
Gap-Crossing Decisions by the Red Squirrel, a Forest-Dependent Small Mammal

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Abstract: *Forest-associated species in fragmented landscapes must traverse potentially inhospitable gaps to move between habitat patches. Although conservation biologists advocate connecting patches with corridors or improving the matrix to make it suitable for movement, little is known about the factors influencing gap-crossing decisions for most species. We investigated gap crossing by the red squirrel (*Tamiasciurus hudsonicus*) in logged landscapes in southeastern Alaska, where the species avoids microhabitats associated with gaps created by clearcutting. We released individuals across clearcuts and determined the routes they took home with tracking spools and radio telemetry. Of 36 adult red squirrels translocated across six clearcuts, 14 crossed clearcuts to reach home. Squirrels were more likely to cross clearcuts if the detour efficiency (distance to home crossing gap divided by distance of forested detour) was low, indicating an ability to compare distances along alternate routes and travel costs or risks in different habitats. No other landscape metrics, such as gap size or crossing distance, predicted crossing behavior. Red squirrels of low body mass were more likely to cross clearcuts, where the probability of encountering conspecifics is low. Distance predicted route choice for squirrels detouring around clearcuts. Indirect evidence suggests that perceived predation risk, energetic costs, or both are higher in clearcuts. Detour efficiency reportedly influences the gap-crossing decisions of some forest-associated birds, but this is the first demonstration of its role in gap-crossing decisions by a mammal.*

Key Words: body mass, connectivity, corridor, forest-dependent mammal, fragmentation, gap crossing, movement behavior, *Tamiasciurus hudsonicus*, territorial mammal

Decisiones para Atravesar Claros de la Ardilla Roja, un Pequeño Mamífero Dependiente de Bosque

Resumen: *Especies asociadas a bosques en paisajes fragmentados deben atravesar claros potencialmente inhóspitos para moverse entre parches de hábitat. Aunque los biólogos de la conservación pugnan por la conexión de parches con corredores o el mejoramiento de la matriz para hacerla adecuada para el movimiento, se conoce poco sobre los factores que influyen en las decisiones para atravesar claros de la mayoría de las especies. Investigamos el cruce de claros por la ardilla roja (*Tamiasciurus hudsonicus*) en paisajes madereros en el sureste de Alaska, donde la especie evita microhábitats asociados a claros creados por la tala. Liberamos individuos en claros y mediante carretes de rastreo y radiotelemetría determinamos las rutas que recorrieron de regreso a su hogar. De 36 ardillas rojas adultas translocadas en seis claros, 14 atravesaron claros para regresar a casa. Fue más probable que las ardillas atravesaran claros si la eficiencia de desvío (distancia al hogar atravesando el claro dividido por distancia vía desvío por bosque) era baja, lo que indica una habilidad para comparar distancias a lo largo de rutas alternativas y costos de viaje o riesgos en diferentes hábitats. Ninguna otra medida del paisaje, como tamaño del claro o distancia de cruce, predijo la conducta de cruce. Ardillas rojas de masa corporal baja tuvieron mayor probabilidad de atravesar claros, donde la probabilidad de encontrar conspecificos es baja. La distancia predijo la elección de ruta para ardillas que se desviaron alrededor de los claros. Evidencias indirectas sugieren que la percepción del riesgo de depredación, los costos energéticos, o ambos son más altos en los claros. La eficiencia de desvío influye supuestamente en las decisiones*

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para atravesar claros de algunas aves asociadas a bosques, pero ésta es la primera demostración de su papel en la decisión para atravesar claros de un mamífero.

Palabras Clave: conducta de movimiento, conectividad, cruce de claros, fragmentación, mamífero dependiente de bosque, mamífero territorial, masa corporal, *Tamiasciurus hudsonicus*

Introduction

Modern conservation strategies for fragmented landscapes rely on the movement of individuals among fragments to rescue populations when declines or local extinctions occur (Brown & Kodric-Brown 1977; Hanski & Gilpin 1991). Such movement requires that animals traverse potentially inhospitable terrain between fragments. Consequently, conservation biologists advocate connecting reserves with corridors or improving the matrix to facilitate movement (e.g., Noss 1987; Franklin 1993; Meffe & Carroll 1994). Movement between fragments has proven difficult to study, and for most species we do not know whether they use corridors preferentially or which features encourage their movement (Lima & Zollner 1996). Our lack of knowledge persists because dispersal and exploration are unpredictable in time and space; researchers generally record locations before and after movements but are unable to determine travel routes (e.g., Arthur et al. 1993; Price et al. 1994; Olson & Van Horne 1998, but see Beier 1995).

Recently, researchers have employed alternative techniques to investigate movement behavior in fragmented landscapes. By following the natural movements of grassland butterflies at forest edges, for example, Haddad (1999) found that species that avoided forest were most likely to use grassland corridors. Researchers tracking insects translocated to habitat edges showed that edge reactions predicted patch emigration rates (Kindvall 1999) and residence times (Schultz & Crone 2001). Many researchers have tested the willingness of forest-associated birds to enter or cross gaps by translocating them across inhospitable terrain or by broadcasting recorded calls, which are known to attract birds, from the opposite sides of gaps. These researchers found that forest specialists were generally more reluctant to enter gaps (Sieving et al. 1996; Rail et al. 1997; Rodriguez et al. 2001) and that detour efficiency (distance across gap divided by distance around gap perimeter) predicted gap crossing for many species (Desrochers & Hannon 1997; St. Clair et al. 1998; Bélisle & Desrochers 2002). Translocations have also been used to study the movements of a few small mammals. Crossing distance did not explain gap crossing by chipmunks (*Tamias striatus*) in unconnected fragments (Bowman & Fahrig 2002), and corridors did not enhance cotton rat (*Sigmodon hispidus*) movements in connected fragments (Bowne et al. 1999). Many of these

movement studies rely on or support the assumption that animals may use corridors as a result of edge-following behavior when encountering gaps.

We investigated the determinants of gap crossing and route choice in the red squirrel (*Tamiasciurus hudsonicus*), a forest-dependent small mammal, by translocating individuals in logged landscapes in southeastern Alaska. In this species, both sexes maintain exclusive feeding territories centered around conifer trees (Smith 1968), exhibit high site fidelity, and home from long distances (>1 km, Bovet 1984; Bakker 2003). Because of their site fidelity, we were able to induce squirrels to make gap-crossing decisions by translocating them across forest gaps (i.e., clearcuts) and releasing them. Unlike passive observation, this approach allowed us to control the landscape conditions presented to squirrels (Bélisle et al. 2001). Red squirrels on unfamiliar ground avoid the microhabitat features in clearcuts, such as dense vegetation, and avoid clearcuts when released at forest-clearcut edges (Bakker 2003). If microhabitat preferences determine movement behavior, red squirrels should use forested detours around clearcuts. Landscape-scale features might influence movement behavior, however, producing more frequent gap crossing than expected based on microhabitat preferences and local edge reactions alone.

We evaluated several landscape-scale features that might influence gap-crossing decisions. Because much conservation planning is based on the configuration of reserves and the composition of the intervening matrix, we assessed the importance of crossing distance, both its absolute length and its length relative to the detour around the clearcut (i.e., detour efficiency), detour distance, clearcut size, and clearcut age. Because red squirrels are territorial, we investigated whether the defensive intensity of conspecifics along forested detours home affected crossing probability. We also evaluated the role of detour length and defensive intensity in route choice by squirrels that detoured around clearcuts. In addition, we investigated body mass, which may indicate ability to prevail in encounters with conspecifics (Stuart-Smith & Boutin 1994); calling rate, which reflects territory quality (Bakker 2003) and probably the motivation to reach home quickly; and sex, which is linked to knowledge of homing routes in that males have higher homing success and presumably larger familiar areas (Bakker 2003). To investigate perception of predation risk and energetic costs as potential mechanisms for avoidance of clearcuts, we evaluated changes in an indirect measure of foraging behavior

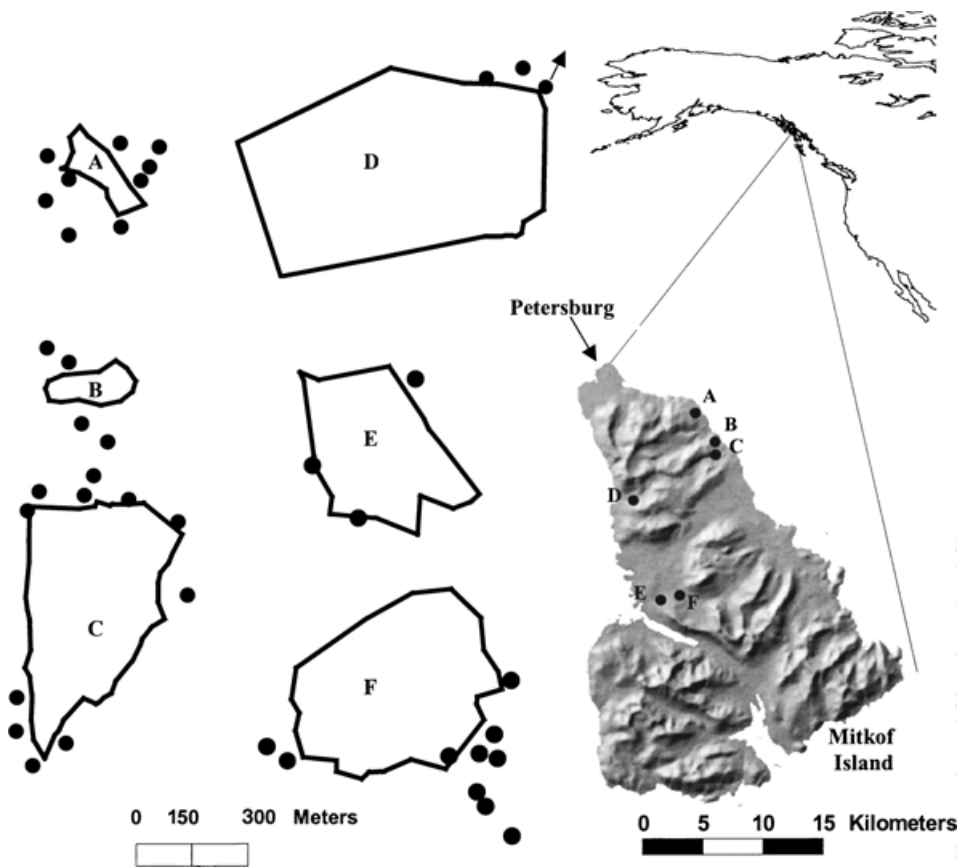


Figure 1. Research sites for study of gap-crossing decisions by red squirrels (*Tamiasciurus hudsonicus*) on Mitkof Island in southeastern Alaska. Squirrels were translocated across six clearcuts, forcing them to make gap-crossing decisions en route to their homes. Dots indicate home range centers of squirrels. The home range center of one squirrel at clearcut D was located 500 m northeast of the clearcut edge, as indicated by arrow.

with distance from the forest edge and compared travel speeds in clearcuts and forests.

Methods

Study Area

The study was conducted on Mitkof Island (56°N, 133°W) in southeastern Alaska from June 1998 to September 2001 (Fig. 1). The 518-km² island is mountainous and supports perhumid rainforest (Alaback 1994), which ranges from low-stature stands (10–20 m) containing shore pine (*Pinus contorta* var. *contorta* Dougl. ex Loud.), Alaska-cedar (*Chamaecyparis nootkatensis* [Lamb.] Spach), western red cedar (*Thuja plicata* D. Don), mountain hemlock (*Tsuga mertensiana* [Bong.] Sarg.), western hemlock (*T. heterophylla* [Raf.] Sarg.), or Sitka spruce (*Picea sitchensis* [Bong.] Carr.) to stands dominated by tall (30–40 m) western hemlock and Sitka spruce. Most late-seral stands have a well-developed ericaceous shrub layer, and peat bogs are common in areas of poorer drainage. Clearcut logging has occurred in most watersheds (USFS 1997).

Trapping and Translocations

Red squirrels inhabit most forest types, and those in forests with large Sitka spruce make more frequent terri-

torial calls, reflecting local variation in defensive intensity (Bakker 2003). We trapped red squirrels with Tomahawk live traps (13 × 13 × 41 cm) baited with peanut butter, oats, and molasses in a range of forest types at six study sites (Fig. 1) located within 500 m of clearcuts <10 years old and 1.7–32.0 ha in size. We radio collared (≤ 4.1 g; Holohil MD-2C and PD-2C, Holohil Systems, Ontario, Canada) adult red squirrels (> 175 g) and calculated the center of their home range (bivariate arithmetic mean) based on an average of 17 telemetry locations (range, 4–33) obtained by signal homing; centers calculated from the first 4 locations were within $23.3 \text{ m} \pm 2.4 \text{ SE}$ of centers from ≥ 20 locations ($n = 17$; V. B., unpublished data).

From July through September of each year, we translocated adult squirrels off their home ranges to the opposite sides of clearcuts, walking through clearcuts directly from capture sites to release sites, located 20–30 m into the forest and 132–887 m away from centers of home ranges (Fig. 1). Squirrels were transported in a mesh trap attached to the top of a backpack (Bovet 1991) in an attempt to provide them with visual information about the location of the most direct route to home (i.e., crossing the clearcut). At the release site, we attached a tracking spool (approximately 225 m of fine, inversely wound thread; 2.4 g; Model 40–2 7B, Danfield Thread, Winsted, Connecticut) to the rump of each squirrel with cyanoacrylate glue. Prior to release, the trap was covered with a dark cloth.

We opened the trap door under the cloth so that the open door was not immediately apparent to the squirrel. We selected release directions randomly and moved ≥ 20 m away in the opposite direction after opening the trap. We determined homing paths with tracking spool traces and simultaneous telemetry by two or three observers at 3-minute intervals or in smaller clearcuts with spool traces alone. Telemetry locations were calculated with Lenth's maximum-likelihood estimator (TRIANG; White & Garrott 1990). We censored locations with confidence ellipses larger than 1 SD from the mean, unless observers recorded high confidence in their bearings and locations fell between previous and subsequent locations. No squirrels were translocated more than once.

Predictors of Gap Crossing

We used the Arcview geographic information system (version 3.2, ESRI 1999) to measure the distance across the clearcut (i.e., crossing distance), detour efficiency ($100 \times \text{distance home across gap} \div \text{detour distance}$), and clearcut size. Detour distance was the shortest distance from release site to home that avoided the clearcut, distance home was the straightline distance from release site to home, and crossing distance was the portion of the straight line transecting the clearcut. To document the defensive intensity of territorial conspecifics, we used callback surveys along the perimeters of four of the clearcuts. We broadcast red squirrel rattle and bark (sensu Lair 1990) calls (Northwood Press 1994) twice at stations established 100 m apart in September 2000 during morning, midday, and evening, and we recorded responses within 2 minutes estimated to be within 50 m. For each translocated squirrel, we calculated a mean response frequency—hereafter, “defensive intensity”—for stations along its chosen route to home (clockwise or counterclockwise around clearcut) to determine whether squirrels tended to cross clearcuts when pursuing routes with high defensive intensity. All squirrels initially attempted to circumnavigate clearcuts. For those that ultimately crossed, we calculated defensive intensity for the route initiated prior to crossing.

Body mass was calculated as the mean of masses recorded during captures within 1 month of translocation (mean $n = 4.3$; range, 1–9). To estimate individual calling rates, we recorded whether squirrels made territorial calls within 5 minutes when approached during home-range telemetry locations. Because calling increases after cones mature (Bakker 2003), by approximately 1 August (Harris 1969), we developed a regression relationship (PROC REG, SAS 8.1, SAS Institute 2000) between calling before (X) and after (Y) 1 August based on squirrels with ≥ 25 observations extending through both seasons ($Y' = 1.031 + \ln[0.430X']$, where both Y' and X' were arcsine-square-root-transformed [Zar 1999], $p = 0.018$, adjusted $R^2 =$

0.842, $n = 5$). We used this equation to standardize calling rates to levels found after 1 August.

We used logistic regression (PROC LOGISTIC) to identify predictors of gap crossing. Prior to analyses, we examined Spearman rank correlations (PROC CORR) and tolerance values for predictors (PROC REG) to identify potential collinearity problems (i.e., $r > 0.7$, tolerance < 0.3 ; Menard 1995). Sequential Bonferroni corrections (Rice 1989) were applied to p values for correlations. After univariate screening for candidate variables ($p < 0.25$; Hosmer & Lemeshow 1989), we examined logit plots and rescaled variables as necessary to achieve linearity of the logit (Hosmer & Lemeshow 1989). We then built a multivariate model, using forward, backward, stepwise, and best subset (score criterion) algorithms to guide model selection. For the former methods, we assigned liberal selection criteria ($p \leq 0.10$ to enter, $p \geq 0.15$ to remove) to ensure that all variables of importance were identified given our relatively small sample size. To assess goodness of fit, we evaluated models that included main effects and their interactions, examined model residual chi-square and residual diagnostics, and performed the Hosmer and Lemeshow (1999) goodness-of-fit test.

Predictors of Detour Route

We used conditional logistic regression (logistic regression for paired data, PROC PHREG; Hosmer & Lemeshow 1989; Stokes et al. 1995) to determine whether distance or defensive intensity influenced routes chosen by squirrels detouring around clearcuts. Each animal was considered a stratum, and for each animal's path we matched data characterizing chosen and alternate routes (clockwise or counterclockwise). Model building and diagnostics followed those for logistic regression.

Predation Risk and Energetic Costs

Red squirrels sometimes forage on conifer cones from felled trees in recent clearcuts adjacent to their territories. To investigate perceived predation risk, we examined the uneaten portion of cones foraged on by red squirrels in clearcuts, similar to giving-up densities, to determine if the amount of foraging decreased with distance from the forest edge (PROC REG), consistent with enhanced perception of risk (Brown 1988; Thorson et al. 1998; Brown 1999). Red squirrels process cones from basal to distal end, nipping off cone scales and eating the two seeds distal to them (Smith 1968). Because cones taper toward the distal end and seeds become smaller (Owens & Molder 1980), foraging efficiency should decline with time for each cone. We counted the number of cone scales remaining on Sitka spruce cones collected in a systematic search of a 2.9-ha 2-year-old clearcut, retaining only cones foraged upon since timber harvest (e.g., cones found on stumps or showing little decay). Given the small size of the clearcut, we that assumed tree size and quality had

been relatively homogeneous and that cone density and seeds per cone did not differ systematically from edge to center. We investigated the latter assumption by regressing cone length on distance from edge. To control for the influence of microhabitat on risk perception, we collected cones only in areas of low overhead shrub cover (<10%).

To investigate energetic costs, we compared speeds of travel in forests and clearcuts (*t* test, PROC MEANS), expecting slower speeds if energetic costs were greater. To calculate speed, we summed elapsed time in forest for squirrels that detoured and in clearcuts for squirrels that crossed, excluding successive locations showing little homeward movement (<20 m). We assumed travel via the most direct route, using detour distance for detourers and crossing distance for crossers. Because telemetry was conducted at 3-minute intervals and some points were censored because of large confidence ellipses, speeds could be over- or underestimated, especially for short paths. Therefore, we excluded from speed comparisons paths of <300 m, which could be traversed in <10 minutes, and paths documented with spool traces alone.

Results

Predictors of Gap Crossing

Of 40 translocated squirrels, 22 detoured around clearcuts, 14 crossed, and 4 followed unknown routes, failing to reach home prior to dusk when radio telemetry was terminated. (Data on gap-crossing decisions and their potential predictors for squirrels translocated across clearcuts are available at www.stikine.org/vjb.) All squirrels homed successfully in <24 hours.

One extrinsic and one intrinsic factor were important in predicting gap crossing in a highly significant logistic-regression model ($p < 0.001$, 88.3% concordant; Table 1; Fig. 2). Detour efficiency was negatively related to gap-crossing probability ($B = -0.130$, Table 1). Red squirrels were more likely to cross clearcuts if the detour was relatively long (i.e., inefficient). The odds ratio indicates that each percentage increase in detour efficiency decreased the probability of gap crossing by >12%.

Body mass was also a strong predictor of gap crossing. To meet assumptions of the logit model (Hosmer & Lemeshow 1989), we transformed body mass to a binary variable, with masses in the first quartile (≤ 190 g) designated as low and all others as high. Squirrels with low body mass were over 12 times more likely to cross clearcuts for any given detour efficiency ($B = 2.545$; Table 1; Fig. 2).

Crossing distance (transformed to short cross, ≤ 100 m; long cross, > 100 m; $p = 0.116$) and clearcut size ($p = 0.204$) were candidate variables after univariate screening, but neither was significant in multivariate models

Table 1. Predictors of gap crossing by red squirrels (*Tamiasciurus hudsonicus*) in southeastern Alaska based on logistic regression.*

| Variable | Odds ratio | Chi-square | p |
|---|------------|------------|-------|
| Detour efficiency | 0.878 | 5.402 | 0.020 |
| Low mass (≤ 190 g) | 12.736 | 4.947 | 0.026 |
| Detour efficiency \times low mass | | 0.725 | 0.394 |
| Clearcut size (ha) | | 0.294 | 0.588 |
| Short crossing distance (≤ 100 m) | | 0.008 | 0.928 |
| ----- | | | |
| Sex | | 1.199 | 0.274 |
| Calling rate ($n = 33$) | | 0.373 | 0.541 |
| Detour distance (m) | | 0.161 | 0.689 |
| Defensive intensity ($n = 29$) | | 0.003 | 0.959 |
| Clearcut age (years) | | 0.001 | 0.973 |

*Odds ratios (shown only for significant variables), obtained by exponentiating the regression coefficient (e^B), indicate the change in crossing probability with each unit increase in the effect. Model $G = 15.819$, $df = 2$, $p < 0.001$, $n = 36$. All variables considered for model building (univariate $p < 0.25$) are shown above the dashed line, including p values when included in the multivariate model. Univariate p value for variables not considered in model building are shown below the dashed line.

(Table 1; Fig. 2). Detour distance, clearcut age, defensive intensity, calling rate, and sex did not meet initial screening criteria (univariate $p > 0.25$; Table 1; Fig. 2). Trials were conducted in existing clearcuts, resulting in correlations between several landscape variables ($r_s = 0.48$ – 0.85 , $p \leq 0.029$). Because clearcuts typically have a limited range of shapes, clearcut size was positively correlated with detour efficiency, crossing distance, and detour distance, and crossing distance was positively correlated with detour distance. Younger clearcuts were smaller, so clearcut age was positively correlated with clearcut size, detour distance, and crossing distance. Finally, clearcut age was negatively correlated with defensive intensity. None of these variables, however, was selected in the final models. Detour efficiency was not correlated with detour distance or crossing distance ($r_s \leq 0.39$, $p \geq 0.210$).

Predictors of Detour Route

For red squirrels that detoured around clearcuts, only distance ($p = 0.081$, odds ratio = 0.992) predicted route choice ($G = 9.150$, $df = 1$, $n = 17$ pairs, $p = 0.003$). Each additional 10 m of distance reduced by 8% the probability of a route being used.

Predation Risk and Energetic Costs

The number of scales remaining on spruce cones eaten by red squirrels in clearcuts increased with distance (0–30 m) from the forest edge ($n = 64$, $B = 0.152$, $p = 0.004$). Distance from the edge, however, explained only 12% of the variation in scale number (adjusted $R^2 = 0.118$). Cone length did not vary with distance from the edge ($B = -0.126$, adjusted $R^2 = 0.009$, $p = 0.222$).

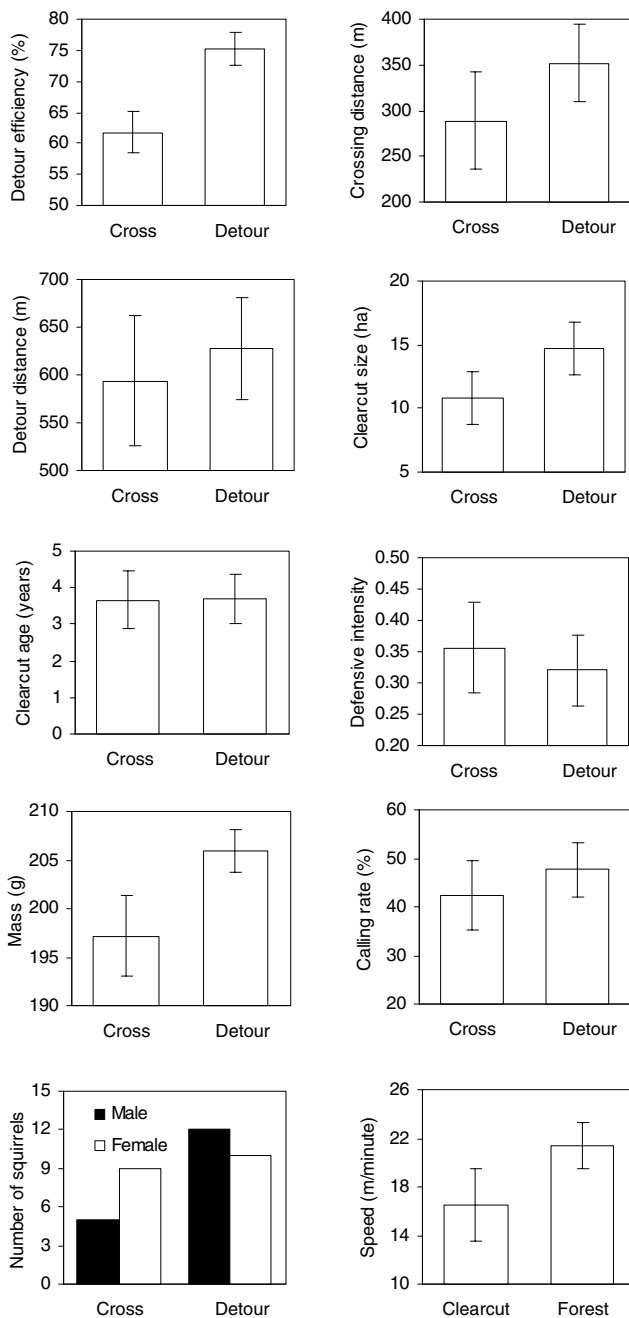


Figure 2. Potential predictors of gap crossing by red squirrels (*Tamiasciurus hudsonicus*) in southeastern Alaska. Mean \pm SE is shown for each predictor except sex, for which a histogram is provided. Graph in lower right shows speed of travel through clearcuts for crossers and through forest for detourers. Defensive intensity is mean response frequency to calls broadcast at stations 100 m apart along the chosen route home or, for squirrels that crossed clearcuts, along the route used prior to crossing.

Squirrels tended to travel more slowly through clearcuts (16.5 ± 3.0 m/minute, $n = 7$) than forest (21.4 ± 1.9 m/minute, $n = 18$), but the difference was not significant ($t = -1.382$, $df = 23$, $p = 0.180$). Power to detect differences ($1 - B = 0.263$) was reduced after we censored six paths <300 m long, four paths identified with spool traces, and one path along which a squirrel stopped overnight.

Discussion

Predictors of Gap Crossing and Detour Route

Detour efficiency predicted gap crossing by red squirrels better than more familiar landscape metrics such as gap size or crossing distance (Fig. 2). Red squirrels traveling on unfamiliar ground confront a variety of challenges, such as risk of predation, risk of conspecific attack, and energetic costs. If they perceive the risks and costs as greater in gaps per meter traveled, red squirrels could minimize these challenges by detouring around gaps when detour efficiencies are high and by crossing gaps when detour efficiencies are low. The greater the risks or costs in the gap, the longer the detour an individual should accept. Red squirrels (except those of low mass; see below) were more likely to detour around clearcuts (i.e., probability >50%) when detour efficiencies exceeded 60%. Similarly, gap-crossing thresholds for forest songbirds ranged from a detour efficiency of approximately 50% for Black-capped Chickadees (*Poecile atricapillus*) to approximately 80% for Red-breasted Nuthatches (*Sitta canadensis*; Desrochers & Hannon 1997).

Lighter red squirrels (≤ 190 g) were nearly 13 times more likely to cross clearcuts than heavier squirrels for any given detour efficiency, circumnavigating clearcuts (probability >50%) only when detour efficiencies exceeded 79%. In forests, lighter squirrels risk chases by heavier conspecifics, and chases reduce vigilance (Milinski 1984; Price et al. 1990; Bernays & Wcislo 1994; Diaz-Uriarte 1999) and may lead to attack and injury (Lair 1990). Thus, the risk of forest travel may be greater for lighter squirrels, decreasing the risk ratio between clearcuts and forests and promoting gap crossing at higher detour efficiencies. Alternatively, lighter squirrels may have lower energy reserves, forcing them to discount predation risk relative to energetic costs by taking shorter routes across clearcuts. Detour efficiency could still be important to gap-crossing decisions based on energetics if energetic costs per meter in clearcuts exceeded those in forest. Finally, lighter squirrels may have difficulty regaining their territories after an absence (Stuart-Smith & Boutin 1994), forcing them to accept greater risks by using shorter routes in an attempt to reach home rapidly. Squirrels crossing clearcuts, however, tended to travel more slowly (see below; Fig. 2), again indicating a role

for detour efficiency in movement decisions. Although lighter squirrels may have been younger and inexperienced in finding routes or assessing risk, all squirrels used in this study were adults and, based on capture history and mass records, all were presumed to be ≥ 1 year old. No increase in adult weight with time was found in this study (year vs. body mass: $R^2 < 0.001$, $p = 0.988$, $n = 37$) or in others (Layne 1954).

Despite the potential importance of avoiding conspecifics, red squirrels apparently did not weigh the intensity with which forested paths were defended in making gap-crossing decisions (Table 1; Fig. 2). Red squirrels may be unable to assess differing defensive intensities across forested habitat on unfamiliar ground, or such differences may be unimportant relative to the large differences between clearcuts and forest. Although call surveys occurred up to three years after translocations, calling is correlated with habitat (Bakker 2003) and should accurately indicate relative differences in defensive levels.

Distance was the most significant predictor of route choice for squirrels detouring around clearcuts. Thus, red squirrels appear able to compare the relative length of paths through forest versus those through clearcut (i.e., detour efficiency) or along different forested routes. As in gap-crossing decisions, squirrels were either uninterested in or incapable of evaluating the intensity of territorial defense along alternate forested routes because this factor did not affect route choice.

Predation Risk and Energetic Costs

Although red squirrels will forage up to 50 m into clearcuts adjacent to their territories (V.B., unpublished data), the positive relationship between the number of seeds they left on cones and distance to the forest edge suggests that they perceive predation risk as greater in the middle of clearcuts. This perceived risk would almost certainly be higher on unfamiliar ground where gap-crossing decisions were made because surface and underground escape routes were unknown. Several other sciurids exhibit higher giving-up densities when foraging in seed trays placed farther from trees (Bowers et al. 1993; Schmidt 2000), which they use as refuges to escape aerial and ground predators (Lima et al. 1985; Temple 1987; Smith 1995). Traversing dense clearcut vegetation might also increase predation risk by visually and audibly revealing squirrels to predators or by reducing visibility for predator detection (Schooley et al. 1996).

Squirrels tended to travel more slowly through clearcuts than forests (Fig. 2); the difference was not significant, but the power to detect differences was low. If travel speeds are lower in clearcuts, several interpretations exist, and all are consistent with greater perceived predation risk or higher energetic costs in clearcuts. With travel speeds in both clearcuts and forests averaging well below the squirrel's capability (17–21 m/minute vs. 250

m/minute; Layne & Benton 1954), squirrels likely paused frequently and numerous short pauses likely went undetected because of the low resolution and precision of the radio telemetry data. Squirrels may have paused more in clearcuts, resulting in lower travel speeds. Pausing rates are higher in riskier habitat as animals stop to scan for predators (McAdam & Kramer 1998; Kramer & McLaughlin 2001; Vásquez et al. 2002). Pausing also allows recovery from energetically demanding travel (Pennisi 2000). Because red squirrels move primarily on the ground when traveling long distances (Bovet 1984; Bakker 2003), dense vegetation in clearcuts as opposed to forest (28 vs. 15 shrub stems/m² and 43% vs. 18% herb cover; Bakker 2003) may have obstructed movement, slowed travel (Schooley et al. 1996), and increased energetic costs. Dense vegetation can also increase vigilance time because visibility is reduced (e.g., Schooley et al. 1996; Sharpe & Van Horne 1998). If dense vegetation hindered route finding, resulting in more tortuous paths, clearcut speeds would appear slower because speed estimates were based on straightline distances; observations of spool traces, however, suggested less tortuous paths in clearcuts.

Even modest differences in energetic costs may have influenced movement decisions because estimated travel costs were substantial. Based on costs of locomotion for similar-sized ground squirrels (Kenagy & Hoyt 1989) and allometric equations for energy expenditures (Speakman 1999), the average translocation required up to 23% of daily energy expenditures. Translocation distances were comparable to forays and dispersal movements of juvenile red squirrels in Alberta (Larsen & Boutin 1994) and to forays of adult red squirrels in southeastern Alaska (Bakker 2003). Thus, energetics would pose similar constraints on natural movements.

Implications and Conclusions

Red squirrels altered their paths in response to habitat and landscape configuration, using forested detours to avoid clearcuts unless detours were very circuitous. Because fragmentation pattern controls detour efficiency, a species' gap-crossing behavior can help predict its movement behavior in fragmented landscapes and can inform reserve design. Behavioral factors underlying decisions to use forested detours may also control corridor use, especially if corridors are wide enough that animals do not perceive both edges. Thus, animals may reject corridors in favor of risky or costly habitat if they require long detours. Habitat specialists are likely to view the risks or costs of travel in the matrix as greater, increasing their willingness to use circuitous detours, than do generalist species.

Red squirrels with low body mass were more likely to cross clearcuts, where the probability of encountering conspecifics is low. The behavior of juvenile red squirrels may mirror that of these lighter squirrels. The

gap-crossing behavior of red squirrels supports a potential role for marginal or unoccupied habitat as movement habitat for territorial species, especially dispersing juveniles, as observed for wolves (*Canis lupus*; Fritts & Mech 1981) and red squirrels (Larsen & Boutin 1994).

Although the importance of detour efficiency in gap-crossing decisions was previously demonstrated for some forest birds (Desrochers & Hannon 1997; St. Clair et al. 1998; Bélisle & Desrochers 2002), this is its first demonstration for a forest mammal, hinting at a potentially more general pattern among vertebrates. Only taxa with large perceptual ranges (Lima & Zollner 1996) are likely to have the capacity to compare distances along alternate routes. Local behaviors at habitat edges predict landscape-scale movement patterns for butterflies (Haddad 1999; Schultz & Crone 2001), which have shorter perceptual ranges (Harrison 1989; Conradt et al. 2000; Schultz & Crone 2001). Species with relatively large perceptual ranges, such as sciurids (Zollner 2000), may exhibit movement behaviors that differ between local and landscape scales because they perceive and respond to habitat edges and the location and configuration of habitat patches across the landscape. Red squirrels, for example, strongly avoided microhabitats associated with clearcuts (Bakker 2003) but readily crossed clearcuts when in some landscape configurations. Research at multiple spatial scales is needed to understand the movement behavior of vertebrates that have large enough perceptual ranges to perceive patterns at microhabitat and landscape scales.

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