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Territory choice and quality in the Yellow Warbler (*Dendroica petechia*). The importance of habitat spatial structure, spatial scale, social factors, and the impact of cattle grazing.

by

Claudio Celada ©

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

in

Environmental Biology and Ecology

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "Territory choice and quality in the Yellow Warbler (*Dendroica petechia*). The importance of habitat spatial structure, spatial scale, social factors, and the impact of cattle grazing" submitted by Claudio Celada in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

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Abstract

Food availability, vegetation type and structure, and the quality of the nesting sites are generally considered as the main characteristics affecting territory choice and quality. The importance of spatial structure of habitat as a component of territory quality has been generally disregarded in previous avian studies. I investigated the effects of spatial structure of habitat at different spatial scales on territory occupancy, territory choice and breeding success in the Yellow Warbler *Dendroica petechia* in a natural patchy landscape. In the aspen parkland of central Alberta, Yellow Warblers live in small patches of willow and aspen surrounded by mixed grassland. They use aspen and willow patches to feed, willow patches to nest, and avoid the surrounding grassland. Some territories consist of more than one habitat patch separated by unsuitable habitat. I found that territory occupancy and consistency of patch occupancy over three years were mainly affected by area and shape of the willow patch within a territory (main patch in multi-patch territories). Territory choice by males and females was mainly affected by area of the (main) willow patch. Vegetation structure of territory was of marginal importance and arthropod abundance and biomass in territories were never significant. Territory occupancy and choice were not affected by spatial structure and vegetation structure at the nest site, except that nests were surrounded by larger amount of willow within 5m than random points, and by spatial structure of the landscape. Models for territory occupancy and choice had little predictive power when tested on another similar landscape. Breeding success was largely stochastic. Territory choice and quality may also be affected by occurrence of members of other species in the surroundings. Multi-species aggregations may provide protection against predators or brood parasites. I found that Yellow Warblers chose patches with ponds occupied by Red-winged Blackbirds earlier than patches with no blackbirds. Presence of Red-winged Blackbirds in patches reduced the incidence of predation at the nests and brood parasitism by the Brown-headed Cowbird. Finally, I investigated the effects of cattle grazing intensity and seasonality on territory quality in the Yellow Warbler, frequency of patch occupancy by other songbird species, and species richness. Only the Red-winged Blackbird appeared to be sensitive to grazing in the study area.

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Chapter 1. Introduction.

Territory choice and quality: are we missing something?

In heterogeneous areas, territories may differ in attractiveness and quality. In migratory species, individuals that arrive at the breeding area earlier will choose territories that contain more or better resources. This view has been formalized in the Ideal Free Distribution and Ideal Despotic Distribution models (Fretwell and Lucas 1970) and tested in the field by several studies (e.g., De Brooke 1979, Petit and Petit 1996, Huhta et al. 1998).

Territory choice (or attractiveness) can be measured as chronological order of territory occupancy and territory quality can be defined based on the breeding success of the territory holder. Several studies have tried to link territory choice and quality, and to identify the features that affect them (e.g., Best and Rodenhouse 1984, Huhta et al. 1998, Morris and Lemon 1998). Features that have been usually considered include food availability (e.g., Verner 1964; Willson 1966), vegetation type and structure (e.g., Holm 1973; Lenington 1980) and several characteristics of the breeding sites (e.g., Zimmerman 1966; Askenmo 1984). Other studies bypassed the direct measurement of the above-mentioned features and inferred habitat quality using the reproductive success in a certain territory over years (Dhondt 1987).

In the last decade, the interest of avian ecologists has gradually shifted from the territory scale to larger spatial scales (i.e. the landscape). Presumably, this move was motivated by the necessity of addressing issues threatening bird populations at larger scales (e.g., habitat loss and fragmentation), but also by the perception that the critical features of territory quality had been clearly identified. A first contribution of this thesis is to include in the assessment of territory choice and quality a previously neglected territory feature, the spatial structure of the territory (i.e. the number of patches of different habitat types within a territory and the size, shape and isolation of these patches) (Chapter 2). Since resources are distributed in space within a territory, spatial structure of territories may alter the costs and benefits of territorial defence. I focus on territory occupancy, chronological order of territory occupancy and breeding success in the Yellow Warbler (*Dendroica petechia*) in the naturally patchy aspen parkland of central Alberta.

Previous avian studies have pointed out the need to include multiple spatial scales in habitat selection studies (e.g., Wiens 1986, Jokimäki and Huhta 1996). Territory choice and quality may be affected by factors that operate at different spatial scales. In Chapter 2, I investigate if and how territory choice and quality are affected by the spatial structure of habitat at different spatial scales (i.e. the nest site, the territory, the surrounding landscape). I also consider vegetation structure at the nest site and territory scale and arthropod abundance and biomass at the territory scale.

Besides intrinsic habitat features, territory attractiveness and quality may also be affected by social factors such as conspecific attraction (see Stamps 1988), dominance (Fretwell and Lucas 1970), and interspecific interactions. Interactions between conspecifics will be only marginally considered in this thesis and in more detail in a companion paper (Celada, C. *unpublished manuscript*). Interspecific interactions may affect bird distribution and habitat use by birds (Sherry and Holmes 1985). Thus, occurrence of individuals belonging to other species within or in the surroundings of a territory may increase or decrease territory attractiveness and quality. For example, the American Redstart (*Setofaga ruticilla*) avoided suitable habitat occupied by the Least Flycatcher (*Empidonax minimus*) in the northern hardwoods forest in New Hampshire (Sherry and Holmes 1985). In Ontario, presence of Red-winged Blackbird (*Agelaius phoeniceus*) colonies reduced the rate of parasitism by the Brown-headed Cowbird (*Molothrus ater*) on Yellow Warbler nests (Clark and Robertson 1979). In Chapter 3, I investigate if the occurrence of Red-winged Blackbirds in patches occupied by territorial Yellow Warblers and in the surrounding landscape affects territory choice and breeding success in the Yellow Warbler.

Cattle grazing is the most common form of public land use in western North America (Platts 1991) and it has occured in the study area since the beginning of the century and probably earlier (Fehr 1982). Because cattle grazing could modify the vegetation structure, arthropod abundance, and the spatial structure of the treed patches (e.g., aspen and willow recruitment at the edge of the treed patches may occur faster in the absence of grazing) its potential impact on the quality and attractiveness of Yellow Warbler territories should be apparent. Because different portions of the study area are subject to different cattle grazing regimes, in Chapter 4 I investigate if grazing intensity and seasonality affects territory choice and territory quality (breeding success) in the Yellow Warbler, and if they interact with other components of territory attractiveness and quality. Studies on the effects of cattle grazing on breeding success in songbirds are extremely rare (but see Wilson *et al.* 1997). I also considered the impact of cattle grazing on the whole songbird community inhabiting the area.

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Chapter 2. The importance of spatial structure of habitat and scale on the territory choice and quality in the Yellow Warbler in a naturally patchy landscape

INTRODUCTION

Landscape spatial structure, which can be characterized by size and shape of patches, heterogeneity, and boundary features (Forman and Godron 1986), affects movements of individual animals (reviewed in Desrochers et al. in press), use of habitat (e.g., Keller and Anderson 1992), foraging behavior (e.g., Zach and Falls 1979), and reproductive behavior (e.g., Wegge and Rolstad 1986, Rolstad and Wegge 1987), but in general, little is known about its effects on fitness of individuals. Several studies, all carried out in human-fragmented landscapes, have related landscape spatial structure to breeding productivity (e.g., see Andrén 1995 for a review on effects of landscape configuration on predation rates, Donovan et al. 1995, Robinson et al. 1995, Tewksbury et al. 1998, Morse and Robinson 1999), but studies set in natural landscape mosaics are extremely rare. For territorial individuals, landscape spatial structure may influence the spatial structure of territories (i.e. the number of patches of different habitat types within a territory and the size, shape and isolation of these patches). Many bird studies have attempted to identify the features of territory quality and to measure their importance to the fitness of the defender. Food availability (e.g., Verner 1964, Willson 1966), vegetation type and structure (e.g., Holm 1973, Lenington 1980), and the quality of nesting sites (e.g., Zimmerman 1966, Askenmo 1984) are the main characteristics affecting territory choice, breeding success, and survival of the territory holder. However, the importance of spatial structure of territories as a component of territory quality has been generally disregarded to date, except for a handful of studies (Newton 1986, Rolstad and Wegge 1987, Wegge and Rolstad 1986, Tjernberg et al. 1993, Redpath 1995, Huhta et al.1998). These studies have focused on human-fragmented landscapes and have not explicitly measured area, shape, and/or isolation of patches belonging to territories (but see Rolstad and Wegge 1987). I tested the hypothesis that, in a naturally fragmented landscape, spatial structure of the habitat can affect territory choice and fitness of territory holders (measured as breeding success).

I focused on patch occupancy, territory choice (measured as chronological order of territory occupancy), and breeding success of the Yellow Warbler (*Dendroica petechia*) in small natural patches of willow and aspen surrounded by unsuitable habitat (mixed grassland). The first aim of this study was to assess the relative importance of measures of territory quality (insect abundance, vegetation structure, occurrence of ponds, patch size, shape, and isolation) on: **a)** pattern of territory occupancy by the Yellow Warbler (territory occupied/ unoccupied); **b)** consistency of patch occupancy over years; **c)** chronological order of occupancy (territory choice); and **d)** breeding success.

Organisms can respond in different ways to different spatial scales and ecological processes are also scale-sensitive (e.g., Wiens 1986, Addicott et al. 1987). Territory choice, predation at the nest, and breeding success in Yellow Warbler may also be affected by the quality of potential nest sites (microscale), and by spatial structure around the territory (landscape scale). However, the effects of landscape spatial structure may reflect the existence of more than one ecological processes that operates simultaneously (e.g., occurrence of larger treed area around a territory may increase insect abundance and increase density of predators in the area). These processes may act at different spatial scales, making it difficult to define a relevant ecological neighborhood (*sensu* Addicott et al. 1987). Therefore, I explored the effects of landscape spatial structure around territories in circular areas progressively increasing in size. The specific questions addressed were: **1.** Do spatial structure and vegetation structure at the microscale (around the nest), and spatial structure of the landscape around the territory affect **a)** territory occupancy, **b)** territory choice by males and by females, and **c)** breeding success in Yellow Warbler?

2. At what spatial extent do they act, if any?

STUDY AREA AND STUDY SITES

This three-year study (1995-1997) was carried out at Rumsey Ecological Reserve and a contiguous tract of aspen parkland, in central Alberta (52° N, 112° W). The two areas, which total 18,350 ha, are part of the largest uninterrupted stretch of aspen-parkland in the region and are completely surrounded by intensively cultivated land, mainly canola fields. The area is a glacial moraine characterized by many hills and depressions, the latter frequently occupied by temporary ponds. Ponds are typically surrounded by patches of willow (mainly *Salix petiolaris* and *S. bebbiana*). Stands of Trembling Aspen, *Populus tremuloides*, occupy depressions and moderately steep slopes, mainly north-oriented. Some isolated Balsam Poplar, *P. balsamifera*, occur in the Aspen stands. *Rosa woodsii, Amelanchier alnifolia,* and *Symphoricarpos occidentalis* dominate the understory in willow patches, whereas *S. occidentalis, R. woodsii, Rubus idaeus,* and *Ribes oxyacanthoides* are the most common shrub species in aspen patches. The area included in the ecological reserve has been under grazing lease since 1917. Different zones have been cattle-grazed with different intensities and 0.8 km^2 were removed from the lease and protected from cattle grazing in 1973.

The study area is a mosaic of ponds, willow patches, and aspen patches embedded in a matrix of mixed grassland. Some of the ponds, aspen, and willow patches form pond-willow or pond-willow-aspen complexes (Fig. 2.1 and Fig.2.2). In the main study area, four study units, one just outside the borders of the ecological reserve (177 ha) and three inside the protected area (220 ha, 38 ha, and 64 ha) were selected to maximize variation in interpatch distance and encompass zones with different grazing intensities. The impact of grazing on vegetation structure, arthropod abundance, occupancy by the Yellow Warbler, and bird community composition in willow patches will be considered in Chapter 4. When considering willow and aspen patches combined, mean patch size was 2,860 m^2 (range 25 - 23,171 m^2) and the mean distance to the nearest patch was 26.1 m (range 5 - 188 m). In 1997, a 357 ha site was added, called hereafter "the southern area"; situated 9 km south of the nearest study site in the ecological reserve. Grazing intensity in this site was homogeneous, and intermediate when compared to the other sites (see study area and study sites, Chapter 4). For this site, mean patch size was 2,178 m^2 (range 25 - 12,053 m^2). Mean interpatch/complex distance was 29.7 m (range 5 - 114 m).

METHODS

Study species

The Yellow Warbler is a neotropical migrant common throughout most of North America. Males reach the study area a few days earlier than females (Kammeraad 1964, Briskie 1995). As soon as they arrive, males establish multipurpose territories (Type A in Nice 1941) that will be used by the pair for foraging, mating, and raising their offspring. Yellow Warblers are strictly insectivorous on the breeding grounds, and forage opportunistically (Frydendall 1967, Busby and Sealy 1979). Prey are mainly pursued by gleaning, and less frequently by hovering and sallying (Frydendall 1967, Busby and Sealy 1979, Hutto 1981). At Rumsey, Yellow Warblers used willow patches to nest and forage, aspen patches to forage only, did not use the surrounding grassland and were never observed foraging on the ground.

Bird censusing and pairing success

Yellow Warblers were censused by point counts (Ralph and Scott 1981) in 208 habitat patches in 1995, and in 283 patches in 1996 and 1997. In 1997, an additional 142 habitat patches were censused daily, in the southern area to obtain a test of the models derived at Rumsey Ecological Reserve for territory occupancy (territory occupied / unoccupied) and the chronological order of occupancy by males. Routes connecting the sampling stations were drawn on detailed maps of the study area. The sampling stations were positioned to cover all the patches and each patch entirely. To minimize disturbance during censusing, sampling stations for smaller patches were usually positioned in the grassland next to the patches, on top of hills, or along hill slopes. In larger patches, one or more sampling stations were situated inside the patch, in order to detect all territorial males. Observers spent six minutes at each sampling station recording and mapping all Yellow Warblers seen or heard, their movements, and activities of territorial significance (e.g., aggressive interactions among territorial conspecifics, singing from an exposed perch) on detailed maps of the study area, ranging in scale from 1:2,000 to 1:3,200. Observer and diurnal variation were standardized by alternating observers on each route and by varying the starting point and direction followed. The standard BTO (British Trust for Ornithology) list of conventions for territory mapping (Bibby and Burgess 1992) was followed. Starting from the date of arrival of the first Yellow Warbler male in the study area, each patch was surveyed six times, once every 3 days, to detect the chronological order of occupancy of different territories. Two days (except for round 3 and 4 in 1997 which took 3 days) were necessary to complete each round. Censuses were conducted from the last week of April until the first week of July, from dawn until 10:00 h. Censuses were not carried out if it was raining or if wind exceeded 30 km/h (level 5 of Beaufort wind scale). Presence/absence of Red-winged Blackbirds (*Agelaius phoeniceus*), at ponds was also recorded, as described for the Yellow Warbler. The rationale for censusing this species is discussed in Chapter 3. Red-winged Blackbirds were not censused in the southern study area.

Yellow Warbler males vary considerably in amount and pattern of brown streaking on their breasts (Studd and Robertson 1985), and these patterns were drawn on a chart whenever observers closely observed an individual male. When neighboring territory holders differed visibly it was possible to identify individual males. Some of the males that were too similar to their neighbors for identification, were mist-netted and individually color-banded (5 in 1995, 11 in 1996, 6 in 1997). Also, 3 and 4 birds that had been previously banded, returned to the study area in 1996 and 1997, respectively. Repeated censuses spread over the breeding period and prolonged behavioral observations (see *Classification of territories*, in *Methods*), identification by sight, in addition to the fact that territorial males were often spatially separated by the landscape matrix, made it possible to identify transient and permanently territorial males. Transient birds were excluded from analyses.

Pairing success was determined by observing male and female interactions such as courting behavior and distance between male and female. A male was considered unpaired if he was solitary for the duration of three 30 min observations separated by at least 4 days. Subsequently, unpaired males were observed continuously for 90 min, toward the end of the breeding season (i.e., right up until chicks fledged from all the nests found) to confirm their mating status (Gibbs and Faaborg 1990).

During settlement, Yellow Warbler females were conspicuous and their presence in patches of habitat could be detected. Starting with the settlement of the first male and for a period of three weeks, patches occupied by males were intensively searched for the presence of females. Patches occupied by both paired and unpaired males were searched every two days, to detect new arrival of females and to confirm the presence of a pair, until the construction of the nest started. A subsample of patches not occupied by males was also searched and were never found to be occupied by females; thus, for females, arrival date and pairing date are similar (see also Bensch and Hasselquist 1991).

Classification of territories

Yellow Warblers can include in their territory more than one habitat patch separated by unsuitable habitat (Fig 2.3). Territories comprised of several habitat patches (multi-patch territories as opposed to single-patch territories) may be chosen later and may be of lower quality because they are more costly to defend in terms of time and energy, since unsuitable habitat has to be crossed to patrol territorial borders. Territory choice and territory quality may be affected, not only by intrinsic habitat quality of the patch(es) composing the territory, but also by the presence of territorial conspecifics in these patches (e.g., Stamps 1988). Consequently, I classified Yellow Warbler territories according to presence of other territorial males in patches as "shared-patch territories" or "unshared-patch territories". These aspects are considered in more detail in a companion paper (Celada, C., *unpublished manuscript*). Presence of Red-winged Blackbirds (RWBB) was also considered a territory feature. The rationale for including presence/absence of Red winged Blackbird is discussed in Chapter 3. To determine which patches belonged to a territory, movements, location of song perches, and aggressive interactions with territorial conspecifics were recorded during at least three 30 min observations, while detecting chronological order of occupancy by Yellow Warbler males, and during four extra observations, for a total of ten 6 min observations. A patch was considered to be included in a territory when a territorial male had been observed singing or actively defending it during a minimum of two observations, separated by at least 5 days (see also Bibby and Burgess 1992). For multi-patch territories the patch in which the territory holder spent more time singing or actively defending his territory was determined to be the "main patch".

Breeding success

Nests were found by intensively searching willow patches. In 1996 and 1997, in one of the study units a nest was found for all the breeding pairs (N = 20 in 1996, and N = 24 in 1997). Since all the nests found were located in willow patches and polygyny does not seem to occur in the study area, it is highly unlikely that the Yellow Warbler nests in aspen patches at Rumsey. Furthermore, females were seldom observed in aspen.

In 1995, 19.4 % of 31 nests, in 1996, 77.6% of 76 nests, and in 1997, 71.6% of 88 nests were found during construction. The rest were found during incubation and a minority during rearing of chicks. Nests were checked every 2-3 days. Number of chicks 9 days old (considered as number of chicks fledged), was obtained for all the nests. When a nest was found empty after the ninth day from hatching, chicks were considered to have successfully fledged.

Since Yellow Warbler chicks may fledge prematurely on day 6 if disturbed (Lozano and Lemon 1996), nestlings were weighed when they were 2 and 5 days old. On day 2, chicks were individually color marked on the leg using a non-toxic marker, so that mean increase in weight could still be obtained if one or several chicks died between day 2 and day 5. At each nest, first and second weighing of chicks were carried out at the same hour of the day (± 1 hr). Predation at the nest between day 2 and 5 was extremely low (10.2%, and 4.0% of nests where chicks were weighed in 1996 and 1997, respectively), suggesting that weighing did not affect breeding success. Subsequent to having their nest depredated, parasitized by the Brown-headed Cowbird (*Molothrus ater*), or destroyed by a storm, some females renested and successfully raised offspring. These nests were counted as preyed upon/parasitized by cowbird, but data from the second nests were not included in analysis for brood size and increase in weight. However, second nests were included in the analysis for overall breeding success of the pair. Potential avian predators occurring in the area include Blue Jay (*Cyanocitta cristata*) Black-billed Magpie (*Pica pica*), American Crow (*Corvus brachyrhynchos*), Common Raven (*Corvus corax*), House Wren (*Troglodytes* *aedon*). Non-avian predators include Red Squirrel (*Tamiasciurus hudsonicus*), Plain Garter Snake (*Thamnopis radix*) and Red-sided Garter Snake (*Thamnopis sirtalis*). Little is known about the occurrence of small mammal species in the area, but some mice and vole species could be egg predators.

Arthropod sampling

Relative abundance of arthropods was determined by sampling in aspen patches (1995 and 1996) and willow patches (1995, 1996, and 1997) during brood rearing, when there were chicks in more than 50% of the active nests. In 1996, sampling was also performed during settlement of birds, starting 3 days after the arrival of the first male (18 May). It took 8 days to sample all the patches. Insect sampling was carried out at the patch level, rather than territory level because territorial borders were not defined during settlement, and during brood rearing exact territorial borders were unknown for some of the territories. For multi-patch territories, only data for the main patch were considered.

A preliminary study was conducted to determine the necessary number of sampling points per patch. Ten patches were sampled at 10 points. Variation in number of arthropods/sample tended to be asymptotic at 8 sampling points. Thus, 8 points were sufficient to adequately sample a patch. Sampling effort was not constant per unit area because I was interested in comparing relative arthropod abundance between patches. Moreover, in smaller patches it was not possible to fit more than 8 non overlapping sampling points (see below). Each patch was divided into 8 zones of equal size and a sampling point was randomly assigned to each zone. At each point, sampling was performed with a standard sweep-net (diameter 37 cm), swept through the willow bush once, over approximately one m, with a firm hand. In aspen, the sweep-net was attached to a 6 m high flexible extensible pole. Height of sweep-netting varied from 0.3-3.5 m in willow and 0.5-8 m in aspen. Sampling effort was evenly distributed along the patch height.

Sweep-netting was selected as the sampling method for the following reasons:

1. Yellow Warblers were frequently observed gleaning in willow and aspen, and they were never observed foraging on the ground, or in the air far from the vegetation;

2. sweep-netting has been found to yield representative samples when assessing the availability of arthropods to Yellow Warblers (Busby and Sealy 1979, Biermann and Sealy 1982).

Arthropod sampling was carried out during sunny weather when the vegetation was dry, between 17:30 and 20:00 h. Arthropods were preserved in 70% ethanol and later classified to order, except for the families Lepidoptera Geometridae (caterpillars), Diptera Chironomidae (midges), and Diptera Culicidae (mosquitos), which were found to be taxa selected in previous studies on Yellow Warbler diet (Frydendall 1967, Busby and Sealy 1979, Biermann and Sealy 1982). Finally, they were dried at 50°C for 24 h (see Zach and Falls 1979) and weighed on an analytical scale to the nearest 0.01 mg. Abundance and dried biomass of Lepidoptera Geometridae, other Lepidoptera larvae, Diptera Chironomidae, and Diptera Culicidae were then analyzed separately. Since Yellow Warblers were frequently observed to feed on Homoptera, mainly Cicadellidae (leafhoppers), this order was also analyzed separately. Coleoptera Coccinellidae were excluded from analysis since they are not eaten by Yellow Warblers (Busby and Sealy 1979).

To make sure that sweep-netting method did not grossly underestimate any taxa, in 1996, willow patches were also censused with a 89 cm x 89 cm beating net, according to the sampling scheme described above. Lepidoptera larvae was the only taxon among those analyzed that lacked correlation between abundance measured with sweep-netting and abundance measured with beating-netting (Appendix 2.1). Thus, for 1996, abundance and biomass of Lepidoptera larvae obtained with beating-net were also included in analysis for territory choice and breeding success. Diptera Culicidae were almost absent in beating-net samples.

Vegetation sampling

Vegetation structure was sampled at all willow and aspen patches after chicks had fledged, in July and the first week of August. Relative abundance of dominant shrub species was quantified in willow patches, but not in aspen patches where birds were only observed perching on top of trees or foraging in the aspen canopy. Since willow structure and understory changed between years, due mainly to variation in pond size, sampling in willow patches was repeated at the end of each breeding season. Aspen patches were sampled once.

Because at the end of the breeding season the approximate territorial borders were known for most territories, vegetation could be sampled at the territory level. In multi-patch territories, vegetation was sampled in all the patches. For < 10% of territories, for which territorial borders were poorly known, sampling plots were placed only in the central part of the territory.

Willow patches: For willow patches, a modified version of the protocol from the BBIRD Program (Martin 1992, see also Schmiegelow et al. 1997, Song 1998) was used. A sample plot was a 5 m radius circle (0.008 ha) divided by 2 perpendicular diameters into 4 equal quadrants. If a nest was present in the patch, the first plot was centered on the nest, otherwise the first plot was randomly selected. The next plot was located 40 m from the center of the first plot, in a randomly selected direction (Appendix 2.2). This procedure was repeated until it was no longer possible to fit plots entirely within the willow patch and that were 40 m apart.

Percent of ground covered by grass/sedge, shrubs, forbs, all green (the sum of these three), leaf litter, and bare ground was visually estimated to the nearest 5% in four 1-m^2 quadrats situated at the extremes of the two perpendicular diameters. Litter depth was measured at four points randomly selected, one point on each of the four quadrants. Numbers of stems of dominant shrub species and total number of stems of all shrubs were counted in the four 1-m^2 quadrats. For all these variables, the mean of the four measures was calculated. Numbers of Trembling Aspen and Balsam Poplar saplings (diameter at breast height [dbh] < 2.5 cm) and poles (2.5<dbh<8 cm), numbers of *Salix petiolaris* and *S. bebbiana* bushes (height >140 cm) within the sample plot were also counted. Height of *Salix* sp. bushes was measured to nearest dm using a graded stick. For each willow bush edge-to edge distance to nearest bush was also measured. Numbers of green and dry stems for each willow were counted. Number of stems for *S. petiolaris* < 2m high and > 2m high was obtained separately, since Yellow Warblers had been seldom observed in bushes < 2m high. *S. bebbiana* < 2m high were almost absent in the area. Percentage of sky obscured by willow was visually estimated to the nearest 10% from the center of the plot. A measure of foliage density was obtained by observing a 5 m graded stick placed in the center of the plot from two extremes of the plot diameter close to the north-south axis. The percentage of the stick hidden by the vegetation was estimated to the nearest 10% and the average of the two measures was recorded (see Villard et al. 1995 for a similar approach). Numbers of live Trembling Aspen and Balsam Poplar trees within the plot were counted, dbh measured using a dbh-tape, and height measured using a clinometer. In total, 48 variables characterizing vegetation structure and composition in willow patches were obtained (Table 2.1). Vegetation around nests and random sample points were compared to determine whether nest sites were selected according to some features of vegetation structure at the microscale.

Aspen patches: The point-centered quarter method (Mueller-Dombois and Ellenberg 1974) was used to sample vegetation structure in aspen patches. Similarly to willow sampling, sampling points in aspen patches were located 40 m apart, in a randomly selected direction (Appendix 2.2). At each plot, distance to the nearest 3 trees in each of the 4 quadrants was measured. Dbh, height, and height of the lowest green branch were taken for the 12 trees considered. Typically, only the highest branches of aspen trees had leaves. Subtracting height of lowest green branch from tree height, a rough relative measure of the green mass for each aspen tree was obtained.

Stage of leaf development in patches: In 1996, aspen trees and willow bushes had started to produce leaves in only some of the patches when the first Yellow Warblers reached the area. Within two days from the arrival of the first male all the patches were classified according to a semiquantitative scale, as completely or mostly green = 3, partially green = 2, and with little/no leaves = 1. A semiquantitative scale was used due to difficulty in measuring the green area in patches.

Nest concealment and placement: To investigate whether predation at the nest and Brown-headed Cowbird parasitism were associated with any microhabitat feature, measurements of nest concealment and variables characterizing nest site were taken after chicks had fledged or predation at the nest had occurred. They included dbh of the main stem of the willow bush on which the nest was located, *Salix* species, willow height, nest height on willow, number of green and dry stems in the nest bush at the nest height level. To simulate nest concealment to an aerial predator or Cowbird, proportion of nest circumference obscured by vegetation was estimated by placing a mirror attached to a pole, 50 cm above the nest. Proportions were converted into a semiquantitative scale of 1-4, where 1 indicated 1% to 25% of nest circumference obscured and 4 indicated 75% to 100% of circumference obscured. To simulate nest concealment to a terrestrial predator, nest visibility was visually estimated to the nearest 10% from 2 m and 5 m from nest, at four cardinal directions, by a kneeling observer. Internal nest diameter, external height of nest, and nest depth were also measured when the nests were intact and could be reached.

Patch definition and measurements of spatial structure

Minimum size of treed patches was defined as 25 m^2. Patches < 25 m^2, which consisted almost exclusively of isolated willow bushes, were not mapped and their vegetation structure and arthropod abundance were not sampled. However, patches < 25 m^2 situated in the proximity of larger patches were occasionally included in territories, although never as main patches. Territories were then classified as multi-patch territories and isolation of the small patches was measured in the field. Although hundreds of isolated bushes were present in the area, over three years only two nests (1%) were found in isolated willow bushes.

Willow patches, aspen patches, and ponds were traced onto transparent paper from 1:10,000 aerial photographs dating from 1988. The thickness of the pencil line used to trace patches was 0.2 mm, leading to a 2 m error. All habitat patches of the study area were ground-truthed to verify if they had been correctly classified and whether their borders had changed considerably since 1988. Only 5% of patches had their borders adjusted on the map after field inspection.

Measurements of spatial structure were obtained with IDRISI (Eastman 1997) and ARCVIEW (Anonymous 1996) geographic information systems. Measurements in circles (see Macroscale below) were obtained using the raster version of the program FRAGSTATS (McGarigal and Marks 1995). Descriptors of spatial structure at the nest, at the patch/territory scale, and at the landscape scale are summarized in Table 2.2.

Nest site scale: For each nest, the following minimum distances were measured: to grassland, to nearest pond/willow edge, to nearest aspen patch, width of willow patch at the nest, and width of willow+aspen at the nest. Starting from nest construction until chicks fledge, Yellow Warbler females spend most of their time within 20 m of the nest (Busby and Sealy 1979). Area occupied by willow, aspen, and pond within nest-centered concentric circles with radius 5 m, 7.5 m, 10 m, 15 m, and 20 m were measured. For each patch, where one or more nests were present, the measurements were also obtained for a set of random points equaling the number of nests.

Patch/territory scale: Area occupied by willow, aspen, pond, total treed area (willow+aspen), and total area (willow+aspen+pond) were measured for each habitat patch. Ponds were included as habitat even though they were not used by Yellow Warblers, because they were thought to affect arthropod abundance. For willow patches, ponds, and treed patches, shape was measured as "Perimeter/√area". For willow patches, shape was also measured as the maximum length of the patch divided by its maximum width perpendicular to the maximum length. This measure quantifies patch elongation and does not depend on perimeter irregularities (Blouin and Connor 1985, Gutzwiller 1992). For multi-patch territories patch size and shape were obtained for the main patch only. Length of pond/willow, willow/aspen, willow/grassland, and aspen/grassland contact edges were also obtained.

Patch isolation was measured as the edge to edge shortest distance to the nearest treed patch and as distance to the nearest willow patch, excluding patches belonging to the same complex. Amount of willow, aspen, and pond (ha) within 50 m and 125 m radius concentric circles centered on territory (pseudo) centers (see Methods, *territory centers*) were measured. These radii represented the range of distances of patches that compose multi-patch territories from the territory center. In multi-patch territories I also measured mean and maximum distance between treed patches and between willow patches belonging to a territory, but not belonging the same complex.

Landscape scale: Amount of willow, aspen, pond, willow+aspen, and total amount of habitat (willow+aspen+pond) was measured in 200 m, 500 m, and 1,000 m radii concentric circles centered on territory (pseudo) centres. The following landscape configuration indices were calculated using FRAGSTATS (McGarigal and Marks 1995; Table 2.2): mean patch size (MPS), and patch size coefficient of variation (PSCV). Mean patch shape (MSI) was computed using a perimeter/√area index adjusted for raster images (McGarigal and Marks 1995). This index increases as patches become more irregular in shape. In a separate GIS layer, willow and aspen patches were reclassified as one habitat type (treed habitat). Besides the above indices, mean nearest neighbor distance (MNN), and nearest neighbor coefficient of variation (NNCV) were obtained for treed patches.

Definition of territory centers and unoccupied territories

By plotting the number of data points against territory size, I determined that 40 data points were necessary to map a territory accurately (i.e., territory size reached an asymptote). For each territory, data points representing movements, location of song perches, and other activities of territorial significance that had been mapped in the field (see Methods, *classification of territories*), were digitized on a GIS coverage of the study area.

Territory borders and territory centers were obtained using CALHOME (Kie et al. 1996) using the adaptive kernel method (Worton 1989). This method describes the home range/territory of an animal using a probability density function, termed the Utilization Distribution (Van Winkle 1975). A grid of points is required to calculate the contours of the area, which are obtained as the harmonic mean of the distance from the grid points to the data points obtained in the field. A 95 % territory utilization distribution (95 % confidence region) was specified. Grid size and an optimal smoothing parameter were automatically estimated by CALHOME, unless data were multimodally distributed, in which case the smoothing parameter was varied until the least-squares cross-validation score was minimized (Worton 1989). Grid size is known to have little effect on kernel estimators (Worton 1989, Hansteen et al. 1997). If the number of data points available was < 40 but > 25, a territory pseudocenter was calculated as described for the territory center.

To analyze pattern of territory occupancy by Yellow Warblers (territory occupied/unoccupied), the unoccupied territories were determined as follows: for a subsample of occupied territories (n = 9 in 1995; n = 17 in 1996; n = 21 in 1997; n = 20 in 1997, southern study area) for which more than 40 data points had been mapped, territorial borders were obtained using the minimum convex polygon method, retaining 95% of observations. These territories and a layer of random points were digitized in IDRISI. For each year, the territories were randomly moved across the GIS coverage of the study area until their centers (previously obtained using the adaptive kernel method) matched a random point. If all patches entirely or partially falling within the template (occupied territory) were unoccupied by Yellow Warblers, an unoccupied territory was defined. If at least one of the patches was occupied, the template was moved to match another random point. Digitized territories were randomly drawn without replacement until all territories had been used as templates. Than a new cycle of drawing was repeated until the area was saturated with unoccupied territories. Seventy-seven unoccupied territories were obtained in 1995, 86 in 1996, 87 in 1997, and 78 in 1997 for the southern area. Vegetation structure, arthropod abundance, and spatial structure of unoccupied potential territories were measured as described for occupied territories in all three years.

Patch size and passive sampling

Larger patches are more likely to be occupied simply because the probability that birds run into them is higher [i.e. passive sampling (Haila et al. 1987,1993)]. To investigate if additional biological effects of size of willow patches were present, the patches of willow were classified as small (0.12-0.19 ha), medium (0.19-0.23 ha), and large (0.23-0.28 ha). Patches larger than 0.28 ha were always occupied and were not included. Total area of willow (the sum of all the patches) was the same ± 0.1 ha for the three classes. If additional biological effects of patch size are present probability of patch occupancy should increase from small patches to large patches class.

Statistical methods

Brief summary of the statistical methods

Given the length and complexity of this section, a short summary of the statistical methods is provided. The reader not interested in the statistical details can omit the following subsections. Latent root regression (Hawkins 1973; Webster et al. 1974) was used to reduce the 48 predictors describing vegetation structure at the nest site scale and territory scale to a subset of 20 that were used in each year in the analyses. Using latent root regressions, descriptors of spatial structure of territories also dropped from 20 to 10. Territory occupancy (territory occupied /unoccupied), chronological order of territory occupancy by males and females, pairing success, number of chicks produced in successful nests, number of chicks produced in all nests, chicks' growth, predation at the nest, and brood parasitism by cowbirds, were analyzed separately in multivariate models in relation to a) vegetation structure and spatial structure at the nest site scale, b) vegetation structure, spatial structure, and arthropod abundance at the territory scale, c) spatial configuration of landscape within 200, 500, and 1000 m from territory center. Logistic regressions were used to analyze territory occupancy, pairing success, predation, and brood parasitism. Chronological order of territory occupancy and number of chicks produced per nest were analyzed with Generalized Linear Models (GLIM). Chicks growth was analyzed using ANCOVA and including number of chicks per nest as main effect, and descriptors of vegetation and spatial structure as covariates. The three scales were first analyzed separately. Variables that were significant in these models were then included simultaneously in a final model if descriptors at more than one scale were significant. Geographic location of territories was also included in models for chronological order of territory occupancy. Models for territory occupancy and chronological order of territory occupancy by males were tested using data from the southern study area. At the nest site scale, vegetation and spatial structure at several spatial extents around nests and random points were compared using logistic regressions. Consistency of patch occupancy over years was analyzed in relation to spatial structure at the territory scale using non-parametric discriminant function analysis. Different components of breeding success were also analyzed in relation to chronological order of territory occupancy by males and females using Spearman rank correlations.

Detailed statistical methods

All the statistical analyses were performed for each year separately. I did not combine years and use years as a factor because of the problem of site fidelity (i.e. the same individuals might be included in more than one year resulting in some pseudoreplication).

Selection of principal variables: Latent root regression (Hawkins 1973; Webster et al. 1974) was used to reduce the number of predictor variables describing vegetation structure of willow patches at the microscale and territory scale, and spatial structure of territories. Latent root regression is a principal component analysis done on the (p+1) set of predictor variables as well as the dependent variable of interest. This technique can be used to produce subsets of variables that retain the bulk of the variance present in the original set of variables, and are not subjected to multicollinearity (Jolliffe 1986). The original variables rather than principal components, whose biological meaning may be difficult to interpret, are then available for subsequent analysis. Details of this analysis are presented in Appendix 2.3.

This procedure made it possible to reduce the 48 predictors describing vegetation structure to a subset of 20 that were used in each year in the analyses (Table 2.3). Descriptors of spatial structure of territories dropped from 20 to 10 and include: "Area of Willow", "Area of Aspen", "Perimeter to √area willow"," Perimeter to √area treed patches", "External perimeter", "Edge willow-pond", "Distance to nearest willow patch", and "Maximum internal distance" (see Table 2.2 for description of variables).

Nest site scale: In all the subsequent analyses $\alpha = 0.05$ was selected as the significance level. Simple and multiple logistic regressions were used to analyze if nests (1, nest present) and random points (0, nest absent) differed in vegetation structure and spatial structure. Only willow patches with nests were included. For each variable, the mean was obtained for the random points and nests (if more than one occurred) for each patch. Thus, each patch contributed one nest and one random point value.

Exploratory simple logistic regressions were run first to compare the relative importance (i.e., deviance explained by different simple regression models) of the spatial explanatory variables at different spatial extents (e.g., "Amount of willow" within 5 m, 7.5 m, 10 m, 15 m, 20 m). Next, a stepwise selection procedure was used to test whether the variables "Amount of willow" within 7.5 m, 10 m, 15 m, and 20 m radius circle, when added in turn as a second variable to the best simple model ("Amount of willow within 5 m" radius circle only), could significantly reduce the residual deviance. The same procedure was followed for amount of aspen and pond in the circles. Finally, other variables describing spatial structure and vegetation structure at the nest site scale, and nest concealment, were added to the model. Wald statistics were used to test for significance of individual coefficients and a goodness-of-fit index to assess the general fit of the model (Hosmer and Lemeshow 1989). Data were analyzed separately for each year (1995, 1996, and 1997).

Chronological order of territory occupancy by males (1995, 1996 and 1997) and by females (1996 and 1997), which were discrete variables ranging from 1 to 7, were analyzed in relation to vegetation structure and spatial structure around the nest using a stepwise GLIM. Pearson Chi-square residuals were plotted against fitted values and explanatory variables to inspect whether any apparent pattern was present (Nicholls 1989). Sensitivity of models to individual observations was also investigated and gross outliers were excluded from the analysis. A Poisson error distribution was initially assumed. Due to slight overdispersion, the parameters of all the GLIM models were then estimated with a quasi-likelihood function (McCullagh and Nelder 1989). Following the same procedure outlined for territory occupancy (territory occupied/unoccupied), pairing success (paired/unpaired), predation at the nest, and parasitism by Brown-headed Cowbirds were analyzed. In 1995 only three parasitized nests were found, hence parasitism was analyzed in 1996 and 1997 only. Pairing success was analyzed in 1995 only, due to the small number of unpaired males in 1996 and 1997. *Salix* species on which the nest occurred was included as categorical variable (*S. bebbiana* or *S. petiolaris)* in logistic models for predation and parasitism. Increase in weight by chicks was analyzed using descriptors of vegetation structures and spatial structures as covariates, one at a time, and number of chicks in the nest as the main effect in ANCOVA (Type I sums of squares). To test whether the effect of predictors was influenced by number of chicks in the nest, the interaction term (e.g., number of chicks x "Area of willow") was also included in models. Covariates were log transformed where necessary.

Number of chicks produced in all nests (range 0 -5) or in successful nests only (range 1 - 5), were analyzed with GLIM, following the same procedure described for chronological order of occupancy of territories.

Territory/Patch scale: For each year, pattern of occurrence of the Yellow Warbler (territory occupied/territory not occupied), was analyzed using stepwise multiple logistic models in relation to spatial structure of the territory, vegetation structure, and arthropod abundance in the territory.

Consistency of patch occupancy over years was analyzed in relation to spatial structure of patches. Vegetation structure in willow patches and arthropod abundance were not analyzed because they varied between years. A patch was considered occupied if it was included in a territory. Since some of the variables tested did not conform to the assumptions of parametric discriminant function analysis (i.e., multivariate normality and equality of the group covariance matrices), one-way nonparametric ANOVA was run on each variable separately, using years of occupancy (0,1,2,3) as a grouping factor. Nonparametric multiple comparisons with unequal sample sizes (Dunn 1964, Hollander and Wolfe 1973) were used to determine which groups were significantly different. Next, nonparametric nearest neighbor discriminant analysis (Cover and Hart 1967, SAS 1989) was performed in a stepwise fashion to detect if the other predictors that were significant in one-way ANOVA improved the classification of observations when added to the variable which had the highest significance in one-way ANOVA, i.e., "Area of willow".

Chronological order of territory occupancy by males (1995, 1996, and 1997) and by females (1996, and 1997) were analyzed in relation to spatial structure of the territory, vegetation structure, arthropod abundance and geographic position of the patch (see below) using stepwise GLIM as described for the nest site scale. Presence of conspecifics in patches (shared/unshared patch), number of patches included in territory (single/multi), stage of development of vegetation (little or no leaves, partially green, mostly green [1996 only]), presence/absence of Red-winged Blackbird in patches were included as categorical variables. For "Area of willow", the quadratic term and interaction terms "Area of willow" x "Single/multi", "Area of willow" x "Shared/unshared", and "Area of willow" x "Presence of RWBB" were also tested. In patches where more than one territorial male was present, the first male was considered.

Geographic position of the territory was tested because at the beginning of the breeding season migrating Yellow Warblers might approach the study area from the same cardinal direction due, for example, to the geographic location of the nearest stopover site. If this is the case, a geographic gradient in chronological order of territory occupancy could exist across the study area. To separate this geographic effect from pure environmental effects, the standardized terms of a cubic trend surface equation (Student 1914) of the form:

$$z = b_1x + b_2y + b_3x^2 + b_4y^2 + b_5xy + b_6x^3 + b_7y^3 + b_8x^2y + b_9xy^2$$

where x and y are geographic coordinates of territory centers, were included in GLIM models (see Legendre 1993). Quadratic and cubic terms were included to model the convoluted topography of the study area. Next, variation explained by environmental variables, geographic variables, and interaction between geographic and environmental variables (variation in common to these two components) was partitioned using partial regression analysis (Legendre 1993). Geographic variables that were significant in GLIM models were regressed onto each significant environmental variable in turn. The residuals were used to model the dependent variable and obtain the fraction of variation explained by the geographic component of the model. In a similar fashion, the residuals for environmental variables and the fraction of variation explained by the pure environmental component of the model were obtained. The interaction fraction was measured as: total explained variation - (pure environmental variation + pure geographic variation) (see Legendre 1993, Legendre and Legendre 1998 for details). Pairing success, predation and parasitism at the nest, number of chicks produced per nest including and excluding unsuccessful nests, and increase in weight of chicks were analyzed as described for the nest site scale.

Landscape scale: Territory occupancy, chronological order of occupancy of territories by males and females, pairing and breeding success, predation and cowbird parasitism at the nest, were separately analyzed in relation to spatial structure of the landscape surrounding the territories (and unoccupied territories for territory occupancy) as described for the microscale. Consistency of patch occupancy could not be analyzed because territory centers changed in position among years. Because I did not have data to support the choice of one or more specific landscape extents, I followed an explorative approach by arbitrarily selecting 200 m, 500 m and 1,000 m radii circles (see also introduction).

Because the circles (landscape extents) surrounding the territories partially overlapped, the problem of pseudoreplication and the potential for positive spatial autocorrelation of observations existed in this analyses. However, I was mainly interested in consistency among years in significance of the individual descriptors.

Model building involved the following steps: **a)** To obtain a first screening of the descriptors included in the analysis, for each circle radius (200 m, 500 m, and 1,000 m) and for each habitat type, a model with all the spatial descriptors was built. This resulted in 12 models (3 radii x 4 habitat types) for each year. **b)** Next, all the variables that were significant in the preliminary models were grouped according to the radius. This resulted in three models (200 m, 500 m, and 1,000 m). Each model contained descriptors of different habitat types. At this step "Total amount of habitat" was also added to the models. **c)** Since the descriptors that were still significant after b) were not strongly correlated

(Pearson's correlation coefficient < 0.55 in all cases), all of them were included in one model. **d)** Since the interest of this study was in detecting any effect of landscape spatial structure while taking into account territory features, and vegetation and spatial structure around the nest, a final model including the significant variables at the nest site scale and territory/patch scale, as well as the landscape descriptors that were significant after c) was developed.

Multi-scale analysis: Since the same sampling plots and the same descriptors had been used to characterize the vegetation structure at the nest site scale and at the territory scale in willow patches, some of the descriptors were highly correlated between scales (Pearson's, correlation coefficient > 0.7, in some cases), and thus multicollinearity could occur. Initially, a separate analysis was performed for each of the two scales. Since the same descriptor was never significant at the two spatial scales in these separate analysis, descriptors regarding the nest site scale and the territory scale were used in the same multivariate models. Geographic position of the territory was included in models for chronological order of arrival at the territory scale. Finally, the descriptors of landscape spatial structure were added to the models for nest site scale and territory scale, which also included geographic position (see *Landscape scale* in this section for details).

Testing models for territory occupancy (presence/absence) and chronological order of occupancy by males: Fitted values of multiple logistic models for territory occupancy by Yellow Warbler males in the main study area were used to predict territory occupancy in the southern study area. First, predicted values obtained from the logistic model for the territory scale were regressed onto observed territory occupancy in the southern area. Next, the procedure was repeated using the fitted values from the model for territory and landscape scale, to analyze if spatial structure of landscape surrounding the territories added predictive power to the model for territory scale. Goodness of fit and percentage of cases correctly classified were used to assess the model. The model for chronological order of territory occupancy by males was tested on the southern area in a similar fashion. Since geographic position of territories in the southern area was not significant in a model independently developed, fitted values of the model for the main area did not include the geographic position.

Pairing success, breeding success,chick growth, predation at the nest and cowbird parasitism in relation to chronological order of settlement by males and females: Pairing success (1995 only), breeding success, predation at the nest, and cowbird parasitism (1996 and 1997 only) were analyzed in relation to chronological order of settlement in territories by males and females. Number of chicks produced, increase in weight by chicks were analyzed with Spearman rank correlation coefficients. Predation at the nest and cowbird parasitism were analyzed with logistic regressions.

Statistical packages used: Univariate non-parametric tests, latent root regressions, logistic regressions, covariance analysis, were performed with SPSS Version 7 (SPSS 1996). Non-parametric discriminant function analysis was performed with SAS Version 6 (SAS 1989). Finally, GLIM were run with S-PLUS Version 4.5 (S-PLUS 1997).

RESULTS

Nest site scale

Chronological order of occupancy and nests vs random points

Chronological order of occupancy of territories by males (N = 36 in 1995, N = 65 in 1996, and N = 72 in 1997; GLIM), and by females (N = 49 in 1996, and N = 53 in 1997; GLIM), was not predicted by vegetation structure and spatial structure around the nest. In 1995, 1996, and 1997 nests were surrounded by a larger "Amount of willow within 5 m" than were random points. "Amount of willow within 5 m" was the most important variable in these models (see R and Wald statistics in Table 2.4) and the only variable that was significant in all three years (P = 0.052 in 1997). No additional effect of amount of willow in larger extents occurred (i.e. Wald statistics did not increase). None of the variables describing vegetation structure were significant in more than one year.

Reproductive success

Number of fledglings produced per nest in successful nests ($N = 19$ nests in 1995, $N = 37$ in 1996, and $N = 50$ in 1997; GLIM), and increase in weight by chicks ($N = 39$ in 1996, and $N = 49$ in 1997; $F_{max1996} = 0.40$, $P > 0.5$; $F_{max1997} = 0.45$, $P > 0.5$, ANCOVA), could not be predicted by any of the variables measured at the nest.

In 1997 only, number of chicks produced per nest, including unsuccessful nests, ($N = 29$ nests in 1995, $N = 71$ in 1996, and $N = 86$ in 1997; GLIM) was larger for nests surrounded by more willow stems, with less area covered by aspen within 10 m, and located closer to the external edge of willow patches (Table 2.5).

Rate of predation at the nest was 41.9% in 1995 ($N = 31$ nests), 39.5% in 1996 ($N = 76$), and 29.5% in 1997 ($N = 88$). Rate of cowbird parasitism was 9.7% in 1995, 13.2% in 1996, 19.3% in 1997. The probability that a nest was preyed upon or parasitized by cowbird was not affected by vegetation structure and spatial structure at the nest scale (logistic regressions). Similarly, nest concealment and nest placement did not affect the probability of a nest being depredated or parasitized (GLIM). Finally, nests situated on *Salix bebbiana* and *S. petiolaris* did not differ in predation and cowbird parasitism rates.

Territory scale

Territory occupancy (presence/absence)

Probability of territory occupancy was mainly affected by the spatial structure of territories. "Area of willow" (area of main willow patch in multi-patch territories) was consistently the most important variable (1995, 1996 and 1997) in models (Table 2.6). Larger willow patches were more likely to be occupied by territorial males. All willow patches larger than 0.23 ha in 1995, 0.50 ha in 1996, and 0.58 ha in 1997 held at least one Yellow Warbler territory. In 1995 and 1996, area occupied by willow within 50 m increased the probability of occupancy. No additional effect of "Amount of willow within 125 m" occurred (Table 2.6). In all three years shape of willow patches had a significant effect; willow patches with higher "Perimeter to $\sqrt{}$area ratio" were more likely to be occupied. Distance to nearest treed patch (or willow patch) and internal distance between patches in multi-patch territories were never significant in models. Indeed, patches characterized by largest distance to nearest patch (up to 127 m) were frequently occupied, and patches as far as 140 m apart were included in the same multi-patch territory.

Probability of territory occupancy was negatively related to vegetation ground cover in willow patches in 1996 and 1997, and positively by foliage density in willow patches in 1997. No other effect of vegetation structure in willow or aspen patches and no effect of arthropod abundance were detected.

Proportion of patches of willow occupied was lower for the small patches class (Fig. 2.4). Because total area of willow was the same in the three size classes considered this indicates that the effect of "Area willow" in models for territory occupancy was not merely due to a passive sampling effect.

Consistency of patch occupancy

Larger patches of willow were occupied more consistently over the years. "Area of willow" alone predicted correctly the number of years of occupancy for 59.9 % of patches. Although area of aspen patches, "Perimeter to √area of treed complexes", "External perimeter of treed complexes", and "Perimeter to √area of willow patches" were significant in univariate analyses (Appendix 2.4), only "Perimeter to √area of willow patches" improved the percentage of patches correctly classified in multivariate analysis, from 59.9% to 65.7% (Table 2.7). Patches of willow with higher perimeter to √area ratio were occupied more consistently over the years.

Chronological order of territory occupancy

Geographic position: In 1997, geographic location (X geographic coordinate) of territories was the single most important predictor of chronological order of territory occupancy by males and females (Table 2.8). Territories situated in the eastern part of the study area were occupied earlier. Once the variation explained by geographic location of territories was partialled out, the pure effect of environmental variables (descriptors of territory quality) and variation in common between the geographic and environmental components of the model was quantified. For both males and females, roughly the same amount of deviance was explained by the pure environmental model and the pure geographic model

(Table 2.9). Variance in common to geographic and environmental components (interaction term) was higher for males than for females (Table 2.9).

Environmental variables: Given that none of the variables were significant at the nest site scale, they were not included in models for the territory scale. Once geographic position was taken into account "Area of willow" was the environmental variable that most affected chronological order of territory occupancy by males and females and the only variable that entered all models (Table 2.8). Territories situated in larger patches of willow were chosen earlier by males and females in all years considered. The quadratic term of "Area of willow" did not improve the models. In 1996, territories with fewer trees in willow patches were occupied earlier. Territory choice by males or females was not affected by any other descriptor of vegetation structure in willow patches or aspen patches, stage of development of vegetation at time of settlement of males (measured in 1996 only), dried biomass or arthropod abundance during territory settlement (1996) or rearing of chicks (1995, 1996, and 1997), dried biomass or abundance of individual arthropod taxa (Appendix 2.5 for Lepidoptera larvae). Territories situated in patches where Red-winged Blackbirds were present were occupied earlier by males (1996 and 1997) and by females (1997).

Given that "Area of willow" was the only variable that was significant in all the models, I then tested to see if "Area of willow" was correlated with any other territory feature. In all three years, there was a positive correlation between "Area of willow" and arthropod abundance per unit area during rearing of chicks ($R_{1995} = 0.22$, $N = 114$, $P = 0.018$; $R_{1996} = 0.36$, $N = 131$, $P < 0.001$; $R_{1997} = 0.23$, $N = 164$, $P = 0.003$) or dried biomass during rearing of chicks ($R_{1995} = 0.27$, $N = 114$, $P = 0.004$; $R_{1996} = 0.24$, $N = 131$, $P = 0.007$; $R_{1997} = 0.22$, $N = 164$, $P = 0.005$, Spearman rank correlation coefficient, two-tailed). None of the descriptors of vegetation in willow patches was consistently correlated with "Area of willow". In 1995 and 1997, "Perimeter to √area willow" was not correlated with arthropod abundance or biomass in willow patches ($R \leq 0.15$, $P \geq 0.788$, Spearman rank correlation coefficient, two-tailed). In 1996, "Perimeter to √area willow" was negatively correlated with arthropod abundance ($R_{1996} = -0.23$, $N = 129$, $P = 0.009$)

and not correlated with biomass sampled during rearing of chicks ($R_{1996} = -0.13$, $N = 129$, $P = 0.14$, Spearman rank correlation coefficient, two-tailed).

Consistency in chronological order of patch occupancy over years

At the patch level, chronological order of occupancy by males among years was correlated ($R_{1995\text{-}96} = 0.36$, $N = 57$, $P = 0.003$; $R_{1995\text{-}97} = 0.35$, $N = 59$, $P = 0.003$; $R_{1996\text{-}97} = 0.48$, $N = 83$, $P < 0.001$, One-tailed Spearman rank correlation coefficient). Chronological order of patch occupancy by females among years was not correlated ($R_{1996\text{-}97} = 0.19$, $N = 45$, $P = 0.111$, one-tailed Spearman rank correlation coefficient). In 1996 and 1997 chronological order of patch occupancy by males and females was correlated ($R_{1996} = 0.591$, $N = 65$, $P < 0.001$; $R_{1997} = 0.76$, $n = 72$, $P < 0.001$, Spearman rank correlation coefficient one tailed test).

Pairing success and reproductive success

Percentage of paired males was 75.8 in 1995, 90.8 in 1996, and 88.1 in 1997. None of the territory features nor date of settlement of males affected pairing success of males in 1995. Data for 1996 and 1997 were not analyzed due to small numbers of unpaired males.

None of the measured variables predicted number of chicks produced per nest, considering successful nests only ($N = 21$ in 1995, $N = 42$ in 1996, and $N = 57$ in 1997; GLIM), number of chicks in all nests ($N = 29$ in 1995, $N = 65$ in 1996, and $N = 85$ in 1997; GLIM), nor increase in weight by chicks ($N = 39$ in 1996, and $N = 49$ in 1997; ANCOVA; $F_{max1996} = 0.86$, $P > 0.50$; $F_{max1997} = 0.19$, $P > 0.50$).

In 1995, nests situated in larger willow patches and in territories surrounded by larger amount of aspen within 125 m from the territory center were more likely to be preyed upon (Table 2.10). No variable was significant in logistic models for predation at the nest for 1996 and 1997. Rate of cowbird parasitism was not affected by any measured variable.

Reproductive success and chronological order of settlement by males and females

Chronological order of settlement in territories by males or females did not affect number of fledglings produced per nest ($R_{\text{males 1995}} = 0.19$, $P = 0.402$, $N = 21$; $R_{\text{males 1996}} = -0.32$, $P = 0.094$, $N = 29$; $R_{\text{females 1996}} = -0.40$, $P = 0.078$, $N = 20$; $R_{\text{males 1997}} = 0.04$, $P = 0.800$, $N = 47$; $R_{\text{females 1997}} = 0.06$, $P = 0.744$, $N = 33$), increase in weight by chicks ($R_{\text{males 1996}} = 0.10$, $P = 0.552$, $N = 35$; $R_{\text{females 1996}} = -0.12$, $P = 0.562$, $N = 25$; $R_{\text{males 1997}} = -0.09$, $P = 0.538$, $N = 46$; $R_{\text{females 1997}} = -0.15$, $P = 0.098$, $N = 32$; Spearman rank correlation coefficient, two-tailed test), or cowbird parasitism rate (logistic regressions). In 1996 and 1997, males that settled in their territory earlier had a lower probability of having their nest preyed upon. However, these models were poor in predicting when a nest would be preyed upon (Table 2.11).

Landscape scale

Territory occupancy (presence/absence) and chronological order of territory occupancy

Landscape models were multi-scale models that included all the variables that were significant at the territory scale and the geographic position of the territory. "Amount of pond within 500 m" was the only landscape variable that was significant (in 1996 only) in models for territory occupancy. However, "Amount of willow within 50 m" and "Perimeter to √area willow" were no longer significant when "Amount of pond within 500 m" was added to the model and the percent of correctly classified observations did not improve when adding "Amount of pond within 500 m" (compare model in Table 2.6 and 2.12).

None of the landscape variables were significant in more than one model for male and female chronological order of territory occupancy (Table 2.13). In general, territories surrounded by patches with higher mean shape index tended to be occupied earlier by males.

Pairing success and reproductive success

Pairing success, (N = 61 males in 1995, N = 109 in 1996, N = 113 in 1997), predation at the nest (N = 30 nests in 1995, N = 70 in 1996, and N = 84 in 1997) , cowbird parasitism (N = 70 nests in 1996, and N = 85 in 1997), clutch size (N = 64 nests in 1996, and N = 83 in 1997), number of chicks produced/nest in successful nests only (N = 31 nests in 1996, N = 51 in 1997), number of chicks produced/nest including unsuccessful nests (N = 42 nests in 1996, and N = 51 in 1997) and increase in weight by chicks (N = 36 nests in 1996, and N = 48 in 1997) were not affected by the spatial structure of landscape.

Test of models for territory occupancy and chronological order of territory occupancy by males on the southern study area

When the models for territory occupancy were tested on the southern study area, they classified correctly 81.3%, 79.9%, and 84.9% of territories, respectively in 1995, 1996, and 1997. However, fit of these models was poor (Table 2.14). A model independently developed for the southern study area, using the full set of predictors, showed that "Area of willow", "Area of aspen", and foliage density affected territory occupancy (Table 2.6). In general, the models classified correctly a higher percentage of occupied territories than of unoccupied territories (Table 2.6). Models for chronological order of territory occupancy by first males had poor (1995) or no predictive power (1996 and 1997) when tested on the southern study area (Table 2.15). The best model for the southern study area included "Area of willow" and "Distance to nearest willow patch" (Table 2.15). Larger willow patches and patches closer to the nearest willow patch were occupied earlier by first males (Table 2.8). "Area of willow" was the only variable that affected territory choice in both study areas. When tested on the southern area, models for territory occupancy and chronological order of occupancy that included territory and landscape variables did not improve the fit of models for territory scale only, and "Amount of pond within 500 m" was not significant. No other landscape descriptor affected territory occupancy or chronological order of occupancy by males in the southern area (logistic regression).

DISCUSSION

Habitat selection can be thought as a hierarchical system of sequential independent decisions that are affected by numerous factors at different spatial scales (e.g., availability of potential nesting sites, vegetation structure of the patch, spatial configuration of the landscape). Alternatively, these factors may act in synergy and simultaneously in a complex way or "Gestalt" (Cody 1985). Territory choice is a form of habitat selection. Whether we think of territory choice as a process that unfolds gradually in time, or as an almost instantaneous complex "decision" that the animal makes, it can be affected by multiple factors that act at different spatial scales. This study quantifies the relative importance of four spatial scales (nest surroundings, territory/patch structure and composition, landscape spatial structure and composition around the territory, geographic position in the study area) to territory occupancy and territory choice. No hierarchy in importance of spatial scales was established *a priori* and the approach followed was to assess simultaneously the relative contribution of the descriptors at different spatial scales. For convenience, my discussion will proceed from the largest spatial extent (main study area) to the smallest (nest site).

Territory choice and geographic position of territory in the study area

In 1997, eastern territories were occupied earlier by both males and females. Geographic position accounted for 37.3% of the explained deviance in models for chronological order of territory occupancy by males, and 45.3% for females (64% and 61.4% respectively, when including the interaction term, Table 2.9). Hence, territory choice was affected by some factor operating at a larger scale. Interpatch distance, which tended to increase from east to west, grazing intensity, which also increased from east to west, occurrence of other unmeasured gradients, and geographic location of stopover sites in the surroundings may all be responsible for the observed geographic trend in territory choice.

It remains to be explained why this occurred only in 1997. In 1997, the first male arrived on 15 May, that is, seven days and three days earlier than in 1995 and 1996, respectively. Migration pattern also differed among years. In 1997, a cold front slowed the migratory flux after a few males had occupied the extreme eastern portion of the study area and new arrivals followed more gradually than in previous years. In these conditions, conspecific attraction at the landscape scale may have led to the observed pattern (e.g, later arriving males that reached the area settled in proximity of the only group of males present in the area).

Territory occupancy, territory choice and landscape

Once the geographic position of the territory was taken into account, many variables describing the spatial structure of the landscape were significant in models for chronological order of occupancy of territories by males and females. This suggests that although the landscape circles overlapped, variation in indices used was sufficient to detect significance in models. None of the landscape variables were significant in more than one year (Table 2.13), however. Since there is no reason to believe that the importance of landscape composition and configuration to territory occupancy and choice by the Yellow Warbler varies between years, the ecological importance of these variables is doubtful (see Knopf and Sedgwick 1994). The same holds for "Amount of pond within 500 m" in the model for territory occupancy (Table 2.12). When this landscape variable was included in the model, two descriptors at the territory scale, "Perimeter to$\sqrt{}$area willow" and "Amount of willow within 50 m" were no longer significant and the fit of the model and percentage of observations correctly classified did not improve. Finally, no landscape variable could predict territory occupancy or chronological order of occupancy by males or females in the southern study area. Hence, I conclude that no descriptor of landscape spatial structure consistently affected territory choice and quality by the Yellow Warblers. However, these results should be interpreted with caution because the power of tests used may have been lower for the landscape scale.

Several studies, all carried out in managed forested or agricultural landscapes have found that bird distribution and breeding success were related to landscape composition (e.g., Askins and Philbrick 1987, Pearson 1993, Donovan et al. 1997, Drapeau *et al.*, *in press;*), or composition and configuration (e.g., McGarigal and McComb 1995, Jokimäki and Huhta 1996, Saab 1999). In a recent review Mazerolle and Villard (1999) found that patch variables were significant predictors of bird response in 93.4% of 25 studies, whereas landscape variables were significant in

59.0% of studies. Nearly all these studies were carried out in agricultural and/or managed forested landscapes. At Rumsey, landscape composition and configuration varies little in space. This could explain the lack of landscape effect on territory occupancy and choice in this study. Edenius and Sjöberg (1997) found that landscape matrix (forest *vs* mire) and landscape composition in natural landscape mosaics of old-growth forest in northern Sweden had no effect on bird distribution.

Territory occupancy, territory choice and territory features

In theory, models at the territory scale may also be affected by short distance spatial autocorrelation, for example if conspecific attraction at the landscape level occurs. However, the fact that suitable patches of habitat were separated by unsuitable landscape matrix should reduce this problem.

Amount of willow and isolation

Size of focal willow patch was the strongest predictor of territory occupancy, chronological order of occupancy by males and females, and consistency of patch occupancy over years. Many other studies have found that larger patches of habitat are more likely to be occupied than smaller ones and that patch size is the main factor affecting the probability of occupancy of a patch (e.g., Van Dorp and Opdam 1987, Blake and Karr 1987, Celada and Bogliani 1993). This may be due to a "passive sampling" effect (Haila et al. 1987, 1993), or to scarcity of suitable habitat in small patches (e.g., Whitcomb *et al.* 1981, Blake and Karr 1987, Villard *et al.* 1995). In my study, the importance of "Area of willow" was not merely due to a passive sampling effect (Fig 2.4). Huhta et al. (1998) found that male and female Pied Flycatcher (*Ficedula hypoleuca*) settled preferentially (earlier) in larger forest stands in Finland, presumably in relation to higher amount of resources (nest sites, mates, food).

Patches that did not meet minimum requirements for holding a full Yellow Warbler territory could still be occupied by being included in multi-patch territories (see Newton 1986, Redpath 1995). "Amount of willow within 50 m" of a territory center affected whether a territory was occupied, but not chronological order of occupancy by males or females. Indeed, most of the patches included in a multi-patch territory were within 50 m of a territory center. Smaller patches with no or smaller area covered by willow within 50 m were less likely to be occupied. "Amount of willow within 125 m" did not affect territory occupancy, probably because patches further than 50 m from territory center were seldom included in multi-patch territories.

Previous studies have found that patch size is more important than isolation to the distribution of bird species (reviewed in Opdam 1991). As the patches of suitable habitat become sparser, dispersal between patches may become problematic and the importance of isolation will increase. Thus the relative importance of patch size and isolation will depend on the spatial configuration of the landscape. Distance to nearest willow patch did not affect territory occupancy by Yellow Warblers and some of the remotest patches (up to 180 m from nearest willow patch) were occupied. Given the short mean distance between treed patches at Rumsey, this is not surprising.

Amount of aspen

Yellow Warblers were frequently observed foraging and advertising their presence from the canopy of isolated aspen trees or from trees situated in aspen patches. However, "Area of aspen" and "Amount of aspen within 50 and 125 m" did not predict territory occupancy and territory choice in the main study area. This suggests that in this area, "Area of aspen" was not as critical as "Area of willow". The presence of aspen trees or patches rather than the size of aspen patches included in a territory is important. This could not be tested because isolated aspen trees in willow patches were not mapped. However, in general "Area of aspen" and vegetation structure in aspen patches was never significant in models.

Patch shape

Territories with higher "Perimeter to √area willow" were more likely to be occupied and more consistently occupied over years. Patch elongation, convolutedness, and occurrence of a pond within willow patches contribute to "Perimeter to √area willow". Patch shape can affect **1.** territory defendability (Eason and Stamps 1992, Eason 1992);

2. proportion of habitat edges in patches of habitat (Forman and Godron 1986);
3. interception of moving organisms, i.e. elongated patches positioned perpendicular to a flux of moving organisms may be more likely to be colonized (Gutzwiller and Anderson 1992). I consider each of these possibilities below.

First, at Rumsey, costs of territorial defence may be lower in willow patches that include a pond because, due to higher visibility, intruders may be detected earlier (see Eason 1992). This should be the case for territories that include one side of the willow patch and do not include the pond. Moreover, for these territories, part of the territorial borders will be adjacent to habitat that is unsuitable to Yellow Warblers. On the other hand, territories including two sides of the willow patch and a pond may be harder to defend because they have more edge. However, intruders may still be easier to detect in these territories given that willow patches are only a few meters wide. Second, many studies have found that proportion of habitat edges may affect arthropod abundance (Gates and Gysel 1978, Hansson 1983, Lovejoy *et al.* 1986, Noss 1991). However, all these studies were carried out in forested habitats. In this study "Perimeter to √area willow", and length of different edge types were not significant in multivariate regressions where "Area of willow", "Area of aspen", "Perimeter to √area willow", "External perimeter", and "Edge willow-pond" were used as predictors of arthropod abundance and dried biomass. Neither length of external patch perimeter nor willow/pond edge affected territory occupancy and chronological order of occupancy by males or females. Third, patch "Elongation" was never significant in models for chronological order of territory occupancy. However, patch orientation was not considered in this study. Thus, only the territory defendability hypothesis could explain why territories with higher "Perimeter to √area willow" were more likely to be occupied and were chosen earlier.

Testing models for territory occupancy and territory choice

Predictive models obtained in habitat selection studies are seldom tested on other study areas. I found that when models for territory occupancy and territory choice were tested on the southern study area they had poor predictive power. "Area of willow" was the only descriptor that predicted territory occupancy and chronological order of occupancy by males in the two study areas and in all the three years in the main study area. Foliage density predicted territory occupancy in the two study areas, but only in one year (1997) in the main study area (Table 2.6). I conclude that even when comparing similar landscapes, models for habitat selection may not be generalized even at small spatial scales. On the other hand, lack of consistency in significant predictors between areas may allow for interesting comparisons. For example, in the southern area, where "Amount of treed habitat" around territory centers was lower (mean "Amount of treed habitat in 500 m" radius circle: southern area = 14.26 ha; main area = 21.10 ha), "Area of aspen" was a positive predictor of territory occupancy, and patches closer to the nearest willow patch were chosen earlier. These two variables were not significant in the main study area. It is plausible that "Area of aspen" becomes important when treed area, thus the total gleaning surface in the landscape, becomes smaller. Also, patch isolation may become important in a landscape where patches of habitat are more sparse. However, results for the southern study area are based on one year only. If Yellow Warblers reoccupy the same territory in consecutive years (Studd and Robertson 1989, Yezerinac et al. 1996) occupancy and choice of a given territory may not be independent among years. This problem could have been solved by removing individual territory holders upon their arrival and describing territory choice for new arrivals (e.g., Thompson 1977, Smith 1987).

Why is "Area of willow" important to territory occupancy and choice?

Birds may assess prey abundance directly, or indirectly using the vegetation structure of a patch as a cue, i.e. the "structural cues hypothesis" (Smith and Shugart 1987). Instead, I propose that birds may use willow patch size as a cue for arthropod (prey) abundance.

Although arthropod abundance and biomass did not affect territory occupancy, territory choice, and breeding success of Yellow Warblers in my study, they may become important if harsher climatic conditions occur (e.g., severe drought or colder than average temperature). For a Yellow Warbler breeding pair, the greatest food demand will likely be during rearing of chicks, and hence arthropod abundance will have its highest effect on territory quality during brood rearing. Because both vegetation structure and arthropod abundance in willow patches can vary dramatically between the times of territory choice and rearing of chicks, a cue that is relatively constant in time (across the breeding season and over years) is needed. "Area of willow" may serve this function if it is consistently (over years) related to arthropod abundance or biomass during brood rearing.

In this study arthropod abundance during settlement of territorial males was weakly correlated with arthropod abundance during rearing of chicks but dried biomass was not correlated between these two periods (Table 2.16). Among the individual taxa considered, only Homoptera abundance showed a highly significant and positive correlation between periods (Table 2.16). It is therefore unlikely that arthropod abundance or biomass during settlement can be used as an indicator of territory quality by Yellow Warblers.

"Area of willow" and arthropod abundance per unit area (or dried biomass) during brood rearing were positively correlated in all the three years of this study. I conclude that Yellow Warblers may use area of focal willow patch as a cue to assess prey abundance during brood rearing. Burke and Nol (1998) also found that Ovenbird density and pairing success were higher in larger woodlots, where prey abundance per unit area was also higher. This difference was attributed to decreased moisture and litter depth in smaller fragments.

None of the descriptors of vegetation structure in willow patches (measured in July) was correlated with arthropod abundance or biomass during rearing of chicks in more than one year. The "Structural cue hypothesis" requires that the relationship between vegetation structure and prey abundance is relatively constant seasonally and over years (Smith and Shugart 1987). Smith and Shugart (1987) found that prey abundance per unit area in forest stands was higher in territory sites than in areas not occupied by Ovenbirds (*Seiurus aurocapillus*). However, Ovenbirds selected territories according to vegetation structure, rather than directly assessing prey abundance. In their study, vegetation structure accounted for 73% of the variation in prey abundance among territories (Smith and Shugart 1987). In Alberta, in the boreal mixedwood forest, the relationship between invertebrate biomass and vegetation structure changed between years (Song 1998). Furthermore, biomass of invertebrates was not related to densities of songbirds, presumably because songbird prey are superabundant in the boreal forest (Song 1998).

In contrast, other studies have found that prey abundance directly affected pattern of occurrence of territory holders (e.g, Nilsson 1979).

Since "Area of willow" is relatively constant between years, it may provide the territory holder with information about the long term quality of a patch, unless dramatic changes in vegetation structure occur. This may be important since familiarity with a territory has been shown to be advantageous to the territory holder. Potential benefits of reoccupying a familiar territory have been reviewed by Eason and Hannon (1994) and include increased foraging gains (Davies and Houston 1981), decreased probability of predation (Hinde 1956, Metzgar 1967), and more effective territorial defence (e.g., Greenwood 1980, Krebs 1982, Maynard Smith 1982). Most birds will choose their territory once or twice in their life, immediately after dispersal or at the beginning of the breeding season (see Danchin et al. 1991 for review). Each year those individuals that bred at a good territory will attempt to reoccupy it, unless its quality has dropped considerably (e.g., Newton and Marquiss 1982, Beletsky and Orians 1987, Bollinger and Gavin 1989, but see Korpimäki 1988 for differences between sexes), therefore a descriptor that provides information on the long term patch/territory quality, such as "Area of willow", may be important.

Nest site selection, territory choice and nest site features

Nests were surrounded by a larger amount of willow within 5 m than random points situated in the same territory. Presumably, vegetation cover immediately around the nest is important. Thus, nest sites were not chosen randomly. However, three nests were found in large isolated willow bushes. Vegetation structure, nest concealment, willow species, and spatial structure around the nest did not affect territory choice by males and females. Thus, nest site selection appears to be subordinate to territory choice by males and females. A possible explanation is that suitable nest sites are not limiting. On the other hand, it is possible that unoccupied territories did not contain suitable nesting sites. According to Lack (1971), open-nesting passerines are not expected to be nest-site limited. However, several studies have shown that nest site selection is an important component of habitat selection in open-nesting passerines (e.g., Martin and Roper 1988, Martin 1992*b*, Steele 1993). Knopf and Sedgwick (1994) found that nest site selection in the Yellow Warbler was based on characteristics of the patch (defined as a clump of uniformly sized bushes surrounding the nest bush), mainly distance between willow bushes, rather than on characteristics of the nest bush itself such as structure and vigor. They also speculated that since Yellow Warblers often reach the breeding area prior to leafing of shrubs, they may not be able to assess vigor of willow. This point is supported by my study.

Distance of the nest to edges and to the nearest aspen patch did not affect territory choice. Nest site may be chosen according to proximity to abundant food sources, such as the willow/pond edge. Arthropod abundance was not sampled at the nest site scale. However, Yellow Warbler males were frequently observed foraging across the entire territory even when their mobility was lowest, i.e., when they had chicks (compare Busby and Sealy 1979). Occasionally, females were also observed foraging far from nest. I conclude that it is unlikely that arthropod abundance/biomass around the nest affected territory choice and nest site selection.

Territory choice: the female perspective

On average, females reached the study area 4 -5 days later than males. Females were never observed alone in patches and in general, territory choice by females mirrored territory choice by males and chronological order of patch occupancy by males and females was correlated (e.g., both sexes were affected by geographic position in 1997). This is expected because male and female settlement periods overlap and females choose territories occupied by unpaired males (see also Brooke 1979). Females may choose territories based on territory attractiveness (e.g., Alatalo et al. 1986, Slagsvold 1986), mate quality (e.g., Catchpole 1980, Gottlander 1987, Lifjeld and Slagsvold 1988), or they may settle randomly (Price 1984, Leonard and Picman 1988, Dale and Slagsvold 1990, Schieck and Hannon 1992). Male quality and territory characteristics are frequently correlated, hence their effects on female territory choice are hard to disentangled (but see Alatalo et al. 1986). In this study male quality was not measured. However, since chronological order of territory occupancy by males and females were strongly correlated it appears that females were essentially using the same cues as males. Alternatively, they may have chosen where to settle according to mate quality.

Territory choice: the relevant scale

Territory choice can now be summarized from the bird's view. Early arriving Yellow Warbler males approaching the area may limit their search for a territory to the portion of the ecological reserve closer to the direction of their place of origin. Consequently, territories may become gradually occupied along a geographic gradient, as happened in 1997. Alternatively, birds may scan a larger area before they settle. This may still result in the pattern observed in 1997, if some spatial gradient in territory quality occurs, or may result in the lack of a geographic effect seen in 1995 and 1996. Once the geographic position has been considered, it remains uncertain if landscape composition and configuration will affect territory choice. If social factors such as conspecific attraction, interspecific interactions, and site fidelity are ignored, territory choice will now be based mainly on "Area of willow" (main patch in multi-patch territories). Higher "Perimeter to$\sqrt{}$area willow", larger "Amount of willow within 50 m" from territory center, low ground vegetation cover, and high foliage density will all contribute to territory attractiveness. Once a territory has been selected, the location of the nest will be random with respect to distance to different edge types, but it will be surrounded by larger amount of willow within 5 m. Some patches may remain unoccupied because few or no sites with willow width < 5 m are available.

Pairing success, breeding success, and habitat features

Landscape composition and configuration, spatial structure of territories and distance to edges did not affect the probability that a nest was preyed upon or parasitized by cowbirds. Presumably, in this study area, where the landscape matrix (grassland) covers 73.5% and treed patches are never larger than 2.3 ha, predators and cowbirds have access to all suitable Yellow Warbler habitat. In contrast, several studies carried out in forested landscapes have found that birds avoided nesting near anthropogenic habitat edges where predation and cowbird parasitism were higher

(Gates and Gysel 1978, Wilcove 1985, Freemark et al. 1995, Wenny et al. 1993, Burke and Nol 1998. In contrast, Song (1988) found that in the mixedwood boreal forest in Alberta predation and cowbird parasitism were not higher near forest/clearcut edges, and edges were not avoided by songbirds. Neither pairing success, nor any of the considered components of breeding success were affected in more than one year by any of the variables measured at the three spatial scales.

Many studies have shown that earlier settlers have higher breeding success (e.g., Alatalo et al. 1986, Barba et al. 1995, Bensch and Hasselquist 1991, Hasselquist 1998, but see Hannon et al. 1988). Males arriving later tended to have higher predation at the nest (1996 and 1997). Quality of parents or increase in number of predators present in the study area as the breeding season progresses may be responsible for this. However, these models had poor predictive power (Table 2.11). In conclusion, breeding success by the Yellow Warbler was largely stochastic. Other studies share this conclusion for other bird species (e.g., Schieck and Hannon 1993).

Why does territory attractiveness not reflect breeding success? Several hypotheses can be put forward. Cold weather at the beginning of the breeding season may put earlier settlers at a disadvantage. Males arriving earlier may have higher extra-pair mating success (Hasselquist 1998). Long-term benefits related to the quality of mate, rather than immediate higher breeding success may be obtained by choosing certain territories (Halliday 1979). Birds may choose their territory to optimize life-time fitness rather than immediate fitness. In Ontario, Yellow Warbler males reoccupied the same territory during up to four consecutive breeding seasons (Studd and Robertson 1989). Of course, extra-pair mating success and long-term benefits could not be measured in this study. Larger willow patches contain higher prey abundance but this could be important only in years with low arthropod abundance. Thus, although more attractive territories do not necessarily guarantee higher immediate breeding success, they may be of higher quality (i.e. allow for higher individual fitness of the territory holder) over the long term.

Conclusions

In this natural mosaic, territory occupancy and choice by the Yellow Warbler were largely affected by one spatial scale, the territory. Nest site features played a marginal role, if any. The importance of landscape spatial structure remains uncertain. However, no single descriptor emerged as constant predictor over years. Models for territory occupancy and choice, when tested even on a similar and close by study area had limited predictive power, suggesting that the processes investigated may be largely landscape-specific or stochastic. This may suggest that landscape spatial structure is indeed important. Territory choice did not reflect breeding success. Long term benefits related to terrritory choice such as genetic qualities of the mate that are inherited by the offspring and that enhance offspring viability (Zahavi 1977, Hamilton and Zuk 1982, Kodric-Brown and Brown 1984) and/or attractiveness (Weatherhead and Robertson 1979, 1981), are difficult to measure but should be included in future studies.

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Table 2.1. Variables describing vegetation structure in willow patches. Variables describing *Salix petiolaris* and *S. bebbiana* separately are available only for 1996 and 1997.

Variable name	**Description of variable**
GROUND COVER	
All green (%)	Percent of ground covered by grass/sedges, shrubs, and forbs.
Grass (%)	Percent of ground covered by grass/sedges.
Shrub (%)	Percent of ground covered by shrubs.
Forb (%)	Percent of ground covered by forbs.
Leaf litter (%)	Percent of ground covered by leaf litter.
Bare ground (%)	Percent of ground not covered by vegetation (woody debris, water, and mud).
Litter depth (cm)	Litter depth.
SHRUBS (10-140 cm)	
#Total shrubs	Total number of shrub stems.
#Rose	Number of *Rosa sp.*stems.
#Saskatoon	Number of *Amelanchier alnifolia* stems.
#Buckbrush	Number of *Symphoricarpos occidentalis* stems.
#Raspberry	Number of *Rubus idaeus* stems.
#Gooseberry	Number of *Ribes oxyacanthoides* stems.
#Aspen shrubs	Number of *Populus tremuloides* stems.
#Willow shrubs	Number of *Salix sp.* stems.
SAPLINGS (dbh<2.5 cm) AND POLES (2.5<dbh<8 cm)	
#Aspen saplings	Number of *Populus tremuloides* saplings.
#Balsam saplings	Number of *Populus balsamifera* saplings.
#Aspen poles	Number of *Populus tremuloides* poles.
#Balsam poles	Number of *Populus balsamifera* poles.
#Total saplings	Total number of saplings.

Variable name	Description of variable
WILLOW BUSHES	
bebbiana height (cm)	Mean height of *Salix bebbiana* bushes.
petiolaris height (cm)	Mean height of *Salix petiolaris* bushes.
Willow height (cm)	Mean height of willow bushes.
Green *stems bebbiana*	Number of green stems of *Salix bebbiana*.
Dry stems *bebbiana*	Number of dry stems of *Salix bebbiana* .
Total stems *bebbiana*	Total number of *Salix bebbiana* stems.
Green stems small *petiolaris*	Number of green stems of *Salix petiolaris* < 2 m.
Green stems big *petiolaris*	Number of green stems of *Salix petiolaris* > 2 m.
Dry stems small *petiolaris*	Number of dry stems of *Salix petiolaris* < 2 m.
Dry stems big *petiolaris*	Number of dry stems of *Salix petiolaris* > 2 m.
Total stems small *petiolaris*	Total number of *Salix petiolaris* stems < 2m.
Total stems big *petiolaris*	Total number of *Salix petiolaris* stems > 2m.
Green stems willow	Total number of green willow stems.
Dry stems willow	Total number of dry willow stems .
Total stems willow	Total number of willow stems.
Willow distance (cm)	Mean distance between willow bushes.
VEGETATION DENSITY	
Foliage density (%)	Foliage density.
Canopy cover (%)	Percent of sky obscured by willow and trees.
Tall stratum (cm)	Taller stratum of willow bushes with constant height (if present).
Low stratum (cm)	Lower stratum of willow bushes with constant height (if present).

Variable name	Description of variable
TREES	
#Aspen trees	Number of *Populus tremuloides* trees.
#Balsam trees	Number of *Populus balsamifera* trees.
#Total trees	Total number of trees.
Aspen height (m)	Mean height of *Populus tremuloides* trees.
Tree height (m)	Mean height of trees
Aspen dbh (cm)	Mean diameter at breast height of *Populus tremuloides* trees.
Tree dbh (cm)	Mean diameter at breast height of trees.

Table 2.2. Spatial structure variables measured at the nest, territory, and landscape surrounding each territory. For multi-patch territories measures at the territory scale refer to the main patch only (see text for explanation).

Variable name	**Description of variable**
NEST SCALE	
Distance to external edge (m)	Shortest distance from nest to landscape matrix (grassland).
Distance to internal edge (m)	Shortest distance from nest to willow/pond edge.
Distance to nearest aspen patch (m)	Shortest distance from nest to nearest aspen patch.
Width willow (m)	Width of willow patch at the nest.
Width willow+aspen (m)	Width of treed area at the nest.
Amount of patch type (willow, aspen, pond) 5...20 m (m^2)	Area covered by patch type (willow, aspen, pond) in 5 m, 7.5 m, 10 m, 15 m, 20 m radius circles centered on nest.
TERRITORY SCALE	
Patch size	
Area patch type (willow, aspen, pond) (ha)	Area occupied by patch type (willow, aspen, pond).
Treed area (ha)	Area occupied by willow and aspen.
Area willow+aspen+pond (ha)	Area occupied by willow, aspen, and pond.
Patch shape and edges	
Elongation	Maximum length of willow patch divided by maximum width perpendicular to the maximum length.
Perimeter to √area willow (m/√ha)	Willow perimeter divided by √willow area.
Perimeter to √area pond (m/√ha)	Pond perimeter divided by √pond area.
Perimeter to √area treed area (m/√ha)	Sum of willow/grassland, aspen/grassland, and willow/pond edge divided by √treed area.
External perimeter (m)	Sum of willow/grassland edge, and aspen/grassland edge.
Edge willow-aspen (m)	Length of willow/aspen edge.

Variable name	Description of variable
Edge willow-pond (m)	Length of willow/pond edge.
Isolation	
Distance to nearest treed patch (m)	Shortest distance from patch belonging to territory to nearest treed patch external to territory.
Distance to nearest willow patch (m)	Shortest distance from patch belonging to territory to nearest willow patch external to territory.
Mean internal distance between treed patches (m)	Mean distance between treed patches belonging to the same multi-patch territory.
Maximum internal dist. between treed patches (m)	Maximum distance between treed patches belonging to the same multi-patch territory.
Mean internal distance between willow patches (m)	Mean distance between willow patches belonging to the same multi-patch territory and not belonging to same treed patch.
Maximum internal distance between willow patches (m)	Maximum distance between willow patches belonging to the same multi-patch territory and not belonging to same treed patch.
Amount of habitat type (willow, aspen, pond) within 50 m and 125 m (ha)	Area occupied by habitat type (willow, aspen, pond) within 50 m and 125 m from territory center.
Amount of treed area within 50 m and 125 m (ha)	Treed area within 50 m and 125 m from territory center.
Territory type	
Shared/unshared (categorical)	Shared patch-territories Vs. unshared patch territories.
Single/multi (categorical)	Single-patch territories Vs. multi-patch territories.
LANDSCAPE SCALE (1)	
Amount of habitat type (willow, aspen, pond, treed habitat) (ha)	Area occupied by each habitat type.
Amount of treed area (ha)	Area occupied by treed habitat.

(1) All landscape variables measured in 200 m, 500 m, 1,000 m radius circles centered on center of territories.

Variable name	Description of variable
Total amount of habitat (ha)	Area occupied by all habitat types (willow + aspen + pond).
Mean patch size (ha) (2)	Amount of habitat type divided by number of patches.
Patch size coefficient of variation (%) (2)	SD in patch size divided by mean patch size, multiplied by 100.
Mean shape index (2)	The mean of the following index, calculated for each patch: Patch perimeter (m) divided by √ patch area (m^2).
Mean nearest neighbor distance (m) (3)	The mean of the shortest edge-to-edge distance to nearest patch, measured for each patch.
Nearest neighbor coefficient of variation (%) (3)	SD in nearest neighbor distance divided by mean nearest neighbour distance, multiplied by 100.

(2) Measured for willow, aspen, pond, and treed habitat separately.

(3) Measured for treed patches only.

Table 2.3. Principal variables for vegetation structure in willow patches derived from latent root regression analysis. Foliage density was also retained for subsequent analysis (see Statistical methods for explanation). ✓ indicates in which year the variable in question was a principal variable.

Principal Variable	1995	1996	1997
Allgreen	✓	✓	
Grass			✓
Shrub	✓		✓
Bare ground	✓	✓	
Litter depth			✓
#Total shrubs		✓	
#Saskatoon			✓
#Aspen shrubs	✓		✓
#Willow shrubs		✓	✓
#Aspen saplings	✓		
#Total saplings			✓
#Balsam poles	✓	✓	
Willow height		✓	
Total stems bebbiana		✓	
Total stems willow		✓	✓
Total stems small †	✓		
Total stems big †	✓		
#Total trees	✓	✓	
#Aspen trees			✓
Tree dbh	✓	✓	✓

† In 1995 data for *S. petiolaris* and *S. bebbiana* were lumped.

Note: Vegetation structure variables, that in none of the three years were selected as principal variables, were excluded from subsequent analysis. Since the main interest was in consistency of significance of predictors over years, all the other variables were retained.

Table 2.4. Logistic regressions for nests *vs* random points and spatial structure, vegetation structure, nest concealment, nest placement and willow species.

Predictor	B (SE)	Wald	P	R
1995				
Constant	-1.90 (0.71)	7.17	0.007	
Amount of willow 5 m	279.26 (110.38)	6.40	0.011	0.22
# Saskatoon	0.26 (0.12)	4.86	0.027	0.18
	X^2	DF	Significance	
Model χ^2	20.34	2	0.000	
Improvement last variable	7.61	1	0.006	
Goodness of fit	62.79	62	$0.25<P<0.50$	
Cases correctly classified	Obs. 0 = 61.3 %	Obs. 1 = 82.4 %	Overall = 72.3 %	
1996	B (SE)	Wald	P	R
Constant	0.05 (0.55)	0.00	0.927	
Amount of willow 5 m	252.00 (76.60)	10.82	0.001	0.21
# Aspen trees	-0.93 (0.35)	7.06	0.008	-0.16
#Total shrubs	-0.03 (0.02)	4.29	0.038	-0.11
Litter depth	-0.28 (0.14)	4.08	0.043	-0.10
#Aspen shrubs	-0.37 (0.55)	4.96	0.026	-0.12
	X^2	DF	Significance	
Model χ^2	36.49	5	0.000	
Improvement last variable	4.86	1	0.028	
Goodness of fit	151.32	137	$0.10<P<0.25$	
Cases correctly classified	Obs. 0 = 73.7 %	Obs. 1 = 68.2 %	Overall = 71.1 %	

Predictor	B (SE)	Wald	P	R
1997				
Constant	0.24 (0.60)	0.16		
Amount of willow 5 m	125.22 (64.47)	3.94	0.052	0.10
Total stems willow	-0.00 (0.00)	3.94	0.047	-0.10
	X^2	DF	Significance	
Model χ^2	8.31	2	0.016	
Improvement last variable	3.89	1	0.049	
Goodness of fit	138.06	136	$0.25<P<0.50$	
Cases correctly classified	Obs. 0 = 59.7 %	Obs. 1 = 67.6 %	Overall = 63.8 %	

Table 2.5. Generalized linear models (stepwise procedure) for production of chicks/nest and vegetation structure and spatial structure around the nest. Unsuccessful nests are included in this analysis. Parameters were estimated with quasi-likelihood method. Distance to external edge was ln transformed.

YEAR 1997	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Number of chicks produced/nest							
Intercept	140.15	85				0.66	0.28
Total stems willow	128.59	84	11.56	7.78	0.007	0.001	0.00
Amount of aspen 10 m	118.85	83	9.74	6.55	0.013	-116.60	61.46
Dist. to external edge	109.87	82	8.98	6.04	0.017	-0.06	0.03

Table 2.6. Logistic regression models for territory occupancy. Territory occupied/not occupied, coded respectively as 1/0, was the dependent variable. Significance of the model was tested with a goodness-of-fit index. Wald statistics were used to test significance of individual coefficients.
R is the partial correlation coefficient between each explanatory variable and the dependent variable. Area willow and Area aspen were ln+1 transformed. Foliage density, expressed as a proportion (p), was arcsin √p transformed.

Predictor	B (SE)	Wald	P	R
1995				
Constant	-56.59 (21.70)	6.80	0.009	
Area willow	6.52 (2.47)	6.99	0.008	0.26
Amount of willow 50 m	27.32 (12.23)	4.99	0.026	0.20
Perimeter to √area willow	16.64 (8.01)	4.32	0.038	0.18
Amount of pond 50 m	12.80 (6.70)	3.65	0.056	0.15
	X^2	DF	Significance	
Model χ^2	48.51	4	<0.001	
Improvement last variable	6.65	1	0.010	
Goodness of fit	20.31	65	1	
Cases correctly classified	Obs. 0 = 66.7 %	Obs. 1 = 94.4 %	Overall = 88.4 %	

1996	B (SE)	Wald	P	R
Constant	-11.38 (2.48)	21.07	<0.001	
Area willow	1.68 (0.32)	27.33	<0.001	0.39
Perimeter to $\sqrt{\text{area}}$ willow	4.77 (1.70)	7.90	0.005	0.19
Allgreen (ground cover)	-0.05 (0.02)	6.82	0.009	-0.17
Amount of willow 50 m	8.51 (3.67)	5.38	0.020	0.14
	X^2	DF	Significance	
Model χ^2	69.99	4	<0.001	
Improvement last variable	5.94	1	0.015	
Goodness of fit	119.57	136	0.75<P<0.90	
Cases correctly classified	Obs. 0 = 68.4 %	Obs. 1 = 93.1 %	Overall = 86.4 %	
1997	B (SE)	Wald	P	R
Constant	-13.04 (2.63)	24.55		
Area willow	1.85 (0.32)	33.96	<0.001	0.40
Foliage density	3.48 (1.11)	9.84	0.002	0.20
Perimeter to $\sqrt{\text{area}}$ willow	1.52 (0.63)	5.91	0.015	0.14
Allgreen (ground cover)	-0.04 (0.02)	4.94	0.026	-0.13
	X^2	DF	Significance	
Model χ^2	95.54	4	<0.001	
Improvement last variable	5.43	1	0.020	
Goodness of fit	122.87	169	0.90<P<0.95	
Cases correctly classified	Obs. 0 = 61.4 %	Obs. 1 = 93.0 %	Overall = 85.0 %	

Southern study area (1997)	B (SE)	Wald	P	R
Constant	-20.22 (4.37)	21.42	<0.001	
Area willow	2.42 (0.52)	21.47	<0.001	0.35
Area aspen	0.26 (0.10)	6.17	0.013	0.16
Foliage density	0.05 (0.03)	4.37	0.037	0.12
	X^2	DF	Significance	
Model χ^2	94.25	3	<0.001	
Improvement last variable	5.16	1	0.023	
Goodness of fit	71.01	112	P = 1	
Cases correctly classified	Obs. 0 = 82.1 %	Obs. 1 = 90.0 %	Overall = 86.2 %	

Table 2.7. Nonparametric nearest neighbor discriminant analysis for number of years of occupancy (0,1,2,3). Mahalanobis distances between vectors of observations were computed. Prior probability of membership was specified as 0.25 for each group. Area willow was entered first; other variables significant in one-way non-parametric ANOVA (see Appendix 4) were entered following a stepwise procedure. Only Perimeter to √area willow improved percentage of cases correctly classified from 59.9% to 65.7%. Number of observations and percent classified are shown in the first and second lines respectively for each observed number of years of occupancy. Observations (N and %) correctly classified are shown in bold.

Model: Area willow

		Classified number of years occupied				
Observed number of years occupied		0	1	2	3	Total
0	N	**48**	17	5	9	79
	%	**60.76**	21.52	6.33	11.39	100
1	N	7	**23**	1	2	33
	%	21.21	**69.70**	3.03	6.06	100
2	N	4	10	**20**	4	38
	%	10.53	26.32	**52.63**	10.53	100
3	N	3	15	14	**45**	77
	%	3.90	19.48	18.18	**58.44**	100
Total		62	65	40	60	227
% observ.		27.31	28.63	17.62	26.43	100
Error rate		0.39	0.30	0.47	0.42	0.40

Model: Area willow+Perimeter to √area willow

		Classified number of years occupied				
Observed number of years occupied		0	1	2	3	Total
0	N	**26**	8	6	2	42
	%	**61.90**	19.05	14.29	4.76	100
1	N	5	**18**	3	1	27
	%	18.52	**66.67**	11.11	3.70	100
2	N	2	5	**24**	3	34
	%	5.88	14.71	**70.59**	8.82	100
3	N	3	9	14	**49**	75
	%	4.00	12.00	18.67	**65.33**	100
Total		36	40	47	55	178
% observ.		20.22	22.47	26.40	30.90	100
Error rate		0.38	0.33	0.29	0.35	0.34

Table 2.8. Stepwise generalized linear models for chronological order of territory occupancy by males and females. Parameters were estimated with a quasi-likelihood method. Only the final model is shown. Area willow and Area aspen were ln+1 transformed. Red-winged Blackbird presence/absence (RWBB), presence of territorial conspecifics in patches, and territory type (single-patch or multi-patch) improved the fit of some of the models. Red-winged Blackbirds were not censused in the southern study area. X is the geographic coordinate of the territory center along the west-east axis.

YEAR 1995	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Male arrivals							
Intercept	77.17	62				3.48	0.67
Area willow	62.46	61	14.70	13.00	<0.001	-0.34	0.09
YEAR 1996							
Male arrivals							
Intercept	100.00	86				2.63	0.42
Area willow	83.63	85	16.68	18.72	<0.001	-0.21	0.06
# Total trees	78.54	84	5.10	5.73	0.019	0.25	0.10
Shared/unshared	73.71	83	4.82	5.41	0.022	-0.32	0.14
RWBB	69.90	82	3.81	4.40	0.039	-0.30	0.16
Female arrivals							
Intercept	58.62	66				2.07	0.46
Area willow	53.57	65	5.05	6.54	0.013	-0.09	0.06
Shared/unshared	49.15	64	4.42	5.73	0.020	-0.32	0.13

YEAR 1997							
Male arrivals							
Intercept	38.74	86				2.19	0.30
X	27.18	85	11.56	47.60	<0.001	-0.17	0.03
Area willow	24.60	84	2.58	8.28	0.005	-0.04	0.06
Single/multi patch	22.98	83	1.62	6.68	0.012	0.04	0.07
Shared/unshared	21.46	82	1.52	6.24	0.014	-0.12	0.03
RWBB	19.45	81	2.01	10.62	0.002	-0.22	0.08
Female arrivals							
Intercept	67.46	68				8.17	1.41
X	55.06	67	12.40	18.85	<0.001	-0.65	0.19
Area willow	45.10	66	9.96	15.13	<0.001	-0.68	0.19
RWBB	42.40	65	2.70	4.10	0.047	-0.80	0.48
SOUTHERN STUDY AREA (1997)							
Male arrivals							
Intercept	283.84	48				3.41	2.58
Area willow	257.31	47	26.53	5.22	0.027	-0.42	0.20
Distance to nearest willow patch	233.95	46	23.36	4.60	0.037	1.28	0.60

Table 2.9. Chronological order of territory occupancy by first males and females (1997). GLIM models for partitioning of deviance explained by geographic variables and environmental variables.

	Residual deviance	DF	Change in deviance	Approximated % of deviance explained
FIRST MALES 1997				
Pure geographic model				18.6
	38.74	86		
Residuals X	31.54	85	19.40	18.6
Pure environmental model				17.9
	38.74	86		
Residuals Area willow	36.29	85	2.45	6.3
Residuals Single/multi patch	35.03	84	1.26	3.3
Residuals Shared/unshared	33.91	83	1.12	2.9
Residuals RWBB	31.82	82	2.09	5.4
Total % deviance explained by original model				49.8
Interaction (geographic and environmental)				13.3
FEMALES 1997				
Pure geographic model				16.8
	224.9	68		
Residuals X	187.2	67	37.7	16.8
Pure environmental model				14.3
	70.70	68		
Residuals Area willow	61.01	66	9.69	13.7
Residuals RWBB	60.60	67	0.41	0.6
Total % deviance explained by original model				37.1
Interaction (geographic and environmental)				6.0

Note: In generalized linear models the residual deviance takes the place of the residual sum of squares in least-squares regressions. If the errors are independent and follow a normal distribution the least-square principle and the maximum likelihood principle are equivalent. In models for 1997, the error distribution did not grossly violate the assumptions of least-square regression. Thus, deviance explained by models can be approximately interpreted as percent variation explained by models.

Table 2.10. Logistic regressions of nests preyed upon *vs* nests not preyed upon and territory features. Area willow was ln+1 transformed. No measured variable was significant in 1996 and 1997.

Predictor	B (SE)	Wald	P	R
1995				
Constant	-29.78 (11.73)	6.45	0.011	
Area willow	3.10 (1.28)	5.81	0.016	0.32
Amount of aspen 125 m	7.46 (2.93)	6.49	0.011	0.35
	X^2	DF	Significance	
Model χ^2	18.71	2	< 0.001	
Improvement last variable	9.49	1	0.002	
Goodness of fit	22.48	26	0.50<P<0.75	
Cases correctly classified	Obs. 0 = 88.2 %	Obs. 1 = 81.8 %	Overall = 85.7 %	

Table 2.11. Logistic regressions of nests preyed upon *vs* not preyed upon and chronological order of settlement by males. Models for males in 1995, and for females (1996 and 1997) were not significant.

Predictor	B (SE)	Wald	P	R
1996				
Constant	-1.72 (0.57)	9.24	0.008	
Order of settlement	0.43 (0.57)	7.03	0.002	0.23
	X^2	DF	Significance	
Model χ^2	8.00	1	0.047	
Improvement last variable	8.00	1	0.047	
Goodness of fit	69.39	68	$0.25< P <0.50$	
Cases correctly classified	Obs. 0 = 69.5 %	Obs. 1 = 50.0 %	Overall = 61.4 %	
1997				
Constant	-2.82 (0.91)	9.49	0.002	
Order of settlement	0.57 (0.24)	5.50	0.019	0.19
	X^2	DF	Significance	
Model χ^2	6.00	1	0.014	
Improvement last variable	6.00	1	0.014	
Goodness of fit	80.44	79	$0.50< P < 0.25$	
Cases correctly classified	Obs. 0 = 87.5 %	Obs.1 = 28.0 %	Overall = 69.1 %	

Table 2.12. Logistic regression models for territory occupancy in relation to territory features and landscape spatial structure. Territory occupied/not occupied coded respectively 1/0 was the dependent variable. Significance of model was tested with goodness-of-fit index. Area willow and Area aspen were ln+1 transformed. Foliage density expressed as a proportion (p) was arcsin $\sqrt{p}$ transformed. Initial models included variables that were significant at the territory scale, and significant variables describing landscape spatial structure (see statistical methods, landscape scale for explanation). Models for the main study area were tested on the southern study area, with data collected in 1997 (N = 115). In 1995, 1997, and in the southern study area no descriptors of landscape spatial structure was significant.

1996	B (SE)	Wald	P	R
Constant	-7.13 (1.52)	22.08	< 0.001	
Area willow	0.81 (0.17)	21.30	< 0.001	0.27
Perimeter to $\sqrt{\text{area}}$ willow	1.27 (0.93)	1.86	0.172	0.00
Allgreen (ground cover)	-0.05 (0.02)	8.95	0.003	-0.16
Amount of willow 50 m	9.96 (3.47)	1.86	0.17	0.00
Amount of pond within 500 m	0.40 (0.11)	12.83	0.003	0.20
	X^2	DF	Significance	
Model χ^2	122.775	5	< 0.001	
Improvement last variable	4.75	1	0.029	
Goodness of fit	142.878	136	$0.50<P<0.25$	
Cases correctly classified	Obs. 0 = 79.8 %	Obs. 1 = 89.6 %	Overall = 85.2 %	

Table 2.13. Stepwise generalized linear models for chronological order of territory occupancy by males and females, in relation to territory features and landscape spatial structure. None of the variables measured at the nest site scale affected chronological order of territory occupancy by males or by females. No descriptor of landscape spatial structure was significant in the southern study area.

YEAR 1995	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Male arrivals							
Intercept	70.91	58				7.70	1.90
Area willow	63.80	57	7.11	6.93	0.011	-0.25	0.01
Mean shape index treed 1,000 m	57.44	56	6.36	6.20	0.016	-2.35	1.04
Mean nearest neighbor treed 1,000 m	53.30	55	4.13	4.03	0.050	-0.04	0.02
YEAR 1996							
Male arrivals							
Intercept	100.07	86				2.62	0.58
Area willow	96.00	85	4.07	4.77	0.032	-0.05	0.04
# Total trees	91.16	84	4.84	5.67	0.020	0.26	0.10
Shared/unshared	85.83	83	5.33	6.24	0.015	-0.13	0.14
RWBB	82.31	82	3.52	4.12	0.046	-0.40	0.17
Mean near. neighb. treed 500 m	77.60	81	4.71	5.51	0.021	0.02	0.01
Mean shape index aspen 200 m	72.40	80	5.20	6.09	0.016	-0.77	0.34
Amount of willow 200 m	67.72	79	4.68	5.47	0.022	-0.32	0.14

YEAR 1996	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Female arrivals							
Intercept	60.84	65				2.96	0.59
Area willow	57.20	64	3.64	4.71	0.034	-0.07	0.06
Shared/unshared	53.06	63	4.14	5.36	0.024	-0.33	0.14
Amount of willow 1,000 m	47.12	62	5.94	7.69	0.007	-0.04	0.02
YEAR 1997							
Male arrivals							
Intercept	38.74	86				2.19	0.30
X	27.18	85	11.56	47.60	<0.001	-0.17	0.03
Area willow	24.60	84	2.58	8.28	0.005	0.04	0.06
Single/multi patch	22.98	83	1.62	6.68	0.012	0.04	0.07
Shared/unshared	21.46	82	1.52	6.24	0.014	-0.12	0.03
RWBB	19.45	81	2.01	10.6	0.002	-0.22	0.08
NO LANDSCAPE EFFECT							
Female arrivals							
Intercept	70.72	68				4.94	0.93
X	57.88	67	12.84	20.86	<0.001	-0.12	0.07
Area willow	48.00	66	9.91	16.11	<0.001	-0.19	0.05
RWBB	45.23	65	2.74	4.45	0.039	-0.27	0.17
Mean shape index willow 500 m	41.05	64	4.18	6.79	0.011	-1.30	0.50

Table 2.14. Testing territory occupancy models on the southern study area. Predictive values for the southern study area were obtained from models for the main study area. To test models for the main area, predictive values were regressed on territory occupancy in the southern area (territory occupied = 1; territory not occupied = 0) using a logistic model. Significance of the model was tested using Goodness-of-fit and percentage of cases correctly classified.

Predictor	B (SE)	Wald	P	R
1995				
Constant	-2.69 (0.49)	30.67	<0.001	
Fitted values	0.06 (0.01)	36.08	<0.001	0.42
	X^2	DF	Significance	
Model χ^2	65.54	1	<0.001	
Goodness of fit	166.63	137	P = 0.05	
Cases correctly classified	Obs. 0 = 82.9 %	Obs. 1 = 79.4 %	Overall = 81.3 %	
1996	B (SE)	Wald	P	R
Constant	-3.15 (0.55)	32.38	<0.001	
Fitted values	0.21 (0.03)	36.22	<0.001	0.42
	X^2	DF	Significance	
Model χ^2	66.21	1	<0.001	
Goodness of fit	169.08	137	0.01<P<0.005	
Cases correctly classified	Obs. 0 = 82.9 %	Obs. 1 = 76.2 %	Overall = 79.9 %	
1997	B (SE)	Wald	P	R
Constant	-2.18 (0.47)	21.25	<0.001	
Fitted values	0.41 (0.07)	31.28	<0.001	0.39
	X^2	DF	Significance	
Model χ^2	72.32	1	<0.001	
Goodness of fit	404.65	137	<0.001	
Cases correctly classified	Obs. 0 = 84.2 %	Obs. 1 = 85.7 %	Overall = 84.9 %	

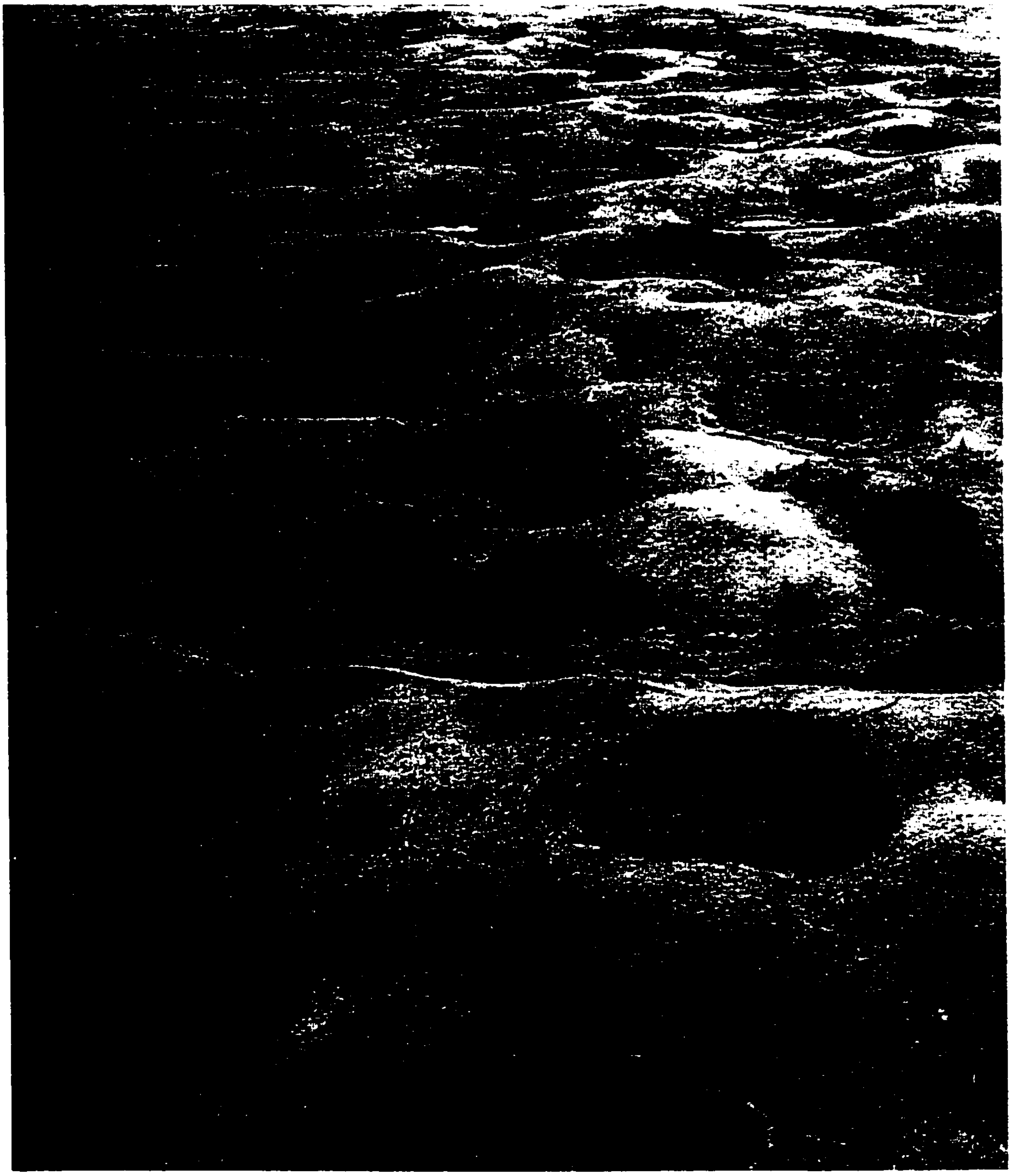
Table 2.15. Testing chronolological order of territory occupancy on the southern study area. Predictive values (fitted values in table) for the southern study area were obtained for models for the main study area using generalized linear models (stepwise procedure). Parameters were estimated with quasi likelihood method assuming a Poisson distribution. Predictive values are regressed on observed chronological order of occupancy in the southern study area to test the models. Red-winged Blackbird presence/absence (RWBB) was not censused in the southern study area and was excluded from models.

	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
1995 - First males							
Intercept	83.48	47				0.60	0.76
Fitted values	72.00	46	11.47	7.33	0.009	2.39	0.88
1996 - First males							
Intercept	83.48	47				2.66	0.63
Fitted values	83.46	46	0.02	0.01	0.92	-0.054	0.55
1997 - First males							
Intercept	81.49	46				0.94	1.02
Fitted values	76.94	45	4.55	2.66	0.11	1.34	0.82

Table 2.16. Correlations between arthropod abundance in territories during settlement of Yellow Warbler males and during rearing of chicks. At settlement arthropods were sampled in willow patches only. Pearson product correlation coefficient-R (one tailed test). All the variables are ln transformed.

	Number of individuals			**Dried biomass**		
	R	N	Sign.	R	N	Sign.
WILLOW PATCHES						
All sampled taxa	0.186	73	0.057	-0.048	74	0.341
Diptera Chironomidae	0.011	76	0.464	0.099	75	0.200
Diptera Culicidae	-0.126	75	0.140	-0.118	75	0.156
Homoptera	0.384	75	<0.001	0.060	74	0.305

Figure 2.1. The study area is characterized by aspen and willow patches embedded in a matrix of mixed grassland. Some of the patches include a pond. Some ponds are covered by grasses and/or cattail.



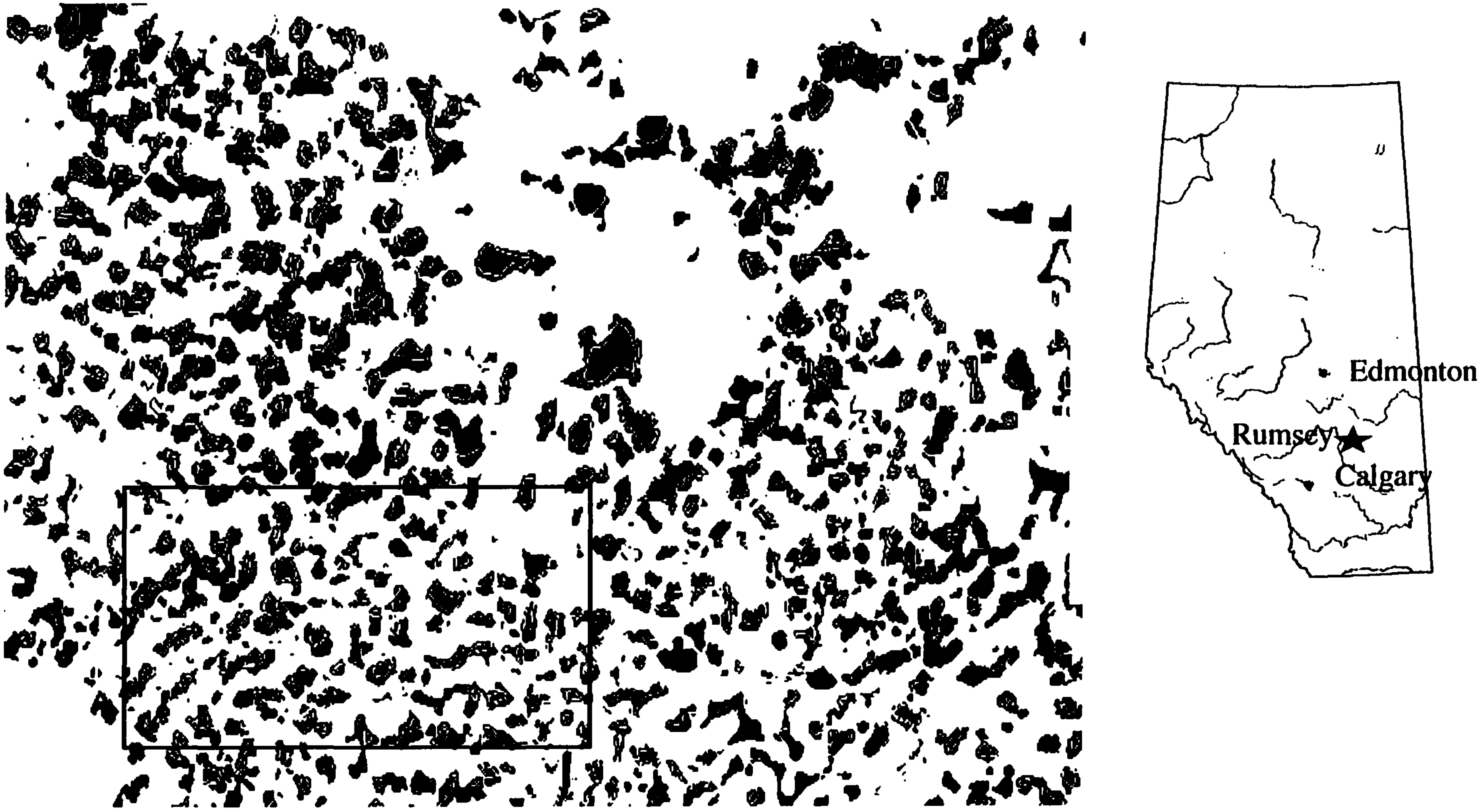


Figure 2.2. The province of Alberta and the location of the study area. A portion of the study area is shown. Blue patches are ponds, light green patches are willow patches and dark green patches are aspen patches. The approximate borders of one of the study units (heavily grazed) are shown in black.

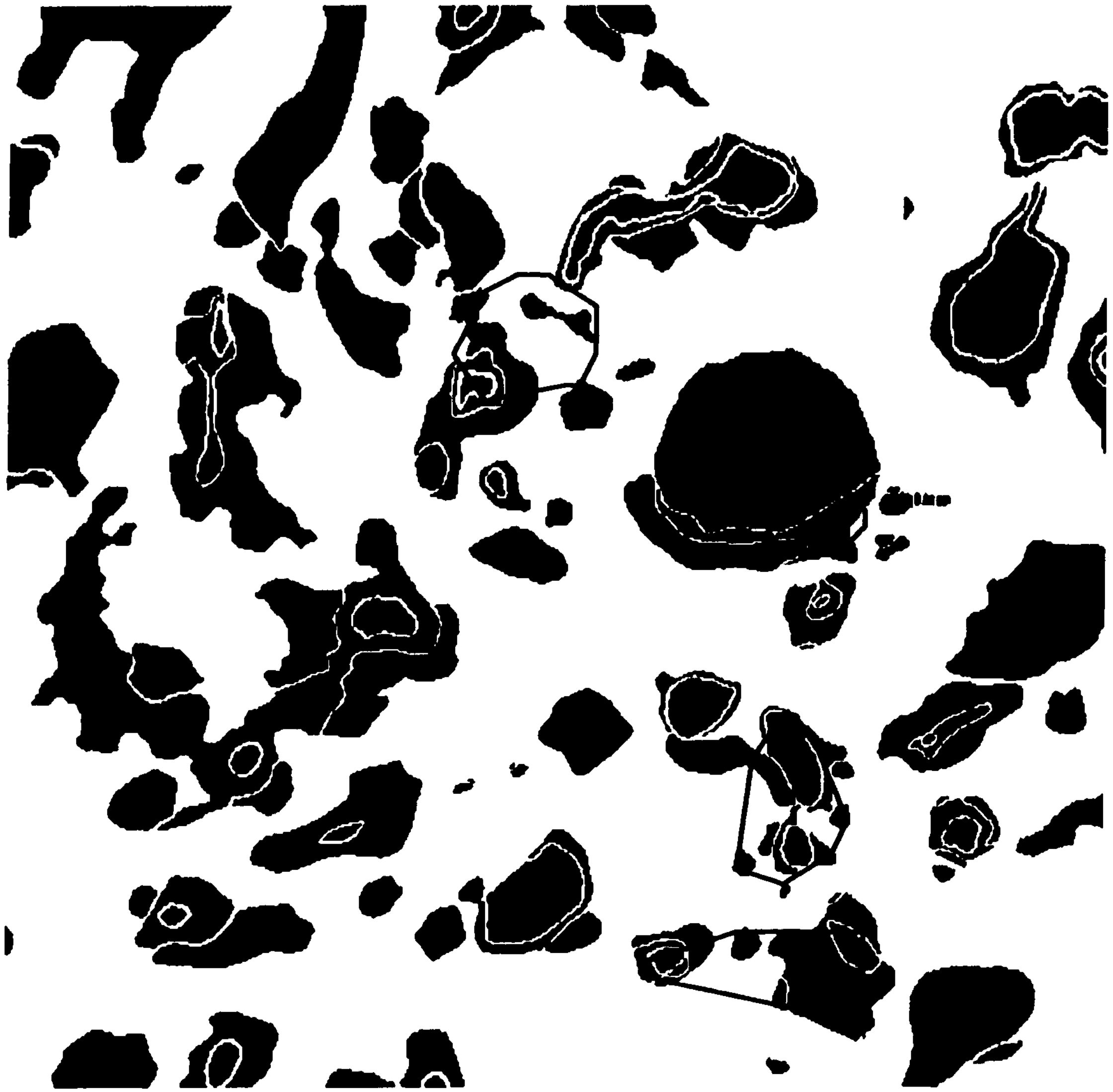


Figure 2.3. Examples of real territorial borders (Minimum Convex Polygon method). Blue patches are ponds, light green patches are willow patches and dark green patches are aspen patches.

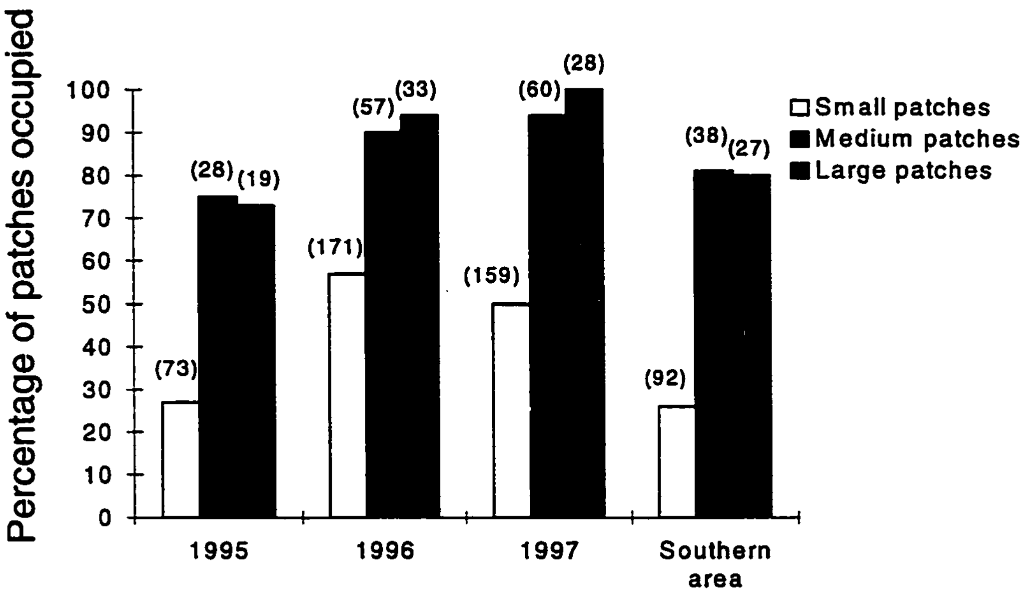


Figure 2.4. Percentage of patches occupied and patch size. Total area sampled was roughly the same (± 0.1 ha) for each size class. Overall, small patches (0.12-0.19 ha) were occupied with lower frequency than medium patches (0.19-0.23 ha) and large patches (0.23-0.28 ha). Patches larger than 0.28 were not included in analysis and were always occupied ($G_{1995} = 5.77$, $P = 0.056$; $G_{1996} = 3.20$, $P = 0.20$; $G_{1997} = 7.25$, $P = 0.027$, $G_{south} = 10.03$, $P = 0.007$)

Chapter 3. Does Red-winged Blackbird occurrence in patches of habitat and in the surrounding landscape affect territory choice and quality in the Yellow Warbler?

INTRODUCTION

Brown-headed Cowbirds (*Molothrus ater*) are brood parasites of at least 220 bird species in North America (Friedmann and Kiff 1985). Cowbird parasitism commonly results in lower breeding success of the host species (e.g., Friedmann 1929; Mayfield 1965; Rothstein 1975; Payne 1977; Weatherhead 1989). Yellow Warblers (*Dendroica petechia*) and Red-winged Blackbirds (*Agelaius phoeniceus*) are both common Brown-headed Cowbird hosts (Friedmann 1929; Bent 1953; Rothstein 1975). After observing aggressive behavior of Red-winged Blackbirds towards Brown headed-Cowbirds, Sutton (1928) suggested that Yellow Warblers may nest in proximity to the larger Red-winged Blackbirds to reduce incidence of cowbird parasitism. More recently, aggressive behavior of the host towards the cowbird has been shown to reduce brood parasitism (Robertson and Norman 1976, 1977; Slack 1976). Clark and Robertson (1979) found that Yellow Warblers nesting in proximity to Red-winged Blackbird colonies, but not in proximity to isolated individuals, had lower rates of parasitism due to aggressive group responses of Red-winged Blackbirds towards cowbirds.

Whether Yellow Warblers "choose" to nest in proximity to Red-winged Blackbirds and whether, in the absence of Red-winged Blackbird colonies, Yellow Warblers can still benefit from the presence of isolated individuals or small groups of Red-winged Blackbirds remains untested. We investigated the effect of Red-winged Blackbird occurrence on Yellow Warbler nest site selection, patch choice, and brood parasitism by cowbirds in a naturally patchy landscape where isolated pairs or small groups of Red-winged Blackbirds are physically separated by unsuitable habitat (mixed grassland). Since we repeatedly observed Red-winged Blackbirds attacking Corvids, we also investigated if Red-winged Blackbirds occurrence could reduce the rate of predation on Yellow Warbler nests.

In our area, suitable habitat for Yellow Warblers (willow patches) was either next to Red-winged Blackbird habitat (pond area covered by cattails *Typha latifolia*) or not (Fig. 3.1). In this study we considered only willow patches including suitable Red-winged Blackbird habitat. Ponds occupied by Red-winged Blackbirds had 1-5 males and occupied willow patches had 1-3 Yellow Warbler pairs. Red-winged Blackbird activity was centered in the ponds, where they nested and perched in cattails. Since ponds were situated in depressions, Red-winged Blackbird males occasionally perched in willow and aspen patches from where they could scan the horizon to detect approaching cowbirds or predators. Since Red-winged Blackbirds arrived first in spring, we could monitor settlement of Yellow Warblers in reference to the presence of Red-winged Blackbirds at the level of the nest site, the patch, and the area immediately around the patch. The breeding periods of the Red-winged Blackbird and Yellow Warbler overlapped chronologically.

We tested the following predictions: **1.** Patches with Red-winged Blackbirds are occupied earlier in spring by Yellow Warbler males and females than patches with no Red-winged Blackbirds (patch choice). **2.** Yellow Warblers nest closer to the pond/willow edge in patches where Red-winged Blackbirds are present than in patches without Red-winged Blackbirds (nest site selection). **3.** Yellow Warblers experience lower cowbird parasitism and nest predation rates in patches occupied by Red-winged Blackbirds. **4.** Patches surrounded by a larger number of Red-winged Blackbirds (landscape scale) are occupied earlier by Yellow Warblers and rate of cowbird parasitism and nest predation at their nests is lower than in patches with fewer Red-winged Blackbirds in the surroundings.

STUDY AREA AND METHODS

The study area is a glacial moraine situated in the aspen parkland in central Alberta, Canada, where an alternation of many hills and depressions exists (Figure 3.1). Depressions are occupied by ponds, where cattail is the structurally dominant macrophyte. Ponds are surrounded by patches of willow, *Salix* spp., and Trembling Aspen, *Populus tremuloides*. Pond size ranges from 0.01ha to 4.46 ha (mean = 0.22

ha). These assemblages of pond, willow, and aspen patches are completely surrounded by mixed grassland which was not used by Yellow Warblers. Red-winged Blackbirds foraged occasionally in the grassland.

In 1995, 1996, and 1997, Yellow Warbler males, Red-winged Blackbird males, and other songbird species occurring in the willow patches and ponds were censused using point counts (Ralph and Scott 1981), five times between 15 May and 30 June. Sampling stations were positioned either next to the patch or on a hill above to sample all patches in their entirety. At each sampling station an observer spent six minutes recording all the birds heard or seen. Cowbirds perching in the patches were also counted to obtain an index of relative cowbird abundance in patches. The maximum number of cowbirds recorded per patch over the five censuses was our measure of cowbird abundance. Given the small size of Red-winged Blackbird groups, the number of males present at each pond could be easily counted. Based on Friedmann (1929,1977) and Lowther (1993) a list of common cowbird hosts was obtained for the study area. Since the rate of cowbird parasitism at Yellow Warbler nests may be potentially affected by abundance of cowbird host nests (i.e. "swamping effect" in Robertson 1973; Clark and Robertson 1979), chronological order of occupancy of willow patches by Yellow Warblers and rate of cowbird parasitism were also analyzed in relation to the total number of common cowbird hosts in the patches whose breeding period chronologically overlapped (at least partially) with that of the Yellow Warblers.

Chronological order of patch occupancy by Yellow Warbler males was obtained by censusing each patch every three days, for 7 times, starting from the arrival of the first male. Since, in a preliminary study, Yellow Warbler females were never observed in patches unoccupied by males, chronological order of patch occupancy by females was obtained by intensively searching, every two days, only those patches where at least one male was present. Censusing terminated when all Yellow Warbler pairs had chicks.

Some Yellow Warbler territories included more than one patch of habitat (willow or aspen) and some patches had more than one Yellow Warbler territory. For the multi-patch territories, the patch where the nest was situated was selected for analysis. For patches containing more than one territory, only the date of arrival of the first male and female were considered. If more than one nest was found in a patch, all the nests were included in the analysis for nest parasitism. This assumes that the probability of a nest being parasitized is not influenced by the fate of the other nests in the patch. Indeed, we never found more than one parasitized nest in a patch. For the same reason all the nests could be included in the analysis for predation at the nests. Yellow Warbler nests were checked every 2-3 days for the presence of cowbird eggs and to detect predation.

Nesting close to an edge, independent of the presence of Red-winged Blackbirds in the patch, may confer several advantages. These include higher prey abundance at the edge (Gates and Gysel 1978; Noss 1991) and structural suitability of potential nest bushes. To determine if Yellow Warblers generally nest close to edges, the nests found were mapped at 1:2,000 scale, a GIS cover of the study area was obtained, and for each willow patch containing at least one nest, a number of random points equal to the number of nests found was obtained. The shortest distance of nests and random points to the pond/willow edge was measured in ARCVIEW (Anonymous 1996) and nests and random points within the same willow patch were compared in a pairwise fashion. Distances were ln+1 transformed. For nests situated very close to the edge, distance was also measured in the field. Discrepancy between the GIS and field measurements never exceeded 2 m. For nests with discrepancies, the mean of the two measurements was considered. Next, distance of nests to the willow/pond edge in patches where Red-winged Blackbirds were present and absent was compared, to test whether Red-winged Blackbird presence affected nest position in Yellow Warblers.

Chronological order of patch occupancy by males (1995-1997) and by females (1996,1997) in relation to patch occupancy by Red-winged Blackbirds was analyzed with a Kolmogorov-Smirnov two sample test. To determine one-tailed significance, the observed maximum difference between the two sample cumulative distributions was tested against a χ^2 distribution with df = 2 (Goodman 1954). This test is conservative for small samples and is used if the two samples differ in size (Goodman 1954). Given the extremely skewed distribution in number of Red-winged Blackbird males per pond, presence/absence data were used in this analysis. Proportion of Yellow Warbler nests parasitized/not-parasitized, and preyed upon/not preyed upon in relation to Red-winged Blackbird occurrence in patches was analyzed with a Randomized G-test with 10,000 randomizations because some cells had observed frequency < 5.

Chronological order of patch occupancy by Yellow Warbler males and females and probability of nest parasitism were also analyzed in relation to the number of Red-Winged Blackbird males occurring at the landscape scale. Nonoverlapping 200 m radius circles, were laid over a GIS cover of the study area (N = 19 for 1995, N = 25 for 1996, and 1997). The 200 m radius was selected because I was interested in analyzing the effect of Red-winged Blackbird abundance in the immediate surroundings of the focal pond. However, circles with radii < 200 m never included more than one pond occupied by Red-winged Blackbirds. Since in another study (Clark and Robertson 1979) Red-winged Blackbirds were found to join group responses towards cowbirds which were initiated up to 57 m from their nest, adjacent circles were positioned 57 m apart (shortest distance between circumferences) in a random direction to minimize the potential problem of non-independence of observations (circles). Number of Red-winged Blackbird males occurring within each circle was counted. This included males occurring in ponds falling partially or entirely within the circle. Only Red-winged Blackbird males were considered because they guard their nests from predators and brood parasites, using exposed perches (Yasukawa *et. al* 1992), and thus their abundance could be presumably assessed by Yellow Warblers when they select a patch. Mean chronological order of occupancy by Yellow Warbler males and females for the patches falling entirely or partially within each circle was obtained. Large patches that fell within two circles were assigned to the circle which encompassed the larger proportion of their area.

Probability of cowbird parasitism at Yellow Warbler nests in relation to the number of Red-Winged Blackbird males occurring in the landscape was analyzed with logistic regressions using quasi-likelihood estimation method. The dependent variable was composed of the vectors: 1) number of nest parasitized in each circle, 2) number of nests unparasitized in each circle. These were converted into a matrix using the command "cbind" in S+, version 4.5 (S+ manual, Version 4.5 1998). This procedure made it possible to obtain proportions of parasitized nests weighed by the sample size at each circle. Due to small sample size nest parasitism could not be analyzed in 1995. Probability of predation at the nests in relation to the number of Red-Winged Blackbird males occurring in the landscape was analyzed in the same way. All the analyses were performed with SPSS Version 7 (SPSS 1996), except for the analyses for probability of predation and parasitism at Yellow Warbler nests in relation to Red-winged Blackbird abundance at the landscape scale which was performed with S+ version 4.5 (S+ manual, Version 4.5 1998).

RESULTS

Cowbird parasitism and Yellow Warbler breeding success

Brown-headed Cowbirds were abundant in the area and parasitized both Yellow Warblers and Red-winged Blackbirds. When looking for potential host nests, cowbirds appeared to scan the ponds, willow and aspen patches from the top of aspen trees. Both host species were observed several times to successfully chase away cowbird males and females.

Rate of parasitism at Yellow Warbler nests in the study area and in the immediate surroundings was 9.7% (N = 30 nests) in 1995, 13.2% in 1996 (N = 76), and 19.3% in 1997 (N = 88). Cowbird parasitism reduced Yellow Warbler breeding success. No Yellow Warbler chicks fledged from parasitized nests in 1995 and in 1996, and in 1997 mean number of chicks fledged was 3.20 for parasitized nests, and 4.15 for unparasitized nests, considering successful nests only ($U = 50.5$, $Z = -2.21$, $N_{paras} = 5$, $N_{unparas} = 47$, $P = 0.013$, one-tailed Mann-Whitney U -test).

Red-winged Blackbird occurrence in patches and nest site selection by the Yellow Warbler

Distance of nests and random points to the pond/willow edge did not differ (Table 3.1), therefore Yellow Warblers at Rumsey did not behave as "edge nesters". In 1995 and 1996, Yellow Warbler nests situated in patches occupied and unoccupied by

Red-winged Blackbird did not differ in distance to the pond/willow edge (Table 3.2). Contrary to what we predicted, in 1997 nests situated in patches unoccupied by Red-winged Blackbird were closer to the willow/pond edge (Table 3.2).

Chronological order of patch occupancy by the Yellow Warbler and Red-winged Blackbird occurrence in patches

Patches occupied by Red-winged Blackbird were occupied earlier by Yellow Warbler males in 1996 and 1997, but not in 1995 (Figure 3.2a,b,c). Chronological order of patch occupancy by Yellow Warbler females was not affected by occurrence of Red-winged Blackbirds at the patch scale (Figure 3.3a, b).

Chronological order of patch occupancy by the Yellow Warbler and relative abundance of Cowbird hosts in patches

Common alternative Cowbird hosts occurring in treed patches were Least Flycatcher (*Empidonax minimus*), Red-eyed Vireo (*Vireo olivaceus*), Warbling Vireo (*Vireo gilvus*), Common Yellowthroat (*Geothlypis trichas*), Grasshopper Sparrow (*Ammodramus savannarum*), Vesper Sparrow (*Pooecetes gramineus*), Savannah Sparrow (*Passerculus sandwichensis*), Song sparrow (*Melospiza melodia*), Chipping Sparrow (*Spizella passerina*), and Clay-colored Sparrow (*Spizella pallida*). No cowbird hosts other than Red-winged Blackbirds nested on the ponds. Mean number of cowbird host per patch was 2.87 in 1995 (range 0-16, N = 150), 2.75 in 1996 (range 0-17, N = 150), and 2.83 in 1997 (range 0-23, N = 150). Chronological order of patch occupancy by Yellow Warbler males in 1995 and 1996 ($R_{1995} = 0.07$, N = 66, P = 0.299; $R_{1996} = -0.14$, N = 97, P = 0.079, one-tailed Spearman rank correlation coefficient) or by females in 1996 ($R_{1996} = -0.02$, N = 70, P = 0.432) were not correlated with number of cowbird hosts in the treed patches. In 1997, patches with a higher number of cowbird hosts were occupied later by males ($R_{1997} = 0.23$, N = 99, P = 0.012) and by females ($R_{1997} = 0.33$, N = 71, P = 0.002). Total number of cowbird hosts did not differ between patches where a parasitized Yellow Warbler nest occurred and where only unparasitized nests occurred (1996: $\text{mean}_{\text{paras}} = 3.89$, SE = 1.23, N =

10; $\text{mean}_{\text{not paras}} = 3.45$, SE = 0.50, N = 62, U = 220.5, Z = -1.51, P = 0.065; 1997: $\text{mean}_{\text{paras}} = 3.60$, SE = 1.26, N = 15; $\text{mean}_{\text{not paras}} = 3.86$, SE = 0.54, N = 58, $U_{1997} = 393.5$, Z = -0.58, P = 0.230; one-tailed Mann-Whitney U-test).

Red-winged Blackbird occurrence in patches, relative abundance of Cowbirds in patches, and breeding success of the Yellow Warbler

Relative abundance of cowbirds in patches was not affected by presence/absence of Red-winged Blackbirds (Table 3.3). Proportion of Yellow Warbler nests parasitized was lower in patches occupied by Red-winged Blackbirds in 1997, but no effect of Red-winged Blackbird occurrence was detected in 1995 and 1996 (Figure 3.4). However, no nest was parasitized in 1995 in patches occupied by the Red-winged Blackbird (N = 9). Proportion of nests preyed upon was lower in patches occupied by the Red-winged Blackbird in 1996, but not in 1995 and 1997 (Figure 3.5). However, post-hoc power analysis (Casagrande *et al.* 1978) indicated that a sample size of 38.8 per sample would have been necessary to achieve a power 0.55. Therefore, for these two analyses the power of the test employed was low in all three years. Although number of chicks produced per nest (including unsuccessful nests) tended to be higher in patches occupied by the Red-winged Blackbird in all three years, this difference was never significant (1995: $\text{mean}_{\text{rwbb abse}} = 1.92$, SE = 0.51, N = 3; $\text{mean}_{\text{rwbb pres}} = 2.00$, SE = 1.15, N = 13, U = 18.5, Z = -0.14, P = 0.444; 1996: $\text{mean}_{\text{rwbb abse}} = 1.38$, SE = 0.26, N = 41; $\text{mean}_{\text{rwbb pres}} = 2.00$, SE = 0.54, N = 11, U = 180.5, Z = -1.07, P = 0.142; 1997: $\text{mean}_{\text{rwbb abse}} = 2.48$, SE = 0.32, N = 40; $\text{mean}_{\text{rwbb pres}} = 3.27$, SE = 0.56, N = 11, U = 168.5, Z = -1.21, P = 0.113, one-tailed Mann-Whitney U-test).

Abundance of the Red-winged Blackbird in the landscape, chronological order of patch occupancy and breeding success in the Yellow Warbler

Number of Red-winged Blackbirds occurring within 200 m radius circles ranged from 0 to 6. Patches surrounded by a higher number of Red-winged Blackbirds within a 200 m circle were occupied earlier by Yellow Warbler males in 1997 ($R_{1997} = -0.38$, N = 25, P = 0.033, one-tailed Spearman rank correlation coefficient), but not in

1995 and 1996 ($R_{1995} = -0.01$, $N = 19$, $P = 0.498$; $R_{1996} = -0.04$, $N = 24$, $P = 0.423$) and not by females ($R_{1996} = -0.110$, $N = 23$, $P = 0.31$; $R_{1997} = -0.14$, $N = 24$, $P = 0.255$). The probability that a Yellow Warbler nest was parasitized (Table 3.4) or preyed upon (Table 3.5) was not affected by Red-winged Blackbird abundance at the landscape scale.

DISCUSSION

Red-winged Blackbird occurrence in patches did not affect nest site selection by Yellow Warblers but it did affect patch choice. Yellow Warblers did not nest closer to the willow/pond edge in patches occupied by Red-winged Blackbirds. Red-winged Blackbird males were frequently observed to scan the pond and vocalize from the top of isolated trees in willow patches or from aspen patches close to the external patch edge (willow or aspen/grassland edge), presumably to detect cowbird or predators' intrusions earlier and to communicate information about them to females (Beletsky *et al.* 1986). This may explain why location of Yellow Warbler nests did not appear to be shifted towards the pond in patches occupied by Red-winged Blackbirds. Since the perches may be used by Red-winged Blackbirds, but also by cowbirds, predicting nest site selection by Yellow Warblers in relation to perch location is not straightforward.

Patches occupied by Red-winged Blackbirds were chosen earlier by Yellow Warbler males in 1996 and in 1997 (Figure 3.2b and 3.2c). As shown in Chapter 2, Yellow Warbler territories situated in patches occupied by Red-winged Blackbirds were occupied earlier after taking into account, in multivariate models, several components of intrinsic territory quality (spatial structure, vegetation structure and prey abundance), nest site features, and spatial structure of landscape surrounding the territory. Although chronological order of patch occupancy by Yellow Warbler females did not differ significantly between patches occupied and unoccupied by Red-winged Blackbirds in 1997, patches where Red-winged Blackbirds were present were all occupied by females within the first four time intervals (Figure 3.3b). Also, in 1997, when chronological order of occupancy by females was analyzed in a multivariate context, occurrence of Red-winged Blackbirds in patches did reduce significantly the residual deviance in a generalized linear model, after intrinsic patch quality was taken into account (Chapter 2).

Aggregation of birds may be an effective means of defence against predation and cowbird parasitism because it makes aggressive group responses possible (Kruuk 1964; Clark and Robertson 1979). Moreover, because a high density of host nests in a patch may lead to a "swamping effect" on cowbirds, (Robertson 1973) resulting in lower probability of being parasitized for each host, patches with high host density may be attractive to Yellow Warblers. Since in our study, unlike Clark and Robertson's (1979), cowbird hosts were abundant, we considered total number of hosts whose breeding period chronologically overlapped with Yellow Warblers' rather than focusing on number of Yellow Warbler pairs nesting synchronously. We did not observe any monospecific or interspecific aggressive group response directed towards cowbirds and we found no correlation between chronological order of patch occupancy by Yellow Warbler males and females and the number of common cowbird hosts in two years (1995 and 1996). Moreover, in 1997 patches with higher number of hosts tended to be occupied later by Yellow Warbler males and females. On average, a larger number of Red-winged Blackbird males within 200 m landscape circles was associated with earlier patch occupancy by males in one year only (1997), and never with earlier occupancy by females. Hence, we conclude that chronological order of patch occupancy by Yellow Warblers is affected by Red-winged Blackbird occurrence mainly at the patch scale.

In 1997, the year in which the highest rate of cowbird parasitism (19.3%) was recorded, the proportion of Yellow Warbler nests parasitized by cowbirds was lowered by the presence of Red-winged Blackbirds in the patch. In 1995, only three parasitized nests were found and all of them were situated in patches unoccupied by Red-winged Blackbirds (Figure 3.4). Relative abundance of cowbirds was not lower in patches occupied by Red-winged Blackbird, indicating that cowbirds did not avoid these patches, rather they were less successful in parasitizing Yellow Warbler nests, presumably due to aggressive interactions with Red-winged Blackbirds. Nest concealment, nest height, intrinsic habitat quality of territory (spatial structure, vegetation structure, and prey abundance), and spatial structure of the surrounding landscape did not affect the probability that a Yellow Warbler nest was parasitized (Chapter 2). Moreover, total number of cowbird hosts did not differ between patches where a parasitized Yellow Warbler nest was present *vs* patches with unparasitized nest(s). Thus, Red-winged Blackbird occurrence *per se* lowered parasitism rate on Yellow Warbler nests in at least one year. In 1996, Red-winged blackbird occurrence in patches also reduced predation rate on Yellow Warbler nests, presumably due to aggressive interactions with Corvids. Number of chicks produced per nest including unsuccessful nests tended to be higher in patches occupied by Red-winged Blackbird. However, this difference was never significant.

Number of Red-winged Blackbird males occurring at the landscape scale (200 m radius circles) never affected cowbird parasitism or predation on Yellow Warbler nests, suggesting that the response range of Red-winged Blackbirds towards cowbirds and Corvids is the patch. Therefore, it is unlikely that Red-winged Blackbirds will leave their pond and cross unsuitable habitat (grassland) to chase cowbirds. Indeed, we never observed this behavior in the field. Although we did observe Red-winged Blackbirds mobbing Corvids far from their breeding pond, these aggressive interactions always initiated when Corvids approached closely (< 50 m) Red-winged Blackbird nests.

Yellow Warblers have been classified as heavily parasitized accepters of cowbird eggs (Rothstein 1975) and brood parasitism for this species is costly (e.g., Weatherhead 1989). Cowbird parasitism reduced Yellow Warbler breeding success considerably in this study area. Moreover, because of the small size of treed patches, breeding patches of Yellow Warblers are entirely accessible to cowbirds. Yellow Warblers, cowbirds, and Red-winged Blackbirds have been sympatric for a few thousands of years in the Canadian aspen parkland. Yellow Warblers have likely been subjected to intense evolutionary pressure to avoid brood parasitism and had time to develop several adaptations to counteract it. The results presented in this paper show that in this area, Yellow Warblers may have used Red-winged Blackbird occurrence in patches as cues to assess patch quality. Although occurrence of Red-winged Blackbirds in patches reduced rate of parasitism and of predation on Yellow Warbler nests in one year, it remains uncertain if individual fitness of Yellow Warblers was increased by the presence of Red-winged Blackbirds in patches.

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Table 3.1. Distance (m) of Yellow Warbler nests and random points to willow/pond edges (Paired t-test). Untransformed mean distance and SE are reported.

	Mean	SE	Mean	SE	Mean	SE
	1995		**1996**		**1997**	
NESTS	6.06	1.35	5.61	0.64	7.20	1.16
RANDOM POINTS	5.62	0.79	5.60	0.90	7.08	1.25
t - value	0.15		-0.47		0.84	
df	29		55		57	
P (two-tailed)	0.88		0.640		0.406	

Table 3.2. Distance of Yellow Warbler nests to the willow/pond edge in patches occupied and unoccupied by Red-winged Blackbird in 1995, 1996 and 1997 (One-tailed Mann Whitney U-test).

Red-winged Blackbirds	Mean (m)	SE	N	U	Z	One-Tailed P corrected for ties
1995						
present	3.68	0.62	5			
absent	7.79	2.35	17			
				30.0	-0.98	0.163
1996						
present	6.45	1.97	9			
absent	5.64	0.77	37			
				164.5	-0.55	0.478
1997						
present	9.87	2.17	10			
absent	4.91	0.77	36			
				95.0	-2.27	0.012

Table 3.3. Relative abundance of Cowbirds in patches occupied and unoccupied by Red-winged Blackbirds in 1995, 1996 and 1997 (One-tailed Mann Whitney U-test).

Red-winged Blackbirds	Mean	SE	N	U	Z	One-Tail P corrected for ties
1995						
present	0.38	0.23	13			
absent	0.72	0.23	32			
				180.5	-0.82	0.205
1996						
present	1.11	0.35	19			
absent	0.88	0.21	66			
				533.5	-1.17	0.122
1997						
present	1.00	0.44	16			
absent	0.87	0.18	60			
				468.5	-0.17	0.432

Table 3.4. Generalized linear models for Cowbird parasitism at Yellow Warbler nests and number of Red-winged Blackbirds within 200 m radius circles. Parameters were estimated with quasi-likelihood method.

Variable	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
1996							
Intercept	4.53	21				-1.45	0.48
Number of Red-winged Blackbirds	4.53	20	0.001	0.001	0.999	-0.02	0.26
1997							
Intercept	4.01	21				-1.22	0.44
Number of Red-winged Blackbirds	3.81	20	0.20	0.26	0.902	-0.24	0.29

Table 3.5. Generalized linear models for predation at Yellow Warbler nests and number of Red-winged Blackbirds within 200 m radius circles. Parameters were estimated with quasi-likelihood method.

Variable	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
1995							
Intercept	3.40	12				0.01	0.66
Number of Red-winged Blackbirds	3.39	11	0.01	0.008	0.999	0.07	0.33
1996							
Intercept	7.42	22				-0.27	0.36
Number of Red-winged Blackbirds	6.20	21	1.22	1.380	0.28	-0.64	0.52
1997							
Intercept	6.41	20				-0.74	0.50
Number of Red-winged Blackbirds	6.37	19	0.04	0.023	0.999	-0.07	0.20

Figure 3.1. An early spring view of one of the assemblages of pond, willow and aspen patches inhabited by Red-wing Blackbirds and Yellow Warblers. The pond is partially covered by cattail.

Figure 3.2. Chronological order of patch occupancy by Yellow Warbler males in relation to patch occupancy by Red-winged Blackbirds (■ = Red-winged Blackbird present, □ = Red-winged Blackbird absent). Each time interval is 3-days. See text for explanation of significance testing. $X^2_{1995} = 0.46$, df = 2, $0.975 < P < 0.99$; $X^2_{1996} = 6.82$, df = 2, $0.025 < P < 0.05$; $X^2_{1997} = 7.32$, df = 2, $0.025 < P < 0.05$, one-tailed Kolmogorov-Smirnov two-sample test.

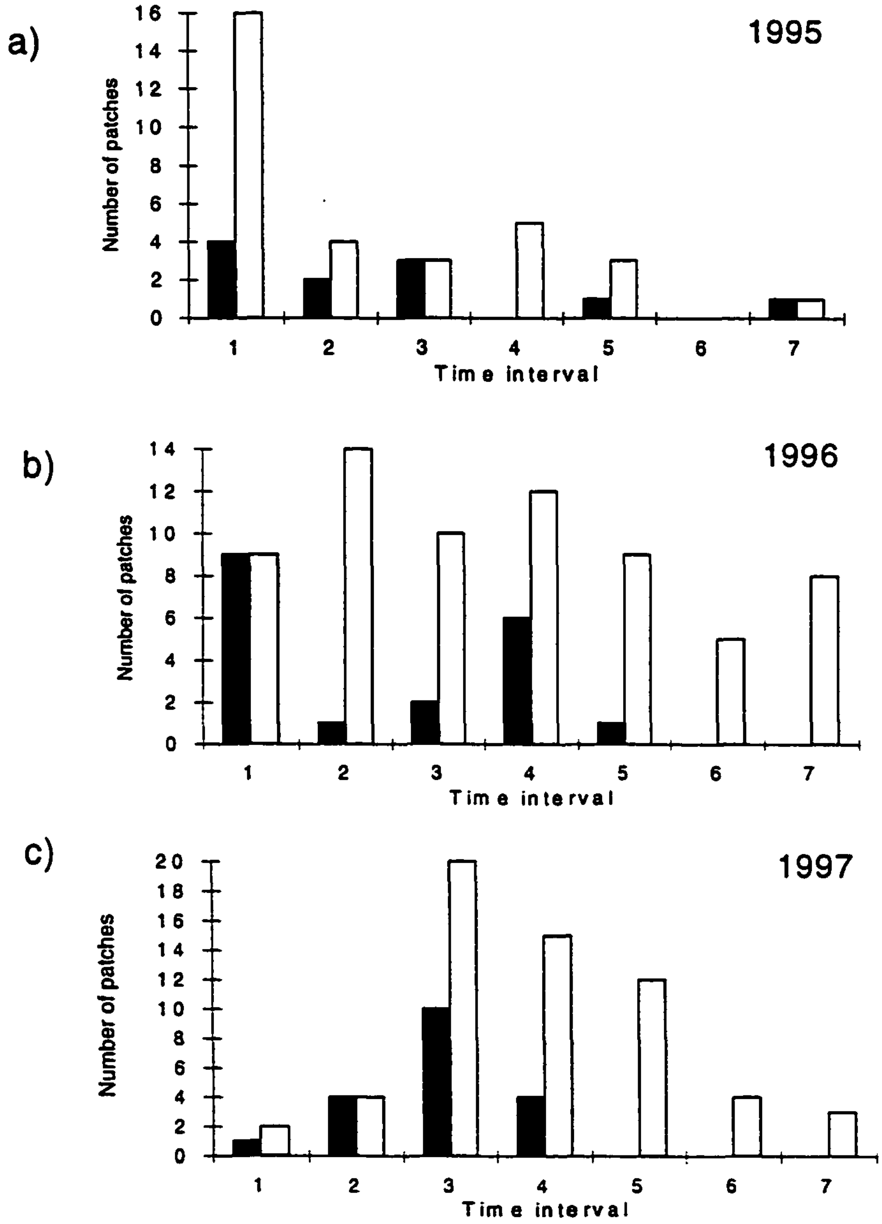


Figure 3.3. Chronological order of patch occupancy by Yellow Warbler females in relation to patch occupancy by Red-winged Blackbirds (■ = Red-winged Blackbird present, ☐ = Red-winged Blackbird absent). Each time interval is 3-days. $X^2_{1996} = 2.16$, df = 2, $0.25 < P < 0.50$; $X^2_{1997} = 2.35$, df = 2, $0.25 < P < 0.50$, one-tailed Kolmogorov-Smirnov two-sample test.

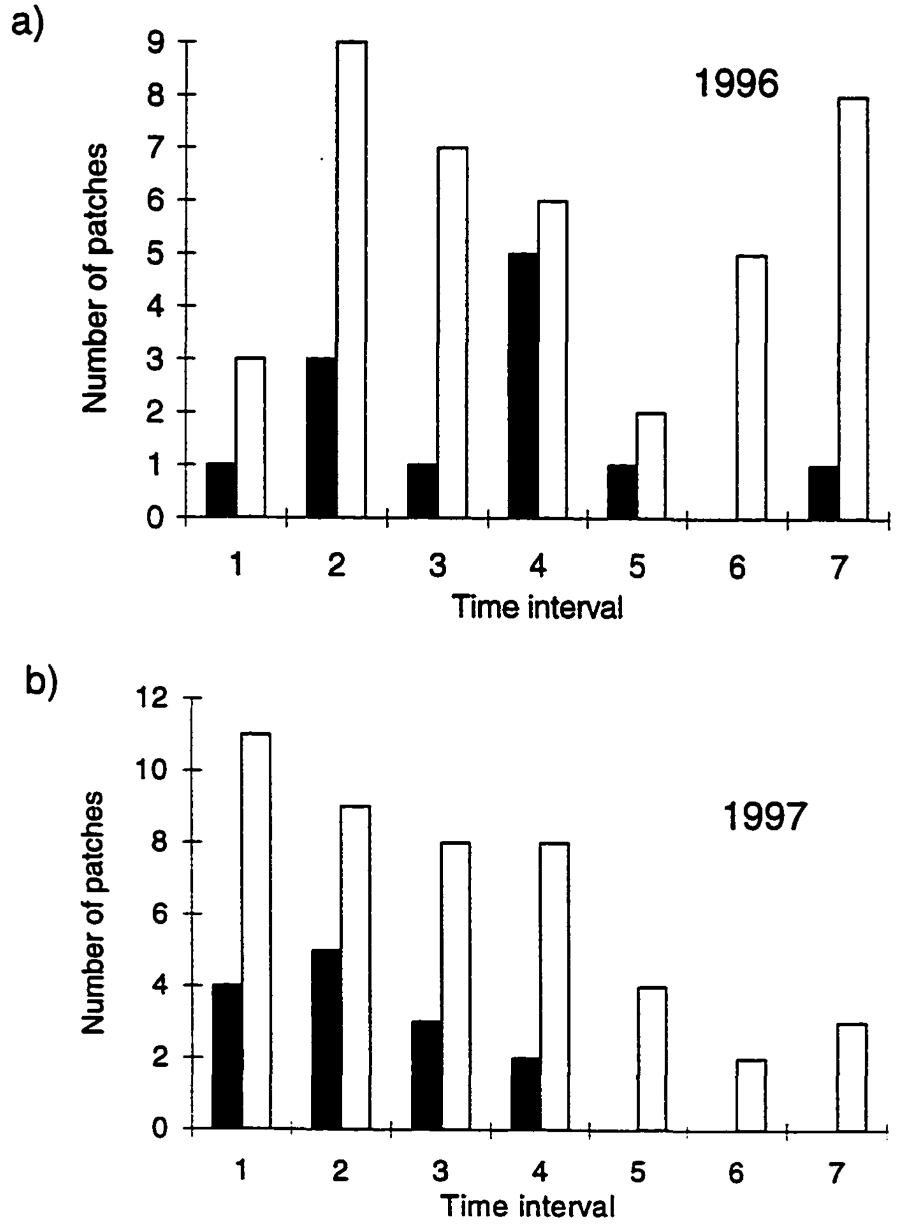


Figure 3.4. Percentage of Yellow Warbler nests parasitized by Brown-headed Cowbirds and occurrence of Red-winged Blackbirds in patches (■ = Red-winged Blackbird present, □ = Red-winged Blackbird absent). **1995**: Red-winged Blackbird present = 0%, N = 9 nests; Red-winged Blackbird absent = 15.8%, N = 19, G = 2.49, P = 0.162; **1996**: Red-winged Blackbird present = 14.3%, N = 14 nests; Red-winged Blackbird absent = 18.0%, N = 50, G = 0.11, P = 0.77; **1997**: Red-winged Blackbird present = 5.0%, N = 20 nests; Red-winged Blackbird absent = 27.9%, N = 43, G = 5.29, P = 0.025.

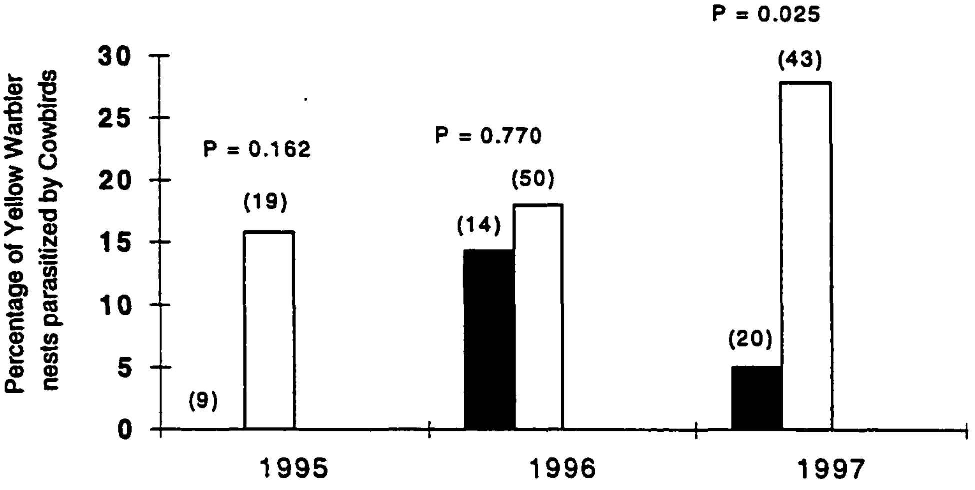
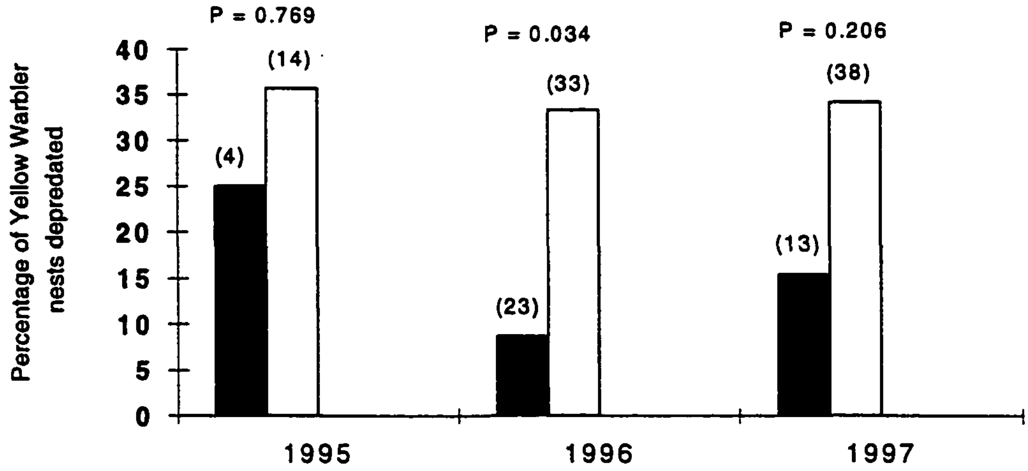


Figure 3.5. Percentage of Yellow Warbler nests preyed upon and occurrence of Red-winged Blackbirds in patches (■ = Red-winged Blackbird present, □ = Red-winged Blackbird absent). **1995**: Red-winged Blackbird present = 25.0%, N = 4 nests; Red-winged Blackbird absent = 35.7%, N =14, G =0.17, P = 0.769; **1996**: Red-winged Blackbird present = 8.6%, N = 23 nests; Red-winged Blackbird absent = 33.3%, N = 33, G = 5.09, P = 0.034; **1997**: Red-winged Blackbird present = 15.4%, N = 13 nests; Red-winged Blackbird absent = 34.2%, N = 38, G = 1.81, P = 0.206.



Chapter 4. Effect of cattle grazing on songbird community composition and on territory quality in Yellow Warblers in the aspen parkland.

Among other detrimental effects to ecosystems, overgrazing by cattle affects bird species diversity and abundance (see Bock *et al.* 1993; Saab *et al.* 1995 for reviews). Although some bird species increase in response to grazing, many species respond negatively (reviewed in Saab *et al.* 1995) and in general, bird species richness is inversely related to grazing intensity (e.g., Kantrud 1981; Mosconi and Hutto 1982; Taylor 1986).

Most previous studies on the impact of cattle-grazing on birds have linked changes in vegetation structure, cover, and vigor caused by grazing, to decreased abundance of local bird populations (e.g., Bock and Webb 1984) and higher predation at nests (Ammon and Stacey 1997). However, changes in vegetation structure and soil nutrients caused by occurrence of livestock may also affect arthropod abundance. Insectivorous bird species, particularly the ones foraging in the lower vegetation strata, may be affected by this change (decrease or increase) in prey abundance. Direct disturbance (physical presence of cattle) may cause destruction of ground nests and to a lesser extent, of shrub nests. Moreover, Brown-headed Cowbirds (*Molothrus ater*) are attracted by cattle (Rothstein *et al.* 1984), thus cattle occurrence may locally increase rate of Cowbird parasitism (Robinson *et al.* 1995).

Grazing can be characterized by its intensity (related to stocking rate or density of animals) and seasonality of use by livestock (duration and timing of grazing over the year) (Saab *et al.* 1995). Both these aspects affect the impact of cattle-grazing on birds (Saab et al. 1995). In this three-year study, I investigated the effects of cattle-grazing intensity and seasonality on habitat quality for songbirds in treed patches in the aspen parkland of central Alberta. The aspen parkland is a vegetation zone unique to Canada, except for a small area extending into the northern US. Since settlement about 90% of Canada's aspen parkland has been altered or replaced by cultivation (North 1976). Overgrazing by livestock has played a major role in this alteration (North 1976). This study took place in a natural area of aspen parkland, where the only disturbances were associated with ranching operations. Different zones of the study area have been grazed with different intensities and seasonality. A quarter section (0.8 km^2) was removed from the grazing lease in 1973 and set aside as a grassland research reserve for the Department of Lands and Forests and the University of Alberta.

The first objective of this paper was to analyze the impact of grazing on a) vegetation cover, vigor, structure and relative abundance of dominant shrub species in aspen and willow patches, and b) relative arthropod abundance and biomass in willow and aspen patches. Next, I assessed the impact of cattle-grazing on a) the number and abundance of songbird species, and b) the pattern of patch occupancy of individual songbird species in willow and aspen patches. I compared vegetation and arthropod abundance between patches situated in units with different grazing intensity and seasonality. Species nesting in willow patches should be expected to be more affected by grazing than species nesting in aspen patches because disturbance caused by the physical presence of cattle (direct disturbance) and the decline in habitat quality (vegetation structure and cover and arthropod abundance) caused by heavy grazing would be more severe in Willow patches than in Aspen patches. Results are discussed grouping species by nest type, nest location, and foraging strategy.

Finally, I selected the Yellow Warbler *(Dendroica petechia)* as a target species and assessed the impact of cattle grazing on habitat quality and breeding success (including brood parasitism by the cowbird) in this species. Data on breeding success in relation to grazing are very scarce for songbirds. In my study area, the Yellow Warbler is strictly dependent on willow patches, where it nests and forages, and on Aspen patches, which are used for foraging only. The surrounding mixed grassland is not used at all by Yellow Warblers. Furthermore, the Yellow Warbler is strictly insectivorous on the breeding grounds and is indicated by Bock et al. (1993) as one of the species whose response to cattle grazing is poorly known and requires further study.

The Red-winged Blackbird (*Agelaius phoeniceus*) was the only species that was found to nest on the ponds. The pattern of occurrence of this species in relation to grazing was also analyzed because cattle regularly enter ponds to drink.

STUDY AREA AND STUDY SITES

This study was carried out at Rumsey Ecological Reserve, in central Alberta. A detailed description of the study area can be found in Chapter 2. The area consists of hundreds of aspen (*Populus tremuloides*) and willow (mainly *Salix petiolaris* and *S. bebbiana*) patches surrounded by mixed grassland (Figure 2. 1). Stands of Trembling aspen occupy depressions and moderately steep slopes, mainly north-oriented. *Rosa woodsii, Amelanchier alnifolia,* and *Symphoricarpos occidentalis* dominate the understory in willow patches, whereas *Symphoricarpos occidentalis, Rosa woodsii, Rubus idaeus,* and *Ribes oxyacanthoides* are the most common shrub species in aspen patches. Treed patches were grazed by cattle. Most of the treed patches included a pond. Some of the ponds that were covered by vegetation (mainly *Carex atherodes, Scolochloa festucacea, Poa palustris,* and *Cirsium arvense*) were grazed and all the ponds were used by cattle as a source of water.

Based on the range evaluation system used by Public Land Services of Alberta (Eastern Slopes Rangeland Seeds Ltd. 1994) the study area is in good to excellent grazing condition, with < 5% in fair conditions. Range condition rating is a measure of deviation from "original conditions" of the range. Several service roads used for ranching operations run across the ecological reserve. A small gas well is present in the area. The five study units were selected according to grazing intensity and seasonality. Grazing intensities (heavy, moderate, light) were defined based on Table 1 in Wroe *et al.* (1988), for excellent/good conditions, in precipitation zone = 355-457mm (14-18 inches in the original Table). Animal unit equivalents (AUE), a standard used to take into account the relative grazing impact of different classes of livestock, were obtained following Wroe *et al.* (1988). Mature cows with or without calves were weighed 1 AUE, yearling heifers and steers were weighed 0.67. A few bulls were present in the area for short periods so that they were not considered in the computation of AUE. The first unit (unit A, 46 treed patches) of 177 ha was situated just outside the border of the ecological reserve and was characterized by moderate grazing (0.4 cattle/ha; 0.4 AUE/ha), during summer only. Cattle were put in this study unit at the beginning of July, when most of songbird species had completed their reproductive season (i.e. chicks had fledged), and were removed at the beginning of September. The same grazing regime was applied for at least 5 years prior to the beginning of this study. A second unit (unit B, 43 treed patches) of 102 ha was characterized by heavy grazing. Cattle were moved into the unit in April where they stayed until about 15 August. Density of cattle ranged from 0.74/ha to 0.93/ha (0.50-0.62 AUE/ha) during my study. Two lightly grazed units of 45 ha and 30 ha, in which a maximum of 0.31 cattle/ha (0.21 AUE/ha) were present (Unit C, 42 treed patches, and Unit D, 20 patches) and with the same grazing seasonality as Unit B were also included. Occasionally, yearlings were wintered in the units B, C and D for short periods (less than a month) when the area was not covered by snow. The grazing regimes described were followed for at least 8 years prior to the beginning of this study in units B, C and D. The last unit considered was a 64 ha unit that was ungrazed since 1973 (Unit E, 38 treed patches). Following the assigned alphabetical order the units were arranged from west to east (Figure 4.1). Study units were interspersed as much as possible in order to minimize interdependence among them. Distance between units ranged from 540 m to 1500 m. Due to logistic constraints this study lacked treatment replication except for the light grazing units.

METHODS

A more thorough description of methods used for this study can be found in Chapter 2 of this thesis, except for the statistical methods. A condensed version of methods is presented in this section.

Bird censusing

In 1995, 1996 and 1997 birds in willow and aspen patches and in ponds were censused five times between 16 May and 5 July using point counts (Ralph and Scott 1981). Sampling stations were positioned along routes designed to cover all the patches. At each station an observer spent 6 minutes recording all the birds heard or seen. Cowbirds perching in the patches were also counted to obtain an index of relative cowbird abundance.

Chronological order of territory occupancy by Yellow Warbler

In addition to point counts, chronological order of territory occupancy by Yellow Warbler males was obtained by censusing each patch every three days, starting from the arrival of the first male. Chronological order of territory occupancy by Yellow Warbler females was obtained by intensively searching every two days patches where at least one male was present.

Measurement of patch size, classification of Yellow Warbler territories and unoccupied territories

Some Yellow Warbler territories included more than one treed patch. For multi-patch territories the patch in which the territory holder spent more time singing or actively defending his territory was determined to be the "main patch". If more than one territory existed in a patch only the date of arrival of the first male and female were considered. For each territory, data points representing movements, location of song perches, and other activities of territorial significance that had been mapped in the field were digitized on a GIS coverage of the study area and territorial borders were obtained with the Minimum Convex Polygon method. Size of treed patches and ponds were also measured from this coverage. Unoccupied Yellow Warbler territories were obtained using borders of actual territories as templates. Templates were moved randomly across the GIS layer of the study area until they included only patches unoccupied by Yellow Warblers. When this occurred, an unoccupied territory was defined.

Breeding success of the Yellow Warbler

Yellow Warbler nests were found by intensively searching willow patches. Number of chicks 9 days old (considered as fledglings) were obtained for all nests. Increase in weight by chicks between day 2 and 5 was obtained in 1996 and 1997. Nests were checked every 2-3 days to detect predation and brood parasitism by Cowbirds.

Arthropod sampling

Relative abundance of arthropods for foliage-gleaning birds in willow bushes and aspen canopy (e.g., Yellow Warbler) was determined by sampling in willow patches (1995, 1996 and 1997) and in aspen patches (1995 and 1996) during brood rearing by the Yellow Warbler. The breeding period of most of the other songbird species occurring in treed patches partially overlapped with the Yellow Warbler's. Arthropods were not sampled on the ground, thus arthropod abundance for ground dwellers and gleaners could not be assessed. For Yellow Warbler territories that included more than one patch, only the main patch was sampled. Each patch was divided into eight zones of equal size and a sampling point was randomly assigned to each zone. At each point, sampling was performed with a standard sweep-net (diameter 37 cm), swept through the willow bush once, over approximately one m, with a firm hand. In aspen, the sweep-net was attached to a 6 m high flexible extensible pole. Height of sweep-netting varied from 0.3-3.5 m in willow and 0.5-8 m in aspen. Sampling effort was evenly distributed along the patch height.

Arthropods were preserved in 70% ethanol and later classified to order or family. Finally, they were dried at 50°C for 24 h (see Zach and Falls 1979) and weighed on an analytical scale to the nearest 0.01 mg. Abundance and dried biomass of Lepidoptera larvae, Diptera Chironomidae, Homoptera, mainly Cicadellidae (leafhoppers), and Hemiptera, which were all abundant in samples, were analyzed separately (see Chapter 2, Methods, Arthropod sampling for rationale).

Vegetation sampling

Vegetation structure was sampled at all willow and aspen patches in July and the first week of August. Since willow structure and understory changed between years, due mainly to variation in pond size, sampling in willow patches was repeated at the end of each breeding season. Aspen patches were sampled once.

Since at the end of the breeding season the approximate territorial borders were known for most territories, vegetation could be sampled at the territory level for the Yellow Warbler. In multi-patch territories, vegetation was sampled in all the patches. For

< 10% of territories, for which territorial borders were poorly known, sampling plots were placed only in the central part of the territory.

Willow patches: For willow patches, a modified version of the protocol from the BBIRD Program (Martin 1992) was used. A sample plot was a 5 m radius circle (0.008 ha) divided by 2 perpendicular diameters into 4 equal quadrants. If a nest was present in the patch, the first plot was centered on the nest. If no nest was present the first point was randomly placed. Other plots were located 40 m from the center of the nearest plot(s), in a randomly selected direction until it was no longer possible to fit more points. Thus, the number of sample points was determined by the size of willow patches. In total, 20 variables characterizing vegetation structure and composition in willow patches were obtained (Table 4.1).

Aspen patches: The point-centered quarter method (Mueller-Dombois and Ellenberg 1974) was used to sample vegetation structure in aspen patches. A first sampling point was randomly placed and the other sampling points, as many as it was possible to fit in the in aspen patches, were located 40 m apart, in a randomly selected direction. At each plot, distance to the nearest 3 trees in each of the 4 quadrants was measured. Dbh and height were taken for the 12 trees considered.

Statistical methods

Vegetation structure, arthropod abundance and grazing intensity: In 1995, 1996 and 1997, the descriptors of vegetation structure, arthropod abundance and biomass in willow and aspen patches were analyzed using one-way ANOVA to assess if they differed between units with different grazing intensity and seasonality (heavy grazing, moderate summer grazing, lightly grazed, and ungrazed). Data for the two lightly grazed units were combined. A Kruskal-Wallis test was used when the variables did not meet the assumptions of a parametric ANOVA. The Bonferroni method was used to determine which groups were significantly different in the parametric ANOVA. Nonparametric multiple comparisons with unequal sample sizes (Dunn 1964, Hollander and Wolfe 1973) were used with the Kruskal-Wallis test. A total of 104 models were run for the three years. For the variables measured in all three years, I retained for subsequent analysis (bird community and Yellow Warbler) only the variables that were significantly and similarly different between grazing units in at least two years (e.g., higher mean for the same group in more than one year). Descriptors of vegetation structure in aspen patches were measured in one year only, thus they were retained in subsequent analyses if they showed a trend in relation to grazing intensity (e.g., increasing values from heavy grazing to ungrazed). For the variables that were measured in two years (e.g., arthropod abundance in aspen patches), I retained those that were significant and consistent in both years, or in one year and had a similar trend in the other year.

Territory occupancy and breeding success of the Yellow Warbler: In 1995, 1996, and 1997 the proportion of territories occupied by Yellow Warbler males in relation to grazing intensity was analyzed using a G-test. For the years in which proportion of occupied territories differed in areas grazed with different intensity, "grazing intensity" was included as a categorical variable in multiple logistic regression models for territory occupancy (territory occupied/unoccupied) together with the descriptors of spatial structure and vegetation structure of territories that were found to be significant in a companion study (Chapter 2). The interactions between "grazing intensity" and the other explanatory variables were also included one by one (in turn) in the models. Analogously, chronological order of territory occupancy by Yellow Warbler males (1995, 1996 and 1997) and females (1996 and 1997) in relation to grazing intensity was analyzed using a Kruskall-Wallys test. Next, "grazing intensity" was included in stepwise GLIM together with the variables that were significant in the corresponding models for chronological order of territory occupancy in Chapter 2. Interactions between grazing and the other descriptors were also considered. Quasi-likelihood estimation (McCullagh and Nelder 1989) was used for these models due to overdispersion of parameters.

In 1995, 1996 and 1997, number of chicks produced per nest including or not including unsuccessful nests was analyzed in relation to grazing intensity using Kruskall-Wallis test. In 1996 and 1997, the increase in weight by chicks was analyzed in GLM including clutch size and grazing intensity as factors. Predation at the nest and brood parasitism by the Brown-headed Cowbird were analyzed in relation to grazing intensity using a Randomized G-test with 10,000 randomizations because some cells had observed frequency < 5. Cowbird parasitism could not be analyzed in 1995 because only three parasitized nests were found. Since none of the components of Yellow Warbler breeding success was found to be affected by territory features in this study area (Chapter 2), grazing intensity did not need to be analyzed in a multivariate context.

Bird Community: Due to low frequency of occurrence of many species, only 10 species could be analyzed for pattern of occurrence in treed patches in relation to grazing intensity. These include Brown-headed Cowbird, Clay-colored Sparrow (*Spizella pallida*), Chipping Sparrow (*Spizella passerina*), Dark-eyed Junco (*Junco hyemalis*), Black-capped Chickadee (*Parus atricapillus*), Least Flycatcher (*Empidonax minimus*), Red-eyed Vireo (*Vireo olivaceus*), House Wren (*Troglodytes aedon*) [American Robin (*Turdus migratorius*), Savannah Sparrow (*Passerculus sandwichensis*) and Vesper Sparrow (*Pooecetes gramineus*) in 1996 and 1997 only]. For each of these a stepwise logistic model for presence/absence in treed patches was built. The model included area of willow patch, area of aspen patch, arthropod abundance and dried biomass in willow and aspen patches, all the variables that were found to differ consistently between grazing units (Table 4.2), and "grazing intensity" as a categorical variable. Interactions between "grazing intensity" and the other explanatory variables were also considered and included one by one (in turn) in the model. Wald statistics were used to test for significance of individual coefficients and a goodness-of-fit index to assess the general fit of the model (Hosmer and Lemeshow 1989). If "grazing intensity" was significant in the multivariate model, a G-test was used to compare the proportion of occupied patches between different grazing units.

Only one species, the Red-winged Blackbird, nested on ponds. A logistic model including area of pond, "grazing intensity" and the interaction term was built for this species. For the three most abundant species, Clay-colored Sparrow, Brown-headed Cowbird, and Least Flycatcher, abundance in patches was also analyzed in relation to grazing intensity using GLIM models and a quasi-likelihood estimation method.

GLIM models were also used to analyze total number of species and individuals occurring in treed patches (including species that are also present in the grassland, see Appendix 4.1), in relation to grazing intensity and patch characteristics as outlined for logistic regressions. For all these analyses, separate models were obtained for 1995, 1996 and 1997.

RESULTS

Effects of grazing on vegetation and arthropods

All models are presented in Appendix 4.2. Models for the variables differing between grazing units are summarized in Table 4.2a and Table 4.2b. In all years the willow patches situated in the heavily and moderate grazed units had a higher percentage of ground covered by vegetation than in the lightly grazed units. Vegetation cover in willow patches was intermediate in the ungrazed unit. Willow patches in unit A (moderate summer grazing) had higher grass cover than the other units (except for the ungrazed unit in 1996), tended to have higher density of rose shrubs, and in two years had lower density of aspen shrubs. Willow patches in unit B (heavy grazing) had higher forb cover than the other units, and lower density of rose shrubs than unit A.

Willow patches in the lightly grazed unit tended to have higher density of Saskatoon shrubs than the other units. Willow patches in the ungrazed unit had consistently higher density of saplings (mainly aspen) and in general, willow patches in the heavily and moderately grazed units had lower density of saplings than in the lightly or ungrazed units. Willow bushes tended to be shorter in the heavily grazed unit. In the aspen patches, distance between aspen trees increased with grazing intensity and the difference between the heavily and moderately grazed units *vs* lightly grazed and ungrazed units was significant.

Willow patches in the heavily and moderately grazed units, particularly in unit B (heavy grazing) had higher relative abundance and dried biomass of Hemiptera. Aspen patches in unit A (moderate summer grazing) tended to have higher total abundance of arthropods and higher abundance and biomass of Homoptera.

Size of willow patches did not differ between grazing units, but size of aspen patches tended to be smaller in the lightly grazed unit and larger in the moderately grazed unit and in the ungrazed unit (Table 4.2)

Yellow Warbler

Results of this and the following sections are summarized in Table 4.7. Detailed results for this section are presented in Appendix 4.3

Territory occupancy and grazing intensity

In 1995, the proportion of territories occupied by the Yellow Warbler did not differ between areas with different grazing intensities ($G = 5.04$, $P = 0.169$; Appendix 4.3a). In general the moderately grazed unit had a lower proportion of patches occupied, whereas a higher proportion of patches were occupied in the ungrazed unit ($G_{1996} = 9.41$, $P = 0.024$, $G_{1997} = 20.24$ $P = <0.001$; Appendix 4.3a). However, neither grazing intensity nor the interactions between grazing intensity and the other explanatory variables were significant when added to multivariate logistic models (Table 2.6, Chapter 2).

Chronological order of territory occupancy and grazing intensity

In 1995 and 1996 chronological order of territory occupancy by males did not differ between units with different grazing intensities ($X^2_{1995} = 2.57$, $P = 0.462$, $X^2_{1996} = 4.11$, $P = 0.250$; Appendix 4.3b). In 1997, territories situated in the ungrazed and lightly grazed units on average were occupied by males significantly earlier than the heavily and moderately grazed units ($X^2 = 18.95$, $P < 0.001$; Appendix 4.3b). In 1997, "grazing intensity" and the interaction "Area of willow x grazing intensity" were significant in GLIM (Table 4.3). In 1996 chronological order of territory occupancy by females was almost significantly different between grazing units ($X^2 = 7.41$, $P = 0.059$, Kruskall-Wallis test; Appendix 4.3b), but "grazing intensity" was no longer significant when added to multivariate models (Table 2.8, Chapter 2). In 1997, territories situated in the moderately grazed unit were occupied later by females than territories situated in the lightly grazed and ungrazed units ($X^2 = 18.95$, $P < 0.001$; Appendix 4.3b). No other variable was significant in GLIM for females. However, chronological order of territory occupancy also reflected the geographic position of the grazing units (see Chapter 2).

Breeding success and grazing intensity

Number of chicks produced per nest in successful nests did not differ between grazing units ($X^2_{1995} = 4.64$, $P = 0.131$, $X^2_{1996} = 1.48$, $P = 0.687$, $X^2_{1997} = 4.62$, $P = 0.202$, Kruskal-Wallis; Appendix 4.3c). In 1997, when including unsuccessful nests, nests situated in the ungrazed unit tended to produce more chicks than in the heavily and moderately grazed units ($X^2_{1995} = 0.73$, $P = 0.866$, $X^2_{1996} = 0.608$, $P = 0.895$, $X^2_{1997} = 7.49$, $P = 0.058$, Kruskal-Wallis; Appendix 4.3c). Increase in weight by chicks did not differ between grazing units ($X^2_{1996} = 5.52$, $P = 0.137$, $X^2_{1997} = 3.66$, $P = 0.301$, Kruskal-Wallis and GLM; Appendix 4.3c). In 1997 a lower proportion of nests were preyed upon in the ungrazed unit (Randomized $G_{1995} = 1.256$, $P = 0.770$, $G_{1996} = 6.106$, $P = 0.120$, $G_{1997} = 9.223$, $P = 0.028$; Appendix 4.3d), and in 1996 the rate of cowbird parasitism was higher in the ungrazed unit than in the light grazing and heavy grazing unit ($G_{1996} = 14.977$, $P = 0.002$, $G_{1997} = 0.501$, $P = 0.917$; Appendix 4.3d).

Bird Community

Pattern of occupancy of individual species, patch features, and grazing intensity

Results of this section are detailed in Appendix 4.4. Pattern of patch occupancy by the Chipping Sparrow, Savannah Sparrow, Dark-eyed Junco, American Robin and Black-capped Chikadeee was never affected by any of the measured patch features or by grazing (Logistic models).

Probability of patch occupancy by the House Wren was affected by the area of aspen patches in two years (Table 4.4) and in 1997, the proportion of patches occupied was higher in the heavily and moderately grazed units than in the lightly grazed and ungrazed units ($G_{1997} = 15.23$, $P = 0.002$; Table 4.4 and Appendix 4.4a). In 1996, percentage of patches occupied by the Red-eyed Vireo was lower in the moderately grazed unit than in the other units ($G_{1996} = 9.15$, $P = 0.040$; Appendix 4.4a). However, trends were not consistent among years for this species. Percentage of patches occupied by the Vesper

Sparrow in 1996 and 1997 was higher in the heavily and moderately grazed units ($G_{1996} = 19.53$, $P < 0.001$; $G_{1997} = 15.15$, $P < 0.001$; Appendix 4.4a). No other feature of patches affected pattern of patch occupancy by the Red-eyed Vireo and the Vesper Sparrow.

Probability of patch occupancy by the Brown-headed Cowbird was not affected by grazing or any other patch feature. However, cowbird relative abundance in patches was positively related to area of aspen or willow patches, density of saplings, and arthropod biomass in willow patches, and negatively with shrub density (Table 4.5). Cowbird abundance was lower in the heavily grazed unit in all three years. However, this result was significant in GLIM in 1996 only ($X^2_{1996} = 24.60$, $P < 0.001$, Kruskal-Wallis test; Table 4.5 and Appendix 4.4b). In general, percentage of patches occupied and abundance of the Clay-colored Sparrow tended to be higher in the moderately grazed unit than in the lightly grazed unit, significantly in 1996 and 1997 ($G_{1996} = 18.80$, $P < 0.001$; $G_{1997} = 17.88$, $P < 0.001$; Appendix 4.4c). Abundance of the Clay-colored Sparrow was also affected by area of willow or aspen patches and vegetation structure ($X^2_{1996} = 15.31$, $P < 0.001$, $X^2_{1997} = 15.46$, $P < 0.001$, Kruskal-Wallis test; Table 4.5 and Appendix 4.4c). In two years, patch occupancy ($G_{1995} = 21.79$, $P < 0.001$; $G_{1996} = 8.97$, $P = 0.032$; Appendix 4.4d) and abundance of the Least Flycatcher in patches were higher in the ungrazed unit and lower in the moderately grazed unit ($X^2_{1995} = 23.64$, $P < 0.001$, $X^2_{1996} = 13.41$, $P = 0.004$, $X^2_{1997} = 8.01$, $P = 0.041$, Kruskal-Wallis test; Appendix 4.4d). However, this effect was not independent of area of aspen patches in 1995 (Table 4.4) and in 1997 (Table 4.5). Total number of saplings (+) and total number of shrubs (-) were also significant in models for occupancy and abundance of the Least-Flycatcher.

Probability of pond occupancy by the Red-winged Blackbird was not affected by pond size. No Red-winged Blackbird was present in the heavily grazed unit in all three years and in 1997 in heavily grazed and moderately grazed units ($G_{1995} = 9.71$, $P < 0.030$; $G_{1996} = 10.27$, $P = 0.028$; $G_{1997} = 21.64$, $P < 0.001$; Appendix 4.4 e).

Species richness and number of individuals

Total number of species and of individuals occurring in treed patches were mainly affected by area of aspen patches and less strongly by area of willow patches (Table 4.6).

Shrub density had a negative effect on species richness and abundance of individuals in 1997, whereas density of saplings was positively related to number of individuals in three years. In 1995 and 1996, grazing was not significant in models for total number of species and of individuals. In 1997, the interaction "grazing intensity x area of aspen" but not the main term "grazing intensity" was significant in models for total number of species and of individuals. In 1997, there tended to be more species in the moderately grazed unit than in the lightly grazed unit ($\chi^2_{1997} = 7.42$, $P < 0.06$, Kruskal-Wallis; Appendix 4.5). Lightly grazed units had lower total number of individuals than ungrazed unit ($\chi^2_{1997} = 9.43$, $P < 0.024$, Kruskal-Wallis; Appendix 4.5).

DISCUSSION

Vegetation structure, vigor and composition in relation to grazing intensity and seasonality

Since the unit grazed only in summer was subjected to different grazing intensity than the other units (intermediate between heavily grazed and lightly grazed units) the effects of grazing intensity and seasonality could not be teased apart. Grazing intensity and possibly seasonality modified ground vegetation structure and composition. Forb cover was highest in the heavily grazed unit and grass cover and density of rose shrubs in the unit with moderate summer grazing. This was not related to canopy cover or foliage density. In the aspen woodland of Alberta, Weatherill and Keith (1969) found that 18 herbaceous species decreased in frequency in aspen woodlots in response to increased grazing intensity, 16 increased with light grazing (0.02-0.27 AUE/ha in their study) but decreased with heavy grazing (0.32-0.54 AUE/ha), 16 increased with grazing no matter its intensity, and two did not respond to grazing. Proportions of grass and forbs were similar in the first three groups. The authors also found that taller plants tended to be replaced by shorter plants, but percentage of ground covered by grass and forbs in relation to grazing intensity was not reported in this study.

Among the dominant shrub species analyzed in my study, Rose reached highest density in the moderately grazed unit (summer only) and lowest density in the heavily grazed unit. The former unit also had lower density of Trembling Aspen shrubs.

Saskatoon was denser in the lightly grazed units. Rose and Saskatoon were both classified as decreasing in response to grazing intensity in Weatherill and Keith (1969). On average, ground vegetation cover was higher in the heavily and moderately grazed units, intermediate in the ungrazed unit and lowest in the lightly grazed unit. This is in disagreement with most of the previous studies on the effects of grazing on vegetation structure (Saab *et al.* 1995).

Upper vegetation strata were also affected by grazing: willow bushes were 30-110 cm shorter in the heavily grazed unit than in the other units. However, grazing intensity and seasonality did not affect vigor of willow and distance between willow bushes. Density of saplings in willow patches was higher in the ungrazed unit. In aspen patches, cattle have been frequently observed to rub against aspen trees. Rubbing and trampling in aspen patches frequently causes tree falls. Consequently, mean distance between aspen trees was > 1 m larger in the heavily and moderately grazed units than in the lightly grazed and ungrazed units. Aspen patches in the ungrazed unit are expanding at the expense of the mixed grassland and aspen recruitment at the edge of patches of aspen appeared to proceed faster in this unit. This may be due to the long term absence of cattle grazing in the area. However, differences in topography between study units may also account for differences in size of aspen patches between units.

Grazing intensity and arthropod abundance/biomass

In general, arthropod abundance increased with grazing intensity. Abundance and biomass of Hemiptera in willow patches was larger in the heavily grazed unit. Soil fertilization by cattle may have affected some unmeasured feature of quality of willow bushes and arthropods may have responded to that. Total abundance of arthropods, and in particular of Homoptera in aspen patches was higher in the heavily grazed unit. Homoptera accounted for 50-80 % of total arthropod abundance in sweep net-samples for aspen patches. I speculate that larger distance between aspen trees (presence of canopy gaps) in the moderately grazed unit (summer grazing only) may have created favorable microclimatic conditions for this taxon.

Territory occupancy in the Yellow Warbler and grazing

Although the proportion of territories occupied by the Yellow Warbler differed between units and decreased with grazing intensity in all three years (Appendix 4.3a), in multivariate models including patch size and shape of willow patches (measured as perimeter to $\sqrt{}$area ratio), amount of willow within 50 m from territory center, ground cover, and foliage density, the probability of territory occupancy were not affected by grazing. Thus, the apparent effect of grazing was likely due to differences in landscape configuration and vegetation structure between study units. However, Krueper (1993) found that in riparian habitat in Arizona, Yellow Warbler density progressively increased within four years from retirement of grazing. In Montana, Yellow Warblers reached higher densities in ungrazed plots than in grazed plots (Mosconi and Hutto 1982). For this species, negative response to grazing has also been found in a riparian site dominated by willow in Oregon (Taylor 1986). However, Page *et al.* (1978) reported increased Yellow Warbler densities in response to grazing in aspen woodlots in California. No response was found by Knopf *et al.* (1988) in willow communities in Colorado, and by Medin and Clary in aspen/willow in Nevada (1991).

Chronological order of territory occupancy by Yellow Warbler males and females and grazing

In 1997, both Yellow Warbler males and females occupied the patches of willow situated in the ungrazed and lightly grazed units earlier than the ones in the heavily and moderately grazed units. In particular, patches in the moderately grazed unit were occupied last. Unfortunately, this pattern also reflected the geographic position of the units along the east-west axis. Thus, it is not possible to assess if chronological order of occupancy was affected by geographic position, grazing regime, or both.

Breeding success in the Yellow Warbler and grazing

Number of chicks produced per nest in successful nests and increase in weight by chicks did not differ between grazing units (Table 4.7). Thus, measured differences in arthropod abundance and biomass, and vegetation between grazing units did not seem to have any effect on productivity in theYellow Warbler. In 1997 predation was lower in the ungrazed unit (Table 4.7). This resulted in an almost significantly higher breeding success in the ungrazed unit in that year (Appendix 4.3c). Since Yellow Warblers nest in willow bushes, vigor and structure of willow bushes may be expected to affect probability of nest predation. However, willow structure and vigor did not differ between the ungrazed unit and the other units (except for willow height in the moderately grazed unit). Alternatively, direct disturbance (physical occurrence of cattle) by cattle approaching the nest may force Yellow Warblers to leave and/or produce alarm calls, which may result in higher nest predation. In 1996 brood parasitism by cowbirds was higher in the ungrazed unit (Table 4.7) but this did not lead to differences in breeding success between grazing units. In 1996, cowbird abundance was higher in the ungrazed unit than in the other units (Table 4.7). I conclude that breeding success by the Yellow Warbler was marginally affected by grazing. Studies on the effects of grazing on breeding success in songbirds are rare. Wilson et al.(1997) found that territory distribution and breeding success of the Skylarks (*Alauda arvensis*) in organic and intensive farmland in southern England was negatively affected by cattle grazing intensity.

Patch occurrence, species abundance and richness in relation to grazing and patch features

Five of the 13 species analyzed were negatively affected by grazing. Surprisingly, none of them was a ground nester (Table 4.8). Previous studies have found that ground nesters experience the most dramatic decline in response to grazing (reviewed in Saab *et al.* 1995). For three of the four ground nesting species present in treed patches (Vesper Sparrow, Savannah Sparrow, Clay-colored Sparrow) the mixed grassland constitutes the primary habitat and all their territories occurred partially in this habitat type. Therefore, for these species impact of grazing on grassland should also be considered. I did not measure vegetation structure and cover in the grassland. However, the ungrazed unit was characterized by a thick continuous layer of dried fescue (*Festuca sp.*), unlike the other units. This may not be advantageous to omnivore ground foragers such as the Clay-colored Sparrow and the Vesper Sparrow. These two species positively responded to heavier grazing intensity. One possibility is that heavy and moderate grazing increased food availability in the grassland.

Four of the five species whose frequency of patch occupancy and/or abundance were negatively affected by grazing were insectivores and three of them foraged in willow or aspen canopy (Table 4.8). However, arthropod abundance in willow and aspen patches tended to be positively related to grazing intensity, and willow and aspen gleaning surface and vigor were probably little affected by grazing.

The only omnivorous species whose frequency of occupancy was negatively affected by grazing was the Red-winged Blackbird. This was also the only species that nested on the ponds at Rumsey. Ponds in the heavily grazed area were intensively used by cattle. Continuous absence of the Red-winged Blackbird from this unit is related to the total absence of cattail (*Typha latifolia*) in ponds caused by trampling and physical disturbance by cattle. Other studies carried out in riparian habitats have all found that Red-winged Blackbirds were negatively affected by cattle grazing (Crouch 1982; Taylor 1986; Knopf *et al.* 1988; Medin and Clary 1990).

Only two cavity nesters were present at Rumsey. This guild is usually the least affected by cattle-grazing (Saab *et al.* 1995). However, since the occurrence of livestock may cause extensive treefalls, the cavity nesters may also be affected by cattle occurrence. However, the Black-capped Chickadee was not affected by grazing and in 1996, the House Wren was more abundant in the heavily and moderately grazed units.

Unexpectedly, in 1996 Brown-headed Cowbird relative abundance was higher in the ungrazed unit than in the lightly and heavily grazed units. Previous studies found that the Brown-headed Cowbird was either not affected by grazing (Kantrud and Kologiski 1982; Kantrud 1981) or responded positively (Reynolds and Trost 1981; Rich and Rothstein 1985; Page et al. 1978; Mosconi and Hutto 1982; Knopf et al. 1988; Schulz and Leininger 1991). Only one study carried out in a willow dominated riparian habitat in Oregon found a negative effect of grazing on cowbird abundance (Taylor 1986).

Together with the Red-winged Blackbird, the Least Flycatcher was the only species that was negatively affected by grazing in more than one year. This species was found in aspen patches only. Least Flycatchers nests between 1 m and 2 m high were frequently found in the area. This would make them vulnerable to physical disturbance by cattle. However, aspen patches were larger in size in the ungrazed unit. The interaction between area of aspen and grazing was found to be significant in some of the models for Least Flycatcher presence/absence and abundance. For species strictly dependent on aspen patches (i.e., Least Flycatcher and Red-eyed Vireo) effect of grazing could be at least partially confounded by differences in spatial configuration of the landscape between grazing units.

Among the measured patch features, area of aspen and willow patches were the most important in models for probability of occupancy and abundance of individual species. In general vegetation structure had little influence and arthropod abundance was never significant in models. When considering species richness and total number of individuals in patches, area of aspen was much more important than area of willow (Table 4.6). Indeed, only the Yellow Warbler nested exclusively in willow patches. The multivariate models for species richness and total number of individuals indicate that grazing had no effect in two years and in one year only the interaction between grazing and area of aspen was significant but of marginal importance compared to area of aspen patches.

Many species show inconsistent responses to cattle grazing among study sites and habitat types (reviewed in Saab *et al.* 1995). I found little consistency between years in bird response to grazing and in general bird distribution and abundance did not reflect differences in vegetation structure and arthropod abundance between units. However, arthropod sampling was representative for foliage insectivores only. The effect of grazing seasonality and intensity could not be disentangled. However, the moderately grazed unit (summer grazing) did not rate better than the heavily grazed unit with regards to bird occurrence, abundance and richness, and breeding success in the Yellow Warbler. The effects of grazing intensity on birds can be considered marginal if compared to other patch features. This may be attributed to overall good range conditions. Perhaps, the most severe effect was on pond vegetation and avifauna, which were only marginally addressed in this paper. Of course, other organisms that live in the ponds and that I did not consider in this study (e.g. amphibians) may be severely impacted by cattle grazing. Admittedly, having sampled one study unit only per grazing treatment (two for lightly grazing) and having selected the patches as sample units the problem of pseudoreplication is present in this study.

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Table 4.1. Variables describing vegetation structure in willow patches.

Variable name	**Description of variable**
GROUND COVER	
All green (%)	Percent of ground covered by grass/sedges, shrubs, and forbs.
Grass (%)	Percent of ground covered by grass/sedges.
Shrub (%)	Percent of ground covered by shrubs.
Forb (%)	Percent of ground covered by forbs.
Leaf litter (%)	Percent of ground covered by leaf litter.
Bare ground (%)	Percent of ground not covered by vegetation (woody debris, water, and mud).
SHRUBS (10-140 cm)	
#Total shrubs	Total number of shrub stems.
#Rose	Number of *Rosa sp.*stems.
#Saskatoon	Number of *Amelanchier alnifolia* stems.
#Aspen shrubs	Number of *Populus tremuloides* stems.
#Willow shrubs	Number of *Salix sp.* stems.
SAPLINGS (dbh<2.5 cm) AND POLES (2.5<dbh<8 cm)	
#Total saplings	Total number of saplings.
#Total poles	Total number of poles.
WILLOW BUSHES	
Willow height (cm)	Mean height of willow bushes.
Green stems willow	Total number of green willow stems.
Dry stems willow	Total number of dry willow stems .
Total stems willow	Total number of willow stems.
Willow distance (cm)	Mean distance between willow bushes.
VEGETATION DENSITY	
Foliage density (%)	Foliage density.
Canopy cover (%)	Percent of sky obscured by willow and trees.

Table 4.2a. One-way ANOVAs for descriptors of patch quality. Only the variables that showed consistency in difference between grazing treatments among years are presented. Kruskal-Wallis test was used when variables did not conform to the assumptions for parametric ANOVA. Means and SE are presented. Groups differing by at least one letter in alphabetical order (e.g., **a** ≠ **b**, but **a** = **ab** and **ab** = **b**) are significantly different.

Variable name	Heavy grazing	Moderate grazing (summer)	Light grazing	Ungrazed	Total df	F (or X^2)	P
VEGETATION IN WILLOW PATCHES							
All green (%) 1995	67.92 **b** (3.78)	57.37 **bc** (3.15)	41.04 **a** (4.15)	51.09 **ab** (3.79)	78	9.11	<0.001
All green (%) 1996	30.40 **a** (1.46)	42.54 **b** (2.81)	32.76 **a** (2.15)	35.88 **ab** (2.13)	181	†13.85	0.003
All green (%) 1997	51.27 **b** (1.42)	49.02 **b** (2.26)	39.10 **a** (2.09)	41.35 **ab** (3.13)	192	†19.13	<0.001
Grass (%) 1995	24.12 **a** (2.10)	46.30 **b** (3.85)	22.39 **a** (2.74)	28.18 **a** (3.88)	78	12.47	<0.001
Grass (%) 1996	9.38 **a** (0.63)	18.97 **b** (1.76)	10.72 **a** (1.19)	15.46 **b** (1.89)	182	†26.90	<0.001
Grass (%) 1997	17.01 **a** (1.13)	25.18 **c** (1.47)	12.17 **b** (1.01)	16.97 **ab** (1.85)	192	†42.80	<0.001
Forb (%) 1995	33.83 **c** (2.78)	4.65 **a** (0.99)	11.90 **b** (1.98)	15.39 **b** (2.37)	78	†46.12	<0.001
Forb (%) 1996	15.57 (1.08)	13.02 (1.16)	24.66 (8.59)	13.04 (1.54)	181	1.00	0.393
Forb (%) 1997	19.48 **b** (0.93)	12.28 **a** (0.78)	13.53 **a** (1.09)	13.71 **a** (1.55)	192	†33.69	<0.001
#Rose 1995	0.94 (0.46)	2.98 (0.65)	2.30 (0.69)	1.72 (0.51)	78	2.48	0.068
#Rose 1996	1.07 **a** (0.44)	4.29 **b** (0.75)	3.02 **ab** (0.52)	2.45 **ab** (0.51)	182	†24.87	<0.001
#Rose 1997	3.88 **a** (0.65)	6.51 **b** (0.76)	3.44 **a** (0.57)	2.40 **a** (0.56)	192	†20.24	<0.001
#Saskatoon 1995	1.63 **ab** (0.49)	0.41 **a** (0.36)	3.74 **b** (1.23)	2.35 **ab** (0.79)	78	†16.19	<0.001
#Saskatoon 1996	0.32 **a** (0.16)	0.56 **a** (0.30)	3.21 **b** (0.71)	1.09 **a** (0.30)	182	†8.06	<0.001
#Saskatoon 1997	0.29 (0.15)	0.04 (0.02)	0.38 (0.12)	0.18 (0.07)	192	†5.90	0.117

Variable name	Heavy grazing	Moderate grazing (summer)	Light grazing	Ungrazed	Total df	F (or X^2)	P
#Aspen shrubs 1995	0.18 ab (0.07)	0.06 a (0.03)	0.58 b (0.15)	0.40 ab (0.24)	78	†8.67	0.004
#Aspen shrubs 1996	0.56 (0.17)	0.30 (0.07)	0.33 (0.09)	1.02 (0.23)	192	†8.06	0.045
#Aspen shrubs 1997	0.56 ab (0.17)	0.30 a (0.07)	0.33 a (0.09)	1.02 b (0.23)	192	†14.84	0.002
#Total saplings 1995	7.54 a (1.55)	6.39 a (1.20)	15.49 b (2.37)	17.13 b (2.72)	78	7.96	<0.001
#Total saplings 1996	4.54 (0.60)	4.10 (0.53)	4.68 (0.68)	7.18 (1.05)	182	†5.48	0.140
#Total saplings 1997	5.71 ab (0.75)	4.65 a (0.68)	5.99 ab (0.99)	8.67 b (1.14)	192	†8.91	0.031
Willow height (cm) 1995	3.29 a (0.12)	4.38 b (0.16)	3.60 b (0.15)	3.72 b (0.19)	78	10.08	<0.001
Willow height (cm) 1996	3.52 (0.11)	3.75 (0.07)	3.64 (0.11)	3.75 (0.14)	182	†2.74	0.434
Willow height (cm) 1997	3.50 (0.11)	3.58 (0.08)	3.31 (0.08)	3.63 (0.12)	192	2.51	0.060
VEGETATION IN ASPEN PATCHES							
Distance to nearest twelve trees (m)	342.31 a (16.43)	369.3 a (16.43)	275.8 b (9.29)	259.2 b (10.82)	179	17.24	<0.001
ARTHROPOD ABUNDANCE IN WILLOW PATCHES							
Hemiptera 1995	9.28 b (1.34)	8.61 b (0.92)	4.78 a (0.62)	4.76 a (0.69)	175	†19.69	<0.001
Hemiptera 1996	18.85 b (2.33)	7.65 a (0.65)	5.68 a (0.81)	6.58 a (1.14)	169	†38.96	<0.001
Hemiptera 1997	20.09 b (1.55)	10.59 a (0.83)	8.88 a (0.61)	9.50 a (1.24)	224	†46.55	<0.001
ARTHROPOD DRIED BIOMASS IN WILLOW PATCHES							
Hemiptera 1995	10.91 b (1.63)	9.99 b (1.31)	3.61 a (0.42)	4.28 a (1.01)	175	†31.28	<0.001
Hemiptera 1996	23.67 b (4.09)	9.26 a (1.33)	3.33 a (0.44)	6.13 a (1.22)	169	†32.27	<0.001
Hemiptera 1997	26.28 b (2.25)	15.38 a (1.54)	11.28 a (0.95)	10.93 a (1.51)	224	†40.95	<0.001

Variable name	Heavy grazing	Moderate grazing (summer)	Light grazing	Ungrazed	Total df	F (or X^2)	P
ARTHROPOD ABUNDANCE IN ASPEN PATCHES							
Total abundance 1995	21.50 (1.89)	24.53 (3.10)	19.78 (3.25)	26.78 (3.62)	79	1.08	0.362
Total abundance 1996	39.50 **a** (3.11)	58.32 **b** (6.32)	34.78 **a** (2.92)	36.57 **a** (4.15)	150	5.40	0.002
Homoptera 1995	10.91 (1.35)	13.12 (1.35)	9.50 (1.49)	11.88 (1.68)	77	0.93	0.431
Homoptera 1996	24.71 **a** (2.48)	41.09 **b** (4.61)	22.0 **a** (2.55)	24.44 **a** (3.73)	155	7.02	0.002
ARTHROPOD DRIED BIOMASS IN ASPEN PATCHES							
Homoptera 1995	17.67 (2.98)	20.52 (2.92)	14.43 (2.58)	17.98 (2.47)	77	0.81	0.490
Homoptera 1996	60.44 **a** (6.56)	100.7 **b** (13.46)	51.26 **a** (6.11)	56.67 **a** (9.61)	156	†11.08	0.011
AREA OF WILLOW PATCHES	1811 (465)	1426 (224)	995 (181)	1717 (307)	156	1.40	0.246
AREA OF ASPEN PATCHES	3288 (598)	1449 (259)	2326 (339)	2729 (712)	156	2.55	0.058

† Kruskal-Wallis test, X^2 corrected for ties.

Table 4.2b. Effect of grazing on the vegetation and arthropods are schematically summarized. Significance value in multivariate models is shown. P values are reported for significant years, in chronological order.

YEAR	1995	1996	1997	P value
Vegetation in willow patches				
All green	H > L, U M > L	M > H, L	H, M > L	<0.001 0.003 <0.001
Grass	M > others	M, U > H, L	M > others H, M > L	<0.001 <0.001 <0.001
Forb	H > others M < others	ns	H > others	<0.001 <0.001
#Rose	ns	M < H	M > others	<0.001 <0.001
# Saskatoon	L < M	L > others	ns	<0.001 <0.001
# Aspen shrubs	L < M	no differ.	U > L, M	0.004 0.045 0.002
# Total saplings	L, UN > H,M	ns	U > M	<0.001 0.031
Willow height	H < others	ns	ns	<0.001
Vegetation in aspen patches				
Distance to nearest twelve trees	H, M > L, U	--	--	<0.001
Arthropod abundance in willow patches				
Hemiptera	H, M> L, U	H > others	H > others	<0.001 <0.001 <0.001
Arthropod dried biomass in willow patches				
Hemiptera	H, M > L, U	H > others	H > others	<0.001 <0.001 <0.001

YEAR	1995	1996	1997	P value
Arthropod abundance in aspen patches				
Total abundance	ns	M > others	--	0.002
Homoptera	ns	M > others	--	0.002
Arthropod dried biomass in aspen patches				
Homoptera	ns	M > others	--	0.011

Note: U = ungrazed, L = light, H = heavy, M = moderate (summer) grazing.

Table 4.3. GLIM models for chronological order of territory occupancy by Yellow Warbler males. Due to error distribution quasi-likelihood estimation method was used. The rationale for including occurrence of red-winged Blackbird in patches is explained in Chapter 3. Grazing intensity and interaction terms were not significant in models for 1995 and 1996.

YEAR 1997	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Intercept		73	34.45			-0.78	1.09
Area willow	0.73	72	33.72	2.42	0.124	0.33	0.14
Red-winged Blackbird	4.29	71	29.43	14.13	<0.001	-0.7	0.09
Grazing intensity	6.06	70	23.37	19.18	<0.001	0.81	0.35
Grazing intensity *Area willow	2.24	69	21.13	7.39	0.008	-0.12	0.05

Table 4.4. Logistic models for presence/absence of individual species in treed patches. Area of aspen and Area of willow were ln+1 transformed. Only significant models are presented.

Predictor	B (SE)	Wald	P	R
House Wren (1995)				
Constant	-4.26 (1.03)	17.21	<0.001	
Area aspen	0.57 (0.14)	17.37	<0.001	0.28
	X^2	DF	Significance	
Model X^2	38.35	1	<0.001	
Improvement last variable	38.35	1	<0.001	
Goodness of fit	124.3	141	0.90<P<0.75	
Cases correctly classified	Obs. 0 = 72.6 %	Obs. 1 = 69.5 %	Overall = 71.3 %	
House Wren (1997)	B (SE)	Wald	P	R
Constant	-1.74 (0.79)	4.93	0.026	
Area aspen	0.30 (0.08)	14.87	<0.001	0.25
Grass	0.04 (0.18)	4.83	0.028	0.12
Grazing intensity	-0.56 (0.20)	8.12	0.004	-0.17
	X^2	DF	Significance	
Model X^2	35.54	3	<0.001	
Improvement last variable	5.04	1	0.015	
Goodness of fit	149.54	151	0.25<P<0.50	
Cases correctly classified	Obs. 0 = 82.3 %	Obs. 1 = 45.8 %	Overall = 68.4 %	

Least Flycatcher (1995)	B (SE)	Wald	P	R
Constant	-2.77 (0.02)	26.60	<0.001	0.37
Area aspen	NS	NS	0.08	0.07
Grazing intensity	NS	NS	0.31	0.00
Area aspen*grazing intensity	0.12 (0.02)	26.60	<0.001	0.37
	X^2	DF	Significance	
Model X^2	36.95	3	<0.001	
Improvement last variable	36.95	1	<0.001	
Goodness of fit	139.79	140	0.50<P<0.75	
Cases correctly classified	Obs. 0 = 86.5 %	Obs. 1 = 53.2 %	Overall = 75.5 %	

Least Flycatcher (1997)	B (SE)	Wald	P	R
Constant	-2.43 (0.77)	10.07	0.002	
Area aspen	0.36 (0.10)	13.56	<0.001	0.24
#Total shrubs	-0.04 (0.01)	9.36	0.002	-0.19
#Total saplings	0.08 (0.03)	6.26	0.012	0.14
	X^2	DF	Significance	
Model X^2	46.86	3	<0.001	
Improvement last variable	6.86	1	0.008	
Goodness of fit	153.40	151	0.10<P<0.25	
Cases correctly classified	Obs. 0 = 78.3 %	Obs. 1 = 63.8 %	Overall = 72.9 %	

Table 4.5. Generalized linear models (stepwise procedure) for species abundance in treed patches. Parameters were estimated with quasi-likelihood method. Area willow and Area aspen were ln+1 transformed.

	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Clay-colored Sparrow (1995)							
Intercept	73.92	55				-2.45	-2.32
Area willow	64.41	54	9.51	12.25	<0.001	0.40	0.14
# Total saplings	53.09	53	11.32	14.58	<0.001	0.03	0.01
Clay-colored Sparrow (1996)							
Intercept	287.19	151				-0.01	0.21
Area willow	264.12	150	23.07	15.86	<0.001	0.09	0.03
#Saskatoon	240.19	149	23.93	16.45	<0.001	-0.15	0.05
Clay-colored Sparrow (1997)							
Intercept	270.75	152				-0.36	0.42
Area willow	255.78	151	14.97	11.91	<0.001	0.09	0.05
Area aspen	225.25	150	30.53	24.28	<0.001	0.13	0.03
#Total shrubs	213.08	149	12.17	9.68	0.002	-0.02	0.01
Grazing intensity	207.48	148	5.60	4.45	0.037	-0.15	0.07
Brown-headed Cowbird (1996)							
Intercept	269.17	121				-3.01	0.68
Area aspen	249.84	120	19.34	10.69	0.001	0.13	0.06
#Saskatoon	223.58	119	26.25	14.51	<0.001	-0.48	0.20
Arthropod biomass in willow patches	207.88	118	15.70	8.68	0.004	0.01	0.00
# Total saplings	200.62	117	7.26	4.01	0.048	0.01	0.03
Grazing intensity	180.97	116	19.65	10.86	0.001	0.50	0.15

	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Brown-headed Cowbird (1997)							
Intercept	292.47	159				-5.02	1.14
Area willow	244.03	158	48.44	29.24	<0.001	0.62	0.14
#Total shrubs	228.78	157	15.25	9.21	0.003	-0.03	0.01
#Total saplings	210.34	156	18.44	11.13	0.001	0.06	0.17
Least Flycatcher (1995)							
Intercept	98.93	55				-5.29	1.11
Area aspen	71.01	54	27.92	29.98	<0.001	0.42	0.13
#Total saplings	66.64	53	4.37	4.70	0.035	-0.01	0.01
Grazing intensity	43.27	52	23.37	25.10	<0.001	0.73	0.15
Least Flycatcher (1996)							
Intercept	233.97	151				-5.14	0.87
Area aspen	165.75	150	68.21	46.79	<0.001	0.39	0.10
#Saskatoon	158.58	149	7.17	4.92	0.028	-0.23	0.11
#Total saplings	147.17	148	11.40	7.82	0.006	0.02	0.02
Grazing intensity	118.18	147	28.99	19.89	<0.001	0.64	0.15
Least Flycatcher (1997)							
Intercept	238.49	152				-10.81	2.84
Area willow	229.62	151	8.87	7.47	0.007	0.00	0.06
Area aspen	162.96	150	66.66	56.11	<0.001	1.31	0.35
#Total shrubs	151.53	149	11.43	9.62	0.002	-0.02	0.01
Grazing intensity	144.11	148	7.42	6.25	0.013	2.38	0.82
Grazing intensity *Area aspen	135.97	147	8.14	6.86	0.010	-0.26	0.10

Table 4.6. Generalized linear models (stepwise procedure) for total number of species and individuals in treed patches. Parameters were estimated with quasi- likelihood method. Area willow and Area aspen were ln+1 transformed.

	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Total number of species (1995)							
Intercept	306.45	142				-0.39	0.20
Area aspen	218.40	141	88.02	73.7	<0.000	0.17	0.03
Area willow	199.05	140	19.37	16.22	<0.001	0.08	0.02
Total number of species (1996)							
Intercept	554.31	151				0.31	0.22
Area aspen	452.04	150	102.27	44.83	<0.001	0.16	0.03
#Saskatoon	394.52	149	57.51	25.21	<0.001	-0.18	0.05
Total number of species (1997)							
Intercept	552.32	152				1.34	0.56
Area willow	536.33	151	15.99	6.92	0.009	0.04	0.04
Area aspen	427.13	150	109.20	47.29	<0.001	0.02	0.07
#Total shrubs	408.95	149	18.18	7.88	0.006	-0.01	0.01
Grazing intensity	405.01	148	3.94	1.71	0.19	-0.60	0.23
Grazing intensity *Area aspen	391.71	147	13.30	5.76	0.018	0.07	0.31

	Residual deviance	DF	Change in deviance	F	P	Parameter estimate	SE
Total number of individuals (1995)							
Intercept	574.65	142				-1.57	0.25
Area aspen	374.24	141	200.41	97.08	<0.001	6.42	0.03
Area willow	332.04	140	42.20	20.44	<0.001	3.21	0.02
#Total saplings	309.51	139	22.53	10.91	<0.001	3.45	0.01
Total number of individuals (1996)							
Intercept	1034.6	151				0.47	0.28
Area aspen	819.1	150	215.60	44.15	<0.001	0.17	0.04
#Saskatoon	734.0	149	85.02	17.41	<0.001	-0.17	0.06
#Total saplings	711.3	148	22.70	4.65	0.033	0.033	0.02
Total number of individuals (1997)							
Intercept	950.83	152				1.45	0.66
Area willow	881.92	151	68.91	16.90	<0.001	0.09	0.05
Area aspen	687.24	150	194.68	47.74	<0.001	-0.001	0.08
#Total shrubs	649.44	149	37.80	9.27	0.003	-0.01	0.01
#Total saplings	633.24	148	16.19	3.97	0.048	0.023	0.01
Grazing intensity	629.86	147	3.39	0.83	0.36	-0.746	0.28
Grazing intensity *Area aspen	602.05	146	27.80	6.82	0.01	0.09	0.04

Table 4.7. Effect of grazing on theYellow Warbler, on the distribution and abundance of other songbird species, and on community composition. Significance value in multivariate models is shown. P values are reported for significant years, in chronological order.

YEAR	1995	1996	1997	P value
Yellow Warbler				
Territory occupancy	ns	ns	ns	
Chronological order of territory occupancy by males	ns	ns	U, L earlier than H, M	<0.001
Chronological order of territory occupancy by females	ns	ns	U, L earlier than M	<0.001
Number of chicks/nest (successful nests)	ns	ns	ns	
Number of chicks/nests (including unsuccessful nests)	ns	ns	U > H, M	0.058
Chicks growth	--	ns	ns	
Predation at the nests	ns	ns	U < others	0.028
Cowbird parasitism at the nests	--	L, H < U	ns	0.002
Proportion of patches occupied by an individual species				
Black-capped Chickadee	ns	ns	ns	
Least Flycatcher	M < U	M < U	ns	<0.001 0.004
House Wren	ns	ns	L, U < H, M	0.004
American Robin	ns	ns	ns	
Red-eyed Vireo	ns	M < others	ns	0.040
Red-winged Blackbird	H < others	H < others	H, M < L, U	0.030 0.028 <0.001
Vesper Sparrow	ns	L, U < H, M	L, U < H, M	<0.001 <0.001
Savannah Sparrow	ns	ns	ns	

YEAR	1995	1996	1997	P value
Chipping Sparrow	ns	ns	ns	
Clay-colored Sparrow	ns	L < M	L < M	<0.001 <0.001
Dark-eyed Junco	ns	ns	ns	
Brown-headed Cowbird	ns	ns	ns	
Species abundance				
Least Flycatcher	M < U	M < U	ns	<0.001 <0.001
Clay-colored Sparrow	ns	ns	L < M	0.037
Brown-headed Cowbird	ns	H < others	ns	<0.001
Species richness and total abundance				
Total number of species in patches	ns	ns	ns	0.060
Total number of individuals in patches	ns	ns	L < U	0.018

Note: U = ungrazed, L = light, H = heavy, M = moderate (summer) grazing.

Table 4.8. Summary of effect of cattle grazing on bird species in relation to foraging guild, nest type and location.

Bird Species	Nest location †	Foraging guild ‡	Nest type	Effect of grazing §
Least Flycatcher	Bushes/trees (a,w)	AI	open	-
Black-capped Chickadee	Trees (a,w)	BI	cavity	ns
House Wren	Trees (a)	FI	cavity	+
American Robin	Bushes/trees (a,w)	GI	open	ns
Red-eyed Vireo	Trees (a)	FI	open	-
Yellow Warbler	Bushes (w)	FI	open	-
Vesper Sparrow	Ground (g)	OM	open	+
Savannah Sparrow	Ground (g,w)	OM	open	ns
Chipping Sparrow	Bushes/trees (a)	OM	open	ns
Clay-colored Sparrow	Ground/shrubs (g,w)	OM	open	+
Dark-eyed Junco	Ground (g,w,a)	OM	open	ns
Red-winged Blackbird	Cattail (p)	OM	open	-
Brown-headed Cowbird	------	GI	----	-

† (a) = aspen patches, (w) = willow patches, (g) = grassland, (p) = pond

‡ AI = aerial insectivore; BI = bark insectivore; FI = foliage insectivore; GI = ground insectivore; OM = Omnivore (based on Saab *et al.* 1995).

§ (+) = probability of occurrence and/or abundance increased with increased grazing intensity; (-) = probability of occurrence and/or abundance decreased with increased grazing intensity. (ns) = not affected by grazing.

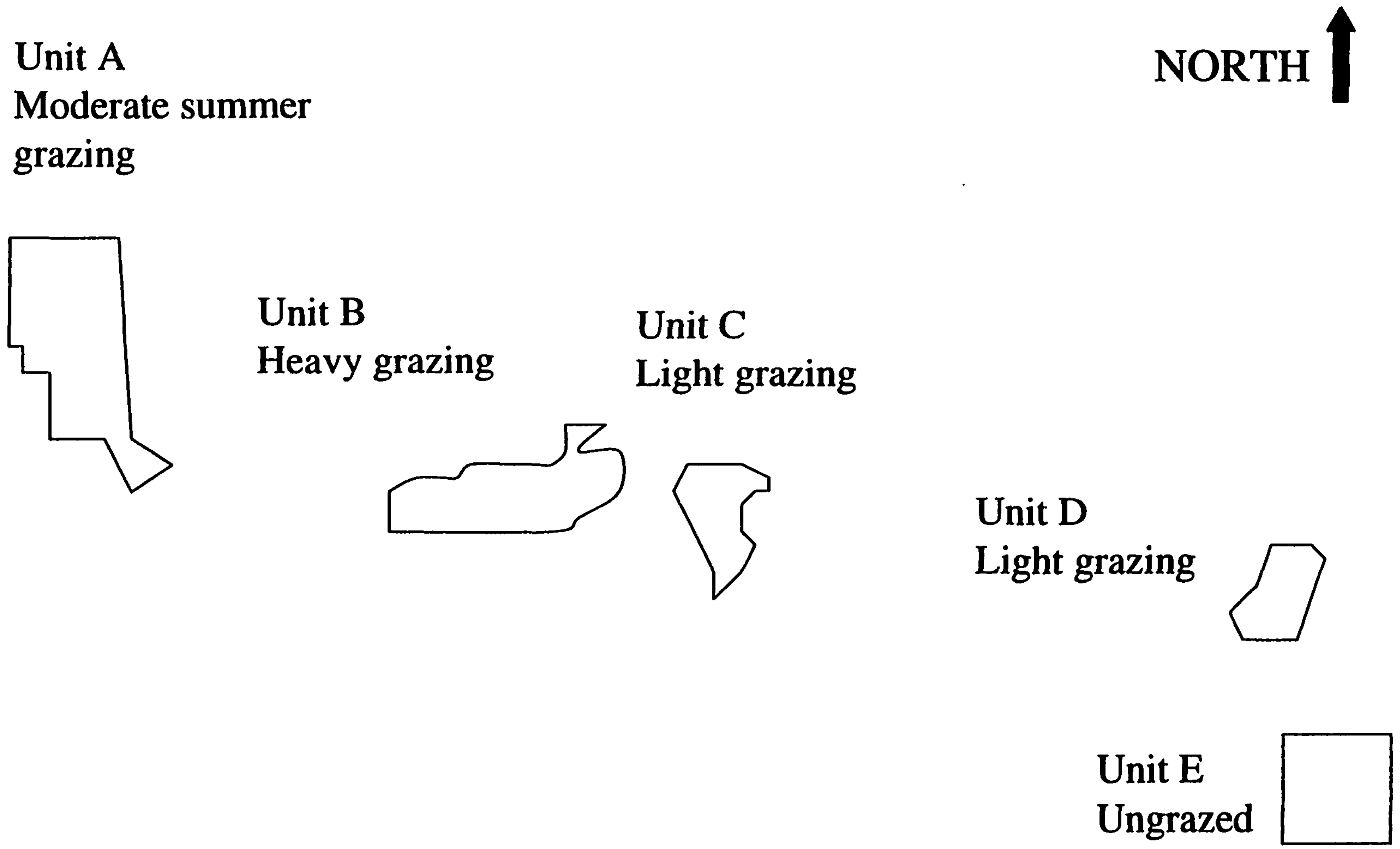

Fig 4.1. The five study units

Chapter 5. Conclusions. Territory choice and quality: spatial structure of territory and social factors do matter.

This study analyzed the effects of several factors on territory choice and quality in the Yellow Warbler in a naturally patchy landscape. These included: **1.** territory features such as spatial structure, vegetation structure and prey abundance, **2.** social factors such as the presence of the Red-winged Blackbird and territorial conspecifics in or adjacent to the territory, **3.** the vegetation and spatial structure at the nesting site, **4.** the spatial structure of the landscape surrounding the territories, **5.** the geographic position of the territory and **6.** the impact of cattle grazing.

Territory occupancy (territory occupied/unoccupied) and territory choice by the Yellow Warbler were mainly affected by the spatial structure of the territories: territories consisting of larger willow patches, in willow patches with higher perimeter to $\sqrt{}$area ratio, and with higher "Amount of willow within 50 m" from the territory center were more likely to be occupied. Territories situated in larger patches of willow were occupied earlier by Yellow Warbler males and females. Social factors (i.e. occurrence of Red-winged Blackbirds and of territorial conspecifics) were not analyzed in relation to territory occupancy.

Overall, territories situated in patches where Red-winged Blackbirds occurred were occupied earlier by Yellow Warbler males and females. Presence of territorial conspecifics in a patch also favoured earlier occupancy. However, spatial structure had a much stronger effect than social factors, as measured by proportion of deviance explained in the models. Grazing did modify the vegetation structure in willow and aspen patches and was positively correlated with arthropod abundance and biomass. A lack of grazing may be responsible for the larger size of aspen patches in the ungrazed zone. However, territory occupancy by the Yellow Warbler was not affected by cattle grazing. In 1997, territories situated in the ungrazed and lightly grazed units were occupied earlier by Yellow Warbler males and females than territories situated in the moderately and heavily grazed units. However, the effect of grazing and Area of willow, could not be disentangled. Among the other songbird species considered, the only species that bred on the ponds (i.e. the Red-winged Blackbird) was more severely impacted by grazing than the species inhabiting the treed patches. Overall, cattle grazing did not modify territory attractiveness and quality for the Yellow Warbler. However, these results should not be extrapolated to other study areas given the generally good range conditions of my study area (see Chapter 4).

Territory occupancy and choice were only marginally affected by the territory features traditionally considered in other studies (i.e. vegetation structure, food abundance and characteristics of the nesting sites). No descriptor of vegetation structure at the territory scale was consistently significant over years and the proportion of deviance explained by the descriptors of vegetation structure was always much lower than the proportion explained by the descriptors of spatial structure. Arthropod abundance and biomass did not affect territory occupancy and choice during the three years covered by this study. However, arthropods may become limiting during rearing of chicks if harsher conditions occur (e.g. Rodenhouse and Holmes 1992). When they settle, Yellow Warblers may use the size of the willow patches as a cue to assess arthropod abundance during brood rearing, since "Area of willow" and arthropod abundance/biomass were consistently and positively correlated over years.

In conclusion, territories were mainly chosen based on the territory features neglected in previous studies, i.e. spatial structure and social factors. I conclude that the spatial structure of territory is an important component of territory attractiveness and social factors can modify the intrinsic territory attractiveness and quality. Therefore, spatial structure and social factors should be included in the measure of "patch/territory suitability" in conceptual habitat selection models such as the Ideal Free Distribution and Ideal Despotic Distribution (Fretwell and Lucas 1970).

Despite the fact that the descriptors of spatial structure of the territory explained a larger proportion of deviance in models for territory occupancy and choice than social factors, the occurrence of Red-winged Blackbirds in patches was the only variable that affected some of the components of breeding success in the Yellow Warbler: rates of predation and Cowbird parasitism at Yellow Warbler nests were lowered by the occurrence of Red-winged Blackbirds in patches. It appears that the descriptors explaining a small amount of deviance in models for territory choice can be important indicators of territory quality. However, it remains uncertain if the overall fitness of the territory holder was also increased by the occurrence of Red-winged Blackbirds in the patches. In one year, the rate of predation was lower at Yellow Warbler nests situated in the ungrazed unit than in the other units. However, the overall effect of grazing on Yellow Warbler breeding success was marginal. A last territory feature typically considered is "availability and characteristics of the nesting sites". Vegetation structure, species of willow supporting the nest, nest placement and concealment, distance of the nest from different types of edges (pond/willow, willow/aspen, willow/grassland) did not affect chronological order of territory occupancy by Yellow Warbler males and females and any of the measured components of Yellow Warbler breeding success. Nests were surrounded by larger amounts of willow within 5 m than random points and it is possible that some willow patches remained unoccupied because their width was < 5 m at any point. However, in general the characteristics measured at the nest site scale had little influence on territory choice and quality.

It remains uncertain if the spatial structure of the landscape surrounding the territory was important. However, no individual predictor of landscape composition or configuration emerged as being constantly significant over years, and the number of Red-winged Blackbirds occurring around the territory (landscape scale) was of little importance. Although in 1997 chronological order of territory occupancy by Yellow Warbler males and females was affected by the geographic position of the territory, the factor(s) responsible for this pattern remain(s) unidentified. Given the geographic position of the study units with different grazing intensity, grazing may be responsible for the observed pattern, but it remains to be explained why geographic position was significant in one year only. Therefore, the effects of grazing and geographic position cannot be separated.

Overall, in this naturally patchy landscape the strongest effects on territory choice and breeding success in the Yellow Warbler were detected at the territory scale.

A greater importance of landscape spatial structure in affecting bird distribution and breeding success might be expected in landscapes where spatial variation in habitat structure and configuration is larger that at Rumsey. This may be the case for many human fragmented landscapes (see Mazerolle and Villard 1999 for a review). Alternatively, the lack of independence between landscape circles may be responsible for these findings. Thus, despite the lack of importance of the nest-site and landscape scale in my study, multiple spatial scales should be considered in future studies.

In a seminal paper Cody (1985) pointed out the complexity of the process of habitat selection, the multitude of factors that could affect it and the implications for the fitness of the individuals that choose certain habitat types over others. In particular, Cody (1985) listed food availability, nesting opportunities, structural features of the landscape and presence of other species as central to the process of habitat selection. The idea of a hierarchical system of sequential decisions was also presented in his paper.

Although the theory of habitat selection (Hildén 1965, Cody 1985) has been central to community and population ecology for the last 35 years, studies that have considered multiple proximate factors that affect birds' choices are rare (e.g., Petit and Petit 1996). There has been a tendency to concentrate on one or few descriptors of the habitat that had been targeted as critical *a priori*. Typically, vegetation structure (e.g., Smith and Shugart 1987), food availability (e.g. Verner 1964), characteristics of nesting sites (Petit et al. 1988) have monopolized the attention of researchers. Furthermore, three important aspects have been neglected by most of the previous studies on territory choice and quality: **1.** the spatial structure of the territory, **2.** interspecific social interactions and **3.** the spatial scale. My results show that it was important to consider these components, and more generally, the necessity of considering the role of multiple aspects (territory features, social factors, spatial scale, human disturbance) when attempting to measure territory attractiveness and quality.

FUTURE RESEARCH

Territory spatial structure and social factors should be considered in future studies on territory choice and quality. Physical characteristics of the study area (e.g, landscape composition and configuration), behavioral and physiological characteristics of the subject species (e.g., mobility and dependance on one or more habitat types) are two of the factors that may determine whether spatial structure of territory and social factors will be important. For example, spatial structure of habitat may become more important as the patches of suitable habitat get smaller in size and more sparsely distributed. Of couse, different species will react (or not react) in different ways to these different situations. Given the poor predictive power of my models when tested on another similar landscape, a great deal of variation in the importance of these factors among landscapes and species should be expected. I briefly outline below some of the points that future research on territory choice and quality should address.

1. Investigate the role of spatial structure of habitat at different spatial scales in human-modified landscapes. I predict that the spatial structure of the landscape surrounding the territory will be more important in landscapes where larger spatial variation in composition and configuration occurs.

2. Similar to what I did in my study, compare landscapes that contain the same habitat types but have different composition and spatial configuration. I emphasize the importance of testing predictive models on different study areas. This has seldom been done in landscape ecological studies. If models are found to have low predictive power when tested on other areas the reason(s) for this should be explored. Critical thresholds in landscape composition and configuration (e.g., Andrén 1994, Fahrig 1997) may become apparent using this approach.

3. Investigate the importance of spatial structure of habitat to species that do not use the landscape as a binary landscape (suitable or unsuitable habitat types), but rather as a mosaic of suitable patches of different quality. In particular, juxtaposition of patches of different habitat types maybe important for species that require different habitat types for different activities (e.g. feeding habitat is different from nesting habitat).

4. Measure the effects of the spatial structure of the territory on the economics of territorial defence (Brown 1964), in terms of time and energy spent patrolling territorial borders (metabolic costs) or defending the territory from intruders (Gibb, 1956; Ewald *et al.*, 1980).

5. Specifically for the Yellow Warbler, investigate other possible interspecific interactions. I repeatedly observed Least Flycatchers chasing away Yellow Warbler males. It seems likely that Least Flycatchers are dominant over Yellow Warblers. Since Least Flycatcher occur mainly in aspen patches, it is questionable whether it is always advantageous to Yellow Warblers to include aspen patches in their territories. For example, if the density of Least Flycatchers is high Yellow Warbler territories close to aspen patches may become suboptimal.

6. Study the effects of conspecific and interspecific attraction at the landscape spatial scale, i.e. does density of territorial conspecifics around the patch affect territory choice and quality (Lima and Zollner 1996) ? In naturally patchy or human fragmented landscapes spatial structure and social factors may act in synergy. For example, at the landscape scale, among other factors, the position and size of a patch of a certain habitat type will determine the probability of recolonization of that patch (e.g., Fahrig and Merriam 1995). Therefore, patches more isolated and smaller in size may be more frequently unoccupied. This effect may be exacerbated by the absence of conspecifics in these patches and in the surroundings (Smith and Peacock 1990, Reed and Dobson 1993). The same argument can be used with regard to the presence of other species that increase the patch quality (e.g., Red-winged Blackbird for the Yellow Warbler) if they have similar habitat requirements.

7. Extra-pair copulations occur in the Yellow Warbler (Yezerinac et al. 1995). Spatial structure of the territory and occurrence of territorial conspecifics in the same patch may affect the probability that extra-pair copulations occur and consequently may affect individual fitness (Davies 1991).

IMPLICATIONS FOR SPECIES CONSERVATION

My results show that conservation of large patches of habitat that include ponds may be important to attract potential breeders. In Canada the currently proposed legislation on federal endangered species focuses on conservation of nest sites. My study suggests that protecting nest sites will not conserve the Yellow Warbler. Moreover, the positive effects of Red-winged Blackbird presence in patches on the Yellow Warbler suggests the need to establish strategies to protect species assemblages rather than individual species, to ensure persistence of beneficial inter-specific interactions.

This study did not address directly if and how the matrix (i.e. grassland) quality affected territory choice and fitness of the territory holder in the Yellow Warbler. However, when comparing Rumsey Ecological Reserve to human-fragmented landscapes some potential adverse effects that were likely absent in my study area should be considered for the latter. For example if roads and urbanized areas are present in the matrix, direct mortality by traffic and clumping of predators (e.g. feral cats and dogs) may occur. This may potentially increase the importance of some descriptors of spatial structure of territories (i.e. patch isolation) to territory choice and quality.

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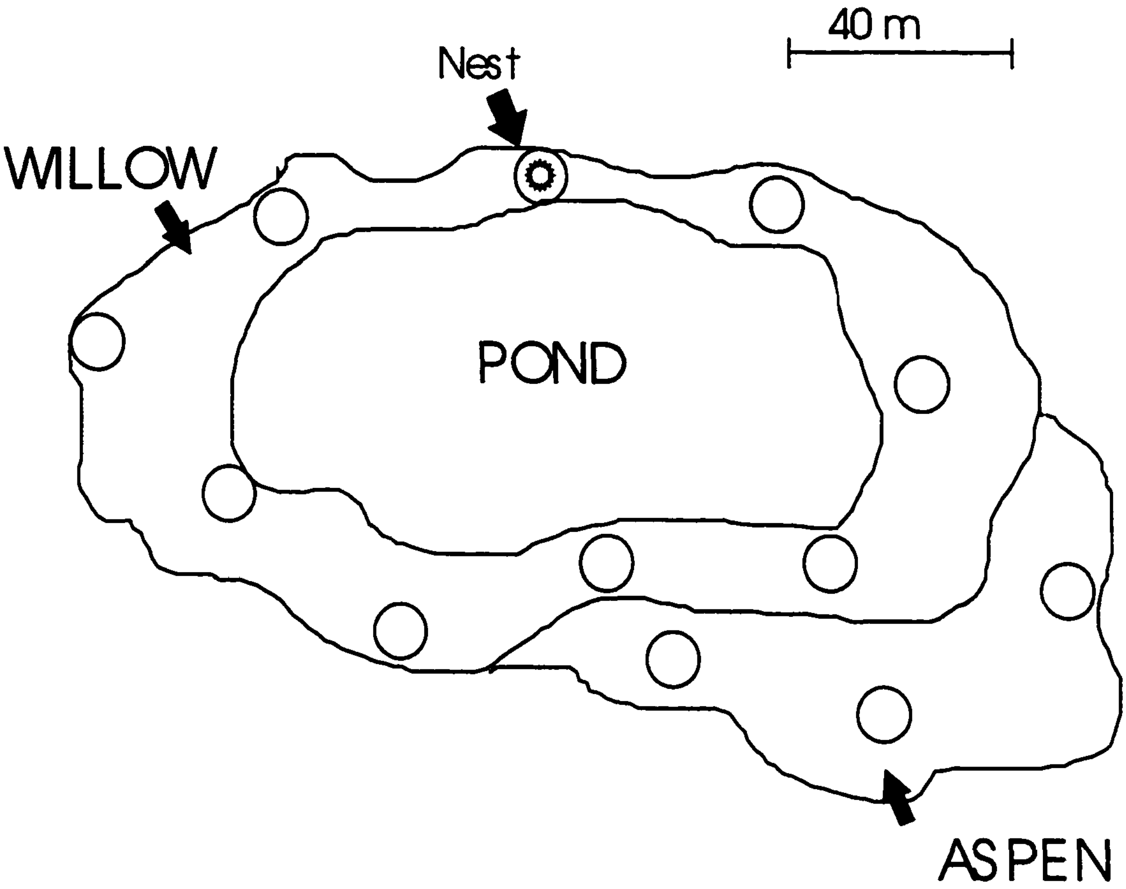
Appendices

Appendix 2.1. Correlations between arthropod abundance (number of individuals) sampled in willow patches by sweep-netting and beat-netting methods. The correlation for total dried biomass is also shown. Data for Diptera: Culicidae were not analyzed because they were almost absent in beat-netting samples. Only data for Homoptera were available for the beat-netting method during rearing. Settlement = sampled during the settlement of Yellow Warbler males in territories. Rearing = sampled during rearing of chicks. Spearman rank correlation coefficient (one -tailed test) was used, unless indicated otherwise.

	Settlement			**Rearing**		
Arthropod taxon	R	N	Sign.	R	N	Sign.
Total arthropod abundance	0.33	24	0.060			
Total biomass of arthropods	0.47	24	0.010			
Diptera: Chironomidae	0.62	26	< 0.001			
Homoptera: Cicadellidae	0.43†	26	0.014	0.66	11	0.013
Lepidoptera: Geometridae	0.08	26	0.344			

† Pearson product correlation coefficient (one-tailed test)



Appendix 2.2. Vegetation sampling design. Willow and aspen patches were sampled as independent units. In both willow and aspen patches the center of each plot was located 40 m away from the center of the nearest plot(s), in a randomly selected direction. A sample plot was a 5 m radius circle. If a nest was present in the willow patch, the first plot was centered on the nest.

Appendix 2.3. Technical aspects of latent root regression analysis.

Because variables had been measured in different units, latent root regressions were run on a correlation matrix. Variables were ln + 1 transformed to approach normality when necessary. Variables expressed in percentages were arcsin$\sqrt{p}$ (where p is a proportion) transformed. Although principal component analysis is known to be robust to non-normality (Ibanez 1971), the presence of variables with many zero values or a strongly skewed distribution may heavily affect this technique by causing the first axis to separate a few objects with extreme values from the other objectes (e.g., Legendre 1998). For this reason #Balsam saplings was excluded from the ordination in 1995, #Saskatoon, #Gooseberry, and Tall stratum in 1996, #Raspberry in 1995 and 1996, and Low stratum in 1996 and 1997. Varimax rotation, which minimizes the number of variables that have a high loading on each factor was used (Pielou 1984). Following Jolliffe (1986), for each axis the variable with the highest loading was selected. The number of axes retained in the analysis was based on a scree plot, (value of each successive eigenvalue against rank order). The axis on which eigenvalues were small and fell along a straight line on the scree plot were considered trivial, except for the first two points on the straight line (Cattell and Vogelmann 1977). However, variables with high loading on predictive multicollinearities (axis explaining little variance but on which dependent variable has high loading) were retained in the analysis (see Appendix 2.3a, 2.3b, 2.3c, and 2.3d for detailed analysis). When two or more variables had a similar loading on a particular component, variable selection was based on their correlation with the dependent variable (Jolliffe 1986), unless one of the variables was thought to be of more general biological meaning (*e.g.* total number of willow stems was selected over number of dry willow stems). Separate analyses were run for vegetation structure and spatial structure. For vegetation structure, the analysis was repeated for each year. Chronological order of occupancy by males was used as dependent variable. Analyses performed successively on other dependent variables (chronological order of arrival by females and several measures of breeding success) did not result in the selection of more predictor variables. Vegetation structure variables, that in none of the three years were selected as principal variables, were excluded from subsequent analysis. Since the main interest was in consistency of significance of predictors over years, all the other variables were retained. When variables that were selected in latent root regressions in different years co-existed in a multivariate model, it was necessary to check for multicollinearity. This problem never materialized in this study. Since no descriptor of vegetation density (Table 1) had been selected by latent root regressions, I decided to select foliage density as it had higher loadings on the first component than the other three descriptors in that group over three years (Canopy cover, Tall stratum, Low stratum) (see Appendixes 2.3a, 2.3b, and 2.3c).

Appendix 3a. Latent root regression for vegetation structure variables in 1995. Loadings were obtained using Varimax rotation. Variables describing *Salix bebbiana* and *S. petiolaris* were lumped for this year (B+P). Two variables (#Raspberry, and #Balsam saplings) were excluded from the analysis because of their highly skewed distribution. Variables selected (Principal Variables) are underlined. Loadings of dependent variable are shown in bold.

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
% Variance explained	23.1	18.6	9.9	9.0	6.7	5.6	4.7	4.6	3.4	2.6
Eigenvalues	9.95	8.01	4.24	3.88	2.89	2.42	2.01	1.98	1.45	1.10
Male arrival	**0.12**	**-0.29**	**-0.24**	**-0.05**	**-0.21**	**0.10**	**0.47**	**-0.43**	**-0.09**	**0.26**
Allgreen	0.18	0.20	0.86	0.16	-0.01	0.05	0.02	-0.31	0.14	0.01
Grass	0.78	0.17	0.14	0.22	-0.09	0.27	-0.42	-0.36	0.08	0.07
Shrub	-0.32	-0.27	0.25	-0.10	0.75	-0.07	-0.84	-0.02	0.12	0.07
Forb	-0.52	0.16	0.75	-0.02	-0.18	-0.21	0.09	0.27	0.54	0.08
Leaf litter	-0.19	-0.19	-0.77	-0.18	0.37	-0.01	0.03	0.32	-0.22	-0.12
Bare ground	-0.28	-0.09	-0.54	-0.02	-0.11	-0.20	-0.15	0.26	0.25	0.48
Litter depth	-0.32	-0.34	-0.66	-0.19	0.01	-0.06	-0.35	-0.07	-0.22	0.23
#Total shrubs	-0.21	-0.36	-0.15	-0.03	0.75	-0.20	-0.22	0.11	0.11	0.23
#Rose	-0.38	-0.26	0.05	-0.22	0.27	-0.18	-0.30	0.23	0.15	0.39
#Saskatoon	0.01	-0.43	-0.24	-0.01	0.76	-0.19	-0.19	0.01	-0.04	-0.06
#Buckbrush	-0.37	0.31	0.36	0.14	-0.01	-0.12	0.05	0.24	0.23	0.38
#Gooseberry	0.13	-0.20	-0.62	-0.01	-0.15	0.01	0.28	-0.28	0.25	0.01
#Aspen shrubs	-0.03	-0.24	-0.18	-0.08	-0.13	-0.12	-0.08	0.10	-0.71	0.01
#Willow shrubs	0.40	-0.6	0.06	0.13	0.72	0.24	-0.15	-0.04	0.11	-0.22
#Aspen saplings	-0.03	-0.16	-0.14	-0.01	0.03	-0.21	0.01	0.89	-0.07	0.10
#Aspen poles	0.68	0.03	0.01	0.47	0.10	0.07	0.16	0.18	-0.35	0.06
#Balsam poles	-0.13	-0.15	-0.02	-0.08	-0.16	0.88	-0.13	-0.02	-0.04	-0.15

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
#Total saplings	-0.11	0.23	-0.14	-0.09	-0.07	0.34	-0.11	0.80	-0.05	0.07
#Total poles	0.47	-0.08	-0.01	0.33	-0.03	0.69	0.05	0.13	-0.32	-0.06
Willow height	-0.88	0.08	0.26	0.17	-0.07	-0.10	0.03	0.01	-0.20	0.18
Green stems small b+p	0.95	0.09	0.14	-0.14	-0.05	-0.06	0.01	-0.02	0.03	-0.07
Green stems big b+p	-0.12	0.88	0.14	0.18	-0.09	-0.02	-0.04	-0.06	0.23	-0.19
Dry stems small b+p	0.90	0.10	-0.01	-0.09	-0.16	-0.09	0.10	-0.16	-0.06	0.10
Dry stems big b+p	-0.08	0.75	0.22	0.03	-0.20	-0.18	0.25	-0.09	-0.12	0.37
Total stems small b+p	0.95	0.10	0.09	-0.12	-0.09	-0.07	0.04	-0.07	0.01	-0.02
Total stems big b+p	-0.12	0.93	0.19	0.14	-0.14	-0.09	0.07	-0.08	0.12	0.01
Green stems willow	0.35	0.78	0.10	0.05	-0.13	-0.09	-0.05	-0.02	0.32	-0.23
Dry stems willow	0.33	0.69	0.16	-0.28	0.26	-0.23	0.27	-0.13	-0.10	0.37
Total stems willow	0.37	0.85	0.21	0.06	-0.17	-0.11	0.08	-0.10	0.10	-0.01
Willow distance	-0.29	-0.01	0.60	0.60	0.01	-0.24	-0.01	0.03	-0.01	0.19
Foliage density	0.27	0.19	0.03	0.21	0.26	-0.28	-0.20	0.03	0.60	0.17
Canopy cover	-0.42	0.16	0.03	-0.13	0.53	-0.05	0.01	0.54	0.10	-0.19
Tall stratum	-0.74	-0.03	0.12	0.35	-0.57	0.08	-0.17	-0.02	-0.39	0.21
Low stratum	0.01	-0.21	-0.65	0.01	0.01	0.18	-0.18	-0.29	-0.60	-0.09
#Aspen trees	0.05	0.24	0.12	0.07	-0.19	-0.17	0.85	0.01	0.02	-0.06
#Balsam trees	0.02	-0.19	-0.11	-0.12	0.04	0.80	0.35	-0.07	0.10	0.08
# Total trees	0.04	0.09	0.04	-0.01	-0.14	0.27	0.91	-0.45	0.05	-0.01
Aspen height	-0.32	-0.01	0.33	0.73	-0.20	0.07	0.17	0.04	0.29	-0.04
Tree height	-0.39	0.17	0.44	0.65	-0.22	-0.04	0.03	0.09	0.30	-0.06
Aspen dbh	0.01	0.16	0.01	0.96	0.05	-0.01	0.01	-0.09	0.03	-0.01
Tree dbh	-0.01	0.12	0.02	0.96	0.05	-0.05	-0.05	-0.11	-0.04	-0.02

Appendix 2.3b. Latent root regression for vegetation structure variables in 1996. Loadings were obtained using Varimax rotation. Five variables (#Raspberry, #Saskatoon, #Gooseberry, Tall stratum, Low stratum) were excluded from analysis because of their highly skewed distribution. Variables selected (Principal Variables) are underlined.

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
% Variance explained	19.2	14.5	11.8	10.9	8.7	7.8	4.2	4.0	3.5
Eigenvalues	8.64	6.50	5.33	4.92	3.91	3.53	1.90	1.82	1.58
Male arrival	**-0.22**	**-0.09**	**0.13**	**-0.06**	**-0.07**	**0.67**	**0.12**	**0.15**	**-0.06**
Allgreen	0.60	-0.07	-0.18	0.08	-0.20	0.08	-0.16	0.41	0.52
Grass	0.64	0.04	-0.18	0.16	0.10	0.12	-0.43	0.35	0.20
Shrub	0.46	0.23	0.17	-0.34	-0.32	0.28	-0.14	0.31	0.08
Forb	-0.11	-0.46	-0.28	0.15	-0.27	-0.20	0.35	0.05	0.43
Leaf litter	-0.77	-0.16	0.12	0.07	0.25	0.22	0.23	0.08	-0.18
Bare ground	0.44	0.07	0.01	-0.18	-0.20	-0.49	-0.20	-0.37	-0.28
Litter depth	-0.33	-0.42	0.34	-0.18	0.09	0.37	-0.03	0.18	-0.18
#Total shrubs	0.17	0.25	0.01	-0.70	-0.23	0.49	0.22	0.04	0.05
#Rose	-0.12	0.16	-0.16	-0.61	0.20	0.50	0.09	-0.17	0.12
#Buckbrush	0.26	0.08	0.07	-0.70	-0.26	0.48	0.16	0.11	0.12
#Aspen shrubs	-0.30	0.07	0.48	-0.47	0.12	-0.16	-0.07	-0.26	-0.02
#Willow shrubs	0.39	0.16	0.25	-0.14	-0.24	-0.57	0.02	0.51	-0.01
#Aspen saplings	-0.60	0.07	0.37	-0.17	0.22	-0.33	0.30	0.22	0.12
#Balsam saplings	0.13	-0.07	0.44	0.36	-0.54	-0.24	0.39	-0.06	0.04
#Aspen poles	-0.36	0.65	0.11	0.17	0.06	0.16	-0.15	0.31	-0.42
#Balsam poles	0.06	-0.24	0.44	0.53	-0.59	0.11	0.06	-0.16	0.07
#Total saplings	-0.45	0.02	0.55	0.04	-0.10	-0.41	0.46	0.16	0.12
#Total poles	-0.35	0.58	0.24	0.32	-0.11	0.19	-0.13	0.27	-0.40
Bebbiana height	-0.37	0.38	-0.15	0.39	0.31	-0.05	-0.29	0.20	0.36

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Petiolaris height	-0.67	-0.03	-0.43	0.31	0.28	0.04	0.09	0.07	0.20
Willow height	-0.72	0.16	-0.34	0.27	0.28	0.01	0.54	0.07	0.21
Green stems bebbiana	0.13	0.83	0.27	0.15	0.28	0.10	0.18	-0.06	0.10
Dry stems bebbiana	0.03	0.80	0.41	0.02	0.25	0.11	0.08	-0.16	0.12
Total stems bebbiana	0.07	0.83	0.36	0.08	0.26	0.11	0.12	-0.12	0.12
Green stems small petiolaris	0.48	0.64	-0.27	0.07	-0.30	-0.02	0.08	-0.04	-0.10
Green stems big petiolaris	0.71	-0.39	-0.02	0.23	0.34	-0.03	0.07	-0.03	-0.23
Dry stems small petiolaris	0.45	0.76	-0.16	0.06	-0.12	0.14	0.14	-0.09	0.11
Dry stems big petiolaris	0.44	-0.57	0.34	0.11	0.41	0.29	0.10	0.09	0.05
Total stems small petiolaris	0.48	0.70	-0.24	0.06	-0.24	0.04	0.10	-0.06	-0.03
Total stems big petiolaris	0.60	-0.55	0.23	0.17	0.42	0.19	0.10	0.05	-0.06
Green stems willow	0.81	0.06	0.03	0.27	0.33	-0.01	0.15	-0.05	-0.19
Dry stems willow	0.49	-0.26	0.47	0.12	0.48	0.34	0.14	0.04	0.10
Total stems willow	0.71†	-0.15	0.33	0.21	0.48	0.22	0.17	0.01	-0.02
Willow distance	0.29	-0.10	0.07	0.04	0.22	-0.16	-0.47	0.02	0.15
Foliage density	0.47	-0.16	0.36	-0.34	-0.22	0.05	-0.15	-0.30	0.12
Canopy cover	0.10	0.36	-0.13	0.51	0.28	0.31	0.06	-0.36	0.20
#Aspen trees	-0.56	0.06	0.20	0.46	-0.23	0.40	-0.25	0.15	0.05
#Balsam trees	0.10	-0.29	0.33	0.57	-0.47	0.23	-0.11	-0.27	-0.05
#Total trees	-0.43	-0.05	0.27	0.56	-0.34	0.40	-0.24	0.03	0.02
Aspen height	-0.44	-0.15	0.55	-0.47	0.11	0.02	-0.27	-0.20	0.13
Tree height	-0.45	-0.15	0.56	-0.46	0.10	0.03	-0.26	-0.20	0.14
Aspen dbh	0.13	0.31	0.78	0.03	0.11	-0.29	-0.14	0.15	0.11
Tree dbh	0.14	0.32	0.77	0.01	0.13	0.30	-0.14	0.16	0.11

† Total stems willow was selected over Green stems willow based on more general biological meaning and correlation between the two variables ($R = 0.80$, $p < 0.0001$; $n=182$; Pearson product-moment correlation coefficient).

Appendix 2.3c. Latent root regression for vegetation structure variables in 1997. Loadings are shown in table. Loadings were obtained using Varimax rotation. One variables (Low stratum) was excluded from analysis because of highly skewed distribution. Variables selected (Principal Variables) are underlined.

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
% Variance explained	25.1	17.6	16.9	12.1	8.5	6.4	4.8	4.1	2.8
Eigenvalues	12.6	8.78	8.47	6.04	4.24	3.18	2.41	2.05	1.42
Male arrival	**0.20**	**0.43**	**0.09**	**0.68**	**-0.45**	**0.18**	**-0.25**	**-0.06†**	**0.04†**
Allgreen	-0.67	-0.28	0.12	0.04	-0.42	-0.01	0.46	0.24	-0.09
Grass	0.28	-0.36	-0.09	0.67	-0.11	0.45	-0.31	-0.10	0.01
Shrub	-0.92	0.12	0.08	0.09	-0.04	0.14	0.18	0.13	0.19
Forb	-0.84	0.12	-0.20	0.19	-0.37	0.04	0.10	0.09	-0.17
Leaf litter	0.48	0.39	0.45	0.36	-0.14	-0.31	0.07	-0.41	0.01
Bare ground	0.21	0.44	-0.52	0.05	0.68	-0.07	0.03	0.10	-0.07
Litter depth	-0.67	0.34	0.21	0.25	0.09	-0.01	0.53	-0.04	-0.18
#Total shrubs	-0.89	0.19	0.26	0.23	0.03	0.02	0.15	0.08	0.14
#Rose	-0.68	0.40	0.36	0.21	0.05	-0.29	-0.02	0.33	0.11
#Saskatoon	0.34	0.11	-0.09	0.28	-0.33	-0.61	-0.07	-0.35	0.08
#Buckbrush	-0.93	0.04	0.17	0.15	-0.02	0.17	0.15	0.10	0.17
#Raspberry	-0.08	0.60	0.48	-0.06	0.53	-0.10	0.10	0.04	-0.30
#Gooseberry	-0.25	0.51	0.46	-0.10	0.56	-0.23	0.05	-0.05	-0.28
#Aspen	0.47	-0.02	0.23	0.12	-0.71	-0.24	-0.12	0.20	-0.27
#Willow	-0.37	-0.20	0.04	0.59	0.41	0.11	0.31	-0.36	0.03
#Aspen saplings	0.03	-0.39	0.42	0.64	0.01	-0.18	-0.08	0.39	0.22
#Balsam saplings	0.69	0.36	0.14	0.37	-0.17	0.41	0.15	-0.06	0.01
#Aspen poles	0.13	0.54	0.62	0.12	0.35	-0.35	-0.19	0.07	-0.06
#Balsam poles	0.59	0.33	0.08	0.31	-0.05	0.57	0.31	0.08	-0.05
#Total saplings	0.28	-0.20	0.46	0.72	-0.03	-0.02	-0.01	0.34	0.19
#Total poles	0.25	0.59	0.61	0.18	0.33	-0.22	-0.12	0.08	-0.06

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Bebbiana height	0.60	0.61	0.11	-0.07	-0.28	-0.14	0.02	-0.28	0.11
Petiolaris height	0.69	0.38	0.52	-0.03	0.16	0.13	0.06	0.08	0.19
Willow height	0.64	0.52	0.48	-0.12	0.11	0.09	-0.02	0.06	0.24
Green stems bebbiana	-0.62	0.54	0.10	-0.43	-0.20	0.29	-0.05	-0.02	-0.02
Dry stems bebbiana	-0.42	0.61	0.24	-0.57	-0.12	0.12	-0.13	-0.05	0.11
Total stems bebbiana	-0.42	0.60	0.24	-0.57	-0.13	0.13	-0.13	-0.05	0.12
Green stems small petiol.	-0.16	-0.01	-0.72	0.30	0.18	-0.32	0.45	-0.18	-0.17
Green stems big petiolaris	0.19	-0.12	-0.86	0.21	0.23	-0.07	0.09	0.25	0.17
Dry stems small petiolaris	0.23	0.29	-0.27	0.16	-0.33	0.42	-0.15	0.27	-0.59
Dry stems big petiolaris	0.72	0.37	-0.49	0.05	0.06	-0.18	0.12	0.18	-0.11
Total stems small petiol.	0.15	-0.11	-0.87	0.22	0.23	-0.10	0.13	0.21	0.17
Total stems big petiolaris	0.72	0.38	-0.49	0.05	0.05	-0.17	0.12	0.18	-0.12
Green stems willow	-0.39	0.36	-0.77	-0.15	0.05	0.15	0.09	0.18	0.15
Dry stems willow	0.56	0.66	-0.40	-0.20	-0.01	-0.12	0.07	0.17	-0.07
Total stems willow	-0.01	0.58	0.74‡	-0.21	0.03	0.05	0.09	0.21	0.07
Willow distance	-0.01	-0.35	0.62	0.10	-0.29	-0.34	0.01	0.52	-0.06
Foliage density	-0.52	0.32	0.25	0.39	0.43	0.12	-0.32	0.33	0.01
Canopy cover	0.04	-0.18	0.43	0.45	0.43	0.52	0.03	-0.30	0.05
Tall stratum	0.64	0.21	0.30	-0.31	0.30	0.10	0.26	0.25	0.20
#Aspen	0.51	-0.12	0.34	-0.60	-0.32	-0.10	0.25	0.07	0.27
#Trees	0.68	0.04	0.32	-0.38	-0.29	0.15	0.35	0.10	0.21
Aspen height	0.18	-0.67	0.43	-0.31	0.16	0.02	0.25	0.08	-0.25
Tree height	0.20	-0.66	0.43	-0.30	0.15	0.04	0.27	0.08	-0.25
Aspen dbh	0.23	-0.78	0.20	-0.45	0.30	0.07	0.05	0.03	-0.01
Tree dbh	0.34	-0.73‡	0.22	-0.40	0.30	0.16	0.11	0.05	-0.02

†PC8 and PC9 are non-predictive multicollinearities.

‡In PC2 Tree dbh was selected over Aspen dbh based on biological meaning and correlation (R = 0.91; P < 0.001 n = 55; Pearson product-moment correlation). In PC3 Total stems willow was selected over Total stems small petiolaris for the same reason (R = 0.38; P< 0.001; n =195). In PC4 Grass, #Willow, and #Aspen were selected due to high loading of Male arrival and low intercorrelation (max R = -0.12; P = 0.09; n=195).

Appendix 2.3d. Latent root regression for spatial structure of territory. Loadings were obtained using Varimax rotation. Variables selected (Principal Variables) are underlined. Loadings of dependent variable are shown in bold.

Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
% Variance explained	27.1	20.5	13.2	8.1	8.1	6.6	3.7	3.0	2.6
Eigenvalues	5.14	3.90	2.51	1.54	1.53	1.26	0.71	0.56	0.49
Male arrival	**-0.07**	**-0.03**	**-0.05**	**-0.12**	**-0.12**	**0.04**	**-0.09**	**0.97**	**0.09†**
Area willow	-0.04	0.42	0.06	0.76‡	-0.11	-0.12	0.36	-0.01	0.07
Area aspen	0.01	0.91	0.13	-0.02	-0.08	-0.30	-0.13	-0.01	0.10
Area pond	-0.08	0.07	0.84	0.13	0.17	0.35	0.06	-0.07	0.06
Treed area	-0.02	0.86	0.12	0.37	-0.11	-0.27	0.09	-0.01	0.11
Area willow+aspen+pond	-0.06	0.69	0.58	0.36	0.01	-0.01	0.11	-0.05	0.11
Elongation	0.27	0.01	0.25	-0.08	0.18	0.23	0.08	0.04	0.23
Perimeter to *area willow	-0.13	0.01	-0.06	-0.21	-0.05	0.05	-0.94	0.10	-0.09
Perimeter to *area pond	0.10	0.23	-0.05	0.28	-0.03	-0.07	0.11	0.11	0.88
Perimeter to area *treed area	0.08	-0.36	0.04	-0.02	0.08	0.82	0.02	0.06	-0.03
External perimeter	0.12	-0.23	-0.88	-0.04	0.14	0.27	-0.01	0.01	0.12
Edge willow-aspen	-0.10	0.35	0.04	0.41	-0.19	-0.67	0.19	-0.01	0.08
Edge willow-pond	0.01	0.09	0.16	0.88	-0.16	-0.08	0.06	-0.15	0.21
Distance to nearest treed patch	0.06	-0.06	0.09	-0.14	0.92	0.15	0.06	-0.04	0.02
Distance to nearest willow patch	0.03	-0.09	-0.07	-0.08	0.96	0.03	-0.01	-0.09	-0.04
Mean internal distance between treed patches	0.91	-0.03	-0.10	0.07	0.02	0.11	0.02	0.05	-0.03
Maximum internal distance between treed patches	0.96	0.03	-0.07	0.02	0.02	0.04	0.07	-0.15	0.11
Mean internal distance between willow patches	0.95	-0.07	-0.03	-0.04	0.02	0.06	0.01	0.10	-0.04
Maximum internal distance between willow patches	0.95	0.01	-0.01	-0.07	0.05	-0.04	0.05	-0.09	0.09

† PC9 is a non-predictive multicollinearity.

‡ Area willow was selected over Edge willow-pond based on biological importance.

Appendix 2.4. One-way nonparametric ANOVA (Kruskal-Wallis) for years of occupancy of patches. Each patch was treated as an independent unit. Multiple comparisons and means for each group are shown.* Indicates significant difference between two groups. X^2 test and multiple comparisons are corrected for tied ranks.

Number of years of occupancy	N	Mean Rank	Mean (m^2)	Multiple comparisons			
Area willow				0	1	2	3
0	79	66.54	267.9	-		*	*
1	33	95.82	549.6		-		*
2	38	127.72	1175.3			-	*
3	77	163.71	1955.3				-

$X^2 = 90.48$; DF = 3; $P < 0.001$

Number of years of occupancy	N	Mean Rank	Mean	Multiple comparisons			
Perimeter to √area willow				0	1	2	3
0	42	55.35	6.77	-			*
1	27	63.07	7.85		-		*
2	34	84.5	9.95			-	
3	75	120.41	13.32				-

$X^2 = 52.86$; DF = 3; $P < 0.001$

Number of years of occupancy	N	Mean Rank	Mean (m^2)
Area aspen			
0	79	90.26	963.5
1	33	99.30	1140.8
2	38	110.63	1446.9
3	77	146.32	3060.0

$X^2 = 30.95$; DF = 3; $P < 0.001$

Number of years of occupancy	N	Mean Rank	Mean (m)
External perimeter			
0	79	75.50	202.5
1	33	95.48	228.1
2	38	123.30	351.0
3	79	158.66	565.3
$X^2 = 65.85$; DF = 3; $P < 0.001$			

Number of years of occupancy	N	Mean Rank	Mean (m)
Perimeter to √area treed area			
0	79	74.69	246.7
1	33	96.65	310.5
2	38	124.07	508.3
3	79	158.61	830.6
$X^2 = 66.73$; DF = 3; $P < 0.001$			

Number of years of occupancy	N	Mean Rank	Mean (m)
Distance to nearest willow patch			
0	79	112.03	31.8
1	33	115.62	34.6
2	38	131.72	39.9
3	78	108.13	34.6
$X^2 = 3.44$; DF = 3; $P = 0.329$			

Appendix 2.5. Sampling of Lepidoptera larvae with beating net method and chronological order of territory occupancy.

Abundance of Lepidoptera larvae during settlement of territorial male was also analyzed for a subsample of territories, using data collected with a beating net (1996). Relative abundance of Lepidoptera larvae (including Geometridae) was not correlated to chronological order of territory occupancy by males (R = 0.12; P = 0.23; N = 38; Spearman rank correlation coefficient, one-tailed test), or by females (R = 0.08; P = 0.341; N = 26; Spearman rank correlation coefficient, one-tailed test). When considering Lepidoptera Geometridae only, again, no correlation was found for males (R = 0.19; P = 0.189; N = 23), or females (R = 0.13; P = 0.309; N = 17).

Appendix 4.1. Species censused in willow and aspen patches at Rumsey Ecological Reserve. Red-winged Blackbird was the only species that nested in the ponds.

Species occurring exclusively in treed patches		**Species occurring also in the mixed grassland**	
Mourning Dove	*Zenaida Macroura*	Eastern Phoebe	*Sayornis phoebe*
Northern Flicker	*Colaptes auratus*	Say's Phoebe	*Sayornis saya*
Yellow-bellied Sapsucker	*Sphyrapicus varius*	Tree Swallow	*Tachycineta bicolor*
Downy Woodpecker	*Picoides pubescens*	Blue Jay	*Cyanocitta cristata*
Hairy Woodpecker	*Picoides villosus*	Black-billed Magpie	*Pica pica*
Least Flycatcher	*Empidonax minimus*	American Crow	*Corvus brachyrhynchos*
Alder Flycatcher	*Empidonax alnorum*	Common Raven	*Corvus corax*
Black-capped Chickadee	*Poecile atricapillus*	Mountain Bluebird	*Sialia currucoides*
Red-breasted Nuthatch	*Sitta canadensis*	Veery	*Catharus fuscescens*
House Wren	*Troglodytes aedon*	Brown Thrasher	*Toxostoma rufum*
Marsh Wren	*Cistothorus palustris*	Cedar Waxwing	*Bombycilla cedrorum*
Swainson's Thrush	*Catharus ustulatus*	Grasshopper Sparrow	*Ammodramus savannarum*
Hermit Thrush	*Catharus guttatus*	Le Conte's Sparrow	*Ammodramus leconteii*
American Robin	*Turdus migratorius*	Vesper Sparrow	*Poocetes gramineus*
Gray Catbird	*Dumetella carolinensis*	Savannah Sparrow	*Passerculus sandwichensis*
Red-eyed Vireo	*Vireo olivaceus*	Song Sparrow	*Melospiza melodia*
Warbling Vireo	*Vireo gilvus*	Chipping Sparrow	*Spizella passerina*
Tennessee Warbler	*Vermivora peregrina*	Clay-colored Sparrow	*Spizella pallida*
Orange-crowned Warbler	*Vermivora celata*	Dark-eyed Junco	*Junco hyemalis*
Yellow-rumped Warbler	*Dendroica coronata*	White-throated Sparrow	*Zonotrichia albicollis*
Yellow Warbler	*Dendroica petechia*	White-crowned Sparrow	*Zonotrichia leucophrys*
Common Yellowthroat	*Geothlypis trichas*	Lincoln's Sparrow	*Melospiza lincolnii*
American Redstart	*Setophaga ruticilla*	Brown-headed Cowbird	*Molothrus ater*
Red-winged Blackbird	*Agelaius phoeniceus*	American Goldfinch	*Carduelis tristis*
Baltimore Oriole	*Icterus galbula*		

Appendix 4.2. One-way ANOVA for grazing treatments. Kruskal-Wallis test was used when variables did not conform to the assumptions for parametric ANOVA. Means and SE are presented. Variables selected for bird analysis are marked in bold.

Variable name	Heavy grazing	Moderate grazing (summer)	Light grazing	Ungrazed	Total df	F (or X^2)	P
VEGETATION IN WILLOW PATCHES							
Allgreen (%) 1995	67.92	57.37	41.04	51.09	78	9.11	<0.001
	(3.78)	(3.15)	(4.15)	(3.79)			
Allgreen (%) 1996	30.40	42.54	32.76	35.88	181	†13.85	0.003
	(1.46)	(2.81)	(2.15)	(2.13)			
Allgreen (%) 1997	51.27	49.02	39.10	41.35	192	†19.13	<0.001
	(1.42)	(2.26)	(2.09)	(3.13)			
Grass (%) 1995	24.12	46.30	22.39	28.18	78	12.47	<0.001
	(2.10)	(3.85)	(2.74)	(3.88)			
Grass (%) 1996	9.38	18.97	10.72	15.46	182	†26.90	<0.001
	(0.63)	(1.76)	(1.19)	(1.89)			
Grass (%) 1997	17.01	25.18	12.17	16.97	192	†42.80	<0.001
	(1.13)	(1.47)	(1.01)	(1.85)			
Shrub (%) 1995	10.05	6.65	8.52	7.98	78	0.88	0.455
	(1.01)	(1.87)	(1.91	(1.39)			
Shrub (%) 1996	6.43	9.71	7.15	8.16	181	†1.77	0.622
	(0.75)	(1.45)	(0.84)	(1.26)			
Shrub (%) 1997	16.33	12.05	13.96	8.89	192	5.66	0.001
	(1.26)	(1.16)	(1.17)	(1.42)			
Forb (%) 1995	33.83	4.65	11.90	15.39	78	†46.12	<0.001
	(2.78)	(0.99)	(1.98)	(2.37)			
Forb (%) 1996	15.57	13.02	24.66	13.04	181	1.00	0.393
	(1.08)	(1.16)	(8.59)	(1.54)			
Forb (%) 1997	19.48	12.28	13.53	13.71	192	†33.69	<0.001
	(0.93)	(0.78)	(1.09)	(1.55)			
Leaf litter (%) 1995	29.48	33.81	50.91	43.85	78	8.44	<0.001
	(3.63)	(2.51)	(3.47)	(3.56)			
Leaf litter (%) 1996	29.60	24.05	31.07	32.44	182	†10.69	0.014
	(1.65)	(2.58)	(2.49)	(2.27)			
Leaf litter (%) 1997	24.80	29.46	28.55	29.60	192	1.46	0.228
	(1.48)	(1.92)	(1.70)	(2.23)			
Bare ground (%) 1995	5.56	8.62	7.94	4.86	78	†2.64	0.451
	(0.87)	(1.54)	(1.68)	(0.95)			
Bare ground (%) 1996	47.37	34.18	34.36	29.30	182	2.33	0.076
	(9.13)	(1.91)	(2.29)	(2.03)			
Bare ground (%) 1997	14.02	14.89	24.06	15.56	192	†28.99	<0.001
	(1.19)	(1.48)	(1.51)	(1.42)			
#Total shrubs 1995	6.06	6.82	9.33	8.12	78	1.55	0.208
	(0.83)	(0.98)	(1.84)	(0.94)			
#Total shrubs 1996	9.71	6.43	7.15	8.16	181	†14.62	0.002
	(1.45)	(0.75)	(0.84)	(1.26)			
#Total shrubs 1997	12.65	14.59	11.24	6.85	192	6.79	<0.001
	(1.19)	(1.28)	(1.13)	(0.99)			

Variable name	Heavy grazing	Moderate grazing (summer)	Light grazing	Ungrazed	Total df	F (or X^2)	P
#Rose 1995	0.94	2.98	2.30	1.72	78	2.48	0.068
	(0.46)	(0.65)	(0.69)	(0.51)			
#Rose 1996	1.07	4.29	3.02	2.45	182	†24.87	<0.001
	(0.44)	(0.75)	(0.52)	(0.51)			
#Rose 1997	3.88	6.51	3.44	2.40	192	†20.24	<0.001
	(0.65)	(0.76)	(0.57)	(0.56)			
#Saskatoon 1995	1.63	0.41	3.74	2.35	78	†16.19	<0.001
	(0.49)	(0.36)	(1.23)	(0.79)			
#Saskatoon 1996	0.32	0.56	3.21	1.09	182	†8.06	<0.001
	(0.16)	(0.30)	(0.71)	(0.30)			
#Saskatoon 1997	0.29	0.04	0.38	0.18	192	†5.90	0.117
	(0.15)	(0.02)	(0.12)	(0.07)			
#Aspen shrubs 1995	0.18	0.06	0.58	0.40	78	†8.67	0.004
	(0.069)	(0.03)	(0.15)	(0.24)			
#Aspen shrubs 1996	0.56	0.30	0.33	1.02	192	†8.06	0.045
	(0.17)	(0.07)	(0.09)	(0.23)			
#Aspen shrubs 1997	0.56	0.30	0.33	1.02	192	†14.84	0.002
	(0.17)	(0.07)	(0.09)	(0.23)			
#Willow shrubs 1995	2.14	0.26	1.82	1.15	78	†9.98	0.019
	(0.66)	(0.11)	(0.51)	(0.69)			
#Willow shrubs 1996	11.92	14.88	15.04	9.50	182	2.18	0.092
	(1.85)	(1.74)	(11.95)	(5.52)			
#Total saplings 1995	7.54	6.39	15.50	17.13	78	7.96	<0.001
	(1.55)	(1.20)	(2.37)	(2.72)			
#Total saplings 1996	4.54	4.10	4.68	7.18	182	†5.48	0.140
	(0.60)	(0.53)	(0.68)	(1.05)			
#Total saplings 1997	5.71	4.65	5.99	8.67	192	†8.91	0.031
	(0.75)	(0.68)	(0.99)	(1.14)			
#Total poles 1995	2.59	1.00	2.53	3.13	78	2.85	0.043
	(0.61)	(0.31)	(0.60)	(0.63)			
#Total poles 1996	3.07	1.26	1.20	2.30	182	†17.13	<0.001
	(0.57)	(0.74)	(0.19)	(0.33)			
#Total poles 1997	2.79	1.32	3.22	2.57	192	†4.01	0.261
	(0.51)	(0.26)	(0.70)	(0.50)			
Willow height (cm) 1995	3.29	4.38	3.60	3.72	78	10.08	<0.001
	(0.12)	(0.16)	(0.15)	(0.19)			
Willow height (cm) 1996	3.52	3.75	3.64	3.75	182	†2.74	0.434
	(0.11)	(0.07)	(0.11)	(0.14)			
Willow height (cm) 1997	3.50	3.58	3.31	3.63	192	2.51	0.060
	(0.11)	(0.08)	(0.08)	(0.12)			
Green stems willow 1995	32.05	33.46	27.30	36.53	78	2.43	0.072
	(2.29)	(1.96)	(1.70)	(3.10)			
Green stems willow 1996	47.74	35.59	48.04	41.50	182	8.13	<0.001
	(2.33)	(1.92)	(2.07)	(1.92)			
Green stems willow 1997	52.48	81.99	72.71	32.35	192	†17.38	<0.001
	(8.24)	(9.85)	(9.48)	(6.57)			

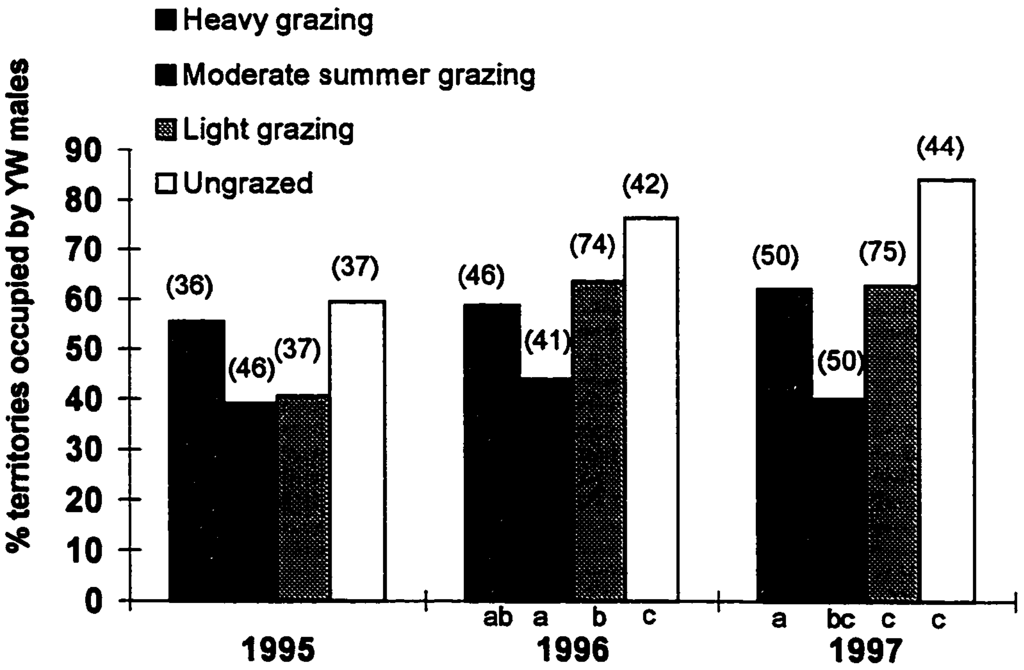
Variable name	Heavy grazing	Moderate grazing (summer)	Light grazing	Ungrazed	Total df	F (or X^2)	P
Dry stems willow 1995	15.03 (1.31)	18.38 (1.35)	10.45 (1.13)	28.88 (3.75)	78	†23.21	<0.001
Dry stems willow 1996	58.32 (2.35)	41.75 (2.22)	46.82 (2.30)	40.91 (3.29)	182	8.36	<0.001
Dry stems willow 1997	127.61 (11.64)	127.42 (9.79)	159.75 (9.96)	154.91 (12.41)	192	2.63	0.051
Total stems willow 1995	47.09 (2.90)	51.83 (3.09)	36.90 (2.60)	65.41 (6.46)	78	†18.68	<0.001
Total stems willow 1996	106.06 (3.87)	77.34 (3.70)	94.86 (3.50)	82.41 (4.25)	182	10.19	<0.001
Total stems willow 1997	96.67 (5.91)	102.07 (5.24)	125.43 (5.25)	103.56 (5.34)	192	5.91	<0.001
Willow distance (cm) 1995	93.96 (12.43)	111.76 (6.29)	78.17 (5.20)	84.52 (6.87)	78	2.72	0.050
Willow distance (cm) 1996	100.45 (4.94)	94.32 (0.71)	114.28 (2.88)	89.36 (4.11)	181	0.73	0.540
Willow distance (cm) 1997	92.39 (4.66)	101.95 (5.81)	95.88 (6.11)	86.86 (4.44)	192	1.14	0.336
Foliage density (%) 1995	47.36 (4.24)	45.46 (3.76)	50.80 (4.69)	48.41 (3.92)	78	0.28	0.843
Foliage density (%) 1996	56.46 (3.69)	56.08 (3.45)	44.67 (3.12)	50.16 (3.75)	182	2.89	0.037
Foliage density (%) 1997	43.31 (2.82)	48.30 (2.02)	60.35 (2.12)	56.58 (2.71)	192	10.92	<0.001
Canopy cover (%) 1995	39.77 (2.48)	50.39 (2.82)	48.63 (3.17)	40.66 (3.17)	78	3.75	0.014
Canopy cover (%) 1996	27.91 (1.96)	23.31 (1.22)	22.81 (1.63)	30.67 (2.67)	182	†9.05	0.029
Canopy cover (%) 1997	31.10 (1.80)	33.68 (2.08)	30.36 (1.80)	27.91 (2.39)	192	1.27	0.287
VEGETATION IN ASPEN PATCHES							
Aspen height (m)	9.63 (0.26)	11.06 (0.41)	11.24 (0.22)	11.04 (0.18)	179	†17.26	<0.001
Aspen dbh (cm)	13.53 (0.36)	12.77 (0.23)	12.57 (0.29)	12.33 (0.46)	179	2.03	0.112
Distance to nearest twelve trees (m)	342.31 (16.43)	369.31 (16.43)	275.84 (9.29)	259.19 (10.82)	179	17.24	<0.001
ARTHROPOD ABUNDANCE IN WILLOW PATCHES							
Total abundance 1995	54.10 (5.10)	68.79 (6.48)	41.24 (6.08)	39.75 (4.88)	118	4.94	0.003
Total abundance 1996	92.29 (10.70)	57.28 (10.70)	63.69 (4.96)	79.67 (9.64)	133	†16.76	<0.001
Total abundance 1997	164.40 (11.35)	133.33 (6.14)	165.95 (14.26)	149.29 (21.10)	165	1.56	0.201

Variable name	Heavy grazing	Moderate grazing (summer)	Light grazing	Ungrazed	Total df	F (or X^2)	P
Homoptera 1995	28.97 (3.60)	30.27 (3.43)	21.24 (3.58)	21.65 (3.04)	115	1.66	0.179
Homoptera 1996	69.15 (9.73)	35.02 (3.73)	37.52 (3.34)	43.29 (6.35)	136	†15.38	0.002
Homoptera 1997	100.58 (6.75)	78.68 (3.81)	99.35 (12.57)	99.04 (17.89)	162	†6.09	0.108
Hemiptera 1995	9.28 (1.34)	8.61 (0.92)	4.78 (0.62)	4.76 (0.69)	175	†19.69	<0.001
Hemiptera 1996	18.85 (2.33)	7.65 (0.65)	5.68 (0.81)	6.58 (1.14)	169	†38.96	<0.001
Hemiptera 1997	20.09 (1.55)	10.59 (0.83)	8.88 (0.61)	9.50 (1.24)	224	†46.55	<0.001
Diptera Chironomidae 1996	2.57 (0.49)	2.64 (0.39)	2.13 (0.81)	2.82 (0.81)	61	0.17	0.918
Diptera Chironomidae 1997	5.72 (0.85)	5.59 (0.88)	8.22 (0.93)	3.67 (0.58)	141	†17.33	<0.001
Lepidoptera 1995	1.00 (0.00)	1.27 (0.14)	1.25 (0.13)	1.00 (0.00)	35	†8.16	0.043
Lepidoptera 1996	1.20 (0.11)	1.27 (0.15)	1.50 (0.17)	1.33 (0.33)	55	0.71	0.551
Lepidoptera 1997	1.45 (0.17)	1.65 (0.85)	1.30 (0.09)	1.20 (0.13)	84	†2.98	0.394
ARTHROPOD DRIED BIOMASS IN WILLOW PATCHES							
Total dried biomass 1995	61.94 (6.95)	74.37 (7.67)	46.72 (8.87)	36.21 (4.72)	118	4.31	0.006
Total dried biomass 1996	100.18 (11.62)	87.13 (13.82)	71.63 (6.51)	106.24 (17.59)	133	†5.82	0.121
Total dried biomass 1997	182.70 (15.10)	152.85 (7.13)	169.59 (14.68)	175.72 (32.47)	165	†3.95	0.267
Homoptera 1995	30.22 (4.70)	23.93 (3.08)	18.31 (3.40)	21.94 (3.40)	115	†3.59	0.309
Homoptera 1996	59.58 (9.77)	32.78 (3.42)	30.47 (2.72)	44.09 (7.39)	136	6.09	<0.001
Homoptera 1997	114.24 (8.94)	85.38 (4.50)	109.04 (12.68)	114.59 (12.69)	162	†5.21	0.157
Hemiptera 1995	10.91 (1.63)	9.99 (1.31)	3.61 (0.42)	4.28 (1.01)	175	†31.28	<0.001
Hemiptera 1996	23.67 (4.09)	9.26 (1.33)	3.33 (0.44)	6.13 (1.22)	169	†32.27	<0.001
Hemiptera 1997	26.28 (2.25)	15.38 (1.54)	11.28 (0.95)	10.93 (1.51)	224	†40.95	<0.001
Diptera Chironomidae 1996	0.31 (0.12)	0.27 (0.09)	0.25 (0.10)	0.55 (0.35)	61	0.54	0.654
Diptera Chironomidae 1997	1.65 (0.27)	2.37 (0.44)	3.09 (0.38)	1.58 (0.48)	141	3.03	0.032

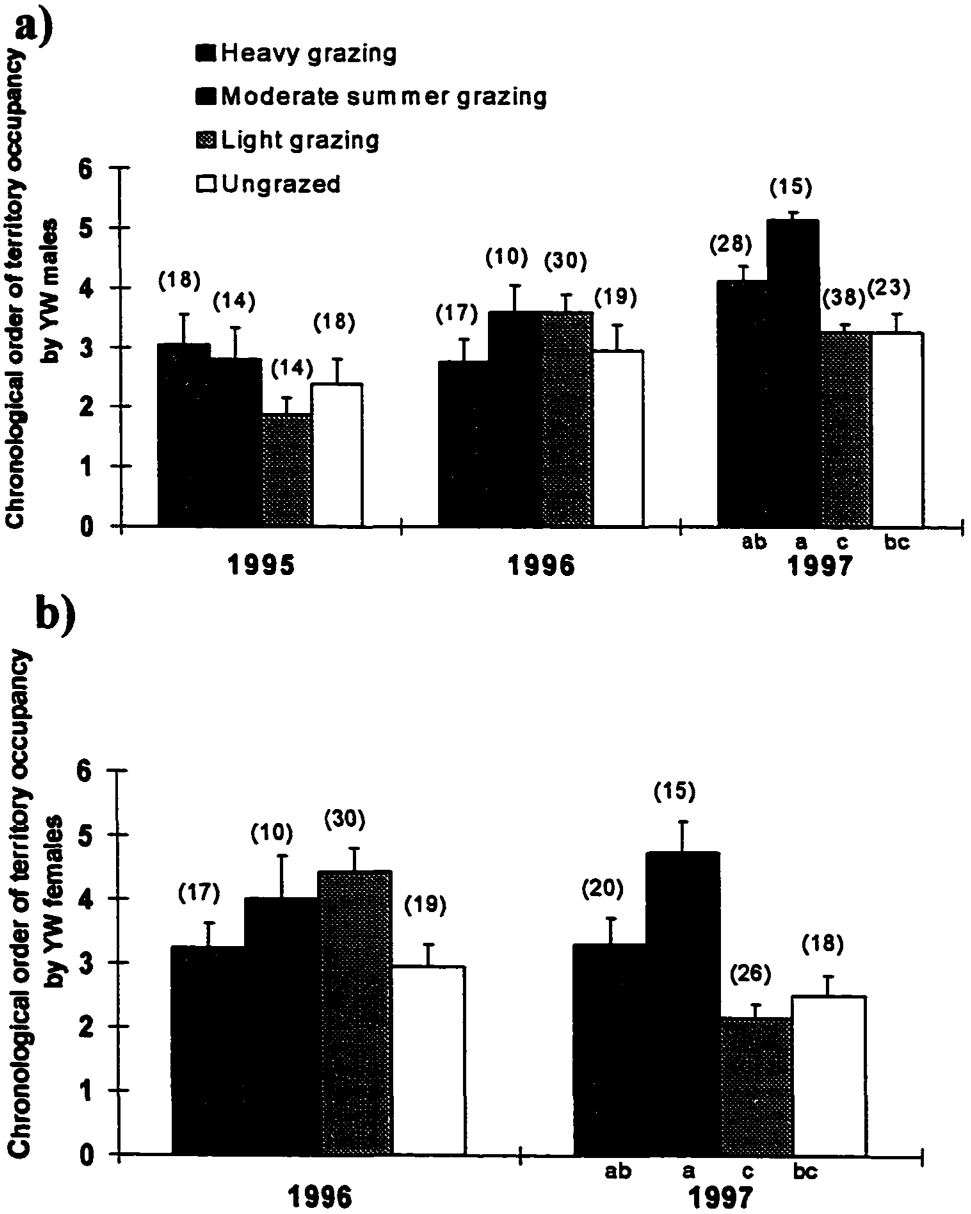
Variable name	Heavy grazing	Moderate grazing (summer)	Light grazing	Ungrazed	Total df	F (or X^2)	P
Lepidoptera 1995	2.01 (0.69)	2.05 (0.56)	8.67 (2.85)	2.59 (1.04)	35	†9.46	0.024
Lepidoptera 1996	3.95 (1.40)	7.81 (1.82)	6.52 (1.65)	14.24 (7.08)	55	2.23	0.096
Lepidoptera 1997	7.60 (1.78)	11.01 (1.77)	7.43 (1.70)	5.71 (2.22)	84	1.32	0.275
ARTHROPOD ABUNDANCE IN ASPEN PATCHES							
Total abundance 1995	21.50 (1.89)	24.53 (3.10)	19.78 (3.25)	26.78 (3.62)	79	1.08	0.362
Total abundance 1996	39.50 (3.11)	58.32 (6.32)	34.78 (2.92)	36.57 (4.15)	150	5.40	0.002
Homoptera 1995	10.91 (1.35)	13.12 (1.35)	9.50 (1.49)	11.88 (1.68)	77	0.93	0.431
Homoptera 1996	24.71 (2.48)	41.09 (4.61)	22.00 (2.55)	24.44 (3.73)	155	7.02	0.002
Hemiptera 1995	2.26 (0.31)	1.94 (0.30)	2.68 (0.88)	2.18 (0.36)	75	0.34	0.799
Hemiptera 1996	1.82 (0.21)	4.72 (2.73)	1.54 (0.16)	1.27 (0.20)	80	0.99	0.403
Diptera Chironomidae 1996	1.800 (0.51)	1.63 (0.38)	2.60 (1.08)	3.40 (1.28)	37	0.76	0.528
ARTHROPOD DRIED BIOMASS IN ASPEN PATCHES							
Total dried biomass 1995	40.34 (7.60)	30.16 (4.69)	24.67 (4.74)	31.57 (8.85)	79	1.05	0.376
Total dried biomass 1996	83.02 (7.36)	132.24 (18.59)	77.26 (8.34)	74.20 (11.40)	150	4.33	0.006
Homoptera 1995	17.67 (2.98)	20.52 (2.92)	14.43 (2.58)	17.98 (2.47)	77	0.81	0.490
Homoptera 1996	60.44 (6.56)	100.68 (13.46)	51.26 (6.11)	56.67 (9.61)	156	†11.08	0.011
Hemiptera 1995	2.42 (0.43)	1.68 (0.44)	3.24 (1.68)	2.52 (0.45)	75	0.45	0.718
Hemiptera 1996	4.51 (1.43)	9.14 (6.22)	1.96 (0.38)	5.47 (3.82)	80	0.70	0.557
Diptera Chironomidae 1996	0.17 (0.04)	0.07 (0.02)	0.27 (0.11)	0.41 (0.20)	37	†1.75	0.626

† Kruskal-Wallis test, X^2 corrected for ties.

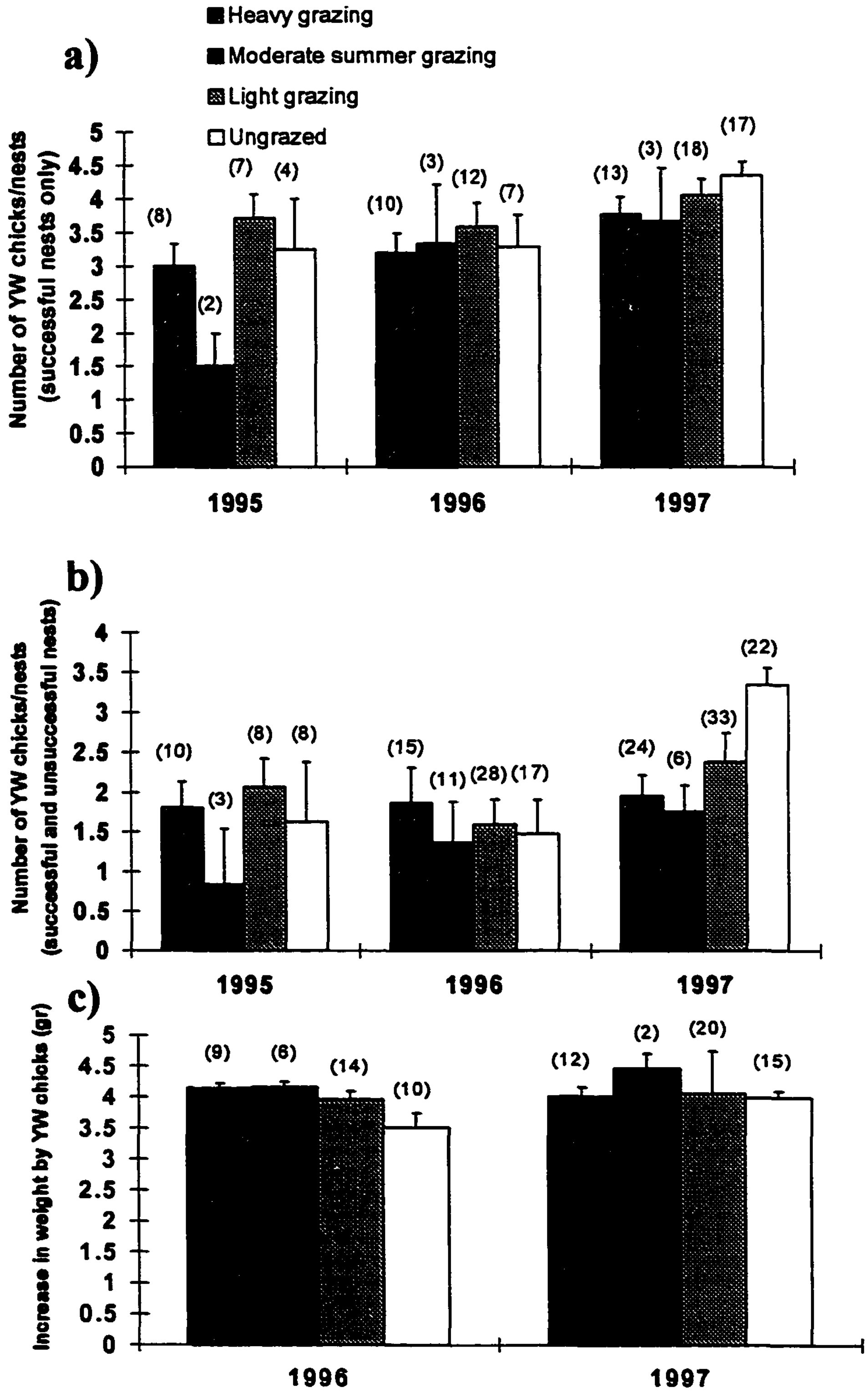
Appendix 4.3a. Proportion of territories occupied by Yellow Warbler males and grazing intensity. Significance refers to the G-test. Groups differing as alphabetical order by at least one letter (e.g., **a** *vs* **b** but not **a** *vs* **ab**) were significantly different in post-hoc comparisons. Significant differences disappeared in multivariate models. (N) above bars denotes the number of territories.



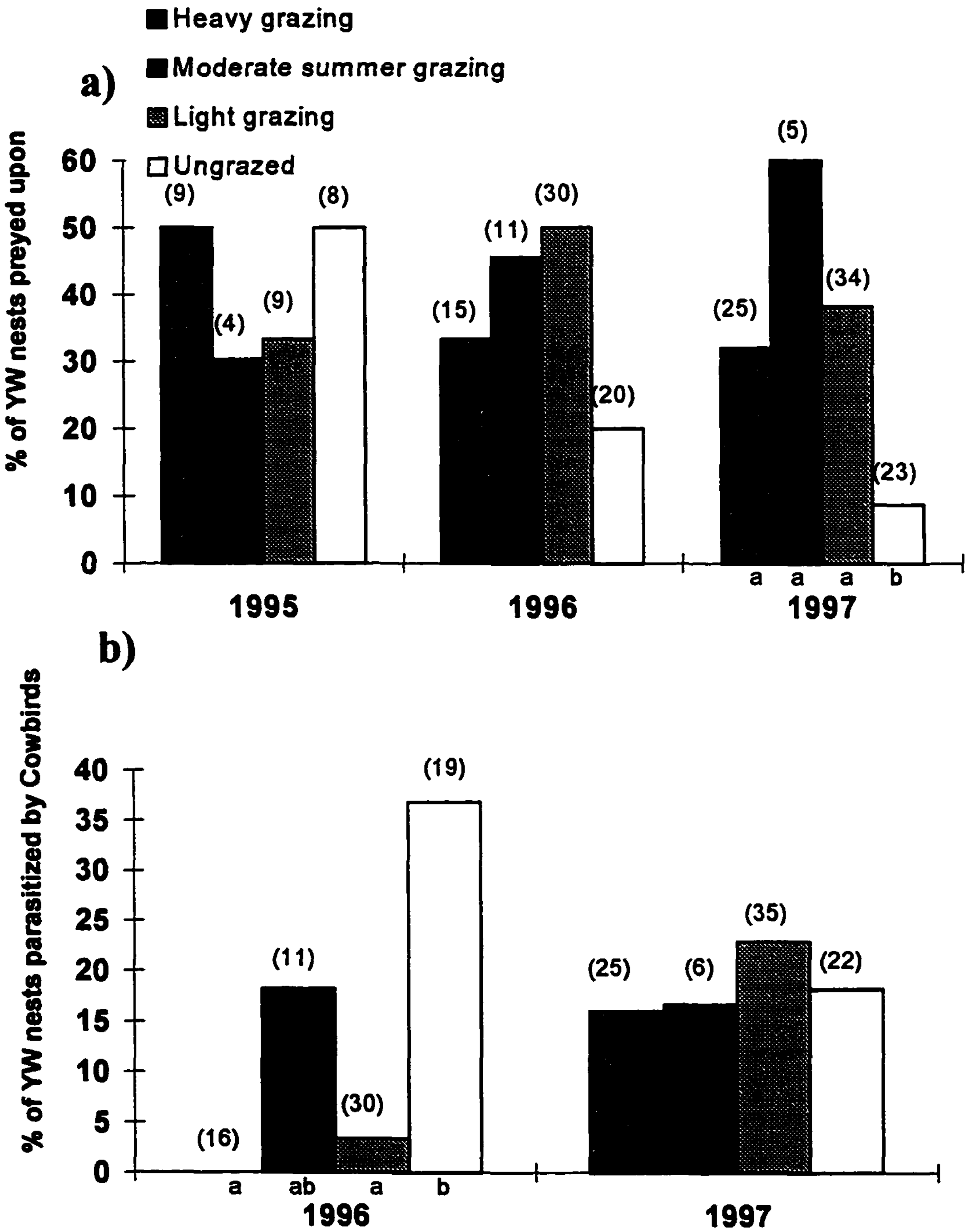
Appendix 4.3b. Chronological order of territory occupancy by Yellow Warbler males (a) and females (b). Significance refers to Kruskall-Wallis test. Groups differing as alphabetical order by at least one letter (e.g., a *vs* b, but not a *vs* ab) were significant in post-hoc comparisons. "Grazing intensity x Area of willow" was significant in multivariate models for males (1997). "Grazing intensity" was the only significant variable in GLIM for females (1997).
(N) above bars denotes the number of territories



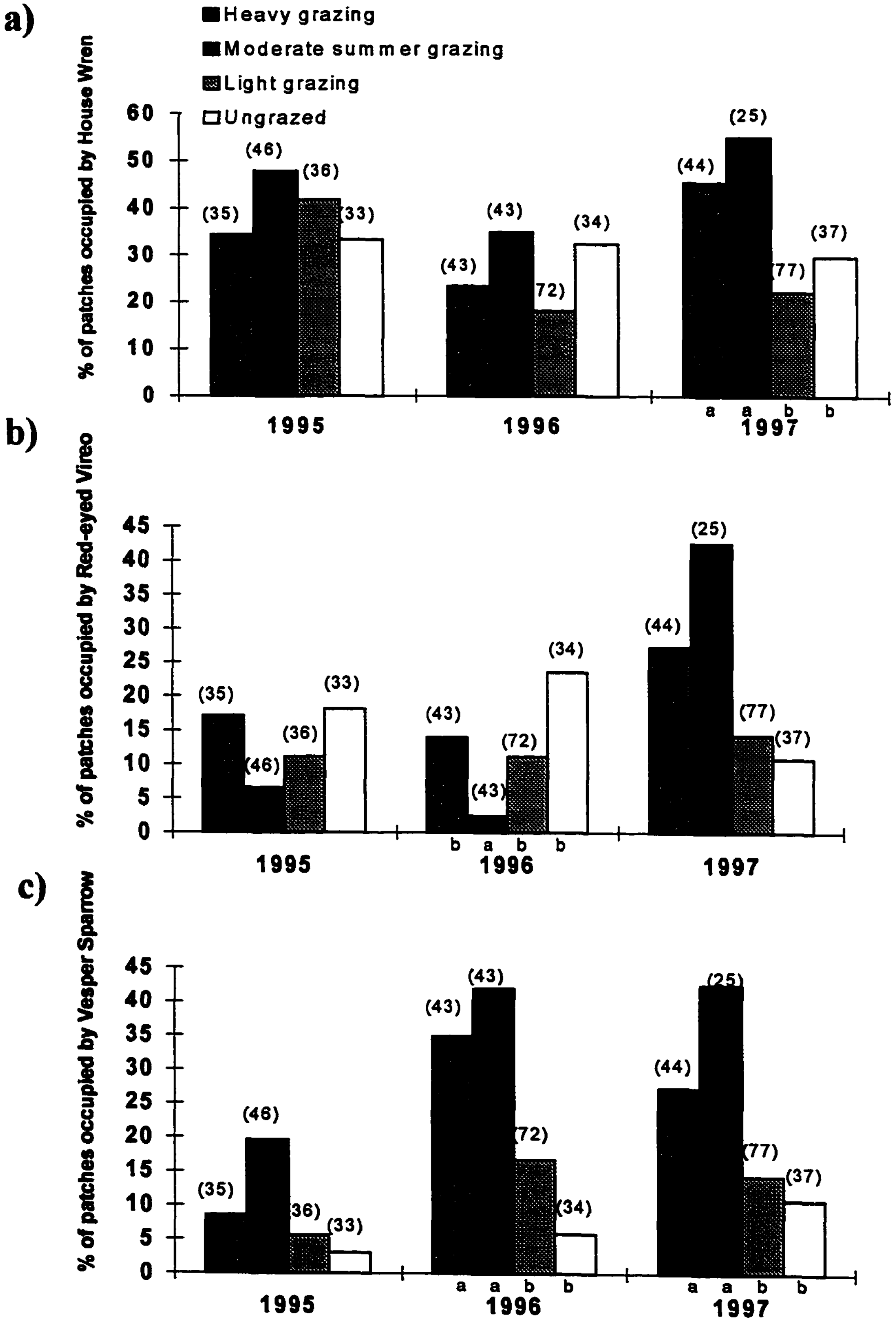
Appendix 4.3c. Breeding success in the Yellow Warbler and grazing. Number of chicks per nest in successful nests (a), number of chicks per nest including unsuccessful nests (b), and increase in weight by chicks between day 2 and 5 (c) did not differ significantly between grazing treatments. (N) above bars denotes the number of nests.



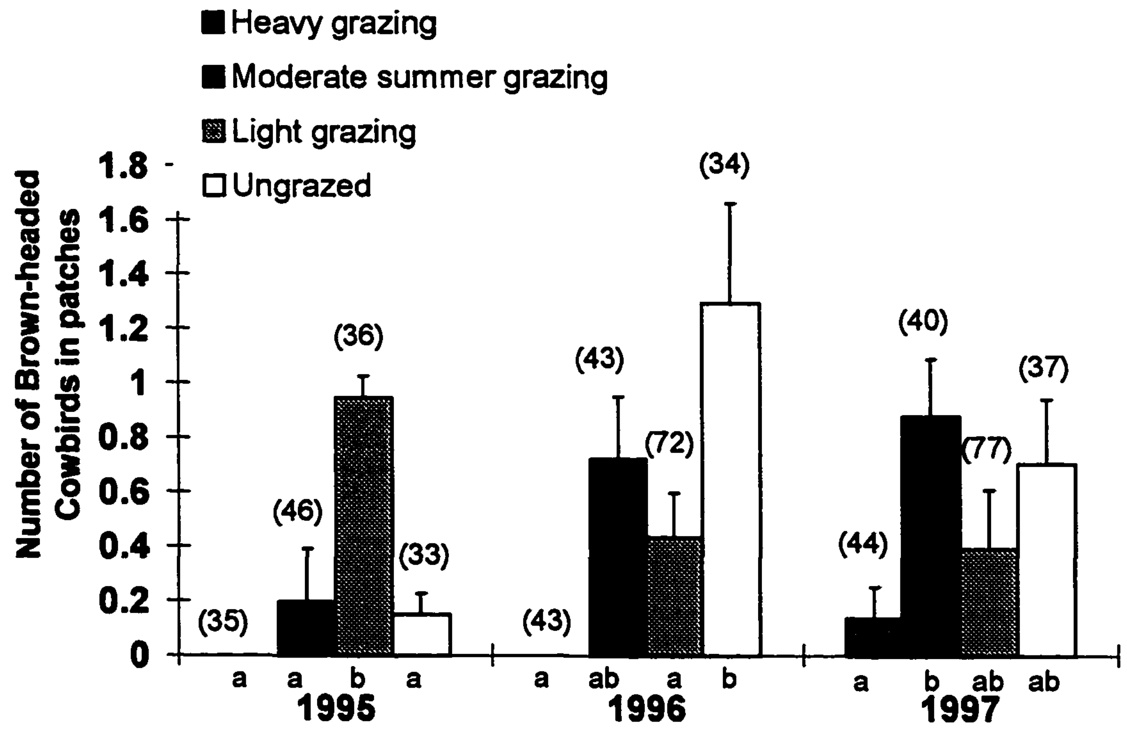
Appendix 4.3d. Percentage of Yellow Warbler nests preyed upon (a) and parasitized by cowbirds (b). (N) above bars denotes the number of nests.



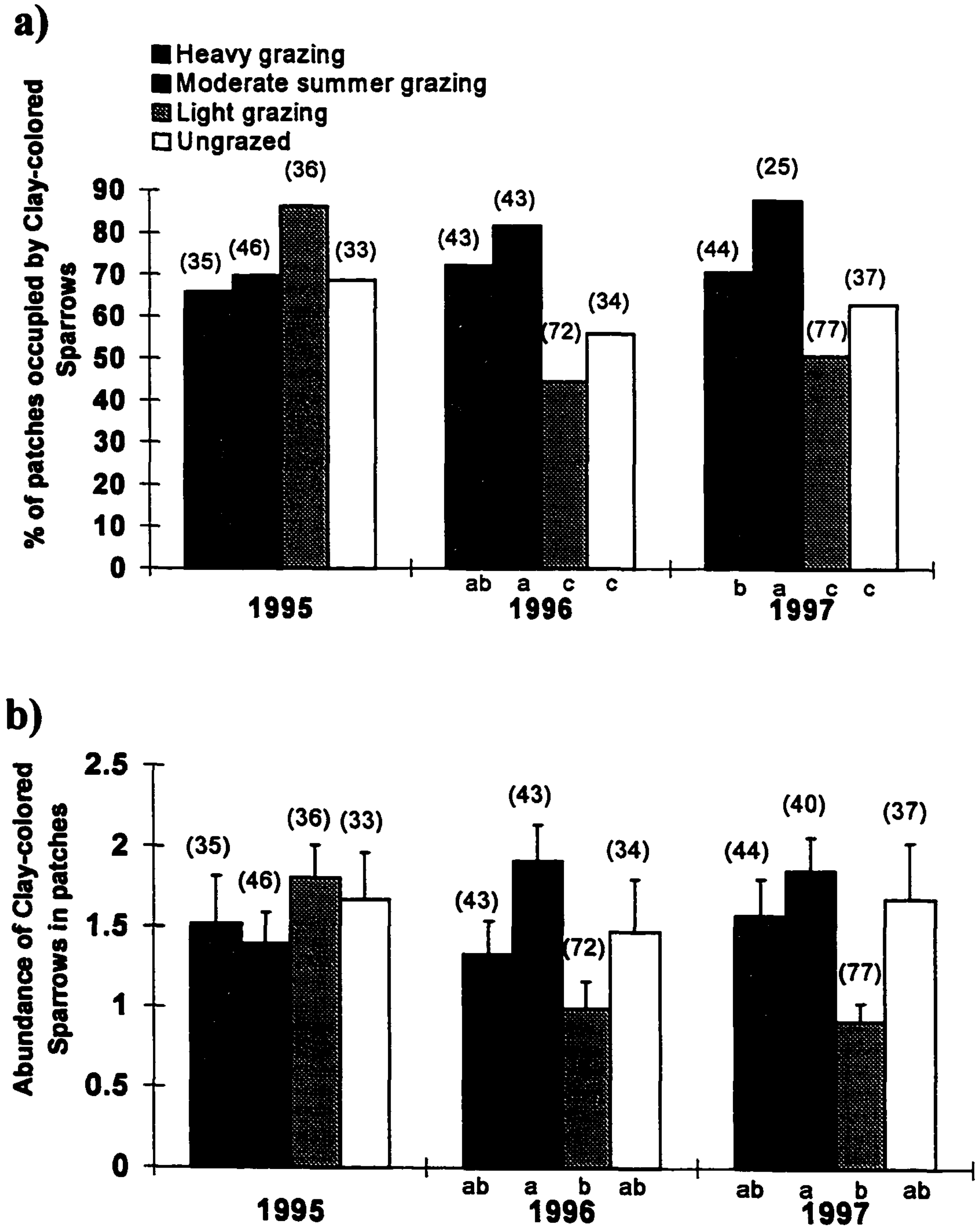
Appendix 4.4a. Grazing and percentage of treed patches occupied by the House Wren (a), the Red-eyed Vireo (b), and the Vesper Sparrow (c). See Appendix 4.3 for the meaning of letters. (N) above bars denotes the number of patches.



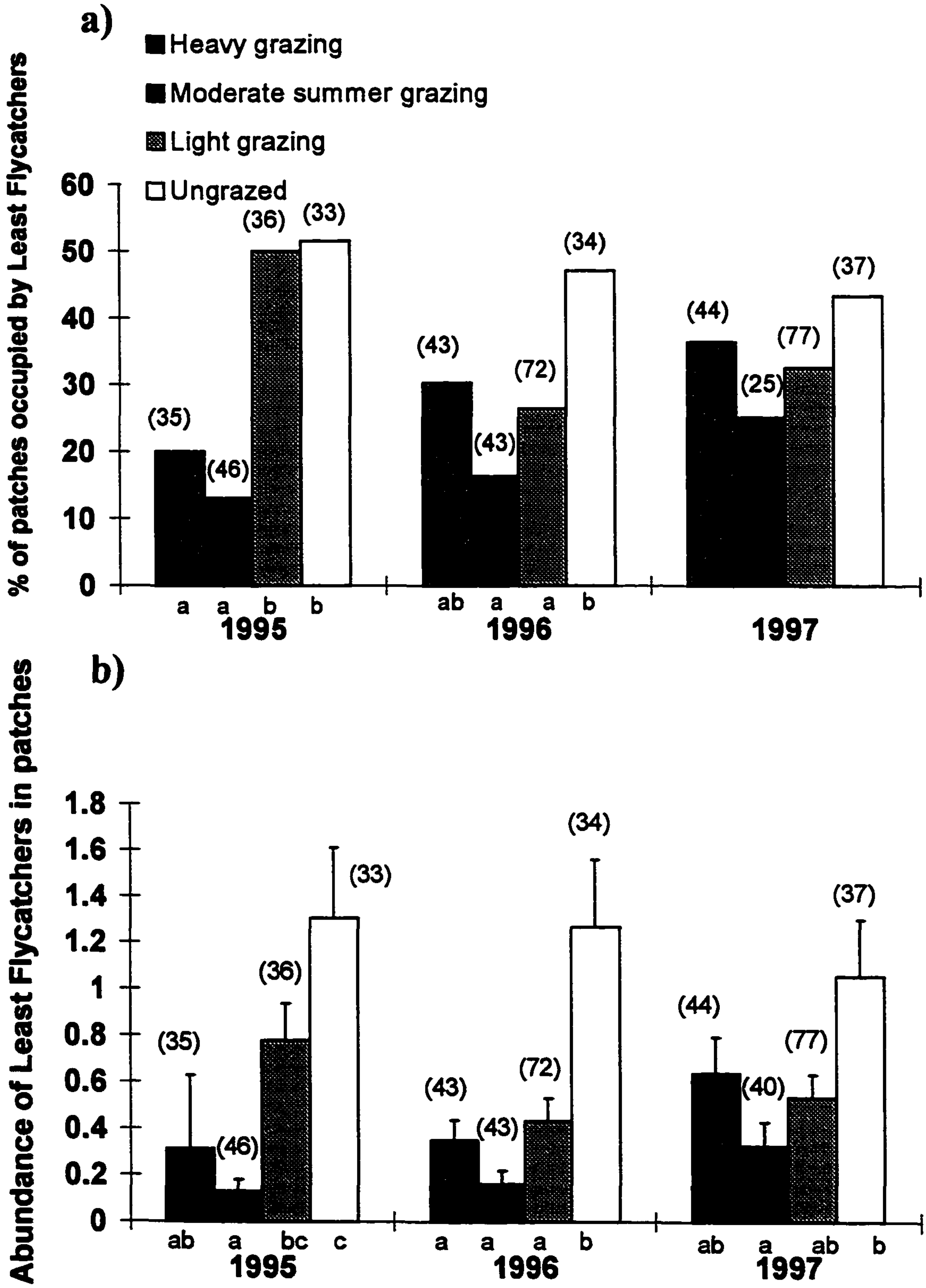
Appendix 4.4b. Number of Brown-headed Cowbirds in treed patches. Mean and standard error are presented Significance is based on Kruskal-Wallis test. (N) above bars denotes the number of patches.



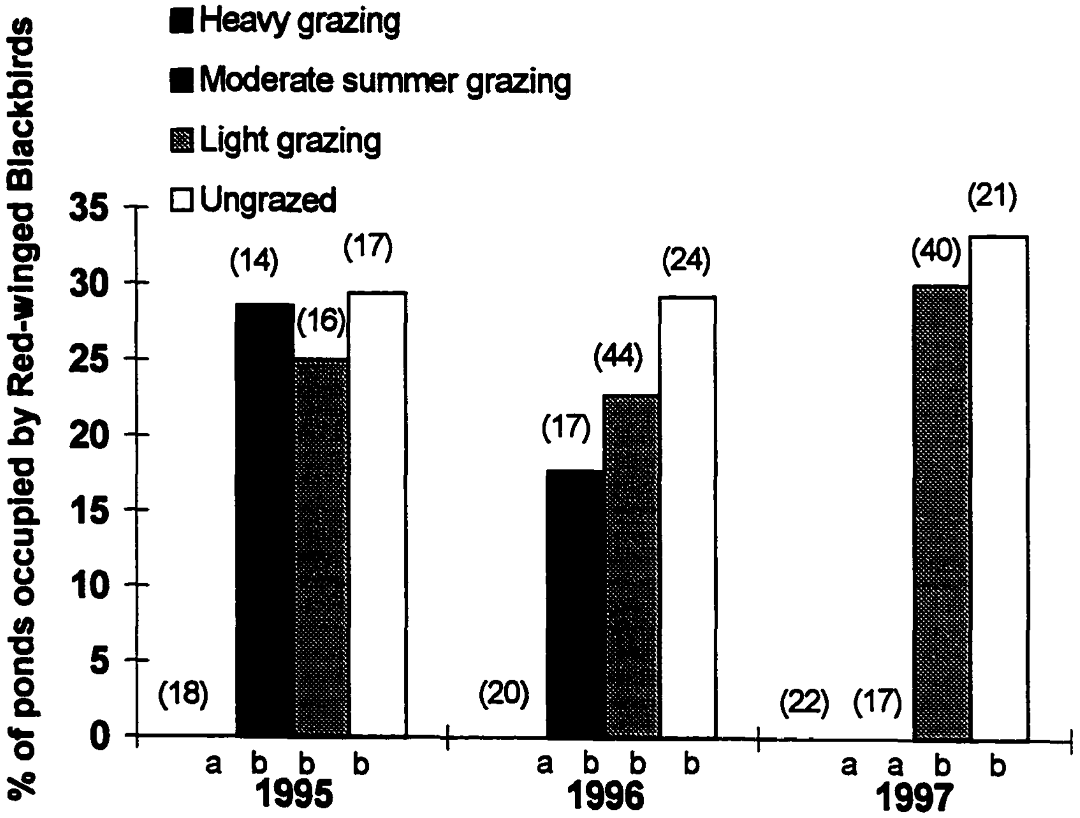
Appendix 4.4c. Grazing and (a) percentage of treed patches occupied by the Clay-colored Sparrow, (b) number of Clay-colored Sparrows in patches. (N) above bars denotes the number of patches.



Appendix 4.4d. Grazing and (a) percentage of treed patches occupied by the Least Flycatcher, (b) number of Least Flycatchers in patches. (N) above bars denotes the number of patches.



Appendix 4.4e. Grazing and percentage of ponds occupied by the Red-winged Blackbird. (N) above bars denotes the number of ponds.



Appendix 4.5. Grazing and (a) species richness and (b) total number of individuals in treed patches. (N) above bars denotes the number of patches.