Gap crossing by chipmunks: an experimental test of landscape connectivity

Jeff Bowman and Lenore Fahrig

Abstract: Eastern chipmunks (*Tamias striatus*) are forest specialists common to eastern North America. Numerous studies suggest that chipmunks require fencerow corridors between woodlots to maintain functional connectivity in agricultural landscapes. We tested this hypothesis by conducting a homing experiment to assess whether chipmunks would cross nonforested gaps of different sizes. Chipmunks in 11 landscapes were translocated a constant distance of 220–250 m across gaps ranging in size from 0 (continuous forest) to 240 m (mostly gap). Logistic regression analysis demonstrated that the probability of an adult chipmunk returning to its home range was not related to the size of the gap that had to be crossed ($\chi^2 = 0.781$, $n = 60$, $P = 0.377$, $\rho^2 = 0.011$). Chipmunks crossed the entire range of gap sizes and there was no evidence of a threshold in connectivity. These results suggest that forest woodlots may be functionally connected for chipmunks even without fencerow corridors, and that landscape configuration in the study area may not have isolating effects on chipmunk populations. More empirical studies are required to identify whether functional connectivity thresholds are present in mammal populations as theoretical studies suggest.

Résumé : Les tamias rayés (*Tamias striatus*) sont des animaux abondants, spécialistes des forêts dans l'est de l'Amérique du Nord. De nombreuses études indiquent que les tamias nécessitent la présence de corridors de haies entre les boisés pour que la connectivité entre les boisés reste fonctionnelle dans les paysages agricoles. Nous avons testé cette hypothèse au moyen d'une expérience de homing au cours de laquelle nous avons vérifié si les tamias traversaient des brèches non boisées de différentes tailles. Des tamias de 11 paysages ont été déplacés sur une distance constante de 220 à 250 m au-delà de brèches mesurant de 0 (forêt continue) à 240 m (surtout des brèches). Une analyse de régression logistique à démontré que la probabilité qu'un tamia regagne son domaine n'est pas reliée à la taille des brèches à traverser ($\chi^2 = 0,781$, $n = 60$, $P = 0,377$, $\rho^2 = 0,011$). Les tamias ont traversé des brèches de toutes les tailles et nous n'avons vu aucun signe de l'existence d'un seuil de connectivité. Nos résultats indiquent que les boisés sont connectés fonctionnellement, même en l'absence de corridors de haies, et que la configuration du paysage dans la région étudiée n'est pas nécessairement un facteur d'isolation pour les populations de tamias. Il faudra procéder à d'autres études empiriques pour déterminer s'il existe des seuils de connectivité fonctionnelle chez les populations de mammifères comme l'indiquent les études théoriques.

[Traduit par la Rédaction]

Introduction

Conversion of forest to nonforest can result in habitat fragmentation and loss for forest dependent species. In eastern North America, this conversion often takes the form of agricultural development, where once continuous tracts of forest may be reduced to structurally isolated woodlots, surrounded by nonforest. Theoretical studies have suggested that movement among such habitat patches as these woodlots is critical to the long-term persistence of populations (e.g., Lefkovitch and Fahrig 1985; Lande 1987). The space that must be crossed between habitat patches is hereinafter referred to as a gap (Dale et al. 1994). There may be a critical gap size for a given species, where distances longer than this critical distance are not crossed (With and King 1999). This has been referred to as a connectivity threshold (Andrén 1994). Connectivity is defined as the degree to which a landscape facilitates or impedes the movement of an individual among resource patches (Taylor et al. 1993). Landscapes where large amounts of habitat have been lost, and where most gap sizes are greater than this connectivity threshold, can have low (or no) connectivity. As a consequence, the probability of persistence for populations using this habitat is much reduced because of isolation effects (Fahrig and Merriam 1994).

Whereas a number of theoretical studies have demonstrated the existence and importance of connectivity thresholds, few empirical studies have actually evaluated movement by organisms across gaps of different sizes (Tischendorf and Fahrig 2000). This is despite the management and conservation importance that often is ascribed to identifying such thresholds (Mönkkönen and Ruenanen 1999; With and King 1999). The empirical studies that have been conducted mostly involve birds. For example, Desrochers and Hannon (1997) demonstrated that the willingness of passerines to travel across gaps is negatively related to gap size. Grubb and Doherty (1999) found that the maximum gap distance crossed was positively related to body size in an Ohio study of eight bird

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species. We have found no studies that explicitly test the effect of gap size on the crossing of gaps by mammals.

Territorial mammals have been shown to return to their home range following experimental translocation (e.g., Murie and Murie 1931). Recent evidence suggests that mammals accomplish this feat by perceiving environmental cues on the outward (displacement) leg of the journey, and reversing these cues on the return leg (Bovet 1995; Thibault and Bovet 1999). Mammals that are prevented from observing environmental cues on the displacement leg will attempt to locate their home range by making a straight-line search in a random direction. The length of these searching trips varies with the individual, corresponding to the usual length that the individual travels on exploratory excursions. Bovet (1995) has referred to this length as the critical distance. If a searching individual reaches this critical distance without finding home, then the animal will make a U-turn, return to the original release site, and search in another direction.

Recognition of familiar terrain seems also to play a part in homing by mammals. Griffo (1961) used "life range" to describe the set of home ranges, dispersal routes, and exploratory excursions that have been used during an individual's lifetime. More experienced mammals have larger life ranges than inexperienced mammals and also return home at a higher rate (Robinson and Falls 1965). In the context of Bovet's (1995) critical distance model, a displaced individual that searches for home in a random direction should have a higher probability of recognizing environmental cues on its searching journey if it is more experienced and thus has a larger life range.

We used the process of homing to test the gap-crossing ability of a forest-dependent mammal, the eastern chipmunk (*Tamias striatus*). Chipmunks have been shown to return home following translocation (e.g., Layne 1957; Seidel 1961; Thibault and Bovet 1999), and they are a featured species in studies of forest fragmentation in eastern North America. A number of authors have suggested that chipmunks might be sensitive to fragmentation as a result of their forest dependence (Forsyth and Smith 1973; Wegner and Merriam 1979; Henderson et al. 1985; Henein et al. 1998), although empirical results are equivocal (Mahan and Yahner 1996, 1998, 1999; Nupp and Swihart 1998; Rosenblatt et al. 1999; Zollner 2000). Chipmunks frequently are assumed to move among woodlots through fencerow corridors, rather than across gaps (Henderson et al. 1985; Bennett et al. 1994). Fencerows are linear landscape elements that occur along the margins of agricultural fields and contain neglected, often woody, vegetation. Henein et al. (1998) ran a simulation experiment that concluded that fencerows were critical to chipmunk population persistence in agricultural landscapes. Their model included the assumption that chipmunks would not cross gaps, and consequently, woodlots without fencerow connections to other woodlots were isolated (zero landscape connectivity). These isolated woodlots were not recolonized after chipmunk populations became locally extinct. Consequently, populations in landscapes without fencerows had a high probability of extinction.

We assumed that, following their experimental translocation, chipmunks would attempt to return home. If chipmunks are translocated using a method that does not allow them to visually observe cues during the experimental dis-

placement, then initial orientation upon release should be random (Bovet 1995). Chipmunks should then return under the following three conditions: (1) if they can perceive familiar terrain across the gap; (2) if they have previously been across the gap and know the way; or (3) through random movements. In any of these cases, we can test the ability of chipmunks to travel across gaps. We predicted three possible outcomes for the relationship between gap size and probability of successful return (Fig. 1). There should be either no relationship between gap size and return probability, a negative relationship, or a negative threshold relationship. A threshold would indicate the important connectivity threshold distance over which probability of persistence of the population in the landscape is reduced. We predicted also that juveniles should have a lower return probability than should adults because juveniles have less prior experience, and therefore, a smaller life range than do adults.
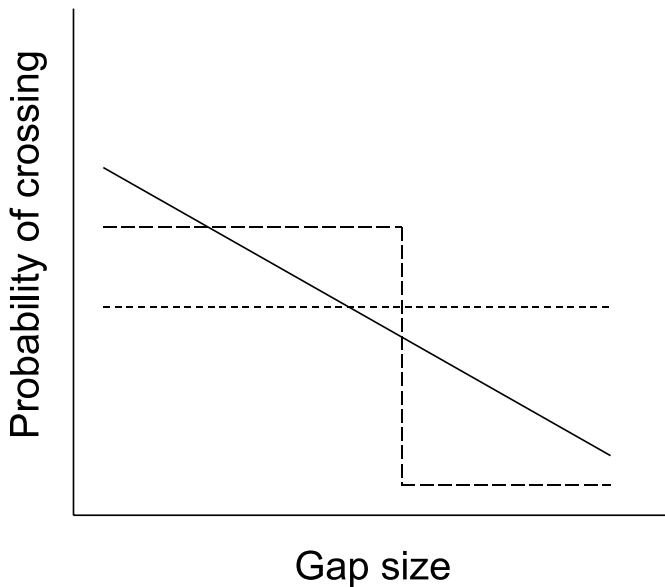
Materials and methods

To study an animal's gap-crossing ability, it is important to be able to discriminate between a gap and a habitat patch from the animal's perspective. Chipmunks are a useful species in this regard because they have been studied often, and show a clear preference for upland hardwood sites over agriculture fields and pasture (Forsyth and Smith 1973; Henderson et al. 1985).

Our study was conducted in the rural landscapes surrounding Ottawa, Ontario, Canada (45°20′N, 75°40′W). Woods were dominated by hardwood overstory, which included *Acer saccharum*, *Fraxinus americana*, *Tilia americana*, *Fagus grandifolia*, and *Quercus macrocarpa*. Understory plants included *Xanthoxylum americanum*, *Prunus* spp., *Rubus* spp., and *Corylus cornuta*. These woods were surrounded by agricultural development, in the form of tilled fields containing soy bean or corn crops, or untilled pasture containing a mixture of grasses.

We captured chipmunks in landscapes with varying forest cover (see details below). Chipmunks were moved a constant distance of 220–250 m from a forested capture site to a forested release site. Between the capture and release sites there were nonforested gaps of between 0 (continuous forest) and 240 m (mostly gap). The selected translocation distance of 220–250 m is about half of the maximum recorded movement distance for the eastern chipmunk (550 m; Seidel 1961); it therefore represents a significant movement distance for this animal, while ensuring that at least some animals would return to the capture site.

Landscapes were selected using four criteria. First, we wanted to have upland hardwood forest (i.e., chipmunk habitat) at both capture and release sites. Second, we wanted any gaps to consist of short (<20 cm) grass pasture, with no connecting fencerows. We also wanted no roads or waterways between the capture and release sites. Finally, we wanted the landscapes to consist of a range of gap sizes, from the minimum of no gap to the maximum 240-m gap. We used a combination of 1 : 50 000 topographic maps and ground-truthing to select 11 landscapes fitting these criteria. Of these, one landscape had a gap that was partially composed of agricultural crops instead of grass. A typical landscape could be thought of as being about 250 m long, of indeterminate

Fig. 1. Three possible relationships between the probability of a mammal crossing a gap and the size of the gap: negative (solid line), negative threshold (large broken line), and no relationship (small broken line).
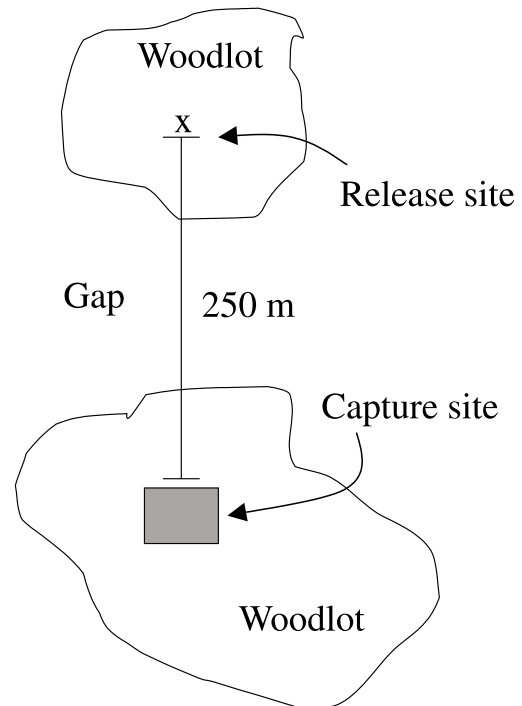

Fig. 2. A typical landscape from an eastern chipmunk (*Tamias striatus*) translocation experiment conducted during 2001 near Ottawa, Canada. Sites were selected such that crossing the gap was necessary to return to the capture site.

width, with upland hardwood patches at either end, a gap of some distance in the middle, and no connecting fencerows (Fig. 2).

At each capture site, we placed 36 folding Sherman box traps in a 6 × 6 grid with 15-m spacing between traps. Traps were baited with a mixture of oats and sunflower hearts, set for 7 consecutive days, and checked twice daily. The landscapes were not all trapped simultaneously; the capture site on each landscape was trapped for a 7-day interval some time between 15 May and 15 August 2001. Captured chipmunks were weighed, sexed, assessed for reproductive condition, and marked with a 1-g monel ear tag (National Band and Tag Co., Newport, Ky.). Juveniles were defined as individuals weighing ≤80 g.

The experimental translocation involved carrying chipmunks in an opaque box for a distance of between 220 and 250 m from the capture site to a release site. This distance was measured from the edge of the trapping grid that was closest to the release site. Direction of translocation was determined by the availability of an appropriate release site an appropriate distance away. We translocated animals from the first day of the 7-day trapping session to the sixth day, all the while monitoring the capture site for returning (i.e., eartagged) chipmunks. No animals were translocated more than once. We avoided translocating pregnant or lactating females. Methods for capture, handling, and translocation of chipmunks were approved by the Carleton University Animal Care Committee.

Our statistical analysis of the data involved two separate approaches. First, we considered each landscape an independent data point, and calculated the proportion of chipmunks that returned to the capture site within the 7-day sample period. This proportion was arcsine transformed and used in a multiple linear regression to test the relationship between the response variable proportion of chipmunks re-
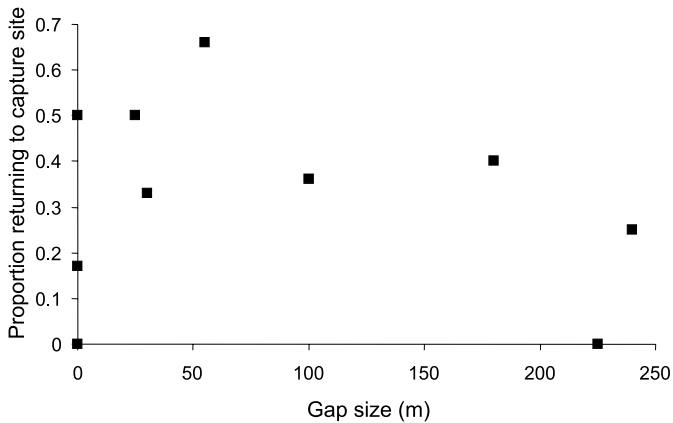
turning to the capture site and the independent variable gap size. Using regression, we tested also for possible confounding effects of chipmunk density at the capture site and Julian date of trapping. Our second approach was to consider each chipmunk as an independent data point. Here, we used logistic regression to test whether the probability of a chipmunk returning to the capture site was related to gap size. The possibly confounding effects that were tested during this analysis included population density at the capture site, date of trapping, and number of days remaining in the 7-day trapping session at first capture. To test our second prediction that juveniles should return at a lower rate than adults, we used a contingency table analysis of successful returns by each of the two age classes. Finally, the mean duration of homing events was estimated as the number of days between initial capture and return to the capture site. We tested whether this value was related to gap size. We used S-Plus 2000 (Insightful Corporation, Seattle, Wash.) for all statistical analyses.

Results

We conducted 2700 trap nights over the 11 landscapes, resulting in 123 chipmunk captures (4.6 captures per 100 trap nights). One landscape had to be omitted from this sample owing to an insufficient number of captures. Between 4 and 15 chipmunks were translocated from each of the remaining landscapes (mean = 7, median = 7). In total, 71 different chipmunks were translocated, 60 adults and 11 juveniles. Seventeen returned within a 7-day sampling period (proportion returning = 0.24). All returning animals were adults

Fig. 3. The proportion of translocated adult eastern chipmunks returning home on 10 different landscapes near Ottawa, Canada. All chipmunks were released a constant distance (220–250 m) from their site of capture. Capture and release sites in each landscape were upland hardwoods separated by a nonforested gap of up to 240 m. Between 4 and 15 chipmunks were translocated from each landscape.
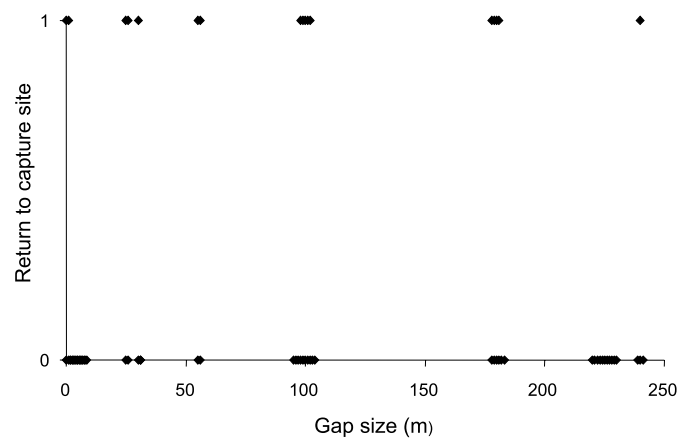

Fig. 4. Fates of individual adult eastern chipmunks translocated near Ottawa, Canada ($n = 60$). Chipmunks were moved a constant distance (220–250 m) from a capture site to a release site, both of which were upland hardwood. Nonforested gaps between capture and release sites varied in size between 0 (continuous forest) and 240 m (mostly gap). Chipmunks either returned (1; $n = 17$) or did not return (0; $n = 43$) to the capture site.

(proportion of adults returning = 0.28). Thus, a larger proportion of adults than juveniles successfully returned ($\chi^2 = 4.099$, df = 1, $P = 0.043$, $\phi = 0.24$). Since no juveniles returned home, we excluded them from further analyses. There was no difference in the proportion of adult males ($n = 11$) and females ($n = 6$) that successfully returned home ($\chi^2 = 0.004$, df = 1, $P = 0.95$), so we combined sexes for the remaining analyses.

When each of the landscapes was considered an independent sample unit, there was no relationship detected between the proportion of chipmunks returning successfully to the capture site and gap size ($F_{[1,8]} = 0.483$, $P = 0.507$, $R^2 = 0.057$, slope = 0.000, intercept = 0.363). Chipmunks crossed the range of gap sizes (Fig. 3). Neither the Julian date of trapping ($F_{[1,8]} = 0.102$, $P = 0.758$, $R^2 = 0.013$, slope = 0.000, intercept = 0.283) nor the population density of chipmunks at the capture site ($F_{[1,8]} = 1.38$, $P = 0.272$, $R^2 = 0.148$, slope = –0.014, intercept = 0.457) were strongly related to the proportion of successful returns in a landscape.

When each chipmunk was considered an independent sample unit, we found no relationship between the probability of a chipmunk returning to the capture site within the 7-day sampling period and gap size ($\chi^2 = 0.781$, $n = 60$, $P = 0.377$, $\rho^2 = 0.011$, slope = –0.003, intercept = –0.609; Fig. 4). The probability of a successful return was not related to Julian date ($\chi^2 = 0.051$, $n = 60$, $P = 0.812$, $\rho^2 = 0.001$, slope = 0.015, intercept = –1.591), chipmunk population density at the capture site ($\chi^2 = 0.533$, $n = 60$, $P = 0.465$, $\rho^2 = 0.007$, slope = –0.035, intercept = –0.489), or number of days remaining in the 7-day sampling period ($\chi^2 = 0.070$, $n = 60$, $P = 0.792$, $\rho^2 = 0.001$, slope = 0.072, intercept = –1.092).

The number of days between first capture and recapture can be used to estimate the duration of the homing event. The mean and median duration of homing were both 2 days (minimum = 0.5, maximum = 4.5). Multiple linear regression demonstrated that there was no strong relationship between the duration of the homing events and gap size ($F_{[1,15]} = 0.96$, $P = 0.34$, $R^2 = 0.06$, slope = 0.004, intercept = 1.650).

Discussion

The probability that chipmunks would return home was not related to the size of the gap that had to be crossed. Chipmunks crossed the range of gap sizes that we tested (Fig. 4). It is possible that a threshold gap size might occur at a larger distance than we measured. Certainly, there is a maximum distance over which chipmunks will home (550 m; Seidel 1961), and this defines a kind of threshold. However, for the Ottawa area, 240 m (the maximum gap size crossed; Fig. 4) is a large gap. We assessed the range of gap sizes between all of the woodlots in a 178-km² region near Ottawa. This area, south of Manotick, encompassed many of our landscapes and many earlier studies of chipmunks (Forsyth and Smith 1973; Henderson et al. 1985; Bennett et al. 1994). The majority of gaps were <240 m (mean = 184 m, median = 170 m, Fig. 5). Further, this distribution was artificially skewed towards larger numbers because of the limits of map resolution. We conclude that chipmunks can move among the majority of woodlots in the area, without fencerows. Thus, landscape configuration in the study area is not expected to have profound effects on chipmunk populations. Fahrig (1997) demonstrated in a simulation model that habitat amount had stronger effects on animal population persistence than did habitat configuration. Our result is consistent with this hypothesis. We predict that configuration would have a stronger effect on chipmunks in a region where habitat amount is lower than it is in Ottawa; further, we predict that these configuration effects would be mediated through the presence of gap sizes greater than the 240 m maximum gap that we tested in the Ottawa area.

A number of authors have assumed that to move among woodlots in agricultural landscapes, chipmunks require fencerow corridors (e.g., Henderson et al. 1985; Bennett et al. 1994). Under this assumption, Henein et al. (1998) demonstrated that simulated chipmunk populations have a high probability of becoming extinct within 25 years in landscapes without

Fig. 5. Distribution of gap sizes between nearest-neighbour wood-lots from a 178-km^2 region south of Ottawa, Canada (mean = 184 m, median = 170 m, n = 137). Gaps are nonforested.
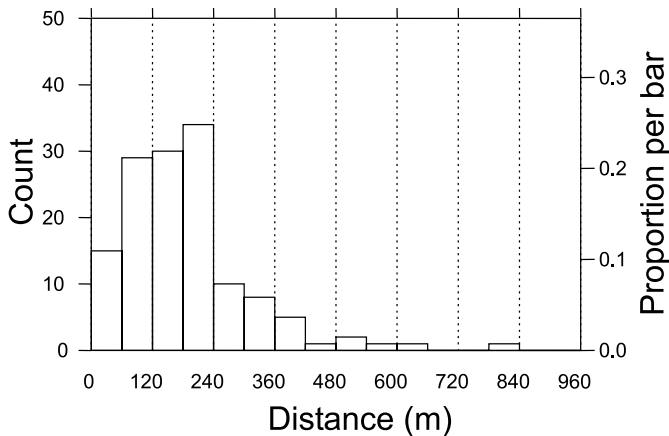
these corridors. In our study, where gap sizes were >0, chipmunks that returned to capture sites had no choice but to cross an open field, as there were no fencerow connections or other wooded routes. Our results suggest that, while chipmunks might prefer fencerows, they do not require them. Thus, chipmunk populations would not necessarily be expected to have a high probability of extinction in agricultural landscapes without corridors. This is intuitive, because despite our study landscapes being under agricultural use for many decades, including many woodlots that are unconnected by fencerows, chipmunks remain one of the most common mammal species. Our results do not lessen the conclusion of Henein et al. (1998) that functionally unconnected chipmunk populations are at an increased risk of extinction. Instead, our results suggest that functional connectivity might be maintained without fencerows, at least over the gap sizes that we tested. In landscapes with larger gap sizes, fencerows might become more important to chipmunk populations for connectivity. We note, of course, that fencerows do make a contribution to habitat amount, and in this way, they may have a large effect on the persistence of chipmunk populations.

A larger proportion of adult than juvenile chipmunks returned home. This result supports previous research suggesting that homing in mammals is accomplished in part, through prior experience. Chipmunks that returned home perceived familiar environmental cues at some point on their journey. Older chipmunks have a larger life range of cues from which to draw. An alternative explanation might be that juveniles were more motivated than adults to disperse, and thus less motivated to return home. We cannot exclude this hypothesis; however, there is convincing accumulated evidence suggesting that prior experience is an important component of successful homing (Robinson and Falls 1965; Joslin 1977; Bovet 1995; Thibault and Bovet 1999; Bowman et al. 2002).

The proportion of chipmunks that were detected after returning home (24% of total sample; 28% of adults) was larger than the proportion detected in a study by Bender (2000) of chipmunk homing (18%). Nonetheless, we suggest that more chipmunks returned home than were detected by us. Some likely returned home during the study and were not captured, and others likely returned home after the 7-day

trapping session. However, we assume that this underestimation of the return rate was consistent across the study landscapes. Generally, experimental translocation provided a useful means of assessing gap crossing by chipmunks. We think the technique has good potential for studying the connectivity of landscapes for mammals. The method could be improved by combining trapping and translocating with radio telemetry, which likely would reduce the potential to underestimate return rate.

Rather than identifying a connectivity threshold, our results demonstrated the behavioural flexibility of chipmunks. Thus, our findings are consistent with studies demonstrating flexibility by mammal species in landscapes that have undergone environmental disturbance (e.g., Linzey 1989; Kirkland 1990; Bayne and Hobson 1998; Bowman et al. 2001). More empirical studies are required to identify whether functional connectivity thresholds are present in mammal populations, as theoretical studies suggest.

Acknowledgements

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