HABITAT SELECTION, ECOLOGICAL ENERGETICS, AND THE EFFECTS OF CHANGES IN WHITE PINE FORESTS ON BREEDING RED CROSSBILLS (*Loxia curvirostra*) IN ALGONQUIN PROVINCIAL PARK, ONTARIO.

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ABSTRACT

Habitat selection by, ecological energetics of, and the effects of changes in white pine (*Pinus strobus* L.) forests on Red Crossbills *(Loxia curvirostra)* were studied in Algonquin Provincial Park, Ontario. Birds were surveyed in several forest habitats and daily activities were observed during the breeding season in the autumn of 1998, a good year for white pine seed production. During the autumn of 1997 and summer of 1998, surveys of white pine stumps from trees harvested in the mid-late 1800s were conducted. Breeding birds foraged in stands with a minimum of 40% white pine, and appeared to prefer stands, both mixed deciduous-coniferous (40-70% white pine) and pine (>70% white pine) along roads. Possible reasons for this were: 1) seeds from trees along the road were more available to birds; 2) open-grown trees along the road had larger crowns with more seeds; and 3) the road provided grit and was adjacent to a favorite foraging area. A time-activity budget indicated that the birds managed to balance energy needs by foraging on white pine seeds for less than 1 hr/day. For a pair of Red Crossbills to breed successfully, they had to rear 3 young to fledging, subsidizing the fledglings' diets for an additional 2 weeks until they could forage on their own. Total cost of successful reproduction for a pair required the consumption of 34, 025 white pine seeds. Surveys of white pine stumps and a GIS based pine-soil model suggested that the area of optimal breeding habitat in Algonquin Park is half of what it was prior to European settlement (1850s). As a result, numbers of potential breeding pairs of Red Crossbills were half of what they likely were before logging of old-growth white pines occurred in the mid nineteenth century. This estimate is conservative. If historical white pine forests produced more seeds/hectare than current forest stands, this would have additional negative impacts, further reducing the potential numbers of breeding birds.

RÉSUMÉ

Ce projet visait à étudier la sélection d'habitat par le bec-croisé des sapins *(Loxia curvirostra)* ainsi que son bilan énergétique et les effets de la perte de vieilles forêts de pin blanc (*Pinus strobus* L.) sur les populations de l'espèce dans le Parc Provincial d'Algonquin, Ontario. Un inventaire des oiseaux a été effectué dans plusieurs habitats et les activités journalières ont été observées pendant la saison de reproduction à l'automne 1998 qui s'est avérée être bonne pour la production de graines de pin blanc. Pendant l'automne 1997 et l'été 1998, un dénombrement des souches de pin blanc coupées pendant le milieu et la fin du 19^e siècle a été effectué dans le but d'estimer les densités historiques des populations de pins. Ces densités furent également estimées à l'aide de modèles pin-sol liés à un système d'information géographiques (SIG), ainsi que par la compilation de données extraites de publications scientifiques. Pendant la saison de reproduction, les oiseaux s'alimentaient davantage dans des peuplements ayant plus de 40% de pin blanc, et semblaient préférer des peuplements mixtes (40-70% de pins) ou des peuplements de pins (plus de 70% de pins) en bordure des routes. Les raisons pouvant expliquer cette situation sont: 1) les arbres le long des routes auraient des graines plus accessibles aux oiseaux; 2) les arbres en milieu ouvert le long des routes auraient des cimes plus grandes et contenant plus de graines; 3) les bordures de routes offriraient une plus grande accessibilité au gravier et à un lieu d'alimentation préférentiel. Les observations des activités journalières ont indiqué que les individus parvenaient à combler leurs besoins énergétiques en s'alimentant de graines de pin blanc pendant moins d'une heure par jour. Pour qu'un couple de bec-croisé parvienne à se reproduire avec succès, il devait élever et alimenter trois jeunes de la naissance jusqu'à l'envol. En plus, il devait partiellement alimenter les jeunes pour une période additionnelle d'environ deux semaines jusqu'à ce qu'ils puissent s'alimenter par eux-même. Les coûts énergétiques totaux pour parvenir à la reproduction nécessitaient la consommation de plus de 34 025 graines de pin blanc. Les résultats des analyses de densités historiques de pins suggèrent que la quantité d'habitats propices à la reproduction du bec-croisé des sapins dans le parc Algonquin aurait diminué de moitié

depuis les coupes intensives de pin blanc survenues au début de la colonisation européenne (milieu du 19^e siècle). En conséquence, les populations reproductrices de l'espèce seraient potentiellement la moitié de ce qu'elles étaient à l'époque. Cet estimé est considéré comme étant conservateur. De plus, on peut émettre l'hypothèse que si les peuplements historiques de pins produisaient davantage de graines que les peuplements actuels, l'estimation des réductions de populations pourrait être encore plus importante.

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PREFACE

Contribution of Authors

This thesis consists of a literature review preceding three manuscripts intended for publication with myself as the senior author, and with Ian D. Thompson and Rodger D. Titman as junior authors. I. D. Thompson and R. D. Titman were involved in experimental design and execution of the research, and analytical and editorial guidance. I was involved in the design of the field research, I collected the data, and I was responsible for data analysis and writing the manuscripts. For literature citations, I used guidelines provided by The Auk, published by the American Ornithologists' Union. As well, each manuscript has its own literature citations. The following is included in accordance with the regulations of the Faculty of Graduate Studies and Research, McGill University:

"Candidates have the option of including, as part of the thesis, the text of one or more papers submitted, or to be submitted, for publication, or the clearly duplicated text of one or more published papers. These texts must conform to the "Guidelines for Thesis Preparation" with respect to font size, line spacing and margin sizes and must be bound together as an integral part of the thesis. The thesis must be more than a collection of manuscripts. All components must be integrated into a cohesive unit with logical progression from one chapter to the next. In order to ensure that the thesis has continuity, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must conform to all other requirements of the "Guidelines for Thesis Preparation" in addition to the manuscripts. The thesis must include the following: a table of contents; an abstract in English and French; an introduction which clearly states the rationale and objectives of the research; a comprehensive review of the literature (in addition to that covered in the introduction to each paper); and a final conclusion and summary".

INTRODUCTION

This thesis focuses on habitat selection, ecological energetics, and effects of logging of old-growth white pine (*Pinus strobus* L.) on populations of Red Crossbills in Algonquin Provincial Park, Ontario. Previous research on this species has considered foraging behaviour, the evolution of the crossed mandible, variability in Red Crossbill types, specialization of food sources, synchronous eruptions, and food profitability. Little is understood about habitat selection, and importance of old-growth and mature forests in eastern Canada as breeding habitats for Red Crossbills. They are the most specialized of the seed-eating birds in this region, hence they are a good candidate as an indicator species of sustainable forest management. As such, it is useful to examine long-term trends in their populations as affected by habitat change from timber harvesting. The objectives of this research were: 1) to better understand habitat selection by Red Crossbills; 2) to determine energetic costs of breeding crossbills in order to estimate conifer seed requirements; and 3) to estimate long-term changes in optimal Red Crossbill habitat and infer effects on potential breeding populations, using Algonquin Park, Ontario, as an example area.

LITERATURE REVIEW

Introduction

The Red Crossbill *(Loxia curvirostra)* is a member of the family Fringillidae, and of the subfamily Carduelinae. Although its plumage can be highly variable, the male is generally reddish overall, the female is grey to yellowish olive, and the juvenile is conspicuously streaked. Its most distinct feature is the bill with crossed tips, which it shares with only one other species in North America, the White-winged Crossbill *(L. leucoptera)*. The evolution of crossed mandibles in crossbills is indicative of their dependence on conifer seeds as a food resource. Many species of finches depend on conifer seeds for food, but crossbills are the most specialized of the seed-eating birds.

In eastern Canada, Red Crossbills are found in the southern boreal forests, and in the Great Lakes-St. Lawrence and Acadian forest regions (Cadman et al. 1987, Erskine 1992). They are most common in pine-dominated habitats, particularly white pine *(Pinus strobus)* forests (Lawrence 1949, Benkman 1987a, b). Although their movements have been called "erratic" and "unpredictable" (Griscom 1937, Bent 1968, Newton 1970, 1972, Payne 1987), they normally occur in an area in response to conifer crops (Reinikainen 1937, Lawrence 1949, Bailey et al. 1953, Newton 1970, Bock and Lepthien 1976, Benkman 1990). Red Crossbills follow large cone crops and in years of abundant cones, they aggregate in large flocks in those regions which have cones.

Variation in Red Crossbills

Eight distinct types of *Loxia curvirostra* have been identified in North America (Groth 1991, 1993). Much effort has been made to classify Red Crossbills into subspecies (Griscom 1937, Monson and Phillips 1981, Payne 1987, Groth 1988), but Groth (1991, 1993) argued that these types are actually separate sibling species. Each type is morphologically distinct and vocally defined (Groth 1991, 1993), and these characteristics do not vary even when individuals of one type are separated by thousands of kilometres (Groth 1993). This suggests that the different forms are reproductively isolated (Groth

1993), even though many types may occur and breed simultaneously in the same area. Reproductive isolation could justify species assignment to the different types. Although renaming of these forms has been suggested by Groth (1993), it would be very difficult because there is some overlap in morphology among types, and differences can be so slight that species division cannot be done with certainty in many situations (Groth 1993).

Evolution of Types

The morphological variation among types of Red Crossbill is exhibited in varying body size, and bill size and shape. Bill size affects time it takes to acquire seeds from cones (Benkman 1987b). Different bill sizes are associated with different conifer species (Groth 1993) because cone structure and seed size have influenced body and bill morphology (Benkman 1993a). "The variety of 'niches' presented by the diversity of conifer cones may be a zone in which adaptive radiation (in bill size) has been possible" (Groth 1993). Important in the evolution of different forms of Red Crossbills is the reliance on seeds of key conifers during periods of food scarcity (*i.e.* late winter, or years of poor seed production) (Benkman 1993a). Each type of Red Crossbill is specialized for foraging on its key conifer because it has either optimal bill size, optimal husking groove width, or both (Benkman 1993a). Key conifers produce seeds regularly from year to year, hold seeds in cones during winter, and have cones that are well protected from species other than crossbills (Benkman 1993a).

Groth (1993) associated crossbill types with subspecies allocations commonly used in published literature. Type 3 is the smallest Red Crossbill, previously called *L. c. minor, L. c. sitkensis* and *L. c. reai* (Payne 1987). The word *minor* is the most prevalent in published sources. Larger forms, Types 1 and Type 4, are likely *L. c. neogaea* and *L. c. vivdor*, but there is some confusion associated with these types (Groth 1993). The largest Red Crossbills are Types 2, 5 and 7, which are *L. c. pusilla*, although synonyms are *L. c. benti, L. c. grinnelli,* and also *L. c. bendirei*. Type 6 has only been named *L. c. stricklandi* and Type 8 consists of Newfoundland birds, *L. c. percna* (Groth 1993).

At least three types (2,3,4) of Red Crossbill are found in northeastern North

America, particularly central Canada (Benkman 1987a, Groth 1993). In the study region for this research project, Algonquin Provincial Park, Ontario, Benkman (1987a, b) observed the foraging habits of types 2 and 3. Type 2 birds foraged on white pine seeds in Virginia and North Carolina (Groth 1988). The subject of this study is Type 2 *Loxia curvirostra* which is reliant on white pines as a food source.

Foraging Technique

Crossbills have relatively large bodies in relation to bill length and depth compared to other carduelines (Benkman 1988a). This is presumably because extracting seeds from cones requires more bill strength than just husking the seed (as other cardueline finches do). As well, Benkman (1988b) determined that the crossed mandible was a clear adaptation for separating the scales and extracting seeds from closed cones. The bird creates a gap between the cone scales by sliding the pointed upper mandible in a biting motion, tearing the closed scale. Its jaws are then spread sideways and bill is opened, increasing and deepening the gap between the scales (Benkman 1987b). Often, the lower mandible is braced against a distal scale while the upper mandible works its way deeper into the gap created. When the seed is exposed, the tongue scoops it towards the bill to be husked (Benkman 1987b). Crossbills remove the seed coat and consume only the seed kernel (Benkman 1987a). Empty seeds are discarded.

Crossbills are the only known carduelines able to forage on closed cones (Smith and Balda 1979), thereby permitting the exploitation of resources that less-specialized finches cannot access. This adaptation also enables crossbills to forage on conifer cones throughout the year (Bock and Lepthien 1976). Benkman and Lindholm (1991) concluded that crossed mandibles of *L. c. minor* increase foraging efficiencies on reclosed and tightly closed scales of closed cones. However, a disadvantage of crossed mandibles is a reduced ability to survive on non-conifer seeds because of increased prying (handling) time (Benkman 1988a). Studies show that foraging efficiency on other types of tree seeds decreases with increased crossing of the mandibles, creating a dependence on specific conifers by this genus (Benkman 1988a, b).

Crossbills forage on cones attached to trees, and navigate branches much like parrots do by using their feet and bills (Newton 1972). They fly from cone to cone and from tree to tree while foraging, and extract and husk seeds while hanging from cones (Newton 1972). Benkman (1987a) measured intake rates (dry mass of seed kernel consumed per second) of Red Crossbills. He concluded that time spent husking a given seed type is constant, and that time spent removing seeds from cones is the most variable and time consuming component of foraging (Benkman, 1987a, b). Stage of ripening is also a main factor affecting foraging rates, although seed size and structure do not change much in various cone stages (Benkman 1987b).

Crossbill Diet

Red crossbills feed predominantly on conifer seeds (Newton 1972, Benkman 1987a) and are inefficient at foraging on other types of food (Benkman 1988a, b). Nevertheless, they have been observed eating buds and insects (Halvorson, 1986). Bailey et al. (1953) recorded crossbills eating almonds, sunflower seeds, hemp, buds of cottonwood, gum, frozen apples and pears, parts of eucalyptus, and insects such as caterpillars, aphids, and tree galls. Interestingly, though, Tordoff and Dawson (1965) stated that crossbills do not need insects in their diet, even for newly hatched young, and it has been documented that crossbills do feed conifer seeds to their young (Bailey et al. 1953, Adkisson 1996). Red Crossbills also consume grit regularly (Benkman 1990), like other granivorous birds.

Interspecific Competition

In the northeast, competition with other seed-eaters is likely highest during the winter for *L.c.sitkensis*, which depends on eastern hemlock *(Tsuga canadensis)* along with White-winged Crossbills (Benkman 1987a). This competition is less evident for larger forms of Red Crossbills, which forage mostly on pines. In years of poor seed production this competition is more apparent (Benkman 1987a). Additionally, during the summer, both Red and White-winged Crossbills forage on white spruce *(Picea glauca)* seeds

(Benkman 1987a). This overlap decreases in the fall, and is minor in winter (Benkman 1987a). Common Redpolls *(Carduelis flammea)* can also compete with Red Crossbills for tamarack *(Larix laricina)* and white spruce seeds (Benkman 1987a).

Reproductive Seasonality and the Timing of Reproduction

Although Red Crossbills can nest during any month of the year (McCabe and McCabe 1933, Bailey et al. 1953), recent studies indicate that they are not purely opportunistic, as was previously thought (Hahn 1995, 1998). Food was considered to be the proximal cue in timing of reproduction (Newton 1973, Benkman 1990). Tordoff and Dawson (1965) suggested that Red Crossbills can reach a partial state of readiness during any photoperiod, but final maturation of gonads depends on food availability. Hahn (1998) proposed that crossbill reproduction is not exclusively regulated by availability of conifer seeds and that crossbills share fundamental similarities with other temperate zone birds. Crossbills have a seasonal reproductive cycle, and "opportunistic responses to favorable conditions are superimposed" (Hahn, 1995). Photoperiod regulates their basic annual cycle, and they exhibit opportunistic responses to supplementary cues (such as food) onto this seasonality (Hahn 1995). This is why Red Crossbills most often breed in late summer or late winter (Halvorson 1986, Hahn 1998), and less often in late autumn. Benkman (1990) suggested that crossbills usually breed in late summer/early fall because foraging profitability increases as preferred cone crops (white pine) mature.

Annual Trends in Conifer Use

Use of conifers by Red Crossbills is somewhat complicated because there are many forms, each with their bill morphology, and they use conifer seeds during various cone stages (Benkman 1987a). Benkman (1987a) studied Red Crossbill foraging ecology in the northeastern United States and Canada, where they exhibit four periods of conifer use. The first occurs in late summer, when they feed on accessible white and red spruce *(Picea rubra)* cones. The second occurs in September-October, although in some years this could be earlier, *i.e.* late August, as was observed in Algonquin Provincial Park in 1998.

As the white pine cones open, Red Crossbills switch to this conifer. In open white pine cones, seeds are more accessible than in red pine cones, but white pine cones shed their seeds faster. As a result, there is a shift from white pine to red pine from late November to January, as number of seeds still in white pine cones declines. This is the third period of conifer use. This switch from white to red pine may be skipped in abundant white pine cone years, when birds use this resource into the spring. If white and red pine seeds are not sufficient, the birds might emigrate in November (Benkman 1987a). During the fourth period of conifer use, from January to late spring or summer, Red Crossbills forage on seeds from a variety of conifer cones, especially other pines including pitch pine (*Pinus rigida)*, Virginia pine (*P. virginiana*) or jack pine (*P. banksiana*). These trends were most typical for *L. c. bendirei* and *L. c. neogaea*. Benkman (1987a) also suggested that *L. c. neogaea* may depend more on spruce and hemlock. *L. c. sitkensis* forages mostly on eastern hemlock (Benkman 1987a).

Foraging Profitability

The rate at which food is consumed, *i.e.*, mass (partitioned among protein, fat and carbohydrates) consumed per unit time, is called the intake rate, or profitability. For Red Crossbills, profitability is, to a certain extent, influenced by cone type and structure, timing of cone opening and subsequent seed release, and available seed mass per tree and in a given forest stand (Benkman 1987a). Breeding in crossbills is clearly a function of the availability of conifer seed in cones, which influences searching time, and ripeness of the cone crop which affects handling time. Crossbills are likely to be time minimizers, reducing the risk of predation by spending as little time foraging as possible. To accomplish this they probably seek out trees with the greatest number of cones, in a stand of trees with a high availability of cones, in order to reduce time spent searching for food and thus reducing total movement. Finches are able to consume large numbers of seeds in brief periods of time, exploiting concentrated food patches rapidly. This enables them to use food resources that are patchily distributed (Benkman and Pulliam 1988). Because crossbill food resources vary annually and regionally, their ability to search for and exploit seed patches of abundant food is important (Benkman and Pulliam 1988).

"Profitability contributes significantly to patterns of crossbill conifer use, and patterns of profitability determine, in large part, local habitat use and movement" (Benkman 1987a). Intake rates affect conifer use by crossbills because they forage on the most profitable conifer, then switch when profitability declines. Benkman (1987a) found that intake rates increased from July to August and September on tamarack and white spruce seeds, as cones matured, but before cones had lost most of their seeds. Use of black spruce *(Picea mariana)* and red spruce was highest from March to May indicating that these species are important winter foods. Crossbills foraged on the most profitable conifer most of the time (Benkman 1987a).

Habitat and Conservation

Population size and status of all but one of the Red Crossbill types (Type 8) is unknown (Adkisson 1996). Red Crossbills have become rare in Newfoundland (Pimm 1990, Benkman 1993b). Competition with red squirrels *(Tamiasciurus hudsonicus)*, previously absent and then introduced to Newfoundland in the 1960s, is one possible reason for the decline in *L. c. percna* (Pimm 1990, Benkman 1993b). Timber-harvesting of old forests, particularly those dominated by spruces and pines, is a more plausible explanation (Montevecchi et al. unpubl.). Logging, insect damage, and forest fires have decreased age and changed the composition of Newfoundland forests. Especially evident is a decline in red pine and white pine, which likely has had a large impact on Red Crossbills (Montevecchi et al. unpubl.). Dickerman (1987) concluded that *L. c. neogaea* nearly became extinct because of the decline of white pine and eastern hemlock from logging by 1900. He also suggested that increases in numbers of *L. c. neogaea* (decades later) were a result of the return of some mature forests of white pine and eastern hemlock in the northeastern USA (and likely in Nova Scotia and New Brunswick, concurrently).

Total area of white pine, red pine, eastern hemlock, black spruce, and white spruce have all declined in the oldest age classes in eastern Canada (Stiell 1978, Aird 1985, Ontario Ministry of Natural Resources (OMNR) 1996, OMNR n.d.). Few data exist on the abundance of crossbills. Recent observations on foraging Red Crossbills in Newfoundland suggested that remnant red pine stands (covering only a few hectares) are some of the only remaining habitats for this species on the island (A. Mosseler, pers. comm.). Montevecchi et al. (unpubl.) and Benkman (1993c) concluded that old-growth conifer forests are important habitat for crossbills because of relative crop stability and high seed production. Holimon et al. (1998) determined that mature western hemlock *(T. heterophylla)* and sitka spruce *(P. sitchensis)* in Alaska were important to Red Crossbills. Yet, no study has examined the importance of mature eastern white pine, *Pinus strobus* L., in Red Crossbill habitat selection. White pine is an important food source for Red Crossbills in the northeast as noted in Ontario (Lawrence 1949, Ross and Ross 1950, Benkman 1987a), Maine (Benkman 1987a), New York (Benkman 1987a), and the southeastern states (Groth 1988). If use of a stand is limited by the number or size of important seed source conifers, particularly to support them during the breeding season (*i.e.* autumn, Griscom 1937, Benkman 1990), then this becomes an important criterion in establishing protected areas, and also for forest management planning.

Benkman (1993c) recommended five actions that could assist the conservation of crossbills: 1) maximize amount of old-growth forests (most productive seed producers); 2) increase rotation ages of logging; 3) leave mature trees when areas are logged; 4) have forest reserves in many distinct climatological regions in order to avoid cone crop failure across all regions; and 5) establish reserves in productive forests.

Concern about crossbill conservation is not unwarranted. Specialist avian species are affected by habitat changes and environmental influences to a greater degree than are generalist species (Paulson 1992, Monkkonen and Welsh 1994). Because crossbills are highly specialized on conifer seeds year round, they are more vulnerable than other seed-eating species that can rely on alternate food sources in times of scarcity (Bock and Lepthien 1976). Also, crossbills likely integrate changes in habitat at the landscape and stand levels. In their wide-ranging search for food they respond to areas that have cone-bearing trees in sufficient density to warrant settling for a period of time, and at the stand level they likely choose stands with the best cone crops. At a broad landscape-level the long-term presence of crossbills may be a strong indicator of sustainable development involving older stands.

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1. HABITAT SELECTION BY RED CROSSBILLS (*Loxia curvirostra*) IN ALGONQUIN PROVINCIAL PARK, ONTARIO, CANADA

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ABSTRACT

Red Crossbills *(Loxia curvirostra)* were observed during the breeding season in the autumn of 1998 in Algonquin Provincial Park, Ontario. To determine stand preferences, surveys were conducted in three forested stand types: pineries with >70% white pine (*Pinus strobus* L.); 2) mixed coniferous-deciduous stands with 40-70% white pine; and 3) mixed coniferous-deciduous stands with < 40% white pine. The stands were classified into one of two categories: 1) interior stands (60-70% stocking, 51-75% canopy cover); and 2) roadside buffer strips (90-100% stocking, 90-100% canopy cover). Red Crossbills only foraged in stands with a minimum white pine composition of 40%. They showed no preference between pine and mixed stands, but the location of the stand was important: there were almost twice as many crossbills in mixed roadside stands than in any of the other categories. Breeding birds preferred mature, dominant trees with large crowns positioned along the road because they appeared to provide an optimal seed source for Red Crossbills in our study region.

INTRODUCTION

Conifer seeds are an important food source for many species of birds, mammals and insects (Smith and Balda 1979). Seed predators vary in their dependence on this resource. Some seed-eaters are more opportunistic than specialized, taking advantage of plentiful seeds in years of high cone abundance, but relying on other food sources during times of cone and seed scarcity. Others, such as the Red Crossbill (*Loxia curvirostra*) have evolved specifically to forage on conifer seeds, and are therefore more specialized. In times of low seed production, when other avian species forage on insects or other resources, Red Crossbills still rely almost entirely on conifer seeds (Newton 1972, Benkman 1987a).

Red Crossbills are most common in pine-dominated habitats, particularly white pine (*Pinus strobus* L.) forests (Lawrence 1949, Benkman 1987a, b). Groth (1993) identified eight distinct types in North America, each with its own call, morphology, and distribution. Each type is associated with one or more 'key conifer' species for which it is morphologically adapted for foraging. Three types (2, 3 and 4) have distributions that include the northeast (Groth 1993), and could have been present in our study region. Type 2 is likely the group that we investigated because of distribution, size of bill, and extended period present in the study region (C. Benkman, pers. comm.).

Pine-dependent crossbills often breed in September and October in eastern North America because cone crops mature then (Griscom 1937, Benkman 1990), and white pine seeds become available for foraging (Benkman 1987a). Although foraging ecology of Red Crossbills has been described (Benkman 1987a, Groth 1988, 1993), habitat selection has not been extensively investigated, especially in eastern Canada. Little information is available on the habitat characteristics that are preferred by crossbills in Canadian forests, and this is viewed as a conservation priority for this species (Adkisson 1996).

It has been suggested that mature forests are important habitat for Red Crossbills (Dickerman 1987, Benkman 1993) because of relative crop stability and high seed production. In eastern Canada, total area of white pine has declined in the oldest age classes (Aird 1985, Ontario Ministry of Natural Resources 1996). Dickerman (1987) suggested that the pine dependent subspecies of Red Crossbill, *L. c. neogaea*, was nearly obliterated by 1900 due to logging of old-growth white pine and hemlock (*Tsuga canadensis*) in the northeastern United States. He proposed that increases in numbers of *L. c. neogaea* decades later were the result of a recovery in mature forest cover.

The objective of this study was to gain a better understanding of the habitats preferred by Red Crossbills by determining Red Crossbill stand use in eastern Canada. We wanted to test the hypothesis that Red Crossbills choose stands with older white pine trees, and to determine whether Red Crossbills prefer pine stands, or whether they simply choose stands based on a minimum number of pines with available cones. A further objective was to determine whether the birds prefer older trees to younger ones for foraging.

METHODS

Study Region

The study area was located in the eastern region of Algonquin Provincial Park, Ontario (48°30' N, 78°40' W). This region is dominated by coniferous and mixed coniferous-deciduous stands. A large white pine cone crop occurred in 1998, and the presence of Red Crossbills in the area was noted as early as July. Study sites were chosen along the main road, between Achray and Lake Traverse.

Survey Sites

Forested stands were initially chosen for Red Crossbill surveys based on accessibility to surveyors. Accessible stands were sampled to determine availability of white pine seeds for foraging crossbills. White pine cones were counted on ten randomly chosen trees per stand. To determine whether crossbills were being selective within the study region, given the presence of cones, we only sampled stands with a minimum of 100 mature cones per white pine tree (on average). We decided on three classifications of type/species composition: 1) pinery (>70% white pine); 2)mixed high (coniferous-deciduous stand with 40-70% white pine); and 3) mixed low (coniferous-deciduous stand with <40% white pine). Because most of the park has been logged, locating old-growth stands was difficult. There are 120 m-wide unlogged 'beauty strips' along the main road called 'Areas of concern'. These roadside buffers served as replacements for mature or old forests. Therefore, we separated the study stands into two categories: 1) interior stands (60-70% stocking, 51-75% canopy cover); and 2) roadside buffer strips (90-100%

stocking, 90-100% canopy cover). Interior stands had white pine trees approximately 109 years old which were harvested (50% selection cut) in 1976 or 1982. Roadside buffers were used to represent older stands because, although of similar age, these stands had no logging history and could be considered 'virgin timber' (B. Pick, pers. comm.). The trees along the road had larger crowns than those in the interior stands, in part because they were open to the road.

Twenty-five stands were surveyed for Red Crossbill presence (Table 1.1). Fifteen areas surveyed were interior stands and ten were roadside buffers. Of these, thirteen were pineries (>70% white pine), ten were mixed high (40-70% white pine) stands, and two were mixed low (<40% white pine) stands. The low number of mixed low stands reflects the nature of the study region; very few of these stand types were present. In addition, five stands (three pineries and two low mixed) were surveyed for Red Crossbill presence even though they did not have sufficient cones to meet our criterion of an average of 100 cones/tree.

Survey Method

Two surveys of 2 hrs duration were conducted in each interior stand and roadside buffer by one of two observers. An observer stood at three or four points for 30-40 minutes. Points were approximately 200 m apart and each was at least 100 m from the stand edge, a road, a wetland, or disturbed area. Numbers of Red Crossbills seen and heard were recorded. Wind speed increased in the afternoons, impairing surveys due to noise, so only morning surveys were used for analysis. Surveys were performed twice in each stand or roadside buffer, in each of two time periods: 08:00 - 10:00 and 10:00 - 12:00. Daylight occurred at about 06:40.

Data Analysis

Average numbers of Red Crossbills seen and heard over the two surveys were calculated per stand for statistical analyses. Red Crossbill count data were not normally distributed, so were log-transformed. We used ANOVA (SAS 1996) to examine Red

Crossbill and cone data by treatment. Main effects included stand type (mixed high or pinery) and location category (roadside buffer or interior stand), and their interaction term. Each of these variables was also compared individually with t-tests (SAS 1996). Surveys conducted in the mixed low category were not included in the analysis because of low sample size (n = 2). Significance of test statistics for observations of Red Crossbills was set at $p < 0.1$ because of small sample sizes, and for cone data at $p < 0.05$.

We examined for possible correlations between Red Crossbill abundance and average number of pine cones per stand type and category. Spearman's rank correlation analysis (SAS, 1996) was performed on cone and untransformed crossbill data.

RESULTS

Red Crossbills were not observed in stands which had no cones, nor were they seen in the mixed low pine stands. These latter stands had similar numbers of cones per tree to other stands, but a low density of pines. Overall, the number of crossbills was significantly different across habitat variables (F = 2.91; $df = 3$; $p = 0.06$). In stands with cones, there were almost twice as many crossbills in mixed roadside buffers ($\bar{x} = 13.6$) than in any other category (Figure 1.1, $\bar{x} = 7.2$ in pinery roadside; 6.2 in mixed high interior stand; 6.8 in pinery interior stand). There was a significant type * category interaction (F = 4.09; $df = 1$; $p = 0.06$), indicating that location of the stand was important. More crossbills were observed in roadside stands, particularly mixedwoods (F = 3.75; $df = 1$; $p = 0.07$). The difference in crossbill numbers in pineries compared to mixed high stands was not significant ($p = 0.22$), regardless of whether pineries were located in roadside buffers or in the interior. T-tests were not significant for either stand type or category at alpha = 0.05.

Cone Abundance

The overall ANOVA model for cones by stand type and category was not significant (F = 2.19; $df = 3$; $p = 0.12$), nor was the stand category*type interaction (F = 0.12; $df = 1$; $p = 0.12$). Main effects in this model were at least marginally significant for stand category (F = 4.33; *df* = 1; $p = 0.05$) and type (F = 2.79; *df* = 1; $p = 0.11$), but individual t-tests for these variables were not significant. Trees along the road had slightly higher numbers of cones compared to interior stands, and pineries had slightly more cones than mixed stands (Table 1.2). We observed a significant positive correlation between the number of crossbills and number of cones in a given stand ($r = 0.35$, $p = 0.01$, n = 23). Low mixed stands also had a similar number of cones per tree ($\bar{x} = 114$, n = 2).

DISCUSSION

Red Crossbills are nomadic and move in search of suitable cone crops (Newton 1970, 1972). These movements are regional in scale and occur across a large range of habitats. Large flocks are often seen invading in fall, when cone crops mature (Bent 1968), as was the case in our study in Algonquin Park during the autumn of 1998. The close association between Type 2 Red Crossbills and white pines normally necessitates annual movements since cone production varies from year to year (Fowells 1965). White pines generally have good seed years only every 3-5 years (Fowells 1965, Wright and Bailey 1982). However, when cone crops are stable in a region for several years, crossbills are capable of becoming resident (Senar et al. 1993), as has been the case in north and central New Brunswick over three years from 1997-1999 (NBDNR, pers. comm.).

On a local scale, habitat use and movements are likely influenced by foraging profitability (seeds eaten per unit time), which crossbills probably aim to maximize (Benkman 1987a). It should follow that crossbills are present in areas with high cone production because cone and seed abundances are strongly correlated, *i.e.*, viable seed is high when cone production is high (Graber 1970, Smith and Balda 1979, McDonald 1992). Our data support the contention that Red Crossbill abundance is highly correlated with cone crop at the stand level (Génard and Lescourret 1987, Holimon et al. 1998). By foraging on trees with abundant cones, crossbills can optimize their intake rates (Benkman 1987b, 1989).

Numbers of crossbills on our study plots were positively related to the abundance of white pine cones. Because we only sampled stands with high numbers of cones, we did not observe large variability among stands. However, a threshold of seed production may exist, above which an increase in seed stock may have little influence on Red Crossbill density (Figure 1.2), as suggested by Génard and Lescourret (1987). This threshold was apparently met or exceeded in our study region, hence the lack of a strong relationship between Red Crossbills and cone numbers. In the low mixed stands and stands with few or no cones, this threshold was not met, and therefore crossbills did not forage in these areas.

Almost twice as many Red Crossbills were observed in mixed roadside buffers than any stand category in our study region, even though the number of cones in the roadside buffers were only slightly higher than in the interior stands (Table 1.2). The trees along the road in the buffers were representative of older white pines because of their large crowns, and we expected them to produce more cones than pines in interior stands. Roadside buffers (Areas of concern) are left in Algonquin Park to improve the aesthetics for park users, and include some of the oldest trees in the area. Cone production is related to tree size and age and older trees produce more cones and more viable seeds than do younger trees (Benkman 1993). In Germany, a 90 yr-old white pine stand produced 5 times more seeds than did a 60 yr-old stand (Messer 1956). Dominant white pine trees (above the general canopy with all sides exposed to sunlight) produce twice as many cones as do subdominant trees (Messer, 1956, Burns and Honkala 1990). Perhaps the marginal age difference (<20 years) of remaining white pines in both roadside buffers and interior stands can help to explain the similarity in cone production. White pines along the road were more exposed to sunlight, since at least 50% of the crown (facing the road) had no competition. Exposed to the sun, their cones may have opened earlier in the season, thus producing seeds which were more available at the time of the study. Crossbills in the Pyrenees were observed in open and dense stands, and it was found that seeds in open stands ripened faster, and therefore attracted more crossbills. After the seeds had been shed, profitability declined, and crossbills switched to denser stands (Génard and Lescourret 1987).

If crossbills strongly prefer mature stands of pine (Dickerman 1987, Benkman 1993), why was a similar trend not more clear in our study? Holimon et al. (1998) suggested that a preference for older trees is not as pronounced in years of good seed production as it is in years of poor production (see also: Manuwal and Huff 1987, Huff et al. 1991). As noted above, our study sites may have surpassed the required threshold of seed production, since white pine cone production was very high. Since average cone production in all four types of stands was similar (112-141cones/tree), all four types likely had sufficient food available (Figure 1.2). Mixed high stands appeared to have adequate amounts of seeds to support similar numbers of crossbills as pineries. In contrast, mixed low stands with <40% white pine apparently had insufficient cone production per stand to support Red Crossbills, since birds were not observed using those stands.

In addition to early seed availability, there may have been other advantages to foraging in mixed roadside buffers. Roadside buffers, because they were located along a gravel road, provided an excellent opportunity for Red Crossbills to forage on available conifer seeds and to obtain grit with minimal additional effort. Crossbills take grit regularly (Benkman 1992) and they spent a considerable portion of the day foraging on grit during this study (J. Simard, unpubl.). Benkman (1990) suggested that crossbills consumed grit as a source of calcium. Small amounts of salt had been applied to the main road (P. Dawson, Ontario Ministry of Natural Resources, pers. comm.) so it is possible that crossbills were also acquiring salt, as has been observed in other studies (Aldrich 1939, Marshall 1940, Bennetts and Hutto 1985). Although Dawson et al. (1965) found that salt was not needed to stay healthy, other authors have suggested that minerals are ingested to compensate for nutritional deficiencies (Pulliainen et al. 1978, Adam and Des Lauriers 1998). Perhaps road edges were preferred by Red Crossbills for other reasons. Helle and Jarvinen (1986) stated that although Red Crossbills avoided edges in their study, they were characteristic of edges during the breeding season (von Haartman et al. 1963).

We noticed three areas where crossbills congregated on a daily basis, all of which were adjacent to small dried-up wetlands characterized by speckled alders (*Alnus incana* var. *rugosa*). There, Red Crossbills foraged on dead alder stumps, consuming the rotted wood and bark. Perhaps crossbills are attracted to such marshes or mineral sources. White-winged Crossbills have been recorded foraging on dead coniferous snags along the edge of a conifer swamp and rotting stumps in marshes in Algonquin Park (Crins and McRae 1998). Pulliainen et al. (1978) observed Parrot Crossbills (*Loxia pytyopsittacus*) consuming wood from decaying logs along a brook bank. Analysis showed that the wood was high in ash and calcium, and consumption was likely to provide mineral nutrients.

It is possible that our results, showing highest Red Crossbill numbers in mixed forest roadside buffers, were a result of observer bias. We usually saw, rather than heard, birds in the buffers, whereas in interior stands most of our data came from hearing birds, but not seeing them. Our survey data were based on combined observations of Red Crossbills seen and heard during the survey period. Observer bias may explain the observed differences between roadside buffers and interior stands, but not the preference for mixed roadside buffer stands. Red Crossbill abundances in interior stands may have been underestimated because they do not vocalize consistently, and therefore are difficult to detect if not visible. We also observed that when a flock flew, not all individuals in the flock vocalized. Therefore, when hearing a flock fly over (but not actually seeing the birds), our estimates ranged from 3-5 individuals, when there could have been more.

In summary, it appears that as long as sufficient cone-producing white pines with large crowns are left in the landscape (following logging), Red Crossbills will use the stands to forage and breed. A minimum of 40% white pine (at least 100 years of age) in each stand appeared to be suitable for Red Crossbill use. Birds often foraged in 'favourite' trees almost daily during the field season (pers. obs.), which supports the idea that a few good cone producing trees are sufficient to attract the birds to a particular stand. It appears that there is a threshold number of cones per stand required by Red Crossbills in an area, above which they may use other cues (such as grit sources) to decide where they will go more often. Cone production is related not only to age, but also to crown size, stand density and position in the canopy. Mature, dominant trees with large crowns positioned along the road were the optimal seed source for Red Crossbills in our study region, in agreement with Benkman's (1993) suggestions.

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Table 1.1: Stands surveyed for Red Crossbills *(Loxia curvirostra)* in Algonquin Provincial Park, Ontario, September-October, 1998.

Stand category	**Stand type**	**N**
Interior stand	Pinery	8
	Mixed high	5
	Mixed low	2
Roadside buffer	Pinery	5
	Mixed high	5

Table 1.2: Average number of cones per white pine (*Pinus strobus*) tree by stand category and type in Algonquin Provincial Park, Ontario, September-October 1998.

Stand category	**Stand Type**	**Mean**	**SD**
Interior stand	Pinery	127.4	21.7
	Mixed high	111.7	11.8
Roadside buffer	Pinery	140.9	19.7
	Mixed high	130.6	15.4

Figure 1.1: Mean number of Red Crossbills *(Loxia curvirostra)* observed in different sites in Algonquin Provincial Park, Ontario, September-October, 1998.

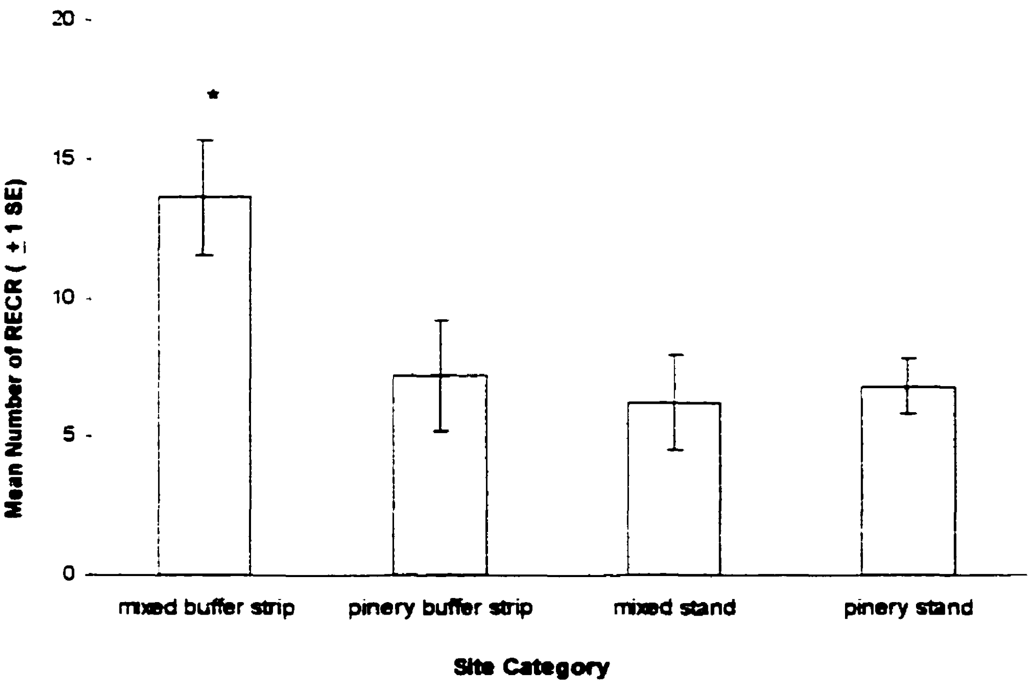
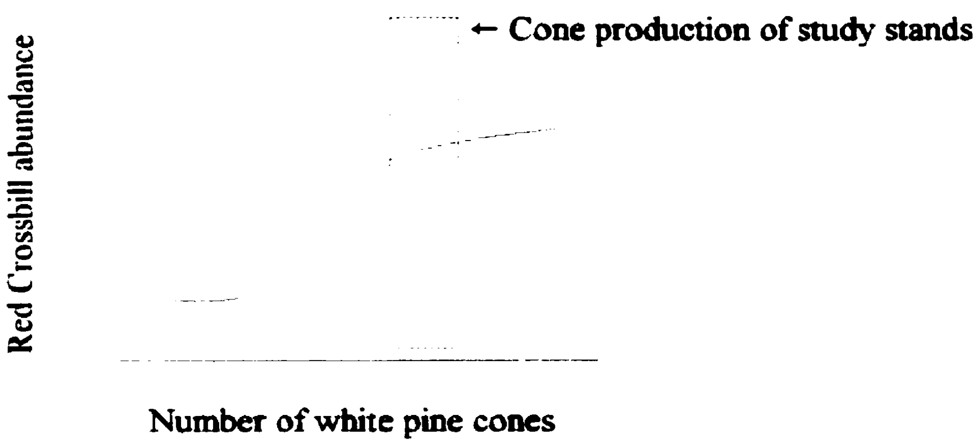


Figure 1.2: Theoretical relationship between Red Crossbill *(Loxia curvirostra)* abundance and number of white pine cones



CONNECTING STATEMENT

Chapter 1 in this thesis, HABITAT SELECTION BY RED CROSSBILLS (*Loxia curvirostra*) IN ALGONQUIN PROVINCIAL PARK, ONTARIO, CANADA examined stand selection by breeding birds, and made inferences about factors influencing choices of foraging areas. The next chapter, ECOLOGICAL ENERGETICS OF BREEDING RED CROSSBILLS *(Loxia curvirostra)* IN ALGONQUIN PROVINCIAL PARK, ONTARIO, CANADA focuses on the daily activities of breeding birds. Estimates of daily energy requirements, represented by numbers of white pine seeds, can help determine the potential number of breeding birds in an area, given seed production of trees in different forested habitats.

2. ECOLOGICAL ENERGETICS OF BREEDING RED CROSSBILLS *(Loxia curvirostra)* IN ALGONQUIN PROVINCIAL PARK, ONTARIO, CANADA

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ABSTRACT

Observations of daily activities of breeding Red Crossbills *(Loxia curvirostra)* were conducted during the autumn of 1998 in Algonquin Provincial Park, Ontario. Energy budgets were calculated based on data collected in the field, other published studies, and laboratory data, and then used to estimate total reproductive cost. Observed intake rates and foraging durations were sufficient to support daily activities, with additional energy available to provide fledged young with food they were not yet able to acquire on their own. Red Crossbills needed to consume 370 seeds/day during the non-breeding season in order to balance energy intake with expenditure. During the breeding season, an estimated 16,787 white pine seeds were consumed by females, and 17,238 by males. Therefore, a total of 34,025 white pine seeds was required for a pair of Red Crossbills to raise three young to fledging.

INTRODUCTION

Activity/energy budgets have been useful in providing insights into avian behavior, population and community ecology, and seasonal patterns of energy use. Activity budgets that estimate daily energy requirements can also be useful in understanding habitat selection by estimating food resources available in patches of habitat.

Red Crossbills *(Loxia curvirostra)* are cardueline finches with bills specialized for acquiring seeds from conifer cones. Several studies have examined Red Crossbill biology and ecology: timing of reproduction (Tordoff and Dawson 1965, Benkman 1990, Hahn 1998); differences in morphology related to foraging ecology (Benkman 1987, Groth 1988, 1993a, 1993b); and their irruptive nature (Newton 1970, Widrlechner and Dragula 1984). Little information exists regarding energy use and partitioning (Adkisson 1996). Dawson and Tordoff's (1964) laboratory effort was the only study that measured basal metabolic rates and examined energy use in relation to temperature in Red Crossbills and White-winged Crossbills (*Loxia leucoptera*). Red Crossbills feed predominantly on conifer seeds (Newton 1972, Benkman 1987) which provide defined yields of energy. Although Red Crossbills are known to breed at any time of the year (Newton 1972), the pine-dependent types breed in September and October in eastern North America because of maturing cone crops (Griscom 1937; Benkman 1990). Benkman (1987) stated that Red Crossbills often switch to foraging on white pine *(Pinus strobus)* seeds in the fall when seeds are most available.

To determine the food requirements of an individual Red Crossbill, it is necessary to compile an activity budget for free-living individuals. This had not yet been done for this species. Benkman (1990) calculated energy thresholds for breeding crossbills, yet, unlike this study, he made assumptions about time spent in activities, and did not observe and measure durations of activities.

Energy budgets can be used to estimate total reproductive cost, which is the total energetic cost of a pair of Red Crossbills raising an average brood of three to independence. We observed Red Crossbills in their natural environment. A principal objective of the field study was to determine how energy was partitioned among requirements for thermoregulation, foraging, and other activities in order to estimate the number of seeds required to support daily activities. Data collected in the field were used to compile the time budget, and other studies and laboratory data were applied to extrapolate what energetic costs of the activities would be. Once this estimate was determined, a prediction of the total population supported by an area can be inferred. The goal of this paper was to calculate the total conifer seeds required to achieve successful (reared to fledgling) reproduction.

METHODS

Field Protocol.

Red Crossbills were observed in an area dominated by mixed and coniferous forests in eastern Algonquin Provincial Park, Ontario, Canada (48°30' N, 78°40' W). Most observations took place in mixed deciduous-coniferous forests, with white pine constituting 40-70% of the species composition, although some observations were in pine forests (>70% white pine), and deciduous forests (<40% white pine). Most data were collected in 'areas of concern': forested stands with no logging history but adjacent to stands logged in 1976 or 1982. White pines used by the birds were over 100 years of age.

Two observers collected and recorded all data using focal animal sampling during daylight hours. Birds were most often observed from roads without the use of a blind, allowing maximum visibility. The individuals did not appear to be affected by our presence at any time, often landing in close proximity to observers on the road. The earliest observation of active Red Crossbills occurred at 07:40, and the latest at 18:03. The birds were studied from 18 September to 29 October, 1998, and total observation time was approximately 31 hours.

Recording entailed one investigator observing a focal individual with a spotting telescope while another recorded time (to the nearest second) and activity (see below). Weather conditions (wind speed, ambient temperature, cloud cover), approximate number of individuals in the flock (crossbills and other species) and in the vicinity, habitat, and any observations of interest (*i.e.* traffic, appearance of potential predators, etc.) were also recorded. An estimate of the total number of Red Crossbills in the immediate area was made before and during observations. Any behaviors of interest were described.

The intake rate while foraging is defined as the dry mass of seed kernel consumed per second (Benkman 1987). When crossbills feed on conifer seeds, they husk the seed coat and consume only the seed kernel. Intake rates were measured sporadically during the field season and calculated from the number of white pine seeds eaten during a defined period of time.

Activities Observed

Seven categories derived from 17 recorded activities were used for calculation of the energy budget: 1) roosting; 2) alert perching; 3) preening; 4) moving (locomotion); 5) flying; 6) foraging: a) for grit and conifer seeds (includes removing seed from cone, husking seed, consuming seed, scanning during foraging, and flying from one cone to another); b) on dead wood; 7) other activities (*i.e.* social interactions, bathing, unknown).

Data Analysis

All individuals observed during the field study were treated independently for the analysis of time allotment per activity. Observations were pooled, and the time spent in each activity was calculated from this total observation time. Data were tested because of the large variation in observation time for individual birds (from 6 sec to >47 min). A Student Newman Keul test (SAS 1996) was used to determine if duration of observation influenced estimates of overall time devoted to each activity.

Daily Energy Expenditure

Field metabolic rate (FMR) estimates the energy expenditure of free-living organisms (Wiens and Farmer 1996). It is based on a time-energy budget (TEB), where total metabolism is calculated based on cost of activities and time spent in each activity (Wiens and Innis 1973). These activities are expressed as multiples of H_{nt} (basal metabolic rate).

$$FMR = H_{nt} * \sum(p_i * A_i)$$

where p_i = the proportion of time engaged in activity i (unitless)

A_i = the metabolic rate during activity i (multiple of H_{nt}; unitless)

H_{nt} = basal metabolic rate (kcal hr^{-1})

FMR = field metabolic rate (kcal day^{-1} $bird^{-1}$)

(Wiens and Farmer 1996)

Calculation of Energy Budget (FMR)

Two energy budgets were calculated. The first model (FMR_{non}) determined energy requirements of nonbreeding individuals (females, males or independent juveniles). The second model (ECR) was used to estimate the total cost for a pair of Red Crossbills to successfully raise 3 young to independence. This model added the FMRs of five stages of reproduction to give entire energetic expenditure. Table 2.1 presents the activities, symbols and equations used to formulate the models. For all of the equations, ti = time spent in activity i (hr), and Hi = energetic cost of activity i (kcal hr $^{-1}$).

Nonbreeding Energy Budget (FMR_{non})

The nonbreeding energy budget model was based on observed time spent in various activities with costs added for thermoregulation and moult of feathers, but it did not incorporate any breeding costs.

$$FMR_{non} = t_{nt}(H_{nt})TR_{nt} + t_{dt}(H_{dt}) + t_{ap}(H_{ap}) + t_{pr}(H_{pr}) + t_{lo}(H_{lo)} + t_{fl}(H_{fl}) + t_{fo}(H_{fo}) + t_{fod}(H_{fod}) + t_{ot}(H_{ot}) + t_{mo}(H_{mo})$$

Additive Model describing Total Energetic Cost of Reproduction (ECR)

In order to calculate the total energetic cost (in kilocalories) of reproduction for a pair of Red Crossbills, the autumnal breeding season was divided into 5 periods: 1) nest construction (FMR_{nc}); 2) egg production ($FMR_{egg)}$; 3) incubation (FMR_{inc}); 4) nestling care (FMR_{nestl}); and 5) fledgling provisioning (FMR_{fledg}). A total reproductive cost was calculated, using the information for activities collected during field observations and energetic costs associated with breeding derived by others (*i.e.* King 1973, Walsberg and King 1978, Rahn et al. 1985, Benkman 1989, Weathers 1992, Williams 1996). The equation defining ECR was:

$$ECR = FMR_{nc} + FMR_{egg} + FMR_{inc} + FMR_{nestl} + FMR_{fledg}$$

The FMR for each reproductive stage was calculated separately for each parent (where they differed) and combined to suggest a total energetic cost for that period, except for nestling care for which a total nestling cost was calculated. Daily costs were calculated separately, where appropriate, for females and males. When young hatched, their costs were added. Each FMR was multiplied by duration of that stage to obtain a total cost for the breeding season. Therefore, for each reproductive stage:

$FMRi = FMR_{ifemale}(d_i) + FMR_{imale}(d_i) + FMR_{iyoung}(d_i)$

where i = the reproductive stage

d = duration of stage i (days)

Type of Red Crossbill. Allometric equations describing metabolic rates of living organisms require weight measurements. Morphological differences, including individual mass, differ significantly between types of Red Crossbill (Groth 1993a), but the types are difficult to identify in the field. Three types of Red Crossbill have distributions that include northeastern North America, and were possibly present in the study area during the field season (Groth 1993a, C. Benkman, pers. comm.). However, because of distribution, size of bill, and the extended period that they were present, the birds observed were most likely type 2 (Groth 1993a, Benkman, pers. comm.). The mean body mass used in metabolic rate calculations (33.0g) was then an approximation of type 2 body masses (Groth 1988, 1993a, Benkman 1990).

Cost Assignments

Mathematical equations for energetic costs are listed in Appendix 1.

Basal Metabolic Rate (H_{nt}). The basal metabolic rate is the "rate of energy utilization by animal organs and tissues at complete rest, unstimulated by the digestion and assimilation of food or by low temperature" (Kendeigh et al. 1977), of a fasting, inactive individual within the thermoneutral zone. Dawson and Tordoff (1964) measured Red Crossbill H_{nt} directly, and their equation was used to calculate the basal metabolism of a 33g bird.

Basal Metabolic Rate or Roosting (H_{nt}). The nocturnal period started at 21:01. To ensure a postabsorptive state, basal metabolic rate commenced 3 hours after the last observed activity at 18:00 (Weathers and Sullivan 1993).

Metabolic Rate during the Day (H_{dt}). Cardueline finches have elevated metabolic rates during the day that are approximately 20% higher than the basal metabolic rate (Aschoff and Pohl 1970). This elevated metabolic rate starts within minutes of light appearing (Pohl 1977, Berman and Meltzer 1978). The daytime (active phase) metabolism period started at 06:00 (approximately one half hour before sunrise) and ended at 21:00.

Thermoregulation

Accurate estimates of thermoregulatory costs in time-energy budgets must account for the effects of shortwave radiation and wind on transfer of heat (Bakken 1976, 1980, Weathers et al. 1984, Williams and Nagy 1984, Buttemer et al. 1986, Weathers and Sullivan 1993). Standard operative temperature (T_{es}), which defines "the thermal equivalence of two environments with different air temperatures, wind velocities, and radiation levels" (Bakken, 1980), uses only one or two parameters to describe the thermal environment, making estimates of thermoregulatory effects easier to calculate. Bakken (1990) developed a general passerine T_{es} scale to determine the effect of wind on energy rates (Eq. 1):

$$T_{es} = T_b - (1 + 0.26\sqrt{u})(T_b - T_e) \qquad \text{(Eq. 1)}$$

where T_{es} = standard operative temperature (°C)

T_b = body temperature (°C)

T_e = operative temperature (°C)

u = wind speed (m/s)

This equation was used to determine the operative temperature for Red Crossbills during the field study, which was then assigned to an equation quantifying the effects of temperature on crossbill energy use.

Thermoregulation during the Day. The daytime operative temperature (calculated from Eq. 1) was, on average, above the lower critical temperature (LCT) of 15 °C (Dawson and Tordoff 1964). This suggests that the crossbills did not have to allocate energy for thermoregulation during the day. Therefore, no thermoregulatory costs were assigned during daylight hours (06:00-21:00).

Thermoregulation at Night. An equation (Eq. 2) describing thermoregulatory costs (Benkman 1990) extrapolated from Dawson and Tordoff (1964) was used to determine transfer of energy in response to operative temperatures below LCT (at night).

$$TR = 1.532 - 0.0423\ [^{\circ}C]. \qquad \text{(Eq. 2)}$$

where [°C] = average daily minimum temperature (replaced by standard operative temperature. T_{es})

The basal metabolic rate was multiplied by TR (thermoregulatory costs). This cost factor (TR) was calculated to be 1.324 x H_{nt}.

Alert Perching. Individuals in a flock often scan for predators while resting. This is what we termed 'alert perching'. It is slightly more costly than being at rest because of head movements. The assigned cost used was an average of conversion factors from 3 studies: 0.5 x H_{nt} (Holmes et al. 1979); 0.7 x H_{nt} (Mugaas and King 1981); and 0.26 x H_{nt} (Weathers and Sullivan 1993). The cost assigned for alert perching was 0.5 x H_{nt}.

Preening. Preening was assigned a cost of 0.8 x H_{nt} (Williams and Nagy 1984). This activity was more costly than alert perching because the bird is more active, but less costly than most other activities.

Locomotion. Red Crossbills hop in order to navigate tree branches and also to forage for grit on the ground. The cost allocated to this activity was 1.0 x H_{nt}, identical to Mugaas and King (1981) and comparable to Weathers and Sullivan (1993) who used a factor of

0.98.

Flight. Using Norberg's (1996) equation for the metabolic cost of flight, the cost conversion used for flight in Red Crossbills was 9.06. This cost factor approximated flight costs allocated by Holmes et al. (10; 1979) and Weathers and Sullivan (10.1; 1993).

Foraging

Foraging on Conifer Cones and for Grit. The cost of foraging on conifer seeds (exclusively white pine (*Pinus strobus* L.) and for grit was 2.5 x H_{nt} (Benkman 1990).

Foraging on Dead Wood (Alnus incana var. *rugosa* and white spruce (*Picea glauca*) bark). Red Crossbills were observed foraging on dead alder (*Alnus rugosa*) each day of the field observations. They also picked at and consumed the bark of dead white spruce. The cost allocated to this activity was 1.5 x H_{nt}. This cost was similar to alert perching, but higher because energy is required to pull wood from the stump, or pull bark off the branch. It was similar to extracting seeds from cones, but probably less costly because less movement was required. We assumed this activity resulted in a net cost in terms of energy acquisition, unlike foraging for seeds, although nutrients were likely obtained during this activity.

Other Activities. Activities such as bathing, social interaction, and playing, which occurred infrequently (often less than 1% of a day), were grouped together and assigned a cost factor of 0.3 (Williams and Nagy 1984).

Moulting. Moulting patterns for North American Red Crossbills are similar to those of European birds (T. Hahn in Adkisson 1996). Red Crossbills commonly undergo definitive prebasic moult from August to October (Bailey and Niedrach. 1953, Newton 1972), and sometimes breed while they are moulting (Newton 1972). Red Crossbills take at least 12 weeks to moult (Newton 1972). An equation derived by Kendeigh et al. (1977) can be used to calculate the total cost of moulting. Although the cost of plumage replacement is independent of temperature, the actual cost to the individual depends on ambient temperature (Kendeigh et al. 1977, Murphy 1996). Therefore, Kendeigh et al.'s formula (1977: Figure 5.9) relating actual cost of moult to average ambient temperature was used to calculate the conversion factor for this process in Red Crossbills. The resulting daily cost was approximately 0.056 x H_{nt}, for 84 days.

Costs Associated with Reproduction

The Five Stages of the Reproductive Cycle

Cost equations and descriptions for reproduction are shown in Table 2.2.

1. Nest Construction (nc)

Since female crossbills generally build the nest (Snyder and Cassel 1951, Snyder 1954, Bent 1968, Newton 1972), energetic costs associated with this task were assigned only to females. To represent this cost, time spent flying was increased by 25% (or 4.65 min). This activity is intermittent and female crossbills often search for nest material close to a nest location, thus requiring few long distance flights (Baily 1953). Studies indicate that duration of nest construction is 3-5 days (Wilson 1932, Baily 1953). Three days was used here since this seemed to agree with data for other small passerines (Welty and Baptista 1990). Male costs during this stage were identical to nonbreeding costs.

2. Egg Production (egg)

Energetic costs for a female during the breeding season usually peak during egg synthesis (Ricklefs 1974, Walsberg 1983). The cost of egg production used was 0.41 x H_{nt} (Rahn et al. 1985), allocated over a 24 hour period. This cost was comparable to King (1973) (0.45-0.58) and Ricklefs (1974) (0.45). We assumed that 7 days were required to produce and lay a 3-egg clutch (Krementz and Ankney 1986, Benkman 1990). There were no additional costs to the male during this reproductive stage.

3. Incubation (inc)

Red Crossbills exhibit assisted gyneparental incubation (Williams, 1996). However, as the female incubates, the male feeds her (Lawrence 1949, Snyder and Cassel 1951, Snyder 1954, Newton 1972). The female rarely gets off the nest while incubating, therefore, to simplify the model, we assumed that she stayed on the nest during the entire incubation period of 14 days (Lawrence 1949, Benkman 1990). Within the thermal neutral zone, females passively supply the heat required to incubate eggs, therefore the cost of keeping the eggs warm is negligible (King 1973, Walsberg and King 1978, Williams 1996). FMR of the female during this period was simply her daily basal metabolic rate (H_{dt}) during the day, plus thermoregulatory costs at night (outside of the thermal neutral zone). These costs were added to the male's energy budget because he was solely responsible for providing her with the necessary energy to survive this period.

4. Nestling Care (nestl)

Weathers (1992) calculated the total energy metabolized (TME) by nestlings, from hatching to fledging:

$$\text{TME} = 28.43\ M^{1.06} \qquad \text{(Eq. 3)}$$

where TME = kJ/fledging, and M = fledging mass (g)

This equation gives the total energy cost of development. The total amount of food that the parents must provide the nestlings in order to meet metabolic needs (ie. heat, production, and growth) can be calculated from this. This cost was divided between both parents who shared provisioning of the nestlings (Lawrence 1949, Baily 1953, Snyder 1954). The resulting cost was multiplied by three to account for the average clutch size (Bailey and Niedrach 1953, Baily 1953, Newton 1972), and then corrected for assimilation efficiency (actual energy metabolized).

5. Fledgling Provisioning (fledg)

Red Crossbills fledge with mandibles not yet crossed (Lawrence 1949), requiring that the parents provide them with food until the bills cross, enabling the young to extract seeds from conifer cones on their own. Because the data indicated that immature crossbills behaved similarly to adults, in accordance with Benkman (1989), the daily activities of immatures were assumed to be identical to nonbreeding adults. Immature crossbills were still being fed by adults (although they attempted to extract seeds from cones), therefore that parental cost was written into this energy budget. The mass of fledglings was estimated to be 84% of adult mass (33.0g), an average of measured weights in three other studies (86% in Baily 1953; 75% in Ternovskij 1954; 90% in Benkman 1989). Adopting this weight, the time to fledge (t_{fl}, in days) was calculated using Weathers (1992):

$$t_{fl} = 7.97\ M^{0.295} = 21 \text{ days}$$

Twenty-one days was in accordance with other studies (Lawrence 1949, Baily 1953, Newton 1972). We assumed that another two weeks were required until the fledglings were able to forage on their own (Lawrence 1949). Three young were considered to have fledged from each nest (Benkman 1989).

Calculation of Seeds Required to meet FMRs

Personnel at the Petawawa Research Forest (Natural Resources Canada) took inventory of the white pine seedfall in the region using seed traps in the fall of 1998. We used average seed weight during the heaviest seedfall period (27 August to 3 September) in our calculations. *Pinus strobus* seeds of this weight released an average of 6.110 kcal/g in a bomb calorimetry analysis performed in the laboratory (Crampton Nutrition Lab, McGill University). This caloric value was in the range (5627-7117 cal/g of dry weight) identified by Long (1934) for various species of *Pinus*. The following equation was used to calculate the number of seeds necessary to meet the FMR*i*:

$$s = \frac{\mathrm{FMR}i}{\mathrm{m(c)}} \qquad \text{(Eq. 4)}$$

where s = number of seeds (seeds day^{-1})

$FMRi = FMR_{non}, FMR_{nc}, FMR_{egg}, FMR_{inc}, FMR_{nestl}$ or FMR_{fledg} (kcal day^{-1})
m = mass * $seed^{-1}$ (g * $seed^{-1}$)
c = caloric value of seed (kcal * g^{-1})

Not all ingested food is metabolized. The metabolizable energy coefficient (MEC) is the rate at which ingested food is digested (Kendeigh et al. 1977). To determine the number of seeds required to meet energetic requirements of Red Crossbills, the amount of energy ingested must be adjusted to determine net energy intake. An assimilation efficiency of 80% was applied to the FMRs (Gibb 1957, Turcek 1959, Myrcha et al. 1973, Willson and Harmeson 1973, Benkman 1990). Although this assimilation efficiency can vary among and even within bird species, specialists such as crossbills experience less variance in their digestive efficiencies (Shuman et al. 1989).

RESULTS

Observational Data

For all categories except flying, moving and foraging in white pine, the effect of duration of observation was insignificant ($p > 0.05$; Student Newman Keul test). In order to simplify the analysis and to make assumptions for an average day, all observations were pooled (Table 2.3).

Period of Thermoregulation

Average temperatures in Algonquin Park were consistently below the LCT at night. The birds had to thermoregulate nocturnally throughout the field study (Table 2.4).

Time Spent in Activities

The birds spent most of their time roosting, and perched (Table 2.5). They foraged on white pine seeds for a small proportion (5%) of daytime hours. Flying, which is the most expensive activity, was limited to approximately 20 minutes/day.

Costs Associated with Reproduction

Additional costs of reproductive activities are highest during the fledgling and reproductive stages (Table 2.6). Female egg production costs were higher than any non-breeding activity.

Calculated FMR

Although on average the fledgling stage required most energy per day during the breeding season (Table 2.7), the total energetic cost of nestlings exceeded fledgling provisioning costs. Incubation was the least costly phase on a per day basis, and nest construction was the least costly phase in terms of total energetic cost. Total energetic requirements for the nestling period were 3 times incubation costs, and almost 5 times egg production needs. Daily nest construction costs were almost identical to nonbreeding costs. Resultant FMR as multiples of basal metabolic rates were as follows: FMR_{non} 1.76 (both sexes); FMR_{nc} 1.79 (female) and 1.76 (male); FMR_{egg} 2.17 (female) and 1.76 (male): FMR_{inc} 1.25 (female) and 1.76 (male); FMR_{nestl} 3.16 (both); and FMR_{fledg} 3.99 (both). The average daily costs of reproduction for the female (31.99 kcal day^{-1}) were 2.71 x H_{nt} and for the male (32.85 kcal day^{-1}) were 2.79 x H_{nt}. Total net cost of reproduction was 3825.19 kilocalories.

Conifer Seed Production (Autumn, 1998) in Algonquin Park and Surrounding Region

Peak seedfall at Petawawa, Ontario, in 1998 occurred during the week of 27 August to 3 September (Table 2.8). Average seed weights were measured and corresponded to weights of large seeds obtained from the Ontario Tree Seed Plant, Angus, Ontario. Corresponding reproductive phases of an average individual were allocated to seedfall stage where relevant (Table 2.8).

Seeds Required to Meet Field Metabolic Demands

The necessary energy intake required (FMR_i /0.80) to meet FMR_i is expressed as the number of seeds and presented in Table 2.9. Highest number of seeds required per day corresponded to most costly periods, per average day (fledgling stage), and in total (nestling stage). The female required an energy intake of 2359.05 kilocalories or 16,787 seeds and the male needed a total intake of 2422.4 kilocalories or 17,238 seeds over the entire breeding season. The total cost of reproduction for the pair was 4781.5 kilocalories, requiring the birds to consume 34,025 white pine seeds (Table 2.9).

Seed Intake Rates

During this study, the average observed intake rate was 2.32 mg/sec, and 61.8% of intake rates were between 1 and 3 mg/sec. Using this average intake rate and the daily nonbreeding FMR requirement of 185 seeds/individual, Red Crossbills could meet their daily energy requirements by foraging for 0.500 hrs. The birds foraged on white pine seeds for approximately 0.753 hr/day.

DISCUSSION

The average Red Crossbill breeding season used for this model lasted 42 days from the start of egg laying to fledging of young, which was similar to what other studies have observed (Baily 1953, Newton 1972, Benkman 1989). The model assumed that no breeding phases overlapped. For example, the female only commenced incubation once all eggs were laid. In temperatures similar to our field season, Red Crossbills started incubating eggs only after all were laid (Baily 1953, Newton 1972).

During reproductive phases when the male was not directly involved (nest construction, egg production, and incubation), his daily activity, and thus energy expenditure, was considered to be identical to that during unmated phases. Males of many species change their behavior during the breeding season (*i.e.* Schnase et al. 1991). However, since crossbills do not defend territories (Newton 1972, Benkman 1988), males were considered to behave similarly to unmated stages during those times.

Time Spent in Activities

Benkman (1990) constructed an energy budget for Red Crossbills with two main activities in his model: flying and foraging. He assumed that 6% of daytime hours were spent flying. However, the birds in this study spent only 2% of daytime hours flying. This time approximation may have been an underestimate of actual time spent flying because it was very difficult to follow the birds once they had taken flight. Birds disappeared from view after a few minutes of flight, and even if they continued to fly, the timing of that particular activity stopped once they were out of view. Only the observed flight time was used in the model, because flight distances varied and could not be estimated once observers lost sight of them.

Red Crossbills spent about 6.9% of daytime hours foraging, compared to an estimated 94% in Benkman (1990). Crossbills, during plentiful cone years (such as this one), probably do not need to spend as much time foraging because of high intake rates, associated with heavy seed weights and high concentrations of seeds. Cones (and therefore seeds) were plentiful in all areas where observations were made, so calculated foraging time allotments appear reasonable. Red Crossbills could meet their daily energy requirements by foraging for 0.50 hrs. The birds were observed foraging on white pine an average of 0.75 hrs/day, so it appears that this foraging rate was adequate to meet nonbreeding energetic needs. During the field season, most birds had already bred, since fledged young were observed during the first week of observations, and adults were observed feeding fledglings on several occasions. This could explain the additional time (0.25 hrs) observed foraging.

Time spent preening (3.78%) was considerably greater than in other studies, (*i.e.* 1.1% for Savannah Sparrows *Passerculus sandwichensis* in Williams and Nagy 1984). Red Crossbills handled conifer cones containing large quantities of sap, probably requiring more preening than other granivorous birds.

Red crossbills appeared to conform to Wilson's (1975) "principle of stringency" (where individuals use uncommitted time as a 'safety net' in case of harsh weather or food shortage) by spending a high percentage (37%) of daylight hours quietly perched.

Presumably this time spent non-active was energy-saving. Individuals from other studies spent similar amounts of time perching (Ettinger and King 1980, Weathers and Sullivan 1989, Schnase et al. 1991).

Foraging on Dead Wood and Grit Consumption

Red Crossbills have been recorded frequenting mineral sources (calcium or sodium) (Aldrich 1939, Marshall 1940, Dawson et al. 1965, Payne 1972, Bennetts and Hutto 1985, Tozer 1994). As well, White-winged Crossbills have been observed foraging on snags of black spruce (*Picea mariana*) and eastern larch (*Larix laricina*), with no evidence of insects, mineral deposits, fungi, or other organisms (Crins and McRae 1998). No organisms were found on the dead alder, although the rotted state of the wood was clear evidence that fungi had reduced the lignin and hemicellulose content of the cell walls, perhaps increasing food value of the wood to the birds. We clearly observed the birds eating the dead wood. Tozer (1994) also observed White-Winged Crossbills eating the exposed inner wood of stumps that may have once been submerged in muddy, roadside water. He suggested that minerals occurred in the wood, attracting crossbills to the mineral source. Parrot Crossbills *(Loxia pytyopsittacus)* have been observed picking at decaying logs whose outer layers were rich in ash and calcium (Pulliainen et al. 1978). Although several reasons have been given to explain unconventional consumption of wood (*e.g.* anti-sap properties (C. Benkman, pers. comm.), taste, mineral deficiencies), a definite benefit has not been identified. However, small concentrations of salt are applied to the main road in the study area during winter (P. Dawson, Ontario Ministry of Natural Resources, pers. comm.). The alder stumps were along that road, in a dry wetland, suggesting mineral runoff. It is possible that the sodium was absorbed by adjacent wetlands and attracted the birds.

Grit is important for grinding seeds, facilitating digestion of this food in granivorous birds. Red Crossbills and other granivorous birds regularly ingest grit (Benkman 1992), as did the birds during this study. Grit may also be a source of calcium (Benkman 1990). The birds foraged for grit for approximately 17 minutes/day, consistent with Benkman's (1990) estimate of 20 min/day. Robel and Bisset (1979) proposed that Bobwhites *(Colinus virginianus)* ate grit for possible soluble nutrients.

Calculated Costs and Resultant Field Metabolic Rates

Basal metabolic rate (H_{nt}) accounted for 64% of total daily energy expenditure by Red Crossbills in the fall of 1998, similar to rates found in the literature (40-60%, Walsberg 1983).

Thermoregulation

Calculated thermoregulatory costs were likely underestimated (32% of H_{nt}). Wind measurements used to determine standard operative temperature (T_{es}) were taken at a lower height than where Red Crossbills foraged in the canopy of large white pine trees, where wind speed was greater. Even modest breezes have a significant effect on metabolic rates. For example, breezes of just 0.1m/s and 0.5m/s increased energy expenditure of Acorn Woodpeckers *(Melanerpes formicivorus)* by 5.6% and 12.0%, respectively (DuPlessis et al. 1994). Interestingly though, Red Crossbills did not appear to alter their behavior in the presence of strong winds during the field season.

Energy Costs during Reproduction

Egg Production

Although the estimated cost of production of eggs was similar to other studies, *i.e.*; 45-58% of BMR (King 1973); 45% (Ricklefs 1974); 38% (Dol'nik and Dol'nik 1981); 41% (Walsberg 1983), this may have been an underestimate. If several eggs at varying stages of completion are being produced in the ovary simultaneously, the cost could be greater than the 41% we applied (Carey 1996). If so, our allocated cost may represent the minimum amount of energy required. During egg production, the female's total daily energy costs were only 29% of costs for nestling care, similar to that found for House Sparrows (*Passer domesticus*) (Krementz and Ankney 1986). It appears that Red Crossbill reproduction was not solely driven by having sufficient energy for egg production, as suggested by Walsberg (1983), because this reproductive period was not the most costly for the female. Since female Red Crossbills assisted in feeding the young, her costs peaked later in the breeding season once the young had hatched.

Incubation

The energy cost of incubation has been debated in the literature for some time. Some authors argue that female incubation costs are similar or even less than those of a non-incubating bird because of heat generated and kept within the nest (King 1973, Walsberg and King 1978, Ettinger and King 1980, Mugaas and King 1981, Walsberg 1983). Incubation likely requires minimal energy expenditure, and for 9 passerine species, incubation costs were typically lower than for other reproductive stages (Weathers and Sullivan 1989).

Parental Effort during Nestling and Fledgling Phases

Parental effort during reproduction peaked during the nestling and fledgling phases, consistent with the literature (Walsberg 1983, Daan et al. 1990). The nestling period is often viewed as the 'bottleneck' in the reproductive cycle (Drent and Daan 1980) and much information exists regarding its costs. Unlike the nestling stage, the fledgling stage has been poorly examined.

Benkman (1990) used an equation from Walsberg (1983) to determine nestling costs to parents. We chose not to use it because resultant nestling costs from this equation appeared to be excessive: they were larger than peak costs calculated using recent information from Weathers (1992). The peak daily metabolizable energy (DME) is "the maximum rate at which parents must provision their nestlings" (Weathers 1992), not an average rate. DME reaches a peak about halfway through the nestling period for most species (Drent and Daan 1980).

Data for 26 bird species feeding altricial young showed that the highest daily energy expenditure occurred while the parents fed the nestlings (Daan et al. 1990). This cost varied according to foraging behavior; aerial foragers having higher feeding costs than ground foragers (Williams and Nagy 1984, Bryant et al. 1985). Weathers and Sullivan (1989) looked at reproductive costs for 9 passerine species and found that the average nestling period cost for parents was 3.38 x H_{nt} (range: 1.8-5.2). Drent and Daan (1980) found that when parents fed young, they increased their energy level by 33-50% over non-reproductive levels. Red Crossbills, on average, expended energy at 3.16 x H_{nt} for the 21 days of the nestling period, for a 79% increase over non-reproductive levels (Table 2.7). This cost may not have been constant every day, or for both parents. During the first 4-5 days after hatching, the female broods the young almost constantly without help from the male (Lawrence 1949, Snyder 1954). The male must provide for her and the three nestlings for those first days, and therefore his peak cost during reproduction occurs during that time (Benkman 1990). This suggests that energetic costs to parents during the nestling period varied, and the first 4-5 days may have been the 'bottleneck' period for the males when most food (energy) was required. While this fact is less important in terms of total energy required for breeding (because the cost is the total for nestlings for the entire nestling period), it is important ecologically because there would have to be sufficient food resources available to the male during the first 4-5 days after hatching.

Parental costs during the nestling period may have, in reality, been higher than what was estimated by this model. Without specific data on feeding rates to nestlings, assumptions about additional energy expenditure due to increased flight activities could not be made. As well as provisioning the young with food required to meet their energetic needs (accounted for in the model), parents likely had increased daily costs associated with gathering this additional food. This would require more flights to and from the nest, reducing time spent perching. Walsberg (1983) suggested that a parent would have to increase its foraging rate 2-3 times its non-breeding rate in order to provide for nestlings. Although increased foraging time during the nestling period was not built into the model, the resulting FMR_{nestl} is indicative of this cost. If Red Crossbills were to meet the average daily nestling energy requirement suggested by the model, they would have to forage for 25 more minutes/day during the nestling period in order to meet their own as well as nestling demands (331 seeds/day, Table 2.9). This represents an increase of 1.79 times their non-breeding foraging rate, similar to what Walsberg (1983) predicted.

Another factor increasing daily energy expenditure of parents during the nestling period is time to fledge. If the young fledge in 2 weeks instead of 3, the daily costs to parents are higher, although total cost/nestling does not change.

The average daily energy required to care for fledglings was higher than during any other period, including the nestling period (Table 2.7). Few studies describe energetic costs to parents during this period, although Smith (1978) found that feeding rates of 13-day old fledgling Song Sparrows (*Melospiza melodia*) were 44% higher than those of 7-8 day old nestlings. Holmes et al. (1979) found equal costs for both periods, and Biedenweg (1983) found results similar to those presented here. On average, for the two weeks, the parents were expending energy at 3.99 x H_{nt}, or a 26% increase above daily nestling period energy expenditures.

Energetic costs during the fledgling period may also have been underestimated. In particular, thermoregulatory costs for fledglings may be higher than estimates used in this study because there is no thermoregulatory assistance from the brood in the nest (Royama 1966, Murphy and Haukioja 1986). As well, the parents may have fed the fledglings for longer than two weeks (*e.g.* 33 days as in Baily 1953) as suggested by Newton (1972) who found that crossbills can only effectively feed themselves on their 45th day. Fourteen days was used because it seemed reasonable given evidence from other field studies that parents only occasionally fed young after this period (Griscom 1937, Lawrence 1949).

More likely, estimated costs for the fledgling period are in excess of true costs. This is because for many species the care given to newly fledged young continues at about the same rate for several days, but then declines gradually until ending completely, 10-14 days after fledging (Kendeigh et al. 1977). We assumed that the costs were the same for every day of the two week period. In reality, their foraging efficiency should have increased as they aged because their ability to extract seeds from cones improves with experience and as their bills grow to cross. When food intake rates were high in White-winged Crossbills, females left males to feed the fledglings on their own and she presumably left to renest (Benkman 1989). If intake rates were low, the female stayed to help feed the fledglings. This suggests that with sufficient resources, the cost for one parent is not excessive.

Average Daily Energy Expenditure during Reproduction (all stages combined)

The average daily energy expenditure for Red Crossbills during reproduction (2.71 x H_{nt} for females, 2.79 x H_{nt} for males) was similar to other reported studies: 2.0 to 5.0 (9 species of passerines; Weathers and Sullivan 1989), 1.89 to 5.59 (26 species; Daan et al. 1990), 3.5 to 4.2 (Drent and Daan 1980), and below the maximum level of 5 (across several taxa) suggested by Bryant (1997). For all stages of reproduction, calculated FMRs were within the ranges suggested above and therefore seem reasonable for this species. Allometric equations have also been used to estimate field metabolic rates (FMR) during reproduction. Nagy's (1987) allometric equation for breeding FMR gives a value of 2.5 x H_{nt}, which is closer to the value of the nonbreeding FMR than any breeding FMR we calculated. However, allometric equations using mass are not desirable for calculating daily energy expenditure because environmental influences and population demography have a significant impact on individual energy costs (Daan et al. 1990).

Many studies have estimated energy expenditure of reproductive birds in nature. Understanding more completely the relative costs of different stages of reproduction can assist in ascertaining limiting factors for breeding birds. Estimates of energy expenditure are often determined from activity budgets resulting from observations in the field, coupled with costs allocated to activities referenced from literature suggesting appropriate energy expenditures. Time-energy budgets based on doubly-labeled water (DLW) have revealed similar results when compared to studies using direct measurements of energy expenditure (Weathers and Nagy 1980, Williams and Nagy 1984, Bryant et al. 1985, Masman et al. 1988). Williams and Nagy (1984) suggested that differences in individuals were more significant than differences among species for varied methods. Time energy budgets are sufficient for making broad assumptions when more specific calculations (*i.e.* DLW) are unavailable.

The accuracy of a time-budget depends on two main factors: the accuracy of the observations (actual *vs.* observed time allocations of activities) and the accuracy of the metabolic assignments (compared to the actual energy expenditure experienced by the individual) (Buttemer et al. 1986). There is always some observer bias associated with measurements of activity, and as a result, there could be inaccuracy related to measured durations of activities (Goldstein 1988). As well, the observation period was assumed to be an actual representation of the entire day. That is, we assumed that individuals behaved similarly when observers were not present, which could be false (Goldstein 1988). There could also be error resulting from the conversion of time to energy, which Goldstein (1988) suggested could be larger than 25%.

FMRs calculated from allometric equations were based solely on mass, and did not take into account two important factors: 1) mass varied daily and between seasons, populations, and individuals; and 2) since most equations were formulated based on studies of several species and were not 'specific' to the Red Crossbill, interspecific differences were not considered (Wiens and Farmer, 1996). The model was not adjusted for mass changes, but the objective was to determine energy requirements of an average Red Crossbill pair, not specific individuals, and therefore was not concerned with individual mass fluctuations. Although energy costs were not specific to *Loxia curvirostra*, many energy equations are based on mass, and are not species-specific (*e.g.* Weathers 1992).

Conifer Seed Production and the Timing of Crossbill Reproduction

Seed Intake Rates

Benkman (1990) measured intake rates of breeding and nonbreeding populations of Red Crossbills. His observed rates for breeding populations were similar to those found here, suggesting that the crossbills were experiencing intake rates high enough for reproduction to occur. Evidence of this was provided by our observations of family groups containing newly fledged young. The seed intake rates recorded were not during maximum seed availability, 27 August to 3 September (Table 2.8), thus rates should have been much greater earlier in the breeding season.

Seed Availability and the Timing of Reproduction

Benkman (1990) suggested that crossbills were sensitive to changes in intake rates, which in turn determined the timing of reproduction. He proposed that because of this sensitivity, breeding began when females had enough energy to produce the eggs and food would still be adequate the first week of the nestling stage. Intake rates must be high during both stages. Since the period of highest energy requirement/day was likely during the first 5 days of the nestling period, when the male provided for himself, his mate, and 3 nestlings, the week with the highest seed availability should be the optimum time for him to meet those energy demands (Table 2.8). Based on this assumption, young should have fledged by the time observations began on 18 September. Newly fledged young were seen during the first week of the field season. Seed availability was also high during 18-24 September when young fledged, another period of elevated energy requirements for the adults.

Limitations affecting Red Crossbill Reproduction

Earlier we suggested that either the nestling or fledgling phase, or both, constitute a critical period that would dictate the start and/or success of Red Crossbill reproduction. The energy constraint for reproduction in Yellow-eyed Juncos (*Junco phaeonotus*; Weathers and Sullivan 1989) was food limitation for fledglings. The inefficiency with which juveniles foraged was crucial because they could not provide for themselves without supplemental feeding from adults, even 4-7 weeks after fledging. Weathers and Sullivan (1993) stated that for many species "reproduction is timed to coincide with peak food availability not because adults are energy-limited but because juvenile birds are such inefficient foragers that they require abundant food in order to balance their energy budgets". This could be the case with Red Crossbills. Measured intake rates during the field season indicated that the adults did not have to forage for very long periods in order to meet energy demands for reproduction, and that fledged young had ample time available for foraging and increasing their efficiency because of plentiful food sources.

Red Crossbills could meet their daily energy demands during the autumn of 1998 in Algonquin Provincial Park, Ontario. Observed intake rates and foraging durations were sufficient to support daily activities, with additional energy available for providing fledged young with food they were not yet able to acquire on their own. Red Crossbills needed to consume 370 seeds/day during the non-breeding season in order to balance energy intake with expenditure. During the breeding season, 16,787 white pine seeds were consumed by females, and 17,238 by males. Therefore, in order for a pair of Red Crossbills to raise three young to a point when fledglings can provide for themselves, 34,025 available white pine seeds were required. Coupled with cone and seed production data for white pines, this information is useful for determining habitat requirements (ie. trees/ha or trees/stand) necessary for Red Crossbills to breed in the study region.

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Table 2.1: Symbols and cost factors used to calculate field metabolic rates (FMR) for Red Crossbill *(Loxia curvirostra)* activities in Algonquin Provincial Park, Ontario, September-October, 1998.

Symbol	Activity	Cost Factor (multiple of H_{nt})
nt	Roosting (night)	1
TRnt	Thermoregulation [a]	1.324
dt	Daytime	1.2
ap	Alert perching [a]	0.5
pr	Preening [a]	0.8
lo	Locomotion [a]	1
fl	Flight [a]	9.06
of	Foraging for seeds and for grit [a]	2.5
fod	Foraging on dead wood [a]	1.5
ot	Other [a]	0.3
mo	Molt [a]	0.056

[a] Conversion factors represent energy costs additional to basal metabolic rate (Hnt).

Table 2.2: Energetic costs associated with breeding stages for Red Crossbills *(Loxia curvirostra)* in Algonquin Provincial Park, Ontario, September-October, 1998.

Reproductive period (*i*)	**Duration (days)**	**Additional reproductive energy costs**	**Female's FMR equation (FMR*i*) ***	**Male's FMR equation (FMR*i*)***
1. Nest construction	3	Female builds nest, increased flying time	t_{fl} x 25%	No additional costs
2. Egg production	7	Female produces eggs	0.41 x H_{nt}	No additional costs
3. Incubation	14	Female incubates eggs alone, male feeds her	No additional costs	Female's FMRnon
4. Nestling care	21	Female broods constantly first 5 days, then shares feeding nestlings with male	TME = 28.43 $M^{1.06}$ kJ/chick x 3 chicks**	TME = 28.43 $M^{1.06}$ kJ/chick x 3 chicks**
5. Fledgling provisioning	14	Both feed fledglings until they are independent	FMR of 3 fledglings**	FMR of 3 fledglings**

*these are additional to daily costs outlined in FMR_{non}

** this is total cost for both adults

Table 2.3: Number of observations and their duration for Red Crossbills *(Loxia curvirostra)*, by age and gender, during September and October of 1998 in Algonquin Provincial Park, Ontario.

Gender	**# Obs**	**% Total observations**	**Total observation time (min)**	**% Total observation time**
Male	93	30.69	695.2	37.76
Female	82	27.06	594.8	32.31
Juvenile	51	16.83	237.7	12.91
Unknown	77	25.41	313.2	17.01
TOTAL	**303**	**100**	**1840.9**	**100**

Table 2.4: Weather data collected during the Red Crossbill *(Loxia curvirostra)* breeding season of 1998 in Algonquin Provincial Park, Ontario.

Time period	**Average wind speed (u) (m/s)**	**Average ambient temperature (°C)**	**Average radiation (% sunlight)**
Day	1.5395	15.96	58.9
Night	0.6963	10.99	0

*Day = 06:00 to 21:00; Night = 21:01 to 05:59

**Wind speed and ambient temperature provided by the Petawawa Research Forest, Petawawa, Ontario

Table 2.5: Time-energy allocation of activities exhibited by *Loxia curvirostra* during September and October, 1998, in Algonquin Provincial Park, Ontario.

Activity	**Percent of 24 hr period spent in activity**	**Total time (hr)**	**Metabolic rate (kcal hr^{-1})**	**Total energetic cost (kcal day^{-1})**
Roosting (nt) and Thermoregulation (TRnt)	37.5	9	0.650	5.851
Daytime BMR (dt)*	62.5	15	0.589	8.838
Alert perching (ap)	23	5.52	0.245	1.355
Preening (pr)	3.78	0.91	0.393	0.357
Locomotion (lo)	0.98	0.24	0.491	0.118
Flight (fl)	1.27	0.31	4.448	1.379
Foraging in white pine (for seeds) and for grit (fo)**	4.3	1.03	1.228	1.264
Foraging on dead wood (*Alnus rugosa* & other) (fod)	4.45	1.07	0.736	0.788
Other (ot)	5.22	1.25	0.147	0.184
Moult (mo)	100	24	0.027	0.656

* daytime BMR was concurrent with all activities except roosting, and was additional to activity costs

** foraging for white pine = 0.753 hr, grit = 0.281 hr

Table 2.6: Energetic costs associated with reproduction for Red Crossbills *(Loxia curvirostra)* in Algonquin Provincial Park, Ontario, September-October, 1998.

Reproductive stage	**Gender affected**	**Energetic cost of reproductive-related activity (kcal day^{-1}) ***
Nest Construction (nest)	♀	0.345
Egg Production (egg)	♀	4.831
Incubation (inc)	♂	no additional
Nestling Care (nestl)	both	32.84
Fledgling Provisioning (fledg)	both	52.35

* these costs are in addition to nonbreeding activities

Table 2.7: Calculated field metabolic rates (FMR) for Red Crossbills *(Loxia curvirostra)* in autumn.

Reproductive phase *(i)*	**Length (days)**	**Individual**	**FMR$_i$ (kcal day^{-1})**	**Cost of *i* (kcal bird^{-1})**	**Total cost of *i* (kcal)****
Nonbreeding		Female	20.79	-	-
		Male	20.79	-	-
Nest Construction	3	Female	21.13	63.39	125.76
		Male	20.79	62.37	
Egg Production	7	Female	25.62	179.34	324.87
		Male	20.79	145.53	
Incubation	14	Female	14.69	205.66	496.72
		Male	20.79	291.06	
Nestling Care*	21	Female	37.21	781.41	1562.82
		Male	37.21	781.41	
Fledgling Provisioning*	14	Female	46.97	657.58	1315.16
		Male	46.97	657.58	
TOTAL ($\sum i$)	**59**	**Female**	-	**1887.24**	**3825.19**
		Male	-	**1937.95**	

* FMR calculated for young is shared among both parents equally

**this total cost is for all individuals for reproductive phase

Table 2.8: Numbers and average weights of white pine seeds calculated from seedfall traps in 1998 at the Petawawa Research Forest, and corresponding reproductive phase of Red Crossbills *(Loxia curvirostra)*.

Date	**Number of seeds/trap**	**Average seed weight (g)**	**Corresponding reproductive phase of *Loxia curvirostra***
Aug. 20 - 27	3	n/a	Incubation (2nd of 2 weeks)
Aug. 28 - Sept. 3	66	0.023	Nestling care
Sept. 4 - 10	50	0.017	Nestling care
Sept. 11 - 17	12	0.018	Nestling care
Sept. 18 - 24	25	0.015	Young fledge
Sept. 25 - Oct. 1	8	0.015	
Oct. 2 - 8	18	0.014	
Oct. 9 - 15	2	0.012	
Oct. 16 - 29	3	0.012	
Oct. 30 - Nov. 19	2	0.019	

** the average weight is calculated from the resultant seedfall of the week leading up to that date

Table 2.9: Corrected field metabolic rates for pair of Red Crossbills *(Loxia curvirostra)* meeting reproductive requirements while foraging on white pine seeds in Algonquin Provincial Park, Ontario, 1998.

Reproductive stage *(i)*	**Total net FMR_i* (kcal day^{-1})**	**Necessary energy intake (kcal day^{-1})**	**Number of seeds required /day**	**Total seeds required for *i***
Nest construction	41.92	52.4	372.8	1119
Egg production	46.41	58.01	412.8	2890
Incubation	35.48	44.35	315.6	4418
Nestling care	74.42	93.03	661.9	13900
Fledgling provisioning	93.94	117.43	835.6	11698
TOTAL ($\sum i$)	**n/a**	**n/a**	**n/a**	**34025**
Nonbreeding	41.58	51.98	370	n/a

*FMR is the total of female and male FMRs

**Number of seeds required was based on average seed weight for heaviest seedfall week (Table 2.8)

See Eq 4 and Appendix 2 for methods for determining actual number of seeds required

CONNECTING STATEMENT

Chapter 2 in this thesis, ECOLOGICAL ENERGETICS OF BREEDING RED CROSSBILLS *(Loxia curvirostra)* IN ALGONQUIN PROVINCIAL PARK, ONTARIO, CANADA described daily activities of Red Crossbills during the breeding season and related energetic costs related to those activities. Chapter 3, THE EFFECTS OF LOGGING OLD-GROWTH WHITE PINE *(Pinus strobus)* ON RED CROSSBILL *(Loxia curvirostra)* DISTRIBUTION AND ABUNDANCE IN ALGONQUIN PROVINCIAL PARK, ONTARIO, CANADA compares historical and current optimal Red Crossbill habitat in the park. Using energetic requirements derived from chapter 2, potential numbers of breeding pairs can be estimated in historical and current stands. It is necessary to couple reproductive costs (in terms of white pine seeds) and availability of seeds in historical and current forest resources in order to better understand importance of habitats to Red Crossbills.

3. THE EFFECTS OF HISTORICAL LOGGING OF OLD-GROWTH WHITE PINE *(Pinus strobus)* ON RED CROSSBILL *(Loxia curvirostra)* DISTRIBUTION AND ABUNDANCE IN ALGONQUIN PROVINCIAL PARK, ONTARIO, CANADA

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ABSTRACT

Red Crossbills *(Loxia curvirostra)* are specialized conifer seed-eating birds which breed in Algonquin Provincial Park, Ontario in years of good white pine *(Pinus strobus* L.*)* seed production. A study was conducted in Algonquin Park to: 1) determine the historical (ca. 1850s) and current extent of Red Crossbill habitat; and to 2) compare potential numbers of breeding pairs supported by early settlement (1850s) and currently available habitat. Field studies determined the number of white pines per hectare in boreal mixed and deciduous stands, currently and historically. A GIS based pine-soils model estimated potential area of pine stands. Results indicate that optimal Red Crossbill habitat (pine stands with >70% white pine) may currently occupy about half of the area it did before logging occurred. Therefore, we suggest that potential numbers of breeding pairs of Red Crossbills are, at a minimum, approximately 50% of what they were during early European settlement.

INTRODUCTION

Several species in six families of birds exploit conifer seeds to varying degrees (Smith and Balda 1979). Many of these are members of the family Fringillidae, and they rely on seeds as an important food source (Newton 1967, 1972). The most specialized of these seed-eating species are the crossbills *(Loxia* spp.). Crossbills are unique for two reasons: 1) they depend on conifer seeds throughout the year (Benkman 1987a) as compared to other seed-eaters that switch to other foods (*i.e.* insects or berries) seasonally or during times of seed scarcity; and 2) they are inefficient at foraging on other food sources (Benkman 1988a), feeding almost exclusively on conifer seeds (Bailey and Niedrach 1953, Bent 1968, Newton 1972, Benkman 1987a, 1990). Crossbills have a highly specialized mandibular structure enabling them to forage for seeds in closed, as well as open, cones (Smith and Balda 1979, Benkman 1988a). As a result of this dependence on conifer seeds, crossbills irregularly undergo large movements in search of sufficient crops (Griscom 1937, Newton 1970, Benkman 1987a, Senar et al. 1993). As well, crossbill densities have been linked to cone crop sizes (Reinikainen 1937, Génard and Lescourret 1987).

Red Crossbills *(Loxia curvirostra)* are commonly associated with pine forests (Lawrence 1949, Benkman 1987a, b). Groth (1991, 1993) identified eight types, each with its own morphology and call. Benkman (1987a) suggested that each Red Crossbill type has an optimal bill size for foraging on its key conifer (Benkman 1993a). In Ontario, eastern white pine *(Pinus strobus* L.*)* seed production is particularly important for Red Crossbills (Lawrence 1949, Ross and Ross 1950, Benkman 1987a). Birds often breed in the autumn when white pine cone crops mature and seeds are available to reproductive birds (Griscom 1937, Benkman 1990).

Benkman (1993b) argued that mature trees (older forests) were crucial to Red Crossbills because of crop stability and high seed production. Dickerman (1987) suggested that the "Old Northeastern" subspecies almost went extinct due to loss of old-growth eastern white pine, and that bird numbers recovered only after sufficient areas of forests had matured. Dickerman concluded this by assessing trends in collected specimens and determining historical abundances from the trends observed. Another method of estimating changes from historical abundance and distribution of Red Crossbills is to evaluate historical vs. current available habitat. Using eastern white pine as a measure of seed production (seeds produced/tree), an estimate of Red Crossbill populations supported by available seeds can be made using number of trees present in a landscape.

Eastern white pine (*Pinus strobus* L.) is, and has been historically, an important softwood timber species in Canada, and demand for it has been high over the years (Wray 1986). Its distribution in eastern North America has undergone significant changes due to human pressure on the landscape, specifically logging. In the mid-1800s it was thought that the white pine supply in Ontario was "inexhaustible" and that it could last 700 years (Wray 1986). Most of the old-growth white pine stands in central Ontario had disappeared by the early 1900s (Aird 1985, Wray 1986).

Algonquin Provincial Park in Ontario has been logged for white pine since the early 1800s. The eastern portion, (approximately one third of the park), has sandy, outwash soils that support aspen or pine forests, mostly white, red *(P. resinosa)* and some jack pine *(P. banksiana)*. This region was predominantly pine in the 1830s when the loggers first arrived, and is still dominated by pine today (Strickland 1993). This side of the park and into the Petawawa region of the Ottawa River valley is the largest, most extensive area of eastern white pine in North America (Rajora et al. 1998). Although the stand types may not have changed, there is one major difference: the gigantic trees that once existed are there no longer.

The western region of Algonquin Park is a different story altogether. Although white pine currently constitutes a small portion of this region, there is considerable information to suggest that it once had a more significant component of white pine than today. White pine was logged intensively on this side of the park and few remaining examples of that historical landscape exist. There used to be a strong white pine component in the west, mixed with hardwoods, but also forming pure stands and groves (Martin 1959). Strickland (1993) said that "big pine dominated just about all of the Algonquin landscape".

The objectives of this study were: 1) to determine historical distribution of mature white pines in three stand types in Algonquin Park; 2) to compare early settlement (1850s) to present day (1990s) white pine distribution and abundance; 3) to determine white pine seed production (both time periods) for stands that Red Crossbills use; and 4) to estimate

Red Crossbill populations that could be supported by historical and current forest resources (white pine seed trees) in the park.

METHODS

Study Region

Algonquin Provincial Park, Ontario (48°30' N, 78°40' W) is located in the Great Lakes-St. Lawrence forest region (Rowe 1972) and consists of 760,000 ha of forest. The park's forests may be divided into the western (two-thirds) and eastern (one-third) sides, based on geological, climatic, and soils differences. The western side has higher rolling hills, may of them over 500 m above sea level, and supports predominantly northern hardwoods (sugar maple *Acer saccharum* and American beech *Fagus grandifolia*) on hills, and coniferous (*e.g.* spruces *Picea spp.*, balsam fir *Abies balsamea*) forests in the lowlands. The eastern side of the park is characterized by large expanses of white pine and red pine forests.

I. Historical Distribution of White Pine

The historical (1850s) distribution of white pine in Algonquin Park was determined using three methods: 1) field studies; 2) a Geographic Information System (GIS) pine-soil model; and 3) a literature search for relevant information. Since white pine can form monospecific stands or, alternately, exist as supercanopy trees in mixed forests of the Great Lakes region (Burns and Honkala 1990), it was necessary to determine white pine abundance in different forest types. The goal of the field study was to estimate historical components of white pine in two stand types: 1) tolerant hardwoods; and 2) mixed deciduous-coniferous forests. The GIS pine-soil model was created as a means to estimate or predict the area of pine stands (>70% pine) that has disappeared since the mid 1800s.

1. ***Field Studies***

Study Area and Selection of Sample Plots

Field work was conducted in September and October of 1997 and May to July of 1998 in Algonquin Provincial Park, in areas dominated by upland deciduous forests. Two related but separate studies were conducted: 1) a random survey and 2) a nonrandom survey.

Random Survey

The first study was a random survey of 4 townships within the park: Lawrence, Dickson, Clancy and Clyde. These townships were chosen because a previous analysis (Leadbitter 2000) of crown surveyors' data from 1860-1890 enabled a comparison of our results to historical records. Each township was divided into four equal quadrats, and 1-3 forested stands were randomly chosen using an overlay grid in three of four quadrats of each township. For logistical reasons, each stand was within 500 metres of an access point (road or trail) and have sufficient area to enable survey methods (about 300 x 200 m minimum size). Each stand was categorized according to the following forest types:
1) tolerant hardwoods: these sites were predominantly deciduous, upland, and fresh to moist sites dominated by sugar maple, American beech, yellow birch *(Betula alleghaniensis)*, and hemlock *(Tsuga canadensis);*
2) boreal-type mixed woods: these sites were typical of boreal forest mixed coniferous–deciduous stands, usually in lowland areas, or cooler, shaded hill slopes and consisting of black spruce *(Picea mariana)*, white spruce *(P. glauca)*, balsam fir, eastern white cedar *(Thuja occidentalis)*, white birch *(B. papyrifera)*, poplar *(Populus tremuloides)*, and red maple *(A. rubrum);*
3) pine forests: these were stands of white pine and red pine, with some jack pine, usually located on sandy soils. Ideally, one stand of each type was sampled in each quadrat within a township, depending on available stand types in quadrats. Some quadrats had no accessible pine stands and therefore could not be sampled.

Nearest Neighbor Sampling Method

For each survey, we assumed that stumps of white pine that had been logged between 1800 and 1890 were still present and distinguishable (Martin 1959, Quinby 1991, D. Voigt, pers. comm.). Martin (1959) noted that white pine stumps left from logging operations in the 19th century were in a "good state of preservation". Based on known periods of logging at locations around the park, we believe that this assumption is valid. Also, loggers in the 19th century used axes or crosscut saws which involved cutting trees higher than with chainsaws (which were used after the 1940s) (Strickland 1996). We therefore only sampled stumps that we believed were cut and existed in the forest before 1940. The exact date that the tree was cut was not important because we were only concerned with whether or not the tree was a mature individual in the 1850s.

At each site (stand), three transects of 250 m length each were sampled in a U shape. Each transect had 5 points, 50 m apart, for a total of 15 points. At each point, a random point was selected within a few metres. From that random spot, the nearest white pine stump, the 'nearest neighbor', was located, and the distance to the centre of the stump was measured (to a maximum search radius of 30 m). Then, from that first white pine stump, the distance to the nearest neighboring white pine stump was measured (to a maximum of 30 m), and from that second stump the distance to a third nearest neighbor white pine stump was also measured. Distances more than 30m were recorded as zero. If possible, the diameter of each stump was measured as well. This method is fully described in Batcheler (1973).

Nonrandom Survey

The second component involved a survey of areas known to have historically been dominated by white pine. The purpose was to determine the density of white pines in those areas that were previously pine stands, but were logged and converted to mostly tolerant hardwoods. These sites were selected based on information provided by Ontario Ministry of Natural Resources staff who were familiar with them because of their high density of white pine stumps. These areas were identified and then surveyed in the same fashion (nearest neighbor sampling method) as the random survey.

To serve as a control for hardwood stands with a white pine component, we sampled a large unlogged stand known as the Big Crow Reserve in the park. This area is characterized by large, 400-500 year-old white pines (they were approximately 350 yrs old in 1953 [Hosie 1953]) that were never harvested, and therefore representative of the mixed tolerant hardwood-pine forests first discovered by loggers in the early 1800s. We sampled this stand using the same method as the other stands (nearest neighbor sampling method), except all species were recorded (not just white pines) and 50 points were located 15m apart. We measured all trees with diameter at breast height (dbh) ≥ 10 cm, and took dbh measurements of the remaining mature white pines (standing and fallen). We counted recently fallen pine (*i.e.* fallen trees with bark mostly intact and branches present) as if they were still standing, because the pines in this area had begun to die and fall just in the past five years. We felt that this gave the most accurate sample of a true unlogged pine-mixed woods stand. This survey in the Crow Reserve was to serve as a control treatment, against which to check the white pine stump data on similar site types collected in the rest of the park.

Analysis of White Pine Stump Data

The nearest neighbor data were analysed using methods outlined in Batcheler (1973, 1975) to calculate white pine stumps per hectare.

2. GIS-Based Pine-Soil Model

In addition to mixed stands, white pine occurs in pineries (stands with >70% white pine). In order to estimate the proportion of Algonquin Park that historically contained pine stands, we used a GIS to overlay and compare soil types of existing white pine stands with areas of similar soil types but that are not pineries. The purpose of this was to estimate the potential proportion of the park that may have had high pine densities prior to logging.

We selected a test area of 2848 km^2 in the northeastern region of Algonquin Park, where the majority of the remaining pine occurs. Maps of forest type (provided by the Algonquin Forest Authority and Ontario Ministry of Natural Resources) were overlaid with soil types from digital maps describing the Quaternary geology of the area (Geddes and McClenaghan 1983-1984). All pine stands were selected with white pine and/or red pine forming more than 70% of the stand, regardless of stand age (under the Forest Resource Inventory mapping of the Ontario Ministry of Natural Resources, this meant 80, 90, or 100% pine). Area of each pine stand on each soil type was extracted into a data base. Total forest area for the test zone was derived from GIS, as was the total area of the park, and total area of existing pine stands. The proportion of soils supporting pinery was calculated for the test area, and for each soil type. This proportion was extrapolated over the entire park to provide an estimate of pineries that might have existed prior to logging.

Age Structure of Historical Forests

Information on the age structure of the historical forests was not available. We converted the stump diameters measured in the field to diameters at breast height (dbh) using the formula given in Myers (1963). We plotted the relative frequencies of the diameters at breast height in order to estimate age structure of the white pines in our study plots prior to logging in the 1800s. We then compared our results with age structures of white pine stands found in the literature (Van Wagner 1978, Holla and Knowles 1988, Quinby 1991).

Comparison of our Data to Crown Surveyors' Records

We used data that were collected and transcribed in Leadbitter (2000) to verify our results. Methods associated with the analysis of the surveyors' notes are detailed in Leadbitter (2000). The survey notes described white pine distribution in two ways: by occurrence and by working group (working group means that a forested stand is dominated by a particular tree species). Much of the *Pinus resinosa* and *P. strobus* information in the surveyors' notes were recorded collectively as "pine" and were not separated by species. As we were only concerned with white pine distribution, we wanted to decipher what proportion of the stands derived from surveyors' notes was white pine. Some of the notes were detailed to species. On average, for every red pine recorded, 1.08

white pines were observed. This ratio was applied to the general pine term to provide an estimate of white pines. For working group data, we applied a 1:4 ratio of red pine to white pine, in order to calculate white pine working group numbers. Approximately 80% of the pine (red or white) working groups found in Algonquin Park are *P. strobus*. Jack pine working group was in a separate category for Clancy township. For the other townships, although the jack pine working group was included in the pine working group category with white and red pine, jack pine stands were so infrequent (at most 1.3%, Ontario Ministry of Natural Resources, unpubl.) that we considered them as zero.

II. Current White Pine Distribution in Townships of Algonquin Park

1. Mixed and Deciduous Stands with White Pine Component

In 1990, data were collected by the Ontario Ministry of Natural Resources (OMNR) in Canisbay and Lawrence townships of the park. Ten 1 km transects in each stand type were surveyed, and data were collected from 55 points in boreal-type mixed stands and 56 points in deciduous stands, using a 2 factor metric prism. Only trees with dbh ≥ 10 cm were included (same criterion as for Big Crow Reserve plot). The basal area information was converted to trees per hectare to correspond to our white pine data using:

$N = 2/(d/2)^2 \times 0.0001$ where N = Number of trees

d = diameter (m) of each tree at a plot or point

2. Pine Stands

We used pine stand (>70% white pine and red pine) information from the Algonquin Park forest resource inventory (OMNR) to compare the historical pine stand results we calculated with current stand information.

The age structure of current pine stands in the park was provided by the Algonquin Forest Authority (2000) (Figure 3.1). That age structure indicated that approximately 92.5% of the pine forests are 50 years old and older (therefore, of good seed-producing age). We also plotted the relative frequencies of white pine diameters at breast height (dbh) measured (by employees at the Petawawa Research Forest) from white pine trees (n = 418) in the study area. We then compared the dbh distribution of current white pines with the dbh distribution of white pine stumps (representing historical age distribution; n = 440) to compare the age structures.

III. White Pine Seed Production

Seed production of white pine was estimated using data from the Petawawa Research Forest (PRF), Petawawa, Ontario, located adjacent to eastern Algonquin Park. White pine seeds were collected by PRF staff from seed traps in study plots at the Meridian Road Silvicultural Area from 1998-2000. The stands from which seeds were trapped were altered with one of three thinning treatments: 1) control plot: not cut, basal area approximately 35 m^2/ha; 2) two crown plot: spacing between trees was equal to two full crowns, basal area was 6-8 m^2/ha; and 3) one crown plot: spacing between trees was equal to one crown, basal area was 14-16 m^2/ha. The pines were approximately 115 years old. The seedfall data for 1998 were corrected for viable seedfall (from gross seedfall trap numbers). The seedfall in 1999 was zero. The seedfall data for 2000 were not yet corrected for viable seeds, so we applied a value of 88.35% to the total seedfall to estimate number of viable seeds. This was based on an average of 86.7% (found in heavy seed year in Graber 1970) and 90% (Noland and Parker, Ontario Forest Research Institute, Sault Ste. Marie, Ontario, unpubl.).

The seed data were classified into three categories: 1) nil (poor seed production, as in 1999); 2) good (or medium seed production, as in 1998); and 3) excellent seed production (as in 2000). Seeds per hectare were calculated by the Petawawa Research Forest (1998-2000, unpubl.). Those data were the only seed data found for Ontario white pines. The data were within ranges quoted from published sources (Fowells 1965, Graber 1970, Krugman and Jenkinson 1974).

Historical and Current White Pine Seed Production in Red Crossbill Habitat

To determine food availability in the 1850s and in the 1990s in Algonquin Park, we first needed to estimate area of suitable breeding habitat for Red Crossbills. Using only stands that we determined would have had sufficient white pines to support breeding birds, based on observations collected in the field (chapter 1), we estimated food availability in various seed years. Three stand types were considered: 1) deciduous stands with less than 40% white pine; 2) mixed deciduous-coniferous stands with 40-70% white pine; and 3) stands with more than 70% white pine. The number of pines per hectare, both historically and currently, in upland tolerant hardwood stands (<40% white pine) was less than the minimum required by the birds during the breeding season (as observed in the autumn of 1998, see chapter 1). Therefore, we did not consider these stand types because they likely would not have supported breeding birds (historically or otherwise). Although Red Crossbills did use stands with 40-70% pine, and current area of these stand types in Algonquin is known, we had no measure of these stand types historically, thus comparing the change in that particular stand type was not possible. Therefore, we used only pine stands (>70% white pine) for seed production calculations because: 1) the birds used this stand type during the breeding season; and 2) we had historical and current estimates of the area in the park covered by this stand type. The best estimate for those stand types historically was derived from the GIS pine-soil model, and other sources (literature and anecdotal). With the highest proportion of white pines, these mature and old pineries then, as now, were likely the optimal Red Crossbill habitat in the park.

We estimated seed production in current and historical forests. There are no available data in the literature suggesting rate of seed production for old-growth white pine stands, which were prevalent in the landscape when the loggers arrived in the area of Algonquin Park. Therefore, we assumed similar seed production in historical forests to current managed forests in Algonquin Park. This provided a conservative estimate. Since the white pines from the Petawawa Research Forest (PRF) were of similar age to the stands currently in the park, we assumed that their seed production was comparable, and we used data collected from the control plot at the PRF. Using the current forest inventory information (Figure 3.1), we assumed that only stands 50 years and older were good seed sources for the birds (Lancaster and Leak 1978), therefore 92.5% of the current pine area was used to calculate seed production. For historical forests, we assumed that approximately 90% of the historical pine forests were of good seed-producing age (>50 years old). In Frelich (1995) it was estimated that 5.4% of the pre-settlement red-white pine forests in Minnesota were 40 years old or less, so our estimate seems fairly conservative.

IV. Red Crossbill Abundance

Historical Red Crossbill Habitat in Algonquin Provincial Park

To determine Red Crossbill numbers that could be supported by the study area, we first identified what stands, historically, were likely good Red Crossbill habitat. During the autumn of 1998, Red Crossbills were observed only in stands with a minimum white pine composition of 40% (see chapter 1). The birds foraged in stands with 94 pines/ha, but not in stands with less than 15 pines/ha (<40% white pine). We did not conduct any observations in stands with between 94 and 15 pines/ha, because they were rare in the study region. Pine distribution seemed to be bimodal: most mixed stands (<70% white pine) had either ≥50% white pine or ≤20% white pine. The threshold number of pines/ha for breeding crossbills is somewhere between 15 and 94, but we were unable to determine exactly what it was. Using data acquired in the field, from published sources, and the GIS pine-soil model, we determined which stands were adequate for breeding Red Crossbills and determined potential numbers of breeding pairs. Stands had to meet two requirements: 1) minimum number of pines/ha for breeding birds (>15); and 2) minimum age for good seed production (50 years and older).

Current Red Crossbill Habitat in Algonquin Provincial Park

Using the same criteria as mentioned above for historical Red Crossbill habitat, we used the current forest inventory information for Algonquin Provincial Park to determine the area of the park covered by pine stands adequate in pine stem density and age to be Red Crossbill habitat.

Determination of Number of Breeding Pairs

Seed production data were coupled with total seeds required by breeding birds to estimate numbers of breeding pairs supported by the historical and current landscape in the park (see chapter 2). To determine total seeds available to the crossbills, we first estimated the seeds eaten by another principal seed competitor, the red squirrel *(Tamiasciurus hudsonicus)*, and subtracted that amount from the total seeds produced. The red squirrel is the only other major competitor (other than White-winged crossbills, *Loxia leucoptera*) that exploits conifer seeds when they are still in the cone (Smith and Balda 1979). Although red squirrels prefer boreal coniferous forests (Rusch and Reeder 1978, Flyger and Gates 1982, Vahle and Patton 1983), they have also been found in red pine forests (Gurnell 1984) and in mixed coniferous-deciduous stands (Yahner 1987, Mahan and Yahner 1992). Red squirrel densities range between 0.3 and 6.8 squirrels/ha (Davis 1969, Rusch and Reeder 1978, Gurnell 1987, Price and Boutin 1993, Price 1994, Stuart-Smith and Boutin 1995). We assumed an average intermediate density of 3 red squirrels/ha, since densities increase to high numbers only after a good cone crop, due to higher survivorship (Halvorson and Engeman 1983). Red squirrels not only consume conifer seeds immediately, but also cut cones from trees in late summer through autumn to store in middens as winter food. These middens contain enough food for a squirrel to survive one to two successive winters, especially in years of crop failure (Gurnell 1984, M. C. Smith 1968). We assumed that an individual red squirrel caches enough seeds to last through one winter. It was expected that red squirrels would depend on white pine seeds during an excellent year, when seeds were very available. We created a model to determine the proportion of seeds taken in an excellent year, and then applied that to a good year (although it would likely be lower because of the decrease in seeds). We used an energetic requirement of 109 kcal/day/squirrel (an average of 100 kcal/day from M. C. Smith 1968 and 117 kcal/day for adult males in C. C. Smith 1968). Energetic requirements were converted to seeds using average seed weights from PRF seed traps in 1998 (0.023g/seed) and 6.110 kilocalories/gram from bomb calorimetry analysis performed in the laboratory (Crampton Nutrition Lab, McGill University).

Seeds unavailable to Red Crossbills = RS = ER*D*n

where:

RS = Total seeds taken by red squirrels (white pine seeds/ha)

ER = daily energy requirements for a red squirrel (white pine seeds/day)

D = number of days from September to April (approximately 210)

n = number of red squirrels/ha

The total seeds available to Red Crossbills in a given year were divided by the number of seeds required for successful reproduction (3 young reared to independence, as defined in chapter 2) (34,025 white pine seeds) to estimate total population that could be supported by available habitat in Algonquin Park.

$$\text{Number of successful breeding pairs} = \frac{\text{Total seeds available}}{\text{Seeds required for successful breeding season}}$$

where Total Seeds Available = Total seeds produced - RS

RESULTS

I. Historical Distribution of White Pine

1. Field Study

Random Plot Results

Thirty stands (439 points) were surveyed in the four townships (Table 3.1). Approximately half (51%) of the data collected were in tolerant hardwood stands, 36% in boreal mixed stands, and 13% in pineries. Average number of white pine stumps/ha for the four townships was 6 in mixed woods (range: 5-7) and 3.5 in deciduous stands (range:

0-11) (Table 3.2). Of interest was the high number (11) of pines/ha in deciduous stands in Dickson township, which was significantly greater than the values for the other three townships (0, 0 and 3). Diameters of white pine stumps ranged from 61 to 79 cm (Table 3.2), averaging 76 cm in mixed stands and 66 cm in deciduous ones. Surveys conducted in pine stands were rejected because most of the stands had previously been burned, likely obliterating many stumps, and hence causing uncertainty in the data. Also, it was not possible to determine if the stumps were old or more recent due to fire scars and damage, nor could we determine species of pine.

Selected Areas of High White Pine abundance

In areas that were selected for their suspected high number of pre-settlement white pines, stump densities were approximately 9 times higher in mixed stands than those in the random survey, and 18 times higher in hardwoods (Table 3.3). Although we were initially led to believe that the West Gate stand (at the western edge of the park) would have a high density of white pines, results indicated that it was similar to the random plots surveyed (Tables 3.2 and 3.3).

Big Crow Reserve

The Big Crow Reserve had 244.2 trees/ha, and was dominated by American beech (33%), eastern hemlock (29%) and sugar maple (22%). Eight (3.28%) trees/ha were large old-growth white pines (Table 3.3). Average dbh of the old-growth white pines was 97 cm (n = 35). No young pines were found in this area.

2. GIS-Based Pine-Soil Model

The GIS-based model of soils supporting pine stands deduced that park soils covering 675.7 km^2 (67, 570 ha) would be ideal for pine (>70% white and/or red pine, all ages) habitat today (Table 3.4). In 1999, Algonquin Provincial Park had approximately 321.5 km^2 (32, 150 ha) of pine stands (>70% white pine and/or red pine, all ages), less than half the area indicated by the GIS model. This suggested that a potential decrease of

52% of pine-dominated stands in the park has occurred. Because we were concerned with white pine stands (>70% white pine), we applied this increase (52%) to the current area of pineries in the park (13,974 ha) to estimate historical extent of this stand type. The model conservatively suggested that there might have been 29,369 ha of white pine-dominated stands in the park.

As a test of our model, we located the Logging Museum plot (Table 3.3), which was historically a high density pine stand (but no longer is) and found that it was characterized by soil type 50 (glacio-fluvial outwash). This suggested that our model was providing adequate predictions of areas previously occupied by pine stands.

Age Structure of Historical and Current White Pines

To describe historical age structure, we plotted the relative frequencies of the stump diameters sampled (converted to dbh's; Figure 3.2) and they represented a normal distribution, a bell-shaped curve. Combining stumps for mixed and deciduous stands, the highest number of stumps (21.55%) were 70-79 cm in diameter. Most (79.68%) of the stumps were 40 to 89 cm in diameter, and 12.54% were over 89 cm. We compared this distribution to current white pine dbh's (Figure 3.2) in mixed and deciduous stands. The peak density was for 40 to 49 cm, with 28.47% of the trees falling in this size class. Only 3.35% of the trees had dbh's between 70-79 cm, an 84% decrease from historical stump distributions. Only 4.55% of today's white pines are over 70 cm dbh, compared to 49.97% of the stumps. None of the trees in our study plots in 2000 were over 89 cm dbh. This suggests that there has been a major shift in age structure from historical pine stands compared to current ones, and that there were many more pines historically in the larger size classes.

Crown Surveyors' Records

According to Crown survey notes (1863-1892), historical distributions of white pine in the four townships we surveyed were similar to each other, and to the park in general (Table 3.5). Stands of pine working group (*i.e.*, dominated by white pine) in

Clancy township were approximately twice that of the other townships, and higher than the park average. Leadbitter (2000) suggested that historical (1890) white pine occurrence decreased approximately 12% in the park, but that stands with white pine as their working group increased by approximately 6% when compared to forest inventory data of 1990 (Table 3.5). However, in his data, some townships, including Lawrence and Clyde, showed substantial (>70%) decreases in white pine compared to historical numbers.

II. Current White Pine Distribution in Townships of Algonquin Park

1. Mixed and Deciduous Stands with White Pine Component

Current white pine abundance in the boreal-type mixed and deciduous stands of the park in Canisbay and Lawrence townships was low (<0.1%, Table 3.6). There was, on average, 1 white pine/ha in the mixed boreal forests, and <1 (0.2) white pine/ha in deciduous stands. These numbers were considerably lower than our estimates of historical white pines from the random pine stump surveys (Table 3.2). If stumps are added to existing numbers of pines/ha, there is an indicated decline of 81.9% and 93.7% of mature white pine in mixed and deciduous stands, respectively, with an average of 88.7% for these two stand types (Table 3.6).

Of the current total productive forests of Algonquin Provincial Park, only 2.3% are stands composed of more than 70% white pine (Table 3.7). An additional 8.9% is characterized by stands with 40-70% white pine, and 88.8% of stands have a white pine composition of 30% or less (Table 3.7). The boreal mixed and deciduous stands examined in the stump survey all fell into the less than 40% pine category, which is by far the most common stand type in the park. Pine stands and mixed stands with ≥40% white pine are currently uncommon in Algonquin.

III. White Pine Seed Production

During an excellent seed year, given 3 red squirrels per hectare consuming only white pine seeds for 7 months (September to April), we determined that red squirrels consumed approximately 488,880 seeds/ha or 21% of the total seed crop (in 2000). This was calculated from a need of 776 seeds/day/squirrel. If the same proportion of seeds was used in years of lower seed production (*i.e.* 1998), then the squirrels would have consumed approximately 8345 seeds/ha over the seven months.

If the park had sustained the area of pineries suggested by our GIS model, then the area of pine stands would have been approximately double the area present today (Table 3.8). We could not estimate mixed (between 40 and 70% white pine) stands historically, but our random survey results (Table 3.2) suggested that these types of forest were not common. If they had been, higher numbers of pines/ha would have been evident in the results of the random surveys. These stands did exist, but were likely not as common as pine stands (>70% white pine) or deciduous stands with <40% white pine. However, we believe that many of these stands (*i.e.*, with 40-70% white pine) probably resulted from selective logging of large pines in stands that had been >70% pine, in the mid 1800s. We considered pine stands, those with >70% white pines, as being the stands with greatest importance to breeding Red Crossbills, and based our calculations of potential numbers of breeding birds on their area.

IV. Red Crossbill Abundance

Numbers of breeding pairs of Red Crossbills in white pine stands (>70%) during good and excellent seed years in Algonquin Park were likely to have been twice the number in 1850 as in 2000 (Table 3.8), based on our estimate of reduction in area covered by pine stands.

DISCUSSION

This is the first study which has attempted to estimate historical forest resources that were available to and affecting the breeding population of Red Crossbills soon after human settlement of eastern Canada. Our results suggest that Red Crossbill habitat has declined in Algonquin Park in two distinct ways. First, there has been a reduction in the area of optimal breeding habitat (*i.e.*, pine forests) of about 50%. Second, there has been a loss of older stands with trees with larger crowns where seed production was significantly higher per unit area. Both of these changes have reduced the overall availability of pine seeds to the birds. Studies have suggested that Red Crossbills are dependent on mature forests (Helle and Jarvinen 1986, Dickerman 1987, Benkman 1993b, Montevecchi et al. unpubl.) because these provide the most seed. Holimon et al. (1998) showed that Red Crossbills favoured larger, older trees in Alaska because of increased seed production, and avoided younger stands. Evidence has indicated that the subspecies of Red Crossbill dependent on white pines in the eastern USA was nearly obliterated due to the loss of mature white pines in the northeast (Dickerman 1987). Dickerman (1987) also suggested that this subspecies only recovered in numbers in the northeast during the 20 years previous to his work, in response to maturing forests. Red Crossbill declines were also linked to the virtual disappearance of white and red pines in Newfoundland (Montevecchi et al. unpubl.). Benkman (1993b) recommended the preservation of mature and old-growth forests which serve as important habitat for Red Crossbills.

We suggest that our estimates of potential numbers of pairs of Red Crossbills are conservative. We did not consider stands with 40-70% white pine in our calculations, and the birds used these stands as regularly as pine stands in the autumn of 1998 (chapter 1). As well, seed production would have likely been high in these stands, because of their lower white pine densities and consequently increased crown size.

Our GIS pine-soil model suggested that, historically, the park may have supported at least double the amount of pine stands than currently. We believe that this estimate is reasonable and conservative because it is based on current site occupation by pines, even though logging over the past 150 years may have converted many pine stands in the test area to mixedwoods. Stands that were historically pine dominated; on sandy soils (especially on the east side of the park which is characterized by sandier soils), are generally still pine stands today (Strickland 1993). Under natural conditions, factors (mostly fire) favour pine-dominated stands on sandy soils (Maissurow 1935, Horton and

Brown 1960, Van Wagner 1978, Barnes 1991). Keddy (1994) showed that presettlement forest types in eastern Ontario were a result of the interaction between tree species and site type/ soil moisture. Activities such as logging, and fire suppression (initiated in Algonquin Park in the 1920s) could eventually cause pine dominated stands to convert to mixed and deciduous stands, as observed in the Big Crow Reserve. Tolerant hardwood forests on these sites that were once pine *(i.e.* Logging Museum site), and predicted with a high and medium probability by our GIS-soils model to still be pine, indicate that many such stands have been lost in the park. Therefore, we suggest that the pine-soil model provided a conservative estimate of the area covered by pine stands.

Other lines of evidence also support our argument. For example, Braun (1950) stated that original white pine forest was often a pure stand. White pines could occur in pure stands extending for several square miles (Nichols 1935). We found evidence for stands that were historically pine stands, but which had been converted by logging to mixed or deciduous stands, at the Logging Museum and Vesper Road sites (Table 3.3). Martin (1959) suggested that an area with at least 74 mature white pines/ha would indicate that it was the leading dominant species of that stand. Our results of 52 and 63 stems/ha are less than that for pure white pine stands, but clearly indicate that pine was a more important component of the historical forest, compared to the forest today. Martin (1959) conducted surveys in Algonquin Park and counted white pine stumps as well. A close examination of his extensive surveys showed that he found several stands with pine stumps which no longer had a significant pine component (Table 3.9). Martin (1959) also detailed several stands of pure white pine within upland deciduous landscapes, notably three specific examples of 10, 6 and 4 ha. Other studies have also suggested large decreases in pine stands compared to presettlement amounts. Our calculated decline of 52% is conservative when compared to Whitney's (1987, 1994) reported decline of 76% from a contrast of white pine proportions in 1836-1859 to 1980 in the Lake States. The presettlement forests of an area along the north shore of Lake Huron in Ontario had pine stands comprising 4.5% of the landscape, compared to 0.9% currently (S. Jones, OMNR, pers. comm.), a decline of 80%. Wray (1986) suggested that the present numbers of old-growth stands in Ontario are a fraction of what existed presettlement.

The disappearance of old-growth pine stands in the northeastern USA has been well documented. Frelich (1995) looked at old-growth in three Lake States (Michigan, Wisconsin and Minnesota) and found that 55% of the red and white pine pre-settlement forests had been old-growth (stands >120 years old) compared to 1.5% in the 1990s. He also showed that only 1.1% of primary forests remained in those states (Frelich 1995). Lorimer and Frelich's (1994) research on a primary forest landscape in upper Michigan showed that 70% of the stands were old-growth (canopies dominated by trees 130-300 years old) and 21% were mature stands. When we plotted the stump dbh distribution, the bell-shaped curve (Figure 3.2) indicated more mid-sized pines than larger or smaller ones in the landscape. The distribution of the diameters of our stumps were similar to a multi-aged distribution, characteristic of undisturbed, mature white pine stands, with continuous recruitment (Holla and Knowles 1988, Quinby 1991). When compared to current diameter distribution, it was evident that size of trees now was generally much smaller than for historical forests.

Guyette and Dey (1995) and Guyette and Cole (1999) examined the age characteristics of white pine coarse woody debris that had fallen into the littoral zones of Dividing and Swan Lakes in Algonquin Park. White pines in Dividing Lake were 267 to 486 years old: 20% of dominant trees sampled were older than 400 years; 52% were 300-400 years old; and 28% were 250-299 years old. In Swan Lake, tree rings of felled white pines indicated that the trees averaged 242 years of age when they died. So, the ages of trees that fell into the water were characteristic of an old-growth forest with diameters similar to the stumps that we recorded (Guyette and Cole 1999). In Swan Lake, no eastern white pine natural coarse woody debris had been created in the last hundred years, which indicated that logging in the nineteenth century caused a loss of large white pines (Guyette and Cole 1999). Studies of some undisturbed old-growth white pine forests elsewhere in Ontario showed that, on certain site types, pine stands had continuous recruitment and were self-replacing, largely due to small scale local disturbances (Holla and Knowles 1988, Quinby 1991). Further, all stands prior to 1920 would have been subjected to ground fires which enhance white pine reproduction (Maissurow 1935). Based on this evidence, our stump data, the Big Crow Reserve, and discussions presented in numerous accounts of the logging industry (*e.g.*, Gillis 1969, MacKay 1996, Strickland 1996), we believe that the majority of the pine forests present in the 1850s, in the landscape in what is now Algonquin Provincial Park, were old-growth forests.

Seed Production

Trees with larger crowns produce more seeds than trees which are constrained within a canopy (Graber 1970, Krugman and Jenkinson 1974, Wray 1986). Younger stands (48% of the current white pine stands in Algonquin are 101-120 years old, 30% are 81-100 years old) have more pines per hectare, but are more dense, with less room for crowns to grow. Older stands (*i.e.* old-growth stands) have fewer pines per hectare (see Horton and Bedell 1960, Figure 44), have more room for bigger crowns, and therefore higher seed production per individual (Graber 1970). Seed collections in two separate studies (Graber 1970, Petawawa Research Forest, unpubl.) showed that stands with smaller numbers of trees produced similar numbers of seeds per hectare to dense stands, because the trees of the former had larger crowns. Graber (1970) found that level of seed production (per hectare) in an intermediate density pine stand (basal area 27.6 m^2/ha, similar to old-growth white pine stand basal areas reported in Holla and Knowles (1988), Day and Carter (1991), Quinby (1991) was 36% higher in a good seed year than in higher density stands. Also, the two crown-spaced (low density) stands at Petawawa Research Forest produced, on average, 62% more seeds/ha in 1998 and 48% more seeds/ha in 2000 than the control plots (Petawawa Research Forest, unpubl.). Further, older trees produce more seeds than younger trees up to about 150 years of age. Messer (1956) found that a 60 year-old white pine stand produced one-fifth the amount of seeds as in a 90 year-old stand. Mature trees also have more stable seed production than younger trees (Benkman 1993b). Stiell (1988) found a strong positive relationship between dbh and cone crop size in red pines. He suggested that this relationship was a reflection of the crown size, on which dbh and cone production were both dependent (Wenger and Trousdell 1958). We suggest that seed production in old-growth pine forests may have been significantly higher than it is in managed pine forests that are currently found in Algonquin. If so, the number of Red Crossbills that could have been supported by pine stands in the 1850s may have been significantly higher than our estimate (Table 3.8). If seed production in old-growth forests was 50% higher than in managed stands of today, numbers of breeding pairs would have been approximately 3.5 times the number estimated to be supported by current pine stands in the park.

Seed production is an extremely variable component of our model. It varies widely in space and time, and even within a given stand type. Cone (and therefore seed) production tends to be spatially synchronous at regional scales (Sirois 2000). In one year, high cone production may be widespread; the next year seed failures might be common (Smith and Balda 1979). When comparing seed crops in two years of seed production in red pines, Stiell (1988) found that although individual tree cone production varied, the overall cones (therefore, seeds) produced/ha was the same. We found few data on white pine seed production in natural systems and across a range of stand types, ages, or structures. Published sources (Fowells 1965, Krugman and Jenkinson 1974, Burns and Honkala 1990) provided general information on seed production intervals, ranges in seed production, seeds per unit mass, and cone biology. Studies of seeds produced per hectare in white pine forests were rare in the literature.

White pines can start producing seeds at 5-10 years of age, although good seed production normally occurs at 20-30 years of age (Fowells 1965, Krugman and Jenkinson 1974, Burns and Honkala 1990). Optimum seed-bearing occurs when pines are 50-150 years (Lancaster and Leak 1978). White pine cones require two years to mature. Good cone production occurs every 3-5 years (Fowells, 1965), usually followed by little or no production. The number of seeds range from 38,600 to 116,800 seeds/kg of cones, with an average crop of 58,400 seeds/kg of cones (Fowells 1965, Burns and Honkala 1990). Most of the seed is dispersed within a month of maturity, in August and September of the second year (Fowells 1965, Burns and Honkala 1990). In one study in Maine, seedfall started in mid-September, peaked in late September-early October, and 98% of the seeds had fallen by the end of November (Graber 1970). Therefore, Red Crossbills must take advantage of the food source to breed within this time period.

Our estimates of numbers of breeding pairs of Red Crossbills were based on seed production data obtained from the Petawawa Research Forest (1998-2000). These numbers do not necessarily reflect precise estimates of crossbills in the historical or current forests of Algonquin Park. Instead, those estimates were intended to reflect changes in potential breeding populations. The number of seeds consumed by red squirrels was a rough estimate, and may be higher or lower than we suggested. Regardless, we suggest that the impact of red squirrels on white pine seed availability was a constant proportion, whether in 1850 or in 2000 forests. Red squirrel impacts on ponderosa pine crops were calculated as 14% of the potential crop (Schmidt and Shearer 1971), which is less than our estimate of 21%. Graber (1970) found that squirrels consumed about 3.6% of the potential crop in high cone crop years. He suggested that in low cone years, the percentage consumed by animals is much higher due to low cone levels. Our calculation was likely an overestimate because we assumed that the squirrels only consumed white pine seeds, when in reality, they eat other coniferous and deciduous seeds, as well as fungi, tree buds and flowers, fruits, insects and other animal material (Hatt 1929, Hamilton 1939, Layne 1954, C. C. Smith 1968, M. C. Smith 1968, Linzey and Linzey 1971, Gurnell 1987). Further, we also assumed that all the remaining seeds would be consumed by Red Crossbills. Again, our intention was simply to provide estimates of changes in potential breeding populations, and the determination of exact numbers of breeding pairs was done to reflect these changes.

Leadbitter (2000) suggested that the occurrence of white pine in Algonquin Park in 1990 was not significantly different than in historical times, based on historical surveyors' notes. He also suggested that the distribution of pine stands had not changed significantly from past to present. This implies that the abundance of white pine in the park, when those surveys were conducted, is nearly identical to that present in 1990 and that pre-settlement pine abundance did not differ significantly from the current amount. We reject this hypothesis, and instead suggest that white pine abundance in the park has declined substantially since the 1800s, probably by 50-80%. One problem with the surveyors' notes is this: because pine are almost always a supercanopy tree (especially in old-growth forests in the 1800s), when the surveyor (who was not a forester by training) looked up to determine species composition, the pines would almost never have been visible. And so in a forest dominated by deciduous trees, even with considerable pine stems, pine would likely have been greatly and regularly underestimated.

A second, even more substantial problem with using the surveyors' notes as Leadbitter (2000) did to estimate "pre-settlement" information, is that in many instances white pine harvesting had occurred before crown surveyors conducted their work, especially in the central and eastern areas of the park. Aird (1985) and Wray (1986) stated that the white pine harvest on Ontario crown forests peaked in the mid 1860s when about 25 million cubic feet (0.77 million cubic metres) of pine were floated down the Ottawa and St. Lawrence rivers (Aird 1985, Figure 2). After 1867, the pine trade moved from square timbers (traded with Britain) to sawlogs (traded with the United States). The peak for white and red pine sawlogs occurred in 1896 in Ontario. Although this peak had 5 times the volume (about 150 million cubic feet or 4.6 million cubic metres) than the earlier peak square timber harvest in 1864, the square timber was much smaller because they logged the prime trees first for sawlogs, and then returned for square timber several years later (Aird 1985). The annual pine harvest dwindled in the 1900s for many reasons, but a main one was the "dwindling supply of virgin pine" (Aird 1985). Eight of the 10 crown surveys for Algonquin were conducted in the 1880s and 1890s, so it is clear that much of the area had already been logged for white pine at the time of those surveys. For example, a map showing the harvest of pine square timber during 1866-67 for the park (Figure 3.3, Strickland 1993) indicated logging during that period in 5 of the 10 townships (Barron, Boyd, Clancy, Dickson, Master) used in Leadbitter (2000) to indicate pine density. These 5 townships were surveyed between 1883 and 1892, and thus, were not "pre-settlement" but indeed "post-harvest" forests. Clyde township survey results support our argument. Clyde township was surveyed in 1863, and, indicated a decrease in white pine stands of 78% (Table 3.5) from pre-settlement times. We believe that this estimate accurately represents pre-settlement forests because Clyde township was surveyed before the initial pine harvest. Maps of pine sawlog harvests in 1871 (Head 1975) support our position that much of the park had been harvested for white pines prior to many of the crown surveys, making their usefulness to indicate pre-settlement forests questionable.

On the other hand, at the extreme west and south of the park, the Gilmour Company only began logging around Tea Lake, Canoe Lake and Burnt Island Lake in 1893 (Long and Whiteman 1998). So, the crown surveyors' notes describing pre-settlement forests in this region of the park would have been more accurate.

Further, a decrease in white pine was clearly evident when we compared the stump data (Table 3.2) to current white pine densities (Table 3.6) in boreal mixed and deciduous forests composed of less than 40% white pine. In boreal mixed forests, white pines have decreased an average of 82% (ranging from 78.4% to 84.5%). In deciduous forests, we found 50 times more white pine stumps than the average in current stands in Dickson township, a decrease of 98 % (Table 3.2). Some deciduous stands likely never had a white pine component, and remain so (*e.g.* stands in Lawrence and Clyde). The northern hardwood forest with scattered white pines is a more stable ecosystem than conifer forests because it is less susceptible to fire and blowdown (Ahlgren and Ahlgren 1983). The change in these forests was gradual after initial logging because the harvest was selective with the white pine removed first (Curtis 1959, Ahlgren and Ahlgren 1983). In the absence of fire and with no seed source, the pine were not replaced (Maissurow 1935). Nichols (1935) stated that white pine was a normal, although perhaps minor component of the climax hardwood-hemlock forest, and in that forest it attained "its finest growth and largest size". It persisted as a supercanopy tree in these forests because it was long lived (Barnes 1991). Loggers arriving on the scene knew that the largest pine was located mixed in with hardwoods on deep, loamy soils (Irland 1986). The long-term effect of selective logging of pines in this stand type is an increase in sugar maple density (Ahlgren and Ahlgren 1983, Whitney 1987) as reported in Leadbitter (2000). He found a significant increase in maple (species and working group) from the 1890s to 1990s. We suggest that the increase in sugar maple may have occurred because of a decrease or loss of white pine.

Our average of 3.5 white pines/ha (range: 0-11, Table 3.2) in deciduous stands (<40% white pine) were similar to the never-logged Big Crow Reserve (Table 3.3). Martin (1959) measured white pine densities in mixed pine-deciduous stands as 0.41 to 2.5 trees per hectare, which is within our estimated value (0-11). Whitney (1994) found that merchantable pine occurred at densities of 2.5- 25 trees/ha in the mixed pine-hardwood forests of Wisconsin and southern Michigan. Composition details of a climax hemlock hardwoods forest in Michigan indicated that white pines made up 2.7% of the canopy, with hemlock at 59.5%, and red maple at 13.5% (Braun 1950).

The processes controlling the nature of deciduous stands was very different than pine stands. Forests dominated by shade-tolerant species could reproduce without large canopy openings (Frelich 1995). This stand type had moist, deep, nutrient rich soils (Frelich and Reich 1996). The climax mixed hardwood stands varied, but the dominant species were sugar maple, hemlock and American beech (Nichols 1935), as observed in our control stand in the Big Crow Reserve. These stands had long replacement intervals (Frelich 1995). Fires are generally small and less frequent in areas where soil is moist (Ahlgren and Ahlgren 1983). Because of this, stand dynamics in the climax mixed hardwood stands were often controlled by the death of a canopy tree (Runkle 1982, Lorimer and Frelich 1989, Whitney 1994). Wind was a major disturbance in this stand type (Frelich and Reich 1996). The natural disturbance regime involved rare catastrophic winds, with frequent low or moderate intensity disturbances that removed a small percentage of the forest canopy (Frelich and Reich 1996). In these forests there were many generations of trees and old-growth conditions could occur for hundreds of years (Frelich 1995, Frelich and Reich 1996).

In the autumn of 1998, we observed that breeding birds did not frequent or forage in stands with less than 15 pines/ha. So, this habitat type (<40% white pine) in the historical landscape may have never been used by breeding crossbills. But, it is also possible that this habitat type was more attractive to Red Crossbills in the historical landscape than it is today for two reasons:

1) white pines in presettlement stands were much older supercanopy trees compared to

those present today (approximately 100 years of age) and their larger crowns would have produced more seeds;

2) the presence of large supercanopy trees was much more prevalent across the landscape than it is currently (comparison of Tables 3.2 and 3.6).

If many stands had small amounts of large pine in the 1800s, they could have been much more important than the small numbers of white pines existing in mixed stands (<40% white pine) in the park today. The white pines found today in this stand type are perhaps too scattered and infrequent to be energetically advantageous to Red Crossbills. Red Crossbills forage in groups, and are energy-maximizing foragers (Benkman 1987a, 1989, Smith et al. 1999). While foraging, they use the behavior of fellow foragers to assess the quality of patches of habitat: "public information" (Clark and Mangel 1984, 1986, Benkman 1988b, Valone 1989, 1993, Smith et al. 1999). They use public information to assess poor patches more quickly then they would if foraging alone, and this strategy is very important in assessing slight differences between good and better patches (Smith et al. 1999). This system of foraging may explain why Benkman (1987b) found that the time spent searching for conifer cones contributed little to overall foraging time, and that time spent removing seeds from cones was the most variable and time-consuming component of foraging. As a result, we would assume that Red Crossbills would forage optimally by choosing areas with high concentrations of seeds, such as in stands with high numbers of pines, over areas with smaller numbers of seed sources. But, the white pines that were present historically may have had sufficient seeds (with their large crowns), and been frequent enough in the landscape to support breeding birds. Red Crossbills often forage in the same trees and revisit trees with many cones, much like Christensen et al. (1991) found for Clark's Nutcrackers *(Nucifraga columbiana)*. Clark's Nutcrackers maximize foraging efficiency by choosing trees with many cones, therefore spending less time handling cones, and travelling within and among trees. White pine trees with sufficient cones and present across the landscape, much more so than today, could have therefore been good seed sources for the birds historically.

Studies investigating pre-settlement landscapes have become prevalent in the literature in recent years as researchers attempt to establish baselines for biodiversity and forest conservation (Christensen 1989, Abrams and Ruffner 1995, Frelich 1995, Frelich and Reich 1996, Jackson et al. 2000, Zhang et al. 2000). Frelich (1995) stated that "presettlement forests can be interpreted as a stable baseline and used to evaluate changes in the landscape caused by humans". The historical forest evolved under natural processes, whereas the post-settlement forest is a result of both natural and human disturbances (Davis 1981, White and Mladenoff 1994). Most of today's white pine forests in Ontario are younger second-growth forests, resulting from logging (Wray 1986), whereas the presettlement forests were predominantly mature and old-growth. The alteration of the original distribution of pine forests in Algonquin Provincial Park, and elsewhere, has greatly decreased potential breeding populations of Red Crossbills. The evidence indicates that the decrease in average age of pine forests has reduced seed production in years when the birds arrive in the park to breed, and therefore reduces the potential numbers of Red Crossbills that could breed successfully. A similar effect is probable across much of the Great Lakes-St. Lawrence forest region of eastern Canada. The alteration of the pre-settlement landscape could have effects that are not only regional, but on much larger scales.

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Table 3.1: Stands surveyed for white pine stumps in four townships of Algonquin Provincial Park, Ontario, May-July, 1998.

Township	**Number of stands surveyed**	**Number of points**			**Total number of points conducted**
		Hardwood	Boreal Mixed	Pine	
Lawrence	7	50	50	0	100
Dickson	8	50	50	15	115
Clyde	9	73	44	15	132
Clancy	6	50	15	27	92
Total	**30**	**223**	**159**	**57**	**439**

Table 3.2: Mean number and diameter of white pine stumps in random surveys conducted in four townships of Algonquin Provincial Park, Ontario, May-July, 1998.

Township	Forest type	White pines/ha (mean ± SE)	Average diameter (cm)
Lawrence	BM	5 ± 2.38	78.59
	D	0	n/a
Dickson	BM	7 ± 3.89	76.3
	D	11 ± 8.14	61.39
Clyde	BM	6 ± 2.88	73.23
	D	0	n/a
Clancy	BM	insufficient data	76.55
	D	3 ± 2.31	70.33
All townships	BM	6	76.17
	D	3.5	65.86

** BM = boreal-type mixedwood. D = deciduous

Table 3.3: Mean number and average diameter of white pine stumps in selected areas of Algonquin Provincial Park, Ontario (1997-1998).

Location	Forest type	White pine stumps/ha (mean ± SD)	Average diameter (cm)
Logging Museum	M	52 ± 11.44	50.61
Vesper Road	D	63 ± 10.08	62.6
Bonfield-Dickson Portage	M	insufficient data	72.51
West Gate	D	5.2 ± 1.77	80.66
Big Crow	D	8 ± 2.80	96.8

Table 3.4: Results of a Geographic Information System pine-soil model: current (1999) and theoretical area of soil types supporting pine stands in Algonquin Provincial Park (AP), Ontario.

Soil type	**Test region area (km^2)**	**Area of pine stands (>70% pine) in test region (km^2)**	**Ratio (area pine/area test region)**	**Total area in AP (km^2)**	**Theoretical area of pine stands in AP (km^2)**
10	459	38	0.082	1360	111.4
20	442	35	0.08	904	72.4
21	310	24	0.076	940	71.9
22	15	2	0.13	114	14.8
30	618	42	0.069	1120	76
31	122	8	0.064	211	13.5
32	4	1	0.258	95	24.4
33	9	0	0	10	0
40	16	2	0.149	68	10.1
41	74	9	0.127	255	32.4
42	9	2	0.187	22	4
50	452	106	0.236	836	197
51	20	3	0.166	77	12.8
52	25	3	0.113	31	3.6
70	21	2	0.082	104	8.5
80	252	11	0.045	513	22.9
Total	**2848**	**288**	-	**6660**	**675.7**

*Key to soil types on page following

Key to soil types of Table 3.4:

10: shallow drift soils over bedrock
2x: Bedrock-drift complex, sufficiently thick drift to subdue bedrock
  20: unsubdivided
  21: mainly till
  22: mainly sand and gravel
3x: Till: silty sand to sand
  30: unsubdivided
  31: compact silty sand
  32: loose to moderately compact silty sand-sand
  33: reworked by fluvial action
4x: Glacial fluvial ice-contact
  40: stratified sand, gravel boulders
  41: kames
  42: eskers
5x: Glacio-fluvial outwash
  50: unsubdivided
  51: mainly sand
  52: sand/gravel
  70: Alluvium: sand, silt, minor gravel
  80: Organic soils, peat, muck

Table 3.5: Historical (1890) *Pinus strobus* distribution determined from Crown surveys compared to recent (1990) forest inventory data in Algonquin Provincial Park, Ontario. Source: Leadbitter 2000.

Township	**% White pine (total occurrence)**		**Change* (%)**	**% White pine (working group)**		**Change* (%)**
	1890	**1990**		**1890**	**1990**	
Lawrence	8.33	0.5	-94	6.49	N/a	N/a
Dickson	5.49	6.01	8.7	5.75	9.98	42.4
Clyde	4.38	1.03	-76.5	5.47	1.2	-78.1
Clancy	7.4	6.78	-8.4	14.14	6.53	-53.8
Average	**6.4**	**3.58**	**-44.1**	**7.96**	**5.9**	**-25.9**
Algonquin Park	**7.23**	**6.36**	**-12**	**9.14**	**9.71**	**5.9**

Surveys occurred from 1863-1892

* Note: "+" indicates an increase in pine, "- " indicates a decrease

Algonquin Park = total of 10 townships, including the 4 mentioned in table.

Table 3.6: Trees and white pine per hectare in the eastern region of Algonquin Provincial Park, Ontario (1990). Source: Ontario Ministry of Natural Resources, unpublished data.

Stand type	**Trees/ha (mean ± SE)**	**White pine/ha (mean ± SE)**	**% White pine**
Boreal mixed	743.61 ± 45.66	1.08 ± 2.41	0.00014
Deciduous	599.49 ± 35.85	0.220 ± 0.10	0.0004

Table 3.7: Stand types of productive forests of Algonquin Provincial Park, Ontario (2000).

Source: Algonquin Forest Authority, Huntsville, Ontario.

Stand type	**White pine composition**	**Area (ha)**
Pinery	>70%	13,974
Mixed	40-70%	54,654
Deciduous	<40%	544,491

Table 3.8: Seeds produced in good and medium seed years and Red Crossbills (RECR)supported by pine stands in Algonquin Provincial Park, Ontario, in 1850 and in 2000. Equal seed production per hectare was applied to managed (year 2000) and old-growth (1850) forests. Total seeds available to RECR were calculated by subtracting seeds consumed by red squirrels.

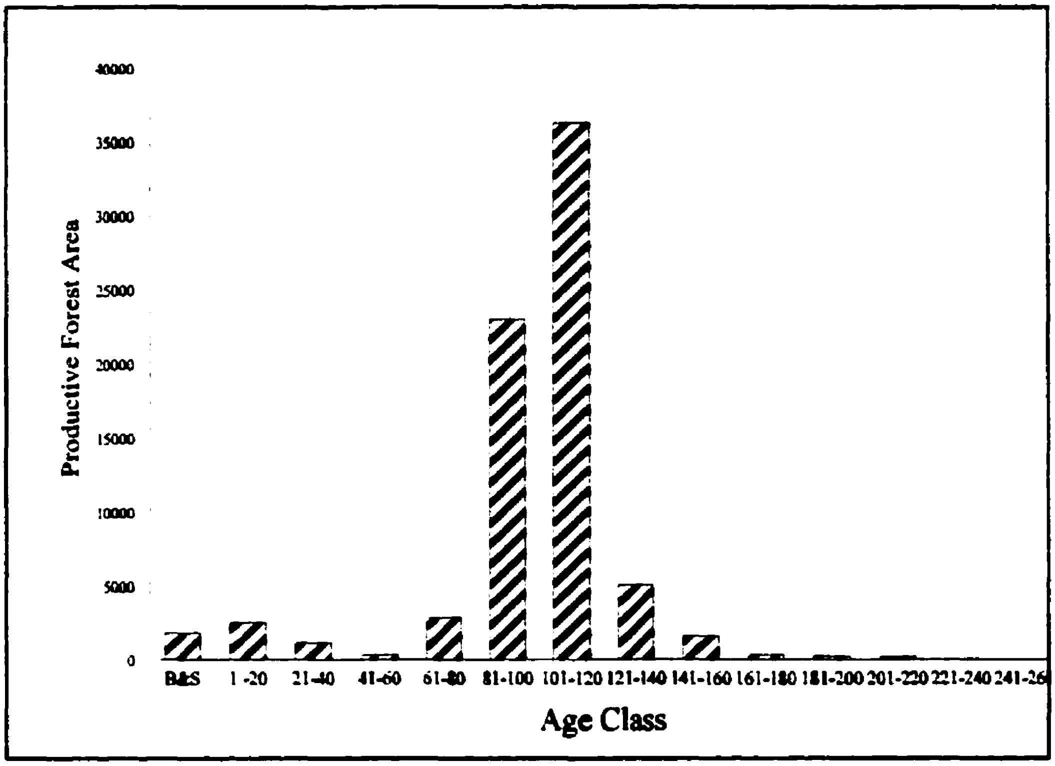
	Area (ha)	**Area of stands >50 years old (ha)[a]**	**Seed year**	**Total seeds per hectare***	**Total seeds available to RECR/ha[b]**	**Total seeds produced (millions) (a x b)**	**Number of breeding pairs of Red Crossbills**
Managed Pine Forests (2000)	13,974	12,926	Good	39,738	31,393	405	11,926
			Excellent	2,301.711	1,818,831	23,510	690,968
Old-Growth Pine Forests (1850)	29,369	26,432	Good	39,738	31,393	829	24,387
			Excellent	2,301,711	1,818,831	48,075	1,412,941

*Seeds per hectare provided by Petawawa Research Forest, unpublished data, Petawawa, Ontario.

Table 3.9: Stands surveyed by Martin (1959) in Algonquin Provincial Park, Ontario: densities of white pine *(Pinus strobus)* stumps, diameters, and historical nature of stands.

Plot	**Stand type (in 1959)**	**White pine (stumps/ha)**	**Diameters of pines (cm)**	**Type of stand historically**
E1-1	Boreal-type mixed	91.4	15-61	White pine
E1-2	Upland deciduous	42		Mixed pine-hardwoods
PB1-1	Poplar-birch upland	160.6		White pine
BS-BP	Betula-*Populus* mixed with *Abies-Picea*	163	>30.5	Pinery (not specified)
BS	Abies-Picea	42		Mixed pine-hardwoods
P1	Immature white pine	650 trees		Hardwood forest
P2	Virgin pine	741	45-76	White pine
P3	Virgin Pine-*Tsuga*	76.6	30.5-122	White pine
other	Virgin Pine with hardwoods	0.4-2.5	122	Mixed pine-hardwoods
BS-H	*Abies-Picea* and hardwoods	27.2		Mixed pine-hardwoods
H1	Upland hardwoods	2.5		n/a
H2	Upland hardwoods	19.8		n/a
HE1	Hemlock	7.4	31.8-123.2	Cedar

Figure 3.1: Age structure of white pine forests in Algonquin Provincial Park, Ontario (2000).



Source: Algonquin Provincial Park, Forest Management Plan for April 1, 2000 to March 21, 2020 by the Algonquin Forestry Authority, Pembroke, ON

Figure 3.2: Relative densities of tree size class (diameter at breast height) distributions for current and historical white pines in mixed and deciduous stands in Algonquin Provincial Park, Ontario.

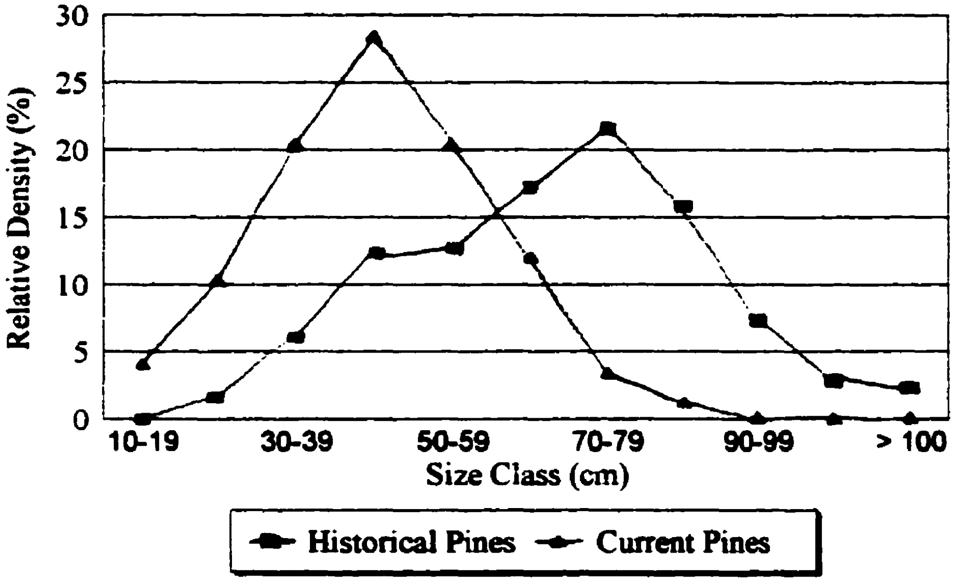
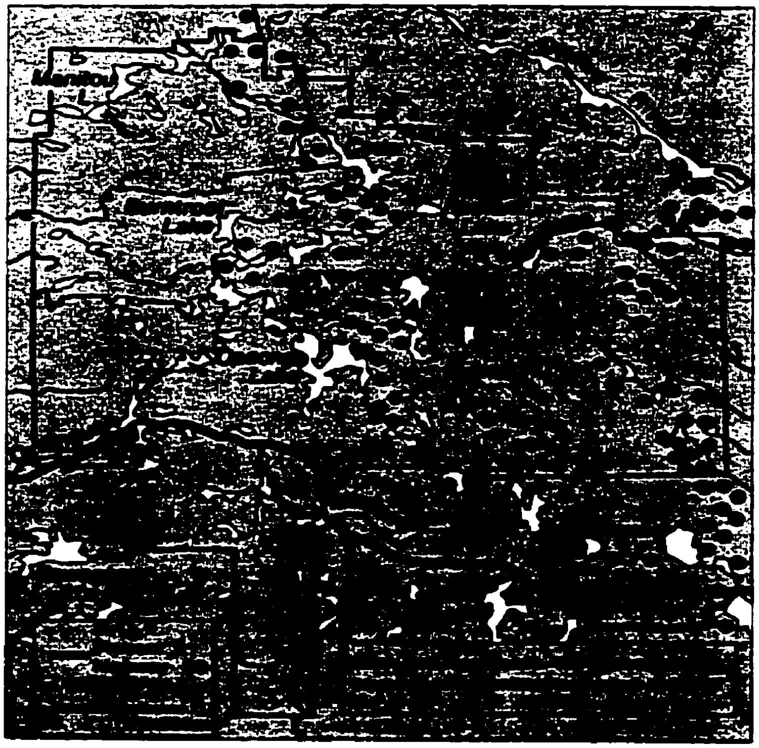


Figure 3.3: The white pine square timber harvest in Algonquin Provincial Park, winter of 1866-7. Map prepared by the Department of Geography, Wilfred Laurier University, Ontario. Source: Strickland 1993.



CONCLUSION

In years of good white pine seed production in Algonquin Provincial Park, Red Crossbills arrive and breed in autumn. A minimum of 40% white pine (at least 100 years of age) in each stand appeared to be suitable for Red Crossbill use. As long as sufficient cone-producing white pines with large crowns were available in stands, Red Crossbills frequented the stands to forage and breed. A threshold number of cones per stand is required by Red Crossbills in an area, above which they may use other cues, such as sources of grit, to decide which stands they use. Mature, dominant trees with large crowns, positioned along gravelled roadways were the optimal seed source for Red Crossbills in Algonquin Park. Observed intake rates and foraging durations were sufficient to support daily activities, with additional energy available for providing fledged young with food they were not yet able to acquire on their own. A successful breeding season for a pair of Red Crossbills (based on raising 3 young to independence) required 34,025 white pine seeds. Optimal breeding habitat in Algonquin Park consisted of stands with a minimum of 94 mature white pines/ha. A GIS pine-soil model estimated that changes in the landscape of Algonquin Park, as a result of human alteration (logging and the suppression of fire), have resulted in a significant decrease (52%) of optimal Red Crossbill breeding habitat. This estimate was supported by other evidence from a survey of historical white pine stumps, and a literature review. Half of the white pine stands in the park are no longer present, compared to the early European settlement period in the mid-1800s, suggesting that potential breeding populations were double the size currently observed. An added effect is the likely probability that seed production rates (seeds/ha) are considerably less in the current, younger, managed forests of the park than they were in the primary old forests when the first settlers arrived. This has an additional, negative impact on numbers of breeding birds, although we were not able to measure it precisely. A similar effect is probable across much of eastern Canada, and the northeastern United States. The alteration of the pre-settlement landscape could have significant effects not only regionally, but on a much larger scale.

APPENDIX 1. Equations used in calculation of field metabolic rate.

Basal Metabolic Rate (H_{nt}) $=(3.1 \text{ ccO}_2 \text{ g}^{-1} \text{ hr}^{-1})(33.0\text{g})(4.8 \text{ cal ccO}_2^{-1})(1 \text{ kcal})(1000\text{cal}^{-1})$

$= 0.491 \text{ kcal bird}^{-1} \text{ hr}^{-1}$ or $11.784 \text{ kcal bird}^{-1} \text{ day}^{-1}$

Daytime basal metabolic rate (H_{dt}) $= 1.20 \times H_{nt} = 1.20(0.491\text{kcal hr}^{-1}) = 0.5892 \text{ kcal hr}^{-1}$

Standard Operative Temperature (Bakken 1990):

Daytime (06:00 to 21:00)

$T_b = 39°C$

T_e = Ta + radiation effect = Ta + average of 58.9% sunlight = 15.96°C + 5.89°C = 21.85°C

$u = 1.5395$ m/s

$$T_{es(daytime)} = T_b - (1 + 0.26\sqrt{u})(T_b - T_e)$$

$$= 39°C - [1 + 0.26(1.5395)^{0.5}](39°C - 21.85°C)$$

$$= 39°C - 22.683°C$$

$$= 16.32°C$$

*radiation effect: If birds are in full sunlight, Te will be about Ta +10° C. If in the shade, Te will approximate Ta (therefore Ta + 0). (Weathers, pers. comm.)

** Tb = 39°C; approximation; Red Crossbills kept body temperature between 38.5 °C and 40°C during the night even though ambient temperatures went from -15 to +28.5°C (Dawson and Tordoff, 1964)

Night (21:01 to 05:59)

$T_b = 39°C$

T_e = Ta = average of 10.99°C

$u = 0.6963$ m/s

$$T_{es(night)} = T_b - (1 + 0.26\sqrt{u})(T_b - T_e)$$

$$= 39°C - [1 + 0.26(0.6963)^{0.5}](39°C - 10.99°C)$$

$$= 39°C - 34.087°C$$

$$= 4.913°C$$

* Te equals Ta because at night Te will be within a couple degrees of Ta (Bakken 1990)

Thermoregulation: Using the equation from Benkman 1990 and substituting standard operative temperature for ambient temperature- Thermoregulatory cost was 0.650 kcal hr^{-1} or 1.32 x Hnt.

Alert perching = 0.5 x Hnt = 0.2455 kcal hr^{-1}(5.52 hr) = 1.355 kcal day^{-1}.

Preening = 0.8 x Hnt = 0.3928 kcal hr^{-1} (0.91 hr) = 0.357 kcal day^{-1}.

Locomotion = 1.0 x Hnt = 0.491 kcal hr^{-1} (0.24 hr) = 0.118 kcal day^{-1}.

Flight (Norberg, 1996): RMR (≈BMR) = $4.02\ M^{0.68} = (4.02)\ (0.033kg)^{0.68} = 0.395$ watts

Pmet (metabolic power required to fly) = $57.3\ M^{0.813} = 57.3\ (0.033kg)^{0.813} = 3.578$ watts

Cost Factor of Flight = Pmet/RMR = 3.578/0.395 = 9.06

Therefore 9.06 x Hnt = 4.448 kcal hr^{-1}, multiplied by 0.31 hr = 1.379 kcal day^{-1}.

Foraging on conifer cones and for grit = 2.5 x Hnt = 1.228 kcal hr^{-1}, and occurred for 1.03 hrs therefore the total cost was 1.264 kcal day^{-1}.

Foraging on dead wood = 1.5 x Hnt = 0.736 kcal hr^{-1}, and occurred for 1.07 hrs therefore the total cost was 0.788 kcal day^{-1}.

Other Activities = 0.3 x Hnt = 0.147 kcal hr^{-1} x 1.25 hr = 0.184 kcal day^{-1}.

Moult (Kendeigh et al. 1977): Total cost of moult (kcal $bird^{-1}$) = NEM = $8.377\ W^{0.9591}$ = 239.6 kcal

At an average ambient temperature of 13.5 °C , the actual cost of moult is approximately 23% of the NEM (figure 5.9 in Kendeigh et al. 1977) = 55.11 kcal.

The moulting costs are divided by 84 days (days in average moulting period, Newton 1972), and the cost is 0.656 kcal day^{-1}, or 5.56% of Hnt (an additional cost to the BMR of 5.57% or 0.0273 kcal hr^{-1}).

Cost of egg production (females) = 0.41 x Hnt, occurring over the entire 24 hours, resulting in a total daily cost of approximately 0.201 kcal hr^{-1} or 4.83 kcal day^{-1}.

APPENDIX 2: Calculation of Field Metabolic Rates

Nonbreeding FMR (FMR_{non}):

$$\begin{aligned} FMR_{non} &= t_{nt}(H_{nt})TR_{nt} + t_{dt}(H_{dt}) + t_{ap}(H_{ap}) + t_{pr}(H_{pr}) + t_{lo}(H_{lo}) + t_{fl}(H_{fl}) + t_{fo}(H_{fo}) + \\ &\quad t_{fod}(H_{fod}) + t_{ot}(H_{ot}) + t_{mo}(H_{mo}) \\ &= 9(0.491)(1.324) + 15(0.589) + 5.52(0.245) + 0.91(0.393) + \\ &\quad 0.24(0.491) + 0.31(4.448) + 1.03(1.228) + 1.07(0.736) + 1.25(0.147) + 24(0.0273) \\ &= 20.79 \text{ kcal day}^{-1} \end{aligned}$$

Nest Construction FMR (FMR_{nc}):

Female: $FMR_{nc} = FMR_{non}$ + 4.65 min of flying = 20.79 kcal day^{-1} + (4.448 kcal hr^{-1})(0.0775 hr) = 20.79 kcal day^{-1} + 0.345 kcal = 21.13 kcal day^{-1}

Male: $FMR_{nc} = FMR_{non}$ = 20.79 kcal day^{-1}

Egg Production FMR (FMR_{egg}):

Female: $FMR_{egg} = FMR_{non}$ + egg production = 20.79 kcal day^{-1} + (0.41)(0.491 kcal hr^{-1})(24 hrs) = 20.79 kcal day^{-1} + 4.83 kcal = 25.62 kcal day^{-1}

Male: $FMR_{egg} = FMR_{non}$ = 20.79 kcal day^{-1}

Incubation FMR (FMR_{inc}):

Female: $FMR_{inc} = t_{nt}(H_{nt})TR_{nt} + t_{dt}(H_{dt})$ = 9hrs(0.491 kcal hr^{-1})(1.324) + 15hrs(0.589 kcal hr^{-1}) = 5.851 kcal day^{-1} + 8.838 kcal day^{-1} = 14.689 kcal day^{-1}

Male: $FMR_{inc} = FMR_{non}$ = 20.79 kcal day^{-1}

(Although the female's FMR_{inc} was allocated to her, it was actually fulfilled by the male who met her energy requirements by feeding her)

Nestling Care FMR (FMR_{nestl}):

Female: $FMR_{nestl} = FMR_{non}$ = 20.79 kcal day^{-1}

Male: $FMR_{nestl} = FMR_{non}$ = 20.79 kcal day^{-1}

Nestlings: FMR_{nestl} = TME = $28.43\ M^{1.06} = 28.43\ (27.72g)^{1.06}$ = 961.92 kJ/fledging = 229.90 kcal/fledging [x 3 fledglings = 689.7 kcal total clutch]

Nestling period - was 21 days - 689.7 kcal / 21 days = 32.84 kcal day^{-1} / 2 parents = 16.42 kcal day^{-1} parent $^{-1}$

Fledgling Provisioning FMR (FMR_{fledg}):

Female: FMR_{fledg} = FMR_{non} = 20.79 kcal day^{-1}

Male: FMR_{fledg} = FMR_{non} = 20.79 kcal day^{-1}

Fledglings: FMR_{fledg} = FMR_{non} (mass of 27.72g instead of adult mass) = 17.45 kcal day^{-1}

[x 3 fledglings = 52.35 kcal day^{-1} total]

Used 14 days for this period - 52.35 kcal day^{-1} (14 days) = 732.9 kcal total for fledgling provisioning [or 26.18 kcal day^{-1} $parent^{-1}$]

APPENDIX 3: Calculation of *Pinus strobus* seeds required to meet Field Metabolic Rates of both parents

$$s = \frac{\text{FMR}i}{\text{m(c)}} \text{ where}$$

$$\text{Nest Construction: } s = \frac{52.40 \text{ kcal / day}}{0.023\text{g / seed}(6.11 \text{ kcal / g})} = 372.8 \text{ seeds/day}$$

$$\text{Egg Production: } s = \frac{58.01 \text{ kcal / day}}{0.023\text{g / seed}(6.11 \text{ kcal / g})} = 412.8 \text{ seeds/day}$$

$$\text{Incubation: } s = \frac{44.35 \text{ kcal / day}}{0.023\text{g / seed}(6.11 \text{ kcal / g})} = 315.6 \text{ seeds/day}$$

$$\text{Nestling Care: } s = \frac{93.03 \text{ kcal / day}}{0.023\text{g / seed}(6.11 \text{ kcal / g})} = 661.9 \text{ seeds/day}$$

Fledgling Provisioning: $s = \frac{117.43 \text{ kcal / day}}{0.023\text{g / seed}(6.11 \text{ kcal / g})} = 835.6$ seeds/day

Nonbreeding: $s = \frac{51.98 \text{ kcal / day}}{0.023\text{g / seed}(6.11 \text{ kcal / g})} = 370$ seeds/day