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SURVIVAL AND BEHAVIOUR OF JUVENILE RED SQUIRRELS, *TAMIASCIURUS HUDSONICUS*

by

Elizabeth Marie Anderson

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Survival and Behaviour of Juvenile Red Squirrels (*Tamiasciurus hudsonicus*)** submitted by Elizabeth M. Anderson in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

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ABSTRACT

Predation is often a major determinant of juvenile survival. Probability of survival may be affected if individuals can assess their risk of predation and adjust their behaviour accordingly. The first objective of the current study was to determine if behavioural and survival differences existed between juvenile red squirrels (*Tamiasciurus hudsonicus*) living along the edge of a forest as compared to juveniles living in the interior of the forest (i.e., are there edge effects?). A basic assumption of many studies that examine the role of predation on behaviour is that individuals performing 'risky' behaviours suffer higher predation rates. The second objective of this study was to test this assumption by determining if various general behaviours (e.g., foraging, travelling, vigilance) predicted survival of juvenile red squirrels. A combination of telemetry, direct observation and live trapping was used to study the behaviour and survival of juvenile red squirrels during the summers of 1997 and 1998 in Kluane, Yukon. There were no survival differences between edge- and interior-born juveniles from birth to emergence and a trend towards higher survival of edge-born juveniles from emergence to weaning. Similarly, there were few behavioural differences from emergence to weaning between these edge- and interior-born juveniles or their mothers. Hence, limited behavioural and survival edge effects could be demonstrated in this population of red squirrels. However, other edge effect studies should still consider the potential implications of behavioural differences between individuals living along a patch edge as compared to those living in the patch interior. Although there may have been behavioural trade-offs between the amount of time spent foraging and resting by juveniles, the behaviour of neither juveniles nor their mothers was not found to be a consistent predictor of juvenile survival from emergence to

weaning or to the end of the summer. This highlights the importance of testing the basic assumptions of predation risk studies.

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CHAPTER 1 - GENERAL INTRODUCTION

BACKGROUND

Juvenile survival rates are often much lower and more variable than survival rates during other life stages (Caughley 1977). Survival from birth or hatching to recruitment into the breeding population may be less than 30% for mammals, 20% for birds and 1% for fish (Lack 1954). A major cause of juvenile mortality is predation. For instance, predation can account for up to 70% of losses among cheetah cubs (*Acinonyx jubatus*) between birth and independence (Laurenson 1994).

Factors known to influence predation risk include behaviour (Daly et al. 1990; FitzGibbon 1990; Skelly 1994; Stuart-Smith and Boutin 1995b) and physical condition (Temple 1987; McNamara and Houston 1987; Sinclair and Arcese 1995). There is an extensive body of theoretical and empirical research examining the ability of animals to assess their risk of being preyed upon and integrate such information into their behaviour (see Lima and Dill 1990 and Lima 1998 for reviews). For example, the influence of predation risk may be manifested in decisions related to foraging behaviour, such as timing of feeding (Brown et al. 1988; Lima 1988; Culp and Scrimgeour 1993), habitat and patch selection (Dill 1987; Ferguson et al. 1988; Jakobsen et al. 1994), diet selection (Lima and Valone 1986; Bowers 1988; Godin 1990) and handling of food items (Valone and Lima 1987). Addtionally, trade-offs between foraging and vigilance may be linked to predation risk (Lima 1987; Bachman 1993; Otter 1994). Decisions regarding group living, such as vigilance level (Elgar 1989; Krause and Godin 1996; Roberts 1996), group size (Ashley et al. 1993; Krause and Godin 1995) and group structure (Abrahams and Colgan 1985; Romey 1995), may also be affected. Although feeding behaviour and group living are well studied with respect to risk of predation, fewer studies have examined the influence of predation risk on reproductive behaviours such as mate choice (Hedrick and Dill 1993; Godin and Briggs 1996), copulation (Berglund 1993; Sih and Krupa 1996) or parental care decisions (Magnhagen 1992; Harfenist and Ydenberg 1995). The general assumption of such predation risk studies is that individuals performing behaviours that expose them to a higher risk of predation will have a lower probability of survival.

This thesis examines behavioural manipulation of predation risk by juveniles. Since juveniles suffer high predation losses, we might expect to see the largest effects of behaviour on survival during this life stage. Chapter 2 explores edge effects from the perspective of juvenile survival and behaviour. If individuals living along the edge of the forest (i.e., potential high predation risk location) can assess their risk of being preyed upon, they may display different behaviours than individuals living in the interior of the forest (i.e., potential low predation risk location). Such a behavioural adjustment could in turn positively affect the survival rates of juveniles living along the edge. Though many edge effect studies have examined differences in survival rates on the edge and interior of a patch, few have considered the possibility of that these rates could be influenced by behavioural differences. Chapter 3 tests the basic assumption of predation risk studies discussed above: individuals exposing themselves to higher predation risk will experience lower survival rates. Although this is a central assumption on which a majority of predation risk studies are based, it is rarely tested (Lima and Dill 1990; Stuart-Smith and Boutin 1995b). One study attempting to do so (Stuart-Smith and Boutin 1995b) suffered from low sample size and a potential methodological problem. This chapter expands upon that work by increasing the sample size in addition to examining the role of mothers' behaviour on juvenile survival.

Red squirrels (*Tamiasciurus hudsonicus*) were chosen as the study species as they exhibit many characteristics ideal for a study examining behaviour and survival. They are highly visible, can be easily trapped, handled, and radio-collared and it is relatively easy to locate and enter their nests. In addition, most squirrels appear to tolerate human observers without altering their behaviour (Price et al. 1986). The major source of mortality in red squirrels, for both juveniles and adults, is predation (Stuart-Smith and Boutin 1995a). Juveniles suffer high mortality from emergence to the end of the summer (Stuart-Smith 1993) and the period from emergence to weaning is thought to be particularly critical (Boutin and Larsen 1993). A preliminary study on juvenile red squirrels found behavioural differences between surviving and depredated squirrels in the amount of time spent resting, being vigilant, traveling off territory, and in the amount of time spent in exposed places (Stuart-Smith and Boutin 1995b). Surviving juveniles thus may have been more sensitive to their risk of predation and adjusted their behaviour accordingly.

NATURAL HISTORY OF THE STUDY POPULATION

This study was conducted in the northern boreal forest near Kluane Lake (61°N, 138°W), southwestern Yukon, Canada (Fig. 1.1). The dominant habitat is open white spruce (*Picea glauca*) forest with occasional stands of aspen (*Populus tremuloides*) and a sparse understory of willow (*Salix* spp.) and bog birch (*Betula glandulosa*) (Douglas 1974). The climate is cold continental with most precipitation falling as snow between October and early-May and an average January temperature of -18°C (Boutin et al. 1995; Stuart-Smith 1993). Predators of red squirrels in the study area include lynx (*Lynx canadensis*), coyote (*Canis latrans*), red-tailed hawk (*Buteo jamaicensis*) and northern goshawk (*Accipiter gentilis*). Great-horned owl (*Bubo virginianus*), weasel (*Mustela* spp.), marten (*Martes americana*), fox (*Vulpes vulpes*) and wolf (*Canis lupus*) are also present at low densities (Boutin et al. 1995).

White spruce cones represent the major food source for red squirrels in Kluane; however, cone production is highly variable from year to year (Fig. 1.2). Hence red squirrels also rely on additional vegetative food resources such as spruce buds, fungi and berries and occasionally eat animal sources such as bird eggs, bones and juvenile snowshoe hares (*Lepus americanus*) (S. Boutin, unpubl. data).

Red squirrels in Kluane actively defend mutually exclusive territories that average 30m in radius (Price et al. 1986). Territory boundaries are consistent from year to year and owner to owner (Price et al. 1986) and represent the minimum territory size required to sustain squirrels in years of poor cone crop (Rusch and Reeder 1978). At the centre of each territory is a midden (cache site) formed through the accumulation of cone debris from several years (Larsen et al. 1997). Although adult red squirrels rarely change territories (Larsen and Boutin 1994; Stuart-Smith 1993), a new owner acquiring a territory maintains the established midden site rather than creating a new midden. A series of tunnels are located throughout the midden in which new cones are stored each fall. The possession of a territory with one or more middens is thought to be crucial to overwinter survival (Kemp and Keith 1970; Larsen and Boutin 1994). Although marginal habitats are often used by dispersing juveniles, they cannot support residents due to the lack of food and middens for overwinter food storage (Rusch and Reeder 1978; Larsen and Boutin 1994).

Female red squirrels do not normally breed until they are at least two years of age (Becker 1992; Larsen 1993); however, it is unknown when males begin breeding (Larsen and Boutin 1994). Adult females are in oestrus for a single day and during this time they tolerate the presence of one or more males on their territory (Lair 1985). Breeding occurs from early-March to mid-June and females give birth to a single litter of 3 or 4 juveniles (range 1 - 7, S. Boutin, unpubl. data) following a 38 day gestation period (Becker 1992; Larsen 1993). Emergence from the natal nest occurs around 42 days (Humphries and Boutin 1996; Chapter 3). Juveniles become increasingly exploratory and wean at about 65 days of age (Humphries and Boutin 1996).

Some juveniles disperse after weaning and establish their own territories (Larsen and Boutin 1994) while others receive part or all of their natal territory from their mothers (Price and Boutin 1993). Although they may begin making exploratory movements of one kilometre or more prior to weaning (Larsen 1993), juveniles do not abandon their natal territory completely until they have established a new territory (Larsen and Boutin 1994; Stuart-Smith and Boutin 1995b). In Kluane, successful dispersers tend to settle < 120m from their natal site and there is no sex difference in the pattern of settlement (Berteaux and Boutin, in press). Similarly, there are no sex differences between juveniles receiving part or all of their natal territory and those who do not receive any of it (Berteaux and Boutin, in press). Females who bequeath their territories tend to do so more often in years of good cone crop and are generally older and have more juveniles at weaning than females who do not bequeath their territories (Berteaux and Boutin, in press).

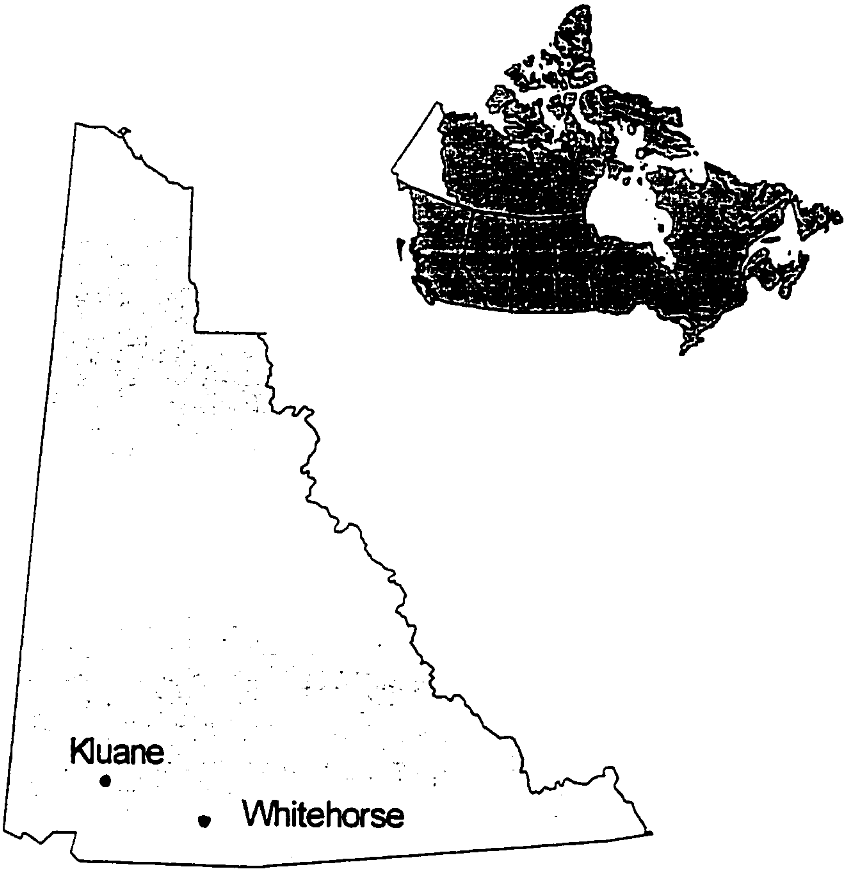

Figure 1.1 Location of study site in Kluane, Yukon Territory, Canada.

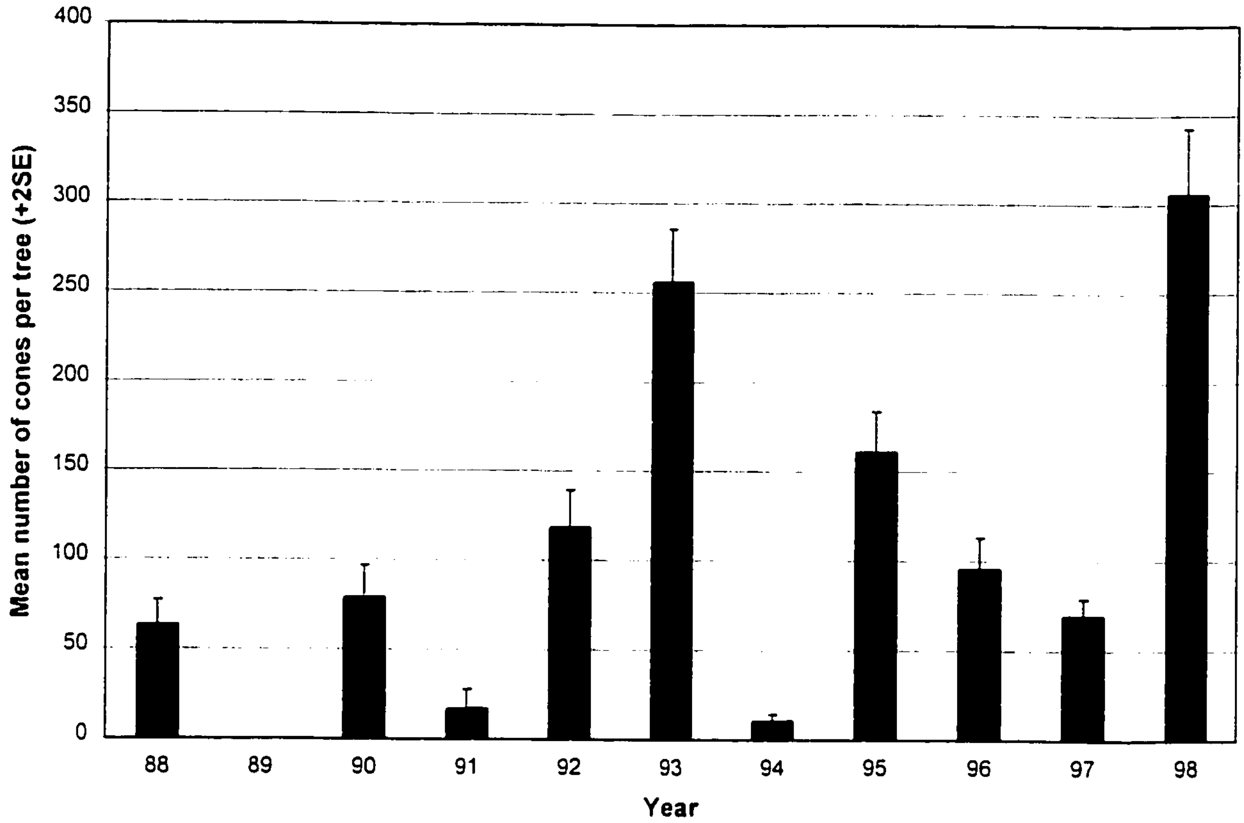

Figure 1.2 Mean number of cones (+2 SE) per white spruce tree each year from 1988 to 1998. There was a complete failure of the cone crop in 1989.

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CHAPTER 2 - SURVIVAL AND BEHAVIOUR OF JUVENILE RED SQUIRRELS ON FOREST EDGE AND INTERIOR

INTRODUCTION

One of the hotly debated topics in the ecological literature today is the presence of edge effects and the degree to which they influence animals living along a habitat boundary as compared to those living in the interior of a habitat patch. Research has focused on birds, with relatively few studies on other classes such as amphibians and small mammals. This bias has stemmed from concern surrounding the decline in populations of neotropical migrants (Voller 1998).

Predominantly, researchers have examined numerical phenomena such as species abundance, richness and diversity as well as rates of nest parasitism and predation. Several studies have documented increases or decreases in the relative abundance, richness and diversity of species living along the edge (e.g., Johnson et al. 1979; Strelke and Dickson 1980; Kroodsma 1984; Gates and Giffen 1991; Sekgororoane and Dilworth 1995; Demaynadier and Hunter 1998) while others have found no evidence of such edge effects (Small and Hunter 1989; Rudnicky and Hunter 1993b; Heske 1995; Bayne and Hobson 1998). Rates of nest parasitism by brown-headed cowbirds (*Molothrus ater*) are often higher along forest edges and this may lead to decreased nest success for individuals nesting in those areas (Gates and Gysel 1978; Chasko and Gates 1982; Brittingham and Temple 1983; but see Hahn and Hatfield 1995; Bielefeldt and Rosenfield 1997). The rate of predation on bird nests may also be influenced by proximity to a forest edge. Although a large body of literature exists (e.g., Gates and Gysel 1978; Yahner and Wright 1985; Angelstam 1986; Andrén and Angelstam 1988; Ratti and Reese 1988; Møller 1989; Yahner 1991; Rudnicky and Hunter 1993a; Pasitschniak-Arts et al. 1998), conflicting results preclude generalizations beyond stating that factors such as nest type (ground, shrub), nest coverage (open, partially covered, cavity), edge type (forest-farmland, forest-clearcut, forest-water) and local predator community may influence the rate of bird nest predation as a function of distance to nearest edge.

Much of this work on parasitism and predation has focused on the egg stage in birds as the use of artificial bird nests allows for easy manipulation of nests and identification of predators (Major and Kendal 1996) and high rates of mortality occur during the early developmental stages in many species of animals (Lack 1954; Caughley 1977). Equivalent life stages in other animals (e.g., juvenile stage in small mammals) are troublesome to study due to the secretive nature of these animals and the difficulties involved in creating artificial nests or locating natural ones.

Although the results are inconclusive, numerical phenomena have been well studied with respect to edges. Behavioural phenomena, on the other hand, have been examined only tangentially. Kroodsma (1984) and Song (1998) mapped songbird territory placement relative to edges to study community-level responses to forest edges. Home range size and residence time of adult females living along patch edges were examined in a study on spatial usage patterns of meadow voles (*Microtus pennsylvanicus*) (Bowers et al. 1996). Møller (1989) examined the relationship between the distance to an edge and nest characteristics (site selection, nest concealment) of various songbirds. Cowbird models have been used to study the responses of the hooded warbler (*Wilsonia citrina*), a forest-interior songbird, to the threat of cowbird parasitism (Mark and Stutchbury 1994). Linzey (1989) studied the effect of transition zones between forested and cleared habitats on the movement behaviour of white-footed mice (*Peromyscus leucopus*). Finally, nest-searching behaviour of red squirrels (*Tamiasciurus hudsonicus*) along a forest edge has also been examined (Pelech 1999).

No studies have addressed the following question: do potential differences in predation pressure affect the behaviour of individuals living on the edge versus the interior? Animals living on the edge of a habitat patch are thought to experience higher predation pressure; however, if they are able to adjust their behaviour according to their current level of predation risk (Lima and Dill 1990), this may result in equivalent survival rates (or nest predation rates) between the edge and interior of the habitat patch. As a result, differences in predation pressure may not result in differences in density, abundance or rates of nest parasitism and predation.

The scarcity of edge effect studies directly examining behaviour is probably influenced by the inherent difficulties in acquiring detailed behavioural data. Many of the animal species examined in previous studies are highly secretive and difficult to capture. Obtaining individuals to mark is often problematic and relocating these individuals, their nests or their young may be virtually impossible. Red squirrels, on the other hand, are ideal organisms for a study examining behaviour and survival. They are highly visible, can be easily trapped, handled, and radio-collared and it is relatively easy to locate and enter their nests. In addition, most squirrels tolerate human observers without altering their behaviour. The major source of mortality in red squirrels, for both juveniles and adults, is predation (Stuart-Smith and Boutin 1995a). Juveniles are known to suffer high mortality from emergence to the end of the summer (Stuart-Smith 1993) and the period from emergence to weaning is thought to be particularly critical (Boutin and Larsen 1993). A preliminary study on juvenile red squirrels found that surviving individuals spent more time resting, more time vigilant, less time travelling off their natal territory and less time in exposed places when compared to those who were eventually depredated (Stuart-Smith and Boutin 1995b). Surviving juveniles may have been more sensitive to their risk of predation. If squirrels can assess and behaviourally manipulate their predation risk, then any negative edge effects on survival may be moderated through differences in the behaviour between juveniles living along an edge and those living in the forest interior.

The main objective of this study was to determine if juvenile red squirrels experience edge effects with respect to survival and behaviour. I compared the survival of juvenile squirrels born along a forest edge to that of juveniles born in the forest interior. I predicted that survival would be lower along the forest edge due to an increased predation risk through use of the edge for travel by predators (Bider 1968). As with most edge effect research on birds (Hartley and Hunter 1998), I assumed higher predation pressure at the edge and consequently did not attempt to quantify predator presence at the edge and interior as it would have comprised an entire study unto itself. Since the survival of juvenile squirrels may be mediated by behaviour (Stuart-Smith and Boutin 1995b), the behaviour of juveniles was also compared to determine if any behavioural differences existed between individuals living along the forest edge and in the forest interior. I predicted that juveniles living along the forest edge would spend more time vigilant and more time resting (particularly in the nest, safe from predation) and less time in attentionattracting behaviours such as traveling, interacting/playing and vocalizing. These behaviours should occur more often under cover (tree or ground) for juveniles living along the edge than for juveniles at the forest interior. Finally, I attempted to determine if any behaviours predicted survival for juveniles in either location.

METHODS

Study Area

The study site was located 20 km southeast of Kluane Lake in southwestern Yukon, Canada (61°N, 138°W) (see Fig. 1.1) and was part of a large study area where long-term research on the reproductive success of red squirrels has been ongoing since 1987. The dominant vegetation is mature white spruce (*Picea glauca*) with a sparse understory of willow (*Salix* spp.) and bog birch (*Betula glandulosa*), and occasional aspen (*Populus tremuloides*) groves. The main squirrel predators in this area include lynx (*Lynx canadensis*), coyote (*Canis latrans*), northern goshawk (*Accipiter gentilis*), and red-tailed hawk (*Buteo jamaicensis*). Also present are great horned owl (*Bubo virginianus*), marten (*Martes americana*), weasel (*Mustela* spp.), fox (*Vulpes vulpes*), and wolf (*Canis lupus*) (Boutin et al. 1995).

Available edges in the study area include an abandoned pipeline, the old Alaska Highway and the new Alaska Highway (Fig. 2.1). Initially cleared in the mid-1950's, the pipeline is approximately 18m wide with a dirt road running down the middle that receives traffic only from researchers working in the area. Regrowth along the pipeline is minimal with short grasses and forbs covering the width and occasional willow bushes along the forest edges. Small piles of stumps and limbs from the initial clearing operation can be found at the edge of the corridor in a few locations. The old Alaska Highway is a gravel road constructed in 1942 to connect Alaska to Canada and ultimately the continental United States. It was last used as a highway in 1967 when a paved road was constructed nearby. Although vehicles rarely travel the 16m wide highway, the roadbed has little regrowth. Some willow and soapberry (*Shepherdia canadensis*) grow along the forest edges. The new Alaska Highway is the main paved highway connecting Alaska to Canada and receives large volumes of commercial and recreational traffic in the summer.

As a result of the road allowance width (approximately 30m), the heavy noise and traffic volume and the potential confounding effects these may have had on squirrels in the immediate proximity, this main highway was not used in the current study.

Evidence from the long-term research project indicates that red squirrels perceive the old highway and pipeline as an edge (S. Boutin, unpubl. data). Red squirrels in Kluane actively defend mutually exclusive territories with an average diameter of 60m (Price et al. 1986). Although territories may abut these edges, no territory has ever incorporated or crossed the edge, whereas clearings in the forest are incorporated within territorial boundaries (S. Boutin, unpubl. data). Edge squirrels were defined as any squirrel whose territory immediately abutted an edge and interior squirrels were squirrels whose territories were at least one territory width away from an edge. This corresponds approximately with the average distance into the forest that edge effects are estimated to penetrate (about 50 - 60m) from the bird (Paton 1994) and vegetation literature (Matlack 1993; Fraver 1994; Young and Mitchell 1994; Stevens and Husband 1998).

Trapping and Identification of Individuals

Each summer from 1987 to 1997, red squirrels living within the study area were trapped and tagged from April to August using live traps (Tomahawk 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanut butter and set on squirrel middens. All individuals caught were tagged with numbered metal eartags (No. 1 Monel tags, National Band and Tag Company, Newport, Kentucky). To facilitate identification at a distance, coloured plastic-coated wires were threaded through the tags so each individual had a unique colour combination. Weight, sex, coat condition and breeding condition were recorded for each capture. Female reproductive condition was assessed as follows: nonbreeder (small, pink nipples), pregnant (large, dark nipples with a distended belly), breeder-lactating (large, pink nipples through which milk can be squeezed and with matted fur around their nipples) or breeder-nonlactating (medium to large dark nipples through which no milk can be expressed).

Pregnant females were radio-collared and trapped at least every three days. After litters were born (as determined by a 10% drop in weight of a female between captures or by the onset of lactation), nests were located using telemetry or visual observation. Nests were examined shortly after parturition and the number and sex of offspring were recorded. Three and a half weeks later (when juveniles weighed 65 - 70g and were about 30 days old), nests were re-entered at which time all offspring were tagged with numbered metal eartags and a unique colour combination of coloured plastic discs threaded through the eartags.

Survival Monitoring

Juvenile red squirrels emerge from the nest at about 42 days of age and wean at 65 - 70 days of age (Humphries and Boutin 1996). Survival of all juveniles after emergence was monitored through weekly trapping, casual observations and complete censuses of all squirrels in the study area during May and August each summer. Individuals were scored as having survived to emergence if they were observed or trapped subsequent to the 42nd day after birth and as having survived to weaning if they were observed or trapped subsequent to the 70th day after birth. Number of individuals surviving from birth to emergence and from emergence to weaning was compared between individuals born on edge territories and those born on interior territories from 1987 to 1997.

Behavioural Observations

During the summers of 1997 and 1998, a sample of juveniles from several edge and interior nests was radio-collared and their post-emergence behaviour was observed (sample sizes shown in Table 2.1). One juvenile (1998) or two juveniles (1997) were chosen randomly from each nest at the time of tagging and equipped with a small radio-transmitter collar weighing 3.8g (Model No. PD-2C, Holohil Systems Ltd., Woodlawn, Ontario, Canada), about 6% of their body mass. These transmitters had a battery life of six months and a transmission distance of 1 to 5km. Beginning at least three days before the anticipated date of emergence, juveniles were located several times daily and the nest tree was searched intensively with binoculars.

Behavioural observations began the first day following emergence and continued for 10 days (Period 1). Observations resumed again for days 15 - 25 post-emergence (Period 2). Period 1 was an indication of early emergence behaviour when juveniles are still highly dependent on their mother and rarely leave their natal territory. Period 2 was an indication of late emergence behaviour when juveniles are weaning and beginning exploratory forays to establish their own territories. I attempted to locate and observe each radio-collared juvenile for twenty 10-min focal animal observations (Martin and Bateson 1993) per period. Focal observations during each period were evenly distributed throughout the morning (0600 to 1200), afternoon (1200 to 1730), and evening (1730 to 2300). In 1998, the mothers of collared juveniles were also radio-collared and their behaviour was observed during Period 1 in the same way as that of juveniles. This allowed me to determine if there were behavioural differences between mothers that might be related to juvenile behaviour during the time in which juveniles were highly dependent on their mothers.

During each 10-min focal observation, the behaviour and exposure of the focal squirrel were recorded every 30 seconds. Behaviour was recorded as one of eight categories (following Stuart-Smith and Boutin 1995b): foraging (eating, caching, handling or searching for food), vocalizing (barking-an alarm call, rattling-a territorial call), traveling (moving quickly in trees or on ground), resting (motionless on a branch with head down and eyes partially closed or in the nest), interacting with another squirrel (playing, chasing, suckling), grooming, vigilant (silent and observant, often standing on hind legs with head up, infrequently foot stomping), and behaviour unknown (or squirrel out-of-sight). Exposure was recorded as one of six categories: in nest, tree-cover (within 1m of the trunk, hidden by branches and difficult to see), tree-exposed (further than 1m from the trunk, easily seen at the tree top or tips of branches), ground-cover (on ground no more than 2m from the tree trunk, under tree canopy), ground-exposed (on ground more than 2m from the tree trunk, in a clearing away from tree canopy), and location unknown (or squirrel out-of-sight). Focal observations occurring on a given day were separated temporally by at least 1½ hours to increase the likelihood they were independent.

For each focal observation, the number of instantaneous samples of each behaviour and of each exposure were divided by the total number of samples the squirrel was observed. These proportions were averaged over each period separately to give the average proportion of samples spent in each behaviour and in each exposure for each individual during Period 1 and Period 2.

Data Analysis

Survival of individual juveniles is dependent on the survival of littermates in some species of mammals (Boutin et al. 1988; O'Donoghue 1994). Since the degree of independence in red squirrel litters was not known, I conducted the analysis described by Boutin et al. (1988). The observed distribution of the number of litters with a given proportion of the litter surviving was compared to the expected distribution assuming independence of littermates. The observed distribution was generated by counting the number of litters falling into each of the following categories of proportion of litter surviving: 0.00-0.20, 0.21-0.40, 0.41-0.60, 0.61-0.80, and 0.81-1.00. The expected frequency distribution of litters with a given proportion surviving was calculated from a binomial distribution using the average survival rate of all litters. For a given litter size, I calculated the probability that 0, 1, 2, etc. young would survive and then multiplied these probabilities by the observed number of litters with that litter size to get the expected number of litters with that proportion of the litter surviving. This was done for each litter size and summed to get the overall expected distribution. I repeated this analysis for each year and tested for independence of litters from birth to emergence and emergence to weaning. The observed and expected distributions were compared using G-tests with Williams correction. The results are shown in Appendices I.1 and I.2.

Log-linear models with Williams correction (Sokal and Rohlf 1995) were used to test the effects of year (1987 - 1997) and natal location (edge, interior) on number of juveniles surviving from birth to emergence and emergence to weaning. The interactions of interest were a significant three-way interaction between year, dead/alive and edge/interior and a two-way interaction between edge/interior and dead/alive. If a three-way interaction was significant, it was redundant to then test for a two-way interaction. As survival of littermates from birth to emergence was not independent (Appendix I.1), I randomly chose one juvenile from each nest for this analysis. From emergence to weaning, survival of littermates was independent (Appendix I.2), hence I performed the analysis using all juveniles in each nest.

Behaviour and exposure data were tested for normality using the Kolmogorov-Smirnov goodness of fit test with Lillefors correction and for homogeneity of variances using Levene's test (SPSS 1998). I normalized the distributions using an arcsin $\sqrt{p}$ transformation, where p is the average proportion of time spent in a behaviour during a Period.

As I collared two juveniles from each nest for behavioural observations in 1997, I needed to determine if I could use both juveniles in my analysis or just one. Hence to determine if littermates behaved more similarly than any two randomly chosen juveniles, I calculated the difference between the mean proportion of time that littermate A spent in each behaviour and the mean proportion of time that littermate B spent in each behaviour. I then randomly chose an equal number of new pairs from the entire pool of juveniles and calculated the differences for the new 'littermates'. This was repeated for each behaviour or exposure during both periods (n = 20 pairs during Period 1 and n = 15 pairs during Period 2). The differences between the observed littermates and the random littermates were compared using independent samples *t*-tests on arcsin $\sqrt{p}$ transformed data. Although there were few differences between the behaviours and exposures of observed and random littermate pairs (Appendices II.1 and II.2), I decided to randomly chose one juvenile from each nest in 1997 for further behavioural analysis to avoid the possibility of psuedoreplication (Hurlbert 1984). The sample sizes used in behavioural analysis are shown in Table 2.1.

To determine if I could pool across years, I tested for differences between years with edge/interior, each behaviour/exposure and each period separately using independent samples *t*-tests. Although the chance of committing a Type I error increases with the number of tests being performed, I kept the acceptable significance level at $p \leq 0.05$ as committing a Type II error would be more serious in this instance than rejecting a true null. Only 3 of 48 tests were significant and these involved behaviours which, when combined, were performed by juveniles on average ≤ 5% of the time. Hence, all subsequent analyses were done with behaviour and exposure data pooled across years.

Behaviour and exposure of juveniles living along the forest edge were compared to that of juveniles living in the interior for each behaviour/exposure and each period separately using independent samples *t*-tests. The same procedures were used to test for edge/interior differences in female behaviour and exposure during Period 1 in 1998. A post-hoc power analysis (Cohen 1988) was performed for each of these comparisons using GPOWER (Faul and Ehrdfelder 1992). I determined the power of the test to detect differences of 10%, 5% and 2% in the proportion of time spent in each behaviour or exposure given my sample sizes and observed variation. These differences were chosen arbitrarily based on the amount of time spent in a range of behaviours. For example, a 10% difference between edge and interior individuals may be relevant for a behaviour in which individuals spend > 50% of their time but not for a behaviour in which they spend < 5% of their time. In this latter situation, a 2% difference may be more applicable.

Logistic regression was used to determine if behaviour and exposure predicted survival from emergence to weaning for individual radio-collared juveniles living on the edge or in the interior. Logistic regression converts dichotomous dependent data (e.g., dead or alive) into a probability value and then based on one or more potential predictors of the dependent, a logistic curve is fitted to the observed data (Glantz and Slinker 1990). To determine if the addition of an independent variable significantly contributes to my ability to predict the dependent variable, I used a likelihood ratio test to compare the likelihood of obtaining the observed data using the model including the predictor to the likelihood of obtaining the observed data if I used a model without the predictor. This is analogous to the overall F test in regression. The likelihood ratio test statistic has been shown to approximately follow a χ^2 distribution and a large χ^2 indicates a significant contribution of the independent variable to my prediction abilities. Following Stuart-Smith and Boutin (1995b), a separate logistic regression was performed for edge and interior juveniles, for each behaviour/exposure and for each period.

All statistical analyses were performed using SPSS (Versions 7.5 or 8.0) and a significance level of $p \leq 0.05$, unless otherwise stated. Results for which $p \leq 0.10$ were considered marginally significant.

RESULTS

Juvenile Survival

Survival of juveniles born along the forest edge from birth to emergence during the 11 year period averaged 65.8% (range: 18% - 100%) while survival of juveniles born in the forest interior averaged 70.6% (range: 35% - 94%) (Fig. 2.2). There was no consistent trend for higher survival on either the edge or the interior. Statistically, there was no significant interaction between year, number surviving and natal location (edge or interior) (G = 10.835, df = 10, p = 0.371) or between number surviving and natal location (G = 13.066, df = 11, p = 0.289). Therefore, there does not appear to be a difference from birth to emergence in the survival of juveniles born on the edge compared to the survival of those born in the forest interior.

The proportion of juveniles surviving from emergence to weaning on the edge averaged 76.6% (range: 33% - 100%) and in the interior averaged 71.8% (range: 60% - 87%) (Fig. 2.3). There was no significant three-way interaction (G = 15.172, df = 10, p = 0.126) but the interaction between number surviving and natal location was significant (G = 19.454, df = 11, p = 0.053) with edge-born juveniles having higher survival. Hence there is a trend towards an effect of natal location on the proportion of juveniles which survive from emergence to weaning and this trend is in the direction opposite to expectation.

Juvenile and Mother Behaviour

Survival of edge and interior juveniles used for behavioural analysis during the summers of 1997 and 1998 is shown in Table 2.2. During Period 1, juveniles spent most of their time resting (70%) and foraging (15%). Although not statistically significant (Table 2.3), juveniles on edges spent slightly less time foraging and traveling and more time resting than interior juveniles (Fig. 2.4a). During Period 2, the same overall proportion (about 85%) of time was spent resting (47%) and foraging (36%) (Fig. 2.4b) and the same trends were evident with respect to edge and interior behavioural differences. The mean proportion of time spent traveling was significantly less and the mean proportion of time spent resting was significantly greater for edge juveniles compared to interior juveniles. The difference in foraging and interacting behaviour was marginally significant, with interior juveniles spending more time in both of these behaviours.

As expected based on the behaviour results, the greatest proportion of time was spent in the nest during Period 1 (62%) and secondarily under tree cover (25%) (Fig. 2.5a). There were no significant differences between edge and interior individuals (Table 2.4). Again during Period 2, the mean proportion of time spent in the nest (36%) exceeded the mean proportion of time spent in any of the other exposures (< 30%) (Fig. 2.5b) and edge juveniles spent significantly more time in the nest.

In contrast to juveniles, mothers spent more time foraging (45%) than resting (39%) (Fig 2.6a). Edge mothers spent more time vocalizing than interior mothers; and this was the only behaviour for which there was a significant difference (Table 2.5). Similarly, behaviour of mothers differed from juveniles in the mean proportion of time spent under tree cover (36%) and in nest (21%) (Fig 2.6b). There were no significant differences between the exposures of edge and interior mothers (Table 2.5). The power of these tests to detect 2%, 5% and 10% differences in behaviour or exposure between edge and interior juveniles or mothers is shown in the corresponding tables.

As the amount of time an individual spends in one behaviour increases, the amount of time available for other behaviours necessarily decreases. Hence, a significant result for one behaviour may also lead to a significant result for a correlated behaviour. For juveniles, traveling/resting, foraging/resting, foraging/traveling (Period 1 only), resting/vigilant (Period 1 only) and for mothers, foraging/resting were highly correlated (r's > 0.5, p's < 0.001) (Appendices III.1 and III.2). For juveniles during Period 1, tree exposed/nest and ground exposed/ground cover and for mothers, tree cover/nest were highly (r's > 0.5) and significantly (p's ≤ 0.001) correlated (Appendices III.3 and III.4).

During Period 1, the proportion of time traveling was positively related to survival for interior juveniles, while the proportion of time vigilant was negatively related to survival for edge juveniles (Table 2.6). During Period 2, the proportion of time traveling was again related to survival for interior juveniles; however, those juveniles who spent more time traveling were less likely to survive. Proportion of time vigilant during Period 2 was negatively related to survival for interior juveniles but not for edge juveniles. Proportion of time spent foraging during both Period 1 and Period 2 was a marginally significant predictor of survival for interior juveniles in both Period 1 and 2 and those juveniles spending more time foraging were more likely to survive.

Proportion of time spent under tree cover during Period 1 was negatively related to survival for edge juveniles and positively related to survival for interior juveniles (Table 2.7). This relationship was opposite for interior juveniles during Period 2 as those spending more time under tree cover tended to have lower survival. Edge juveniles spending more time on the ground but under cover during Period 2 tended to have higher survival.

DISCUSSION

Pre-emergence Juvenile Survival

Survival from birth to emergence did not differ between juveniles born along the forest edge and those born in the forest interior. Factors which could influence survival prior to emergence for red squirrels include predation of juveniles or mother and malnourishment of juveniles or mother (Stuart-Smith 1993). Pre-emergence predation of juveniles has not been demonstrated in red squirrels (Stuart-Smith and Boutin 1995a, E. Anderson, unpubl. data). Predation of adults, as estimated from midden turnover rates, does occur, but it is not higher along the forest edge than in the interior (S. Clare and K. Larsen, unpubl. data). Juvenile malnourishment has also been postulated as a major source of partial or complete litter loss in some years (Stuart-Smith 1993; Stuart-Smith and Boutin 1995a). If a breeding female has depleted her cone supply by the breeding season, she may have difficulty providing adequate nourishment to her litter when alternative food sources such as conifer buds, berries or fungi are not abundant (Boutin and Larsen 1993; Stuart-Smith 1993). Pelech (1999) found higher spruce bud biomass at the forest edge but no difference in spruce cone production. Hence, malnourishment should be worse in the forest interior if cone supplies are depleted, as females living along the forest edge would have access to additional conifer buds. This does not appear to occur, perhaps because malnourishment is only a significant factor in years immediately following a poor cone crop (e.g., years of cone crop failure: 1989, 1991, 1994; Fig 1.2).

There appears to be a trend towards higher survival of edge juveniles prior to 1992 and higher survival of interior juveniles from 1992 onward. Although it is possible that differences in the two main mortality factors of pre-emerged juveniles (maternal food supply or predation pressure) may have differed pre- and post-1992, it is unlikely. As discussed above, Pelech (1999) found no differences in cone production between trees along the forest edge and in the interior and cone failures occurred both pre- and post-1992.

Densities of the snowshoe hare predators, lynx, coyote, goshawks and great-horned owls, have been found to track the densities of their main prey source with the predator densities remaining high for several months after the hare numbers have begun to decline (Keith et al. 1977; Krebs et al. 1995). Red squirrels represent a source of alternative prey for these predators; however, slight increases in predation on adult squirrels as hare numbers declined do not affect squirrel densities (Stuart-Smith and Boutin 1995a). The pattern of higher pre-emergence survival of juvenile red squirrels living along the edge prior to 1992 and higher pre-emergence survival of juveniles living in the forest interior after 1992 does not appear to be correlated with any particular point in the hare cycle: hare and predator numbers were increasing during 1987 - 1989 (a period of higher edge juvenile survival) and during 1995 - 1997 (a period of higher interior juvenile survival) (Krebs et al. 1995; C. Krebs unpubl. data). Similarily, the first peak in hare densities occurred during 1989 (higher edge juvenile survival) and 1990 (higher interior juvenile survival) and the second peak occurred during 1997 (higher interior juvenile survival). Finally, during the crash phase of the snowshoe hare cycle (1991 and 1992), edge juveniles had higher survival in one year and interior juveniles had higher survival in the other year.

Alternatively, one must consider the sample sizes contributing to this data set. As survival of littermates was not independent prior to emergence, it was necessary to use only one juvenile from each nest, reducing the sample size from 2032 to 671 juveniles over the 11-year period. During the first years of this study (1987 - 1989), the study area was smaller, field techniques were not as efficient as in later years and hence sample sizes were relatively low. Eliminating these early years completely from analysis does not change the conclusions of no differences in pre-emergence survival between edge and interior juveniles; however, it does eliminate the appearance of edge juveniles having higher survival pre-1992 and interior juveniles having higher survival post-1992.

Post-emergence Juvenile Survival

The major source of post-emergence juvenile mortality in red squirrels is predation; disease and starvation have little direct impact (Stuart-Smith and Boutin 1995a). If predation pressure is higher along an edge due to the use of forest edges as travel ways by predators (Bider 1968), we would predict lower survival along the edge. However, there were no significant differences between survival of juveniles born along the edge as compared to the survival of juveniles born in the forest interior and, in fact, the trend was toward higher survival of edge juveniles. One major shortcoming of this and most bird nest predation studies (Hartley and Hunter 1998) is the lack of a measure of predator abundance or relative predator pressure on the edge versus the interior. Although attempts were made to record casual predator and alternative prey sightings, the resulting data were coarse and there are differences in detectability between the forest edge and the forest interior.

Though relative predation pressure on edge and interior is unknown, one can still consider habits of the local predators. None of the predators in this system are edge-specialized predators. Coyote and lynx use the corridors as travel routes in the winter due to snow conditions (Murray and Boutin 1991; O'Donoghue et al. 1998); however, in summer, the frequency of travel along these routes compared to the forest interior is unknown. Although northern goshawks may incorporate edges into their home range (Kenward 1982; Palmer 1988), they are adept fliers and often hunt in mature forest (Kenward 1982; Widén 1989). Red-tailed hawks, on the other hand, may capture most of their prey in more open habitats (Palmer 1988). Thus, the nature of the predator community may be such that rates of predation-induced juvenile deaths along the forest edge are not higher than for juveniles in the interior.

Although much nest predation work has focused on survival of natural and artificial nests on the forest edge and in the interior, small mammal studies have tended to focus on density, abundance and diversity at edges (Johnson et al. 1979; Heske 1995; Mills 1995; Sekgororoane and Dilworth 1995; Bayne and Hobson 1998; Stevens and Husband 1998). Only one study has looked at survival of small mammal young along a forest edge. Hansson (1998) used recapture rates to estimate survival and found that immature yellow-necked wood mice (*Apodemus flavicollis*) and immature bank voles (*Clethrionomys glareolus*) suffered higher mortality in forest edge zones. Edge effect studies on birds generally examine nest predation over a range of 7 to 14 days and are meant to simulate the laying and incubation period of many songbird species (Paton 1994; Major and Kendal 1996). Survival of nestlings from hatching to fledging with respect to edges has rarely been examined with natural nests (Gates and Gysel 1978) and is impossible to study with artificial nests. Small mammals, on the other hand, are virtually impossible to study in the field while they are still in the nest; survival can usually only be studied after emergence. This study allowed the opportunity to examine survival of juvenile red squirrels born along the forest edge and in the forest interior both prior to and after emergence from the natal nest.

Behavioural Compensation of Increased Predation Risk

Lack of post-emergence survival differences could also arise if predation risk was indeed higher along the forest edge due to increased prey visibility or predator efficiency at forest clearings, but edge individuals compensate for the increased risk by adjusting their behaviour (Lima and Dill 1990). As predicted, edge juveniles did spend more time resting, less time traveling and they also spent less time foraging during Period 2 than interior juveniles. Contrary to my predictions however, no differences existed in proportion of time vigilant and vocalizing and there were no significant behavioural differences during Period 1. Mothers living along the edge and those living in the forest interior did not differ behaviourally. Similarly, the only exposure that differed significantly between edge and interior juveniles was the proportion of time in the nest during Period 2. This compliments the previous finding that edge juveniles rested more than interior juveniles during Period 2, but fails to support my predictions that edge juveniles would spend more time under tree and ground cover. Edge and interior mothers did not differ in their exposures.

One possible explanation for the differences in juvenile foraging and resting behaviour during Period 2 is that food quality or quantity may be higher at the edge. This may allow edge-born juveniles to forage less than individuals in the forest interior and consequently spend more time resting. Conversely, if edge juveniles spend more time resting, their energy demands may be lower requiring less time spent foraging. Irrespective of location, these potential trade-offs between time spent foraging and time spent in the nest are supported by a strong correlation ($r > 0.65$) between these behaviours. As discussed previously, individuals living along the edge have access to more spruce buds early in the season; however, availability of cones does not differ between the edge and interior (Pelech 1999). The quality of the edge food resources compared to the interior is unknown. The lack of differences in the foraging behaviour of mothers indicates that there may not have been large differences in food quality or quantity. Overall however, the relative lack of post-emergence behavioural differences between edge and interior juveniles seems to indicate that behavioural compensation for increased predation risk does not occur.

One critique of this analysis arises from the fact that a significant result in one behaviour may lead to a significant result in a correlated behaviour. This problem of correlations between behaviours and exposures could be treated using principal components analysis (PCA), an analysis designed to account for such correlations by producing axes which represent new independent variables (SPSS 1998). However, the axes produced by PCA's are often difficult to interpret or depict graphically and the application of this technique maybe more beneficial to studies which incorporate more than seven variables. Hence, I simply analyzed each variable separately while taking into consideration the correlations and associated limitations. Correlations between variables likely do not render this study fruitless as there are few significant results.

Edge effects may have been present but my methods of measuring behaviour were ineffective at detecting differences in behaviours (e.g., if edge juveniles are more efficient at vigilance than interior juveniles) or the variation between individuals swamped my ability to detect differences (i.e., low power). One way to overcome the first problem would be to develop another method of measuring behaviour, particularly vigilance. This solution is more complicated than at first glance. Unlike many songbird species for which eating (head down) and vigilance (head up) are mutually exclusive behaviours, red squirrels can handle and eat food while simultaneously maintaining a level of vigilance. Hence, given my present method of quantifying the amount of time spent performing each behaviour, it was necessary to arbitrarily categorize such behaviour as one or the other according to preset guidelines. Secondly, I usually had high power (> 0.75) to detect differences of 10% in the behaviours and exposures in which juveniles spent the majority of their time (foraging, resting, nest, tree cover). Based on the results of Stuart-Smith and Boutin (1995b) and Humphries (1996), I could expect to find 15 – 20% differences in these behaviours between study groups. For behaviours and exposures in which juveniles spent less than 10% of their time, my power was generally high to detect differences of 5% but much lower to detect differences of only 2%.

The most parsimonious explanation for lack of behavioural differences is simply that edge effects do not occur in this population of red squirrels. Although the human-induced edges in this study were hard, distinct edges, the study area is quite patchy with a many softer, natural edges. Squirrels in this area may be adapted to living in proximity to habitat edges, resulting in the lack of behavioural differences between individuals that lived along human-induced edges and those that did not. Since there are no predators that specialize on edges in this system, predation risk may not be perceived as higher along the human-induced forest edge and thus, edge squirrels do not need to compensate behaviourally to reduce their risk.

Unlike nest predation, predation risk for parent birds provisioning nests has not been studied extensively (Lima 1987: Magnhagen 1991). A few studies indicate that parents provisioning nestlings suffer higher predation risk (Ainley and DeMaster 1980) and may adjust provisioning activity relative to the risk of predation (Harris 1980; Harfenist and Ydenberg 1995). Yet bird nest predation studies have overlooked the fact that individuals tending nests along a forest edge may adjust their behaviour so nesting activity is less conspicuous to predators. In doing so, the rate of nest predation may be lowered to a level equivalent to that at the interior of the forest. Songbird species which build partially covered nests tend to live closer to woodland edges than species which build open nests (Møller 1989); however individual differences in nesting behaviour and subsequent nest success have not been examined in birds with respect to edges. Although

Pelech (1999) examined individual behavioural differences in red squirrels living along a forest edge, she was doing so with squirrels as predators rather than prey. The present study was the first to examine individuals living along the forest edge and in the interior to determine if potential differences in predation risk influence their behaviour or spatial locations and thus considers a behavioural alternative to numerical edge effects.

Edge juveniles in Period 1 and interior juveniles in Period 2 who spent more time vigilant were less likely to survive than their counterparts. Although the relationship was in the same direction for interior juveniles in Period 1, it was not significant and for edge juveniles in Period 2, there was no trend. Contrary to my results, a previous study found a positive relationship between the proportion of time spent vigilant and the survival of juveniles (Stuart-Smith and Boutin 1995b). I am uncertain why that relationship was not consistent between periods in the current study.

Proportion of time traveling during each period predicted the survival of interior juveniles only. During Period 1, those interior juveniles spending more time traveling were more likely to survive while during Period 2, those juveniles spending less time traveling were more likely to survive. These Period 2 results concur with previous studies (Larsen and Boutin 1994; Stuart-Smith and Boutin 1995b) that found traveling, particularly off the natal territory, to be risky. The opposite relationship during Period 1 could arise if the time spent traveling is an indication of an attempt to avoid predation by taking refuge either in a covered location or in the nest. Interior juveniles who spent more time under cover during Period 1 were indeed more likely to survive. During Period 2, juveniles may have learned that covered locations are inherently safer and hence spend more time in covered locations and less time traveling from an exposed to a covered location. However, this is not supported by the behavioural data as both surviving and depredated juveniles spent less time in the nest during Period 2 and more time in all other exposures. Although there were no significant differences for surviving and depredated interior juveniles during Period 2, the trends for the two marginally significant exposures were in the opposite direction to what one would predict (i.e., juveniles spending more time under tree cover had lower survival and juveniles spending more time on the ground exposed had higher survival).

The results for the effect of proportion of time spent under tree cover on survival are equally enigmatic: edge juveniles spending less time and interior juveniles spending more time under tree cover during Period 1 were more likely to survive. The results for interior juveniles make intuitive sense but those for edge juveniles do not. Finally, edge juveniles spending more time under cover on the ground during Period 2 tended to have higher survival. This result supports the expectation that spending more time in covered locations would enhance survival.

One possible explanation for the complex results from the logistic regression analysis is that though the sample sizes were relatively high in each period for both edge and interior, only a few individuals (< 20%) died. The distribution of alive versus dead individuals was thus highly skewed. The resulting logistic regression models were good at predicting who would survive but rarely succeeded at predicting who would die. Alternatively, these results may simply represent stoichasticity in the system.

Conclusions

There no pre-emergence and limited post-emergence survival differences, as well as few behavioural differences between juvenile red squirrels born along a forest edge as compared to juveniles born in the forest interior. Hence edge effects were not convincingly demonstrated in this population of red squirrels. However, future studies of edge effects should adopt a behavioural approach to determine if individuals, particularly birds, living along a forest edge behaviourally mediate their risk of predation as compared to individuals in the forest interior.

Table 2.1 Edge and interior sample sizes used in juvenile behavioural analysis during Periods 1 and 2 in 1997 and 1998.

Period	Location	1997	1998
1	Edge	7	17
1	Interior	14	23
2	Edge	5	16
2	Interior	12	20

Table 2.2 Survival of edge- and interior-born juveniles used for behavioural analysis in 1997 and 1998.

Year	Location	Alive	Dead
1997	Edge	5	2
1997	Interior	9	5
1998	Edge	16	1
1998	Interior	21	2

Table 2.3 Results of *t*-tests on juvenile behavioural differences between edge and interior for each behaviour and period separately. *t*-tests were performed on arcsin $\sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined. Also shown is the power of the test to detect a 10%, 5% and 2% difference in the proportion of time spent in each behaviour given my observed sample sizes and variation.

Period	Behaviour	*t* statistic	df	p value	Power to detect difference of		
					10 %	5%	2%
1	Forage	-1.253	59	0.215	0.973	0.494	0.122
	Vocalize	0.520	59	0.605	1.000	0.764	0.189
	Travel	-1.477	59	0.145	1.000	0.993	0.426
	Rest	1.581	59	0.119	0.683	0.230	0.078
	Interact	-0.771	59	0.444	1.000	1.000	0.979
	Groom	-1.038	59	0.303	1.000	1.000	1.000
	Vigilant	-0.024	59	0.981	0.987	0.552	0.133
2	Forage	-1.705	51	0.094	0.819	0.301	0.089
	Vocalize	-0.709	51	0.482	1.000	1.000	0.978
	Travel	-3.082	51	0.003	1.000	0.995	0.439
	Rest	2.730	51	0.009	0.840	0.315	0.091
	Interact	-1.668	51	0.101	1.000	1.000	0.905
	Groom	0.071	51	0.943	1.000	1.000	1.000
	Vigilant	0.039	51	0.702	1.000	1.000	0.617

Table 2.4 Results of *t*-tests on juvenile exposure differences between edge and interior for each exposure and period separately. *t*-tests were performed on arcsin $\sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined. Also shown is the power of the test to detect a 10%, 5% and 2% difference in the proportion of time spent in each exposure given my observed sample sizes and variation.

Period	Exposure	*t* statistic	df	p value	Power to detect difference of		
					10%	5%	2%
1	Nest	1.548	59	0.127	0.603	0.199	0.073
	Tree Cover	-0.198	59	0.844	0.844	0.318	0.091
	Tree Exposed	-1.213	59	0.230	0.806	0.292	0.087
	Ground Cover	-0.088	59	0.930	1.000	0.994	0.428
	Ground Exposed	-1.187	59	0.240	1.000	1.000	0.808
2	Nest	2.247	50	0.029	0.755	0.263	0.083
	Tree Cover	-1.062	50	0.294	0.725	0.249	0.081
	Tree Exposed	-1.647	50	0.106	1.000	0.773	0.192
	Ground Cover	-0.632	50	0.532	0.983	0.532	0.129
	Ground Exposed	-0.556	50	0.581	0.990	0.573	0.138

Table 2.5 Results of *t*-tests on behaviour and exposure differences between edge and interior mothers for Period 1 during 1998. *t*-tests were performed on arcsin $\sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined. Also shown is the power of the test to detect a 10%, 5% and 2% difference in the proportion of time spent in each behaviour or exposure given my observed sample sizes and variation.

Behaviour/Exposure	*t* statistic	df	p value	Power to detect difference of		
				10%	5%	2%
Forage	-0.396	36	0.695	0.489	0.162	0.067
Vocalize	2.083	36	0.044	1.000	1.000	0.936
Travel	-0.919	36	0.364	1.000	1.000	0.695
Rest	0.230	36	0.820	0.580	0.191	0.072
Interact	0.231	36	0.818	1.000	1.000	0.860
Groom	0.277	36	0.784	1.000	1.000	1.000
Vigilant	0.606	36	0.548	1.000	0.853	0.226
Nest	-0.022	36	0.982	0.682	0.230	0.078
Tree Cover	-0.197	36	0.845	0.512	0.169	0.068
Tree Exposed	1.051	36	0.300	0.995	0.619	0.148
Ground Exposed	0.144	36	0.886	0.675	0.227	0.077
Ground Cover	-0.503	36	0.618	0.998	0.677	0.162

Table 2.6 Results of logistic regressions of behaviour variables on survival from emergence to weaning. Sample sizes were 24 and 35 for edge and interior, respectively, during Period 1 and 21 and 32 for edge and interior, respectively, during Period 2. All df = 1. p values significant at $p \leq 0.05$ are underlined.

Period	Behaviour	Edge		Interior	
		χ^2	p value	χ^2	p value
1	Forage	0.577	0.447	2.615	0.106
	Vocalize	1.675	0.196	0.355	0.551
	Travel	0.106	0.745	4.519	0.034
	Rest	0.003	0.958	0.060	0.806
	Interact	1.875	0.171	0.103	0.749
	Groom	0.767	0.381	0.023	0.878
	Vigilant	3.908	0.048	1.988	0.159
2	Forage	0.126	0.723	3.103	0.078
	Vocalize	1.708	0.191	1.481	0.224
	Travel	0.666	0.415	7.887	0.005
	Rest	0.026	0.873	0.431	0.511
	Interact	0.978	0.323	1.166	0.280
	Groom	0.025	0.874	2.211	0.137
	Vigilant	0.283	0.595	7.066	0.008

Table 2.7 Results of logistic regressions of exposure variables on survival from emergence to weaning. Sample sizes were 24 and 35 for edge and interior, respectively, during Period 1 and 21 and 32 for edge and interior, respectively, during Period 2. All df = 1. p values significant at $p \leq 0.05$ are underlined.

		Edge		Interior	
Period	Exposure	χ^2	p value	χ^2	p value
1	Nest	1.023	0.312	0.045	0.831
	Tree Cover	4.201	$\underline{0.040}$	5.159	$\underline{0.023}$
	Tree Exposed	1.462	0.227	2.294	0.130
	Ground Cover	0.073	0.787	0.001	0.981
	Ground Exposed	1.235	0.267	0.126	0.722
2	Nest	0.693	0.405	1.301	0.254
	Tree Cover	0.057	0.811	3.192	0.074
	Tree Exposed	2.266	0.132	0.051	0.822
	Ground Cover	8.423	$\underline{0.004}$	0.647	0.421
	Ground Exposed	0.464	0.496	2.805	0.094

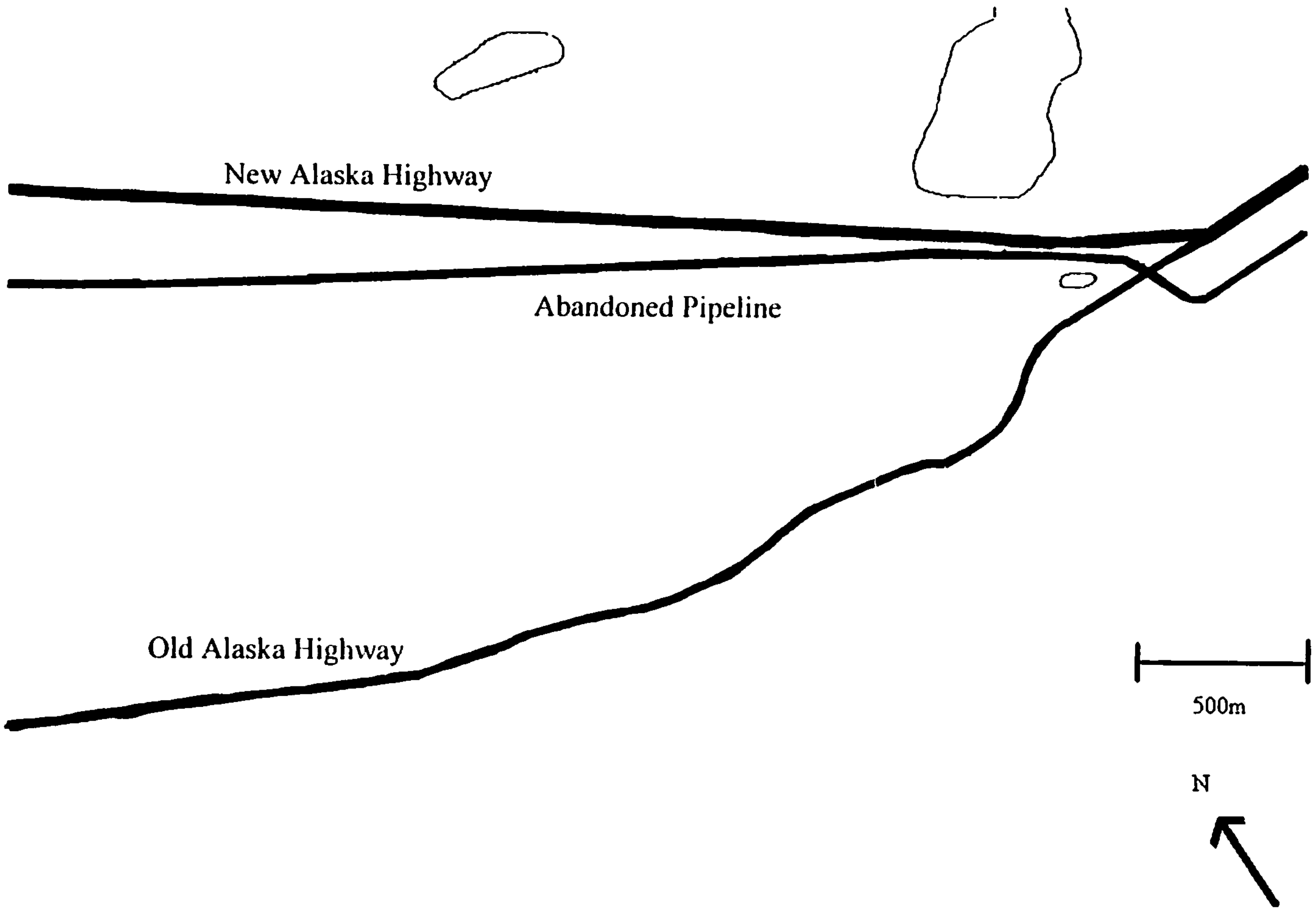

Figure 2.1 Location of forest-pipeline and forest-road edges in the study area.

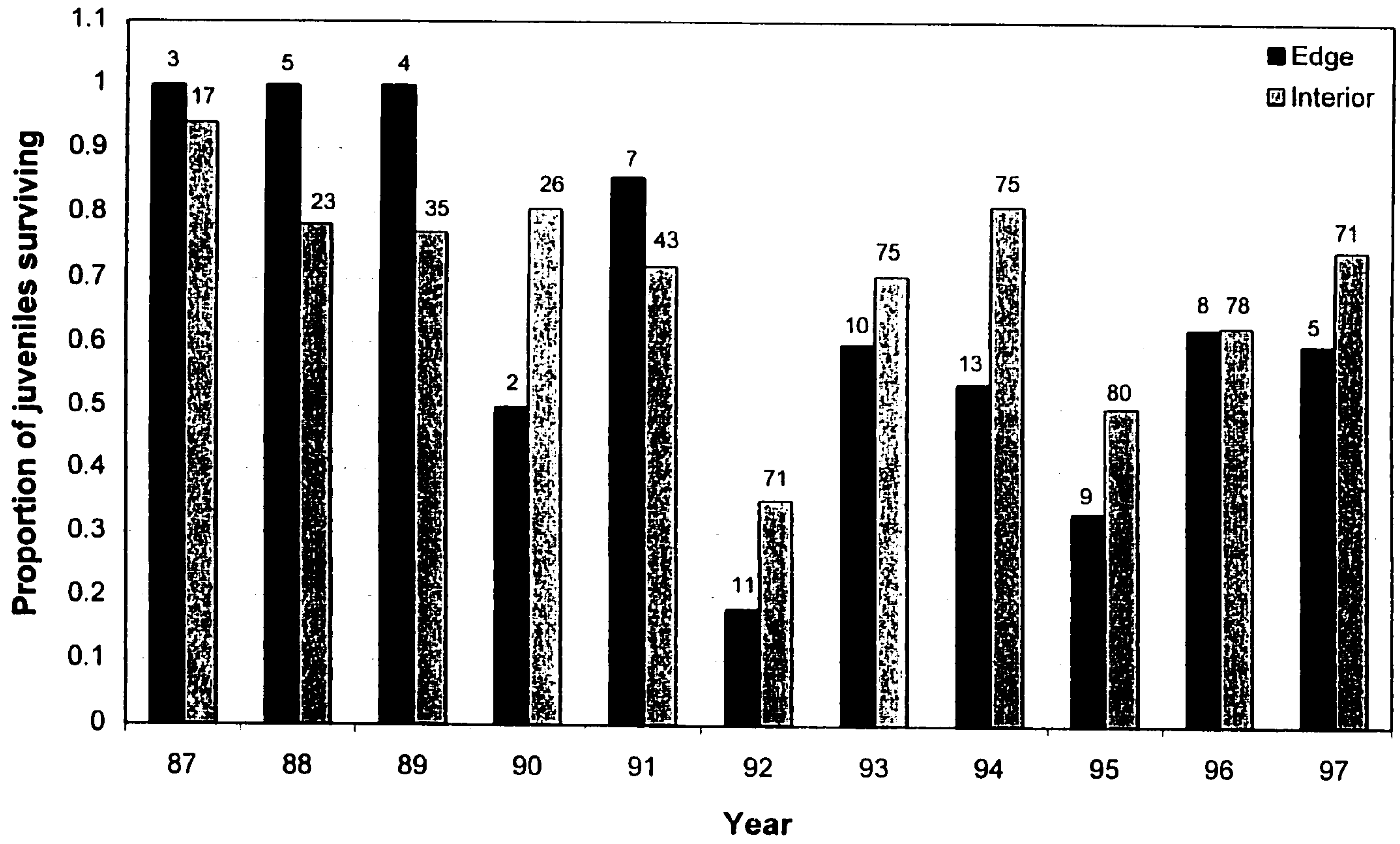

Figure 2.2 Proportion of juveniles surviving from birth to emergence each year from 1987 to 1997 when analyzed using one randomly chosen juvenile per nest (n = 671). The numbers above the bars are the sample sizes in each category.

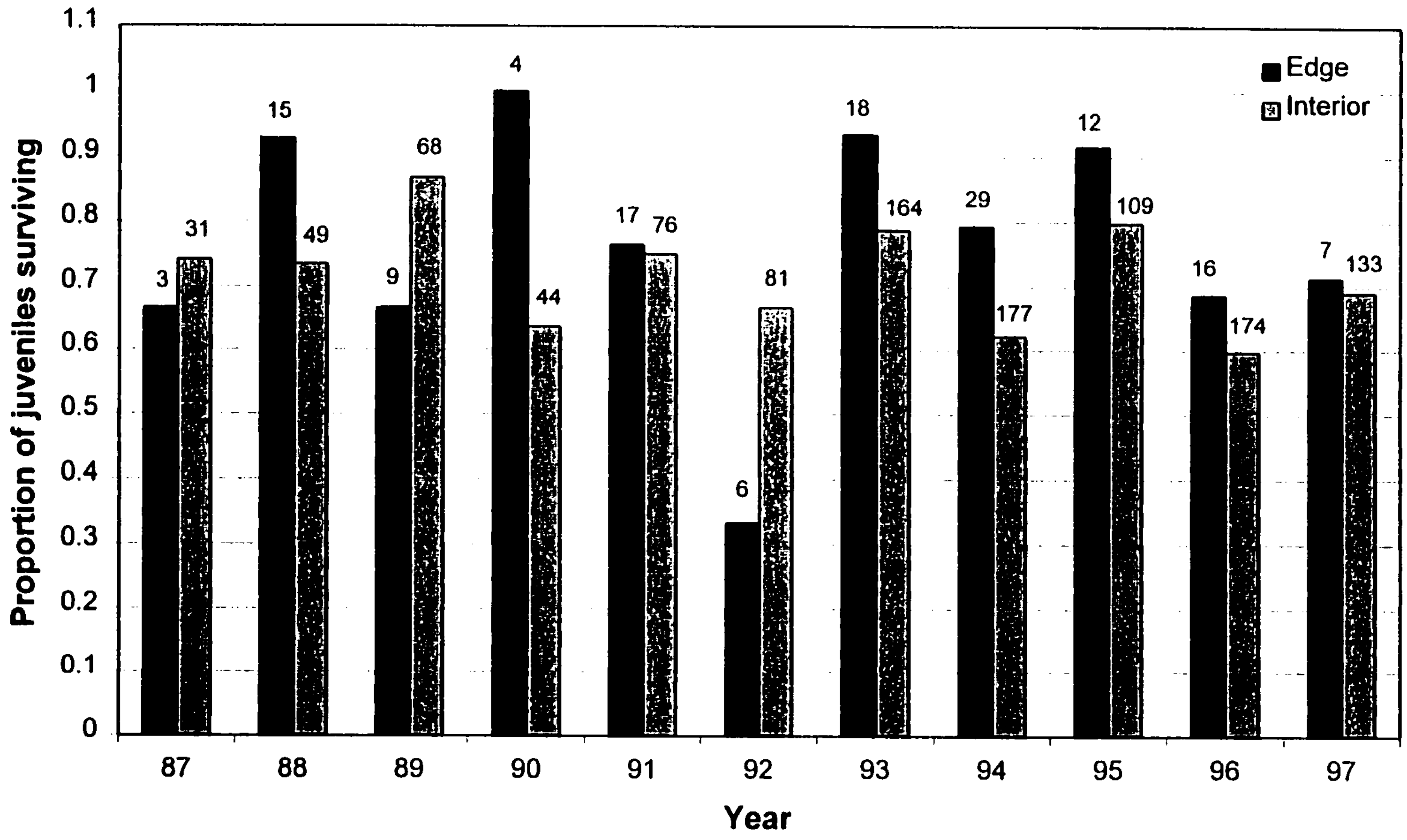

Figure 2.3 Proportion of juveniles surviving from emergence to weaning each year from 1987 to 1997 when analyzed using all juveniles known to emerge (n = 1242). The numbers above the bars are the sample sizes in each category.

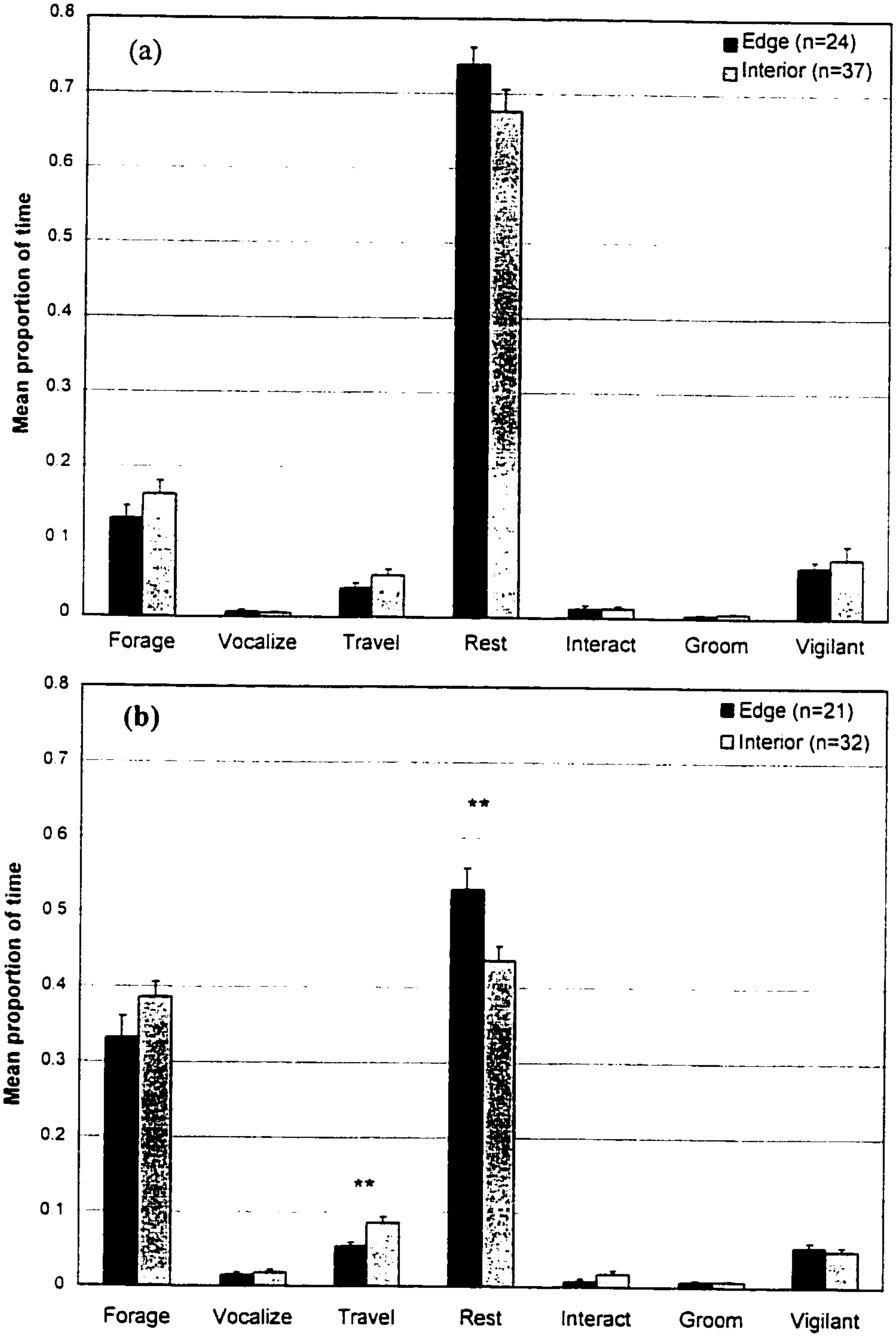

Figure 2.4 Mean (+SE) proportion of time spent in each behaviour by juveniles during Period 1 (a) and Period 2 (b).** $p \leq 0.01$.

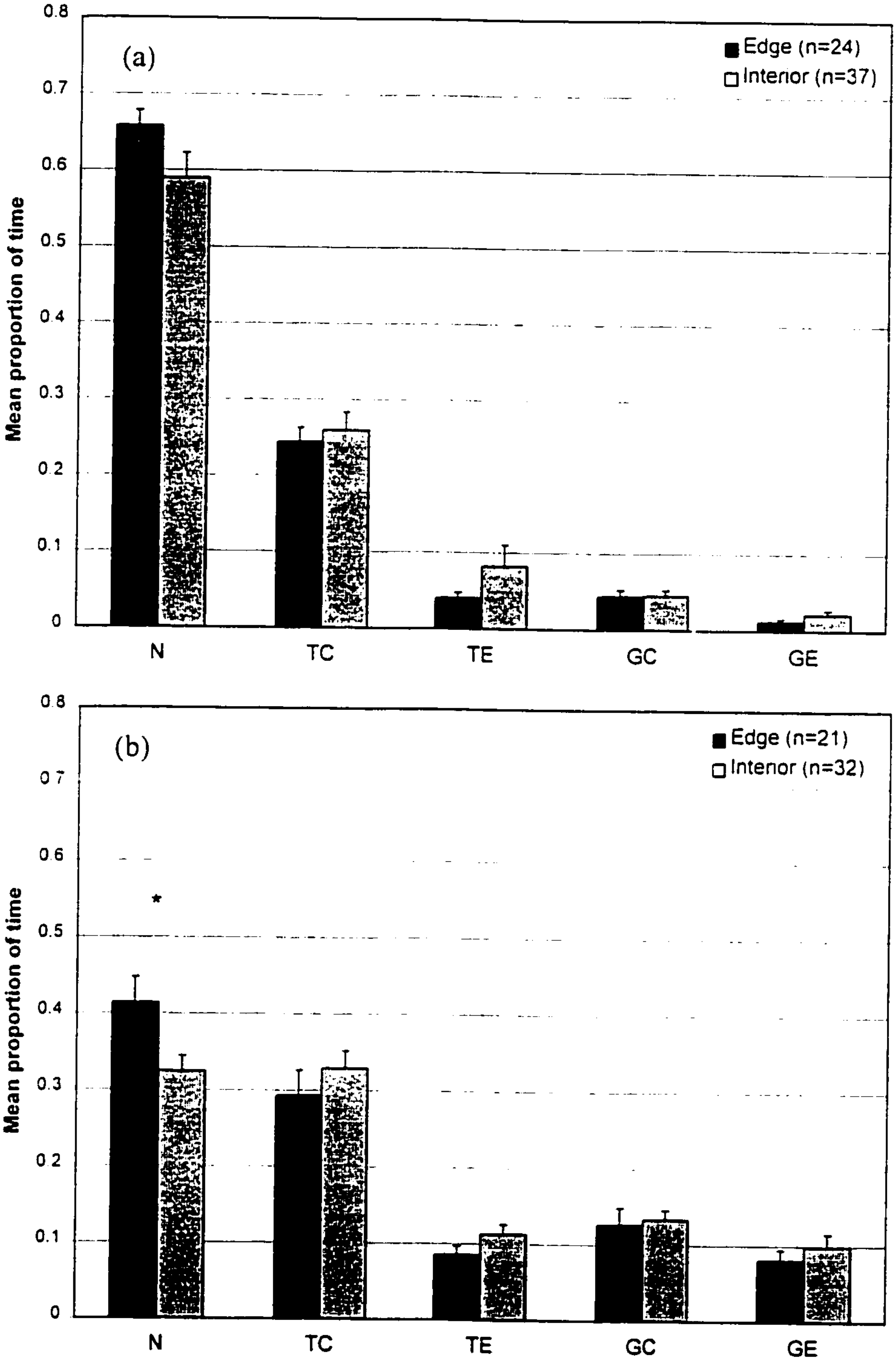

Figure 2.5 Mean (+SE) proportion of time spent in each exposure by juveniles during Period 1 (a) and Period 2 (b). N = Nest; TC = Tree Cover; TE = Tree Exposed; GC = Ground Cover; GE = Ground Exposed. * $p \leq 0.05$.

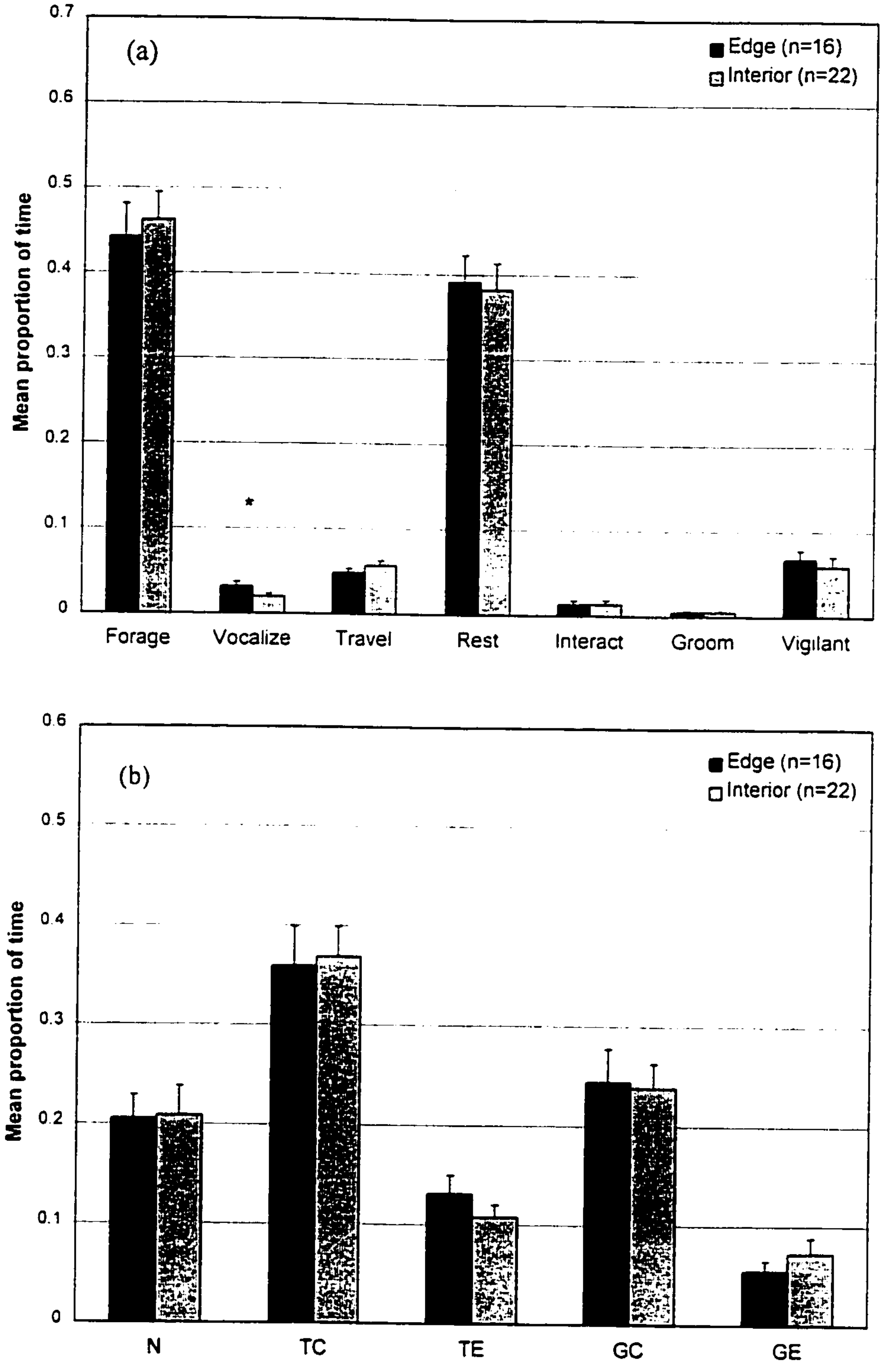

Figure 2.6 Mean (+SE) proportion of time spent by mothers in each behaviour (a) and exposure (b) during Period 1 in 1998. N = Nest; TC = Tree Cover; TE = Tree Exposed; GC = Ground Cover; GE = Ground Exposed. * $p \leq 0.05$.

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CHAPTER 3 - DOES BEHAVIOUR PREDICT SURVIVAL OF JUVENILE RED SQUIRRELS?

INTRODUCTION

Studies of many different animal species have found that the survival of juveniles is lower and more variable than during other life stages (Lack 1954; Caughley 1977). For mammals in particular, much research has examined how juvenile survival to independence is influenced by factors ranging from parental age, experience and social status (Webb 1988 in Webb 1993; Wauters and Dhondt 1989; Mech and McRoberts 1990; Derocher and Stirling 1994; Doolan and MacDonald 1997) to rates of predation (Harcourt 1992; Laurenson 1994; Stuart-Smith and Boutin 1995a). Although many factors that may influence juvenile survival are not under the juvenile's immediate control (e.g., birthdate, litter size, prevalence of disease), risk of predation may be manipulated by the individual.

Manipulation of predation risk can occur, for example, by altering behaviours or use of spatial locations perceived as unsafe (Lima and Dill 1990). Two major reviews (Lima and Dill 1990; Lima 1998) have summarized studies examining the role of predation risk on the behaviour of feeding animals primarily, but also on other areas such as social behaviour (i.e., group size and structure), vigilance and escape behaviour, reproductive behaviour, predator-prey interactions, and patterns of activity. A general assumption of studies that relate behaviour to predation risk is that individuals performing less risky behaviours will suffer less predation and therefore have higher survival. Rarely, however, is this assumption tested by following individuals until their death (Stuart-Smith and Boutin 1995b; Lima 1998). A preliminary study which related the behaviour of juvenile red squirrels (*Tamiasciurus hudsonicus*) to survival (Stuart-Smith and Boutin 1995b) seemed to support the assumption: Individuals who spent relatively more time vigilant, resting and on their natal territory and less time in exposed locations were more likely to survive to weaning. However, sample sizes were low (n = 15 individuals of which only 3 were depredated) and there was some disagreement on the date of emergence from the natal nest as identified in that study and in a later study on the same population of squirrels (Humphries and Boutin 1996).

The current study was designed to test the basic assumption of studies relating behaviour to predation risk (i.e., risky behaviour leads to lower survival rates) as well as expand upon the work of Stuart-Smith and Boutin (1995b) in determining what behaviours predict survival of squirrels. The behaviour of juvenile red squirrels was the focus of study as high mortality occurs between birth and weaning (Boutin and Larsen 1993) and the largest source of mortality for emerged juveniles is predation (Stuart-Smith and Boutin 1995a). Additionally, I examined the behaviour of the corresponding mothers during the early post-emergence period and its relationship with juvenile survival as it has been shown that females may alter their behaviour to reduce predation on juveniles (FitzGibbon 1990; Laurenson 1994).

Numerous behaviours may negatively influence survival of juvenile red squirrels. Traveling, particularly off the natal territory, may be costly for several reasons. Active individuals are likely more conspicuous to predators than stationary individuals (FitzGibbon 1990; Skelly 1994; Martel and Dill 1995). Traveling relatively long distances may expose individuals to predators and unfamiliar habitat more often than traveling within the home range (Metzgar 1967; Gaines and McClenaghan 1980). For instance, kangaroo rats (*Dipodomys merriami*) that traveled further between successive telemetry locations suffered higher predation rates (Daly et al. 1990). Most depredated juvenile red squirrels were found off their natal territory (Larsen and Boutin 1994) and juveniles spending more time off their natal territory were more likely to be depredated (Stuart-Smith and Boutin 1995b). Hence, I predicted that juvenile red squirrels who spend more time traveling and who travel further from the natal midden should suffer higher predation rates than juveniles who are more conservative in their traveling behaviour.

Vocalizing and interacting with other squirrels may attract the attention of predators or reduce the vigilance of the participating individuals. Nestling begging behaviour has been shown to increase nest predation rates (Haskell 1994) and most depredations of fur seal pups (*Arctocephalus australis*) have been found to occur when juveniles are playing (Harcourt 1991). Thus, juvenile red squirrels that spend more time vocalizing and interacting should be more likely to be depredated. Juveniles spending relatively more time visible to predators in exposed locations away from canopy cover, whether in the trees or on the ground, should suffer higher predation rates than those spending relatively less time in such locations.

Behaviours which should be positively related to survival include vigilance and resting (Stuart-Smith and Boutin 1995b). It is intuitive that individuals spending more time vigilant should have higher survival rates (FitzGibbon 1988). Similarly, juveniles spending more time resting should have higher survival as most resting by squirrels occurs in the nest, safe from predators. Finally, juveniles spending more time under cover should have higher survival rates than those who spend less time under cover.

METHODS

Study Area

I used the same population of red squirrels as Stuart-Smith and Boutin (1995b) to reduce the potential variability in our results due to population-level behavioural differences. The study site was located 20 km southeast of Kluane Lake in southwestern Yukon, Canada (61°N, 138°W) (Fig. 1.1). The dominant vegetation is mature white spruce (*Picea glauca*) with a sparse understory of willow (*Salix* spp.) and bog birch (*Betula glandulosa*), and occasional aspen (*Populus tremuloides*) groves. The main squirrel predators in this area include lynx (*Lynx canadensis*), coyote (*Canis latrans*), northern goshawk (*Accipiter gentilis*), and red-tailed hawk (*Buteo jamaicensis*). Also present are great horned owl (*Bubo virginianus*), marten (*Martes americana*), weasel (*Mustela* spp.), fox (*Vulpes vulpes*), and wolf (*Canis lupus*) (Boutin et al. 1995).

Identification of Individuals

During the summers of 1997 and 1998, adult red squirrels living within the study area were trapped, marked and breeding condition of females assessed as described in Chapter 2. Pregnant females were trapped regularly and radio-collared (Model No. PD-2C, Holohil Systems Ltd. Woodlawn, Ontario, Canada) shortly before or immediately following parturition (as determined by a 10% drop in weight of a female between captures or by the onset of lactation). Natal nests were then located using telemetry or visual observation and entered to record the number and sex of the offspring. The nests were re-entered when juveniles were about 30 days of age (65 - 70g) and all offspring were tagged with numbered metal eartags and a unique colour combination of coloured plastic discs threaded through the eartags. One juvenile (1998) or two juveniles (1997) were randomly chosen from each nest at the time of tagging and equipped with a small radio-transmitter collar similar to that used on adult females.

Behavioural Observations

Beginning at least three days before the anticipated date of emergence, radio-collared juveniles were located several times daily and the nest tree was searched intensively with binoculars. Behavioural observations began the first day following emergence and continued for 10 days (Period 1). Observations resumed again for days 15 - 25 post-emergence (Period 2). Period 1 was an indication of early emergence behaviour when juveniles are still highly dependent on their mother and rarely leave their natal territory. Period 2 was an indication of late emergence behaviour when juveniles are weaning and beginning exploratory forays to establish their own territories. I attempted to locate and observe each radio-collared juvenile for twenty 10-min focal animal observations (Martin and Bateson 1993) per period. Focal observations during each period were evenly distributed throughout the morning (0600 to 1200), afternoon (1200 to 1730), and evening (1730 to 2300). Focal observations occurring on a given day were separated temporally by at least 1½ hours to increase the likelihood that they were independent. In 1998, mothers of collared juveniles were also radio-collared and their behaviour was observed during Period 1 in the same way as that of juveniles to determine if differences in the behaviour of mothers predicted the survival of their juveniles.

During each 10-min focal observation, the behaviour, exposure and location of the focal squirrel were recorded every 30 seconds. Behaviour was recorded as one of eight categories (following Stuart-Smith and Boutin 1995b): foraging (eating, caching, handling or searching for food), vocalizing (barking-an alarm call, rattling-a territorial call), traveling (moving quickly in trees or on ground), resting (motionless on a branch with head down and eyes partially closed or in the nest), interacting with another squirrel (playing, chasing, suckling), grooming, vigilant (silent and observant, often standing on hind legs with head up, infrequently foot stomping), and behaviour unknown (or squirrel out-of-sight). Exposure was recorded as one of six categories: in nest, tree-cover (within 1m of the trunk, hidden by branches and difficult to see), tree-exposed (further than 1m from the trunk, easily seen at the tree top or tips of branches), ground-cover (on ground no more than 2m from the tree trunk, under tree canopy), ground-exposed (on ground more than 2m from the tree trunk, in a clearing away from tree canopy), and exposure unknown (or squirrel out-of-sight). Locations were recorded to the nearest 3m on a 30m-interval grid system established in three 40ha patches of forest in the study area. Locations for observations off the grids were estimated by pacing back to the grid.

Individual Survival

Survival of juveniles was followed until weaning (65 – 70 days of age) through daily telemetry locations. From weaning until the end of the summer (August 31), survival was monitored through weekly trapping and casual observations on the grids. In addition, ownership of all middens was censused using these methods in August.

Data Analysis

For each focal observation, the number of instantaneous samples of each behaviour and of each exposure were divided by the total number of samples the squirrel was observed. These proportions were averaged over each period separately to give the average proportion of samples spent in a particular behaviour or a particular exposure for each individual during Period 1 and Period 2.

The location data for each individual was summarized as several movement indices. (1) For each focal, I calculated the proportion of locations that were on the individual's natal territory and averaged these for each period. This was an indication of the propensity of an individual to remain on their natal territory. (2) Though I tried to only observe behaviour when it appeared a squirrel was not responding to my presence, it is possible that over the course of a 10min observation period, a squirrel may have attempted to move me towards or away from their territory (e.g.,, mother trying to lure observer away from juveniles). To circumvent this potential problem, I used the first location from each focal observation to calculate the proportion of first locations that were on the individual's natal territory during each period. (3) Similarly using first location from each focal. I calculated the distance from that location to the natal midden location and averaged these distances for each period. This was used as an indication of the propensity of an individual to move away from their natal midden. The further an individual moved, the more likely it was to be in unfamiliar habitats or territories. (4) Finally, individuals will occasionally move off the natal territory to a consistent location (e.g., an off-territory nest location or feeding site) and thus may appear to move large distances from the natal midden, as summarized in the previous movement index. This relatively consistent movement pattern can be contrasted with an individual who moves off the natal territory to unpredictable locations. To discern the propensity of an individual to move around between consecutive focal observations, I calculated the distance from the first location of a focal to the first location of the previous focal and averaged these distances over each period.

Logistic regression (Glantz and Slinker 1990) was used to determine if differences in the proportion of time spent in each behaviour, exposure and movement (by mothers and juveniles) predicted survival for individual radio-collared juveniles. Following Stuart-Smith and Boutin (1995b), a separate logistic regression was performed for each behaviour, exposure and movement variable during each period. Additionally, all variables (behaviour, exposure and movement tested separately) were entered in a forward stepwise logistic regression to determine which variables were the most important determinants of survival. Survival was analyzed over two time periods: from emergence to weaning and from emergence to the end of the summer. All statistical analyses were performed using SPSS (Versions 7.5 or 8.0) and a significance level of $p \leq 0.05$, unless otherwise stated. Results with a p value of $p \leq 0.10$ were considered marginally significant.

RESULTS

The average date of emergence among nests with collared juveniles (n = 62) was 42 days of age (range: 35 - 49). Of the 81 collared juveniles, 65 (80%) survived to weaning and 50 (62%) survived until the end of summer. Preweaning survival was followed using telemetry and the main mortality source was found to be predation: Only

2/16 (12%) individuals were known to succumb to other natural causes (i.e., disease and exposure). Postweaning survival was followed using casual observations and regular trapping on the grids, as radio-collars were removed at weaning for rotation to other study individuals. Since most juveniles settle < 120m from their natal territory (Berteaux and Boutin, in press) and thus within the bounds of the study area, any disappearances (3/16) were assumed to indicate mortalities, most likely due to predation (Stuart-Smith and Boutin 1995a).

Sample sizes used in the logistic regression analyses are shown in Table 3.1. Correlations between behaviours of juveniles (Appendix III.1), exposures of juveniles (Appendix III.3), behaviours of mothers (Appendix III.2) and exposures of mothers (Appendix III.4) are presented and discussed in Chapter 2.

Juvenile Behaviour and Survival

Behaviour - Behavioural differences between surviving and depredated juvenile squirrels and the results from the corresponding single variable logistic regressions are shown in Figure 3.1 and Table 3.2, respectively. Juveniles spending more time foraging were significantly more likely to survive from emergence to weaning but there was no effect on survival from emergence to the end of the summer. There was no significant effect of proportion of time spent traveling on survival except that juveniles who spent more time traveling during Period 2 had lower survival to weaning. Differences between the proportion of time spent resting by individuals who survived and those who were eventually depredated were not significant. Very little time was spent vocalizing and though surviving juveniles vocalized slightly more than depredated juveniles, it was only significant for the effect of Period 1 vocalizations on survival from emergence to the end of summer. As juveniles spent more time interacting, their probability of survival increased, though it was only marginally significant for the effect of Period 1 interactions on survival from emergence to the end of the summer. Grooming, like vocalizing and interacting, was performed infrequently and was only positively related with survival to weaning for behaviour Period 2. Finally, juveniles spending more time vigilant during Period 1 had significantly lower survival from emergence to weaning and there was no effect on survival otherwise. When multiple logistic regressions were used to determine the strongest predictors of survival, the results were as follows (Table 3.3): survival from emergence to weaning was predicted by the proportion of time spent vigilant during Period 1 and the proportion of time spent traveling and resting during Period 2, while only the proportion of time spent vocalizing during Period 1 predicted survival from emergence to the end of summer.

Exposure - Juveniles spending more time in tree-cover during Period 1 had marginally higher survival from emergence to the end of the summer (Fig. 3.2). The proportion of time spent under tree-cover had no effect on survival otherwise (Table 3.4). The proportion of time spent in the tree-exposed and ground-cover categories did not significantly predict survival to the end of either survival period. Although the differences were only marginally significant, juveniles spending more time on ground-exposed during Period 1 had lower survival from emergence to the end of the summer while those spending less time on ground-exposed during Period 2 had lower survival from emergence to weaning. The proportion of time spent in the nest did not significantly predict survival to either weaning or the end of summer. If the tree-cover and ground-cover categories are combined to give an overall-cover variable, and tree-exposed and ground-exposed combined to give an overall-exposed variable, the results were similar to when the four variables were analyzed separately. No variables entered a multiple logistic regression as significant predictors of survival.

Movement - There were few differences between surviving and depredated juveniles in the movement variables (Fig. 3.3, Fig. 3.4). Neither the first location nor the average of all locations on the natal territory from Period 1 or 2 significantly predicted survival during either of the survival periods (Table 3.5). Only the average distance between focals during Period 2 significantly predicted survival from emergence to the end of the summer in both the single variable (Table 3.5) and multiple variable (model $\chi^2 = 6.806$, df = 1, p = 0.009) logistic regressions and no variables predicted survival from emergence to weaning.

Behaviour of Mothers and Juvenile Survival

Behaviour – The proportion of time spent foraging, vocalizing, interacting, grooming or vigilant by mothers did not significantly predict the survival of their juveniles from either emergence to weaning or to the end of summer (Fig 3.5, Table 3.6). Juveniles of mothers who traveled more tended to have with higher survival during both survival periods while mothers who rested more had juveniles with significantly lower survival from emergence to the end of summer. The only variable which was a significant predictor of survival from emergence to the end of summer in a multiple logistic regression was the proportion of time spent traveling (model $\chi^2 = 8.433$, df = 1, p = 0.004). No variables predicted survival from emergence to weaning.

Exposure - Mothers who spent more time in tree-cover had juveniles with significantly higher survival from emergence to weaning (Fig. 3.6, Table 3.7). Consistent and significant over both survival periods was the positive relationship between the proportion of time spent by mothers on ground-cover and juvenile survival. Mothers who spent more time in the nest had juveniles with significantly lower survival and mothers who spent proportionately more time under overall-cover had juveniles with significantly higher survival over both time periods. The proportion of time spent in tree-exposed, ground-exposed and overall-exposed by mothers did not predict the survival of juveniles. The multiple logistic regressions showed that the greater proportion of mothers' time spent under overall-cover, the higher the survival of offspring from emergence to weaning while the greater the proportion of mothers' time spent in the nest, the lower the survival of offspring from emergence to the end of the summer (Table 3.8).

Movement – There were no significant relationship between the proportion of first locations or the average proportion of a mother's locations on the territory and juvenile survival during either period (Fig. 3.7, Table 3.9). Juveniles with mothers who traveled less between focals tended to have higher survival from emergence to weaning (Fig. 3.8) but effect was only marginally significant (Fig. 3.8) and the distance of the mother to the natal midden was not a significant predictor of juvenile survival during either survival period. No movement variables entered the multiple logistic regression as significant predictors of survival.

DISCUSSION

This study indicates that the behaviour of both juveniles and mothers may predict juvenile survival from emergence to weaning and from emergence to the end of the summer. However, there was no single behaviour, exposure or movement variable that repeatedly appeared as a consistent predictor of survival. This study also suggests that the relationships between behaviour/exposure/movement and survival identified by Stuart-Smith and Boutin (1995b) may not be universal predictors of juvenile red squirrel survival.

Emergence of juvenile red squirrels from the natal nest was thought to occur at about 50 days of age (Smith 1968; Boutin and Larsen 1993; Stuart-Smith 1993; Larsen and Boutin 1994). Yet, two recent studies which determined the exact date of emergence found it to be 42 days (Humphries and Boutin 1996; this study). As Stuart-Smith and Boutin (1995b) found an average emergence date of 56 days of age, it is possible that they missed the emergence of most juveniles by up to two weeks. During the first two weeks after emergence juveniles spend around 70% of their time in the nest and when out of the nest, they are often sedentary and easily overlooked (E. Anderson, pers. obs.). All references in Stuart-Smith and Boutin (1995b) to 'days after emergence' should thus be adjusted by 14 days. In doing so, the dates at which juveniles were depredated are well after weaning. Hence their analysis of the effect of behaviour on survival from emergence to weaning must be interpreted cautiously and, perhaps more appropriately, as the effect of behaviour on survival from emergence to the end of summer.

Influence of Behaviour on Survival

The most consistent but unexpected behavioural difference between surviving and depredated juveniles in this study was the positive relationship between proportion of time spent foraging and juvenile survival. If survival is food-limited, juveniles spending more time foraging would be in better body condition and suffer death due to starvation less often than juveniles spending less time foraging. Since the number of starvation deaths is minimal (Stuart-Smith and Boutin 1995a; this study), this is likely not an appropriate explanation. It is becoming increasingly evident from both modeling and empirical studies that neither food availability nor predation can be considered as the single most important factor in population limitation (McNamara and Houston 1987; Desy et al. 1990; Sinclair and Arcese 1995) but rather often they interact to regulate animal numbers. This premise may apply here: less time spent foraging leads to food stress but this does not act as a direct mortality cause; instead, it acts indirectly to increase an individual's susceptibility to predation. However, I have no data on the body condition of surviving versus depredated juveniles and thus cannot relate proportion of time spent foraging to body condition.

Traveling, particularly off the natal territory, may be costly in terms of predation risk (Gaines and McClenaghan 1980; Daly et al. 1990; Larsen and Boutin 1994; Stuart-Smith and Boutin 1995b). This study did not find such a cost: the proportion of time spent traveling (during Period 2) only negatively influenced survival from emergence to weaning. Examining the low sample size (n = 4, Table 3.1) and large standard error (Fig. 3.1a) for depredated juveniles during this survival period, I suspect this result is under the strong influence of one or two juveniles who traveled extensively. In contrast, mothers who spent more time traveling had juveniles with significantly higher survival. Although traveling rapidly around the territory could be used by mothers to distract predators or alert offspring to potential danger, similar to alarm calling in ground squirrels (e.g., Shields 1980; Hoogland 1983; Sherman 1985), red squirrels seldom interact directly with their juveniles. A more plausible explanation is that mothers spending more time traveling secure additional territory, and thus food, resources for bequeathal to their offspring. This would subsequently allows for higher juvenile survival (Boutin et al. 1993; Berteaux and Boutin, in press).

Greater proportions of time spent resting or in the nest by mothers appeared to negatively affect juvenile survival. Although there are correlations between mother and juvenile resting behaviour (Appendix V.1), the proportion of juvenile time spent resting or in the nest did not significantly affect survival. Time spent in the nest is completely safe from predation and thus we would predict that juveniles who spend more time resting would be depredated less often (Stuart-Smith and Boutin 1995b). If mothers with juveniles who are eventually depredated are in poor body condition and not supplying adequate nourishment to their offspring (i.e., the juveniles are food stressed), these juveniles may be more susceptible to predation, as discussed above.

Influence of Exposure on Survival

Although there were several marginal results, there were no significant effects of juvenile exposure on survival from emergence to weaning or to the end of the summer. Since resting generally occurs in the nest, it is not surprising that the relationship between mother's nest exposure and juvenile survival is similar to that between mother's resting behaviour and juvenile survival. Additionally, the proportion of time spent under cover (tree, ground or overall) by mothers was a positive predictor of juvenile survival during both periods. This result may have been confounded by the availability of cover or density of trees on natal territories. Tree density on the natal territory may positively influence the survival of juveniles (Larsen 1993). As the natal territory and its available vegetation are common to family members, mothers who spent more time under cover, simply because they had proportionately more available, may have had juveniles with higher survival. Furthermore, the availability and use of more vegetation on some territories may explain why there were correlations between the proportion of time spent under cover for mothers and juveniles (Appendix V.2). If these results are simply due to the confounding effect of availability of vegetation, rather than an active behavioural decision to use less exposed locations, it is surprising that there was no effect of juvenile exposures on survival.

Influence of Movement on Survival

There was little influence of movements by either mothers or juveniles on survival from emergence to weaning or to the end of the summer. Only the average distance between focals showed any influence on survival with depredated juveniles traveling further between focals during Period 2 than survivors. Individuals who moved around more between focals may have been more conspicuous to predators thus suffering higher predation risk (FitzGibbon 1990; Skelly 1994; Martel and Dill 1995); however, the traveling behaviour data does not support this as it shows no effect of traveling on survival. It was surprising to find no survival cost of movement as Stuart-Smith and Boutin (1995b) found that juveniles spending more time off their natal territory were more likely to be depredated and Larsen and Boutin (1994) found the carcasses of most depredated juvenile squirrels off their natal territory.

The main predators of squirrels in this study also prey upon snowshoe hare (*Lepus americanus*). Stuart-Smith and Boutin's study (1995b) was conducted during 1992 when the population density of snowshoe hares crashed in Kluane, requiring the lingering high numbers of predators to switch to other food resources (Boutin et al. 1995). My study was conducted during 1997 and 1998, years of increasing and peak snowshoe hare densities (C. Krebs, unpubl. data) and likely high predator densities. Though predator numbers were high during both studies, the availability of their dominant prey was quite different. If red squirrels perceive high predator abundance as high predation risk, we would not predict any behavioural differences between the two studies. However, if the squirrels perceive high snowshoe hare abundance to result in a lower predation risk, we would predict squirrels to perform riskier behaviours more often during my study. Juveniles spent approximately the same amount of time in each behaviour and exposure category during both studies and thus did not behaviourally appear to perceive the different predation conditions.

Juveniles begin emergence completely reliant on their mothers for nourishment and shelter. By weaning, juveniles must be able to locate ample food to sustain themselves and complete growth. By the end of the summer, they need to have established their own territory to survive the winter (Larsen and Boutin 1994). Survival from emergence to weaning should be most strongly influenced by an individual's ability to avoid predators, particularly during the first days after emergence. The strongest predictors of survival from emergence to weaning were the proportion of time spent vigilant during Period 1 (early emergence) and the proportion of time spent traveling and resting during Period 2. However, traveling was the only behaviour which responded in the predicted direction. Survival from emergence to the end of summer should be influenced not only by the ability to avoid predation but also by an individual's ability to obtain adequate food and territory resources. These latter requirements would involve considerable foraging, vocalizing, traveling and interacting with neighbors, all potentially risky behaviours. Only the proportion of time spent vocalizing during Period 1 and the average distance moved between focals during Period 2 were significant predictors of survival from emergence to the end of the summer.

No strong behavioural predictors of survival appeared from any of these results. Stuart-Smith and Boutin (1995b) were able to detect significant behavioural predictors of juvenile survival based on a sample size of n = 15. Accordingly, my sample sizes should have been sufficiently large (n = 81) to detect predictors if they were present. These apparent conflicts between the results of our studies do not appear to be caused by differences in predation conditions or differences in methodology. Nonetheless, these discrepancies lead to questions about the universality of results that could not be replicated using the same population of red squirrels.

Finally, this study indicates the importance of testing the basic assumption of predation risk studies that individuals exposing themselves behaviourally to higher predation risk will have lower survival. My results indicate that this may not be the case and in fact the opposite situation may sometimes occur (e.g., juveniles spending more time in the nest had lower survival).

Table 3.1 Sample sizes used in logistic regression analyses.

	Period	Alive	Dead	*Total*
Emergence to weaning	1	65	16	81
	2	65	4	69
Emergence to end of summer	1	50	31	81
	2	50	19	69

Table 3.2 Results from single variable logistic regressions predicting the effect of juvenile behaviour on survival. See Table 3.1 for sample sizes. All df = 1. p values significant at $p \leq 0.05$ are underlined.

		Emergence to Weaning		Emergence to End Summer	
Period	Behaviour	χ^2	p value	χ^2	p value
1	Forage	4.590	0.032	0.040	0.842
	Vocalize	0.721	0.396	5.983	0.014
	Travel	0.441	0.507	0.226	0.634
	Rest	0.157	0.692	0.111	0.739
	Interact	0.651	0.420	2.929	0.087
	Groom	0.667	0.414	0.322	0.570
	Vigilant	5.084	0.024	2.126	0.145
2	Forage	4.522	0.034	2.585	0.108
	Vocalize	0.577	0.447	0.611	0.435
	Travel	4.011	0.045	1.566	0.211
	Rest	0.700	0.403	1.064	0.302
	Interact	0.758	0.384	1.848	0.174
	Groom	4.273	0.039	1.146	0.284
	Vigilant	1.440	0.230	1.862	0.172

Table 3.3 Results from multiple logistic regressions predicting the effect of juvenile behaviour on survival. The model χ^2 tests the null hypothesis that the coefficients of all variables in the model are not different from zero. The $\Delta\chi^2$ value tests the null hypothesis that the coefficient for that single variable is not different from zero. See Table 3.1 for sample sizes.

	Period	Variable entered first	Variable entered second	Model χ^2	df	p value
Emergence to weaning	1	Vigilant ($\Delta\chi^2$=5.085, p=0.024)		5.084	1	0.024
	2	Travel ($\Delta\chi^2$=4.336, p=0.037)		4.011	1	0.045
		Travel ($\Delta\chi^2$=11.288, p=0.001)	Rest ($\Delta\chi^2$=7.153, p=0.008)	9.007	2	0.011
Emergence to end summer	1	Vocalize ($\Delta\chi^2$=6.131, p=0.013)		5.983	1	0.014
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Table 3.4 Results from single variable logistic regressions predicting the effect of juvenile exposure on survival. See Table 3.1 for sample sizes. All df = 1.

Period	Exposure	Emergence to Weaning		Emergence to End Summer	
		χ^2	p value	χ^2	p value
1	Tree Cover	1.904	0.168	3.623	0.057
	Tree Exposed	0.842	0.359	2.095	0.148
	Ground Cover	0.179	0.672	0.001	0.970
	Ground Exposed	2.310	0.129	2.989	0.084
	Nest	0.008	0.931	0.004	0.951
	Cover	1.898	0.168	3.007	0.083
	Exposed	1.466	0.226	3.540	0.060
2	Tree Cover	0.292	0.589	0.366	0.545
	Tree Exposed	0.404	0.525	0.421	0.516
	Ground Cover	0.019	0.890	0.401	0.527
	Ground Exposed	3.626	0.057	0.642	0.423
	Nest	0.359	0.549	2.244	0.134
	Cover	0.191	0.663	0.955	0.329
	Exposed	3.436	0.064	1.124	0.289

Table 3.5 Results from single variable logistic regressions predicting the effect of juvenile movements on survival. See Table 3.1 for sample sizes. Pp1stlocterr = proportion of first locations on natal territory; Avgppterr = average proportion of locations on natal territory; Avgfocfoc = average distance from first location of one focal to first location of previous focal; Avgfocmid = average distance from first location of a focal to natal midden. All df = 1. p values significant at $p \leq 0.05$ are underlined.

		Emergence to Weaning		Emergence to End Summer	
Period	Movement	χ^2	p value	χ^2	p value
1	Pp1stlocterr	0.132	0.716	1.339	0.247
	Avgppterr	0.557	0.455	2.059	0.151
	Avgfocfoc	1.959	0.162	1.795	0.180
	Avgfocmid	0.204	0.652	0.114	0.736
2	Pp1stlocterr	0.083	0.773	0.532	0.466
	Avgppterr	0.085	0.770	0.440	0.507
	Avgfocfoc	1.254	0.263	6.806	$\underline{0.009}$
	Avgfocmid	0.183	0.669	0.111	0.739

Table 3.6 Results from single variable logistic regressions predicting the effect of mothers' behaviour during Period 1 in 1998 on juvenile survival. Sample size is 40 from both emergence to weaning and emergence to the end of summer. All df = 1. p values significant at $p \leq 0.05$ are underlined.

	Emergence to Weaning		Emergence to End Summer	
Behaviour	χ^2	p value	χ^2	p value
Forage	0.030	0.862	2.038	0.153
Vocalize	0.655	0.419	0.040	0.842
Travel	3.464	0.063	8.433	0.004
Rest	0.216	0.642	3.855	0.050
Interact	0.112	0.737	0.160	0.689
Groom	2.479	0.115	0.942	0.332
Vigilant	1.091	0.296	0.124	0.725

Table 3.7 Results from single variable logistic regressions predicting the effect of mothers' exposure during Period 1 in 1998 on juvenile survival. Sample size is 40 from both emergence to weaning and emergence to the end of the summer. All df = 1. p values significant at $p \leq 0.05$ are underlined.

	Emergence to Weaning		Emergence to End Summer	
Exposure	χ^2	p value	χ^2	p value
Tree Cover	2.828	0.093	1.591	0.207
Tree Exposed	0.805	0.370	0.011	0.918
Ground Cover	4.238	0.040	7.480	0.006
Ground Exposed	0.031	0.860	0.545	0.460
Nest	6.953	0.008	12.397	0.000
Cover	10.457	0.001	12.389	0.000
Exposed	0.328	0.567	0.232	0.630

Table 3.8 Results from multiple logistic regressions predicting the effect of mothers' exposure during Period 1 in 1998 on juvenile survival. The model χ^2 tests the null hypothesis that the coefficients of all variables in the model are not different from zero. The $\Delta\chi^2$ value tests the null hypothesis that the coefficient for that single variable is not different from zero. Sample size is 40 from both emergence to weaning and emergence to the end of summer.

	Variable entered first	Variable entered second	Model χ^2	df	p value
Emergence to weaning	Cover ($\Delta\chi^2$=12.660, p=0.000)		10.457	1	0.001
Emergence to end summer	Nest ($\Delta\chi^2$=12.942, p=0.000)		12.397	1	0.000

Table 3.9 Results from single variable logistic regressions predicting the effect of mothers' movements during Period 1 in 1998 on juvenile survival. Sample size is 40 from both emergence to weaning and emergence to the end of summer. Pp1stlocterr = proportion of first locations on natal territory; Avgppterr = average proportion of locations on natal territory; Avgfocfoc = average distance from first location of one focal to first location of previous focal; Avgfocmid = average distance from first location of a focal to natal midden. All df = 1.

	Emergence to Weaning		Emergence to End Summer	
Movement	χ^2	p value	χ^2	p value
Pp1stlocterr	0.295	0.587	0.043	0.835
Avgppterr	0.046	0.830	0.096	0.756
Avgfocfoc	2.667	0.102	1.408	0.235
Avgfocmid	1.005	0.316	1.660	0.198

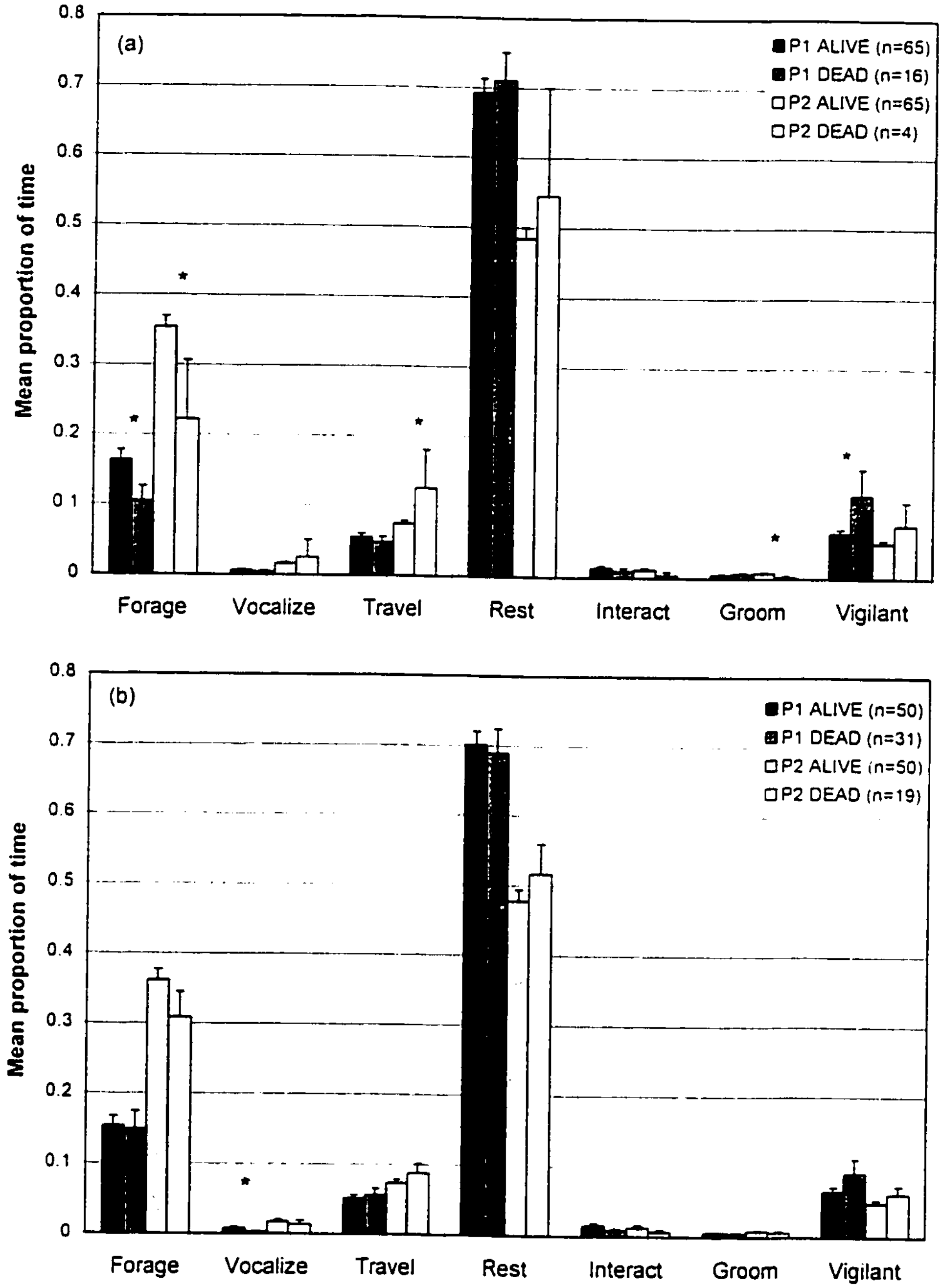

Figure 3.1 Mean (+SE) proportion of time spent in each behaviour during Period 1 (P1) and Period 2 (P2) for juveniles surviving from emergence to weaning (a) and to the end of the summer (b). Asterisks indicate differences that were identified as significant predictors of survival at $p \leq 0.05$ by single variable logistic regressions.

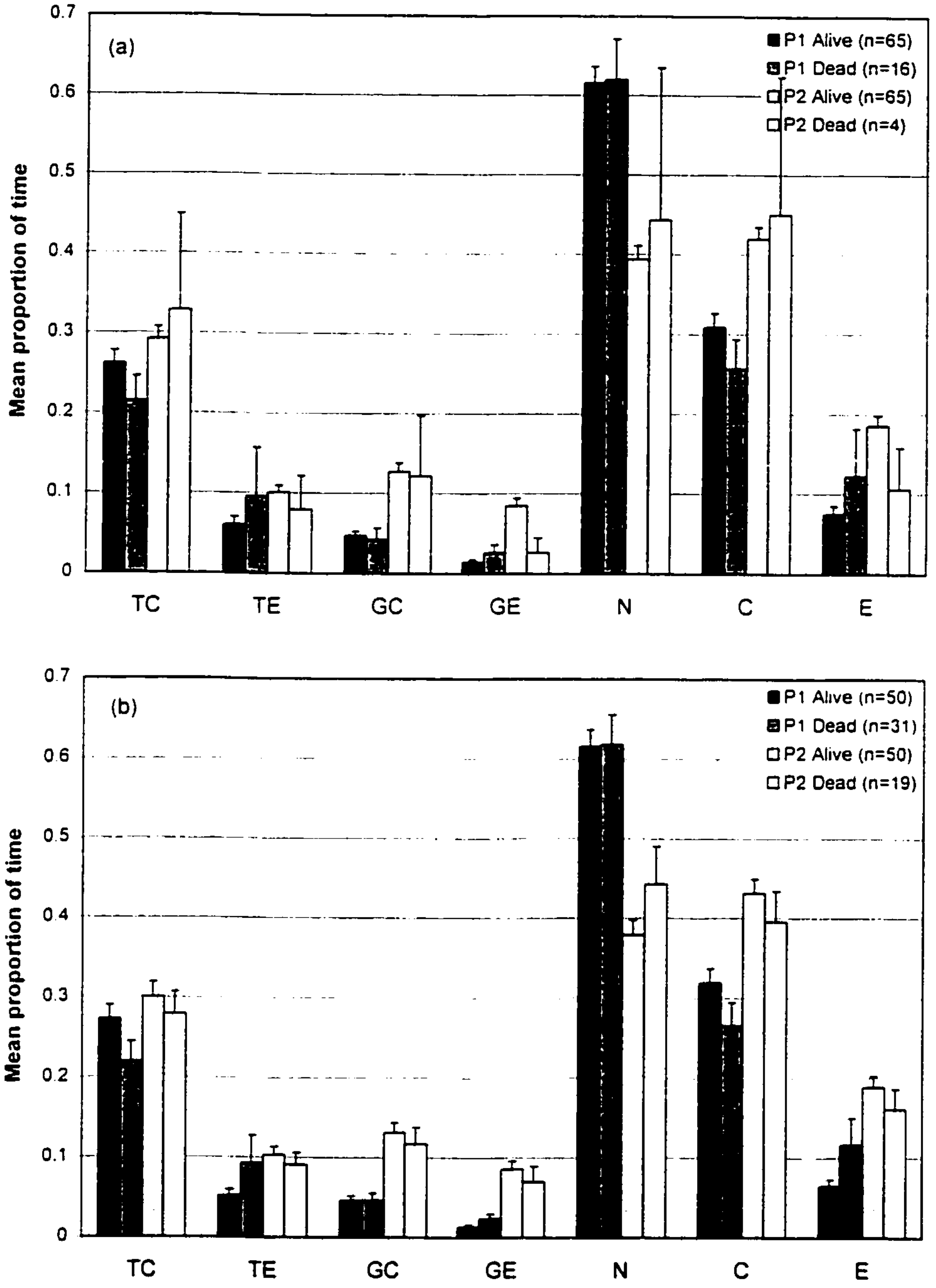

Figure 3.2 Mean (+SE) proportion of time spent in each exposure during Period 1 (P1) and Period 2 (P2) for juveniles surviving from emergence to weaning (a) and to the end of the summer (b). TC = Tree Cover; TE = Tree Exposed; GC = Ground Cover; GE = Ground Exposed; N = Nest; C = Overall Cover; E = Overall Exposed. No differences were identified as significant predictors of survival at p ≤ 0.05 by single variable logistic regressions.

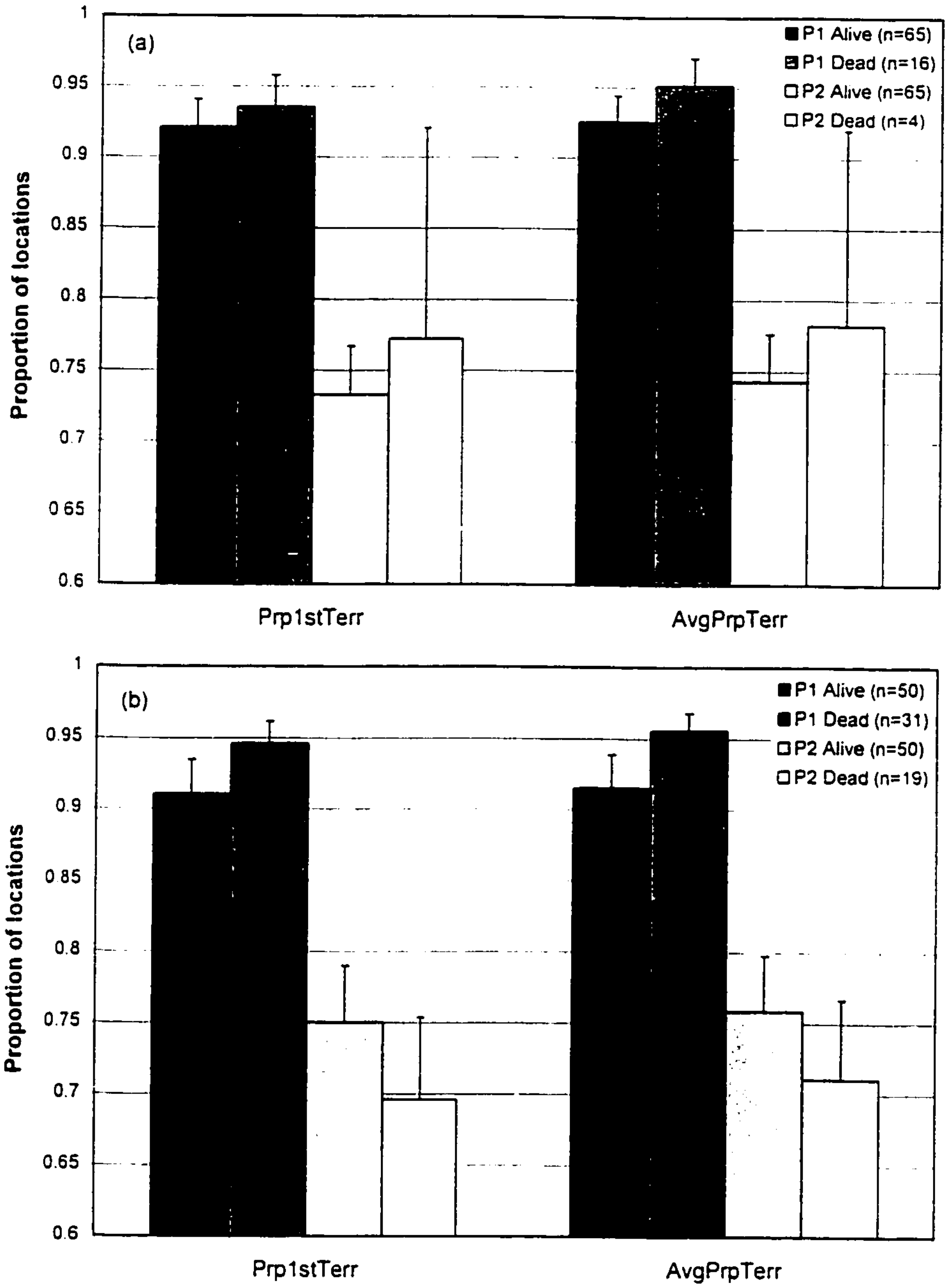

Figure 3.3 Mean (+SE) proportion of locations on the natal territory during Period 1 (P1) and Period 2 (P2) for juveniles surviving from emergence to weaning (a) and to the end of the summer (b). Prp1stTerr = proportion of first focal locations during a given period on the natal territory; AvgPrpTerr = average proportion of locations during a focal on the natal territory. No differences were identified as significant predictors of survival at $p \leq 0.05$ by single variable logistic regressions.

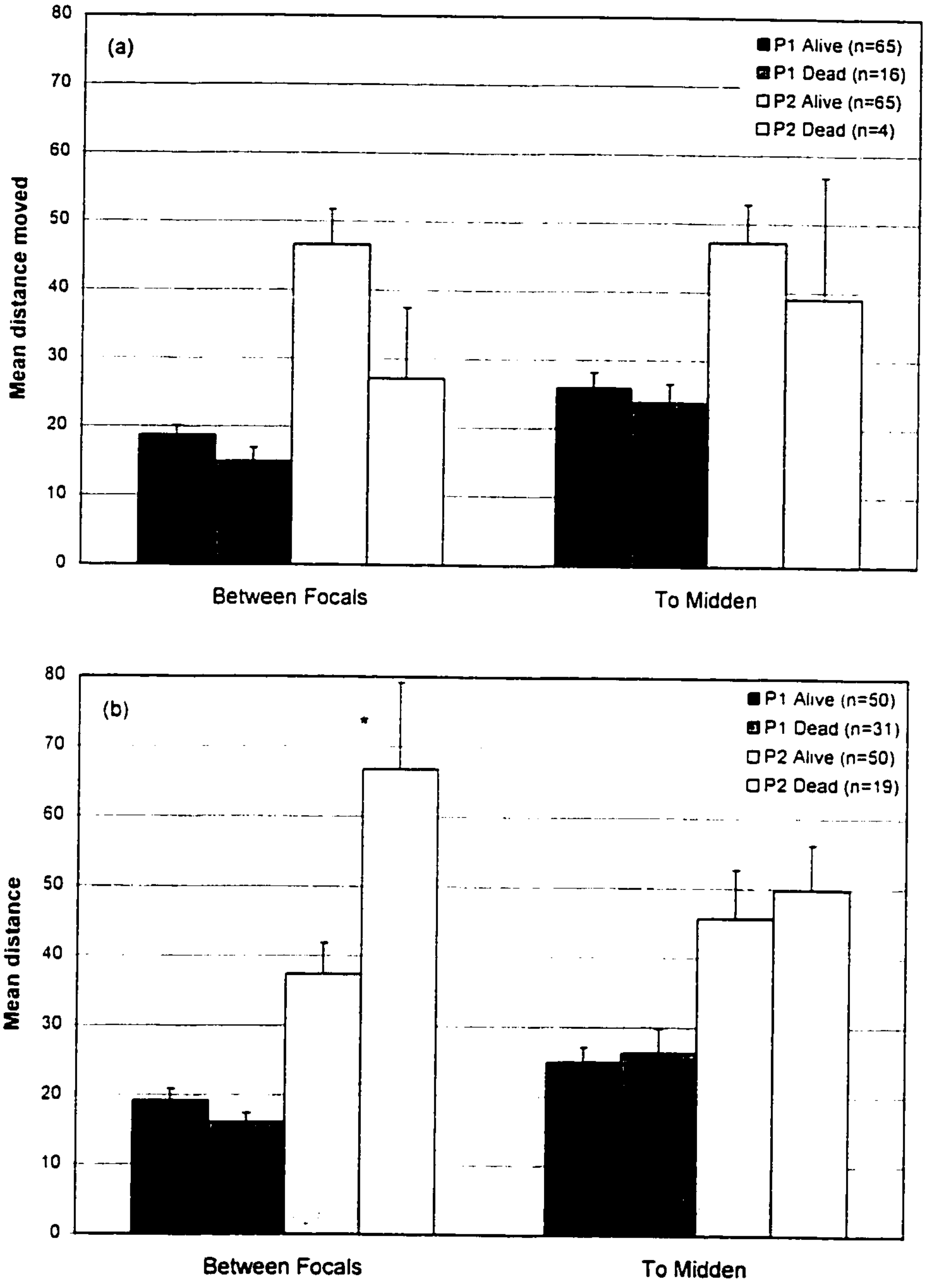

Figure 3.4 Mean (+SE) distance (m) moved between focals and from the first observation to the midden during Period 1 (P1) and Period 2 (P2) for juveniles surviving from emergence to weaning (a) and to the end of the summer (b). Asterisks indicate differences that were identified as significant predictors of survival at $p \leq 0.05$ by single variable logistic regressions.

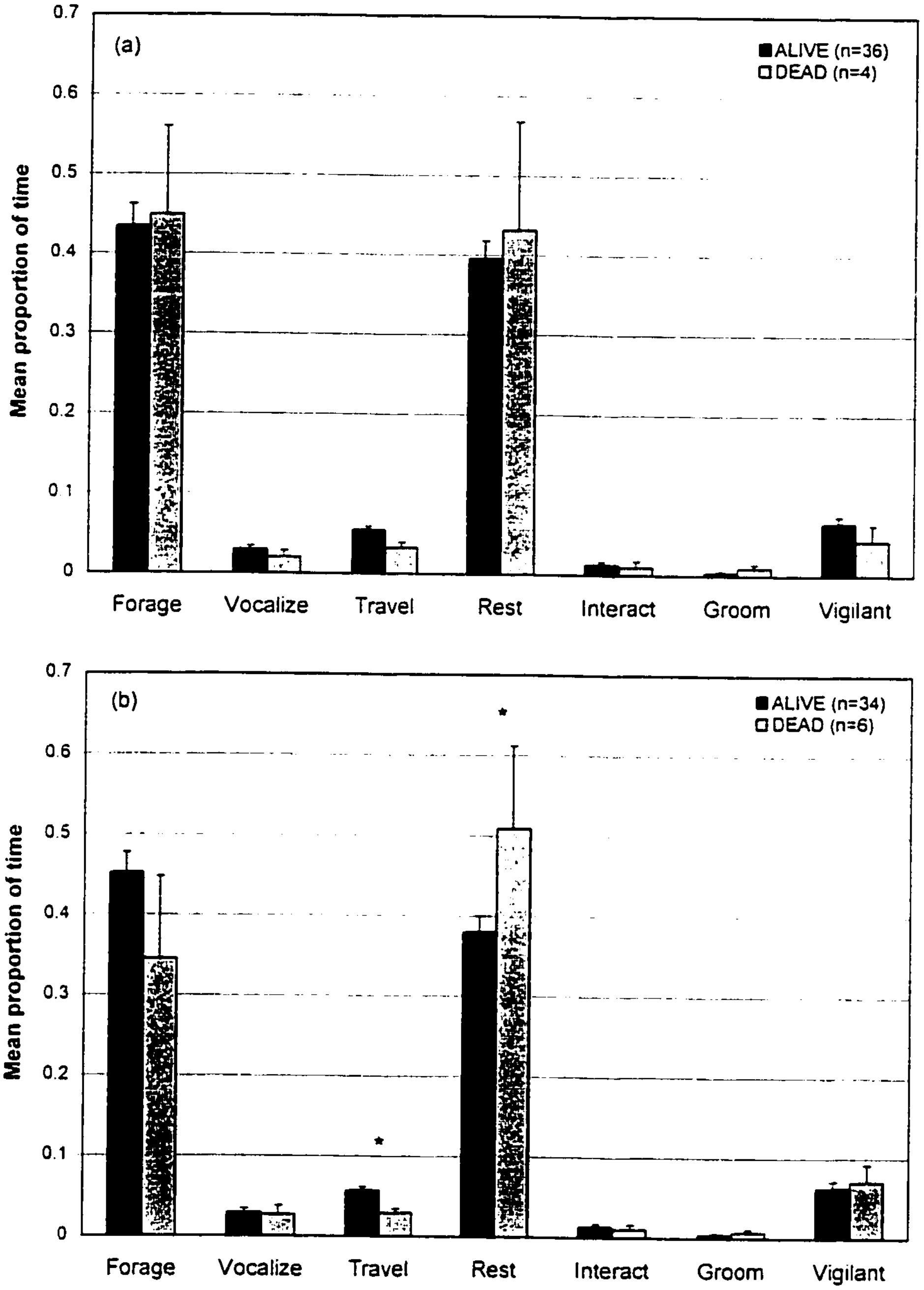

Figure 3.5 Mean (+SE) proportion of time spent by mothers in each behaviour during Period 1 in 1998 for juveniles surviving from emergence to weaning (a) and to the end of the summer (b). Asterisks indicate differences that were identified as significant predictors of survival at $p \leq 0.05$ by single variable logistic regressions.

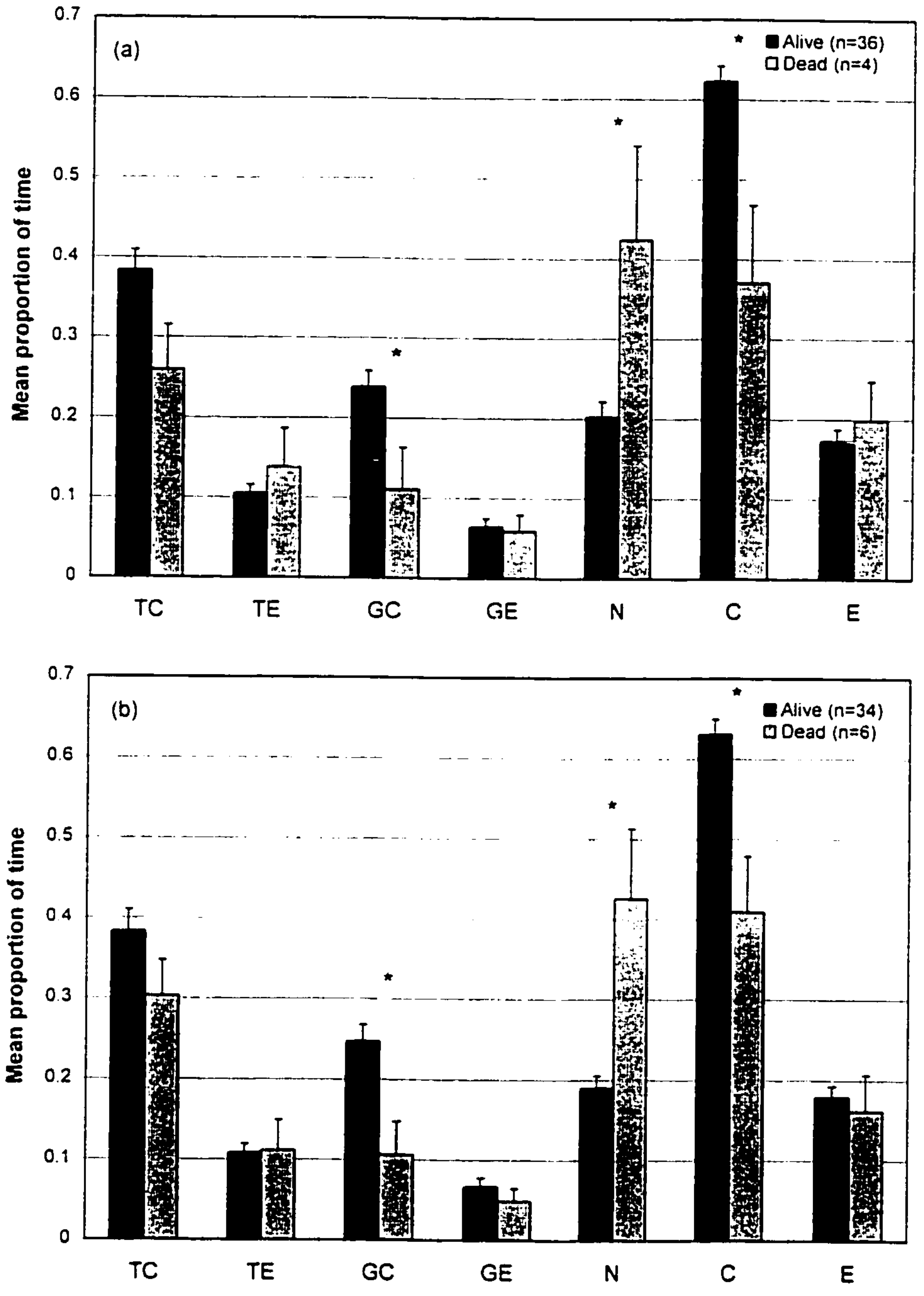

Figure 3.6 Mean (+SE) proportion of time spent in each exposure by mothers during Period 1 in 1998 for juveniles surviving from emergence to weaning (a) and to the end of the summer (b). TC = Tree Cover; TE = Tree Exposed; GC = Ground Cover; GE = Ground Exposed; N = Nest; C = Overall Cover; E = Overall Exposed. Asterisks indicate differences that were identified as significant predictors of survival at $p \leq 0.05$ by single variable logistic regressions.

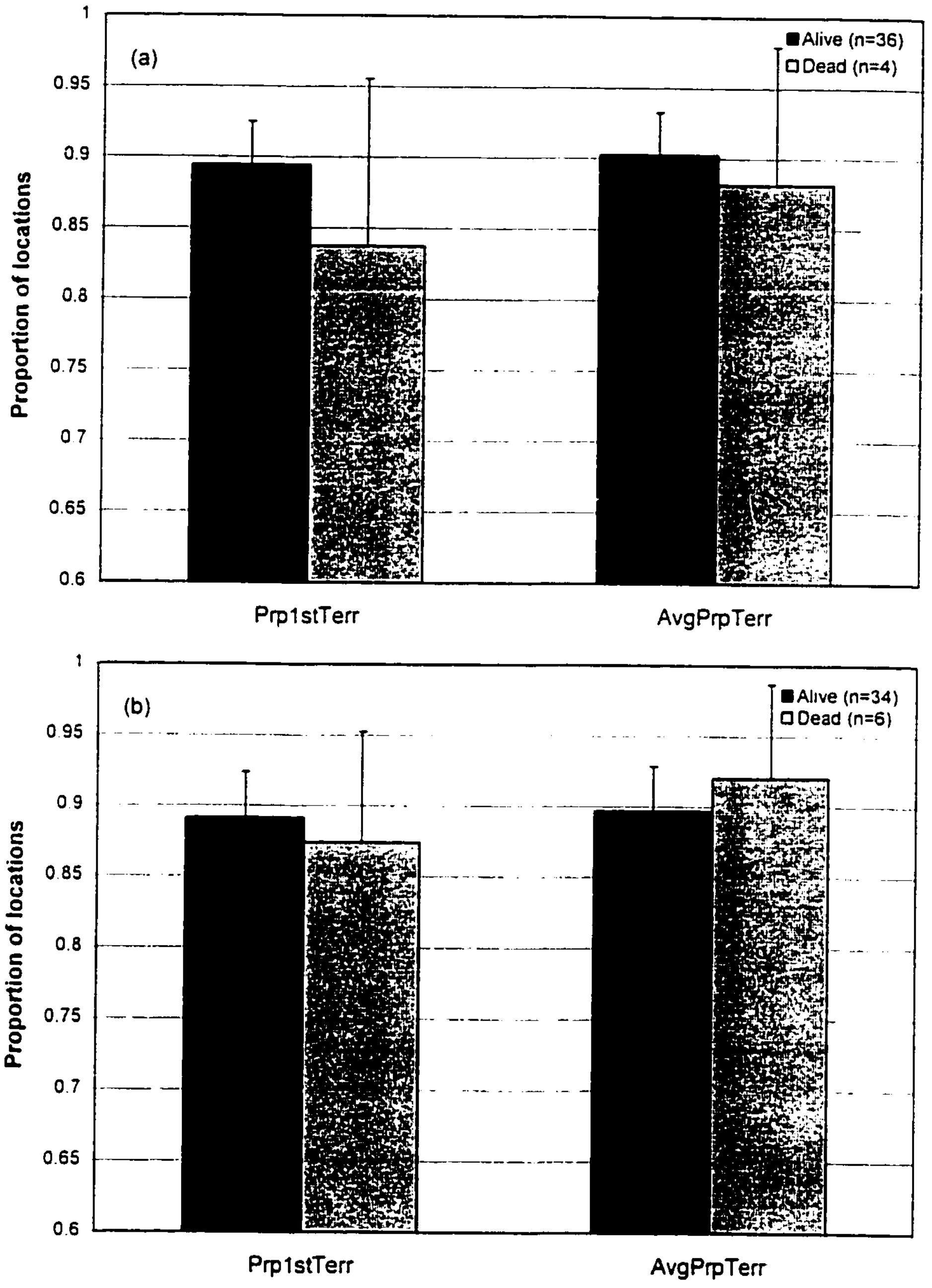

Figure 3.7 Mean (+SE) proportion of mothers' locations on the natal territory during Period 1 in 1998 for juveniles surviving from emergence to weaning (a) and to the end of the summer (b). Prp1stTerr = proportion of first locations during a given period on the natal territory; AvgPrpTerr = average proportion of locations during a focal on the natal territory. No differences were identified as significant predictors of survival at $p \leq 0.05$ by single variable logistic regressions.

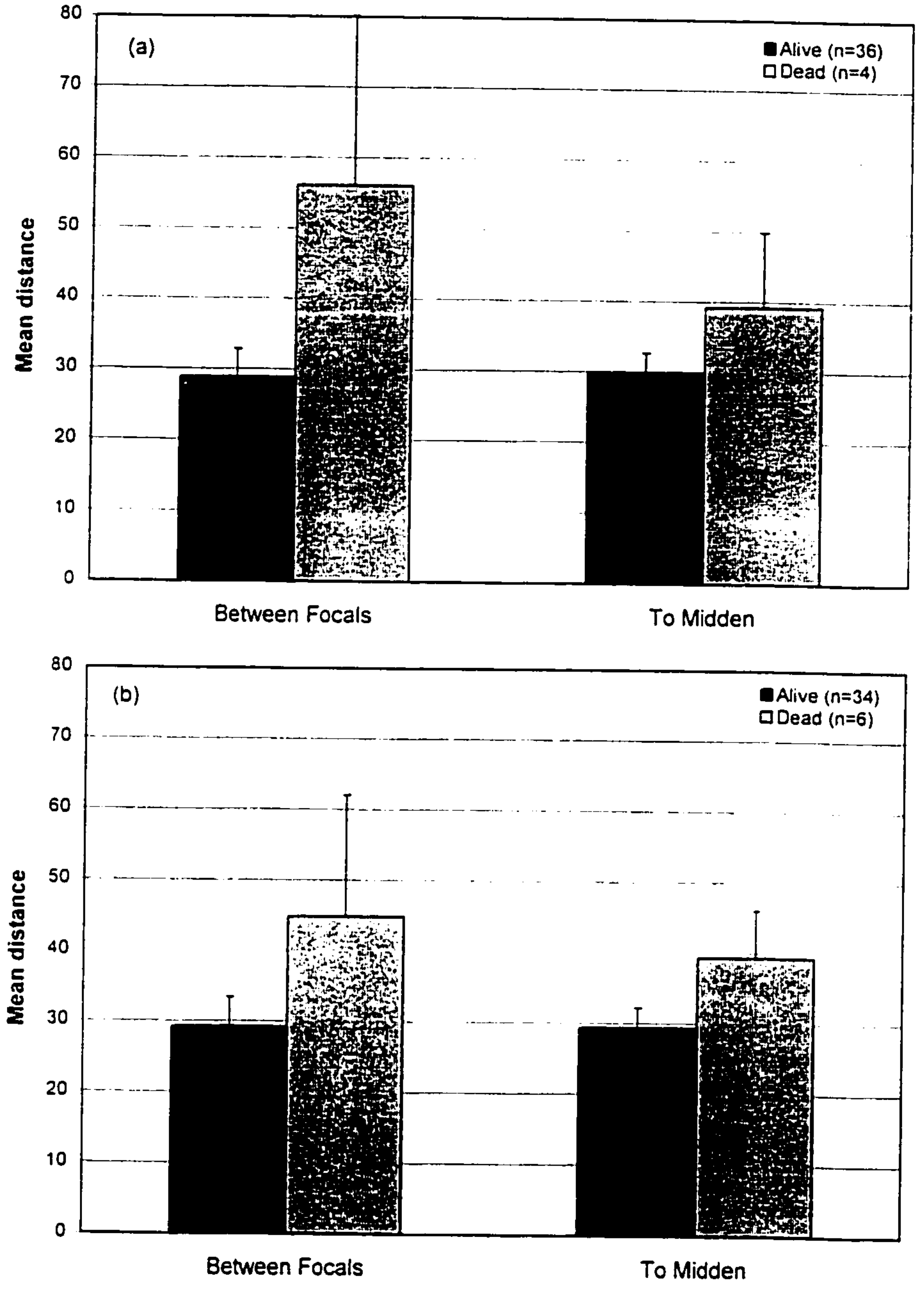

Figure 3.8 Mean (+SE) distance (m) moved between focals and from the first observation to the midden by mothers during Period 1 in 1998 for juveniles surviving from emergence to weaning (a) and to the end of the summer (b). No differences were identified as significant predictors of survival at $p \leq 0.05$ by single variable logistic regressions.

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CHAPTER 4 – GENERAL DISCUSSION

GENERAL CONCLUSIONS

This study found no significant effects of the forest edge on the survival or behaviour of juvenile red squirrels (Chapter 2). This lack of behavioural differences could arise from methodological problems with techniques for measuring the applicable behaviours, in particular vigilance, or from an inability to detect differences if they were indeed present. However, a more likely explanation is that there are no edge effects occurring in this population of squirrels. The local landscape is relatively patchy and individuals may be adapted to living in proximity to patch edges. In addition, the nature of the predator community in this system may be such that predation pressure is no higher on the forest edge than at the interior of the forest, requiring no behavioural compensation for increased risk.

Lack of differences, however, does not indicate lack of scientific contribution. One is often frustrated with statistical insignificance when in fact the phenomenon under scrutiny may not be relevant for the population or habitat in which it is being studied. This may be the situation with edge effects in the boreal forest. Recent research on bird nest predation (Huhta et al. 1998; Song 1998), small mammal abundance (Bayne and Hobson 1998) and now small mammal survival and behaviour failed to find differences between the edge and interior in studies conducted in the boreal forest. Edge effects may not be limit or otherwise influence populations living in the boreal forest. The value of this study may lie in the novel approach of applying a behavioural perspective to edge effect research. Although not present in this population of red squirrels, behavioural edge effects may exist in other species or other populations. This is especially pertinent with respect to the results of previous edge effect studies on nest predation. If parents living at the edge or interior of a habitat patch can adjust their nest provisioning behaviour according to the perceived level of predation risk, previous results on nesting success, particularly insignificant results, may acquire alternative interpretations.

This study did not find any behaviour, exposure or movement variables relating to either juveniles or their mothers to be strong or consistent predictors of juvenile survival from emergence to weaning and emergence to the end of the summer (Chapter 3). Stuart-Smith and Boutin (1995) found significant relationships between survival and the proportion of time spent resting, vigilant, travelling off the natal territory and in exposed locations. My results indicate a potential trade-off between the proportion of time spent resting, foraging and vigilant; however, the evidence is tenuous and precludes any sweeping generalizations.

Two of the basic premises of scientific investigation are repeatability of results and validation of assumptions. This study attempted to replicate the results of a single study (Stuart-Smith and Boutin 1995) and test a basic assumption underlying many predation risk studies (i.e. individuals performing risky behaviours will suffer higher predation-induced mortality). In neither ambition did I obtain the anticipated results: my results were not consistent with the work of Stuart-Smith and Boutin (1995) and individuals performing risky behaviours did not necessarily suffer higher predation rates. Admittedly, such discrepancies may be due to some factor specific to my study or years of data collection. Yet, we should not lose sight of the importance of testing the underlying premises of our scientific method, however unglamorous such studies may be.

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APPENDICES

Appendix I.1 Independence of littermate survival from birth to emergence tested using G-tests with Williams correction. The numbers in each category are the observed number of litters with that proportion of the litter surviving. The numbers in parentheses are the expected number of litters with that proportion of the litter surviving. p values significant at $p \leq 0.05$ are underlined.

Year	0.00-0.20	0.21-0.40	0.41-0.60	0.61-0.80	0.80-1.00	Total # of litters	Average proportion of litter surviving	G stat	df	p value
1987	1 (0.46)	0 (0.04)	0 (0.49)	0 (0.85)	19 (18.16)	20	0.95	0.428	4	0.980
1988	4 (0.43)	0 (1.07)	1 (2.48)	0 (6.56)	23 (17.46)	28	0.84	12.738	4	0.013
1989	6 (2.09)	2 (2.89)	0 (3.21)	5 (10.25)	26 (20.57)	39	0.77	8.321	4	0.081
1990	3 (1.58)	2 (1.62)	2 (4.58)	4 (5.41)	17 (14.81)	28	0.76	1.724	4	0.786
1991	4 (1.54)	3 (3.68)	4 (7.30)	10 (11.64)	27 (23.84)	48	0.76	2.359	4	0.670
1992	45 (23.95)	8 (31.05)	5 (12.48)	10 (12.37)	16 (4.15)	84	0.34	31.331	4	0.000
1993	14 (3.67)	10 (10.15)	6 (15.88)	9 (28.64)	46 (26.97)	85	0.69	26.786	4	0.000
1994	7 (1.91)	6 (6.28)	5 (8.69)	18 (28.86)	52 (42.25)	88	0.78	7.383	4	0.117
1995	37 (18.25)	7 (27.46)	10 (18.65)	16 (17.17)	19 (7.48)	89	0.43	26.875	4	0.000
1996	13 (3.49)	9 (11.05)	5 (13.63)	18 (30.51)	42 (28.31)	87	0.69	15.767	4	0.003
1997	11 (5.02)	11 (9.95)	8 (13.02)	9 (22.01)	37 (26.00)	76	0.67	10.849	4	0.028

Appendix I.2 Independence of littermate survival from emergence to weaning tested using G-tests with Williams correction. The numbers in each category are the observed number of litters with that proportion of the litter surviving. The numbers in parentheses are the expected number of litters with that proportion of the litter surviving.

Year	0.00-0.20	0.21-0.40	0.41-0.60	0.61-0.80	0.80-1.00	Total # of litters	Average proportion of litter surviving	G stat	df	p value
1987	5 (3.29)	1 (0.95)	0 (2.10)	0 (2.21)	13 (10.47)	19	0.70	5.512	4	0.239
1988	3 (1.18)	2 (2.21)	0 (2.75)	6 (6.82)	13 (11.04)	24	0.74	4.348	4	0.361
1989	0 (0.99)	2 (0.75)	2 (2.62)	6 (5.02)	23 (23.98)	33	0.87	1.702	4	0.790
1990	3 (3.25)	1 (0.90)	6 (5.35)	2 (2.19)	13 (13.31)	25	0.71	0.057	4	0.999
1991	3 (2.88)	4 (1.36)	7 (8.58)	2 (4.82)	28 (26.37)	44	0.78	2.587	4	0.629
1992	6 (4.65)	2 (2.86)	6 (6.79)	6 (6.94)	18 (16.76)	38	0.68	0.461	4	0.977
1993	5 (3.96)	4 (2.51)	12 (10.38)	5 (14.09)	45 (40.06)	71	0.79	5.138	4	0.273
1994	10 (7.38)	9 (8.53)	13 (15.02)	14 (19.13)	35 (30.94)	81	0.67	1.564	4	0.815
1995	2 (2.29)	2 (1.09)	3 (5.28)	9 (7.35)	37 (36.99)	53	0.85	0.999	4	0.910
1996	14 (9.95)	9 (8.37)	10 (17.47)	12 (14.81)	29 (23.40)	74	0.61	3.577	4	0.466
1997	10 (9.50)	3 (4.03)	12 (11.17)	10 (9.86)	30 (30.45)	65	0.68	0.192	4	0.996

Appendix II.1 Results of *t*-tests between observed and random littermate pairs in the difference of the mean proportion of time spent in each behaviour during each period separately. *t*-tests were performed on arcsin $\sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined.

Period	Behaviour	*t* statistic	df	p value
1	Forage	-1.331	38	0.191
	Vocalize	-0.459	38	0.649
	Travel	-2.343	38	0.024
	Rest	-0.748	38	0.459
	Interact	0.112	38	0.911
	Groom	-0.083	38	0.934
	Vigilant	-1.197	38	0.239
2	Forage	-2.296	28	0.029
	Vocalize	0.126	28	0.901
	Travel	0.011	28	0.991
	Rest	0.558	28	0.581
	Interact	0.528	28	0.602
	Groom	-0.890	28	0.381
	Vigilant	-0.615	28	0.543

Appendix II.2 Results of *t*-tests between observed and random littermate pairs in the difference of the mean proportion of time spent in each exposure during each period separately. *t*-tests were performed on arcsin √p transformed data.

Period	Behaviour	*t* statistic	df	p value
1	Nest	-1.158	38	0.254
	Tree Cover	-0.511	38	0.612
	Tree Exposed	-0.490	38	0.627
	Ground Cover	-0.417	38	0.679
	Ground Exposed	0.042	38	0.967
2	Nest	-1.712	28	0.098
	Tree Cover	-0.752	28	0.458
	Tree Exposed	-0.283	28	0.780
	Ground Cover	-0.521	28	0.607
	Ground Exposed	-0.450	28	0.657

Appendix III.1 Pearson correlation coefficients for the correlations between juvenile behaviours. Period 1 values (n = 61) lie above the diagonal and Period 2 values (n = 53) lie below the diagonal. Correlations were performed on arcsin √p transformed data using one juvenile per nest. * $p \leq 0.05$; ** $p \leq 0.01$.

	Forage	Vocalize	Travel	Rest	Interact	Groom	Vigilant
Forage		-0.091	0.575**	-0.667**	0.311*	0.340**	-0.172
Vocalize	0.138		0.105	-0.050	-0.134	0.056	0.161
Travel	0.134	0.336*		-0.580**	0.212	0.342**	-0.052
Rest	-0.869**	-0.315*	-0.503**		-0.261*	-0.338**	-0.538**
Interact	-0.112	0.031	0.056	0.008		0.077	-0.083
Groom	-0.103	-0.169	-0.091	0.168	0.341*		0.012
Vigilant	-0.395**	-0.237	0.064	0.154	-0.189	-0.344*	

Appendix III.2 Pearson correlation coefficients for the correlations between behaviours of mothers during Period 1 in 1998 (n = 38). Correlations were performed on arcsin $\sqrt{p}$ transformed data. * $p \leq 0.05$; ** $p \leq 0.01$.

	Forage	Vocalize	Travel	Rest	Interact	Groom
Forage						
Vocalize	-0.076					
Travel	-0.151	0.237				
Rest	-0.903**	-0.188	-0.020			
Interact	-0.110	-0.151	-0.263	0.084		
Groom	0.013	0.311	-0.041	-0.068	-0.158	
Vigilant	-0.362*	0.287	0.075	0.015	-0.049	-0.026

Appendix III.3 Pearson correlation coefficients for the correlations between juvenile exposures. Period 1 values (n = 61) lie above the diagonal and Period 2 values (n = 52) lie below the diagonal. Correlations were performed on arcsin √p transformed data using one juvenile per nest. * $p \leq 0.05$; ** $p \leq 0.01$.

	Nest	Tree Cover	Tree Exposed	Ground Cover	Ground Exposed
Nest		-0.422**	-0.657**	-0.162	-0.042
Tree Cover	-0.400**		-0.287*	0.196	-0.029
Tree Exposed	-0.306*	-0.006		-0.155	-0.147
Ground Cover	-0.363**	-0.341*	-0.159		0.533**
Ground Exposed	-0.306*	-0.466**	-0.071*	0.347*	

Appendix III.4 Pearson correlation coefficients for the correlations between exposure of mothers during Period 1 in 1998 ($n = 38$). Correlations were performed on arcsin $\sqrt{p}$ transformed data. * $p \leq 0.05$; ** $p \leq 0.01$.

	Nest	Tree cover	Tree exposed	Ground cover
Nest				
Tree Cover	-0.526**			
Tree Exposed	-0.070	0.137		
Ground Cover	-0.299	-0.477**	-0.461**	
Ground Exposed	-0.147	-0.446**	-0.367*	0.379*

Appendix IV.1 Pearson correlation coefficients for the correlations between Period 1 and Period 2 juvenile behaviour ($n = 69$). Correlations were performed on arcsin $\sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined.

Behaviour	Correlation coefficient	p value
Forage	0.299	<u>0.013</u>
Vocalize	0.076	0.535
Travel	0.214	0.078
Rest	0.487	<u>0.000</u>
Interact	0.036	0.766
Groom	0.067	0.584
Vigilant	0.090	0.460

Appendix IV.2 Pearson correlation coefficients for the correlations between Period 1 and Period 2 juvenile exposure ($n = 69$). Correlations were performed on arcsin $\sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined.

Exposure	Correlation coefficient	p value
Tree Cover	0.175	0.151
Tree Exposed	0.273	0.023
Ground Cover	0.430	0.000
Ground Exposed	0.325	0.006
Nest	0.412	0.000
Cover-Overall	0.228	0.060
Exposed-Overall	0.129	0.290

Appendix IV.3 Pearson correlation coefficients for the correlations between Period 1 and Period 2 juvenile movement ($n = 69$). Correlations were performed on arcsin $\sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined.

Movement	Correlation coefficient	p value
Prop. of 1st locations on territory	0.360	0.002
Avg. prop. of locations on territory	0.437	0.000
Avg. distance from focal to focal	0.060	0.623
Avg. distance from focal to midden	0.151	0.215

Appendix V.1 Pearson correlation coefficients between juvenile Period 1 or Period 2 behaviour and mothers' behaviour during Period 1 in 1998. Sample sizes are 40 and 36 during Periods 1 and 2, respectively. Correlations were performed on arcsin $\sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined.

	Period 1		Period 2	
Behaviour	Correlation coefficient	p value	Correlation coefficient	p value
Forage	0.367	0.020	0.003	0.985
Vocalize	0.213	0.188	0.097	0.575
Travel	0.363	0.021	0.062	0.720
Rest	0.475	0.002	-0.046	0.791
Interact	0.151	0.352	-0.080	0.644
Groom	0.209	0.195	0.194	0.257
Vigilant	0.370	0.019	0.364	0.029

Appendix V.2 Pearson correlation coefficients between juvenile Period 1 or Period 2 exposure and mothers' exposure during Period 1 in 1998. Sample sizes are 40 and 36 during Periods 1 and 2, respectively. Correlations were performed on $\arcsin \sqrt{p}$ transformed data. p values significant at $p \leq 0.05$ are underlined.

	Period 1		Period 2	
Exposure	Correlation coefficient	p value	Correlation coefficient	p value
Tree Cover	0.294	0.069	0.280	0.098
Tree Exposed	0.206	0.209	0.372	0.026
Ground Cover	0.397	0.012	0.389	0.019
Ground Exposed	0.219	0.180	0.186	0.277
Nest	0.175	0.287	0.210	0.218
Cover-Overall	0.397	0.012	0.229	0.179
Exposed-Overall	-0.008	0.963	0.164	0.347

Appendix V.3 Pearson correlation coefficients between juvenile Period 1 or Period 2 movement and mothers' movement during Period 1 in 1998. Sample sizes are 40 and 36 during Periods 1 and 2, respectively. Correlations were performed on arcsin √p transformed data. p values significant at $p \leq 0.05$ are underlined.

	Period 1		Period 2	
Movements	Correlation coefficient	p value	Correlation coefficient	p value
Prop. of 1st locations on territory	0.255	0.112	0.177	0.303
Avg. prop. of locations on territory	0.095	0.561	0.061	0.925
Avg. distance from focal to focal	0.116	0.477	-0.212	0.214
Avg. distance from focal to midden	0.364	0.021	-0.144	0.403