Area-sensitive forest birds move extensively among forest patches

Gail S. Fraser *, Bridget J.M. Stutchbury

Biology Department, York University, Toronto, Ont., Canada M3J 1P3

Received 1 November 2002; received in revised form 2 May 2003; accepted 19 June 2003

Abstract

Habitat fragmentation is thought to create a barrier to individual movements particularly for area-sensitive species which, by definition, prefer to breed in large tracts of forest. For two breeding seasons, we radio-tracked an area-sensitive species, the scarlet tanager Piranga olivacea, in a fragmented landscape in northeastern PA. We found that scarlet tanagers made extensive and frequent movements among fragments. Paired males were less likely to leave their capture fragment, and traveled shorter distances. Unpaired males in fragments had two distinct tactics we labeled: “Sedentary” and “Mobile”. Sedentary males stayed at one fragment and sang at high rates, while mobile males spent 58% of the total time tracked off their capture fragment and traveled over a kilometer away from the capture site over open fields and through forests. Mobile males were not floaters per se because they were territorial (i.e., singing) in multiple sites. Habitat structure of a fragment did not correlate with the percent time a male spent off the capture fragment. Males in fragments experienced lower pairing success and were more likely to be first time breeders compared to males in continuous forest. Our results suggest that movements by scarlet tanagers in fragmented landscapes are not restricted during the breeding season, and that these movements are related directly to pairing status and indirectly to population density.

© 2003 Elsevier Ltd. All rights reserved.

Keywords: Forest fragmentation; Neotropical migrant; Pairing success; Corridors; Radiotelemetry; Space-use; Scarlet tanager; Piranga olivacea

1. Introduction

Many North American songbird populations are declining as result of habitat fragmentation on their breeding grounds (e.g., Robinson et al., 1995). Many studies suggest that Neotropical migrant species that prefer larger tracts of forests (“area-sensitive” birds; see Villard, 1998) are especially sensitive to forest fragmentation (e.g., Askins et al., 1987; Freemark and Collins, 1992; Lee et al., 2002). Area-sensitive birds are expected to (1) experience lower reproductive and pairing success with a decrease in forest area (e.g., Gibbs and Faaborg, 1990; Porceluzi et al., 1993; Villard et al., 1993; Robinson et al., 1995; Roberts and Norment, 1999); (2) frequently be absent in small forest fragments (e.g., Askins et al., 1987; see also Brown, 1984); and (3) prefer to use corridors and frequently avoid crossing open, non-forested areas (Sieving et al., 1996; Desrochers and Hannon, 1997; Bélisle et al., 2001; Bélisle and St. Clair, 2001). While the effects of fragmentation on the distributions of Neotropical migrant species (e.g., Lynch and Whigham, 1984; Blake and Karr, 1987; Freemark and Collins, 1992), and factors influencing reproductive success (e.g., Robinson et al., 1995; Friesen et al., 1999) have been extensively studied, little work has been done on how individuals move within and among fragments.

Community-level, temperate breeding studies have driven concepts on how populations are affected by forest fragmentation in Neotropical migrant research (Hunter, 1992), but an important gap in our understanding concerns how individuals of different species move through a mosaic environment (Wiens, 1994). Individual movements and habitat selection are key components in understanding the effects of forest fragmentation on population dynamics (Wiens, 1994). For example, edge avoidance, or a reluctance to cross open areas, are considered typical traits of area-sensitive and/or forest interior Neotropical migrants breeding in the temperate eastern forests of North America, yet for most species we have little or no empirical data to
support these ideas (Villard, 1998). Although edge avoidance or a reluctance to cross open areas appear uncharacteristic for migratory bird species, some evidence suggests that migratory birds, upon arriving at the breeding grounds, do not disperse or colonize new areas as rapidly as resident bird species (Bensch, 1999), and many of these species are particularly sensitive to habitat fragmentation (e.g., Freemark and Collins, 1992). Low breeding dispersal rates or colonization into new areas may be linked to behaviors such as site fidelity (Bensch, 1999) or higher predation risks when crossing open areas (Wiens, 1994; Grubb and Doherty, 1999).

Recent radio-tracking studies on two area-sensitive bird species demonstrate that movements between fragments are not only possible, but can occur regularly (Bayne and Hobson, 2001a; Norris and Stutchbury, 2001). Norris and Stutchbury (2001) found that male hooded warblers Wilsonia citrina leave their small forest fragments on a daily basis through the incubation and nestling stages. They crossed gaps up to 460 m in search of extra-pair copulations, despite being paired and having an active nest. Bayne and Hobson (2001a) observed no differences in the amount of movement made by male ovenbirds Seiurus auricapillus in continuous forest compared to fragmented habitat in the post-fledging period. However, males with fledglings moved less compared to those without young and rarely crossed open areas and consequently those on forest fragments were restricted in their movements compared to males in continuous forest. These studies suggest that moderate fragmentation and isolation of forest patches on the breeding grounds may not inhibit movement among patches by birds during certain periods of the breeding season. Clearly, more data on habitat use are required to understand how area-sensitive species behave in fragmented landscapes and to facilitate better strategies for their conservation.

We chose to study scarlet tanager Piranga olivacea behavior in forest fragments because this species is negatively influenced by forest fragmentation (Rosenberg et al., 1999), and scarlet tanagers are canopy birds that prefer mature forests (Mowbray, 1999). There are a number of studies that describe a positive relationship between forest area and the presence of tanagers (e.g., Robbins et al., 1989; Askins et al., 1987; Freemark and Collins, 1992; Rosenberg et al. (1999, Project Tanager) found a positive relationship between forest cover at the landscape scale and the occurrence of tanagers, although the response of scarlet tanagers to forest fragmentation varied among regions. Roberts and Norment (1999) recorded a complete absence of scarlet tanagers in fragments less than 10 ha in a highly forested area (northwestern NY). Although tanagers can occur in small woodlots (e.g., 3 ha, Galli et al., 1976; 6.5 ha, Blake and Karr, 1984), it is unclear whether these birds were breeders or vagrants (see Mowbray, 1999) because none of these studies involved radio-tracking of individuals. Here, we present the results of a radio-tracking study on scarlet tanagers in northwestern PA and describe the movements and pairing success of individuals in a fragmented landscape.

2. Methods

2.1. Study area

We studied scarlet tanagers at the Hemlock Hill Biological Research site (41°46′N, 79°56′W) and surrounding region (approximately 740 km²) in Crawford County, northwestern PA in 2000 and 2001. Male scarlet tanagers were located on 10 small isolated woodlots (<10 ha, mean = 5.3 ± 2.5 ha, range 3.2–9.6 ha), 2 mid-sized fragments (44 and 75 ha), and 2 relatively large forest plots (150, 165 ha), hereafter referred to as continuous forest. All fragmentation in this area was caused by agricultural activities and eight fragments were patches completely isolated by fields or roads, while four woodlots were connected to other forest habitat by small (<40 m wide) corridors. Mean distance to nearest forests for the 12 fragments was 138 ± 21.9 m (range 10–325 m).

We calculated the area and perimeter-area ratio of forest woodlots with a planimeter (Planix 7) from 1993, 1:40,000 aerial photographs. Perimeter-area ratio was calculated as the ratio of edge (m) to area (ha) for each fragment. Percent forest cover within 1 km of each woodlot was also estimated from aerial photographs. Based on USGS topographical maps, total forest cover for the region (740 km²) was approximately 39%. Although forest cover in some areas has increased slightly (<1%) since the production of these maps (personal observation), all of the fragments used in the study appeared to be the same size as shown on the 1993 aerial photographs. Furthermore, no major logging has occurred in any of the fragments except for one that was selectively logged (i.e., the fragment is still the same size) in the past ten years. We concluded that there has been little change in forest cover in the region since the early nineties.

The four most predominant tree groups in the forests fragments were maple Acer spp., hemlock Tsuga canadensis, American beech Fagus grandifolia, and hickory Carya spp. In the continuous forest plots the mixture was similar except elm Ulmus spp. was more common than American beech.

2.2. Radio-telemetry

We captured tanagers with song playbacks, a tanager decoy (taxidermic mount), and one 12 m long mist-net placed at standard height. Each bird was banded with a
US Fish and Wildlife aluminum band, and an individually distinct color band combination. We measured wing chord, tarsus length, and body mass (using a 50 g Pesola scale) of each adult. We aged tanagers based on plumage coloration; second-year (SY) males have brown on their primaries, whereas after second-year males (ASY) have all black primaries (Mowbray, 1999). Males (n = 31; Table 1) were fitted with a small (1.4 g), BD-2G radio transmitter (Holohil Systems Ltd, Carp, Ont., Canada) attached with a figure-8 cotton embroidery thread harness (see Rappole and Tipton, 1991). The transmitter and harness together weighed about 5% of adult body mass (average ~30 g) and the harness was designed to fall off by the end of the field season. Transmitters lasted up to 8 weeks and the range was approximately 1.5 km.

While we attempted multiple recaptures of all tanagers at the end of each season to remove the transmitter, we had a low success rate (n = 3). Nine transmitters (5 in 2000; 4 in 2001) fell off before the end of the study. In the continuous forest, males with transmitters left on at the end of the 2000 season experienced a similar return rate (67%, n = 6) to males with transmitters removed (57%, n = 7). Surprisingly, 3 males with transmitters attached in 2000 returned with transmitters still in place upon arrival on the breeding grounds in 2001 (continuous forest plot, all ASY males in 2000). These three males were the first to return in 2001, attracted females within a few days, and lost the transmitters within a month of arriving. Also, all males that were recaptured at the end of each study year had a mass that was within 1 g of initial capture mass (mean initial capture mass = 27.8 ± 1.0 g; mean recapture mass = 27.8 ± 0.29 g, n = 3). From these data, we concluded that scarlet tanagers were not negatively affected by wearing a radio transmitter (see also Powell et al., 2000).

We radio-tracked tanagers in 2 h bouts between 06:00 and 14:00, usually on foot 20–30 m away from the focal bird, however on a few occasions (2.6% of total tracking time) tanagers were tracked by car. Observations were not made during wet weather. We had a total of 359 tracking hours and each male used in our analyses had a minimum of 6 hours of tracking time (Table 1). For both years, birds were tracked between 13 May and 30 June.

Because many studies have described scarlet tanagers as forest interior or area-sensitive birds, we were particularly interested in documenting whether males moved off the isolated woodlots. We report these results, for paired and unpaired males, in percent time off capture fragment (minutes off fragment divided by total minutes tracked), and the rate off capture fragment (number of trips off fragment per hour tracked). Percent time off fragment for paired males was not divided into different breeding stages because only two of 11 pairs fledged young during our study and nests were difficult to locate, so stage of nesting was most often unknown. We also calculated percent time off territories for males in continuous forest and compared them to paired males in forest fragments with a t test. The distance traveled was calculated from topographical maps (fragments) or from grid marks (continuous forest; see below) and reported as average values. When relevant, we also reported corridor use as a percent of time tracked. All averaged values are reported with ±1 SE.

We determined whether a male was paired based on repeated sightings of a female with the focal male, or seeing her carry nest material, on a nest, or carrying food for young. We used a χ² test to compare age distribution and pairing success between fragments and continuous forest. We measured song rate (number of song bouts during a tracking period) during the radiotelemetry observations from males on forest fragments and compared paired and unpaired male rates with a t test.

We had two different methods for recording the location of a male during a tracking session and determining subsequent territory size, depending on which plot a male was tracked in. The 150 ha forest had conspicuous grid marks every 50 m; the location of a male tracked on this plot was recorded by noting the closest grid mark whenever the bird moved. We measured territory size with a planimeter for each tracking session and reported the average territory size for each male. The location of males in forest fragments or in the 165 ha plot were recorded by noting their position relative to

Table 1
A summary of telemetry on scarlet tanagers in Northwestern PA

<table>
<thead>
<tr>
<th>Year</th>
<th>Continuous</th>
<th>Fragment</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>110.8</td>
<td>114.2</td>
</tr>
<tr>
<td>2001</td>
<td>30.1</td>
<td>104.1</td>
</tr>
<tr>
<td>Mean tracking time (h ± SD)</td>
<td>11.1 ± 3.6</td>
<td>12.7 ± 4.5</td>
</tr>
<tr>
<td>Mean range of tracking time (all males)</td>
<td>6–14.7</td>
<td>6–19.5</td>
</tr>
<tr>
<td>Number of males tagged</td>
<td>10</td>
<td>9c</td>
</tr>
</tbody>
</table>

*a Males tracked on 150 ha plot only.
*b Males tracked on 150 and 165 ha plots.
*c One male each year was captured in a fragment and then settled in continuous forest.
obvious landmark features. At the end of each season, we mapped all movements for males, measured the extent of these movements with a 50 m tape and used a planimeter to determine territory size (i.e., area defended with song). Movements off territories for continuous forest males were assumed when males moved greater than twice the distance away from the perimeter of their territory (i.e., usually 100 m or more) and were in other males’ territories. Movements off fragments for males in forest fragments were considered time off territory and these movements were not included in the area estimate. Four males used and defended an entire woodlot, therefore we considered the whole fragment to be their territory.

We found that some males in fragments not only gained a partner mid-season, but that they also switched territories mid-season (i.e., from a fragment to continuous forest); therefore, we report the final status (e.g., paired or not, and in fragment or continuous forest) of male tanagers as they were by the end of the telemetry work (30 June for both years, or sooner if the transmitter fell off).

2.3. Habitat structure and movements off territories

Habitat structure, which can influence prey abundance (Smith and Shugart, 1987), may also determine how often males leave their fragments or territories. We examined (1) whether there was a relationship between amount of movement off a forest fragment and the fragment’s habitat features, (2) whether movements in continuous forest were related to the habitat features of territories, and (3) whether paired males’ habitat differed between continuous forest and forest fragments. We measured habitat characteristics with the James and Shugart (1970) method. For each territory we used 5–0.02 ha plots. The initial plot was positioned at the center of the territory, while the other 4 plots were positioned 50 m from the center, in each cardinal direction. For each territory we determined tree density (number of trees per ha), average diameter of tree at breast height (cm), number of tree species, total log basal area, % canopy cover, canopy height (m), and shrub density (number of shrub stems per ha). Many of our variables were correlated, therefore we log transformed all the variables and used a Principle Components Analysis (PCA; correlations matrix) to collapse our dataset (McGarigal et al., 2000). We used principle components (PC) I and II, % forest cover within 1 km, and perimeter–area ratio, in a backwards step-wise regression with percent time off fragment (arcSin transformed; Zar, 1996) as the dependent variable for males on 12 fragments (Mobile males not included, see Section 3). If a fragment had more than one male in both study years (n = 3), we averaged the percent time off territory for all males in the fragment. In addition, if a fragment had more than one vegetation plot (n = 1), we averaged the values for this analysis.

We repeated the PCA and backwards step-wise regression for 13 territories in continuous forest, excluding perimeter–area ratio as a variable with the dependent variable as percent time off territory. Percent forest cover was included in the regression because some males were on the edge of the forest (n = 5). We included edge and interior territories in one step-wise regression because we found no difference in percent time off territory between males in the two areas (p = 0.8) and because of our limited sample sizes. Finally, we compared habitat features (canopy cover and height, log total basal area, and shrub and tree density) between continuous forest (n = 12) and fragment plots (n = 10) for paired males in a series of t tests.

2.4. Occupancy of forest fragments

We used a playback system to survey 13 woodlots in May 2000 (mean area ± SD = 10.1 ± 19.6, range 3.0–75 ha) and 15 woodlots in May 2001 (mean area = 11.9 ± 19.6, range 3.0–75 ha) to estimate percent occupancy of isolated forest fragments. Fragments with tanagers (either banded or unbanded) observed more than once were considered occupied. In all but two cases each year, the males with transmitters were the only color-banded individuals present in the fragments.

3. Results

3.1. Radio-telemetry

3.1.1. Movements of males in forest fragments: paired versus unpaired behavior

Paired males were less likely to leave their capture fragment than were unpaired males (t test, n = 11, 8; t = −2.8, p = 0.01) and traveled shorter distances than unpaired males (t test, n = 6, 8; t = −3.15, p = 0.01; Table 2). Paired males also had significantly lower song rates than unpaired males (paired: mean = 0.4 ± 0.1 songs/min; unpaired: mean = 2.5 ± 0.3 songs/min; (t test, n = 11, 6; t = −7.4, p < 0.001). We found no differences in territory size between paired and unpaired males (Mobile males not included—see below) in fragments (t test, n = 11, 4; t = −2.0, p = 0.06; Table 2).

Observations of paired males off territories (i.e., off fragment) can provide insights into the reasons for these movements. Only six of 11 paired males moved off their forest fragments and we observed considerable variation in the number of times these movements occurred. Three paired males only left once out of the total time tracked (24.2 h; mean per male = 8.1 h): two males (with no young) left for unknown reasons (no visual observations of them) and the third (nesting status unknown) was
observed foraging off territory. One paired male (with no young) left twice out of total time tracked (12.1 h), and on one of these occasions he was engaged in a male-male chase. The last two paired males left multiple times (>3) over the course of the total time tracked (33.7 h; mean per male = 16.9 h). One male spent 17% of his time in a neighboring fragment (200 m away) and was also observed there with a female. This pair also spent 52% of their time in an adjacent corridor (40 × 10 m) where on one occasion, they were observed foraging with fledglings on ripe elderberry berries (Sambucus nigra). The second male increased his time off the capture fragment from 2% during incubation stage to 28% during the fledgling stage. He was observed singing during the incubation stage in a neighboring fragment and foraging during the fledgling stage in this same fragment and once more in another nearby forest.

We found that tanager pairs (4/11) on forest fragments sometimes moved territories mid-season. Two males disappeared immediately after nest predation events, and they were not subsequently observed (either visually through playbacks or by radio transmitter signals) in their fragment or in nearby forests for the remainder of the field season. Two other pairs moved three times to different territories within a season. Final territories were 300 and 400 m away from the original territories and were entirely off the capture fragments; one pair moved to a neighboring fragment (approximately twice as large as the capture fragment), the other pair moved to continuous forest.

We found that unpaired males (all SY; n = 8) adopted one of two distinct tactics that we describe as: (1) Sedentary and (2) Mobile. Sedentary males (n = 4) spent the majority of their time in their capture fragment singing at high rates (Table 2). Mobile males (n = 4) moved over open fields and through forests and were off their capture fragment more than 50% of the time tracked (e.g., Fig. 1(a); Table 2). Unlike secretive floaters (e.g., Zack and Stutchbury, 1992), Mobile males advertised by singing on the original capture fragment (territorial behavior that allowed us to initially capture them). Mobile males were difficult to follow because we did not know where they would be from one day to the next and they were often out of transmitter range (approximately 1.5 km) at the time of a scheduled tracking session. For example, one male was out of transmitter range 11 out of 18 days we attempted tracking and he was located in the capture fragment on only three out of the remaining seven days. Yet when he was on the capture fragment he would respond to playbacks (i.e., was territorial). A conservative estimate of the total area utilized by Mobile males (n = 3) averaged 122 ± 99 ha. The fourth Mobile male likely had a similar range as the other males, but we only located him once off the capture fragment and consequently could not estimate the total area traveled.

The mating status of unpaired males sometimes changed comparatively late in the breeding season. Three males gained females mid-season (two Sedentary – 14 June and 7 July; one Mobile – 18 June). The two Sedentary males (both the sole occupants of each fragment) were counted as unpaired in the data analysis because one male’s transmitter fell off before pairing occurred and the other male gained a female after the end of our study. The one Mobile male we were able to track after he was paired behaved

| Table 2 |
| Movements of radio-tracked male scarlet tanagers in fragments and continuous forest |
| Continuous | 
| Paired | Unpaired |
| No. of males | 12 | 1 |
| Percent time off fragment or territory | 4.7 ± 4.3** | 1.1 |
| No. times off fragment or territory per hour | 0.2 ± 0.2 | 0.17 |
| Distance traveled (m)** | 106 ± 16.5** | 25 |
| Territory size (ha)b | 0.9 ± 0.2* | 0.6 |

| Fragment | 
| Paired | Unpaired |
| Stay and sing | Move and sing | Total |
| No. of males | 4 | 4 | 8 |
| Percent time off fragment or territory | 5.7 ± 2.2 | 6.7 ± 2.6 | 57.8 ± 8.5 | 32.3 ± 10.5 |
| No. times off fragment or territory per hour | 0.2 ± 0.07 | 0.2 ± 0.09 | N.A.* | 0.2 ± 0.09 |
| Distance traveled (m)** | 173 ± 27 | 467.0 ± 144.8 | 1120 ± 204 | 793.4 ± 169.1 |
| Territory size (ha)b | 1.6 ± 0.3 | 3.2 ± 0.9 | N.A.* | 3.2 ± 0.9 |

Values are mean ± SD.

**Corridors were not used in movements. Distances are calculated as one-way trips. Sample sizes differ from number of males tagged because mean distance traveled is only from males that left their territory.

bTerritory size calculated from tagged males only.

*Because Move and Sing males were off their capture fragment more than 50% of the time tracked and did not make discrete movements related to their capture fragment we did not calculate the number of times off fragment per hour or territory size. t Tests between paired males in fragments versus paired males in continuous forest.

*p = 0.05.

**p = 0.04.
similarly to paired males observed at the beginning of the season (Fig. 1).

3.1.2. Age structure and pairing success: fragments versus continuous forest

SY males were more likely to be in forest fragments (14/17), whereas ASY males were more likely to be found in the continuous forest (27/30; $\chi^2 = 24.6, p < 0.0001$; Table 3). SY males (9/17) also experienced lower pairing success than ASY males (28/30; $\chi^2 = 10.6, p = 0.001$; Table 3). All three ASY males in forest fragments were paired, while only one SY male in continuous forest was unpaired.

### Table 3

<table>
<thead>
<tr>
<th></th>
<th>Continuous forest</th>
<th>Forest fragments</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. males*</td>
<td>30</td>
<td>17</td>
</tr>
<tr>
<td>Age ratio (SY:ASY)</td>
<td>3:27</td>
<td>14:3</td>
</tr>
<tr>
<td>No. paired males</td>
<td>27 (2, 25)</td>
<td>10 (7, 3)</td>
</tr>
<tr>
<td>(SY, ASY)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Pairing success</td>
<td>90%</td>
<td>59%</td>
</tr>
</tbody>
</table>

One SY unpaired male was captured in a fragment, but settled with a female in continuous forest (see Fig. 1). Another ASY paired male was initially in a fragment for two weeks (20 May–3 June) then moved to continuous forest with, presumably, the same partner. Both of these males were placed in the continuous forest category.

*Includes all birds intensively followed from both study years, including individuals that were not banded. For radio-tagged birds location and pairing status of males is that at end of study (30 June).

3.2. Habitat structure, movements off territories, and corridor use

Principle component scores I and II explained 64% of the variance in the data matrix for forest fragment habitat. We interpreted PCI to be representative of canopy height and cover (magnitudes of loading 0.52, 0.49, respectively; all other variables < ±0.42) and PCII to be representative of tree density (loading 0.77; all other variables < ±0.34) for forest fragment habitat. Canopy height and cover (PCI), tree density (PCII), edge density, or the amount of forest cover within 1 km did not influence the probability of a male leaving his territory (backward stepwise regression, no variables remained in model, $R^2 = 0.00, n = 12$; does not include Mobile males).

Principle component scores I and II explained 65% of the variance in the data matrix for continuous forest territories. We interpreted PCI primarily as diameter at breast height (DBH) (loading 0.61; all other variables < ±0.42) and PCII was most influenced by canopy height and the number of tree species (loading 0.51, 0.49, respectively; all other variables < ±0.47). DBH (PC I), the number of tree species and canopy height (PC II), or the amount of forest cover within 1 km did not influence the probability of a male leaving his territory (backward stepwise regression, no variables remained in model, $R^2 = 0.00, n = 13$).

Paired males in continuous forest resided in forests with significantly taller canopy and increased total basal area compared to paired males in fragments (Table 4). In the two years of our study, we tracked scarlet tanagers in 12 fragments. In four fragments we captured both paired and unpaired males in both study years. Because both paired and unpaired males were captured on these fragments, we suggest that there are no special habitat features related to pairing success. In six fragments, we captured only single paired males, and in the last two fragments we captured only single unpaired males (Table 4).
Four fragments had forest corridors available for tanagers to use in their movements. Six males (two unpaired, four paired) were tracked on these fragments (Table 5). Two males were observed using (or flying in the direction of) a corridor when leaving the same fragment (different years). The first male just went into the corridor and no further. The second male not only used a corridor to go to an adjacent fragment, but he also spent 52% of the time tracked in the corridor and we considered this area part of his territory (Section 3.1.1). All other movements, on both the remaining fragments with corridors and the eight fragments without corridors, during tracking sessions, were across fields and roads (Table 5).

3.3. Occupancy of fragments

In May of 2000 and 2001, 77% (10/13) and 73% (11/15) of the fragments surveyed were occupied. Eighty-one percent (9/11) of fragments of <10 ha were occupied in 2000 and 83% (10/12) were occupied in 2001.

4. Discussion

Current theory predicts that area-sensitive, or forest-interior birds, occur more frequently in larger habitat patches, experience lower pairing success with a decrease in forest area, and avoid crossing open gaps. Yet scarlet tanagers in our study made extensive and frequent movements among fragments without using corridors and had a high occupancy rate in small forest fragments <10 ha, observations not supportive of current predictions for area-sensitive species. On the other hand, some of the patterns we observed were consistent with the negative effects of fragmentation: the proportion of SY tanagers was greater in forest fragments than in continuous forest and males in fragments experienced lower...
pairing success. Tanagers in large forests had higher pairing success and were more likely to be ASY, but SY males on forest fragments were not restricted in their movements by the fragmented landscape.

4.1. Movements off fragments

Tanagers’ movements were not restricted to their capture fragment. Movements off fragments seemed to have a variety of causes including foraging, male-male chases, and mate searching. Paired males were less likely to leave their capture fragment than were unpaired males, which suggests that a primary motivation for unpaired male movements off fragments was to find a mate. The extreme of this behavior was the Mobile male strategy. Because there was no difference in the amount of movement off territories for paired males in fragments and continuous forest, we conclude that paired males react similarly to the surrounding landscape independent of whether they are in fragments or continuous forest.

Comparisons to other radio-tracking studies are limited because very few exist for Neotropical migrants on the temperate breeding grounds (Norris and Stutchbury, 2001; Norris et al., 2000 and Bayne and Hobson, 2001a). Compared to hooded warblers, paired tanager males left their fragments less frequently. Norris and Stutchbury (2001) found that both paired and unpaired male hooded warblers left their fragments and returned, as much as once every two hours, and crossed gaps in search of extra-pair matings through the incubation and nestling stage.

Some tanager movements off fragments were permanent changes in territory location after nest failure. In the two cases where we were able to follow the birds, both moved to areas where other tanagers were present and one moved into continuous forest. Changing territory sites may be an attempt to increase the likelihood of success of the second nesting attempt, and this behavior has been noted in other species. For example, prairie warblers (Dendroica discolor) frequently changed mates and territories within a breeding season in association with nest failure (Nolan, 1978).

We discovered a previously undescribed behavior used by forest birds to search for mates, Mobile males. We found that Mobile males moved and advertised their position among both fragments and continuous forest in search of a mate, a form of continuous dispersal throughout the breeding season. Both mate finding tactics (i.e., Sedentary and Mobile) sometimes were successful at attracting females mid-season and this success was likely related to re-nesting attempts, although only three of the nine unpaired males found mates. The success of Sedentary males in attracting a female suggests that females were also moving among forest fragments. Males that pair later in the breeding season might still have an opportunity to rear chicks because we have preliminary evidence that at least some scarlet tanagers in this area will double brood and re-nest (unpublished data). Thus, scarlet tanager females may be reproductively available for longer periods of time than in single-brooded species. With some level of double brooding and re-nesting, scarlet tanagers may be able to maintain viable populations in some fragmented habitats, as Friesen et al. (1999) concluded for wood thrush (Hylocichla mustelina) breeding in small forest fragments in southern Ontario. More work is needed to understand the role that female tanagers have in nest site selection in a fragmented landscape, and in mate choice and retention within and between seasons.

Our study demonstrated variation in male scarlet tanager behavior was mostly related to pairing status. Unpaired males were much more likely to leave their capture fragment and sing in multiple sites, which may mean that during annual breeding bird surveys (Sauer et al., 2002) tanager densities may be overestimated. However, paired males had significantly lower song rates than unpaired males, so they may go undetected more often during breeding censuses. These two effects may partially cancel each other out.

4.2. Age structure and pairing success

Pairing success can be influenced by factors such as age (e.g., Sherry and Holmes, 1989; Bayne and Hobson, 2001b) and location of breeding territory (i.e., fragment or continuous forest). In our study, 83% of scarlet tanager males in forest fragments were SY birds that experienced lower pairing success compared to males in the continuous forest plot. Although most males in the fragmented habitat were unpaired SY males, ASY males with territories in forest fragments (n = 3) experienced 100% pairing success, suggesting that age is also an important factor in female mate choice in scarlet tanagers. Roberts and Norment (1999) observed lower pairing success for tanagers in smaller forest fragments (areas <1000 ha), though pairing success was higher in their forest plots compared to ours (see below). Differences in pairing success due to area effects has been documented in ovenbirds (Villard et al., 1993; Van Horn et al., 1995), but Villard et al. (1993) suggest that low pairing success for males in forest fragments may also be related to higher local population density.

4.3. Habitat structure, movements off capture fragments, and corridor use

In their extensive study on tanagers, Rosenberg et al. (1999) found that regional forest cover affects the sensitivity of scarlet tanagers to forest fragmentation. In areas with higher amounts of regional forest cover, such as the US northeast, tanagers may occur in smaller
As population density increases SY males may have less opportunity to establish a territory on preferred larger forest patches through competitive interactions with ASY males (see Sherry and Holmes, 1989) and consequently experience lower pairing success. It follows that as density decreases the occupation of smaller forest fragments should also decrease, but the proportion of paired SY males should increase (Weins, 1976; Brown, 1984; Villard et al., 1993). The differences we observed in scarlet tanager pairing success, patch size occupancy, and territory size between our study and one conducted less than 150 km away in upstate NY (Roberts and Norment, 1999) implicates regional population density as a major factor in determining these differences. Roberts and Norment (1999) found that scarlet tanagers were not present in forest fragments of less than 10 ha in upstate NY, whereas we frequently found scarlet tanagers moving among fragments. Thus, our findings appear to support Project Tanager's (Rosenberg et al., 1999) conclusions on the importance of regional forest cover, and help explain why scarlet tanager area-sensitivity varies across regions.

Our results show that a species exhibiting an “area-sensitive” pattern of fragment occupancy (e.g., Roberts and Norment, 1999) cannot be assumed to be limited to forest-interior habitat. Based on Project Tanager results (Rosenberg et al., 1999), and the fact that scarlet tanagers are canopy birds that prefer mature forests (Mowbray, 1999) we would never have predicted that scarlet tanagers would move around extensively once they established a territory in a fragment. This kind of empirical work challenges long-held assumptions about how birds behave in fragmented landscapes, how far they move, and to what extent gaps represent a barrier to daily movements. To date, three of three “area-sensitive” birds studied (hooded warbler, ovenbird, and scarlet tanager; Norris and Stutchbury, 2001; Bayne and Hobson, 2001a, this study, respectively) are actually not area-sensitive in terms of movements. Nonetheless, species may still be considered area-sensitive if their probability of occurrence increases with habitat patch size. However, area-sensitive species should not be assumed to avoid edge habitat, rely on corridors, or avoid crossing open fields (Villard, 1998).

Many researchers emphasize the importance of core forest area, or forest interior, when assessing how bird populations and nesting success are affected by fragmentation. We suggest that small fragments are more important to these forest birds than previously appreciated. In our study area, smaller forest patches located amongst larger forested areas appeared to allow SY unpaired males to readily move around and prospect for breeding sites or mates in different locations and they may be particularly important in regions with higher population densities. If regional density can be estimated, managers may be able to make informed decisions about how important smaller fragments are for tanagers and potentially use tanagers as a model for other Neotropical migrants (Wiens, 1994). In our study area, all but one of the fragments was privately owned, which emphasizes the importance of private land in reserve networks (Wiens, 1994). Landowners educated about the importance of these woodlots could choose to make informed decisions on tree harvesting. For example, one landowner in the area harvested two large trees off 3.7 ha fragment, but removed them in a relatively non-destructive manner (using a horse) leaving the canopy fairly intact.

Rosenberg et al. (1999) stress caution in extrapolating results from one study to the whole species because of the variation in tanager response to fragmentation among different regions. Observed variation in breeding
behavior just within one region (US northeast; Roberts and Norment, 1999, this study) is further support for caution in suggesting broad recommendations on habitat management for scarlet tanagers. From this study, we concluded that many of the reasons for movements in a fragmented habitat are related to breeding adult dispersal. However, our study also demonstrates the need to understand: (1) the array of behavioral responses to fragmentation in various regions with different levels of forest cover and population densities; (2) whether smaller forest fragments are reproductive “sinks” rather than “sources” (see Pulliam, 1988); and (3) how fledging dispersal may be affected by fragmented habitat.

Acknowledgements

We thank Hemlock Hill Biological Research Area and all of the land owners for permission to conduct research. This project was funded by awards to BJMS from the Molson Foundation, the Premier’s Research Excellence Award, and the Natural Sciences and Engineering Research Council of Canada. Bianca Capuano, Kevin J. Cooper, Ryan Norris, and Mari Ortwerth all provided excellent field assistance. A special thanks to M. Ortwerth and K. Cooper for their hard work. Thanks to Steve Woolfenden for his help in calculating territory and fragment sizes, and to Eugene Morton and Bonnie Woolfenden for lively tanager discussions. Bev Brown, Laurence Packer, Scott Robinson, Scott Rush, and two anonymous reviewers contributed useful comments on an earlier draft.

References


