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Proc. R. Soc. B 2009 **276**, 3361-3367 first published online 1 July 2009

doi: 10.1098/rspb.2008.1958

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Mortality risk increases with natal dispersal distance in American martens

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The assumption that mortality risk increases with dispersal distance has rarely been tested. We compared patterns of natal dispersal in the American marten (*Martes americana*) between a large regenerating forest landscape and an uncut landscape that was dominated by more mature forest to test whether mortality risk increased with dispersal distance, and whether variation in mortality risk influenced dispersal distance. Mortality risk increased with dispersal distance in both landscape treatments, but the distance-dependent increase in mortality in the regenerating landscape was twice that in the uncut landscape. Differences in body condition, supported by other data on foraging efficiency, suggested that juveniles from the regenerating landscape were less able to cope with the energetic demands of dispersal compared with juveniles from older forests. Juveniles travelled shorter distances in the regenerating versus uncut landscape. These results implied that dispersal was costly in terms of juvenile survival and that mean dispersal distance was shaped, in part, by mortality risk.

Keywords: dispersal; survival; Cox proportional hazard model; commercial trapping; refuges; boreal forest

1. INTRODUCTION

The movement of juveniles across landscapes (natal dispersal, *sensu* Greenwood 1980) is a key factor influencing population demography. The shape of the distribution of natal dispersal distances can determine the rates of population spread and recruitment, with a strong impact on population persistence (Botsford *et al.* 2001; Bowler & Benton 2005; Ronce 2007; Phillips *et al.* 2008). Our ability to explain variation in dispersal distances across species and under changing conditions is limited, however, because the fitness costs of dispersal remain largely unknown (Bowler & Benton 2005; Ronce 2007).

Most studies have reported that the distribution of natal dispersal distances is leptokurtic, with relatively few juveniles moving long distances and most moving short distances (Wiens 2001; Rousset & Gandon 2002; Bowler & Benton 2005; Ronce 2007). Many researchers have suggested that short-distance dispersal is selectively advantageous because of high fitness costs incurred while in transit (Murray 1967; Waser 1985; Rousset & Gandon 2002; Stamps *et al.* 2005; Stamps 2006). Increased time and energy investment, coupled with increased risk of predation, is thought to reduce the probability of survival among long distance dispersers. Accordingly, most juveniles should settle close to the natal area to reduce the risk of dying (Murray 1967;

Waser 1985; Rousset & Gandon 2002). A corollary of this hypothesis is that dispersers should move shorter distances when mortality risks are elevated.

We compared patterns of dispersal by a mustelid carnivore, the territorial American marten (*Martes americana*), in two boreal forest landscapes in northern Ontario, Canada, to assess the impact of mortality risk on dispersal distances. Conifer forests of 80 or more years old dominated the uncut landscape, whereas the regenerating landscape was younger by comparison, having been logged and replanted 20–60 years ago. Several field studies suggest that forests older than 80 years provide better marten habitat than younger forests (Buskirk & Powell 1994; Thompson & Harestad 1994). Adult densities are higher in mature forest than in younger forest (Thompson & Colgan 1987; J. Fryxell, I. Thompson & J. Baker 2001–2005, unpublished data). Martens are more successful at obtaining prey (Andruskiw *et al.* 2008) and experience lower mortality (Thompson 1994) when living in more mature forests.

Juvenile martens disperse from their natal territory at 4–6 months of age and dispersal can take longer than four months to complete (Johnson 2008). Juvenile martens must forage during dispersal because they have limited fat reserves (Brown & Lasiewski 1972; Buskirk & Harlow 1989). Given that martens hunt less efficiently in younger forests than older forests, we predicted that martens should have shorter dispersal distances in a landscape dominated by regenerating forests compared to an uncut, mature forest landscape. Poor body condition, whether an artefact of maternal condition, juvenile condition prior to dispersal or reduced foraging efficiency

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during dispersal, should exacerbate energetic costs and reduce a disperser's ability to survive dispersal and find and compete for suitable areas for settlement (Holekamp 1984, 1986; Barbraud *et al.* 2003; Stamps *et al.* 2005; Stamps 2006).

Juvenile martens were live-captured, immobilized and equipped with radio-collars during dispersal (Johnson 2008). We defined all juveniles as dispersers due to variation in capture times and because adult marten territoriality probably pre-empts philopatry under most circumstances. We tested for overall differences in juvenile body condition between landscapes, predicting poorer body condition in the regenerating landscape than in the uncut landscape. We compared the distribution of dispersal distances to test whether dispersal distance was shorter in the regenerating landscape than in the uncut landscape. We then used Cox proportional hazard models to test whether mortality risk increased with dispersal distance and to identify factors that influenced variation in mortality risk between the regenerating landscape and the uncut landscape. More specifically, we predicted that mortality risk should increase with dispersal distance in both landscapes because of the accumulated energetic costs associated with movement, but that the risk should be greater for juveniles from the regenerating versus uncut landscape owing to poor body condition.

Martens are commercially harvested for their fur. The commercial harvesting of martens has been shown to have a profound effect on juvenile recruitment (Hodgman *et al.* 1994; Thompson 1994). Dispersing juveniles may be particularly vulnerable to commercial harvesting because of increased hunger and an increased probability of encountering traps that are baited with food. To reduce the impact of this, we paid trappers in our study areas to suspend marten trapping for the duration of the study. Non-trapping refuges were used to minimize the effects of commercial trapping on our study populations. We, nevertheless, expected some juveniles to disperse beyond the boundaries of the non-trapping zone. We evaluated the vulnerability of juveniles to commercial harvesting and the efficacy of non-trapping refuges at reducing disperser mortality in both landscapes.

2. MATERIAL AND METHODS

The study was conducted on two large landscapes of the boreal forest near the town of Ear Falls, Ontario, Canada (50°38' N, 93°13' W; figure 1). The uncut landscape (approx. 1800 km²) was composed mostly of forests 80 or more years old with some recent timber clear-cutting. The regenerating landscape (approx. 1900 km²) was younger, having been selectively logged and clearcut 20–60 years earlier with small remnant patches of mature forest representing less than 20 per cent of the landscape (Thompson *et al.* 2007).

Commercial fur trappers in both landscapes were contacted at the onset of the study and most agreed not to harvest martens within core areas of the study site during 2001–2004. The size and number of the non-trapping refuges differed between the landscapes. There was one large refuge measuring 590 km² in the uncut landscape and two smaller refuges in the regenerating landscape, measuring 260 km² in total.

Juveniles were live-trapped in both landscapes from August 2001 to November 2005. Over 80 per cent (950 out of 1181)

of the live traps were located in the non-trapping refuges. We included all live-trapping data in our analysis because restricting the analysis to juveniles captured in the refuges yielded qualitatively similar results (Johnson 2008). Animals were sedated with a ketamine–xylazine mixture. Their sex, body length (cm) and mass (g) were recorded, and the first lower premolar was extracted for cementum ageing (Archibald & Jessup 1984). Young martens are born in March–April and mature sexually, at the earliest, in their second summer of life (greater than 1 year old; Thompson & Colgan 1987). We defined juvenile martens as animals 1 year old or less and adults as greater than 1 year old, using 1 May to designate juvenile transition to adulthood (Smith & Schaefer 2002). Martens were fitted with 30 g radio collars prior to their release. Radio-collared animals were monitored via ground and/or aerial telemetry until December 2005. Commercial fur trappers from both landscapes provided additional information about the fate of radio-collared animals, including the time and location of death, until February 2006.

We used an individual's mass adjusted for body length as an index of body condition. Mass and length measurements were available for 194 juveniles (regenerating landscape: $n = 94$; uncut landscape: $n = 100$). We tested for differences in body condition between juvenile martens using ANCOVA, with body length as a covariate (García-Berthou 2001) and sex as an independent variable because marten body size is sexually dimorphic.

We defined natal dispersal distances operationally as the Euclidean (straight line) distance between a juvenile's first capture location and where it died or was first located as an adult (i.e. greater than 1 year old). Dispersal distances were calculated for all juveniles. We provide the diameter of adult female home ranges in the uncut (2.9 km) and regenerating (1.9 km) landscapes as a reference for interpreting juvenile dispersal distances. Individual dispersal distances were calculated for 111 juvenile marten from the uncut landscape (48 females, 63 males) and for 92 juveniles from the regenerating landscape (48 females, 44 males).

We first compared observed distributions of natal dispersal distances between the sexes within each landscape because patterns of dispersal are generally male biased in polygynous mammals like martens (Greenwood 1980; Dobson 1982). We then compared the distributions of natal dispersal distances between the landscapes using two datasets: first including all juveniles and second solely juveniles known to have survived to adulthood. The latter analysis allowed us to test whether short dispersal distances were an artefact of juveniles dying in transit, before completing the process of dispersal, and to assess how many juveniles survived the settlement period.

We tested whether dispersal distributions differed between the landscapes using bootstrapping, because this offers a more powerful alternative to non-parametric tests (Manly 1991). Chi-squared statistics were used to quantify the differences between landscape distributions. We used the uncut landscape to generate the null distribution because old-growth forests represent undisturbed marten habitat (Buskirk & Powell 1994; Thompson & Harestad 1994). We used a similar procedure for the comparison between the sexes within each landscape, using data from juvenile males to generate the null distribution.

We used Cox proportional hazard models to identify factors influencing variation in mortality risk between the landscapes (Murray 2006). Cox proportional hazard models

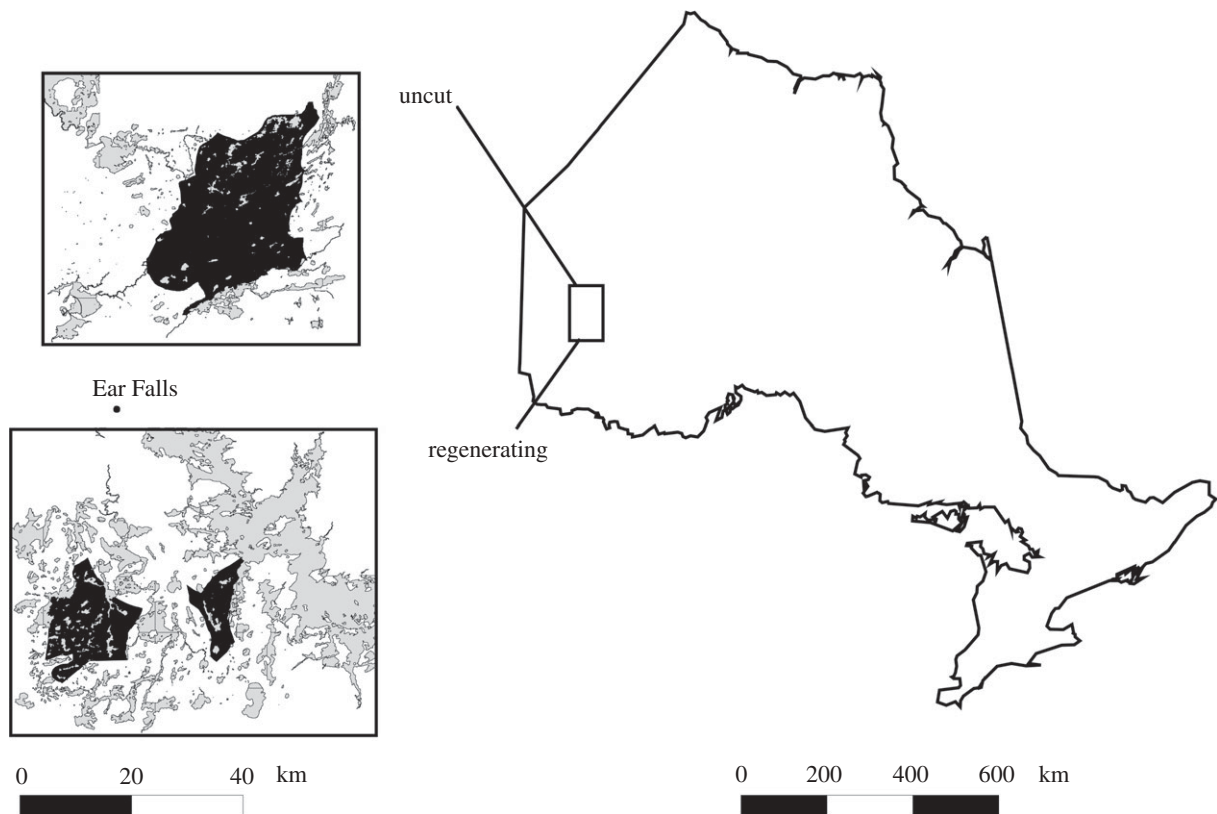


Figure 1. Location of study area and the uncut versus regenerating landscape. Grey, water; black, non-trapping refuges.

are often used to evaluate the instantaneous risk of mortality at a given time (t), conditional on survival to that time (x_i)

$$h_1(t) = h_0(t) \exp(\beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_p x_{ip}),$$

with h_0 denoting the estimated hazard rate per unit of time in the absence of any covariates (termed the baseline hazard rate) and β_p the effect of covariates included in the model (Murray 2006).

We included a Cox model testing changes in the baseline hazard rate as a function of time spent dispersing (Model 1, table 1). We substituted time for dispersal distance (d) to create a model evaluating changes in the baseline hazard rate per unit distance ($h_0(d)$) (Model 2, table 1). We predicted that dispersal distance should explain more variation in disperser mortality risk for juvenile martens than time owing to the accumulation of energetic costs associated with long distance movement.

All other Cox models developed included landscape, body condition and/or sex as covariates to evaluate their relative effects on the mortality risk associated with dispersal distance (table 1). We hypothesized that mortality risk should increase with dispersal distance in both landscapes, but that reduced foraging efficiency (Andruskiw *et al.* 2008) during dispersal would increase the mortality risk for juveniles in the regenerating landscape compared with those in the uncut landscape (Model 3, table 1). Several studies have implicated body condition as an important predictor of dispersal distance and settlement success (Stamps *et al.* 2005; Stamps 2006). Some studies have reported that heavier juveniles are more mobile (Holekamp 1984, 1986) and survive better than lighter counterparts (Barbraud *et al.* 2003). Other studies have suggested that the superior competitive ability of heavier juveniles may force juveniles in poorer condition to disperse

farther in search of vacant sites for settlement (Gaines & McClenaghan 1980), potentially exacerbating the mortality risk of long-distance dispersal. We used the residuals from our weight-length ANCOVA to test whether or not enhanced body condition attenuated mortality risk among long-distance dispersers. We included a landscape by body condition interaction to accommodate the possibility that the effect of body condition might vary between the landscapes (table 1). We also included sex as a covariate and a sex by landscape interaction term (Greenwood 1980; Dobson 1982; Jones 1988).

We compared 14 Cox proportional hazard models (table 1) and evaluated their relative ability to predict changes in mortality risk using Akaike's information criterion (AIC) (Burnham & Anderson 2002). Models were corrected for small sample sizes and overdispersion (QAIC_c; Burnham & Anderson 2002). The resultant Akaike weights were used to identify the most parsimonious model among those examined (Burnham & Anderson 2002). Model averaging was used to estimate parameters for models with a $\Delta\text{QAIC}_c < 10$ (Burnham & Anderson 2002). We included 142 juveniles in the Cox proportional hazard models, 54 of which were censored (survival not known). The effect of each covariate is presented as the hazard ratio ($\exp(\beta)$). For dichotomous variables, such as landscape, the hazard ratio can be interpreted as the ratio of risk for dispersers from the regenerating landscape (1) relative to that from the uncut landscape (0), controlling for other covariates in the model.

We evaluated the efficacy of the non-trapping refuges at reducing disperser mortality by using the first and last telemetry location of each individual to create a dichotomous variable, indicating whether juvenile martens dispersed beyond the boundary of the non-trapping refuges. Differences in survival between individuals dispersing within and

Table 1. The fourteen Cox proportional hazard models, predicted outcomes, and relative rankings using AIC developed to explain variation in mortality risk among juvenile martens. The models are presented in increasing order of complexity. The footnotes 1–5 refer to the predictions for variables in the model. All models were corrected for small sample sizes and overdispersion (QAIC_c). The landscape (L) model (1) is the most parsimonious model. $h_0(t)$ is the baseline hazard with dispersal time, $h_0(d)$ is the baseline hazard with dispersal distance, BC refers to body condition and S to sex.

model	predicted model outcome	pseudo- R^{2a}	Δ QAIC _c
1 $h_0(t)$	mortality risk increases with dispersal time		31.8
2 $h_0(d)$	mortality risk increases with dispersal distance		1.3
3 L	higher mortality risk in regenerating landscape ¹	0.09	0
4 BC	heavier juveniles disperse farther, attenuating mortality risk with increasing dispersal distance ²	0.01	2.9
5 L, BC	L and BC influence variation in mortality risk ^{1,2}	0.10	2.0
6 L, BC, L × BC	L and BC influence variation in mortality risk; ^{1,2} however heavier juveniles outcompete lighter juveniles for nearby vacant sites in regenerating landscape, exacerbating increase in mortality risk with distance ³	0.11	3.1
7 S	higher mortality risk in females than males ⁴	<0.01	3.3
8 L, S	variation in mortality risk with L and S ^{1,4}	0.11	1.7
9 L, S, L × S	L and S influence variation in mortality risk; ^{1,4} however males in the regenerating landscape experience greater risk than males in uncut landscape (reduces sex differences in risk) ⁵	0.11	3.7
10 BC, S	BC and S influence variation in mortality risk ^{2,4}	0.02	4.8
11 L, BC, S	variation in mortality risk with L, S and BC ^{1,2,4}	0.11	3.7
12 L, BC, S, L × S	L, BC and S influence variation in mortality risk, but the effect of S varies with L ^{1,2,4,5}	0.11	5.7
13 L, BC, S, L × BC,	L, BC and S influence variation in mortality risk, but the effect of BC varies with L ^{1,2,3,4}	0.13	4.9
14 L, BC, S, L × BC, L × S	L, BC and S influence variation in mortality risk, with both the effect of S and BC varying with L ^{1,2,3,4,5}	0.14	9.6

^aCalculated from the likelihood ratio. Measures the improvement in the model with covariate(s) compared to the model estimating the baseline hazard rate as a function of increasing dispersal distance (model 2).

outside the refuges were analysed using a logistic regression. We included a landscape by refuge interaction to test whether the large refuge area in the uncut landscape was equally effective as the two smaller refuges in the regenerating landscape at protecting juvenile dispersers from commercial fur trapping.

3. RESULTS

We captured most juveniles in October about 1–2 months after the onset of dispersal (Johnson 2008). The distribution of month of capture was similar in both landscapes (Kolmogorov–Smirnov test: $Z = 0.80$, $p = 0.55$), suggesting that there were no temporal biases between the landscapes.

(a) Body condition

As predicted, juveniles from the regenerating landscape were in poorer condition than those from the uncut landscape ($F_{1,189} = 4.34$, $p = 0.04$). Juveniles from the regenerating landscape weighed, on average, 27 g less than their counterparts from the uncut landscape of similar body lengths. Sex accounted for a large proportion of the variation in body condition (ANCOVA: $F_{1,189} = 104.87$, $p < 0.01$) with juvenile males weighing, on average, about 200 g more than juvenile females after adjusting for body length. The effect of sex on body condition did not vary between the landscapes ($F_{1,189} = 0.27$, $p = 0.61$). There was an overall increase in juvenile body mass with increasing body length ($\beta \pm \text{s.e.} = 1.30 \pm 0.18$).

(b) Natal dispersal distances

We did not detect significant differences in dispersal distances between the sexes in either the regenerating ($\chi^2 = 3.38$, $p = 0.20$) or uncut ($\chi^2 = 5.31$, $p = 0.30$) landscape. Juvenile females from the regenerating landscape moved a mean of 6 km ($\sigma^2 = 201$; maximum distance = 96 km), which was the same as males ($\sigma^2 = 205$; maximum distance = 91 km). In the uncut landscape, females moved an average of 4 km ($\sigma^2 = 932$; maximum distance = 181 km) compared with 18 km for males ($\sigma^2 = 1243$; maximum distance = 214 km).

Dispersal distributions differed between the landscapes ($\chi^2 = 15.50$, $p = 0.02$), with greater distances recorded for martens in the uncut landscape. Most juveniles remained within 5 km of their first capture site, regardless of landscape (figure 2a). About 60 per cent of juveniles moved further than the diameter of an adult female territory after initial capture (figure 2a). Juveniles from the regenerating landscape dispersed 8 km ($\sigma^2 = 288$), on average, compared with 16 km ($\sigma^2 = 1104$) on the uncut landscape. The maximum dispersal distance in the regenerating landscape (96 km) was less than that in the uncut landscape (214 km).

Restricting the analysis to juveniles that survived the transition to adulthood also showed that the distribution of dispersal distances differed between landscape treatments ($\chi^2 = 12.87$, $p < 0.01$; figure 2b). Dispersers from the regenerating landscape that survived to adulthood moved 4 km ($\sigma^2 = 22$) on average, with a maximum dispersal distance of 15 km, whereas those from the uncut

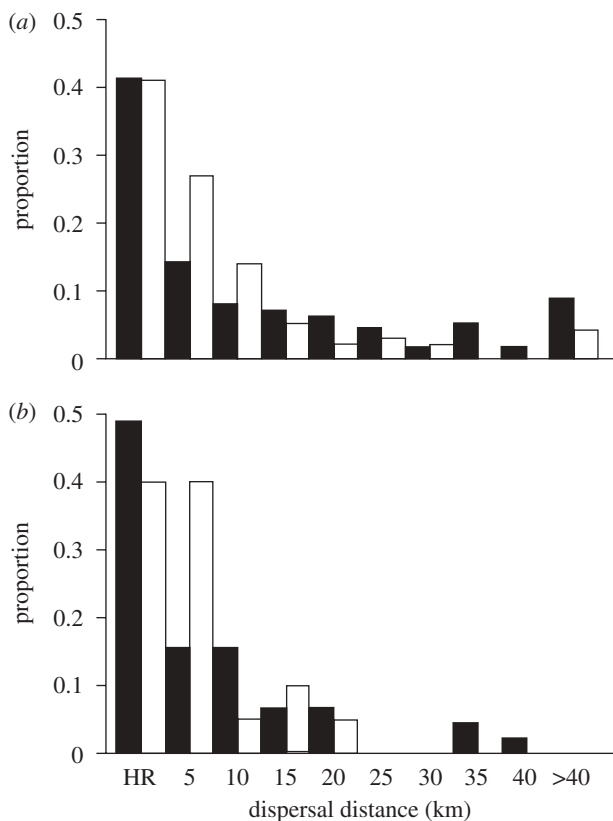


Figure 2. Distribution of natal dispersal distances for the uncut (filled bars) and regenerating (unfilled bars) landscapes; (a) for all dispersers and (b) for dispersers that survived to adulthood. The mean diameter of adult female home ranges (HR) was 2.9 km in the uncut landscape and 1.9 km in the regenerating landscape.

landscape moved an average of 7 km ($\sigma^2 = 97$), with one juvenile travelling 48 km from its capture location.

(c) Mortality

The most parsimonious model among the 14 candidate Cox models included landscape as the sole covariate influencing patterns of mortality risk with increasing dispersal distance (Model 3, table 1). Mortality risk increased with increasing dispersal distance in both landscapes (Model 2, figure 3). The mortality risk of dispersal was almost twice as high in the regenerating landscape as it was in the uncut landscape (model average: $\exp(\beta) = 1.8$; 95% confidence limits (1.21–2.78)). Indeed, only 25 per cent (17 out of 67) of the dispersers from the regenerating landscape successfully survived to adulthood, compared with 49 per cent (37 out of 76) in the uncut landscape. Including landscape as a covariate in the distance-dependent model (Model 3, table 1) explained an additional 9 per cent of the variation in mortality risk than dispersal distance alone (Model 2). Neither variation in body condition within each landscape (Model 5: $\exp(\beta) = 1.82$; 95% confidence limits (0.25–13.49)), nor sex (Model 8: $\exp(\beta) = 0.75$; 95% confidence limits (0.48–1.17)) improved the explanatory ability of the landscape + distance-based model. All other models, including the time-dependent model, were poorly supported (table 1).

Trapping was the major cause of juvenile mortality despite the refuges. Commercial trapping of martens

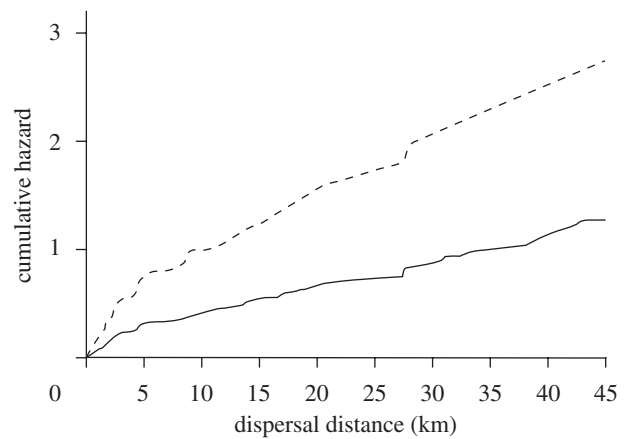


Figure 3. Estimated changes in the cumulative hazards for juveniles from the regenerating landscape (dashed line) and uncut landscape (solid line) dispersing less than 45 km.

accounted for 60 per cent (57 out of 95) of juvenile fatalities and did not vary between landscapes ($\chi^2 = 0.25$, $p = 0.56$). Nevertheless, the non-trapping refuges appeared to reduce disperser mortality. The odds of surviving to adulthood increased about fivefold for dispersers remaining within non-trapping refuges, compared with those dispersing beyond the refuge boundaries ($\exp(\beta) = 4.91$; 95% confidence limits (1.97–12.21)). This effect of refuges on survival did not vary between landscapes ($\exp(\beta) = 0.50$; 95% confidence limits (–0.12 to 2.01)), suggesting that the two smaller refuges in the regenerating landscape were equally effective as the large reserve in the uncut landscape at protecting juvenile dispersers from commercial fur trapping.

4. DISCUSSION

Our results suggested that dispersal is costly to juvenile American martens. Juveniles from the younger, regenerating landscape dispersed shorter distances and experienced lower survival than juveniles from the uncut landscape. The landscape difference in dispersal distances was similar when the analysis was restricted to juveniles that survived to adulthood, suggesting that the short dispersal distances in the regenerating landscape were not solely the result of the premature death of juveniles in transit. Short dispersal distances in the regenerating landscape could result from high territorial vacancies created by higher adult mortality (Thompson 1994) and low adult densities (Thompson & Colgan 1987; J. Fryxell, I. Thompson & J. Baker 2001–2005, unpublished data). Juveniles may have reduced mortality risks associated with dispersal by using a simple, fixed behavioural rule to settle in the first vacant site (Murray 1967; Waser 1985), assuming that a higher proportion of suitable home ranges were vacant in the regenerating versus uncut landscape. Alternatively, dispersers may have engaged in habitat selection and enhanced fitness by adaptively adjusting the number of sites sampled to the mortality risk during dispersal (Luttbeg 2002; Rousset & Gandon 2002; Stamps *et al.* 2005). More specifically, our body condition results suggested that juveniles from the regenerating landscape might disperse short distances because they sampled fewer sites to reduce the risk of starvation. The fact that dispersal

patterns were similar when the analysis was restricted to juveniles surviving to adulthood suggests that this sampling strategy may provide the additional benefit of reducing settlement costs (Stamps *et al.* 2005). Regardless, our results are consistent with the more general hypothesis that dispersal distances are, in part, shaped by mortality risks.

Although the mortality risk associated with dispersal is often hypothesized to increase with dispersal distance (Rousset & Gandon 2002; Stamps *et al.* 2005; Ronce 2007), few studies have demonstrated this fundamental assumption. Juvenile survival in the common goldeneye (*Bucephala clangula*) is unrelated to dispersal distance, perhaps because flight reduces dispersal time and consequently exposure to mortality risk (Pöysä & Paarsivaara 2006). Dispersal affects subsequent levels of avian fecundity rather than survival (Bélichon *et al.* 1996), suggesting that avian dispersers may be more susceptible to deferred dispersal costs (*sensu* Stamps *et al.* 2005). In contrast, the mean age of death decreased with increasing dispersal distance among trapped juvenile foxes (*Vulpes vulpes*) (Harris & Trewhella 1988), implying higher mortality rates. Mortality risk also increased with dispersal distance among juvenile kangaroo rats (*Dipodomys spectabilis*) (Jones 1988). Differences among these studies indicate a clear need for more empirical work, testing whether variation in mortality risk increases with dispersal distance and assessing the impact of mortality risk on dispersal distance (Ronce 2007).

Dispersal distance explained more variation in mortality risk than the time spent dispersing for juvenile martens. Mortality risk increased with dispersal distance in both landscapes, but the distance-dependent increase in mortality was two times greater in the regenerating versus uncut landscape, presumably because juveniles were in poorer condition. Individual variation in body condition did little to improve the explanatory power of Cox proportional hazard models, after the landscape differences were taken into account. The correlation between juvenile condition and landscape makes it difficult to determine the nature of the body condition relationship. Reduced rates of energy gain (Andruskiw *et al.* 2008) may have caused dispersing juveniles from the regenerating landscape to start off in poorer condition than those in the uncut landscape. Alternatively, juveniles from both landscapes might have started off in similar condition, but those from the regenerating landscapes might have experienced greater losses in condition while searching for a suitable area for settlement. Our data are inadequate to discriminate between these alternative hypotheses.

Commercial fur harvesting of martens accounted for most of the juvenile mortality. This was somewhat surprising given the size of the refuges. Nevertheless, the odds of survival were five times higher for juveniles dispersing within a refuge than for those that ventured outside. Our results corroborate previous findings suggesting that commercial trapping can have a profound effect on juvenile recruitment in martens (Thompson & Colgan 1987; Hodgman *et al.* 1994). Two small refuge areas in the regenerating landscape were equally effective at reducing juvenile mortality as one large area in the uncut landscape, possibly because dispersal distances were shorter in young forests. Similarly, Botsford *et al.* (2001) found that two small marine reserves exceeding

the mean dispersal distance of the target species could be equally effective as one large reserve.

In summary, we found that juveniles from young, regenerating forests dispersed shorter distances and suffered higher mortality risk with increasing distance compared with juveniles in the older uncut forests. Reduced foraging success (Andruskiw *et al.* 2008) and poorer body condition probably also contributed to the reduced disperser survival in the regenerating landscape. Too few studies have tested whether mortality risk increases with dispersal distance to determine whether this is the predominant pattern among mammals, but consistency with two other studies (Harris & Trewhella 1988; Jones 1988) suggests that this may be a reasonable inference.

All experiments described herein are in accordance with the guidelines of the Canadian Council on Animal Care and have been approved by the Animal Care Committee at the University of Guelph.

This work was supported by research grants from the NSERC Industrial Partnership Program, Canadian Forestry Service, Forest Ecosystem Science Cooperative Inc., Ontario Ministry of Natural Resources, Sustainable Forest Management Network, and an FCAR Doctoral Scholarship and an OGSST scholarship awarded to C.A.J. B. Daziel developed the program used for the bootstrapping analysis. We are indebted to R. Routledge, P. Wiebe, J. Oakes, J. Ellis and numerous other field technicians for helping with data collection. We are also grateful for the support of the Ear Falls Trappers Association. C.A.J. specially thanks C.A. MacDonald and members of the Guelph Nudds/Fryxell laboratory for their helpful comments and encouragement. We appreciated the constructive comments from two anonymous reviewers.

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