research Council of Canada (grants to J.B., J.R.M., and P.J.W.), the Ontario Living Legacy Trust (grants to J.B. and P.J.W., and J.R.M. and G.L.H.), the OMNR Climate Change Fund, the Ontario Species-at-Risk Program, the OMNR Wildlife Research and Development Section, and the Brown Fund of Haliburton Forest and Wildlife Reserve. We are especially indebted to individuals who provided data from additional studies within Ontario, including Emma Followes and other Aurora District OMNR staff, Sandy Dobbyn of Rondeau Provincial Park, and Steve Patterson of Glaucomys.org. We thank Judith Eger, Steve Holmes, Brian Naylor, Tara McEachen, Derek Potter, Norm Quinn, Carrie Sadowski, staff of the Algonquin Park Wildlife Research Station, staff of Algonquin, Killarney, and

Mark. S. Burnham Provincial Parks, OMNR District staff, Peter Schleifenbaum and staff of Haliburton Forest and Wildlife Reserve, and the Algonquin Forestry Authority for field and technical support. Numerous field assistants helped with the work, including Lisa Bridges, Crystal Ling, Kim McNeilly, Julia Monkman, Mark Newman, Meghan O'Neill, Dave Pearce, Jeremy St. Onge, Njal Rollison, Charlotte Sharkey, and Sue Tully. Finally, we thank all the land owners for allowing us access, including Trent University, several Conservation Authorities, the Federation of Ontario Naturalists, and numerous private citizens, as well as two anonymous reviewers for helpful comments on an earlier draft of the manuscript.

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Appendix A

Table A1. Results of livetrapping surveys for northern (*Glaucomys sabrinus*) and southern (*Glaucomys volans*) flying squirrels in Ontario, Canada, during 2002–2004.

Site	Year	Latitude (°N)	Longitude (°W)	<i>G. sabrinus</i>		<i>G. volans</i>		Total trap-night
				No. per 100 trap-night	No. of unique individuals (no. of captures)	No. per 100 trap-night	No. of unique individuals (no. of captures)	
Clear Creek ^a	2003	42.523	81.628	0	0	5.27	38 (79)	1 500
Clear Creek	2004	—	—	0	0	13.67	11 (16)	117
Bronte Creek ^b	2004	43.408–43.411	79.749–79.745	0	0	0	0	69
Hilton Falls ^b	2004	43.520–43.524	79.996–79.993	14.04	6 (8)	0	0	57
Upper Canada College ^b	2004	43.656–43.657	79.878–79.874	0	0	0	0	66
Silver Creek ^b	2004	43.693–43.696	79.969–79.965	1.75	1	0	0	57
Belfountain/Dufferin ^b	2004	43.794–43.802	80.017–80.008	20.45	22 (27)	0	0	132
Grey County	2003	44.000–44.600	81.000–80.300	1.41	2 (2)	0	0	142
Bruce County	2003	44.000–45.200	81.589–81.000	10	13 (13)	0	0	130
Ganaraska	2003	44.091–44.106	78.543–78.494	1.5	4 (4)	0	0	266
Ganaraska	2004	—	—	5.27	16 (24)	0.66	3 (3)	455
Keene Road	2004	44.223–44.227	78.251–78.249	0	0	0	0	55
Henderson Line	2004	44.298–44.300	78.208–78.205	5.63	3 (4)	1.41	1	71
Burnham Provincial Park	2004	44.303	78.268–78.267	1.67	1	0	0	60
Oliver Property	2002	44.570–44.576	78.497–78.491	0	0	5.88	4 (4)	68
Oliver Property	2003	—	—	0	0	22.99	15 (20)	87
Oliver Property	2004	—	—	0	0	1.67	1	60
Kawartha Highlands	2002	44.687–44.688	78.336–78.333	1.09	2 (2)	7.1	8 (13)	183
Kawartha Highlands	2003	—	—	0	0	23.33	17 (28)	120
Kawartha Highlands	2004	—	—	3.33	1 (2)	11.67	7 (7)	60
Leslie M. Frost	2002	45.160–45.178	78.849–78.842	0.65	1	5.19	8 (8)	154
Leslie M. Frost	2003	—	—	0.68	3 (3)	13.86	48 (61)	440
Leslie M. Frost	2004	—	—	0	0	2.00	7 (9)	449
Haliburton Forest	2004	45.224–45.360	78.641–78.458	0.66	19 (25)	0.07	2 (2)	2 865
Killbear Provincial Park	2003	45.351	80.228	0	0	13.33	4 (4)	30
Algonquin Hwy. 60	2002	45.441–45.651	78.825–78.327	0.24	7 (12)	1.27	37 (64)	5 043
Algonquin Hwy. 60	2003	—	—	0.64	34 (61)	4.18	227 (397)	9 499
Algonquin Hwy. 60	2004	—	—	0.68	20 (77)	0	0	11 295
Algonquin Achray	2002	45.875–45.951	77.827–77.591	0.81	11 (25)	0.87	19 (27)	3 094
Algonquin Achray	2003	—	—	1.57	15 (36)	0.57	11 (13)	2 286
Algonquin Achray	2004	—	—	0.11	1	0	0	900
Algonquin North	2003	46.000–46.008	78.853–78.828	0	0	0.97	9 (9)	930
Algonquin North	2004	—	—	0	0	0	0	128
Killarney Provincial Park	2003	46.029–46.063	81.349–81.239	1.63	6 (6)	2.18	7 (8)	367
Killarney Provincial Park	2004	—	—	0	0	0	0	180
Mattawa	2003	46.373–46.431	78.956–78.892	2.54	7 (8)	18.41	50 (58)	315
Mattawa	2004	—	—	0.45	2 (2)	0	0	442
Nipissing Preserve	2003	46.659–46.703	79.939–79.743	3.57	4 (5)	0	0	140
Emerald Lake	2003	46.934–46.950	80.351–80.291	6.09	21 (21)	0.87	3 (3)	345
Latchford	2004	47.165–47.289	79.860–76.650	3.82	10 (12)	0	0	314
Total				0.88	232 (376)	1.94	538 (827)	42 971

Note: Sites are listed in increasing order of latitude, and coordinates are omitted for repeat visits to sites in subsequent years. Data collected by authors except those indicated by footnotes.

^aCollected by L. Pasma and S. Dobbyn in 2003 for a study of the southern flying squirrel at Clear Creek forest for the Nature Conservancy of Canada.

^bCollected by Emma Followes and the Aurora District staff, Ontario Ministry of Natural Resources.