

Response to clear-cut logging by northern waterthrushes

Ian G. Warkentin, Allison L. Fisher, Stephen P. Flemming, and Shawn E. Roberts

Abstract: We examined the distribution and foraging behaviour of northern waterthrushes (*Seiurus noveboracensis*) in recently harvested and intact landscapes of Newfoundland. Data were collected along six 1-km segments of stream and adjoining upland habitat resulting in four treatments (harvested or intact, upland or stream) with three replicates each. Although known as a riparian specialist, we found waterthrush territories equally distributed across intact upland and riparian habitats. However, few waterthrushes occupied harvested uplands, while large numbers packed into riparian buffer strips adjacent to these 5- to 10-year-old postharvest clearcuts. Arthropod abundance and biomass were highly variable between years and across the four treatments, generating significant year \times treatment interaction effects. Riparian habitat (in both intact and harvested areas) had consistently greater numbers of arthropod prey and more biomass than either upland habitat type. Northern waterthrushes foraging in riparian habitat adjacent to harvested uplands had lower attack rates and more frequent long flights than waterthrushes foraging in the intact treatment types. Prolonged packing of individuals into riparian buffer strips, and apparent adverse effects on waterthrush foraging efficiency, raise concerns about the effectiveness of buffer strips for sustaining viable populations of terrestrial riparian habitat specialists.

Résumé : Nous avons examiné la répartition et le comportement alimentaire de parulines des ruisseaux (*Seiurus noveboracensis*) dans des paysages récoltés récemment et des paysages intacts à Terre-Neuve. Des données ont été récoltées le long de six segments de 1 km d'habitats riverains de ruisseaux et d'habitats non riverains adjacents pour un total de trois répétitions de quatre traitements (récolté ou intact, riverain ou non riverain). Malgré que la paruline des ruisseaux soit reconnue comme spécialiste du milieu riverain, nous avons trouvé autant de territoires dans les habitats riverains et non riverains intacts. En revanche, peu de parulines ont occupé les habitats non riverains récoltés tandis qu'elles se sont entassées en grand nombre dans les lisières boisées riveraines adjacentes aux coupes à blanc vieilles de 5 à 10 ans. L'abondance et la biomasse d'arthropodes variaient beaucoup entre les années et les traitements, ce qui a donné des interactions significatives années \times traitements. Le milieu riverain (dans les paysages intacts et récoltés) avait des nombres de proies (arthropodes) et des biomasses nettement plus élevés que le milieu non riverain. Les parulines des ruisseaux s'alimentant dans les habitats riverains adjacents à des coupes attaquaient moins souvent et faisaient plus de longs vols que celles s'alimentant dans les milieux riverains et non riverains intacts. L'entassement prolongé des individus dans les lisières boisées riveraines, de même que les effets adverses apparents sur l'efficacité d'alimentation des parulines, soulèvent des inquiétudes quant à la capacité des lisières boisées à maintenir des populations viables de spécialistes des habitats riverains terrestres.

[Traduit par la Rédaction]

Introduction

Riparian zones with natural disturbance regimes are critical sources of ecological diversity on a regional scale (Naiman et al. 1993). Many jurisdictions across North America now require that forestry operations incorporate practices that recognize the importance of this habitat (Knopf et al. 1988; Canadian Forest Service 1993). Thus, in forested landscapes undergoing timber harvesting, buffer strips of undisturbed native vegetation along lakeshores,

and streams are maintained to protect aquatic habitats and species as well as water quality. However, the extent to which these buffer strips are an effective means of preserving terrestrial wildlife communities is unclear. One area of research arising from the latter point concerns the width of buffer strips required to protect terrestrial wildlife. Many studies have found that the level of biological diversity for terrestrial species such as songbirds is closely associated with the width of the buffer strip preserved through these modified timber harvesting practices (e.g., Stauffer and Best 1980; Darveau et al. 1995; Hagar 1999; Pearson and Manual 2001). But since few such studies have focussed on the terrestrial species that specialize on riparian habitat (Wiebe and Martin 1998; Whitaker and Montevecchi 1999), it is difficult to determine the effectiveness of buffer strips for conserving riparian-dependent species.

One species widely identified as a riparian habitat specialist in North American boreal forests is the northern waterthrush (*Seiurus noveboracensis*). Studies in northern British Columbia (Wiebe and Martin 1998), southern Que-

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bec (LaRue et al. 1995), and western Newfoundland (Whitaker and Montevecchi 1997) all found this species to be most closely associated with the band of deciduous riparian vegetation immediately adjacent to boreal forest streams. Further research by Whitaker and Montevecchi (1999) suggested that northern waterthrushes use of 20- to 50-m-wide buffer strips was similar to their use of the same band of riparian habitat adjacent to intact upland forest.

We examined the distribution, reproduction, and foraging behaviour of northern waterthrushes in riparian and upland habitat of disturbed and intact forested areas of western Newfoundland. Our objective was to evaluate the response of this riparian habitat specialist to forestry practices that create large clearcuts but retain buffer strips in the resulting postharvest landscape. This project expanded upon the work of Whitaker and Montevecchi (1997, 1999) by using multiple response variables that, when examined together, may show greater sensitivity to habitat disturbance than transect-derived density measures. Specifically, we measured reproductive parameters and foraging behaviours of northern waterthrushes in intact riparian forest and adjacent upland areas. We compared these values with those obtained for waterthrushes breeding in riparian buffer strips and the recently cleared, adjoining upland habitat. Habitat specialists may be more sensitive to disturbance than generalists. Thus, evaluating the effectiveness of buffer strips for maintaining viable northern waterthrush populations will aid our understanding of how this forestry practice contributes to the successful management of biodiversity in Canada's boreal forests.

Study areas

We conducted this study on the west coast of insular Newfoundland, Canada. The boreal forest of the Western Newfoundland Ecoregion (Damman 1983) is dominated by 50- to 100-year-old balsam fir (*Abies balsamea*). Forest fires are uncommon and natural succession is insect driven (Meades and Moores 1994). Many stands regenerate directly to balsam fir canopies, although black spruce (*Picea mariana*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*), red maple (*Acer rubrum*), and eastern larch (*Larix laricina*) occur where site conditions are suitable. Ground cover ranges from moss-dominated poor-quality sites to rich layers of herbaceous plants and ferns. Bogs, fens, and other wetlands are common and the topography is typically rolling to rugged. Riparian zones frequently are bordered by dense shrub stands heavily dominated by alder (*Alnus crispa* and *Alnus rugosa*). The climate is wet, with annual precipitation averaging nearly 1200 mm (Damman 1983) and a mean annual temperature of 5.2°C (Scruton et al. 1995).

Clear-cut harvesting is the primary method of timber extraction in Newfoundland; it occurs on a large scale (>25-ha plots) and typically involves cutting adjacent stands in rapid succession and in close proximity to each other (cf. Whitaker and Montevecchi 1999). This results in watersheds with extensive clearings broken by riparian buffer strips at least 20 m wide as well as remnant patches of trees on steep slopes, wet soils, or high ground. Vegetation regrowth on these clearings typically results in a dense stand that, in the

5- to 10-year postharvest period, includes regenerating balsam fir, white birch, trembling aspen (*Populus tremuloides*), and wild raspberry (*Rubus idaeus*), along with various herbaceous species.

We conducted this research along six 1-km segments of streams and in adjoining upland habitat. The locations of disturbed and intact stream segments were chosen based on the similarity of stream features among sites and were not allocated at random. Three study areas (referred to hereafter as disturbed) were southwest of Corner Brook (approximately 48°55'N, 58°03'W) immediately adjacent to cut-blocks that had been harvested from 5 to 10 years previously (i.e., 1990 for site 1, 1992 for site 2, and 1994 for site 3). Subsequent harvesting within a 3-km radius for site 1 did not occur after 1995. Site 2, located 3.2 km from site 1 and 10.1 km from site 3, had no harvesting within a 3-km radius from 1995 until 2000 when a large area extending from just inside the 3-km-radius boundary and outward was harvested. For site 3, located 10.6 km from site 1, there was ongoing harvesting within 3 km during the winters prior to all three years of our study. Our control areas (referred to hereafter as intact) were approximately 60 km away, located in and adjacent to Gros Morne National Park of Canada (approximately 49°27'N, 57°40'W) where forests are largely free from clearing with the exception of some small-scale (<<1-ha plots) domestic harvesting which was ongoing in the vicinity of our study areas. These intact sites were 7.1, 9.8, and 14.8 km apart from each other. Each of the six stream segments was marked off at 50-m intervals to aid in the mapping of territories. In addition, we marked the perimeter of the upland habitat from stream edge to 300 m away on one randomly chosen side of each 1-km stream segment.

Materials and methods

Prey abundance

We determined arthropod abundance and biomass for five locations at 200-m intervals along each 1-km stream segment and for appropriate locations (i.e., where waterthrushes had been seen foraging) 40–75 m away in the adjacent upland habitat. Data were collected 30 June – 7 July 1999 and 28 June – 6 July 2000. For all locations, we took samples representing substrates (foliage, soil–litter surface, and air) that correspond to waterthrush foraging activities reported by Craig (1984). At stream-side sites, we also took samples from stream sediment surfaces and the stream surface itself to correspond to the aquatic foraging activities of waterthrushes (Craig 1984). Sampling protocols were as follows. (i) For arboreal-dwelling arthropods, the outer 25 cm of foliage from deciduous and coniferous branches at 1 and 2 m heights were separately bagged and then clipped and shaken vigorously to remove loose arthropods (Ramsay et al. 1999). We then removed the branches from the bag and inspected them visually to collect any other arthropods present. We added 70% ethanol to the bag to kill and preserve the arthropods for later identification, counting, and measurement. Branch clippings were collected in early morning. (ii) To sample ground-dwelling arthropods, we left a pitfall trap (250-mL jar with 50 mL of 70% ethanol, sunk so that the top was flush with the ground) for 24 h at each site (Atlegrim and Sjöberg 1995). (iii) Flying arthropods were

sampled using sticky traps (Skagen et al. 1998). Opposite sides of a 12 × 18 cm piece of cardboard were coated with Tanglefoot® and suspended for 24 h in vegetation 0.5 m from the ground. Boards were bagged and frozen for later identification, counting, and measurement of arthropods. (iv) For stream-side locations, we sampled aquatic sediment surfaces at three spots within 10 m of the location using a 1-m² Surber sampler with a 240-µm-mesh net (Surber 1937; Baumgartner and Waringer 1997). Arthropods collected from all three spots were washed with 70% ethanol from the net into a Whirl-pak bag for storage. (v) Additionally, we sampled the stream surface by sweep-netting over a 10-m distance in triplicate with a 240-µm-mesh net. The captured arthropods were washed with 70% ethanol into a Whirl-pak bag for storage.

We identified arthropods to order and recorded the number and length (to the nearest 0.5 mm) of each individual for those orders that have been identified as part of the normal northern waterthrush diet (Eaton 1957; Craig 1987). Biomass for each individual was estimated based on applying the formula $M = 0.0305L^{2.62}$, where M is the biomass (mg) and L is the length (mm) (Skagen et al. 1998).

Territories and nests

Teams of three trained observers conducted surveys for singing males at each site on an approximately weekly basis from mid-May through late June 1998–1999 and mid-May through mid-June 2000. Observers systematically walked along the stream and through adjacent upland habitats for 18 search-hours per week at each site. We mapped the territories of singing males (aided by some colour banding but most often by the simultaneous singing of males on adjacent territories; Bibby et al. 2000) and located nests when possible. We considered any mapped area where a male was heard singing on at least four visits to be an occupied territory (Vickery et al. 1992). The survey period coincided with the first arrival of male northern waterthrushes into the region (detection by independent sources of first singing male heard varied from 17 to 20 May over the three years) as well as median first egg dates of 1 June in the Corner Brook area ($n = 11$, range 25 May – 10 June) and 6 June in the Gros Morne area ($n = 9$, range 31 May – 17 June). The minimum length of occupancy and timing of surveys largely ensured that all detected northern waterthrushes were on established breeding territories, although not that they were producing young. Territories that bordered the main stream or encompassed smaller streams and ponds in the upland zone were considered to be occupying riparian habitat; all others were classified as occupying upland habitat for the purposes of data analyses. Nests (inventoried only in 1998 and 1999) were monitored every 3–4 days as needed to determine laying dates, clutch size, and reproductive output for each territory. Young that reached day 6 of the 9-day nestling phase (Eaton 1995; I.G. Warkentin, unpublished data) were considered to have successfully fledged (although most were visited at least on day 7). We compared nest success during the incubation and nestling periods, as well as overall, between intact and disturbed habitats (riparian and upland combined) using descriptive statistics from the Mayfield method (Mayfield 1975; Johnson 1979).

Foraging behaviour

We conducted focal animal sampling of foraging individuals on an opportunistic basis from mid-June through mid-July 1999 and 2000. Observations were collected using binoculars and a portable cassette player to record location (intact versus disturbed), foraging manoeuvre–attempt (e.g., probes, gleans, and other foraging techniques as defined by Remsen and Robinson 1990), movements (steps, hops, and flights more than 2 m), and the length of the observation (seconds). A maximum of 10 min per individual was included in data analyses; observation segments less than 30 s long were excluded. In addition to examining the data for each variable standardized for time, we assessed differences between individuals in intact and disturbed habitat in terms of the number of prey attacks per step.

Statistical analyses

Except where noted, the comparison groups were intact riparian, intact upland, disturbed riparian, and disturbed upland with three replicates of each treatment. We performed repeated-measures analysis of variance (ANOVA) using PROC GLM (SAS Institute Inc. 1988) on $\log(x + 1)$ transformed data for number of arthropod prey (per order and combined across orders) and prey biomass (per order and combined across orders) and territory density. The data were subject to post hoc examination using Student–Newman–Keuls (SNK) tests to assess variation across treatments within years (Zar 1996). Because of limited sample sizes for observations of foraging individuals, we based these analyses on pooling individuals across replicates and years; thus, n reflects the number of observed foraging sequences for each habitat type. These foraging data ($\log(x + 1)$ transformed, as arcsine transformations were unsuccessful in normalizing the data) were analysed using one-way ANOVAs to examine the number of foraging attempts, steps, hops, and flights per second as well as the number of foraging attempts per step. Nest success data for intact and disturbed habitats were compared using a Fisher exact test (Zar 1996).

Statistical tests involving prey abundance, territory number, and nest success were considered significant at $P = 0.05$. Given the small sample size for our foraging observations, we consider these to be exploratory analyses and set the level of significance at $P = 0.10$ (Steidl et al. 1997).

Results

Prey abundance

Arthropod abundance and biomass were highly variable from year to year across treatments when examined both at the level of individual orders and for values combined across orders. We identified 5951 individuals from 13 orders (Table 1) that normally occur in the diet of northern waterthrush as summarized by Eaton (1995). Repeated-measures ANOVA of abundance data revealed one order (Orthoptera) with a significant treatment effect (i.e., different values among the four treatments: intact riparian, intact upland, disturbed riparian, and disturbed upland), five orders for which numbers differed significantly from year to year within treatments, and five orders with significant year × treatment interaction effects (Table 1). Similar assessment of prey biomass revealed two orders (Orthoptera and Coleoptera)

Table 1. Results of repeated-measures ANOVA comparing numbers and biomass of prey for 13 arthropod orders occurring in the diet of northern waterthrushes across intact and disturbed riparian and upland habitats.

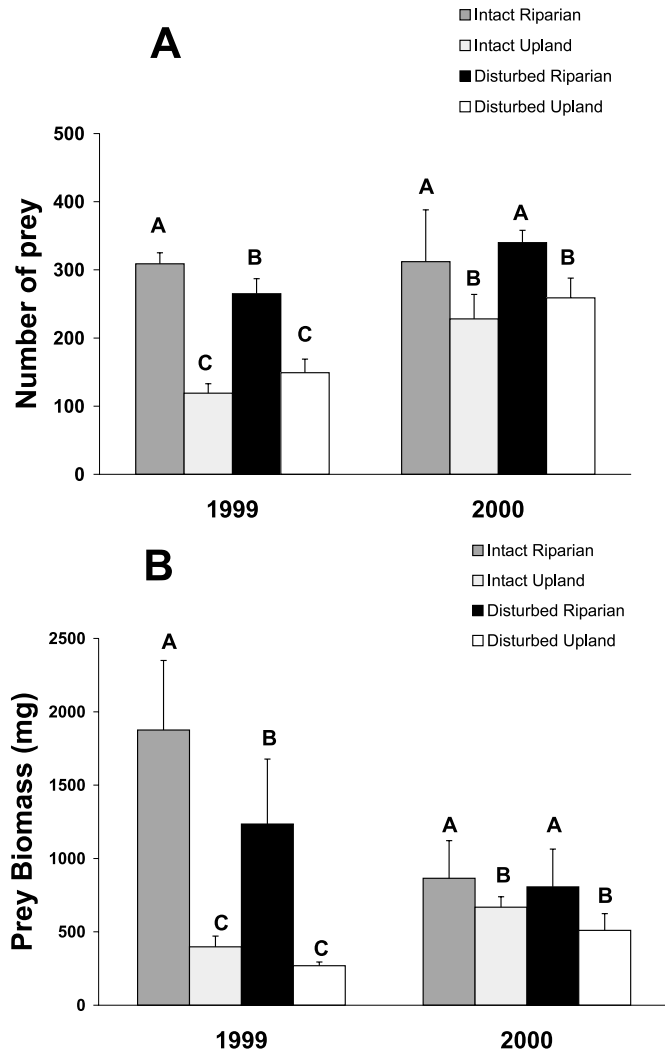
Order	Effect	Number of individuals		Biomass	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Araneae	Treatment	$F_{[3,8]} = 0.41$	0.7477	$F_{[3,8]} = 0.88$	0.4927
	Year	$F_{[1,8]} = 18.67^*$	0.0025*	$F_{[1,8]} = 2.10$	0.1853
	Interaction	$F_{[3,8]} = 2.78$	0.1099	$F_{[3,8]} = 8.33^*$	0.0076*
Collembola	Treatment	$F_{[3,8]} = 1.70$	0.2443	$F_{[3,8]} = 2.83$	0.1066
	Year	$F_{[1,8]} = 11.52^*$	0.0095*	$F_{[1,8]} = 4.44$	0.0682
	Interaction	$F_{[3,8]} = 1.25$	0.3558	$F_{[3,8]} = 6.66^*$	0.0144*
Ephemeroptera	Treatment	$F_{[1,4]} = 0.00$	0.9736	$F_{[1,4]} = 0.74$	0.4377
	Year	$F_{[1,4]} = 60.14^*$	0.0015*	$F_{[1,4]} = 35.70^*$	0.0039*
	Interaction	$F_{[1,4]} = 0.17$	0.6972	$F_{[1,4]} = 0.20$	0.6769
Odonata	Treatment	$F_{[1,4]} = 2.88$	0.1647	$F_{[1,4]} = 0.28$	0.6244
	Year	$F_{[1,4]} = 0.51$	0.5140	$F_{[1,4]} = 0.36$	0.5834
	Interaction	$F_{[1,4]} = 1.58$	0.2774	$F_{[1,4]} = 4.26$	0.1079
Plecoptera	Treatment	$F_{[1,4]} = 0.03$	0.8697	$F_{[1,4]} = 0.75$	0.4365
	Year	$F_{[1,4]} = 54.19$	0.0018	$F_{[1,4]} = 2.32$	0.2026
	Interaction	$F_{[1,4]} = 16.00^*$	0.0161*	$F_{[1,4]} = 13.69^*$	0.0208*
Orthoptera	Treatment	$F_{[3,8]} = 5.85^*$	0.0205*	$F_{[3,8]} = 4.58^*$	0.0378*
	Year	$F_{[1,8]} = 4.02$	0.0800	$F_{[1,8]} = 0.51$	0.4964
	Interaction	$F_{[3,8]} = 2.78$	0.1099	$F_{[3,8]} = 1.44$	0.3013
Hemiptera	Treatment	$F_{[3,8]} = 5.75$	0.0214	$F_{[3,8]} = 9.04$	0.0060
	Year	$F_{[1,8]} = 1.19$	0.3079	$F_{[1,8]} = 5.32$	0.0500
	Interaction	$F_{[3,8]} = 4.78^*$	0.0341*	$F_{[3,8]} = 9.02^*$	0.0060*
Homoptera	Treatment	$F_{[3,8]} = 3.18$	0.0849	$F_{[3,8]} = 3.16$	0.0856
	Year	$F_{[1,8]} = 62.34^*$	<0.0001*	$F_{[1,8]} = 11.28$	0.0100
	Interaction	$F_{[3,8]} = 0.98$	0.4473	$F_{[3,8]} = 8.04^*$	0.0085*
Coleoptera	Treatment	$F_{[3,8]} = 0.95$	0.4622	$F_{[3,8]} = 10.02^*$	0.0044*
	Year	$F_{[1,8]} = 67.40$	<0.0001	$F_{[1,8]} = 0.91$	0.3677
	Interaction	$F_{[3,8]} = 7.73^*$	0.0095*	$F_{[3,8]} = 3.13$	0.0875
Hymenoptera	Treatment	$F_{[3,8]} = 0.10$	0.9565	$F_{[3,8]} = 0.16$	0.9224
	Year	$F_{[1,8]} = 44.76$	0.0002	$F_{[1,8]} = 25.41^*$	0.0010*
	Interaction	$F_{[3,8]} = 15.83^*$	0.0010*	$F_{[3,8]} = 0.67$	0.5951
Tricoptera	Treatment	$F_{[1,4]} = 1.67$	0.2661	$F_{[1,4]} = 1.29$	0.3187
	Year	$F_{[1,4]} = 0.48$	0.5264	$F_{[1,4]} = 0.66$	0.4609
	Interaction	$F_{[1,4]} = 0.02$	0.8994	$F_{[1,4]} = 0.09$	0.7746
Lepidoptera	Treatment	$F_{[3,8]} = 1.12$	0.3951	$F_{[3,8]} = 0.36$	0.7806
	Year	$F_{[1,8]} = 1.79$	0.2182	$F_{[1,8]} = 1.31$	0.2855
	Interaction	$F_{[3,8]} = 5.04^*$	0.0300*	$F_{[3,8]} = 5.19^*$	0.0279*
Diptera	Treatment	$F_{[3,8]} = 0.67$	0.5914	$F_{[3,8]} = 1.16$	0.3816
	Year	$F_{[1,8]} = 13.00^*$	0.0069*	$F_{[1,8]} = 4.55$	0.0655
	Interaction	$F_{[3,8]} = 2.29$	0.1553	$F_{[3,8]} = 0.35$	0.7905

Note: Three replicates for all four treatments were collected over 2 years, but only stream-side treatments were collected for aquatic orders (Ephemeroptera, Plecoptera, Odonata, and Tricoptera). Asterisks show statistically significant effects.

with significant treatment effects, two orders with significant year effects, and six orders with significant year \times treatment interaction effects (Table 1). There was no consistent ranking pattern of treatments for those orders that had a significant treatment effect, based on either number of individuals or biomass. When we combined these data sets

across orders for each replicate (i.e., summing all individuals or biomasses within a replicate), repeated-measures ANOVA produced significant year \times treatment interaction effects for both arthropod abundance ($F_{[3,8]} = 5.81$, $P = 0.024$) (Fig. 1A) and biomass ($F_{[3,8]} = 13.31$, $P = 0.001$) (Fig. 1B). Within years, riparian habitat had consistently

Fig. 1. Mean (\pm SE) (A) number and (B) biomass of arthropod prey captured during sampling in the four habitat types over 2 years in western Newfoundland. Means with the same letter are not significantly different based on SNK comparison within years.

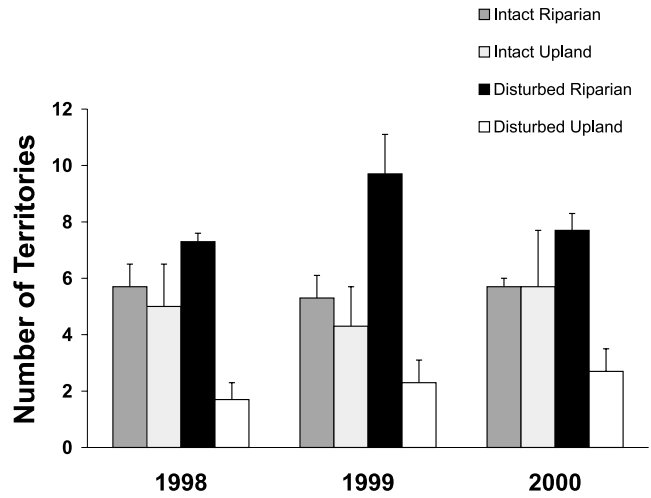


greater numbers of individuals and more biomass for 1999 and 2000. This significant interaction effect, and the high ranking of riparian habitat based on both variables, held even when we removed data for the aquatic orders (Ephemeroptera, Plecoptera, Tricoptera, and Odonata) from the analyses of the two variables.

Number of territories

Over 3 years, we identified 189 northern waterthrush territories along 6 km of stream and in the adjacent upland habitat. Despite the apparent variability in food supply, waterthrush territory numbers in the four treatments were highly consistent from year to year. There was a significant difference between treatments in the number of territories established ($F_{[3,8]} = 6.06, P = 0.018$) (Fig. 2) but no significant year ($P = 0.47$) or year \times treatment interaction ($P = 0.46$) effects. Similar numbers of territories were identified in intact riparian and upland habitats, but there were few waterthrushes occupying disturbed upland habitat and rela-

Fig. 2. Mean (\pm SE) number of waterthrush territories identified in the four habitat types over three years in western Newfoundland.



tively large numbers packing into disturbed riparian habitat. When data for the two intact habitats were combined by replicate and compared with similar pooled data for the two disturbed habitats, there was no significant difference in the average total number of territories per replicate surveyed.

Nest success

We identified 25 nests in 1998–1999 for which there was a known outcome; two of these were in upland habitat. The total includes two nests where the pair abandoned their initial nest cup and re-nested 10–15 m away. Six of the nests were depredated at the egg stage (three in intact and three in disturbed habitat) and one nest in disturbed habitat was depredated at the nestling stage. Two additional nests were abandoned prior to egg-laying with no known re-nesting attempt, a further nine nests were discovered for which the outcomes were unknown (found late in the season), and at least one recent fledgling was observed on another five territories. There was no significant difference between intact and disturbed habitats in the proportion of failed nests (3 of 10 versus 4 of 15, respectively; Fisher exact test, $P = 0.6$). However, due to the small sample size, power was extremely low (power = 2%). Mean and median number of young produced per nest (known outcomes only) were 2.6 and 3.5, respectively, for intact habitats ($n = 10$) and 2.8 and 4, respectively, for disturbed habitats ($n = 15$). Using the Mayfield method to compare nests in riparian habitat only, the probability of a nest surviving through both the incubation and nestling periods in intact habitat was 40.2% (0.402×1.000), while that in disturbed habitat was 56.8% (0.676×0.841). These again were based on limited samples and produced large, overlapping 95% confidence intervals (Table 2).

Foraging behaviour

We collected a total of 58 foraging sequences averaging 168 s. The number of attacks directed towards prey was higher in intact riparian and upland habitat than in the two disturbed habitats (Table 3). There were also differences between treatments in the number of flights per unit time, with birds in disturbed riparian habitat moving longer distances

Table 2. Limited interpretable differences in nest success values, based on the May-field method, for the 12-day incubation and 9-day nestling periods of northern waterthrushes occupying intact and disturbed riparian habitat.

Habitat	Incubation period	Nestling period
Intact	41 nest-days ($n = 6$)	37 nest-days ($n = 6$)
	3 lost = 0.073/nest-day	None lost
	40.2% probability of survival	100% probability of survival
	95% CI = 13.3–100.0	No 95% CI (none lost)
Disturbed	31 nest-days ($n = 5$)	52 nest-days ($n = 11$)
	1 lost = 0.032/nest-day	1 lost = 0.019/nest-day
	67.6% probability of survival	84.1% probability of survival
	95% CI = 30.5–142.5	95% CI = 49.4–125.3

Note: Ninety-five percent confidence interval (CI) for probability of survival calculated on the basis of Johnson (1979).

Table 3. Foraging patterns for northern waterthrushes across treatments standardized per minute (except attacks per step).

Habitat	Attacks	Steps	Hops	Flights	Attacks/step
Intact riparian ($n = 11$)	7.5±1.0a	8.8±2.9	2.1±0.7	1.6±0.2a	1.3±0.2
Intact upland ($n = 23$)	11.1±1.5a	29.8±6.4	4.5±1.0	2.4±0.6a	1.8±0.9
Disturbed riparian ($n = 19$)	6.5±0.7a	25.9±4.6	2.1±0.7	4.0±0.5a	0.6±0.2
Disturbed upland ($n = 5$)	6.0±1.4a	19.3±11.9	1.6±0.2	2.3±0.4a	0.9±0.5
$F_{[3,54]}$	3.32*	2.17	2.01	2.58*	1.48
P	0.0265*	0.1028	0.1237	0.0630*	0.2297

Note: Values are means ± SEs; number of observed foraging sequences are reported for each habitat type. Letters are results from SNK comparisons for significant tests (with asterisks) where means with the same letter are not significantly different.

more often than birds in any of the other three habitat types. SNK post hoc comparisons failed to distinguish among treatments for these two behaviours, which may be due to insufficient sample sizes (Zar 1996).

Discussion

Although typically identified as a strong riparian habitat specialist (Eaton 1995; LaRue et al. 1995; Whitaker and Montevecchi 1997, 1999; Wiebe and Martin 1998), northern waterthrushes made extensive use of the habitat in our intact upland sampling areas. Established waterthrush territories were about equally split between intact upland and riparian habitats. The presence of various forms of nonriparian surface water and the moist Maritime climate associated with this insular boreal biome seem to create abundant opportunities for arthropods in upland habitats of western Newfoundland. Thus, waterthrushes in intact forests make use of upland locations, for both foraging and breeding, that are unexpected for this species based on previous research (Eaton 1995; LaRue et al. 1995; Whitaker and Montevecchi 1997; Wiebe and Martin 1998). However, industrial forestry substantially alters the landscape and appears to result in the packing of northern waterthrush territories into the remaining forest stands along the riparian buffer zone in western Newfoundland. Similar packing or crowding into forest fragments, or buffer strips, following disturbance has been seen in studies across a variety of taxa (reviewed by Debinski and Holt 2000).

The long-term nature of the territory packing by northern waterthrushes that we observed was unexpected based on the

results from other studies. Temporary packing or crowding of birds into forest fragments immediately after clear-cut logging has been studied experimentally in tropical systems (Lovejoy et al. 1984). Bierregaard and Lovejoy (1988, 1989) found initial rapid increases in the densities of resident forest birds in the remaining forest fragments, following clearing, as displaced individuals moved to the next nearest suitable habitat. Subsequent declines in density over a 200-day period led to postclearing densities that fell to, or below, those initially recorded for the area prior to logging, depending on fragment characteristics. Darveau et al. (1995) found similar patterns for migratory species that breed in riparian buffer strips left in otherwise clear-cut boreal areas in Quebec. Over a 3-year period, densities of forest-dwelling birds within buffer strips peaked in the first year following clear-cutting of the adjacent upland forest and then declined to below initial densities in all but the widest buffer strips. Hagan et al. (1996) suggested that with a 60- to 80-day residency period on the breeding grounds each year by most neotropical migrants, a response to changes in forest cover (i.e., clear-cutting) over 3 years by such individuals would not be unexpected. Assuming no further arrivals of displaced individuals from surrounding forest due to logging activities, those who initially found refuge in the fragment would die and not be replaced until densities reached lower stabilized levels. Schmiegelow et al. (1997) documented short-term (i.e., 2-year) relative crowding of isolated forest remnants following small-scale local clearing in mixed-wood forests of north-central Alberta. But while neotropical migrant abundance varied substantially in an immediate response to harvesting activities, Schmiegelow et al. (1997) found that

the abundance of short-distance migrants and residents was relatively stable. These different responses may have resulted from the presence of large tracts of undisturbed forest in the immediate vicinity of the study site.

In addition to the studies outlined above, which indicate initial crowding of remnants followed by decreased densities in the 2- to 3-year period following clearing, Whitaker and Montevecchi (1999) found no difference in northern waterthrush densities between 4- to 5-year-old postharvest buffer strips and control riparian sites in western Newfoundland. In contrast, our disturbed study sites, which were in and adjacent to clearcuts between 5 and 10 years postharvest, still displayed strong signs of packing into the riparian buffer strips and no indication of the relaxation in densities seen elsewhere. Ongoing logging activities in the wider landscape (i.e., within 3 km) might lead to a continued displacement of upland individuals into these riparian buffer strips. However, we did not find a discernible pattern to suggest increased packing associated with subsequent harvesting. Thus, Hagan et al.'s (1996) suggestion that ongoing harvesting in the vicinity of a refuge prolongs elevated plot population densities may only explain our results for one of three disturbed study areas.

Our data on prey abundance and biomass suggested a limited impact of forest clear-cutting on arthropod populations. The abundance of arthropods varied significantly from year to year within and between sites, and this variability itself may have important longer-term consequences in terms of the quality of a given habitat. However, the absence of a significant difference between intact and disturbed upland habitats in overall prey number or biomass suggests that food was not limiting in disturbed habitat. Our finding that riparian habitat (both intact and disturbed) tended to support higher prey abundance than upland habitat concurs with the general perception that riparian areas have greater food resources for birds (e.g., Wiebe and Martin 1998; Pearson and Manuwal 2001). However, in contrast with the findings of Whitaker and Montevecchi (2000) that the abundance of flying insects (primarily Diptera and Hymenoptera) was greater in riparian buffer strips than in undisturbed shoreline canopies, we found no treatment effects for these two flying insect orders (Table 1) and no conclusive differences when all taxa included in the study were combined. While our sampling was completed at roughly the same time of year, we did not sample as high in the canopy (6–12 m) as Whitaker and Montevecchi (2000) because of the foraging behaviour of our target species. This difference in sampling regime may account for some divergence in the results between the two studies.

With an influx of displaced individuals into riparian buffer strips, a decline in productivity might be expected due to social disruption and the problems associated with either establishing or defending a territory in crowded conditions (Hagan et al. 1996). As well, there may be difficulties associated with attracting a mate to what might be perceived by females to be lower-quality territories (Gibbs and Faaborg 1990; Van Horne et al. 1995; Burke and Nol 1998). Hagan et al.'s (1996) study in central Maine found that densities of ovenbirds (*Seiurus aurocapillus*) breeding in fragments recently formed through logging were higher than those of nonfragmented habitat. At least temporarily, productivity in

that ovenbird population was inversely related to breeding densities, possibly as a consequence of behavioural dysfunction linked to the crowding. The data that we have on nesting success (using 25 nests to compare either the proportion of nest failures or our Mayfield statistics) suggest that territory packing may have no impact on northern waterthrushes occupying disturbed riparian habitat. However, our statistical power was limited.

Crowding may lower foraging success through a number of mechanisms. Reduced access to high-quality foraging sites or increased interference competition with increasing competitor density (e.g., Cresswell 1998) could result in lowered foraging efficiency. Prey were equally abundant in intact and disturbed riparian habitats, and we found indications of lowered attack rates per unit time in disturbed habitats and more frequent flights by birds in riparian buffer strips. However, more data are required to identify the specific cause(s) for decreased foraging success in disturbed habitats.

Management implications

In a related paper, Warkentin et al. (2003) found that predated northern waterthrush nests had less concealment due to lower numbers of coniferous trees within 5 m and that waterthrush nests in buffer strips had improved nesting cover with greater numbers of smaller trees. Moreover, in the current study, we also found that high densities of northern waterthrush territories were being maintained for extended periods of time in buffer strips, contrary to other studies of this type. These findings suggest a potential benefit of riparian buffer strips. However, our data also suggest that crowding of disturbed riparian buffer strips may lower foraging success through as yet unidentified mechanisms. Thus, the potential benefits concerning nest predation may be offset by lower foraging success associated with higher territory density. Hence, our results indicate that previous assumptions about the temporary nature of territory packing in response to harvesting activity may not hold for all songbird species in every habitat. This calls into question the longer-term viability of northern waterthrush populations, and that of other terrestrial riparian habitat specialists, in such disturbed habitats.

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References

- Atlegrim, O., and Sjöberg, K. 1995. Effects of clearcutting and selective felling in Swedish boreal coniferous forest: response of invertebrate taxa eaten by birds. *Entomol. Fenn.* **6**: 79–90.

- Baumgartner, A., and Waringer, J.A. 1997. Longitudinal zonation and life cycles of macrozoobenthos in the Mauerbach near Vienna, Austria. *Int. Rev. Gesamten Hydrobiol.* **82**: 379–394.
- Bibby, C.J., Burgess, N.D., Hill, D.A., and Mustoe, S.H. 2000. Bird census techniques. 2nd ed. Academic Press, London, U.K.
- Bierregaard, R.O., Jr., and Lovejoy, T.E. 1988. Birds in Amazonian forest fragments: effects of insularization. *In Acta XIX Congressus Internationalis Ornithologici*. Vol. II. *Edited by H. Ouellet*. University of Ottawa Press, Ottawa, Ont. pp. 1564–1579.
- Bierregaard, R.O., Jr., and Lovejoy, T.E. 1989. Effects of forest fragmentation on Amazonian understory bird communities. *Acta Amazonica*, **19**: 215–241.
- Burke, D.M., and Nol, E. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk*, **115**: 96–104.
- Canadian Forest Service. 1993. The state of Canada's forests 1993: 4th report to Parliament. Canadian Forest Service, Communications Division, Ottawa, Ont.
- Craig, R.J. 1984. Comparative foraging ecology of Louisiana and Northern Waterthrushes. *Wilson Bull.* **96**: 173–183.
- Craig, R.J. 1987. Divergent prey selection in two species of waterthrushes (*Seiurus*). *Auk*, **104**: 180–187.
- Cresswell, W. 1998. Relative competitive ability changes with competitor density: evidence from feeding blackbirds. *Anim. Behav.* **56**: 1367–1373.
- Damman, A.W.H. 1983. An ecological subdivision of the island of Newfoundland. *In Biogeography and ecology of the island of Newfoundland*. *Edited by G.R. South*. Junk Publishers, The Hague, Netherlands. pp. 163–206.
- Darveau, M., Beauchesne, P., Bélanger, L., Huot, J., and LaRue, P. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. *J. Wildl. Manage.* **59**: 67–78.
- Debinski, D.M., and Holt, R.D. 2000. A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* **14**: 342–355.
- Eaton, S.W. 1957. A life history study of *Seiurus noveboracensis*. *Sci. Stud. St. Bonaventure Univ.* **19**: 7–16.
- Eaton, S.W. 1995. Northern Waterthrush (*Seiurus noveboracensis*). *In The birds of North America*. No. 182. *Edited by A. Poole and F. Gill*. Academy of Natural Sciences, Philadelphia, Pa., and American Ornithologists' Union, Washington, D.C.
- Gibbs, J.P., and Faaborg, J. 1990. Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. *Conserv. Biol.* **2**: 193–196.
- Hagan, J.M., Vander Haegen, W.M., and McKinley, P.S. 1996. The early development of forest fragmentation effects on birds. *Conserv. Biol.* **10**: 188–202.
- Hagar, J.C. 1999. Influence of riparian buffer width on bird assemblages in western Oregon. *J. Wildl. Manage.* **63**: 484–496.
- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk*, **96**: 651–661.
- Knopf, F.L., Johnson, R.R., Rich, T.D., Sampson, F.B., and Szaro, R.C. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bull.* **100**: 272–284.
- LaRue, P., Bélanger, L., and Huot, J. 1995. Riparian edge effects on boreal balsam fir bird communities. *Can. J. For. Res.* **25**: 555–566.
- Lovejoy, T.E., Rankin, J.M., Bierregaard, R.O., Jr., Brown, K.S., Jr., Emmons, L.H., and Vandervoort, M.E. 1984. Ecosystem decay and Amazon forest remnants. *In Extinctions*. *Edited by M.H. Nitecki*. University of Chicago Press, Chicago, Ill. pp. 69–117.
- Mayfield, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* **87**: 456–466.
- Meades, W.J., and Moores, L. 1994. Forest sites classification manual: a field guide to the Damman forest types of Newfoundland. 2nd ed. Can. For. Serv. For. Resour. Dev. Agreement Rep. 003.
- Naiman, R.G., Decamps, H., and Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecol. Appl.* **3**: 209–212.
- Pearson, S.F., and Manuwal, D.A. 2001. Breeding bird response to riparian buffer width in managed Pacific northwest Douglas-fir forests. *Ecol. Appl.* **11**: 840–853.
- Ramsay, S.M., Otter, K., and Ratcliffe, L.M. 1999. Nest-site selection by female Black-capped Chickadees: settlement based on conspecific attractions. *Auk*, **116**: 604–617.
- Remsen, J.V., Jr., and Robinson, S.K. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. *Stud. Avian Biol.* **13**: 144–160.
- SAS Institute Inc. 1988. SAS/Stat user's guide, release 6.03. SAS Institute Inc., Cary, N.C.
- Schmiegelow, F.K.A., Machtans, C.S., and Hannon, S.J. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. *Ecology*, **78**: 1914–1932.
- Scruton, D.A., Clarke, K.D., McCarthy, J.H., Forsey, S., Whitaker, D.M., Cowan, G.I. McT., Baggs, E., Montevecchi, W.A., Green, J.M., Bell, I., and Moores, L.J. 1995. The Copper Lake Buffer Zone Study: project site description and general study design. *Can. Tech. Rep. Fish. Aquat. Sci.* 2043.
- Skagen, S.K., Melcher, C.P., Howe, W.H., and Knopf, F.L. 1998. Comparative use of riparian corridors and oases by migrating birds in southeast Arizona. *Conserv. Biol.* **12**: 896–909.
- Stauffer, D.F., and Best, L.B. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. *J. Wildl. Manage.* **44**: 1–15.
- Steidl, R.J., Hayes, J.P., and Schaubert, E. 1997. Statistical power analysis in wildlife research. *J. Wildl. Manage.* **61**: 270–279.
- Surber, E.W. 1937. Rainbow trout and bottom fauna predators in one mile of stream. *Trans. Am. Fish. Soc.* **66**: 193–202.
- Van Horne, M.A., Gentry, R.M., and Faaborg, J. 1995. Patterns of ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *Auk*, **112**: 98–106.
- Vickery, P.D., Hunter, M.L., Jr., and Wells, J.V. 1992. Use of a new reproductive index to evaluate the relationship between habitat quality and breeding success. *Auk*, **109**: 697–705.
- Warkentin, I.G., Roberts, S.E., Flemming, S.P., and Fisher, A.L. 2003. Nest site characteristics of northern waterthrushes. *J. Field Ornithol.* **74**. In press.
- Whitaker, D.M., and Montevecchi, W.A. 1997. Breeding bird assemblages associated with riparian, interior forest and nonriparian edge habitats in a balsam fir ecosystem. *Can. J. For. Res.* **27**: 1159–1167.
- Whitaker, D.M., and Montevecchi, W.A. 1999. Breeding bird assemblages inhabiting riparian buffer strips in Newfoundland, Canada. *J. Wildl. Manage.* **63**: 167–179.
- Whitaker, D.M., and Montevecchi, W.A. 2000. Elevated numbers of flying insects and insectivorous birds in riparian buffer strips. *Can. J. Zool.* **78**: 740–747.
- Wiebe, K.L., and Martin, K. 1998. Seasonal use by birds of stream-side riparian habitat in coniferous forest of north central British Columbia. *Ecography*, **21**: 124–134.
- Zar, J.H. 1996. Biostatistical analysis. 3rd ed. Prentice-Hall, Upper Saddle River, N.J.