

FACTORS AFFECTING NEST PREDATION OF ARTIFICIAL AND REAL
SAGEBRUSH BREWER'S SPARROW (*Spizella breweri breweri*) NESTS IN THE
SOUTH OKANAGAN AND SIMILKAMEEN VALLEYS, BRITISH COLUMBIA

By

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ABSTRACT

Predation is the predominant cause of nest failure for the Brewer's Sparrow (*Spizella breweri breweri*; BRSP), a provincially red-listed shrub-steppe species that has experienced significant declines throughout most of its range (Breeding Bird Survey). The factors that influence nest survival are often species and context specific. Therefore, it is important to examine the dynamics of Brewer's Sparrow nest survival in British Columbia (BC) so that appropriate management strategies can be devised.

I monitored Brewer's Sparrow nests to test if nest density and avian nest predator activity influenced Brewer's Sparrow nest survival. I also conducted an artificial nest experiment to assess potential nest predation risk relative to Brewer's Sparrow abundance and to determine whether increased avian nest predator activity was associated with reduced nest survival. In addition, within site factors such as tree encroachment, timing, and nest concealment were modelled to determine their effects on the survival of real Brewer's Sparrow nests at all nesting stages and for three nest predator categories - avian, mammalian and pooled (all predators combined) using artificial nests. The study was conducted at six sites in the South Okanagan region of BC.

My results showed that increased avian nest predator activity was associated with reduced survival of artificial nests. Avian predation of artificial nests was also highest at sites with few Brewer's Sparrows, suggesting that Brewer's Sparrows may avoid nesting at sites with many avian nest predators. Artificial nest predation by small mammals did not vary with Brewer's Sparrow abundance.

Survival analysis revealed that nest initiation date was an important predictor of real nest survival, because depredation increased later in the season. Pooled predators and mammalian depredation of artificial nests mirrored this trend. Avian predation risk was reduced through the season but only in combination with less nest cover. Late in the season, artificial nests placed close to trees experienced less mammalian predation and more avian predation. Tree density was related negatively to the survival of real Brewer's Sparrow nests at the nestling and pooled nesting stages.

Overall, my results suggest that Brewer's Sparrows nested in sites lower in avian nest predator activity. This trait resulted in the relative importance of other predators, such as small mammals, becoming more apparent. The importance of nest concealment and tree encroachment on real nest survival may be circumvented by Brewer's Sparrows nesting far from trees, in micro-sites with ample cover, and nesting in sites with low avian nest predator activity.

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CHAPTER 1 General Introduction

Like many songbird species in shrub-steppe habitat, Brewer's Sparrow (*Spizella breweri* spp.; BRSP) numbers are declining throughout most of their range (Sauer *et al.* 2001). There are two geographic subspecies in BC, *Spizella breweri taverneri*, the timberline subspecies, is darker and larger than *Spizella breweri breweri*, the sagebrush subspecies. The *taverneri* subspecies breeds in northern British Columbia, and in the mountains of southeastern British Columbia, whereas the *breweri* subspecies (or Sagebrush Brewer's Sparrow) breeds in the South Okanagan region of BC (Cannings *et al.* 1987). All further references to Brewer's Sparrows in this thesis refers to the *breweri* subspecies.

Brewer's Sparrows are red-listed in British Columbia (BC), due to small population size, restricted breeding range and threatened sagebrush habitats (Sarell and McGuiness 1996). Sauer *et al.* (2001) noted a slight increase in Brewer's Sparrow numbers over the last 30 years (3.1 % per year, $p = 0.84$, $n = 2$) in BC. Although this trend is not significant, it indicates a relatively stable population when compared to the survey wide results, which show an estimated decline of 3.2 % per year ($n = 450$, $p < 0.00$; Sauer *et al.* 2001). The BC population is at the northern extent of the species' range. This peripheral population of Brewer's Sparrows may play a role as a source population for declining populations in the south (Lomolino and Channell 1995). It is therefore important to understand the factors that affect this population and to address problems that may reduce population size further.

Predation is considered an important factor shaping reproductive ecology and behaviour of avian populations (Martin 1995). Nest predation reduces recruitment rate; thus, reducing nest predation rates may be important in recovering stressed populations. In the South Okanagan throughout 1997-1999, N. Mahony (unpub. res.) observed a mean predation rate of 34 % on Brewer's Sparrow nests; a rate which is typical for open cup nesters in similar habitat (Davison and Bollinger 2000). Similar estimates were found by O'Connor (1991; 33% of nests lost to predation in 74 studies) and Martin (1993a; 41% of nests lost to predation in 55 species).

Most declines in passerine populations have been a consequence of habitat destruction (Hagan *et al.* 1996), with nest predation acting as a secondary factor on already reduced populations. Anthropogenic changes in the South Okanagan have placed pressures on nesting habitat for shrub-steppe birds through heavy grazing and clearing of sagebrush to improve forage or for urban development. Human activities can also indirectly alter predation pressure at the nesting grounds. For example, fire suppression and subsequent increases in tree density in the sagebrush habitat (Turner and Krannitz 2001), and may contribute to higher rates of nest predation by providing nesting and foraging sites for avian nest predators (Krannitz and Rohner 2000).

The most commonly known nest predators of temperate-zone songbirds are in the family Corvidae and, in the South Okanagan, this includes the American Crow (*Corvus brachyrhynchos*; AMCR), Common Raven (*Corvus corax*; CORA), and Black-billed Magpie (*Pica pica*; BBMA). Other studies have implicated corvids as predators of Brewer's Sparrow nests (Petersen and Best 1987, Rotenberry and Wiens 1989).

However, many other nest predators may also threaten the reproductive success of nesting Brewer's Sparrows (Appendix I).

Brewer's Sparrows are small (9-12 g) insectivorous birds, virtually devoid of any conspicuous markings. This muted plumage of buff-brown streaking presumably enables the birds to blend into the sagebrush habitat and reduce detection by predators. The benefits of nest cover and camouflage from nest predators might be why Brewer's Sparrows nest primarily in big sagebrush (*Artemisia tridentata*; Rich 1980, Wiens and Rotenberry 1981). Brewer's Sparrow nests are small (mean diameter 87 mm, depth 41 mm; Rotenberry *et al.* 1999) and composed of grasses, weed stems, and rootlets, with the outside material consisting mainly of sagebrush (Baicich and Harrison 1997). The 2-5 blue-green eggs with brown speckles (Baicich and Harrison 1997) are only exposed if a vigilant female is disturbed by a predator and reluctantly leaves the nest unattended. Spacing out or clumping nests in response to predator species and corresponding foraging strategy are other possible methods of reducing the probability of nest predation. In BC, Brewer's Sparrows breed in loose colonies, patchily distributed throughout shrub-steppe habitat of the South Okanagan.

Several studies have assessed nest placement and nest site characteristics for Brewer's Sparrows (e.g., Knick and Rotenberry 1995, Petersen and Best 1985). Only a few studies have attempted to determine what influence habitat differences have on Brewer's Sparrow nesting success (e.g., Mahony (unpub.), Reynolds 1981). However, in these studies sample sizes were small and associations were only tested at the nest shrub or nest patch level.

In Chapter Two, I investigate site level factors that affect the daily survival rate of real and artificial nests. I determine whether nest density is associated with nest survival for Brewer's Sparrows. Additionally, I test the 'direct avoidance' hypothesis regarding the effects of predator presence on nest distribution and nest survival.

In Chapter Three, I investigate within site factors and model the effects of tree encroachment, seasonality, and nest concealment on the survival of real nests at egg, nestling, and pooled stages. Models were also derived for artificial nest predation separating predation by predator types; avian, mammalian and pooled predators.

In Chapter Four, I conclude by discussing management implications for Brewer's Sparrows nesting in the South Okanagan region.

CHAPTER 2 Does Nest density and/or Predator Activity Explain Nest Distribution and Nest Survival in Brewer's Sparrows?

2.1 INTRODUCTION

Predation is a predominate factor driving the life history traits and habitat use of many avian populations (Martin 1995), with about one third of nest failures caused by predation on average (O'Connor 1991). It is therefore important to discern the extent and manner that nest predators influence the distribution and survival of Brewer's Sparrow nests. This chapter approaches two questions regarding nest survival and distribution; (1) is nest density associated with nest survival and (2) can predator presence and/or predation risk explain nest distribution at the site level.

Answering the first question will establish whether or not nest density has a positive, negative, or no effect on Brewer's Sparrow nest survival. Generally, increasing nest density has been associated with increased nest predation in songbirds (Keyser *et al.* 1998, Hagan *et al.* 1996, Major *et al.* 1994, Knapton 1979). I refer to this effect as a 'negative density effect'. A 'negative density effect' may result from an increased foraging efficiency of nest predators at higher prey densities (Tinbergen *et al.* 1967) or when nesting densities remain high in an area because the birds are unable to respond to or move away from acute changes in amount of predation. An example of a factor that might induce this effect is the availability of nesting habitat, which may be limited due to factors such as habitat fragmentation. In such cases, birds may have to nest at

abnormally inflated densities (Larivière and Messier 1998, Hagan and Johnston 1992).

The result may be elevated predation pressure with increased density.

Fretwell (1972) theorized that at higher nest densities, predation might decrease due to group benefits of colonial nesting. Such a 'positive density effect' is possible under two hypotheses, which I refer to as the 'indirect avoidance' hypothesis and the 'direct avoidance' hypothesis. The 'indirect avoidance' hypothesis suggests that birds breeding in colonies are advantaged by reduced risk of predation indirectly through group benefits (reviews in Brown *et al.* 1990, Wittenberger and Hunt Jr. 1985). Some of the mechanisms that result in these 'indirect' benefits include cooperative detection and repulsion of predators (Wiklund and Anderson 1994, Hoogland and Sherman 1976, Pulliam 1973, Kruuk 1964), central nest position (peripheral nests receive higher predation rates; Picman *et al.* 2002), reduced probability of attack per prey or dilution (Foster and Treherne 1981) and predator satiation (Lima and Dill 1989, Nisbet and Welton 1984). The 'indirect avoidance' hypothesis is not tested in this chapter, but may be a possible alternate hypothesis to the 'direct avoidance' hypothesis explained below. Birds clustering in high quality habitat can also produce a 'positive density effect' by increasing nest survival independent of the influences of nest predators. I controlled for differences in habitat quality between sites by using sites that had comparable habitat features and characteristics known to be associated with Brewer's Sparrow abundance (Paczek 2002).

Direct avoidance of nest predators, through nest site selection, may be another reason for coloniality (Brown *et al.* 1990, Ward and Zahavi 1973). I refer to this as the 'direct avoidance' hypothesis. Direct avoidance of nest predators, by nesting where

predator activity is low, may result in a 'positive density effect' if birds cluster in areas of low predator activity but might also result in 'no density effect' if predators that forage in high prey density areas are avoided. It is possible that birds nest in loose colonies because they are taking advantage of the few sites that have reduced nest predator activity in an area. This makes it difficult to assess whether or not predator avoidance, rather than nest density, is the stronger mechanism for reducing nest predation because the two hypotheses are not mutually exclusive. To avoid this problem I used the number of nests per site instead of nest density to test the 'direct avoidance' hypothesis. Nest number better reflects the number of breeding birds that are occupying a nest site than does nest density, because sites with high nesting densities can have varying numbers of nests.

This forms the foundation for answering the second question: can predator presence explain nest distribution and differences in nest survival, between nest sites. The 'direct avoidance' hypothesis predicts that high nest predator activity will be associated with sites that have fewer nests. The consequence of avoiding high predator activity should be increased nest survival at sites with more nests and less predator activity.

The Brewer's Sparrow is an appropriate species to address questions regarding nest density, because Brewer's Sparrows nest in loose colonies, with a wide natural range of breeding densities have been reported (~3 to 20 birds per 100 ha; Harvey 1992, Cannings *et al.* 1987). Nest predation is the greatest cause of nest failure for Brewer's Sparrows, proximately influencing recruitment rates, and may represent the main selective factor for Brewer's Sparrow nest site selection (Rotenberry and Wiens 1989).

Research has been conducted to determine which habitat is suitable for breeding Brewer's Sparrows (Paczek 2002). Previously, it has been noted that several areas that apparently had suitable nesting habitat remained unoccupied by Brewer's Sparrows (Wiens *et al.* 1985). These areas may have been avoided for other reasons such as the presence of predators, or because they were clustering in other areas to take advantage of any benefits of coloniality.

Previous studies have found that the effect of nest density on nest survival varied with nest predator type (Hogstad 1995, Wiklund and Anderson 1994). For instance, large mammals and avian nest predators may be able to key into high density nesting patches, resulting in a bulk attack and a 'negative density effect' (Pelech 2000, Larivière and Messier 1998, Hogstad 1995, Tinbergen *et al.* 1967, Kruuk 1964,). In contrast, solitary predators such as snakes and small mammals are thought to forage for eggs and nestlings in nests independent of the nearest nest neighbour and with minimal prey search image, resulting in a 'no density effect' (Wiley and Wiley 1980). It was therefore important to identify predator type in this study, which was possible with the use of artificial nests and clay eggs.

Although artificial nests may not accurately reflect the exact predation rates of Brewer's Sparrow nests, they are useful for determining trends and patterns (Wilson *et al.* 1998), as well as identifying potential predators (Donovan *et al.* 1997). However, predators respond differently to artificial nests and real nests (Ortega *et al.* 1998). It is therefore important to validate the findings of artificial nests with the use of real nests, as some predators may be overestimated - as in the case of small mammals (Maier and DeGraaf 2001), or under-represented - particularly in the case of snakes (Davison and

Bollinger 2000). I have approached my hypothesis testing in two ways: by conducting an experiment using artificial nests and secondly, by monitoring natural nests to validate the artificial nest findings.

2.2 METHODS

2.2.1 Study Area

Research was conducted from May to August 2000 in the South Okanagan region, BC, Canada. This region encompasses an area of approximately 90km long by 30 km wide and includes parts of both the South Okanagan and Lower Similkameen valleys. The study was conducted in shrub-steppe habitat, which is found in patches throughout the ponderosa pine and bunchgrass biogeoclimatic zones (Meidinger and Pojar 1991). These biogeoclimatic zones include arid habitat from the valley bottom to about 600-1000 meters in elevation (Meidinger and Pojar 1991). The undulating topography of the study area is dominated by big sagebrush with an understory of grasses and forbs. Common conifer tree species that can be found scattered throughout the landscape include ponderosa pine (*Pinus ponderosa*), douglas-fir (*Pseudotsuga menziesii*), and rocky mountain juniper (*Juniperus scopulorum*), which can grow to a shrubby tree up to 10 meters tall.

Artificial Nest Experiment Sites

Six sites located in the region between the village of Keremeos (49°12'N, 119°49'E) and Okanagan Falls (49°20'N, 119°34'E) were used for the artificial nest experiment (Table 2-1; Figure 2-1). These sites were selected based on previous

knowledge of nesting Brewer's Sparrow abundance (Mahony unpub., Paczek 2002, Harvey 1992), and ease of access . To compare nest predation rate and patterns, I selected six sites where the relative abundance of Brewer's Sparrows was known; three sites were known to have 'low' Brewer's Sparrow relative abundance, and three sites with 'high' relative abundance (Paczek 2002). All six sites had comparable habitat features and characteristics known to be associated with Brewer's Sparrow abundance (Paczek 2002). All of the sites had comparable silky lupine (*Lupinus sericeus*), parsnip-flowered buckwheat (*Eriogonum heracleoides*), and big sagebrush (*Artemisia tridentata*) cover but varied in litter cover. It was assumed that litter cover did not affect the distribution of avian nest predators. Litter cover may influence snake and mammal predation or nest predation rate, as Paczek (per. comm.¹) noticed more garter snakes (*Thamnophis sirtalis*) where there was thick litter cover. This would expect to increased nest predation at high abundance Brewer's Sparrow sites, as litter cover was greater at these sites.

Armstrong Creek is just north of Keremeos and has both a 'low' and 'high' site that are separated by approximately two km from edge to edge. The Armstrong low (ARL) site was located just south of Keremeos Columns Provincial Park and was leased by ranchers (Figure 2-1). Armstrong high (ARH) site was situated at a slightly higher elevation than ARL (Table 2-1). The White Lake area was a 10-km² tract of shrub-steppe habitat with varying densities of breeding Brewer's Sparrows throughout. Both sites were at the same elevation (Table 2-1). No Brewer's Sparrow nests were found at

¹ Susan Paczek did her Master's degree on Brewer's Sparrows see Paczek 2002.

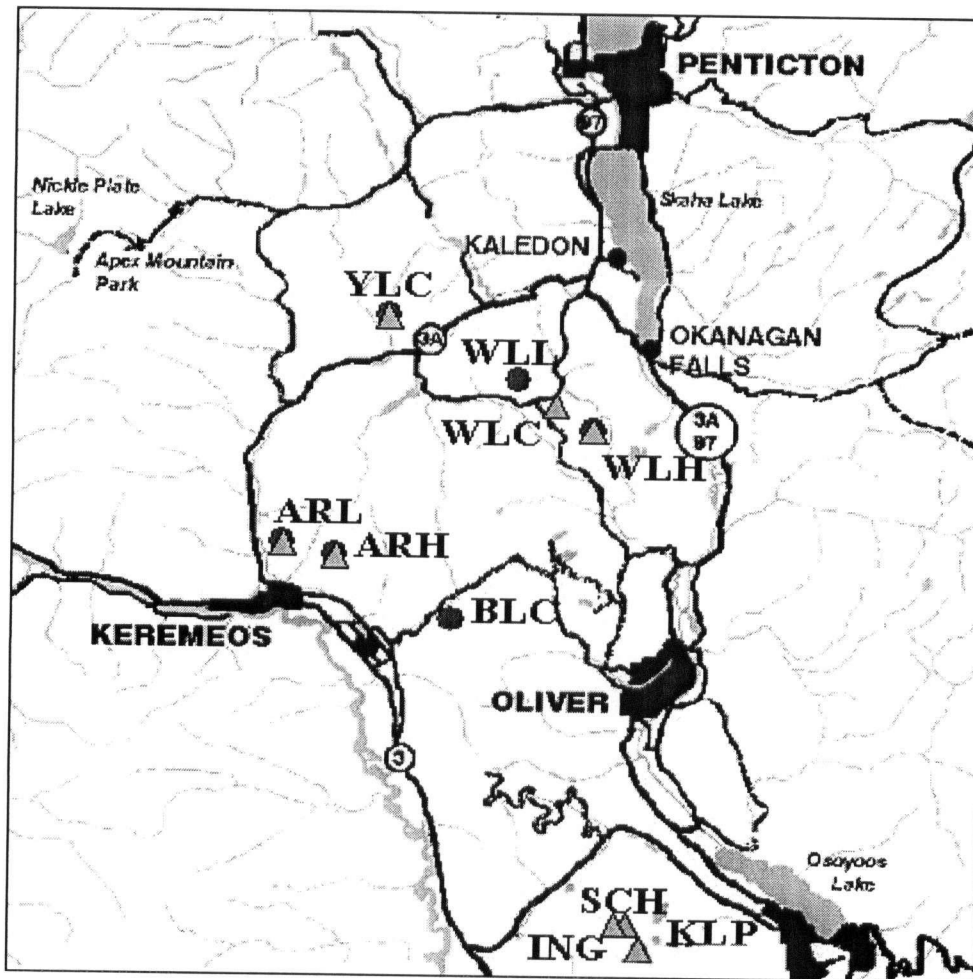


Figure 2-1 Map of the study area. Triangles show where the real nests were monitored, and circles where the artificial nest experiment was conducted. Site acronyms are ARL – Armstrong low, ARH – Armstrong High, BLC – Blind Creek, ING – International Grasslands, KLP - Kilpoola, SCH – Schneider, YLC - Yellow Lake Creek, WLC - White Lake Center, WLL - White Lake low, WLH - White Lake High

the White Lake low (WLL) site, although Paczek (2002) heard singing males there in 1998. The White Lake high-density (WLH) Brewer's Sparrow site was situated southeast of WLL. A breeding population of Brewer's Sparrows, in an area identified as White Lake centre (WLC), occurred between the two artificial nest sites (Table 2-1). WLC was used in the real nest study; however, artificial nests were not placed at this site so as not to interfere with concurrent Brewer's Sparrow research at this location. The

last two sites were Yellow Lake Creek (YLC), which was high density, and Blind Creek (BLC), which was low Brewer's Sparrow density (Table 2-1). These sites were separated by approximately 12 km (Figure 2-1). Yellowlake Creek had the highest density of Brewer's Sparrows (1.0 nests/ha) of the artificial nest study sites. No Brewer's Sparrow nests were found at the Blind Creek site, though singing males were found there two years ago by Paczek (2002).

Real Nest Monitoring Sites

Real nest searching and monitoring was conducted at six study sites (Figure 2-1). The real nest study was hindered by a lack of suitable sites in the South Okanagan region. In order to have a reasonable sample size, survival data from four additional sites (Table 2-1) were supplied by Mahony (unpub. data) and were included in the analysis. Kilpoola (KLP), Schneider (SCH), and International Grasslands (ING) were clustered within 5km of each other and were adjacent to the Washington State border (Figure 2-1). At 1.7 nests/ha, Kilpoola had the highest density of Brewer's Sparrow nests of all 10 sites in the South Okanagan region. International grasslands was a large tract of grassland, but only a 13 ha portion was used in this study (Table 2-1). The density of nesting Brewer's Sparrows was high, despite being recently burned (see results). White Lake centre (WLC) was flanked by the WLL and WLH sites and was adjacent to White Lake (Figure 2-1).

Artificial nest experiments and real nest monitoring were conducted simultaneously from 1 May to 31 July 2000, coinciding with the Brewer's Sparrow breeding season (Cannings *et al.* 1987). Three artificial nest trials of 12 day duration

were run, the first trial ran from May 22 to June 3, the second trial from June 12 to June 24, and the third trial from July 3 to July 15.

Table 2-1 Sites used in the artificial nest experiment and real nest monitoring. ‘A’ refers to where the artificial nest experiment was conducted and ‘R’ refers to where the real nest monitoring was conducted. Predation data from the asterisked sites ‘*’ were supplied by Mahony (unpub.). ‘Site Area’ is the approximate size of the site, which was used for the artificial nests experiment.

Site	Artificial and/or real	Lat/long	Elevation in meters	Site Area in ha
ARH	A & R	49° 13’/119° 45’	1175	11
ARL	A & R	49° 14’/119° 48’	958	11
BLC	A & R	49° 12’/119° 42’	824	17
*ING	R	49° 0’/119° 37’	900	13
*KLP	R	49° 1’/119° 34’	870	17
*SCH	R	49° 1’/119° 35’	900	14
YLC	A & R	49° 21’/119° 44’	1071	17
*WLC	R	49° 19’/119° 38’	480	18
WLH	A & R	49° 18’/119° 37’	628	10
WLL	A & R	49° 19’/119° 39’	686	17

2.2.2 Artificial Nest Design, Protocol and Analysis

I established eight transects of artificial nests at each of the six sites. Each transect consisted of six artificial nests placed at 5, 30, 55, 80, 105, and 130 meters (25 meters increments), from the base of isolated conifer trees, that had a mean height of 16 meters (range 5-30m). Every attempt was made to mimic the dimensions and construction of Brewer’s Sparrow nests to provide a similar search image for predators. I used commercially purchased realistic woven-grass canary nests (approximately 10cm in

diameter and 4cm deep; Hagen© item B-1980) for my artificial nests. The nest rims were painted a dull grey to blend into the sagebrush, and the nests were weathered outside for one week before being placed in the field to reduce artificial scents. Nests were wired into shrubs (mean shrub height of 73cm; 5-189cm range) at an approximate height of 30 cm from the ground (mean of 30.5cm; 9-71cm range), and two coloured clay eggs were placed in the centre of each nest.

Modelling clay provided an excellent substrate for recording tooth or beak imprints. Additionally, artificial eggs were easily sized, shaped, coloured by mixing different coloured clays, and were painted with brown speckles to convincingly mimic Brewer's Sparrow eggs. I used 2 kinds of non-toxic clay with negligible odour: Sculpey II ©, which is useful because it can be permanently hardened by baking, and Aken plastaline © (Plastaline modelling clay; Van Aken international, Rancho Cucamonga, CA), which is the clay most typically used in artificial nest predation studies (Haskell 1995). Concerns regarding the exclusion of small predators were addressed by using clay eggs only, because clay eggs are palatable and small (17mm; DeGraaf and Maier 1996).

Clay eggs were placed in nests for a 12-day cycle, based on the approximate incubation period for Brewer's Sparrows of 11 days (Rotenberry and Wiens 1991). The nests were checked between sunrise and noon on the 3rd, 6th, and 12th day of each trial. A nest was considered depredated if one or both eggs were missing, or if eggs were marked with direct evidence of predation - such as beak, tooth, or scratch marks. Predation events were classified into avian, mammalian and unknown, as well as a category for nests that were disturbed (trampled) by cows. . Snake predation is generally

excluded from artificial nest studies (Marini and Melo 1998) but if snake predation occurred, it would be grouped with unknown events because scratch marks from snakes are indistinguishable from other predators. Missing eggs were assumed to be taken by avian predators because twelve eggs with bill imprints were found scattered throughout the study sites. In the artificial nest analysis, avian, mammalian, and pooled predators were assessed. Pooled predators included all predation events by all possible predators.

Marked eggs were removed after a depredation and the nests were reset with new eggs. However, only the first predation events were included in the analysis to avoid pseudo-replication (Hurlbert 1984). Untouched eggs were removed on the last (12th) day. After being left empty for 8 days, the nests were moved 5-10 meters in random directions to ensure independent observations between trials. All artificial nests were handled in the same manner to avoid bias. To avoid alerting visual predators to nest locations, nest markers were placed 10-30 meters from the nest. A precautionary approach was taken to avoid scent paths to the nests by taking different paths to the nests upon each visit. Hands were rubbed with sagebrush before handling eggs and nests to reduce human scent.

2.2.3 Monitoring of Real Nests

Real nest searching was conducted by using either the 'stalking' or the 'tapping' techniques at all ten sites. The tapping technique consisted of several people walking back and forth across the site in a line, gently tapping on shrubs to flush incubating birds. The stalking technique involved following and observing the birds from a distance. A

combination of both techniques was employed until I felt confident I had found all the nests in an area.

Once a nest was found, the condition, location, and clutch size was determined. Subsequent monitoring was conducted on a three-day rotation between two sites. Nests were considered successful if they were found empty after the expected fledging date (8-9 days after hatching), and signs of a successful fledge were observed. Indications of fledging success were: parents feeding a fledgling; agitated parents; sounds of begging calls or 'chips' nearby; presence of one or more fledglings in the immediate area; or a flattened nest rim. The area surrounding the nests was intensely searched for clues to confirm the nest's status including: nests found empty before the end of the expected fledgling period; nests disturbed with the lining pulled out; or nests with a hole through the bottom. Occasionally, dead chicks or depredated eggs were found in or around the nests, making the nest failure obvious. Nests that were abandoned with all eggs intact were removed from the analysis, as this could not be categorized as depredated or not. To avoid pseudo-replication (Hurlbert 1984), only first nesting attempts were used in the data analysis, and re-nests were disregarded. All the nests at my sites were visited once every three days and once every four days for the other researcher's sites.

2.2.4 Estimating Daily Survival Rate

Comparisons between real and artificial nests, as well as the effects of breeding pair density, nest density, and avian predator activity estimates were assessed in relation to nest survival by computing the daily survival rate for each site and using a correlation analysis. Daily survival rates for each site were estimated using the program

SURVIVAL - Mayfield Version 5.1 (Krebs 2000). The program calculates the Mayfield daily survival rate as well as providing the Bart and Robson (1982) maximum likelihood estimator of survival rate (MLE) and 95 % confidence intervals. MLE is the preferred estimate of survival rate as it resolves the bias in Mayfield method (Bart and Robson 1982), caused by the fact that nests were visited periodically and the exact date of depredation was unknown. Units are reported in finite daily survival rates (DSR); with the number of nests not depredated at the end of the day divided by the number of nests not depredated at the start of the day. Spearman rank correlation analysis (r_s) was used to test potential associations with DSR.

2.2.5 Density and Survival of Real Nests.

The effects of population size and density of Brewer's Sparrows on nest survival were investigated using two measures of density: 1) nest density (#nests/ha), and 2) breeding pair density (number of singing males/ha). Additionally, the area used by each local population was calculated to determine the potential effects of nesting patch size on nesting success.

Nest density was calculated from the number of nests divided by nesting patch area (the polygon area around the peripheral nests). Precise geographical nest locations were obtained by measuring the distances and direction of nests from field markers such as a landmark (rocks, fence posts etc.), survey grid markers (from the Brewer's Sparrow survey) and/or isolated trees in the landscape. Nesting patch size was derived by using AutoCAD (Autodesk 2002). A minimum convex polygon was drawn around the

peripheral nests and the inside area was calculated. To estimate each site's nest density, the number of nests was divided by the calculated area.

Breeding pair density was estimated from the number of singing males (based on survey data) divided by the area surveyed. Brewer's Sparrow surveys were conducted at each of the six sites once per month, totalling three surveys per site over the study period. Surveys were conducted between 0600 and 1000 h, under satisfactory weather conditions; good visibility, with little or no precipitation, and wind less than Beaufort 3 (12.9-19.3 km/h; light breeze, leaves and twigs move around). Using a marked grid of 600 by 200 m, five 200 meters parallel transect lines were established 100 meters apart and 50 meters wide and surveyed at each site using a combination of transect and point count methods. This method of surveying included walking at a rate of 10 m/min, totalling 20 min per 200 meters transect. Auditory detections of any male Brewer's Sparrows were recorded. To avoid double detections, locations based on the grid markers were estimated. If more than one Brewer's Sparrow was detected within 50 meters of another, only the first detection was included. This decreased the chances of over-estimating the numbers by birds or double counting birds.

The effect of nest density on nest survival was tested using nest density and breeding pair density in relation to daily survival rate of nests. The number of nests was not used, as sites that have high numbers of nests may not necessarily have high nest densities. A positive association between nest survival and density would refute 'negative density effect' prediction and support the 'positive density effect' prediction.

2.2.6 Direct Avoidance Hypothesis

Avian Nest Predator Activity Index in Relation to Real Nest Number.

Potential nest predators were monitored throughout the study at six sites using a measure of activity level. To produce an avian nest predator activity index, each observer independently recorded potential predators encountered while conducting fieldwork, the frequency of observations, and the number of hours spent in the area. Moving predators were recorded only where first seen, and repetitive daily sightings of the same species in the same place were recorded only once by that person for that day. To avoid overestimates, duplicate auditory or visual detections coming from the same direction were omitted. Results for all observer-days were combined to calculate the average number of predators seen per hour (encounter rate). Counts were not conducted during inclement weather. Potential avian nest predators were mostly within the family Corvidae and included American Crow, Common Raven, and Black-billed Magpie.

Predator activity was compared to the number of Brewer's Sparrow nests present at the site to determine if there were fewer predators at sites 'high' in Brewer's Sparrows. Sites designated as 'low' Brewer's Sparrow sites had less than five nests per site and 'high' Brewer's Sparrow sites had greater than five nests. It is important to note that nest number and not nest density is used here, as sites with high density do not always have more nests. A high number of nests may indicate a site preference where density does not. Nest number refers to the total count of all nests at a particular site. In this study nest density and the total number of nests at the site are highly correlated making the terms interchangeable, however, number of nests is used, since this makes more sense in terms of the 'direct avoidance' hypothesis.

Avian Nest Predator Activity Index in Relation to Nest Survival of Real and Artificial Nests

To test the 'direct avoidance' hypothesis, I determine if nesting at sites with fewer avian nest predators is beneficial to Brewer's Sparrows. I compared predator distributions between 'high' and 'low' Brewer's Sparrow sites and, tested the association of DSR, from real and artificial nests, in relation to avian nest predator activity. Kaplan-Meier survivorship was also used to estimate the survival rate of real and artificial nests (Pollock *et al.* 1989). This method was used because it addresses assumptions that are inherent in constant survival distributions (Kaplan and Meier 1958, Cox and Oakes 1984) such as DSR. Cox's F- test was used to compare the survival times (Lee 1980) of two groups: 'high' abundance (greater than or equal to 5 nests per site) and 'low' (less than 5 nests per site) abundance of Brewer's Sparrows. Each predator type was analysed separately for artificial nests. All statistical tests, apart from the DSR estimates, were performed using STATISTICA© (Statsoft 1999) for this chapter.

2.3 RESULTS

2.3.1 Daily Survival Rate of Artificial and Real Nests

Of 858 artificial nests, 70.3 % (603 nests) were depredated; 28.2 % (242 nests) by birds, 37.4 % (321 nests) by mammals. An additional 1 % (9 nests) were trampled by cows. The predators of the remaining 31 nests (3.6 %) were unknown. The mean overall daily survival rate for the artificial nests due to avian predation was $0.96 \text{ DSR} \pm \text{SD } 0.03$). The lowest nest daily survival rate was at Blind Creek (BLC; $0.91 \pm \text{SE } 0.01$),

which was a 'low' Brewer's Sparrow site (Table 2-2). The highest survival rate ($0.99 \pm \text{SE } 0.003$) was at the Yellow Lake Creek (YLC), a 'high' Brewer's Sparrow site (Table 2-2). Daily survival rates of artificial nests attributed to avian predation did not significantly vary between the six sites (ANOVA $F = 2.51$ $n = 18$, $p = 0.09$) and did not vary significantly between trials (ANOVA $F = 0.64$ $n = 18$, $p = 0.542$).

One hundred and seventy active real nests were found across ten sites, but only 122 were used in the analysis since the remaining nests were known renesting attempts. Of the 122 nests that were used in the analysis, 29.5 % (36 nests) of the nests were depredated, and 70.5 % (86 nests) were censored (meaning that they survived the observation period and were presumed to have fledged successfully). For real nests, the mean DSR was 0.93 ($n = 8$), similar to that of artificial nests. However, the lowest survival was not at BLC, but at another 'low' Brewer's Sparrow site, ARL at 0.87 and the highest was at SCH 0.95 (Table 2-2). Nest predation was assumed to be the primary cause of nest failure, based on the evidence left at disturbed nests. DSR did not differ significantly between the egg and nestling stages of the real nests (Mann-Whitney U-test; $z = 0.84$ $p = 0.40$). Thus, all nesting stages were pooled for real nest analysis.

The daily survival rate from avian, mammalian, and pooled predation did not vary significantly between artificial and real nests (Mann-Whitney U-test; $z = -1.81$ $p = 0.07$, $z = -1.55$ $p = 0.121$ and $z = 1.42$ $p = 0.16$, respectively; Table 2-2). However, the amount of depredation of artificial nests (70.8 %) was much higher than that of real nests (29.5 %). The DSR of artificial nests did not differ from that of real nests because of differences in sampling intervals and sample sizes which is an inherent problem of using this kind of survival analysis (Krebs 2000).

Table 2-2 Daily survival rates for artificial nests with avian, mammalian and all predator types. Real nests are also presented. Sites without real Brewer's Sparrow nests are not included, as Daily Survival Rate (DSR) could not be computed.

Sites	Avian DSR	Mammalian DSR	All predators DSR	Real nest DSR
ARH	0.956	0.966	0.916	0.920
ARL	0.951	0.961	0.917	0.874
BLC	0.914	0.944	0.869	-
WLH	0.988	0.927	0.915	0.928
WLL	0.940	0.921	0.878	-
YLC	0.990	0.956	0.944	0.947
ING	-	-	-	0.943
KLP	-	-	-	0.935
SCH	-	-	-	0.953
WLC	-	-	-	0.914

Table 2-3 Mean Brewer's Sparrow densities from both survey techniques. Mean Breeding Bird Density is the number of Brewer's Sparrows per hectare and was derived using a combination line/point count survey technique and the mean number of nests per hectare was derived from the number of first nests found, divided by the nest patch area. Nest patch area was derived from the inside area of the polygon around all peripheral nests at a site. Predator activity index is also presented in corvids observed per hour.

Sites	Breeding bird density	Nest density	Nest Patch Area	Number. of nests	Predator Activity
ARH	0.49	0.78	8.94	7	0.52
ARL	0.18	0.37	10.9	4	8.82
BLC	0.00	0.00	0.0	0	5.68
WLH	0.40	0.85	9.4	8	0.16
WLL	0.02	0.00	0.0	0	1.75
YLC	0.89	1.06	16.0	17	0.13
ING	N/A	1.13	13.3	15	N/A
KLP	N/A	1.67	17.4	29	N/A
SCH	N/A	1.32	14.4	19	N/A
WLC	N/A	1.26	18.2	23	N/A

2.3.2 Nest density and Breeding Pair Density in Relation to Survival of Real Nests

Spearman rank order correlations showed significant correlations between the methods of estimating Brewer's Sparrow density; nest density (number of nests per hectare) and breeding pair density (number of singing males per hectare; $n = 6$, $r_s = 0.93$, $p < 0.01$), indicating that the methods of estimating density were in close agreement and likely had similar biases. Number of Brewer's Sparrow nests was positively correlated to

nest density and breeding pair density ($n = 10$ $r_s = 0.98$ $p < 0.001$ and $n = 6$ $r_s = 0.93$ $p < 0.01$, respectively).

Although survival of real Brewer's Sparrow nests was not associated significantly with either nest density or breeding bird density (Table 2-4), the trend in each case was positive.

Table 2-4 Spearman Rank Correlations between the daily survival rate (DSR) of real nest density and breeding bird density estimates, as well as nest patch area. Breeding bird density is the number of singing male Brewer's Sparrows per hectare and was derived using a combination line/point count survey technique. The mean number of nests per hectare was derived from the number of first nests found, divided by the nest patch area. Nest patch area was derived from the inside area of the polygon around all peripheral nests at a site.

Site level variables	DSR Real		
	n	r_s	p
Nest density	8	0.55	0.16
Breeding Bird density	4	0.80	0.20
Nesting patch area	8	0.21	0.61

2.3.3 Direct Avoidance Hypothesis

Avian Nest Predator Activity Index in Relation to Real Nest Number.

Of 467 observations of corvids during encounter surveys, 71.1% (332) were Common Ravens, 14.6% (68) were Black-billed Magpies and 14.4% (67) American Crows. Nest number confirmed sites designated as 'low' or 'high' in Brewer's Sparrow abundance. 'Low' Brewer's Sparrow sites had less than five nests and included ARL, BLC, and WLL (Table 2-3). 'High' Brewer's Sparrow sites had greater than five nests and included sites ARH, WLH, YLC (Table 2-3).

'Low' Brewer's Sparrow sites had greater avian nest predator activity (5.41 corvids/hr) when compared to 'high' Brewer's Sparrow sites (0.27 corvids/hr, Mann-Whitney U-test; $n = 6$, $z = 1.96$, $p < 0.05$). This was confirmed by a negative correlation between avian nest predator activity and number of Brewer's Sparrow nests found at the site ($n = 6$, $r_s = -0.81168$ $p < 0.05$; Figure 2-2). The analysis used the total count of Brewer's Sparrow nests found at each site. Nest density measures were not used here, because I am comparing the number of birds nesting at the sites, and sites with a high density do not necessarily have a high number of nesting birds. However, the relationship of avian nest predator activity to nest density is the same ($n = 6$ $r_s = -0.81$ $p < 0.05$) because nest density is highly correlated to nest number ($n = 10$ $r_s = 0.98$ $p < 0.001$).

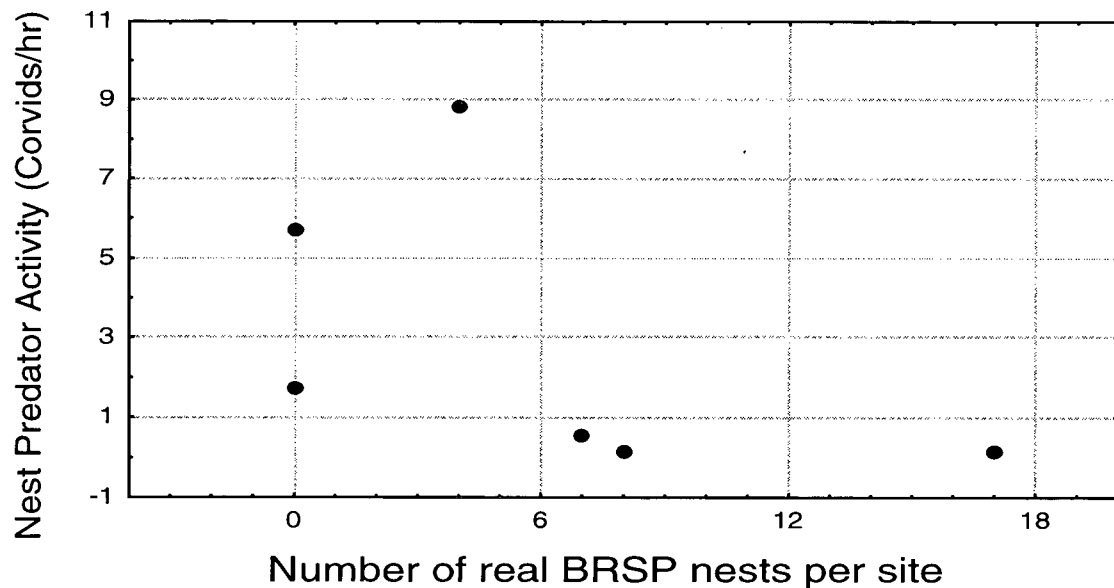


Figure 2-2 Correlation between avian nest predator activity (the number of corvids per hour) and the number of real Brewer's Sparrow nests at six sites, ($n = 6$ $r_s = -0.81$ $p < 0.05$). The number of real Brewer's Sparrow nests is the total count of nests found at each site.

Avian Nest Predator Activity Index in Relation to Nest Survival of Real and Artificial Nests

As expected from increased predator activity at 'low' Brewer's Sparrow sites, my results from the experiment with artificial nests indicate that sites lower in Brewer's Sparrow nest number had significantly more avian nest predation than sites with a 'high' number of Brewer's Sparrow nests.

The percentage of artificial nests depredated by avian predators was 40.3 % (173 nests) for 'low' Brewer's Sparrow sites and 16.1 % (69 nests) for 'high' sites (Mann-Whitney u-test $z = 6.15$ $p < 0.001$; Figure 2-3). The same trend was found when all nest predators were considered. The percentage of artificial nests depredated by pooled predators was 61.8 % (265 nests) for 'high' Brewer's Sparrow sites and 79.7% (342 nests) for 'low' Brewer's Sparrow sites (Mann-Whitney u-test $z = 4.551$ $p < 0.001$). This difference was mostly attributable to the strong differences in avian predation.

Mammalian predation pressure was relatively constant between 'high' and 'low' Brewer's Sparrow sites at 38.9 % (167 nests) and 35.9 % (154 nests) respectively; Mann-Whitney u-test $z = -0.77$, $p = 0.44$; Figure 2-3).

Similar results were found when analyzed using Cox's F-test. Artificial nests placed in 'low' Brewer's Sparrow sites had reduced survival times due to avian predation (Cox's F-test $F = 2.99$ $p < 0.001$; Figure 2-4) compared to those in 'high' Brewer's Sparrow sites. A similar significant difference was found in survival time attributed to pooled predators (Cox's F-test $F = 1.70$ $p < 0.001$). Survival rate of nests attributable to

mammalian predation was not affected by the abundance of nesting Brewer's Sparrows (Cox's F-test $F = 1.09$ $p = 0.23$).

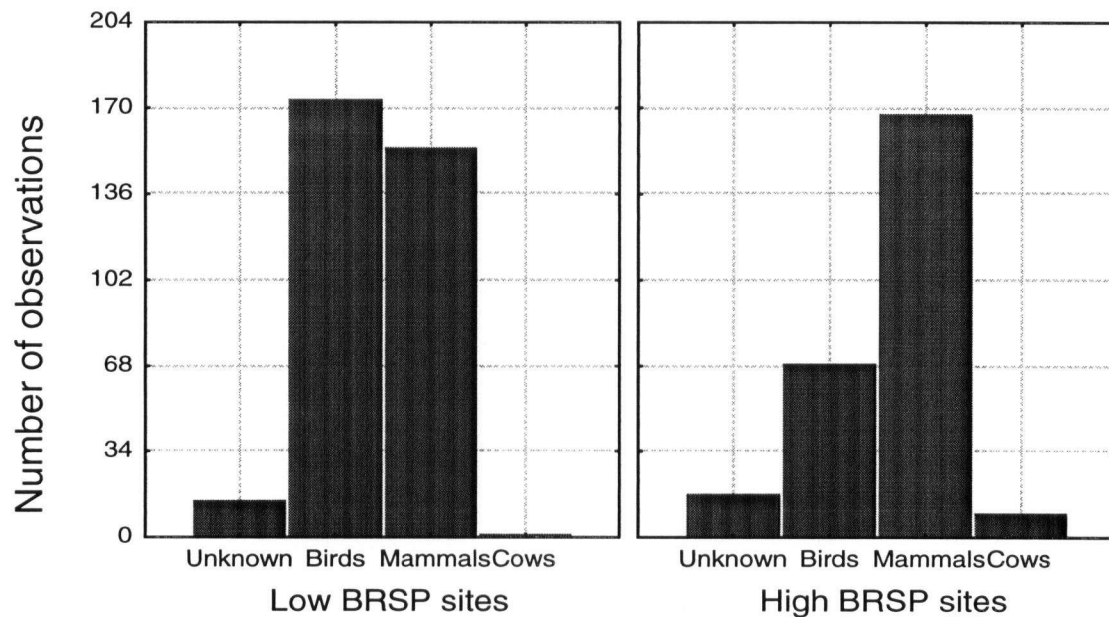


Figure 2-3 The number of predation events observed in the artificial nest experiment for each predator type in relation to Brewer's Sparrow (BRSP) abundance.

Survival of artificial nests, attributable to avian predation, was higher at sites with more nest predator activity for trials 1 and 2 ($n = 6$, $r_s = -0.83$ $p = 0.04$ and $r_s = -0.94$ $p = 0.005$, respectively; see Figure 2-5) but not in trial 3 ($n = 6$ $r_s = -0.70$ $p = 0.13$). When all trials were pooled, the relationship was significant ($n = 6$ $r_s = -0.83$ $p = 0.04$). This shows that my underlying assumption of increased predation with increased nest predator activity is supported allowing me to test the 'direct avoidance' hypothesis. In addition, there was support for this assumption by the real nest results, as survival of real nests was also negatively associated with increased avian nest predator activity. The DSR

decreased with increased avian nest predator activity although a sample size of four is too small for a definitive conclusion (Figure 2-6).

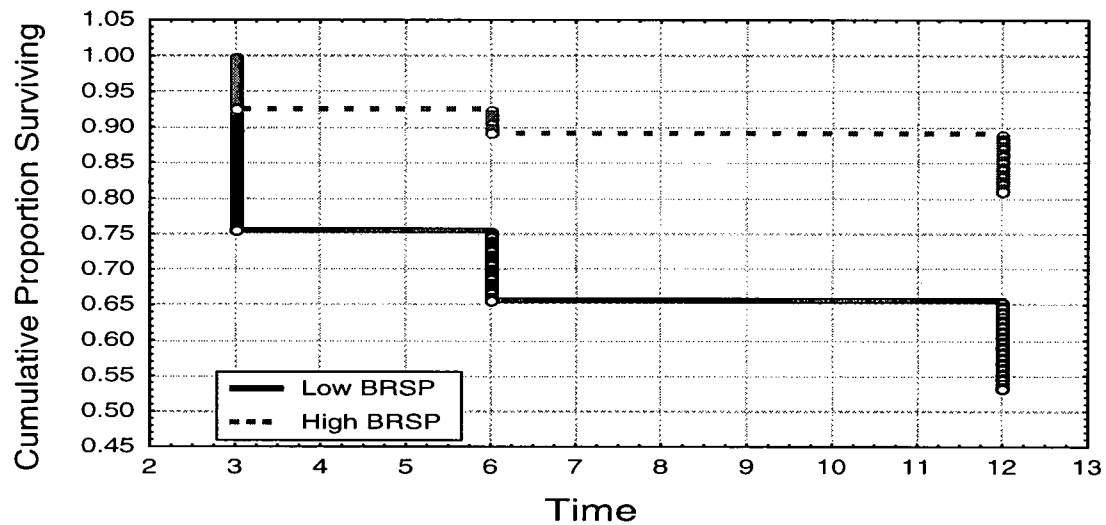


Figure 2-4 Kaplan-Meier plot of the cumulative proportion surviving in each group ('high' versus 'low' Brewer's Sparrow sites) for avian predation of artificial nests. Artificial nests placed in sites with 'high' Brewer's Sparrow (BRSP) sites had a better survival rate due to reduced avian predation as compared to nests placed in 'low' Brewer's Sparrow sites (Cox's F-test $F = 2.99$ $p < 0.001$). Dashed line indicates the nest survival plot of 'high' Brewer's Sparrow sites; the solid line indicates the 'low' Brewer's Sparrow sites.

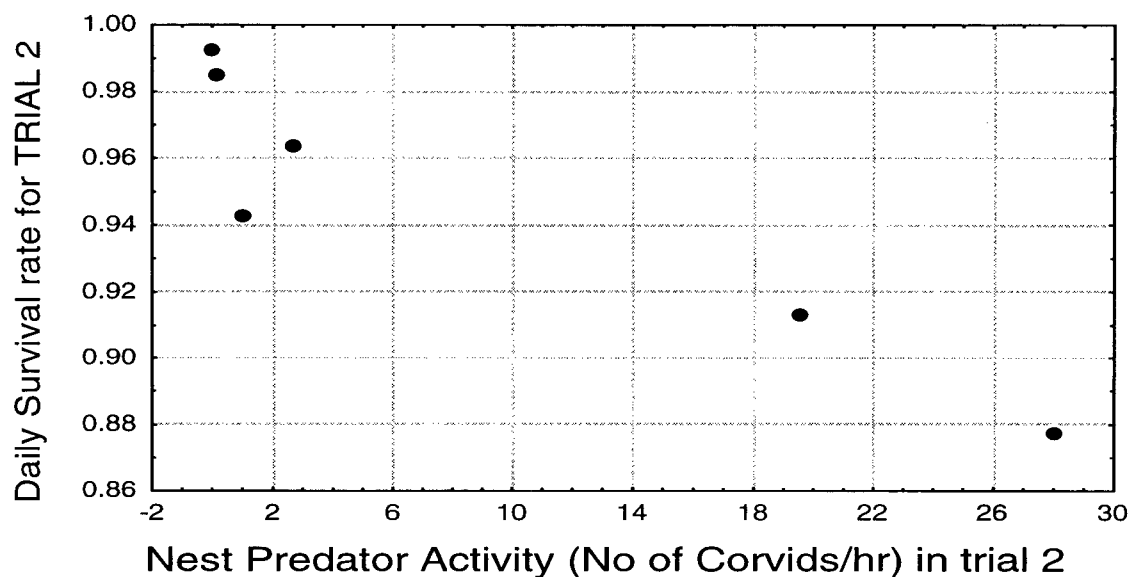


Figure 2-5 Survival of artificial nests attributable to avian predation in relation to nest predator activity index (number of corvids observed per hour). Daily survival rate (DSR) for trial 2 was negatively correlated to predator activity through trial 2 ($n = 6$, $r_s = -0.94$, $p = 0.005$).

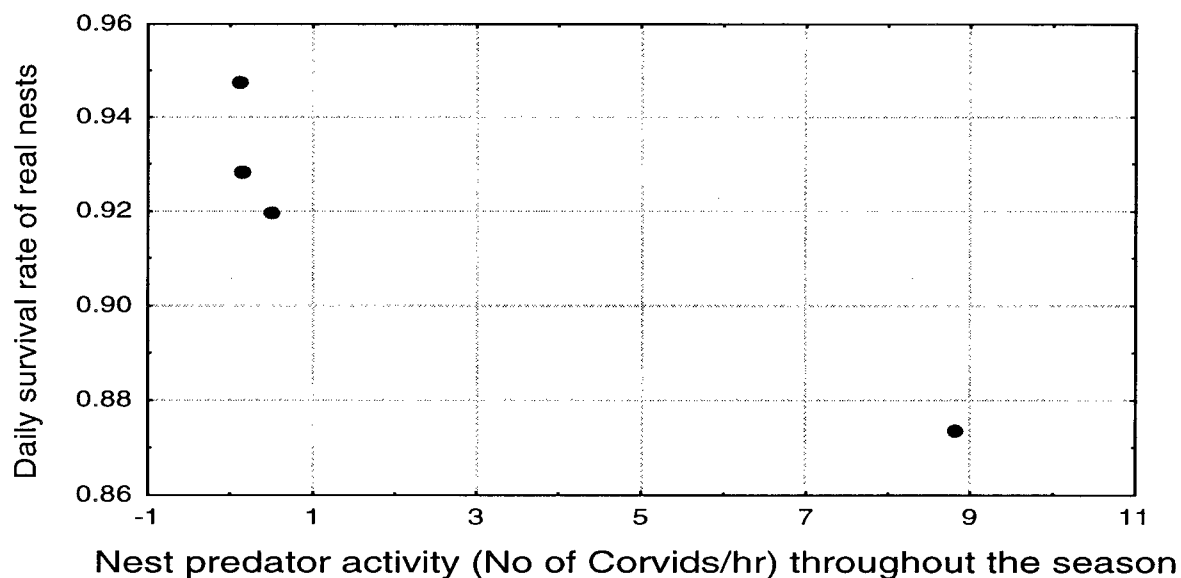


Figure 2-6 Survival of real nests in relation to nest predator activity index (number of corvids observed per hour), indicating a trend of reduced DSR with increased avian nest predator activity.

2.4 DISCUSSION

I considered two questions regarding nest survival and distribution of real and artificial Brewer's Sparrow nests; (1) is nest density associated with nest survival and (2) can predator presence and/or predation risk explain nest distribution at the site level. Nesting density did not have a strong effect on nest predation rate. I determined that artificial nests at sites high in avian nest predator activity suffered greater nest predation. This could be a cue for Brewer's Sparrows to nest in areas that are lower in nest predator activity. This was supported as I found that there were few Brewer's Sparrows nesting at sites with many nest predators. Unfortunately, there were not enough real Brewer's Sparrow nests at sites with many nest predators to make the final link to predation risk of real nests.

2.4.1 Nest density and Breeding Pair Density in Relation to Survival of Real Nests

The 'positive density effect' hypothesis predicted that sites with higher nesting densities would have increased nesting success. I found a non-significant positive trend between nest survival and Brewer's Sparrow density. This result lends some support to the 'positive density effect' hypothesis. It is likely that the weak 'positive density effect' detected in this study resulted because Brewer's Sparrows nested at sites low in avian nest predators (see section 2.4.2), which are thought to improve their foraging efficiency with increasing prey nest density (Sugden and Beyersbergen 1986). In the case of high Brewer's Sparrow density sites, which had few corvids, other predators such as snakes and mammals may have played a more important role in Brewer's Sparrow nest success.

These solitary predators detect nests at close range and forage independent of nest density, opportunistically taking one nest at a time (Wiley and Wiley 1980).

Nest density may not have been strongly correlated with the success of real Brewer's Sparrow nests for several other reasons. First, avian and large mammal predation might have been density dependent but the influence of small mammals and snake predation may have diluted this trend as real nest predation is a combination of all predators. Secondly, density relationships may not have been evident in the real nest study because Brewer's Sparrows may have adjusted their nest density in response to predator activity, which may have masked the effect of nest density. Lastly, Buler and Hamilton (2000) indicated that corvids could easily form search images for artificial nests. However, the degree to which search images would be used to locate natural nests that are well camouflaged, such as Brewer's Sparrow nests, is unknown. Angelstam (1986) indicated that eggs contribute less than one percent of a predator's food requirements, suggesting that the development of a search image for real Brewer's Sparrow nests may not be strongly selected for.

The 'negative density effect', which predicted an increase in predation with increasing nest density, was refuted by this study because there was a slight positive trend in increased Brewer's Sparrow nest survival with increasing Brewer's Sparrow nest density. However, the 'no density effect' cannot be refuted because there was only a non-significant positive effect, and the 'direct avoidance' hypothesis could also explain the slight positive trend.

2.4.2 Direct Avoidance Hypothesis

Avian nest predators were virtually non-existent at Brewer's Sparrow sites with many nests, which suggests that Brewer's Sparrow nests are frequently located in sites with reduced avian nest predator activity. 'Direct avoidance' would be likely to increase the survival of real nests, as was indicated by my artificial nest results. Artificial nest survival rates showed that there was a high cost to nesting at sites with many avian nest predators. The relationship between nest predator activity and nest predation rates is consistent with other studies (Zanette and Jenkins 2000, Andrén 1992, Angelstam 1986), and supports the notion that surveys of nest predators can increase the understanding of predation risk at particular sites (Sloan *et al.* 1998). Andrén (1995) stressed the importance of knowing predator community composition for understanding changes in predation patterns, especially since differences in spatial patterns of nest predation with predator types has been well documented (Hannon and Cotterill 1998, Haskell 1995, Nour *et al.* 1993).

The positive relationship between nest predator activity and nest predation should place a selective force on Brewer's Sparrows to nest in areas that are lower in nest predator activity. Unpublished data from Paczek (2002) shows that Brewer's Sparrow numbers were negatively correlated to avian nest predators, American Crows, Common Ravens, and Black-billed Magpies ($n=159$ $r_s = -0.48$ $p < 0.001$). However, what Brewer's Sparrows are cueing into to avoid sites high in avian predators can only be speculated on at this point. Brewer's Sparrows may be able to assess avian predation risk by identifying areas where corvids are nesting, as corvids start nesting long before Brewer's Sparrows (Cannings *et al.* 1987) and avoid these areas.

My artificial nest data suggest that small mammals might have been important Brewer's Sparrow nest predators, because sites with high Brewer's Sparrow numbers experienced nearly twice as much mammalian predation than avian predation. It is unlikely that Brewer's Sparrows could avoid small mammal predation through nest site selection because small mammal predation risk, based on the artificial nest data, was consistently high across all sites. Small mammals are important nest predators in shrub-steppe communities and are known to consume eggs of small passerines (DeGraaf and Maier 1996, Guillory 1987, Maxson and Oring 1978). However, the extent to which passerines are depredated by small mammals remains unclear because the clay eggs used in artificial nests are easier to mark than the eggs of passerines, which are generally thick shelled. This may cause an overestimation of predation risk from small mammals (Maier and DeGraaf 2001). Additionally, Brewer's Sparrows will defend their nests against small mammals. For instance, Rotenberry (pers. comm.; as cited in Rotenberry *et al.* 1999) noted adult Brewer's Sparrows aggressively responding and pursuing weasels, chipmunks and ground squirrels. More research is needed to determine the effects of small mammals on Brewer's Sparrow nests.

Despite designing the artificial nests to closely mimic real nests in terms of nest structure, egg colour, egg size, and nest height, other visual cues such as concealment (Leimgruber *et al.* 1994) and nest appearance (Martin 1987) could elicit different predator species and predation patterns (Willebrand and Marcstrom 1988). For instance, snakes are considered important predators in shrublands (Best 1978, Thompson III *et al.* 1999), but are rarely attracted to artificial nests (Marini and Melo 1998), which could lead to an underestimation of nest predation for grassland birds (Bergin *et al.* 1997,

Davison and Bollinger 2000). This demonstrates the importance of comparisons between real and artificial nests (Sloan *et al.* 1998).

2.4.3 Conclusions

This study identified potentially important correlations between Brewer's Sparrows and avian nest predators that suggest predator avoidance might be related to site selection/natural selection. This predator avoidance merits further investigation, especially because avian nest predators are increasing in many areas due to anthropogenic changes. Continued assessment of predator communities in relation to prey species is needed to determine the generality of the 'direct avoidance' hypothesis. Although the artificial nest results are correlational, this study identified the importance of artificial nests in determining predation patterns and potential risks, as real nesting birds may be pre-adapted to predation pressure at nest sites. Nest predator removal experiments may provide insight into understanding why Brewer's Sparrows avoid sites that appear otherwise suitable for nesting and to see if Brewer's Sparrows might expand their nesting range into previously unoccupied but suitable nesting areas.

CHAPTER 3 Using Survival Analysis of Artificial and Real Brewer's Sparrow Nests to Model Factors Associated with Nest Success.

3.1 INTRODUCTION

The importance of nest predation as a potential agent limiting reproductive success (Martin 1995) should be considered when formulating management plans for species at risk. Nest predation patterns are influenced by numerous ecological factors and can vary spatially and temporally for different predator types (Chalfoun *et al.* 2002) and nesting stages (Pietz and Granfors 2000a). Additionally, nest predation patterns are species-specific for both prey and predators (Chalfoun *et al.* 2002). Deciphering and understanding the ecology of nest predation is a crucial step before devising management plans for species at risk, as nest predation influences recruitment rates and thus may sway the population's recovery or demise.

In this chapter, I investigate the relative importance of ecological and nest concealment factors on predation of real and artificial Brewer's Sparrow nests for the different nesting stages and predator types. The objectives of this study were to determine the effects of tree encroachment (distance to closest tree and tree density), timing (clutch initiation date), and nest placement (nest concealment and nearest neighbour) on nesting survival of real and artificial Brewer's Sparrow nests. I predicted that tree encroachment would reduce nesting success due to increased pressure from avian nest predators. Timing was predicted to influence nest survival by decreasing nesting success through the season, a pattern found in many species (Lepage *et al.* 1999).

And the importance and influence of nest placement characteristics on nest survival are expected to vary with predator type.

The generality of environmental factors such as edge effect (Lahti 2001), timing (Lepage *et al.* 1999), and nest placement characteristics (Burhams and Thompson III 1998, Martin 1992) on predation risk continues to be debated. My study evaluates proximately to trees, timing and nest placement factors in relation to nest predation risk specifically for Brewer's Sparrows in the South Okanagan region, since predation is often context-dependent (Chalfoun *et al.* 2002).

Many studies have assessed changes in nest predation risk due to edge effects at forest ecotones (Winter *et al.* 2000, Danielson *et al.* 1997, Suarez *et al.* 1997, Keyser *et al.* 1998, Paton 1994, Nour *et al.* 1993). However, grassland and shrub-steppe habitats have unique challenges for testing edge effects. There are often isolated trees scattered in the open areas, producing 'soft' edges. Knowledge of the effects of the individual trees on nest predation patterns is poor. Isolated trees may provide predator perch and nesting sites, which will obscure edge effects. Söderström *et al.* (1998) noted that proximity to the nearest tree predicted the incidence of nest predation better than proximity to forest edge for grassland birds in Western Europe. The few studies examining the response of prey populations to supplemental avian perches found that the perch increased predation resulting in a decline in the density of small mammals (Wolff *et al.* 1999, Kay *et al.* 1994). Some species avoid nesting in areas where conifers have invaded the sagebrush habitat. For example, Commons *et al.* (1998) found that Sage Grouse (*Centrocercus urophasianus*) avoid areas with conifers, apparently to reduce predation pressure. Several studies have established that edge has a significant effect on

predation rates of grassland birds (Burger *et al.* 1994, Johnson and Temple 1990), which may relate to the increased availability of perch sites as well as increased predator nesting sites. In this study, I tested the effect of proximity to individual trees on Brewer's Sparrow nest survival, in order to recognize potential consequences of tree encroachment, which is an identified concern in this study region (Krannitz and Rohner 2000). I predicted that nests placed closer to trees would experience greater predation risk than nests placed further away.

My study models the effects of tree encroachment, time of the season, and nest concealment, on nest survival for the different nesting stages of real nests. Predation rates of real nests are usually calculated based on the entire nesting period, clumping incubation and brooding periods. The assumption that predation rate is constant between these stages has been supported by some studies (Zanette and Jenkins 2000, Cresswell 1997a, Roper and Goldstein 1997, Zimmerman 1984), but not supported by other studies that have found either higher predation during the incubation period (Martin 1992, Best and Stauffer 1980) or through the brooding period (Morton *et al.* 1993, Schaub *et al.* 1992). These differences in predation rate between incubating and nestling stages are most likely determined by the behaviour and activity level of the parents and nestling birds, and are probably species specific. Increased predation on nestlings has been attributed to increased adult activity and begging calls of the nestlings (Cresswell 1997a, Roper and Goldstein 1997). However, Brewer's Sparrow nestlings do not call and the differences between predation rate of incubating and nestling stages is unknown. This study separates the egg and nestling stages and compares them to overall nest predation rates and patterns.

Artificial nests are thought to display similar spatial and temporal patterns of real nest predation, but suffer different absolute amounts of predation (Bayne *et al.* 1997, Sullivan and Dinsmore 1990). However, there is little consensus over the generality of this assumption. Many studies have found a lack of correlation between relative predation rates and comparable predation patterns of real and artificial nests (Part and Wretenberg 2002, Zanette 2002, Davison and Bollinger 2000, Major and Kendall 1996, Reitsma 1990), as well as a lack of correlation of absolute predation rates (Ortega *et al.* 1998, Sloan *et al.* 1998, Wilson *et al.* 1998). More recent studies that used artificial nests, which closely mimicked real nests, had similar predation patterns of real nests (Davison and Bollinger 2000), probably because they attracted similar nest predator species (Part and Wretenberg 2002). The ambiguities surrounding the use of artificial nests make it essential to validate the results with real nests. In this study, I used realistic artificial nests to determine the effects of nest and site habitat characteristics on predation of Brewer's Sparrow nests. I then compared these results to the model derived for real nests. Artificial nests experimentally tested the effect of distance from trees, tree density and other habitat variables, on nest predation.

3.2 METHODS

Research was conducted in the South Okanagan Valley, British Columbia, Canada during the spring and summer of the year 2000. The same study sites were used as described in Chapter Two. The same artificial nest design and protocol, as well as real nests monitoring methods and techniques, were used as described in Chapter Two.

Predator type on artificial nests was separated into avian, mammalian, bovine (trampling) and unknown (reptilian is likely omitted from artificial nests) using imprints left in the modelling clay eggs. Nesting stages for real nests were separated into eggs and nestlings to determine if predation effects differed according to nest stages. Clutch initiation date was determined from either nest observations or counting backwards from the hatching or fledging date. The hatching date for Brewer's Sparrow eggs is 10-12 days with a mean of 11 days (Rotenberry and Wiens 1991, Reynolds 1981) and was used to calculate laying date or the start of the egg stage. Fledging was expected to occur between 7-9 days after hatching. Thus, an eight day (Rotenberry and Wiens 1991) mean fledging time was used to calculate hatching date, the start of the nestling stage. Fledging time was used to determine if the nest was successful with the addition of other clues (see Chapter 2 methods).

3.2.1 Tree Encroachment

To determine the effect of tree encroachment on nest predation, tree density and horizontal distance to the closest tree were measured using a Nikon Laser 800 Rangefinder directed perpendicularly to the trunk of a tree. Tree density was the count of all trees greater than five meters high (conifer and deciduous) within 100 meters of the nest. Tree density estimates were grouped categorically; 0-5 trees was low tree density, 6-10 trees was medium density and high tree density was greater than or equal to 11 trees within 100 m. Measurements were recorded for all artificial and real nests.

3.2.2 Timing

The artificial nest experiment was divided into three trials (see Chapter Two for details). Artificial nest experiments and real nest monitoring were conducted simultaneously, from 1 May to the end of July. Real nests were divided into early (on or before June 15) and late nesters (after June 15) based on clutch initiation date.

3.2.3 Nest Concealment and Nearest Neighbour

To assess other factors associated with predation risk, characteristics of nest placement were measured: height of above the ground (m), plant height (m), plant species in which the nest was built or placed, number of supporting branches, and percentage overhead cover. These characteristics were measured for every real and artificial nest. To prevent abandonment, measurements were taken once a nest became inactive.

Nest height was measured from the ground to the rim of the nest with a meter stick. Plant height was measured from the ground to the top of the plant that the nest was built or wired in. Cover height was calculated by subtracting the difference between plant height and nest height. Percent overhead cover was estimated from the amount of vegetation covering the nest one meter above the nest. To avoid observer bias, one person estimated percent overhead cover and counted the number of supporting branches for all of the nest sites. However, percent cover estimates and branch counting were prone to measurement error and were not used in the model building process; rather they were used to compare general nest characteristics between real and artificial nests.

Precise geographical locations of all nests were measured and mapped in AutoCAD© (Autodesk 2002). This provided an estimate of the distances between nests or distance to the nearest neighbour. Nearest neighbour was used as an individual nest variable in the analysis of real nests only. It was not used in the artificial nest analysis because the artificial nests were all placed equal distances apart, at 25 meters increments.

3.2.4 Testing of Independence Between Nests and Interactions Between Trial, Sites and Treatment.

It is important to test for independence between each nest since survival analysis, such as Cox's regressions which were used in this chapter, treats nests as the experimental unit, as estimated survival functions for survival data are recorded for individuals. Comparing an expected binomial distribution to the frequency distribution of predation rates for real and artificial nests tested for the independence of individual nests (see Buler and Hamilton 2000 for methods). Since the data fitted a binomial distribution this indicates that nests were depredated independently of each other.

Before survival analysis was performed, predation data were analysed using analysis of covariance (ANCOVA) to assess effects and interactions between distances to the nearest tree, site, and trial differences on the proportion depredated. Predation data were converted to 'proportion depredated' by pooling all transects at each site. To determine if the distance – predation rate relationship was curvilinear, distance squared was incorporated into the model. If distance squared is important then the effect of distance from trees on predation rate may be a non-linear relationship such as an exponential model and warrants further investigation.

Since percentages form a binomial, rather than a normal distribution, an arcsine square root transformation was used to transform the predation data. The dependent variable (probability of predation) was still not normally distributed after the transformation was applied. However, the remaining departures were not large enough to seriously violate the assumptions of a parametric test, as the Shapiro-Wilks (Zar 1996) 'W' test statistics was 0.93 for the transformed variables. Statistical comparisons were performed with GLM procedures using STATISTICA© (Statsoft 1999).

3.2.5 Survival Analysis and Model Building

Model building using failure time survival analysis under Cox's Model (Muenchow 1986) in combination with a forward stepwise selection process was used to determine which factors most strongly influenced nest predation rate. Akaike's Information Criterion (AIC) was used at each step of the modelling process to evaluate and select the most parsimonious model that best fit the data (Burnham and Anderson 1998) and to determine the contribution of each variable to the model (Collett 1994).

Cox's Proportional Hazard Regression (CPHR), which considers when predation occurred, was used because it does not make assumptions regarding the shape of the relationship (non-parametric) and can accommodate censored data, which are nests that have survived the observation period (Muenchow 1986, Manolis *et al.* 2000). The analysis was stratified by trial (three groups) since the ANCOVA showed differences in predation patterns between trials. Every nest was treated as a separate observation as no interaction between transects was found within sites. Only independent variables were included in the analysis and significantly correlated variables (Spearman Rank at $\alpha =$

0.05) were reduced to a single variable by selecting the most easily measured, and thus the most accurate variable. For example, plant height was correlated to nest height as well as to cover height for both real and artificial nests ($r > 0.5$). Thus, plant height was retained because variation in plant height was within tens of centimetres whereas the variation in nest height was smaller and harder to distinguish (differences were in millimetres).

A second order AIC was not used for the artificial nest experiment because sample size (n) was large with respect to the number of estimated parameters (k). However, for the real nest data a second order or bias adjusted AIC_c was used because the n/k ratio was < 40 (Hurvich and Tsai 1989).

There were several cases where the models were tied for best fit (AIC within 1 or 2 units); I assessed the uncertainty around the models selected using Akaike Weights (w ; Burnham and Anderson 1998) for a model. The variables entered into the Cox's Regression Models were: distance from tree (Distree), tree density within 100 meters from the nest (Dentree), plant height (as a measure of nest placement and concealment; Planthgt), distance to the nearest neighbour (Disnest) for real nest predation only, and Julian date of clutch initiation (Time). The variable selection procedure followed Collett's (1994) recommended strategy.

Kaplan-Meier survivorship statistical methods were used to explore the effects of individual variables (or univariate analysis) outside of the modelling process. This method is useful to graphically illustrate relationships and is a robust comparison between groups (Pollock *et al.* 1989). Additionally this type of survival analysis reduces the assumption of constant survival distributions that are inherent in the Mayfield method

(Cox and Oakes 1984). Cox's F- test was used to compare the survival or failure time of two groups, near (80 meters or less) and far (greater than 80 m) from the base of the closest tree. Each nest was treated as a separate experimental unit. Each predator type was analysed separately for artificial nests and each trial was reported separately. All of the statistical tests were performed using STATISTICA© (Statsoft 1999).

3.3 RESULTS

Of 858 artificial nests placed in the field 70.3 % (603 nests) were depredated; 28.2 % (242 nests) by birds, 37.4 % (321 nests) by mammals and 1 % (9 nests) by cows. The predators for the remaining 31 nests (3.6 %) were unknown.

One hundred and seventy real nests were found across 10 sites but only 122 were used in the analysis since the remaining nests were known re-nesting attempts. Of the 122 nests that were used in the analysis, 29.5% (36 nests) of the nests were depredated and 70.5% (86 nests) were censored meaning that they survived the observation period and were presumed to have fledged successfully. One hundred and twenty one nests were observed through the egg stage. Thirteen (10.7%) were depredated at the egg stage and 108 (89.3%) went on to the nestling stage, at which point 22 (20.4%) were depredated and 86 (79.6%) survived to fledging stage.

The majority (75%, 91 nests of 122 first nests) of the nest clutches were initiated between 14 May and 15 June (Figure 3-1). One hundred and fifty three of the 170 real nests were found before 1 July. Of the 17 nests found after 1 July, only nine were first nesting attempts. Individuals may have nested earlier and their first nest may have been

over-looked but this was the first recorded nesting attempt recorded for the season for that pair.

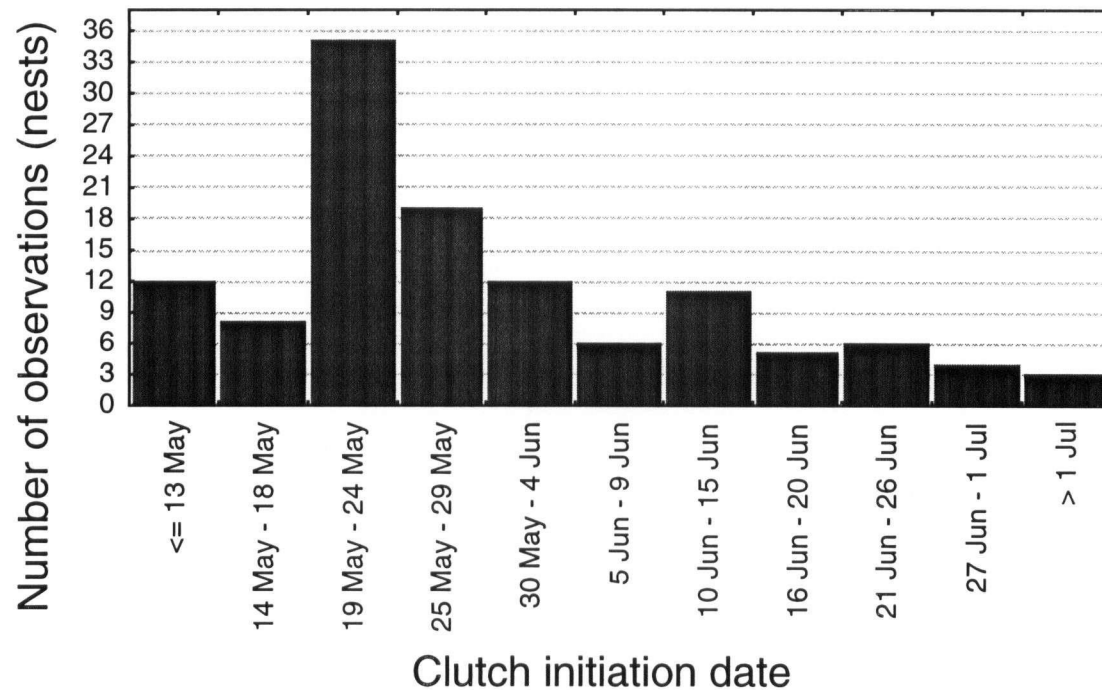


Figure 3-1 The number of real Brewer's Sparrow nests found through time at all of the 10 study sites. The mean date that the real nests were found was 2 June (min 6 May, max 4 Jul). Only first known nesting attempts were reported.

3.3.1 Comparing Nest Characteristics of Real and Artificial Nests.

Nest height was comparable between real and artificial nests with a mean height of $32 \text{ cm} \pm 15.7 \text{ SD}$ ($n = 122$) from the ground for real and $31 \text{ cm} \pm 10 \text{ SD}$ ($n = 848$) for artificial nests (Table 3-1). There were significant differences between plant heights, percent overhead cover and cover heights between real and artificial nests (Table 3-1). Real nests were placed in plants that had a much higher mean height ($87.39 \pm 25.4 \text{ SD}$)

than what has been documented in other studies (69 cm \pm 15 SD, n = 58, Petersen and Best 1985; 66.9 cm \pm 11.3 SD, n = 27, Rich 1980; 71.36 cm \pm 1.23 SD, n = 89, Rotenberry *et al.* 1999). Artificial nests were placed in shrubs closer in height to that of other Brewer's Sparrow nests in other regions (73 cm \pm 26.4 SD).

Table 3-1 Summary of nest characteristics for real and artificial nests. Mean distance to the closest tree, nest height, plant height and percent overhead (OH) cover height are reported for real and artificial nest. Distree stands for distance to the closest tree. Min and max values proved the range in values. Statistical comparison between real and artificial nests were made using Mann-Whitney U-test. Asterisks indicate the significance levels * indicates $p < 0.05$, ** indicates $p < 0.01$, * indicates $p < 0.001$.**

	Real nests			Artificial nests			Mann-Whitney U test
	Mean	Min	Max	Mean	Min	Max	z
Nest height	31.87	8	100	30.53	9	71	-0.61
Plant height	87.39	40	182	73.04	22	189	5.82***
% OH cover	65.11	5	99	33.17	0	100	10.64***
Cover Height	55.51	17	164	42.51	0	143	7.02***
Distree	139.38	7	647	67.70	5	130	7.41***

A majority (81%) of the 122 real nests were built in big sagebrush, (*Artemisia tridentata*), four percent in common snowberry (*Symphoricarpos albus*) and three percent in three-tip sagebrush (*A. tripartita*). Where big sagebrush was scarce, such as in areas that were recently burned, nests were placed in other shrubs and tall herbaceous plants. These included rabbit brush (*Chrysothamnus nauseosus*), pasture sage (*Artemisia frigida*), tarragon (*Artemisia dracunculus*), bluebunch wheatgrass (*Pseudoroegneria*

spicata), parsnip-flowered buckwheat (*Eriogonum heracleoides*); single nests found in silky lupine (*Lupinus sericeus*), lemonweed (*Lithospermum ruderales*), diffuse knapweed (*Centaurea diffusa*), arrow-leaved balsamroot (*Balsamorhiza sagittata*), and squaw currant (*Ribes cereum*).

3.3.2 Tree Encroachment

The mean distance to the closest tree was significantly greater in real nests (mean 139 m) than the average artificial nest (68 m; Table 3-1). However, the range of artificial nest placement (5-130 m) reflected that of real nests. The closest real nest was placed within 7 meters of the base of the tree, 18 % (22 nests) were placed within 50 m, 36 % (44 nests) were placed beyond 135 meters and the remaining 54 % were between 50 and 135 meters (Figure 3-2).

Nest placement variables (nest, plant or cover height) did not vary with distance from trees for real nests (Table 3-2). Likewise, artificial nest placement variables did not vary with distance from trees (Table 3-2).

Tree density surrounding the nests did not vary between artificial and real nests (Mann-Whitney u-test $z = -0.51$ $p = 0.61$). Both the majority of real (80 %, 97 nests) and artificial nests (79 %, 674 nest) were located in low tree density areas (less than five trees within 100 m).

Avian nest predation of artificial nests was higher closer (<80m) to trees for trial 3 only (Figure 3-3). In contrast, mammalian predation of artificial nests was lower closer to trees but in trial 3 only (Cox's F-test; $F = 1.51$ $p = 0.003$). All other trials showed no effect of distance from tree for avian or mammalian predation. Trial 1 only showed an

increase in predation close to trees for pooled predators (Cox's F-test; $F = 1.36$ $p = 0.03$).

There was no change in predation risk for real nests with distance from trees for pooled nesting stages (Cox's F-test; $F = 1.22$ $p = 0.27$).

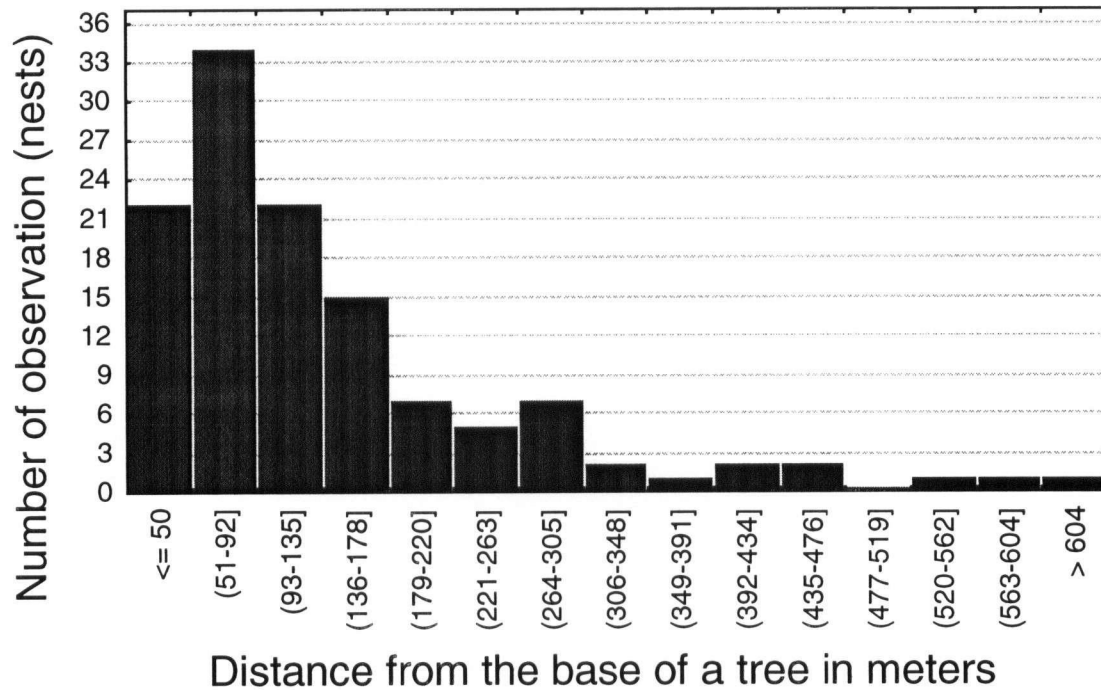


Figure 3-2 The distribution of real nests with distance to the closest tree.

Table 3-2 Spearman correlation of nest characteristics with distance from the base of the closest tree. All the relationships were non-significant.

Variable	Real Nests			Artificial nests		
	n	r_s	p-value	n	r_s	p-value
Nest Height	122	-0.01	0.91	848	0.04	0.28
Plant Height	122	0.00	0.33	848	-0.00	0.93
Cover Height	122	0.13	0.14	848	-0.02	0.54

3.3.3 Nest Concealment Relationships

There were seasonal changes in the nest height of real Brewer's Sparrow nests, with early nesters nesting at lower mean nest heights (29.83 cm) than later nesters (mean nest height 39.39 cm; Mann-Whitney U-test $z = -2.75$ $p = 0.006$). However, both plant height and cover height did not differ between early and late nesters (Mann-Whitney U-test $z = -0.70$ $p = 0.49$ and $z = 0.40$ $p = 0.69$, respectively). Cover height did not vary with nest height (Figure 3-4).

Nests in taller plants were higher off the ground and had increased cover. Plant height of real nests was correlated to nest height ($n = 122$ $r_s = 0.56$ $p < 0.001$) and cover height (Figure 3-5). Interestingly these correlations are also true for artificial nests (Plant height with nest height $n = 848$ $r_s = 0.71$ $p < 0.001$ and cover height $n = 848$ $r_s = 0.92$ $p < 0.001$, respectively).

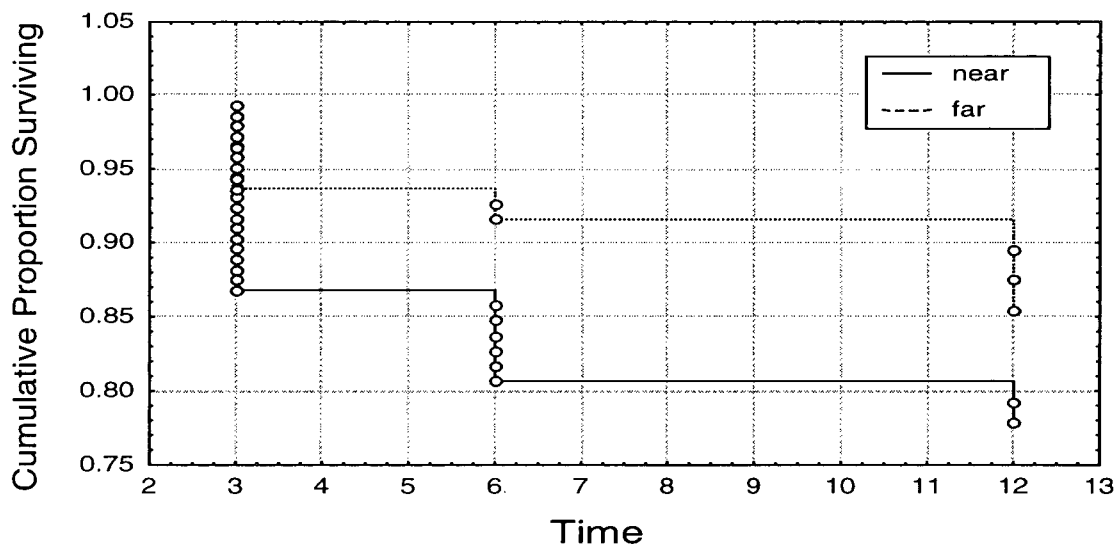


Figure 3-3 Kaplan-Meier cumulative proportion surviving in each group (near (<or equal to 80m; indicated by the solid line) versus far (>80 m; indicated by the dashed line) distance from the closest tree). This graph showed that there was a significant increase in survival due to lower avian predation in nests that are greater than 80 meters from the base of a tree for trial 3 only (Cox's F-test $F = 2.01$ $p = 0.02$)

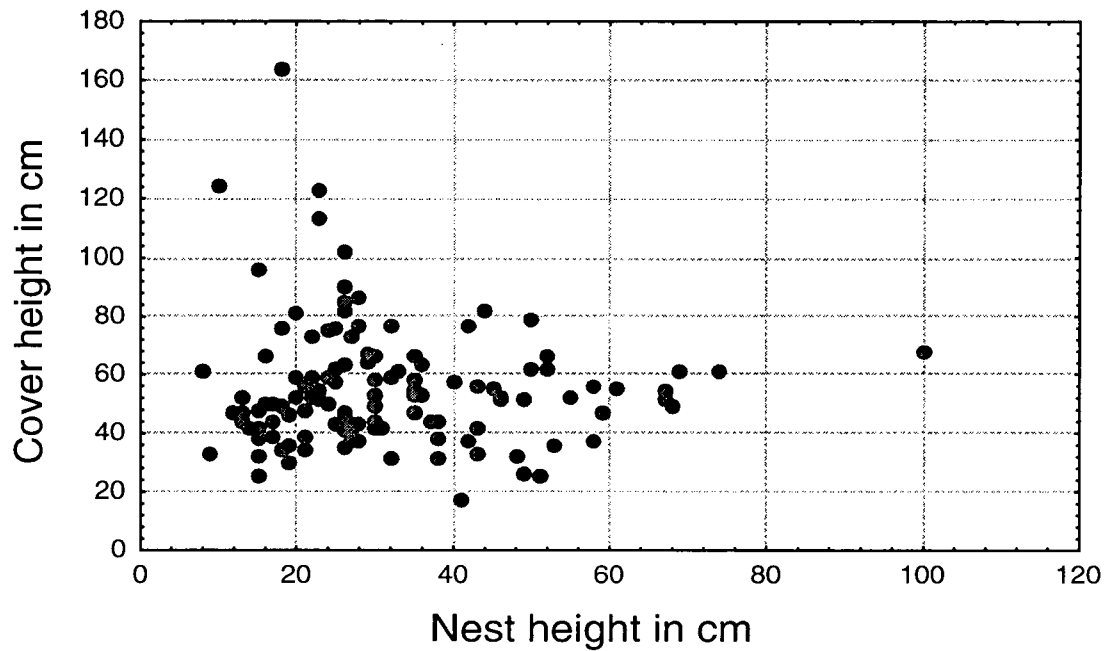


Figure 3-4 Association between nest height and cover height (plant height – nest height) for real nests ($n = 122$ $r_s = 0.02$ $p = 0.83$).

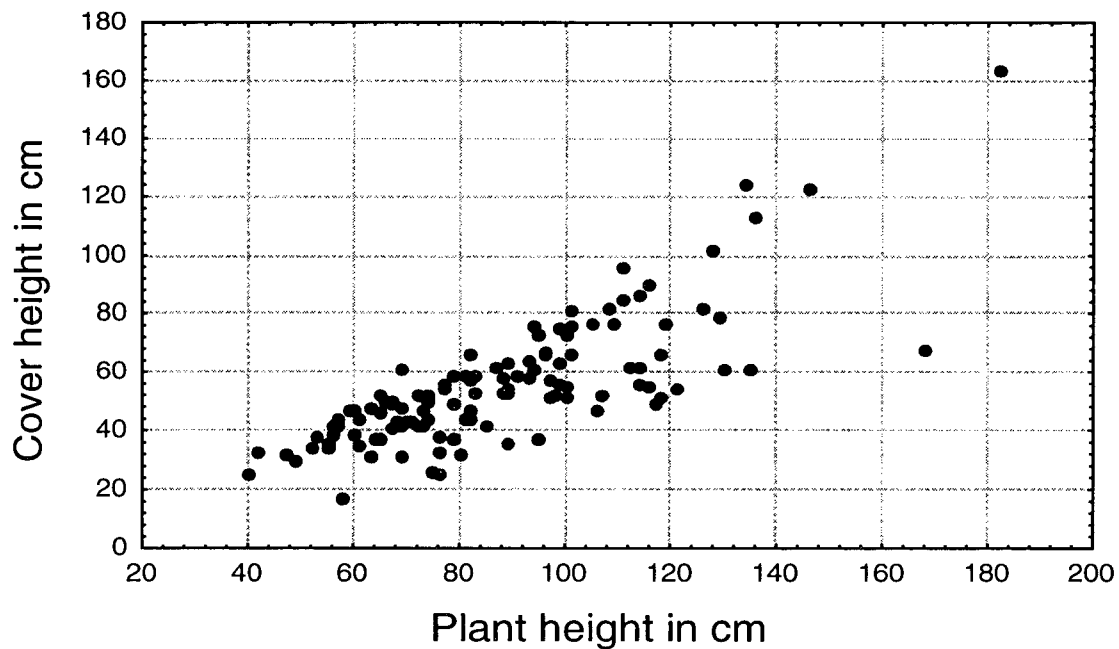


Figure 3-5 Correlation between plant height and cover height (plant height – nest height) for real nests ($n = 122$ $r_s = 0.79$ $p < 0.001$). Generally, if plant height increases the amount of cover over the nest increases.

3.3.4 Analysis of Covariance

Meeting the assumptions of subsequent statistical tests, predation rates for real and artificial nests (all predators) did not differ from a binomial distribution ($\chi^2 = 0.17$, d.f. = 4, $p > 0.99$ and $\chi^2 = 0.09$, d.f. = 4, $p > 0.99$, respectively) indicating that predation was random and thus fates of individual nests were independent of other nests.

Although predation rates of artificial nests were significantly different between sites, no distance/site interaction was found; sites differed in predation rate, but not in how distance from tree affected predation rate. Additionally, a significant interaction between site and trial was detected; thus the trials were not be pooled and were treated separately (Table 3-3).

Predation rates varied between trials, indicating seasonal changes. Avian nest predation risk declined through the trials (Kruskal-Wallis test: $H = 41.75$ $p < 0.001$), while the number of mammalian predation events increased significantly through the season (Kruskal-Wallis test: $H = 130.15$ $p < 0.001$; Figure 3-6).

Table 3-3 Analysis of covariance (ANCOVA) results for avian predation of artificial nests to assess effects and interactions between distances to the nearest tree, site, and trial differences on the proportion depredated. Predation data were converted to 'proportion depredated' by pooling all transects at each site. To determine if the distance – predation rate relationship was curvilinear, distance squared (Distance2) was incorporated into the model. Site is a categorical variable. Transformed proportion of nests depredated at a site, the dependent variable. Distance from trees and distance squared are covariables. Asterisks indicate the significance levels * indicates $p<0.05$, ** indicates $p<0.01$, * indicates $p<0.001$.**

General Effect	Degrees. Of freedom	MS	F
Intercept	1	5.05	97.64***
Trial	2	0.89	17.26***
Site	5	0.23	4.53***
Trial*Site	10	0.26	5.01***
Distance	1	0.01	0.30
Distance2	1	0.00	0.01
Site*Distance	5	0.07	1.34
Site*Distance2	5	0.06	1.21
Error	78	0.05	

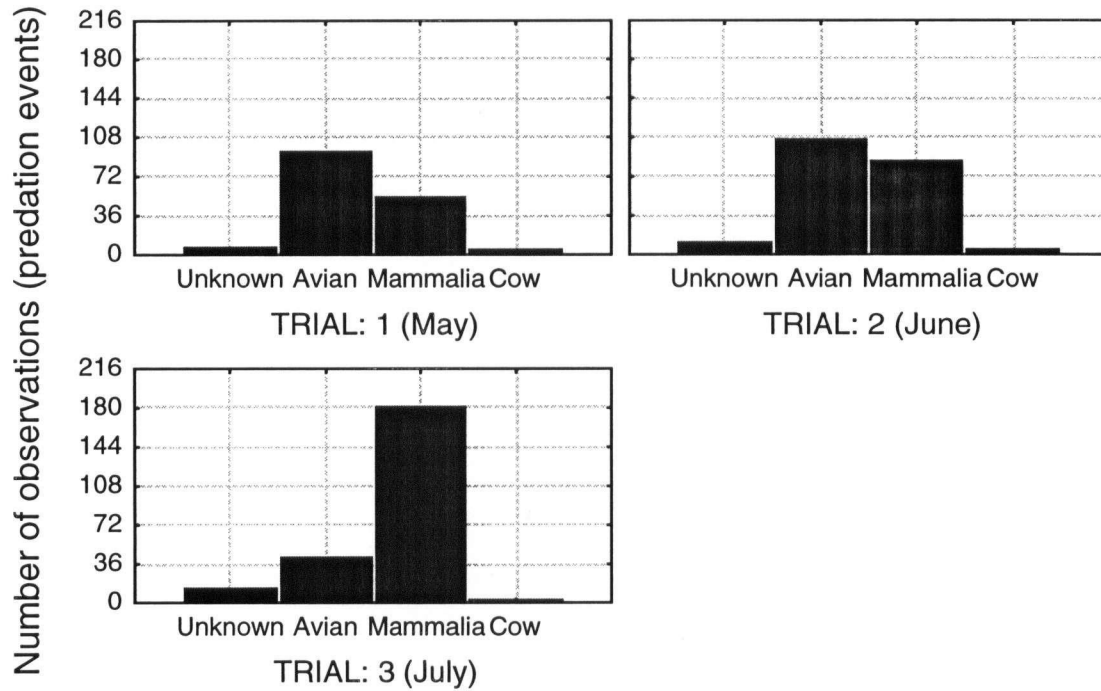


Figure 3-6 The number of observed predation events for each predator type through the season.

3.3.5 Model Building

For real nests, clutches initiated earlier in the season had a greater chance of survival than later nests according to the AIC selection process ($\Delta AIC_c = 0.00$ $w = 0.36$ $p = 0.06$; Table 3-4). The artificial nest results were less definitive. For pooled predators ($\Delta AIC = 1.62$ $w = 0.26$ $p = 0.01$; Table 3-5), and mammalian predation on its own ($\Delta AIC = 0.00$ $w = 1.00$ $p < 0.001$; Table 3-5), the same trend was observed of increased predation through the season. However, for avian predation of artificial nests there was a weak decrease in predation through season but only in combination with plant height (Table 3-5).

Plant height alone was an important predictor of artificial nest predation attributable to avian predators, as nests placed in taller shrubs experienced less predation (Table 3-5). Plant height in combination with time was a competing (or tied) model, as artificial nests placed in taller shrubs and initiated later experienced less avian predation (Table 3-5). Plant height alone did not influence predation rates by pooled or mammal predators at artificial nests. Predation of artificial nests by pooled predators decreased with increased plant height, but only in combination with time (Table 3-5). Plant height was not an important variable for real nest survival (Table 3-4).

Modelling of real nests for pooled nesting stages indicate that clutch initiation date is the mostly likely model, with predation increasing through the season (Table 3-4). Increasing tree density also reduced survival time and is a plausible alternate model (Table 3-4). Both of these models are within two AIC units of the null model, thus p-values are used to determine if the models are statistically significant. Modelling of real nest predation was also conducted with the exclusion of the WLC site from the data. This site was problematic as it was surrounded on two sides by telephone poles that may be acting as nest predator perches and lookouts. Telephone poles as perch sites were not included in the tree density estimates. When the models were built without WLC, the effect of tree density ($\Delta AIC_c = 0.00$ $w = 0.48$ $p = 0.04$) became more important than timing for nest survival ($\Delta AIC_c = 1.86$ $w = 0.19$ $p = 0.11$) for pooled nesting stages.

When the nesting stages were divided into egg and nestlings, derived models showed a significant change in the variables selected for the best model. At the egg stage, none of the models were significant and all of the models were tied for best-fit model including the null model (Table 3-4). Four models were tied for best fit for the

nestling stage with nearest nest variable 41% more likely than those models based on time, combination of distance to tree and density of trees, or distance to closest tree alone (Table 3-4). There were no significant changes in the models when WLC was excluded from the analysis for the egg and nestling stages.

Table 3-4 Models for real nests predation derived using Cox's proportional hazard regression using Akaike Information Criterion (AIC) as the model selection process. The models with the lowest change in AICc are the best models. Models that are tied for best fit (AIC within 1 or 2 units) can be assessed by the uncertainty around the models reported as Akaike weights = 'w'. P-values are derived for Cox's proportional hazard regression indicates whether the models are statistically significant independent from the AIC selection process. A positive relationship indicates an increase in predation with an increase in the factor.

Model	Change in AIC _c	'w' = Akaike Weights	p-value	Relationship less (-ve), more (+ve)
Pooled nesting stages				
None	1.65	0.16		
Distree	3.37	0.07	0.58	+ve
Dentree	1.03	0.22	0.10	+ve
Plant height	3.57	0.06	0.74	-ve
Nearest Nest	2.07	0.13	0.20	+ve
Time	0.00	0.36	0.055	+ve
Egg stage only				
None	0.34	0.24		
Distree	2.15	0.10	0.63	-ve
Dentree	1.95	0.11	0.51	+ve
Plant height	1.56	0.13	0.37	-ve
Nearest Nest	1.59	0.13	0.38	-ve
Time	0.00	0.29	0.12	+ve
Nestling stage only				
None	2.41	0.10		
Distree	1.61	0.15	0.09	+ve
Dentree	3.57	0.06	0.35	+ve
Plant height	4.45	0.04	0.97	-ve
Nearest Nest	0.00	0.33	0.04	+ve
Time	1.82	0.13	0.11	+ve
Distree & Dentree	1.07	0.19	0.07	+ve

Table 3-5 Models for artificial nests predation derived using Cox's proportional hazard regression using Akaike Information Criterion (AIC) as the model selection process. The models with the lowest change in AIC are the best models. Models that are tied for best fit (AIC within 1 or 2 units) can be assessed by the uncertainty around the models reported as Akaike weights = 'w'. P-values are derived from Cox's proportional hazard regression indicate whether the models are statistically significant independent from the AIC selection process. A positive relationship (+ve) indicates an increase in predation with an increase in the factor.

Model	Change in AIC	'w' = Akaike Weights	p-value	Relationship less (-ve), more (+ve)
Avian predation				
None	7.76	0.01		
Distree	7.88	0.01	0.17	-ve
Dentree	8.30	0.01	0.23	-ve
Plant Hgt	1.82	0.26	0.005	-ve
Time	7.40	0.02	0.12	-ve
Time & Plant Hgt	0.00	0.66	0.003	-ve
Distree & Dentree	6.38	0.03	0.07	-ve
Mammalian Predation				
None	30.56	0.00		
Distree	31.20	0.00	0.24	+ve
Dentree	32.48	0.00	0.78	-ve
Plant Hgt	32.56	0.00	0.95	-ve
Time	0.00	1.00	0.00	+ve
All predators				
None	6.72	0.02		
Distree	8.00	0.01	0.40	-ve
Dentree	7.70	0.01	0.31	-ve
Plant Hgt	3.50	0.10	0.02	-ve
Time	1.62	0.26	0.008	+ve
Time & Plant Hgt	0.00	0.59	0.005	

3.4 DISCUSSION

My results show that clutch initiation date was the most important factor affecting real nest survival. Other factors such as proximity to the nearest tree, and nest concealment did not influence the overall survival of real nests. When artificial and real nest models are compared, the artificial nest experiment identified possible adaptive nesting strategies of Brewer's Sparrows to avoid predation risk. Predation risk may not always be identified through the study of real nests alone, as birds respond to predation pressures through adaptive nest placement, and thus negate the effect of factors such as nest concealment and distance to the nearest tree. However, it may still be important to understand how habitat factors might affect predation risk, as habitat modifications and loss can lead to unexpected changes in predation rates and risk that can lead to acute changes in selection pressures.

3.4.1 Tree Encroachment

For artificial nests the model building results indicated that nest predation was not affected by the distance to the closest tree or tree density for all nest predator groupings (avian, mammalian and all predator combined). However, my prediction, of increased predation close to trees, was supported later in the season when distances to the nearest tree were categorized into near versus far, for avian predation of artificial nests. There was an opposite effects of proximity to trees for mammalian. Artificial nests results suggest that perhaps only individual trees, and not an increase in tree density, are

necessary to increase nest predation. This may be a result of isolated trees providing corvids with perch sites, nesting sites or stop over sites (Salathé 1986).

In testing the effects of tree encroachment on real nests, none of the distance to trees or tree density models were statistically significant. However, using the AIC selection process for modeling of real nests, I found a marginal effect of the distance from trees for the nestling stage, and found that increased tree density led to an increase in real nest predation for pooled nesting stages. Additionally, tree density did significantly reduce nest survival when the site WLC was excluded from the data.

This relationship of tree density and reduced real nest survival is supported by other studies that have shown avian nest predators increase with increasing tree density (Krannitz and Rohner 2000). The reduced effect of distance to the closest tree on real nest predation rate could be attributable to avoidance of trees by Brewer's Sparrows, as the mean distance from trees for real nests was 139 m, and the majority was built beyond 50 meters from the base of the tree. Edge effect tends to occur within 50 meters from the edges (reviewed by Paton's 1994; Winter *et al.* 2000). The artificial nest study indicated that nests placed within 80 meters from the nearest tree experienced increased avian predation risk late in the season. This suggests that edge effect occurs within a distance of 80 m, which is comparable to similar studies in shrub-steppe habitat (75 meters edge effect; Vander Haegen and DeGraaf 1996), meaning that edge effect may not affect real nests, since most of the nests were built beyond that range.

Alternatively, the lack of effect may also be attributable to the low abundance of avian nest predators at the sites with more Brewer's Sparrows (Chapter Two). Sullivan and Dinsmore (1992) found that crows forage up to 382 meters from their nests in

Manitoba. Ravens showed a similar foraging distance with the majority of their foraging occurring within 400 meters of the nest during their breeding season (Sherman 1993). If Brewer's Sparrows can nest beyond the crows' foraging range then the effects of distance from tree would not be detected in real nests.

In a recent review of effect of edges on nest predation risk, it was determined that no predictive patterns have emerged in the last 20 years of research (Lahti 2001). Some studies support the theory of edge effect, while others, either report a lack of edge effect or a negative edge effect. The results from the artificial nest experiment indicate the distance to nearest tree effect, whether positive or negative, was nest predator specific. In general, corvids are thought to forage close to trees (Hannon and Cotterill 1998), but this was supported by the artificial nest study in July only. However, different corvid species may forage differently with regard to trees and may reduce the effect early in the season, when predation is highest. As edge effect is species-specific for both prey and predators, Chalfoun *et al.* (2002) stress the importance of 'customizing' management of edge effect for nest predator species and for the species being managed.

3.4.2 Timing

Timing was the predominate factor affecting real Brewer's Sparrow nest survival with survival highest early in the nesting season. Seasonal declines in nesting success have been found in many species (Lepage *et al.* 1999, Robertson 1973) and are likely linked to biotic and abiotic changes in conditions through the nesting season.

The same seasonal decrease in nest survival was observed for the mammalian predation of artificial nests. Seasonal declines in nesting survival may be attributed in

part to seasonal increase in abundance and dispersal of juvenile small mammals (Briese and Smith 1974). As discussed in Chapter Two, small mammals are important nest predators in shrub-steppe communities, and are known to consume the eggs of small passerines (DeGraaf and Maier 1996, Guillory 1987, Maxson and Oring 1978). However the extent to which passerine nests are depredated by small mammals remains unclear, as artificial nests contain artificial eggs that are easier to mark than the thicker shelled eggs of most passerines. This may cause an overestimation in predation risk by small mammals (Maier and DeGraaf 2001). More research is needed to determine the effects of small mammals on Brewer's Sparrow nests. An alternate explanation that warrants further investigation, is the possibility that seasonal increases in nest predation may have resulted from predators learning to find and depredate nests (Pelech 2000).

Snakes are important predators in shrub lands (Thompson III *et al.* 1999, Best 1978), but are rarely attracted to artificial nests (Marini and Melo 1998). Thus, increased predation in real nests over time might also be attributable to snakes, but this cannot be documented using artificial nests.

In contrast to my results, a reverse pattern of decreased predation through time has also been documented. Increased nest predation early in the season has been linked with the dispersal of juvenile avian nest predators (Sloan *et al.* 1998, Patnode and White 1992, Zimmerman 1984). Corvids breeding in the spring will use eggs of other species to supplement the diet of their nestling or fledging young (Boarman and Heinrich 1999). In this study, avian predation of artificial nests did increase through the season, but only in combination with changing plant height. In other words, timing, as a single variable

independent from plant height, did not have a strong effect on the avian predation rate of artificial nests.

3.4.3 Nest Concealment

In the artificial nest study, the importance of nest placement on nesting success varied with predator type, which is similar to what has been documented in other studies (Martin 1993a), and predicted for this study. Artificial nests placed in taller shrubs were preyed upon less by avian predators than nests in lower shrubs. This relationship was probably a result of increased cover height as when plant height increased, the associated cover height also increased. Increased cover is generally important in reducing predation from avian sources as they are visual predators (Littlefield 2002, Sugden and Beyersbergen 1986), but not mammalian predation because small mammals hunt using olfactory cues (Clark and Nudds 1991). This was supported by this study, as concealment was not important for predation of artificial nests by small mammals.

Concealment of real nests was not related to the survival of real Brewer's Sparrow nests for any nesting stage, whereas nest concealment affected avian predation of artificial nests. The real nest findings were contrary to previous work (Martin 1992), which found that artificial and real nests that are more concealed are less likely to be depredated. However, other studies have found an effect of nest concealment in artificial nests but failed to find an effect in real nests (Cresswell 1997b, Storaas 1988).

There are three possible explanations for this contradiction. 1) Concealment may be important for Brewer's Sparrows but they are selecting for overall cover at the nest patch scale (see Martin 1992, Martin and Roper 1988) which was not measured in this

study. 2) Shrub cover for real nests was already at an optimal level, thus the range in cover did not provide enough statistical evidence to detect minor changes in predation rate. 3) Avian predation was not as important as predation by ground-dwelling predators, which would make the influence of overhead cover negligible. Each of these possible explanations will be more fully explored below.

Nest concealment may not be an important predictor of predation risk as Brewer's Sparrows may select for overall shrub cover within a nesting patch area. Habitat selection models for Brewer's Sparrows generally describe shrub cover as an important predictor for the occupancy of Brewer's Sparrows (Vander Haegen *et al.* 2000, Knick and Rotenberry 1995). However, occupancy may be misleading and may not be linked to reproductive success, since anthropogenic changes in the landscape and associated habitat can lead to a decoupling of habitat selection and suitability (see Chapter Two, Misenhelter and Rotenberry 2000). Thus, the historical contribution of habitat selection should be considered (Knick and Rotenberry 2000). This is especially true in species that exhibit site fidelity, such as in Brewer's Sparrows (Peterson and Best 1987). Nesting success provides a better indication of suitable nesting habitat (Tyre *et al.* 2001). Generally, shrub cover is important for overhead concealment from predators. However, cover may also be important for food, protection of fledglings and adults from the elements, and heat (Rich 1980). Predation rate tends to decrease with increased nest concealment, and increases with greater structural complexity in surrounding vegetation (Martin 1993b, Yahner and Scott 1988, Bowman and Harris 1980; but see Clark and Nudds 1991). However, this was not supported by my real nest results.

Brewer's Sparrows may already select the optimal amount of cover as they tend to nest in taller and denser shrubs. Petersen and Best (1985) and Best (1972) suggested that cover might be the most important factor influencing Brewer's Sparrow nest placement. If Brewer's Sparrows are nesting with an optimal amount of cover, the changes within the range of cover may not be extreme enough to alter predation rates. Sullivan and Dinsmore (1990) found that cover height reduced crow predation up until 20cm, and beyond 20 cm of cover height there was no substantial reduction in predation. Cover height for the real nests were on average 55 cm with a range from 17-164 cm. This is a key consideration in assessing real nesting success, as nest concealment may still be important but will not be detected since all nests are already well concealed. This apparent lack of influence of nest concealment, which is frequently found in nest survey studies (Cresswell 1997b, Storaas 1988), could lead to poor management decisions and must be approached with caution.

Lastly, nest concealment might not be important if, as I postulated in Chapter Two, Brewer's Sparrows avoid areas high in avian nest predators. This would diminish the influence of avian predators, making the influence of nest cover negligible. Additionally, ground dwelling predators such as snakes or rodents, which are unaffected by nest cover, may pose more of a hazard to Brewer's Sparrow nests.

The nest height found in this study was consistent with other studies, as an average nest height of 30 cm from the ground is typical for Brewer's Sparrow nests (Cannings *et al.* 1987, Rich 1980). Nest height increased through the season for real nests. This seasonal increase in nest height has been documented in other studies (Best and Stauffer 1980, Best 1978), and usually corresponds with a decrease in concealment

(Best and Stauffer 1980). However, this study did not support this, as concealment did not vary with seasonal change in nest height. The apparent lack in change of cover despite increased nest height is probably to maintain cover for avoidance of avian predators and to provide shade in a heat stressed environment. An increase in abundance of mammalian and reptilian ground-dwelling nest predators, and selection of larger shrubs by Brewer's Sparrows may explain the seasonal increase in nest height. This is supported by similar studies which found snake and mammal predation did not vary with overhead cover (Wray II and Whitmore 1979, Best 1978), but may be affected by nest height and concealment or obstruction from below (Burhams and Thompson III 1998).

3.4.4 Nearest Neighbour

Nearest neighbour effects were only observed for the nestling stage of real nests. Nests built close together experienced less predation than nests with longer nearest neighbour distances, indicating a group benefit in nesting close together for the nestling stage only. This relationship with nearest neighbour and reduced nest predation risk is supported by similar studies for other species (Meilvang *et al.* 1997). Nestling Brewer's Sparrows, do not beg vocally or give warning calls. Adults, in contrast, will chirp in the presence of predators (Rotenberry *et al.* 1999), which may help warn nestlings to huddle and to cease begging behaviour thus reducing predation risk. Additionally, difference between nesting stages maybe a consequence of changes in predator response to behavioural difference in adults and nestlings at each nesting stage.

3.4.5 Comparing Artificial and Real Nests

Artificial nests in this study had less cover, were more evenly spaced, and were placed closer to the nearest trees than real nests. Despite these differences, artificial nest models were useful in understanding changes in spatial and temporal changes in predation risk for each predator type. Predation risk by each predator type between artificial and real nests were likely not comparable. My results support suggestions that birds are the primary predators for artificial nests, but small mammals may be the dominant predator of real nests (MacIvor *et al.* 1990, Willebrand and Marcstrom 1988) as well as snakes. Small mammal predation may have been overestimated (Maier and DeGraaf 2001), and snake predation likely entirely unmeasured (Davison and Bollinger 2000, Marini and Melo 1998, Bergin *et al.* 1997) in the artificial experiment. However, without the artificial nest data to help understand the mechanisms behind the patterns, interpretations of real nest predation becomes purely conjectural.

Artificial nests reflected similar patterns of nest predation for some predator types. Daily survival rates of real nests did not differ significantly from that of artificial nests (Chapter Two). However, predation rates of artificial nests was much higher than that of real nests. This is contrary to other studies in similar habitats that have found that artificial nests underestimate predations of real nests (Davison and Bollinger 2000, Bergin *et al.* 1997).

Real nests may not reflect the full range of predation risks present at sites, as the birds have already adapted to predators and conditions at a site. For instance, cover may not be perceived as an important variable for nest predation risk in real nests because Brewer's Sparrows have already selected an optimal amount of cover. Nest predation

must place a strong selective force for all birds and existing modifications to nesting variables may not be recognized in unaccompanied real nest studies. Artificial nests are useful in identifying this risk, which may be over looked with real nest analysis only. This demonstrates the importance of comparisons between real and artificial nests (Sloan *et al.* 1998).

Reviews of artificial nest experiments have largely described the failings of artificial nests to accurately mimic predation rates and patterns of real nests (Zanette 2002, Weidinger 2001, Wilson *et al.* 1998, Major and Kendall 1996, Martin 1987). Artificial nest experiments have come a long way in addressing several biases that have been identified by reviewers; however, it is unlikely that any observed nest, real or artificial, will ever be free from the bias involved in conducting any level of research on wild populations. When working with small populations, such as the Brewer's Sparrow in BC, researchers are limited in sample size and real nests cannot be easily manipulated without a cost to seasonal fecundity of the population. However, it is often most important to discern information on which habitat variables influence the survival of nests for species at risk. Artificial nests have provided insight into predation risks and habitat variables that may contribute to nest survival for different predator types.

CHAPTER 4 Conclusions

4.1 MANAGEMENT IMPLICATIONS

This study is in agreement with many studies that indicate that timing of nesting is an important predictor of nesting success. The underlying mechanisms for seasonal changes in nesting success are most likely linked to several biotic and abiotic factors. This study identified that peak seasonal emergence of mammals might be avoided by nesting early, and I speculate that nesting early also allows Brewer's Sparrows to evade predation by emerging snakes. Changes in nest predator community and abundances should be considered in managing nesting areas. Avian predation is highest early in the season, and the results from Chapter 2 indicate that Brewer's Sparrows can avoid these pressures by nesting at sites where corvid activity is lower. Alternatively, Brewer's Sparrows may have already been displaced from these areas. Anthropogenic changes could lead to an increase in corvid number. If corvid numbers increase, this could potentially increase early season predation when other predators are not yet active.

Loss of habitat through urbanization and conversion into agricultural land poses a direct threat to nesting habitat for Brewer's Sparrows. Indirect effects, such as increased density of nest predators, may also contribute to elevated nest predation rates, and thus lowered reproductive success. Density of avian nest predators tends to increase proportionally with the conversion of natural habitat into agricultural land (Andr n 1992). Further research in the South Okanagan is required to determine the effects of increasing conversion of habitat into agricultural land, on corvid numbers. Agricultural land and human settlements offer reliable food sources for corvids (Marzluff *et al.* 2001,

Restani *et al.* 2001), permitting nest predator populations to thrive (Marzluff *et al.* 1994, Engel and Young 1989). Breeding bird survey results for British Columbia from 1966 to 2000 indicate that there is a significant increase in the number of Common Ravens (2.4% per year, $p = 0.03$, $n = 87$; Sauer *et al.* 2001). American Crows are also increasing across North America (1.1% per year, $p < 0.001$, $n = 3109$; Sauer *et al.* 2001); however, the trend is not significant for BC (0.7% per year, $p = 0.23$, $n = 61$; Sauer *et al.* 2001). Black-billed Magpies are declining at a rate of 2.3% per annum in BC, but the trend is not significant (Sauer *et al.* 2001). Since corvids are effective nest predators, there is concern that their increase will place more predation pressure on species at risk. Corvids have been documented as nest predators of several endangered and threatened species (Powell and Collier 2000, Snyder and Snyder 2000, Berry 1985, Scott and Morrison 1978).

If Brewer's Sparrows require sites that are low in corvid numbers to nest in, an increase in avian nest predators throughout the South Okanagan may make it difficult for Brewer's Sparrows to nest in sites low in corvids. Many management plans for endangered species have proposed different methods of controlling or reducing corvid numbers to help protect species at risk from nest predation, with varying degrees of success (see Côté and Sutherland 1997). This study indicates that Brewer's Sparrows may be able to avoid sites high in avian predator activity. However, it is advised that long term monitoring of avian nest predator populations should be conducted, and the influence of avian nest predators should be a consideration when evaluating the impacts of urban sprawl and agricultural conversion in the South Okanagan.

Tree encroachment due to fire suppression may also be a contributing factor to the increase in density of nest predators, as well as a reduction in suitable nesting habitat (Hutto 1995). Fire suppression causes changes in herbaceous cover and ground litter that will often lead to an expansion of pine (*Pinus spp.*) and juniper (*Juniperus spp.*) into sagebrush habitat (Davenport *et al.* 1998, Miller and Wigand 1994). Encroaching trees provide perching and nesting sites for a number of avian nest predators such as corvids (Sullivan and Dinsmore 1990, Loman and Göransson 1978). Several studies have linked increased conifer densities with reduced nest survival, apparently because of increased predator predation (Krannitz and Rohner 2000, Bayne and Hobson 1997). The number of perching sites has increased with both human and tree encroachment in the South Okanagan. Human-made perching and nesting sites such as telephone poles and fence lines could potentially contribute to increased nest predation risk (Marzluff *et al.* 1994).

While the influence of distance from trees on nest survival was not conclusive because there seems to be a seasonal effect, my real nest results suggest that tree density may reduce nesting success at the nestling stage. Managers should use baseline surveys to measure trends in corvids, and other nest predators, to quantify increased predation risks due to human and tree encroachment into shrub-steppe habitat (Turner and Krannitz 2001). Care should be taken to avoid attracting corvids to areas by inadvertently providing man-made perching and nesting sites (such as telephones and fence lines). This identifies the importance of continued research and monitoring in the shrub-steppe ecosystem as well as maintaining natural processes, such as fire, to prevent tree encroachment into shrub-steppe habitat.

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Appendix I A list of possible nest predators on the South Okanagan region.

Avian

American Crow	<i>Corvus brachyrhynchos</i>
Black billed Magpie	<i>Pica pica</i>
Brown Headed Cowbird	<i>Molothrus ater</i>
Common Raven	<i>Corvus corax</i>
Gray Jay	<i>Perisoreus canadensis</i>

Small Mammals

Great Basin Pocket Mouse	<i>Perognathus parvus</i>
Yellow-pine Chipmunk	<i>Tamias amoenus</i>
Eastern Fox Squirrel	<i>Sciurus niger</i>
Red Squirrel	<i>Tamiasciurus hudsonicus</i>
House Mouse	<i>Mus musculus</i>
Deer Mouse	<i>Peromyscus maniculatus</i>
Striped Skunk	<i>Mephitis mephitis</i>
Short-tailed Weasel	<i>Mustela erminea</i>
Least Weasel	<i>Mustela nivalis</i>
Long-tailed Weasel	<i>Mustela frenata</i>
American Badger	<i>Taxidea taxus</i>

Large mammals

Black Bear	<i>Ursus americanus</i>
Coyote	<i>Canis latrans</i>
Grey Wolf	<i>Canis lupus</i>
Common Raccoon	<i>Procyon lotor</i>
Red Fox	<i>Vulpes vulpes</i>
White-tailed deer	<i>Odocoileus virginianus</i>

Reptilian

Common Garter Snake	<i>Thamnophis sirtalis</i>
Gopher Snake	<i>Pituophis melanoleucus</i>
Racer	<i>Coluber constrictor</i>
Rubber Boa	<i>Charina bottae</i>
Western Rattlesnake	<i>Crotalus viridis</i>
Western Terrestrial Garter Snake	<i>Thamnophis elegans</i> (Mahony per comm. ² .)

² Mahony is a PhD candidate at the university of British Columbia studying Brewer's Sparrow population viability.