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High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern saw-whet owls

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ABSTRACT

Studies of the effects of habitat fragmentation have been heavily biased toward population and community questions, with less attention on the effects of habitat loss and fragmentation on individual behaviour and reproduction. We studied the effects of habitat amount and configuration on the foraging behaviour, provisioning rates and physiological condition of breeding male northern saw-whet owls (*Aegolius acadicus*) nesting in the fragmented aspen parkland of central Alberta, Canada. We then examined the relationship between provisioning behaviour and both reproductive success, and juvenile physiological condition. Males nesting in areas with little forest cover and large inter-patch distances spent more time perching, maintained smaller home ranges, and provisioned their nests less frequently. However, home range size and provisioning rates levelled off in landscapes with moderate to high forest cover. Male owls breeding in areas with low forest cover, and those raising large broods, also exhibited higher levels of chronic stress, as measured by heterophil/lymphocyte (H/L) ratios. Predictably, males that provisioned the nest less often fledged fewer young, which, in turn, exhibited higher variation in physiological condition. These results suggest that low levels of habitat loss and fragmentation may be beneficial to saw-whet owls, potentially by increasing prey abundance. However, high levels of habitat loss and fragmentation appeared to reduce the foraging efficiency of male saw-whet owls, increase their levels of physiological stress, and reduce their reproductive success. Increasing habitat loss and fragmentation may ultimately decrease population sizes of saw whet owls in this area and other species that are similarly affected by changes to in habitat composition or configuration.

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1. Introduction

Habitat fragmentation is often used to describe two different, but linked processes: a reduction in the amount of habitat (composition) and changes in the configuration of the remaining patches (Wiens, 1994). The relative influences of

habitat composition and configuration have been difficult to separate (Andr en, 1994; Fahrig, 1997; Villard et al., 1999; B elisle et al., 2001), and attract ongoing attention (Schmiegelow and M onkk onen, 2002; Fahrig, 2003; Cushman, 2006). Theoretical work suggests that habitat configuration is often important only below some threshold of habitat amount

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(With and Crist, 1995; Fahrig, 2003), but both attributes appear to be important to the persistence of diverse bird populations (Radford et al., 2005).

Beyond the distinction between habitat composition and configuration, the majority of studies that address the effects of habitat fragmentation have focused on community and population effects (see reviews by Fahrig, 2003; Cushman, 2006). Habitat fragmentation is frequently associated with reductions in species richness within communities (e.g., Schmiegelow and Mönkkönen, 2002; Fahrig, 2003; Stewart, et al. 2004). Loss in species richness presumably results from the effects of habitat fragmentation on populations for which there may be reductions in genetic diversity (e.g. Gibbs and Stanton, 2001), population growth rates (Donovan and Flather, 2002), or population sizes (e.g. Rolstad, 1991; Bender et al., 1998; Donovan and Flather, 2002). Within populations, however, less is known about how habitat fragmentation affects reproductive success (reviewed by Stevens et al., 2003), and very little is known about how the behaviour of individuals influences population responses.

Recent work on birds has shown that habitat loss increases movement costs to individuals, (Bélisle et al., 2001; Ruiz et al., 2002) and decreases breeding success (Hinsley et al., 1999). Although these effects have received the most attention in the context of individuals whose home range is encompassed within a single patch (e.g. Matthysen and Curie, 1996; Brooker et al., 1999; Bélisle and Desrochers, 2002), the effects of habitat loss and fragmentation can also apply to individuals that maintain home ranges that encompass multiple patches. These individuals may actually be more vulnerable to fragmentation effects than individuals whose home ranges are contained within a single patch (Grubb and Doherty, 1999; Hinsley, 2000). For individuals maintaining multiple patch home ranges, smaller and more isolated patches of habitat may require that they consistently travel farther for resources. Indeed, use of multiple patches of habitat within a home range appears to convey substantial costs for several bird species (Redpath, 1995b; Hinsley et al., 1999). These costs may accrue from increased energy expenditure to detour around gaps in habitat (e.g. St. Clair et al., 1998; Bélisle and Desrochers, 2002), and higher predation risk (Lima and Dill, 1990; Nonacs, 2001; Redpath, 1995b; Siffczyk et al., 2003; Turcotte and Desrochers, 2003), both of which may lower foraging efficiency and increase physiological costs as a result of chronic stress (Ruiz et al., 2002; Turcotte and Desrochers, 2003). When impediments to movement are associated with critical life stages, such as provisioning young, habitat fragmentation is more likely to reduce the reproductive success of individuals and, potentially, population viability (Rolstad, 1991; Hinsley, 2000).

The northern saw-whet owl (*Aegolius acadicus*) provides an excellent opportunity for examining how habitat fragmentation affects the movements, foraging efficiency and reproductive success of a species whose home range typically encompasses multiple habitat patches. These owls are considered to be forest specialists (Cannings, 1993) and thus, may generally be more vulnerable to the effects of habitat fragmentation (Harris and Reid, 2002). Although saw-whet owls can hunt from forest edges, habitat loss and fragmentation may reduce perch availability, alter prey availability (Bay-

ne and Hobson, 1998; Silva et al., 2005) and increase predation by open-area species such as the great horned owl (*Bubo virginianus*; Cannings, 1993). Because males are the sole provisioners to the nest for the bulk of incubation and brooding (Cannings, 1993), northern saw-whet owls present a relatively simple system for studying foraging and provisioning behaviour and their effects on reproductive success with varying degrees of forest fragmentation.

Optimal foraging theory (*sensu* Stephens and Krebs, 1986) offers several unexplored predictions about how owls foraging in multiple patches might behave in a fragmented landscape. In particular, the Marginal Value Theorem suggests that individuals that travel farther between successive patches will spend longer periods of time foraging within a given patch (*sensu* Charnov, 1976). As increasing habitat loss and fragmentation isolates resources into patches (Bruun and Smith, 2003), individuals may simultaneously be obliged to forage farther from their nests (Frey-Roos et al., 1995; Bruun and Smith, 2003), and maintain larger home ranges (Redpath, 1995b), resulting in fewer provisioning trips to the nest (Frey-Roos et al., 1995; Bruun and Smith, 2003). Conversely, landscapes may contain so little habitat that the distance between patches may exceed a species' gap-crossing tolerance (e.g., Desrochers and Hannon, 1997; Harris and Reid, 2002). In these cases, territorial movements may be constrained to reduce the sizes of home ranges, putting a greater strain on available resources. Either effect should ultimately reduce the rate at which individuals can provision their young (Frey-Roos et al., 1995; Tella et al., 1998; Hinsley, 2000; Bruun and Smith, 2003) with consequential effects on their own or their offspring's growth and condition (Tarlow et al., 2001). Travelling through fragmented areas may also result in increased stress to the provisioning parent as a result of increased predation risk (Lima and Dill, 1990) and higher movement costs (Hinsley, 2000), which may be expressed physiologically (Bélisle et al., 2001; Ruiz et al., 2002) as a decrease in body mass relative to size (Perez-Tris et al., 2004) or in an immunological response (Ruiz et al., 2002).

The objective of this study was to examine how variation in habitat composition and configuration affect foraging decisions, provisioning behaviour and physiological condition of male northern saw-whet owls. We also examined how male provisioning behaviour relates to individual reproductive success and juvenile condition prior to fledging. Based on these objectives, and combined with the theory described above, we generated five specific predictions. (1) As the distance between foraging perches and patches increases, the time an individual spends at a perch or in each patch will also increase. (2) Male home range sizes and foraging radii will vary quadratically, increasing as lower forest cover and increasing distance between patches spreads out resources, but then decreasing when the distance between patches exceeds the gap-crossing tolerance of individuals. (3) A reduction in forest cover and an increase in the distance between remaining patches will be reflected in lower provisioning rates. (4) Males that provision the nest less frequently will fledge fewer young and produce fledglings in poorer physiological condition. (5) Males breeding in areas with low forest cover and greater distances between remaining patches will also exhibit poorer physiological condition.

2. Materials and methods

2.1. Study area

Field data were collected between 2002 and 2005 in the transition zone between boreal forest and aspen parkland north and east of Edmonton, Alberta, Canada (53°32'N, 113°33'W). In this 3040 sq km study area, approximately 250 nest boxes have been erected since 1985 to support a long-term monitoring project for northern saw-whet owls (R. Cromie, pers. comm.). This region is characterized by predominantly flat terrain with a patchy distribution of mature mixedwood forest, interspersed with cropland, pasture and human development. Forest patches are dominated by trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) mixed with white and black spruce (*Picea glauca*, *Picea banksiana*). Landscapes within 800 m of nests ranged from 10% to 85% forest cover (our metric of composition). The mean patch size of these 800 m landscapes varied from 3.6 to 286 m² and the mean edge to edge nearest neighbour distance between patches ranged from 15.3 to 122.2 m.

2.2. Home range and foraging behaviour of adult males

Home range size and foraging behaviour were determined by tracking breeding male saw-whet owls using radio telemetry. Individuals were captured while provisioning their nests using a box trap placed over the entrance to the nest box (Saurola, 1987). Traps were deployed prior to sunset and left on the nest box until the male was caught or two hours after sunset. This trap design blocks the female and young inside the box and a trap door is triggered when the male arrives with food (Saurola, 1987). Males were trapped as soon after hatching as possible, ranging from early May to mid-July depending on when the nest was initiated.

Once captured, males were banded with US Fish and Wildlife Service bands and fitted with backpack PD-2P transmitters (Holohil) using a harness made of Teflon strapping and lightweight polyester material. The transmitter was encased in a polyester sack and was placed on the back between the scapulae and the straps passed over the shoulders, crossing in an X over the breast before being sewn to the transmitter sack at the back. This design did not include a quick release and we were required to recapture males at the end of the breeding season to remove the transmitter. Of the 21 males we banded, only three transmitters were not recovered; all others were either removed from the recaptured bird ($n = 7$), found dropped after the bird had torn through the sack ($n = 8$) or removed from a recovered dead bird ($n = 3$). After release, males were given a minimum of five days to acclimate to the transmitter and then were tracked for a minimum of three focal bouts during the chick-rearing period. Each observation period began after sunset and lasted a minimum of 3 h. Although saw-whet owls tend to exhibit crepuscular activity patterns, with highest activity exhibited just after dusk and again before dawn (Cannings, 1993), we focused on this first activity peak due to logistical constraints. Within this period, two stationary observers continuously and simultaneously monitored an individual owl using hand-held VHF receivers to record all movements between perches and to

and from the nest (after Redpath, 1995a; Graham, 2001). Position sensors in the transmitters alerted us to each movement and simultaneous bearings were taken once the individual had settled on a perch. A combination of triangulated and observed locations during these focal periods was used to calculate the distance between successive perches, time spent at each perch, and the maximum radius from the nest of each foraging trip.

We estimated telemetry error using a sub-sample of telemetry fixes on roosting birds that we also located by sight. We calculated mean linear error, standard deviation (SD) of bearing deviations and tested for directional bias in bearing error using a one-sample *t*-test, testing for a significant deviation from zero degrees (after White and Garrott, 1990).

Home range size was estimated from all position fixes during focal bouts and at daytime roosts during the breeding season using a fixed kernel estimator (Seaman and Powell, 1996) and the Home Range Extension for ArcView GIS (Rodgers and Carr, 2001). Although kernel estimators of home range size assume statistical independence between position fixes (Swihart and Slade, 1997), a number of studies have found little difference in home range size estimated using statistically independent locations and those estimated using autocorrelated data (Anderssen and Wrongstad, 1989; Gese et al., 1990; Reynolds and Landré, 1990). Thus, it is likely that home range estimates based on autocorrelated data are valid, provided fixes are collected over the entire timeframe of interest (Kernohan et al., 2001). In this study, we used groups of autocorrelated fixes from temporally independent focal bouts as well as independent daytime roost sites over the course of the entire nestling season to retain more information about individual movement (Kernohan et al., 2001). Bandwidth (smoothing parameter) was calculated using the least squares cross validation method (Seaman and Powell, 1996). Because the value for this method is dependent on home range size and number of fixes (Kenward, 2001), which ranged from 30 to 75 per individual, we first calculated a smoothing parameter for each male's set of positions individually and then calculated the median of these values. Finally, we recalculated home range size for each male using the median value as the smoothing parameter to allow for comparison among males (Kenward, 2001).

2.3. Physiological Condition

Male physiological condition was assessed in 2004 and 2005 using the residuals generated from a regression of body mass against tarsus length (Ots et al., 1998) and the ratio of white blood cells, specifically heterophils to lymphocytes (H/L) ratios. This ratio has been identified as a reliable indicator of a bird's response to chronic stress, increasing as stress increases (Gross and Siegel, 1983; Hórak et al., 2002) and appearing to be less affected by short-term handling stress than corticosterone levels (Gross and Siegel, 1983). Blood samples were taken upon capture by puncturing the ailar vein using a 27½ gauge needle and collecting less than one cc of blood in a heparinized capillary tube. One to two whole blood smears per bird were made using a 2-slide wedge method on site (Campbell, 1988) and then stored for examination later. Smears were stained within four months of preparation

using a Wright stain, buffered using a 2% solution of Giemsa stain in deionized water (Sigma). We then performed leukocyte differential, classifying a random count of 100 white blood cells into each of five cell types: heterophils, lymphocytes, monocytes, eosinophils and basophils. The ratio of heterophils to lymphocytes was calculated from the number of each cell type in that count (after Bortolotti et al., 2002; Ruiz et al., 2002; Suorsa et al., 2004).

2.4. Provisioning rates

Nightly provisioning rates were measured using an automated weighing system installed in occupied nest boxes. Each scale consisted of a weighing platform inserted into the base of the nest box and connected to an external controller. The device measured and logged the relative mass of the box contents at 1-min intervals on a removable memory module, making it possible to record when prey weighing more than 10 g were added to the nest. We used a 10 g cut off because it the smallest mass that we could discern reliably from background variation in the scale data and could also encompass a majority of the prey types that the owls were likely to consume. Deer mice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*) are the primary prey of saw-whets in this study area (H. Hinam, unpublished data) and elsewhere (Cannings, 1993), and range in mass between 10 and 40 g (Burt and Grossenheider, 1980).

We calculated provisioning rates for each nest as the number of food deliveries each night. We defined night as the period between sunset (as recorded by Environment Canada at Edmonton, Alberta) and one half hour after sunrise. We did not use mass of prey deliveries as our measure of provisioning rate because the accumulating pad of pellets regurgitated by the developing young reduced the accuracy of the scales during the later nestling period.

2.5. Reproductive success and juvenile condition

Each nest was monitored every 2–7 days from the day of discovery until the last of the young fledged, approximately 30 days after hatching. Most nests fledged at least one juvenile (75 of 78 nests monitored for the entire study period). We visited the nest just prior to fledging, when the oldest chick was approximately 30 days old to assess reproductive success and collect blood samples. We assessed juvenile condition with H/L ratios measured from whole blood smears as for males. We used both the mean H/L ratio of each nest and the standard deviation of H/L ratios (H/L SD) within each nest as measures of juvenile pre-fledging condition. The latter was used because saw-whet young hatch asynchronously (Cannings, 1993) and it is possible that physiological stress may be manifested not only by higher H/L ratios for the whole nest, but also by a greater difference in H/L ratios between older and younger nestlings (Blas et al., 2005).

2.6. Habitat composition, configuration and prey density

We compared the dependent variables of male home range size, perch time, H/L ratios and provisioning rates to a set of continuous habitat composition (forest amount) and configura-

tion metrics that were calculated for landscapes centred on each nest. We defined the landscape size as a radius of 800 m radius from the nest. This radius was based on the mean foraging distance from the nest of the males followed during this study ($n = 14$). We overlaid each nest-centred landscape on a GIS forest layer of the study area. This layer was created by enhancing black and white Indian Remote Sensing (IRS) data with a false-colour LANDSAT layer from 1998 and digitizing it into a binary layer of habitat (forest) and non-habitat (all other types). The minimum mapping unit of the LANDSAT data was 30 m². However, the 4-m² resolution of the IRS layer allowed us to identify fine-scale habitat features such as small woodlots. Based on their perceived importance to owl behaviour and condition, we selected three nest patch metrics, one landscape-level composition metric (percent forest cover), and five landscape configuration metrics to describe each nest-centred landscape. Patch metrics included nest patch size and nest patch shape index, which describes the complexity of the edges of the nest patch, representing the potential prey availability through good hunting locations (Cannings, 1993), as well as predation risk that is often associated with edges (Andreassen and Ims, 1998), and nest patch proximity index (after Bender et al., 2003), which describes how connected the nest patch is to the rest of the landscape. We described landscape configuration using mean patch size and patch density, which together describe how dissected the landscape is. We also used edge density, landscape shape index and mean edge-to-edge nearest neighbour distance as representatives of potential predation risk associated with increased landscape complexity.

A final independent variable was an index of prey density. Because saw-whet owls mainly eat small mammals (Cannings, 1993), the effects of forest fragmentation on the behaviour and reproductive success of northern saw-whet owls may be modified by fluctuations in prey density (Redpath, 1995a; Hakkarainen et al., 1997). Consequently, we estimated relative prey density in 2003 and 2004 using small mammal trackplates (King and Edgar, 1977; Mabee, 1998). Each trackplate was contained within a 30 cm length of 3.7 cm diameter PVC pipe. The trackplate itself consisted of a plastic board with a two-part chemical dye in the middle and treated paper on either side to record the tracks of any small mammal moving passively through the tube.

Due to logistical constraints, track plating was carried out only during the last two weeks of June in 2003 and 2004, which corresponded to the late nestling period of most nests. Ten to 30 plates were deployed in within the 800 m radius of the nest along 200 m transects (five per transect). Half of the transects in each landscape were placed along edges and the other half in the forest interior (more than 200 m from the edge). Because landscapes with low forest cover did not offer enough space to place the same number of trackplate transects as landscapes with high forest cover, sampling intensity varied with the amount of forest cover within each landscape with two transects (one interior, one edge) in landscapes with forest cover up to 30%, four transects (two interior, two edge) in landscapes with forest cover between 31% and 60% and six transects (three interior, three edge) in landscapes with greater than 61% forest cover. Although small mammals are present in open areas (Silva et al., 2005), the

lack of perches presumably made these areas difficult for saw-whets to exploit and so we did not sample these areas. Trackplates were left out for 10 days (± 2 days) and then removed. Because it was typically impossible to identify individual paths, we estimated small mammal density with the number of prints/trackplate/day for each landscape (Whisson et al., 2005).

2.7. Statistical analysis

Statistical analyses were conducted using either SPSS 11.5 (SPSS, 2001) or SAS 9.1.3 (SAS Institute Inc., 2004). We examined the relationships among travel distance, and time spent at a perch both within and among forest patches using general linear mixed models, while including individual males as a categorical random effect. We modelled the relationship between each dependent variable (male home range, perch time and condition) with the independent variables specifying habitat composition (percent forest cover) and configuration (nest patch size, nest patch shape, nest patch proximity index, edge density, mean patch size, patch density, mean nearest neighbour distance, landscape shape index). We constructed statistical models using Hosmer and Lemeshow (2000) model building approach modified for general linear models. In brief, we began by identifying significant main effects with a liberal $\alpha = 0.25$, then fit a forced entry model including all possible effects and identified those that remained significant at $\alpha = 0.05$. We then fit a reduced model with only the remaining significant factors. We examined the linearity of effects graphically (James and McCulloch, 1990; Bissonetti, 1999) and compared the fit of linear models to either quadratic or natural log relationships when necessary. Finally, we tested for any biologically plausible interaction between the remaining main effects in each model.

Changes in forest amount are often correlated with changes in forest configuration (Fahrig, 1997). Thus, before beginning the model building process, we examined all habitat variables for correlations between habitat composition (percent forest cover) and our five configuration variables (above). When correlation coefficients exceeded 0.60, we regressed configuration metrics against forest cover using simple linear regression and then using the residuals as corrected independent variables in the model building process (after Villard et al., 1999; Bélisle et al., 2001).

We assessed parental provisioning by modelling the relationship between the number of prey deliveries per night (nightly provisioning rate) and the habitat variables described above using a general linear mixed model, again using the model-building approach of Hosmer and Lemeshow (2000). Because parental provisioning rates are often affected by the age of the young (Hedd et al., 2002), we included the approximate age of the oldest nestling (days since hatch ± 3 days) as a covariate. We accounted for pseudoreplication within nests by using nest as a random factor. We used a similar approach to examine the relationships between nightly provisioning rate (feeds per night) and mean perch time for foraging males, as well as between mean provisioning rate (feeds/night) and both individual reproductive success and juvenile condition, introducing clutch size as a covariate when appropriate (after Tremblay et al., 2003).

3. Results

We obtained foraging behaviour and enough data points (>30 ; Seaman et al., 1999) to estimate home range size from 14 male owls between 2002 and 2005. We calculated telemetry error based on 37 locations of live, tagged owls that were between 26 and 1 484 m away from the observers. Telemetry bearing error was unbiased (mean difference between actual and estimated bearings = 0.39° ; $t = 0.289$, $p = 0.774$, $df = 77$), and the standard deviation of errors was 22.5° . Mean linear error was 62.8 m (± 52.6 SD, $n = 38$).

3.1. Effects of habitat characteristics on male behaviour

Mean perch time and inter-perch distance were calculated for each male from an average of 29 ± 15.5 inter-perch movements per bird ($n = 14$). The distances males travelled between consecutive perches varied widely from 19 to 1700 m (mean = 320.5 m ± 257.2 , $n = 398$). The time a male spent at each perch ranged from 1 to 60 minutes (mean = 10.9 ± 8.2 min, $n = 398$). When the variation among males was controlled with a random effect, the time spent at a perch increased significantly with distance to the next perch ($F_{1,370} = 4.7$, $p = 0.048$; Table 1). A significant interaction between perch distance and individual males indicates that the strength of this relationship varied among individuals ($F_{13,370} = 1.9$, $p = 0.026$; Table 1).

At the patch level, males foraged for two to 104 min in each forest patch (mean = 22.7 min ± 17.8 SE, $n = 69$) and the distance between consecutively used patches ranged from 11.2 to 1431.2 m (mean = 131.1 m ± 223.3 , $n = 69$). Patches ranged in size from 0.3 to 438.8 ha (mean = 71.2 ha ± 107.3 , $n = 69$). Once the effect of individual male was accounted for, patch residence time increased most strongly with the size of the patch; but it also increased significantly as the distance to the next patch increased (Table 1). Males moved 0 to 10 times between consecutive perches within a given patch (mean = 2.3 ± 2.1 , $n = 68$). The distance to the next patch did not influence the number of movements a male made between perches within that patch (Table 1). As expected, the number of movements increased significantly as patch size increased (Table 1).

Movement between perches and foraging behaviour were also related directly to landscape metrics of habitat amount and configuration. The mean time a male spent at a perch while foraging decreased significantly in landscapes with greater forest cover, which accounted for 55% of the variation in the data ($r^2 = 0.55$, $F_{1,12} = 14.5$, $p = 0.002$). The mean foraging radius of owls decreased significantly as edge density increased and this relationship explained 35% of the variation in the data ($r^2 = 0.35$, $F_{1,12} = 6.4$, $p = 0.026$).

Analyses of all telemetry fixes for each male provided information on home range size. Home range sizes were estimated from an average of 46.4 telemetry fixes per bird ± 18.4 ($n = 14$) and varied dramatically from 11.7 to 137.0 ha (mean = 89.4 ha ± 40.2 , $n = 14$). Using an area accumulation curve, we found that sampling saturation was reached between 27 and 42 fixes per individual (mean = 33.5 fixes ± 4.9 ; $n = 12$), consistent with the suggestion of 30 fixes by Seaman et al. (1999). Saturation was not reached within the existing

Table 1 – Summary results of three general linear mixed models of the effects of: (1) the effects of distance to the next perch on the perch time of individual males (n = 14); patch size and distance to the next patch on (2) individual patch residence time of foraging males (n = 14) and (3) the number of sequential perches a male visits within a patch

Dependent variable	Parameter	β	df	F	P
Perch time	Distance to next perch	0.01	1	4.7	0.048
	Individual male		13	1.4	0.148
	Distance \times male		13	1.9	0.026
	error		370		
Patch residence time	Patch size	0.07	1	20.1	<0.001
	Distance to next patch	0.02	1	4.2	0.045
	Individual male		11	0.7	0.754
	Error		55		
Number of sequential perches in a patch	Patch size	0.01	1	38.3	<0.001
	Distance to next patch	0.00	1	0.2	0.684
	Individual male		11	1.6	0.140
	Error		54		

number of fixes for two individuals. Although there was some evidence of a positive relationship between the number of fixes obtained per bird and the amount of forest in a landscape ($r = 0.56, p = 0.06$), there was no relationship between the number of fixes and our the calculated home range size ($r = 0.06, p = 0.85$); the relationship that might have introduced a systematic bias to our results.

Contrary to prediction, home range size did not exhibit a quadratic relationship with increasing forest cover in nest-centred landscapes. Instead, home range size increased with forest cover, levelling off in more contiguous landscapes

($F_{1,10} = 13.2, p = 0.005$; Fig. 1) and decreased with both increases in edge density ($F_{1,10} = 9.8, p = 0.010$; Fig. 1) and the complexity of the nest patch edge ($F_{1,10} = 10.0, p = 0.010$; Fig. 1). Neither nest patch shape index nor edge density was significantly correlated with percent forest cover ($r = -0.18, p = 0.53$ and $r = 0.24, p = 0.404$ respectively, $n = 14$). These three factors explained 85% of the variation in male home range size ($r^2 = 0.85, F_{3,9} = 16.9, p < 0.001$).

3.2. Effects of habitat and male behaviour on provisioning rates and reproductive success

Scales were installed in 43 nests between 2002 and 2004, but malfunctions resulted in provisioning data from only 29 nests. At many nests with functioning scales, there were gaps in the data produced and, as a result, nightly provisioning rates (feeds in a night) were calculated over a range of 5–25 days per nest (mean = 11.6 days \pm 5.0, $n = 29$). Males provided between 3 and 10 prey deliveries per night (mean = 7.4 \pm 1.2 feeds, $n = 336$ nights from 29 nests). The number of deliveries in a night decreased as nestlings aged ($\beta = -0.03; F_{1,305} = 11.2; p = 0.001$).

Larger broods were associated with higher provisioning rates ($F_{1,305} = 27.9, p < 0.001$; Fig. 2), once the effect of nestling age was accounted for. Provisioning rates also increased significantly with the proportion of forested habitat in the landscape and decreased significantly with increases in the nearest neighbour distance among patches ($F_{1,305} = 5.4, p = 0.021$ and $F_{1,305} = 5.6, p = 0.019$ respectively; Fig. 2).

Males spent less time at a perch, on average, with increasing forest cover and patch proximity (above). Once the variation associated with nest was accounted for, longer perch times led to a decrease in the number of nightly prey deliveries ($F_{1,82} = 16.3, p = 0.001$; Fig. 3). There was no significant relationship between male provisioning rates and either their mean foraging radius ($F_{1,81} = 0.1, p = 0.471$) or home range size ($F_{1,81} = 0.2, p = 0.129$) once the within-nest variation and nestling age was accounted for.

Among the nests for which we could link mean male provisioning behaviour (feeds/night) and nest success, clutch size ranged from 3 to 9 eggs (mean = 5.8 eggs \pm 1.2, $n = 27$).

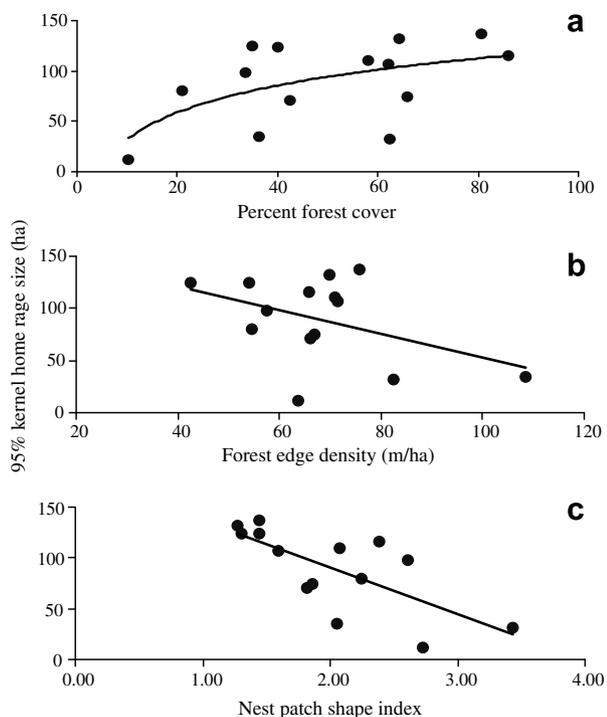


Fig. 1 – The effect on home range size of male saw-whet owls (95% fixed kernel estimator) and of each of: (a) percent forest cover, (b) forest edge density and (c) nest patch shape index.

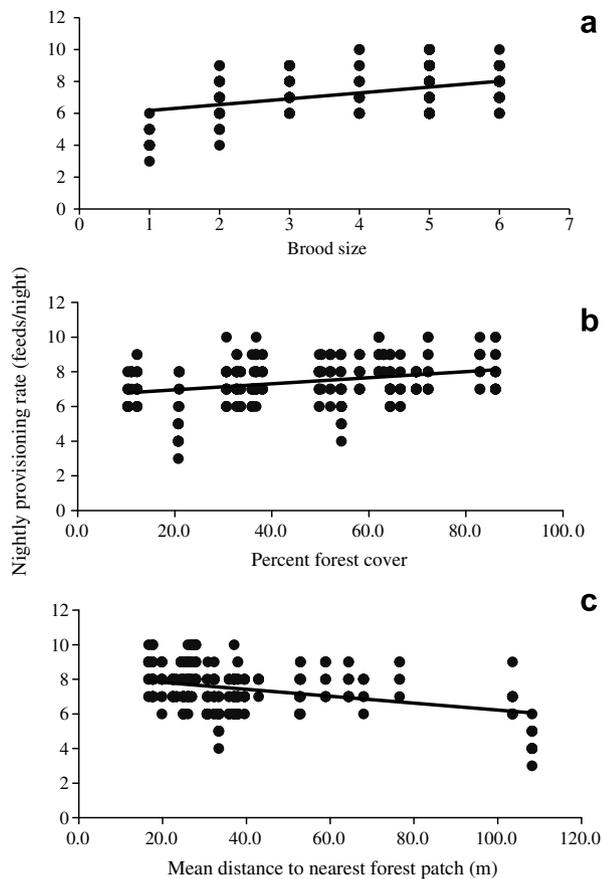


Fig. 2 – The effect on nightly provisioning rate (number of feeds/night) for 29 males of: (a) brood size, (b) percent forest cover and (c) mean edge-to-edge nearest neighbour distance (metres).

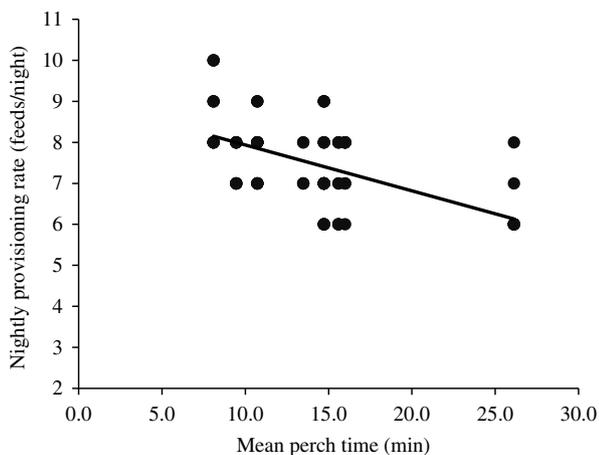


Fig. 3 – The relationship between the nightly provisioning rate (number of feeds/night) and the mean time spent at a perch (min) by each foraging male for which there was corresponding scale data ($n = 8$).

These nests fledged from 1 to 6 young (mean = 4.3 fledglings \pm 1.4, $n = 27$). As expected, there was a significant positive relationship between clutch size and the number of young fledged. However, once clutch size was accounted for,

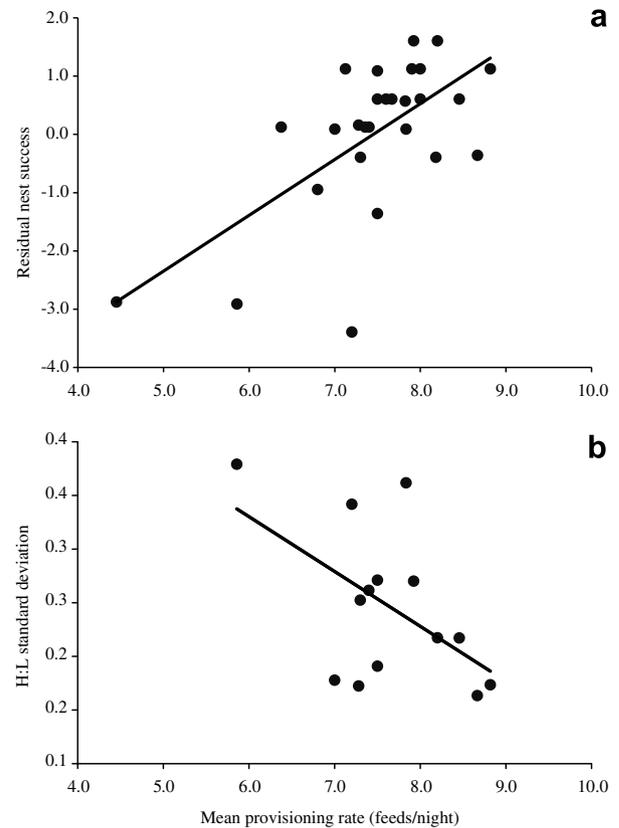


Fig. 4 – The relationship between nightly provisioning rate (number of feeds/night) and (a) residual nest success (measured as the number of fledglings produced after accounting for clutch size, $n = 26$) and the standard deviation of the ratio of heterophils to lymphocytes (H:L standard deviation) among chicks within broods ($n = 15$).

there was also a significant positive relationship between the mean number of feeds per night by the male and the number of young that successfully fledged from a nest (Fig. 4). Together, these two variables accounted for just over 50% of the variation in the data ($r^2 = 0.51$, $F_{2,24} = 12.4$, $p < 0.001$; Fig. 4).

There was no relationship between the mean ratio of heterophils to lymphocytes (H/L ratio) of juveniles in the nest and provisioning rates ($F_{1,12} < 0.1$, $p = 0.957$). However, the within-nest variation in nestling H/L ratios decreased significantly as provisioning rates increased ($r^2 = 0.29$, $p = 0.044$, $n = 15$; Fig. 4), suggesting that there was more variation in the condition of chicks within nests that experienced low provisioning rates.

3.3. Effect of habitat and parental effort on male physiological condition

We collected blood samples from 24 males including radio-tagged individuals during the early nestling stage between 2004 and 2005 to obtain H/L ratios. These ratios varied between 0.48 and 3.13 (mean = 1.29 ± 0.14 , $n = 24$). Higher H/L ratios, which are indicative of chronic stress, increased with brood size and decreased in areas with greater forest cover (Table 2). These two variables accounted for 65% of

Table 2 – Results of a general linear model of the effects of landscape variation and brood size on immunological condition (heterophils:lymphocytes) and residual body mass (mass regressed against tarsus length) of breeding male owls

Dependent variable	Parameter	β	SE	t	P
Heterophils:lymphocytes	Percent cover	−0.02	0.01	−4.89	<0.001
	Brood size	0.17	0.07	2.38	0.027
	Intercept	1.61	0.46	3.52	0.002
Residual body mass	Edge density	0.17	0.06	3.01	0.008
	Mean patch size residual	0.07	0.02	3.61	0.002
	Intercept	−10.75	3.7	−2.90	0.010

the variation in the data ($r^2 = 0.65$, $F_{2,21} = 19.1$, $p < 0.001$). Male body mass ranged from 70.5 to 87.0 g (mean = 79.8 ± 1.05 g, $n = 22$), tarsus lengths ranged from 26.6 to 31.1 mm (mean = 28.2 ± 0.26 mm, $n = 22$). Residual body mass (i.e. after being regressed against tarsus length) increased significantly with both the edge density of the landscape and the residual mean patch size (Table 2). These combined effects accounted for 48% of the variance in the data ($F_{2,18} = 8.33$, $p < 0.001$).

3.4. Effect of prey availability on male behaviour and condition

As evidenced above, print density, measured through track plating in 2003 and 2004 did not enter into any models explaining male behaviour or physiological condition. However, a mixed model analysis (including each nest-centred landscape as a random effect) of the relationship between print density and landscape metrics revealed that the density of small mammal prints per trackplate per day increased significantly with residual mean patch size ($F_{1,32} = 12.2$, $p = 0.001$; $r^2 = 0.28$).

4. Discussion

As predicted by the Marginal Value Theorem (Charnov, 1976; Stephens and Krebs, 1986), owls spent more time at a perch as the distance to the next perch increased. However, there was considerable variation both within and among males. For males living in landscapes with large forest patches, most inter-perch movements occurred within patches and owls also perched for less time on average, perhaps because they could move more easily within these more contiguous habitats. Similarly, tawny owls (*Strix aluco*), foraged longer at a perch with increasing interperch distance, with the effect being more pronounced in highly fragmented areas (Redpath, 1995a).

The effect of interperch distance on perching time was most apparent when the next perch was across a gap in the habitat. Indeed, all males in this study spent more time foraging in a patch as patch size increased, or as the distance to the next patch increased, as would be predicted by the Marginal Value Theorem (Charnov, 1976; see also Stephens and Krebs, 1986). Similar relationships have been reported for species as diverse as insects (e.g., Cresswell and Osborne, 2004) and large mammals (e.g. Shipley and Spalinger, 1995). For owls, larger patches may offer more perch options, and possibly a greater abundance of some small mammal prey (Mills, 1995; Sunde and Redpath, 2006). In this study, small mammal print density increased with the size of nest-centered patches, but

our sampling design prevents us from knowing whether this increase was due to mammal density or sampling intensity.

In addition to potential increases in foraging opportunities afforded by larger patches, the increase in patch residence time as gap sizes increased may reflect movement costs. These costs could stem from either an increase in the physiological cost of traveling over larger distances (Hinsley, 2000) or an increase in predation risk (Bélisle and Desrochers, 2002; Harris and Reid, 2002). Indeed, higher survival associated with remaining in a patch may partially explain why individuals of diverse species remain longer in patches than the Marginal Value Theorem would predict (Nonacs, 2001). For saw-whet owls, predation risk associated with gaps is likely more important than movement costs because foraging owls often travelled much longer distances within forest patches than among them and were often observed stopping at a forest edge before leaving a patch. Saw-whet owls are sometimes preyed upon by long-eared owls (*Asio otus*) and are likely also vulnerable to predation from opportunistic great-horned owls (*B. virginianus*) and barred owls (*Strix varia*; Cannings, 1993), all three of which occur in the study area (Grossman, 2003).

Our results were consistent with our predictions that residence time would increase with the distance between both perches and patches. However, they only partially supported our prediction that home range size would vary quadratically with habitat composition and configuration. The home range sizes of male saw-whet owls dropped dramatically in landscapes with low forest cover and large amounts of edge, and home range sizes were much larger in landscapes of moderate forest cover and fragmentation. However, home range size levelled off rather than decreased in the highest ranges of forest cover and decreased with increasing edge density. These results contrast with several other avian studies in which home range sizes were largest in landscapes with low habitat cover and high fragmentation (Redpath, 1995b; Bruun and Smith, 2003; Siffczyk et al., 2003).

One explanation for the discrepancy among studies in the shape of the relationship between forest cover and home range size may be provided by the distribution of prey. For some prey species, such as deer mice, landscapes with high forest cover and low edge, may provide poor habitat (Bayne and Hobson, 1998; Silva et al., 2005), forcing male owls to expand their home ranges in search of more resources (Redpath, 1995b; Siffczyk et al., 2003). However, saw-whet owls do not specialize on a single prey species (Cannings, 1993) and thus lower numbers of one prey species in landscapes with less edge habitat may be offset by increases in abundance of other small mammal species that prefer contiguous forest

(Mills, 1995). Indeed, a study of space use by four different raptor species, including some prey specialists, found no effect of small mammal abundance on where individuals foraged and suggested that the need to provision a central place a more important determinant of space use (Thirgood et al., 2003). Thus, instead of expanding their home ranges to offset the effects of patchy resources under conditions of low forest cover, owls in our study area may have restricted their movements as a result of a greater risk of predation associated with crossing open areas (Bayne and Hobson, 2001; Turcotte and Desrochers, 2003; Fraser and Stutchbury, 2004), resulting in smaller home ranges in areas of extreme forest loss and fragmentation.

The effects of landscape composition and configuration on male foraging behaviour were also apparent through the effects of these variables on provisioning rates and subsequent reproductive success. As predicted, males breeding in more contiguous landscapes with a greater proportion of forest cover provisioned young more frequently than males nesting in more fragmented landscapes. This pattern has been observed in a number of breeding birds (Bruun and Smith, 2003; Luck, 2003; Suorsa, 2003; Tremblay et al., 2005). Although provisioning rates were not related to the distance males travelled while foraging (in contrast to Bruun and Smith, 2003; Tremblay, 2005), they were closely tied to the mean perch time of foraging males. This increase in perch time may reflect a reduction in foraging efficiency (above), either through a decrease in prey availability (Luck, 2003) or an increase in predation risk in more fragmented areas (Ruiz et al., 2002). In addition to the effects of landscape, male provisioning rates increased with brood size as they do in many bird species (Cucco and Malacarne, 1995; Olsen et al., 1998; Dawson and Bortolotti, 2003).

Predictably, males that delivered prey less often fledged fewer young, once the effect of clutch size was controlled for. A causal link between delivery rates and fledging success assumes that the number of nest visits is a reliable proxy for the biomass provided to the chicks (Nolan et al., 2001). This assumption seems reasonable in small species like saw-whet owls that are limited in the volume of prey that can be carried. Thus, our results are consistent with the studies that link provisioning rates to reproductive success (Ens et al., 1992; Henderson and Hart, 1993; Frey-Roos et al., 1995; Mairgret and Murphy, 1997) and support the contention that energy requirements of the young is an important factor limiting the productivity of nesting birds (Martin, 1987; Wiehn and Korpimäki, 1997).

Aside from the number of chicks that fledged, the immunological condition of chicks may provide additional insight into the reproductive success of males because it may be correlated with subsequent chick survival (Christe et al., 1998; Suorsa et al., 2004). Higher levels of chronic stress, as measured through haematological parameters, have been linked with lower juvenile recruitment (Lobato et al., 2005). In this study, there was no relationship between the rate of food deliveries to the nest and the mean juvenile heterophil/lymphocyte ratio within a nest. However, males who provisioned the nest less frequently fledged broods with a greater variation in physiological condition among nestlings. Lower provisioning rates may increase food stress for young within the nest leading to a higher incidence of antagonistic behaviour among nestlings (Mock and Parker, 1997). These behaviours

are associated with spikes in blood corticosterone levels (Kitayski et al., 2001), and repeated spikes may result in chronic stress, manifested by higher heterophil/lymphocyte ratios (Gross and Siegel, 1983) in marginalized nestlings.

Variation in landscape characteristics also affected the male condition, as reflected by body size and H/L ratios. Contrary to expectations, males were heavier relative to body size in landscapes with greater amounts of habitat edge and larger patch sizes. Body mass may be a function of competing influences of prey availability and predation risk (Ots et al., 1998). Landscapes with higher habitat edge may offer high small mammal availability (Mills, 1995; Bayne and Hobson, 1998; Tallmon et al., 2003), promoting an increase in body mass, but these landscapes may also promote higher predation risk (Andreassen and Ims, 1998).

As predicted, chronic physiological stress measured through H/L ratios was higher in males breeding in landscapes with lower amounts of forest cover. In these habitats, stress may result from an increased rate of encounters among conspecifics or with predators (Ruiz et al., 2002; Perez-Tris et al., 2004). Because lymphocytes are responsible for an individual's immune response, low lymphocyte numbers may reduce immunocompetence and expose individuals to an increase in infection and parasitism (Gross and Siegel, 1983; Hórak et al., 1998; Ruiz et al., 2002). Even birds exposed experimentally to predators exhibited reduced immunocompetence and increased parasitism (Navarro et al., 2004). Alternatively, saw-whet males may have been more stressed because they lived in areas with less prey or lower prey availability, causing nutritional stress that may be manifested immunologically (Suorsa et al., 2004). Although we found no significant effects of prey density on owl condition, our methods may not have provided an adequate measure of prey abundance or availability.

The effect of landscape composition, which we assessed with the percent of forest cover, on male physiological condition was exacerbated by brood size. Males feeding larger broods had significantly higher H/L ratios suggesting that higher brood demands generate chronic stress. This effect of increased brood size on parental costs of reproduction is ubiquitous in birds (Hegner and Wingfield, 1987; Hórak et al., 1998; Ardia, 2005) and mammals (Huber et al., 1999; Oksanen et al., 2002; Koivula et al., 2003). Whether from landscape or brood characteristics, higher levels of chronic stress are likely to reduce the health of males with cascading fitness implications. Other field studies of birds have shown that a reduction in immunocompetence as a result of higher levels of chronic stress can reduce subsequent survival (e.g., Saino et al., 1997) and reproductive success (Hanssen et al., 2003; Hanssen et al., 2005). Unfortunately, male site fidelity in northern saw-whet owls is low both in this study and in other areas (Cannings, 1993; Marks and Doremus, 2000) and so it was impossible to determine the relationship between immunocompetence in one season and fitness in subsequent years.

In sum, this study has shown that northern saw-whet owls exhibit changes in behaviour and reproductive success in response to variation in habitat composition and configuration. Saw-whet owls nesting in landscapes with low forest cover and high fragmentation maintained smaller home ranges and spent more time perching during foraging activi-

ties, which led to lower provisioning rates. Lower provisioning rates were associated with males that fledged fewer young and broods with a wider variation in chick condition. Finally, males breeding in landscapes with low forest cover and high fragmentation exhibited high levels of immunological stress and males inhabiting landscapes with high edge density and larger mean patch size were heavier. The changes in behaviour, physiological condition, and reproductive success we documented provide information about the mechanisms that may cause the declines in population sizes and species diversity others have documented (see reviews by Fahrig, 2003; Cushman, 2006; Ewers and Didham, 2006). In addition to explaining declines that have already occurred, our results suggest that more attention needs to be paid to the determinants of population persistence in highly fragmented habitats for common, as well as rare, species. The lower success of saw-whet owls in landscapes with low forest cover and high degrees of fragmentation may be an early warning of eventual population declines in these areas. On the other hand, our results also suggested that owls benefit from moderate levels of fragmentation, possibly through increases in potential foraging areas. Our research suggests that saw-whet owl populations would be best served by management strategies that mimic the moderately fragmented landscape that characterized the aspen parkland before European settlement.

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