A MULTI-SCALE APPROACH TO NEST PREDATION OF THE LEAST BELL'S VIREO (*Vireo bellii pusillus*)

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GENERAL INTRODUCTION

The Least Bell's Vireo (*Vireo bellii pusillus*) is an endangered, neotropical migrant that nests exclusively in riparian habitat. It was once a common species in California (Grinnell and Miller 1944), but in 1986 was listed as federally endangered as its numbers had decreased to 300 pairs statewide (Fish and Wildlife Service 1998). The current breeding range for this species is limited to southern California and northern Baja California, Mexico. Increased habitat protection, habitat restoration and control of the brown-headed cowbird (*Molothrus ater*) have allowed the Least Bell's Vireo to increase in numbers (Kus 1999) in recent years. Nest predation is currently the leading cause of nest failure for Least Bell's Vireo; therefore, understanding the factors that influence nest predation will aid in its recovery.

Several factors thought to influence nest predation have been well studied. These include nest concealment (Martin and Roper 1988, Howlett and Stutchbury 1996) and edge effects (Gates and Gysel 1978, literature review by Lahti 2001) and results from these factors are variable. Landscape features, such as the land use surrounding breeding habitats, have been less studied, but still results are varied (Wilcove 1985, Danielson et al. 1997). Skutch (1949) hypothesized that increased parental activity at the nest would increase nest predation, although recent research has found that increased activity by the adults during the nestling stage does not increase nest predation (Martin et al. 2000). Several studies have stressed the importance of identifying the major nest predators and their foraging patterns prior to examining factors that influence nest predation (Donovan et al. 1997, Lahti 2001, Heske et al. 1999).

The overall objective of this study was to determine the potential and active predator community and examine the habitat correlates of nest predation. In the first section, three methods were used to investigate nest predators of the Least Bell's Vireo. Point counts and tracking stations were used along a 5-kilometer corridor of the San Luis Rey River in San Diego County, CA, to identify the potential predators in the area. Videophotography was used in the same area to document actual nest predators. Adult Least Bell's Vireo behavior at the nest was quantified using data collected on video. The objectives were: (1) to determine the potential predators in the Least Bell's Vireo breeding area, (2) to determine the actual nest predators of the Least Bell's Vireo, (3) to compare the ability of the three methods in determining nest predators, (4) to determine whether nest condition after predation can be used to identify specific predators, and (5) to determine whether parental behavior at the nest prior to depredation influences the likelihood of nest predation.

In the second section, factors influencing nest predation of Least Bell's Vireo were examined at three spatial scales to determine what nest-site, habitat or landscape characteristics were affecting the likelihood of nest predation in a western riparian system. Fine-scale measurements included nest height, species of host plant, nest concealment within 1 meter of the nest, and two measures of vegetative cover within 15 meters of the nest (% cover below 2 meters and % canopy above 2 meters to the top of the canopy). Edge (intermediate scale) was measured as the distance from each nest to the outermost edge of the riparian habitat. A second measure of edge that included edges associated with gaps within the riparian habitat was also quantified. On the broad scale, the relative composition of landscape features was categorized within 400 meters of each nest. These landscape features included 13 different land use types including agriculture, urban development, roads, trails and native land uses such as riparian habitat and coastal sage scrub. The objectives were: (1) to determine the effects of nest concealment, edge and surrounding land use on nest predation, and (2) to determine the spatial pattern of nest predation.

DETERMINING NEST PREDATORS OF THE LEAST BELL'S VIREO THROUGH POINT COUNTS, TRACKING STATIONS AND VIDEOPHOTOGRAPHY

Nest predation is the major cause of nest failure in open nest birds (Ricklefs 1969, Martin 1992) and is therefore an important process to study when attempting to increase populations of an endangered species. Much of the current literature on nest predation includes studies on the effects of habitat fragmentation and associated edge effects. Recent studies suggest that prior to determining landscape or edge effects on nest predation, one must first identify, and understand, the active predator community (Donovan et al. 1997, Heske et al. 1999, Lahti 2001). The objective of this paper is to determine the potential predators of the Least Bell's Vireo, establish the actual nest predators and compare the results. This paper also investigates the possibility that nest predation is influenced by adult behavior at the nest.

A large array of animals can make up the predator community in a particular area and can include mammals, birds and snakes. Knowing what nest predators are present at a site can aid in identifying the potential mechanisms that influence nest predation. Predators have different habitat requirements and search for prey in different manners, and thus are likely to differ in the factors that influence their occurrence and activity. Nest predators can also vary with the egg size (Keyser et al. 1998, DeGraaf et. al. 1999), nest location (Wilcove 1985, Martin 1987) and even type of nest of each individual species (Martin 1987).

The diversity of potential predators can make determining potential and actual nest predators a difficult task. Several methods have been used with varied success. A very general method, used by some nest monitors, is to evaluate the condition of the nest after predation. This method identifies the predator as a bird or snake if the nest is intact and as a mammal if the nest is torn or removed. Tracking stations have also been used to sample the community of potential mammalian predators (Heske et al. 1999, Dijack and Thompson III 2000).

Several studies identified nest predators more directly by using artificial nests containing clay eggs (Haskell 1995, Donovan et al. 1997, Keyser et al. 1998). Predators are identified by teeth and beak marks left on the eggs after a predation event. Artificial nests may indicate what nest predators are active in a specific area, but there is some question as to whether they sample the whole suite of predators (Paton 1994, Willebrand and Marcstrom 1988, Haskell 1995). Willebrand and Marcstrom (1988) demonstrated that avian predators, using visual cues, were the main predators of artificial nests, while mammals, which combine visual and olfactory cues, were the key predators of natural nests.

One way to conclusively determine active nest predators is to use cameras to witness actual depredation events at natural nests. Video cameras have been used in this capacity in a number of studies, with a great deal of success (Sloan et al. 1998, Innes et al. 1994, Brown et al. 1998, Thompson et al. 1999).

The use of video cameras also allows for the examination of parental activity at the nest. Skutch (1949) hypothesized that the risk of nest predation is increased with increased parental activity at the nest. If a nest predator locates nests using visual cues, then an increased number of trips to a nest by parents would give rise to increased nest predation. This increase can be observed in most species between the egg and nestling period. In addition, individuals of a specific species may vary with regard to degree of activity at nests. Martin et al. (2000) studied parental activity of ten common open-nesting birds in Arizona and found that as parental activity increased from egg to nestling stage, nest predation did not. In studies of brood parasitism of the Willow Flycatcher (*Empidonax traillii*), it was found that quieter individuals were less likely to attract the Brown-headed Cowbird (*Molothrus ater*) to their nest (Uyehara and Narins 1995), suggesting that singing near the nest can attract visual predators.

Several methods were used in this study to investigate potential and actual nest predators of the Least Bell's Vireo (*Vireo bellii pusillus*), an endangered, neotropical migrant that nests in willow riparian woodlands in southern California and northern Baja California, Mexico. The Least Bell's Vireo nests in the dense understory of the riparian in areas of high nest concealment. It builds an open cup nest in a V-shaped portion of a branch about one meter from the ground. Both the male and female incubate the eggs and care for the nestlings. The breeding period for this vireo is between late March and early August. The nesting cycle usually takes a month from the beginning of nest building until fledging. The Least Bell's Vireo will renest several times, particularly when first nests are depredated.

In this study, two methods were used to investigate the community of potential nest predators of the Least Bell's Vireo. Point counts and tracking stations were used to identify potential avian and mammalian nest predators, respectively, and their abundance. A third method, videophotography, was used to determine actual nest predators. This information was used to compare the ability to predict actual nest predators by sampling the potential predator community. The use of video cameras to film nests also allowed for examination of potential partial nest predations and the causes of any nest abandonment. Nest condition after depredation was matched to the actual nest predators recorded on videotape. Parental activity (singing and movement) at the nest was quantified from video recordings to determine if these behaviors contributed to nest predation.

METHODS

Least Bell's Vireos and their predators were studied along a 5-kilometer section of the San Luis Rey River and a 2-kilometer reach of one of its tributaries, Pilgrim Creek, (Figure 1) in northern San Diego County, California. The major potential predators of the Least Bell's Vireo at these sites include birds, snakes and mammals. Avian predators include Western Scrub-Jay (*Aphelocoma californica*), Yellow-breasted Chat (*Icteria virens*), Cooper's Hawk (*Accipiter cooperii*), American Crow (*Corvus brachyrhynchos*), Common Raven (*Corvus corax*) and Greater Roadrunner (*Geococcyx californianus*). Mammalian predators include raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and skunks (*Mephitis mephitis*), long-tailed weasel (*Mustela frenata*), gray fox (*Urocyon cinereoargeneus*), coyote (*Canis latrans*), deer mice (*Peromyscus maniculatus*) and domestic cats (*Felis domesticus*). Snake predators include gopher snake (*Pituophis melanoleucus*), racer (*Coluber constrictor*), garter snake (*Thamnophis hamondii*), red coachwip (*Masticophis flagellum*), California kingsnake (*Lampropeltus getulus*) and rattlesnakes (*Croatalis sp*.).

Tracking Stations

Ten tracking stations were set up along the San Luis Rey River (Figure 1). Stations were placed at least 250 meters apart along the edge of the riparian habitat. Each station consisted of a 1-meter diameter circular plot. This plot was cleared of all vegetation and debris, and a thin layer of powdered gypsum applied. Commercial attractants (Russ Carman's Pro Choice and Canine Call) were placed on a small rock in the center of each station. The bait attracts potential predators from a distance of 100-200 meters. Pro Choice is a general attractant used to attract mammals such as opossums, skunks and raccoons, and Canine Call is an attractant specifically for attracting coyotes. Because attractants were used, the tracking stations were placed at least 20 meters away from any Least Bell's Vireo territories along the edge of the riparian system. The gypsum was used to preserve tracks for species identification.

Tracking stations were set up at the beginning of May, June and July, 2000, and run

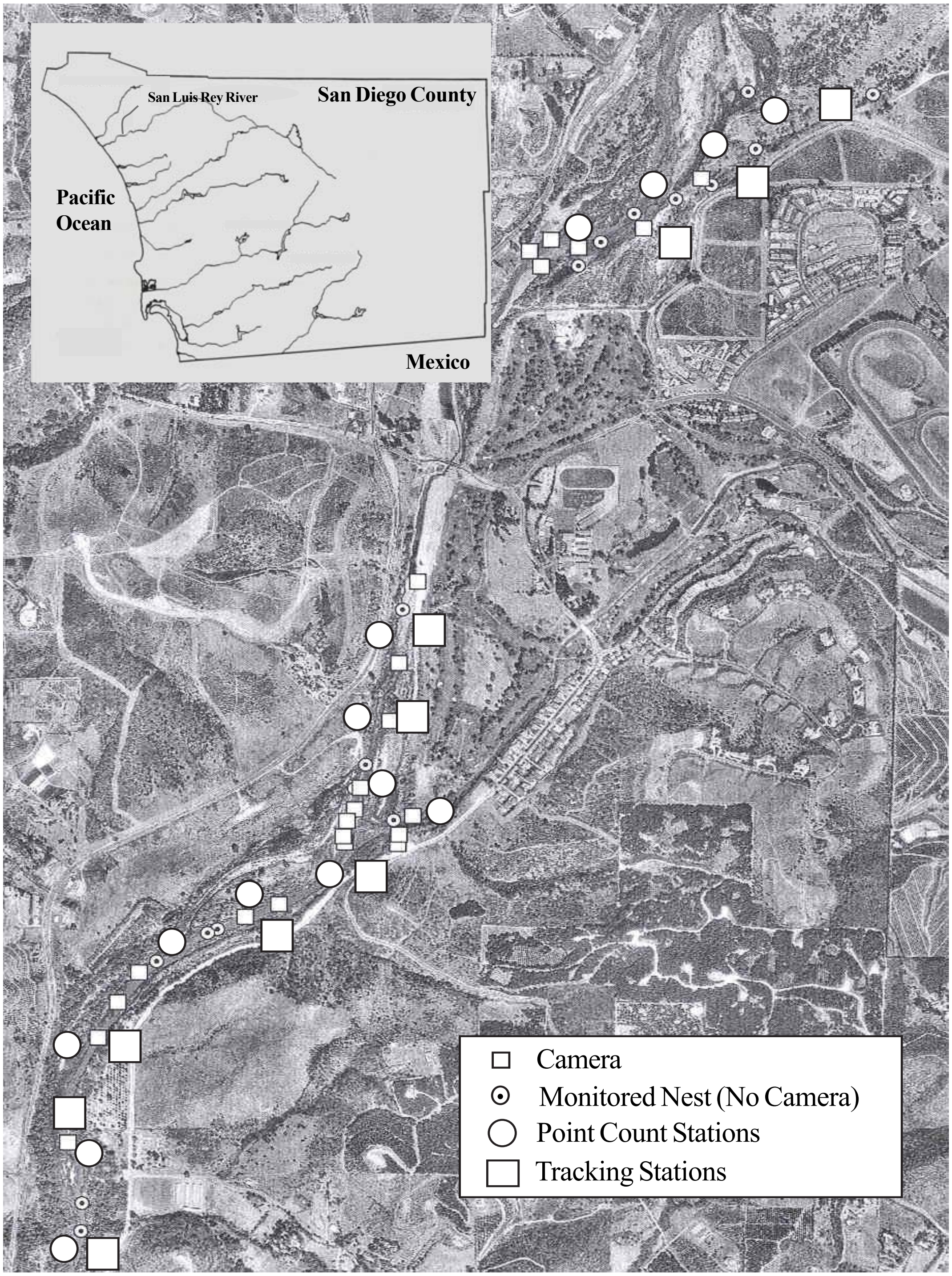

Figure 1: Aerial photograph of all nests monitored, nests with video cameras (n=23), point count stations (n=14), and tracking stations (n=10) along a 5-km stretch of the San Luis Rey River in 2000.

for three consecutive days on the days immediately following setup. Presence of each species was recorded by visiting each station daily. After tracks were examined and recorded, the station was refreshed by smoothing or adding gypsum as necessary. The bait was replaced on daily visits if required and was replaced at all stations at the end of the second day.

Point Count Stations

Fourteen point counts stations were set up along the same stretch of the San Luis Rey River as the tracking stations (Figure 1). Point count stations were placed at least 250 meters apart in order to prevent overlap of data between stations. All potential avian predators (Yellow-breasted Chat, corvids and hawks) seen or heard within a 100-meter radius of each point were recorded during 3-, 5- and 10-minute intervals. Although not known to be a nest predator at the San Luis Rey River, Yellow-breasted Chats were included because they were documented as nest predators in Arizona using video cameras (Paradzick et al. 2000). Data were collected between 15 minutes after local sunrise and noon. A total of five surveys were conducted on May 5, May 17, June 3, June 16 and July 4, 2000. The order in which stations were visited was alternated between surveys in order to alleviate any bias associated with time of day.

Videophotography

Cameras were placed at 25 Least Bell's Vireo nests during the 2000 breeding season, including 23 nests along the San Luis Rey River (Figure 1) in the same area as the point counts and tracking stations, and two nests at Pilgrim Creek. Cameras were placed at nests found early in the nesting cycle and were left in place until the nest was no longer active.

The video systems (Sentinel Video System by Sandpiper Technologies and Fieldcam by Fuhrman Diversified) consisted of a small, specialized camera mounted within a meter of the nest, with a cable connecting the camera to a video recorder and battery hidden 25-50 meters away. The camera recorded in time-lapse mode, taking several pictures per second, allowing the videotape to record continuously for 24 hours. Infrared light enabled the recording of nocturnal predators. Tapes were replaced daily without approaching the nest and later viewed to ensure that the nest was still active.

Following depredation events, the tapes were reviewed and the identity of the nest predator, stage (egg or nestling) of nest, time of day and date were recorded. Tapes were also reviewed following discovery by nest monitors of eggs or nestlings missing from a nest. When the camera was being removed, the condition of the nest was recorded as either torn or intact.

Parental Behavior

Adult Least Bell's Vireo behavior at the nest prior to depredation was analyzed by reviewing videotapes all nests depredated during daytime hours. Two measures of adult behavior were quantified: activity and singing at the nest. Activity was defined as the number of trips an adult made to or from the nest. Singing was recorded as occurring or not occurring during the observation period. Activity and singing were quantified during the one-hour interval prior to depredation for all nests depredated during daytime hours. Nests depredated at night were not analyzed because at night, the bird is inactive and at the nest constantly, leaving only at the approach of the predator. Each depredated nest was paired with a successful nest during the same one-hour time period and stage in nesting cycle in order to control for the possibility of activity varying throughout the day or cycle.

Data Analysis

Data from the tracking stations and point counts were analyzed using an index of abundance to allow comparisons between mammalian and avian potential predators. The index of abundance (Linhart and Knowlton 1975, Crooks and Soule 1999) was calculated by dividing the number of days a species was present at a station by the total number of station days. Point count data were further analyzed by calculating the average relative abundance of each species at each station. Average relative abundance was calculated by dividing the number of individuals per species per station by the total number of count days.

The effect of cameras on nest predation was analyzed using χ^2 analysis, by comparing monitored nests with cameras (n=23) and those without cameras (n=131) along the San Luis Rey River in 2000. Activity data were analyzed using a paired t-test. Singing at the nest was analyzed using Fisher's exact test (two-tailed).

RESULTS

The results for this section are divided into potential predators (tracking stations and point count stations), confirmed predators (cameras), depredation descriptions (as observed on the video tapes), nest condition, and parental behavior

Potential Predators

Four potential mammalian predators and one avian predator were recorded at the tracking stations. They included coyote, striped skunk, Virginia opossum, long-tailed weasel and greater roadrunner. Of these, the coyote was the most common potential predator and was detected at all tracking stations. Striped skunk was detected at half of the tracking stations, while the Virginia opossum was detected on three non-adjacent stations. There was only one observation of the long-tailed weasel. The greater roadrunner was detected at only one station, but was detected at that station four different times. The indices of abundance were coyotes: 0.29, striped skunk: 0.09, Virginia opossum: 0.04, long-tailed weasel: 0.01 and Greater Roadrunner: 0.04 (Figure 2).

Five potential avian predators were recorded at the point count stations: Yellow-breasted Chat, Western Scrub-Jay, American Crow, Common Raven and Cooper's Hawk (Figure 3). Greater Roadrunners were not detected during point counts even though they occurred in the area (Figure 2). Yellow-breasted Chats were recorded at all stations and had the highest overall index of abundance (0.63). The Western Scrub-Jay was the second most abundant predator, but its overall index of abundance was low, at 0.20. It was detected at 64% of the point count stations. The remaining birds exhibited very low abundance (Figure 3).

Both Yellow-breasted Chats and Western Scrub-Jays occurred in numbers greater than one at point count stations where they were observed. Yellow-breasted Chats were observed at all point counts and had a relative abundance of 1.4 individuals per station per count day. Western Scrub-Jays were not as widespread and had a relative abundance of 0.29 individuals per station per count day.

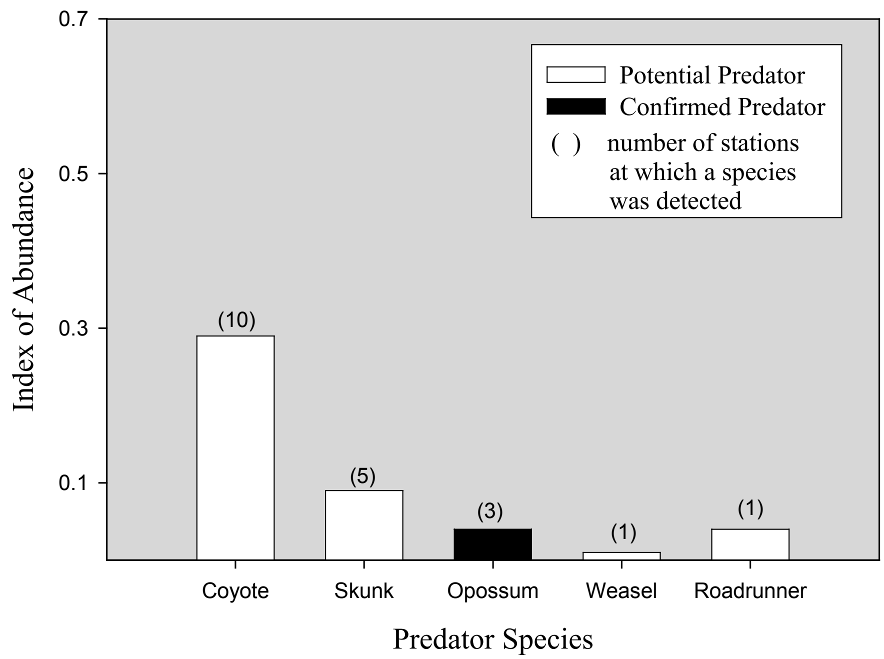

Figure 2: Index of abundance (number of occurrences per species/total number of station days) of predators identified at tracking stations. Confirmed predator observed by camera.

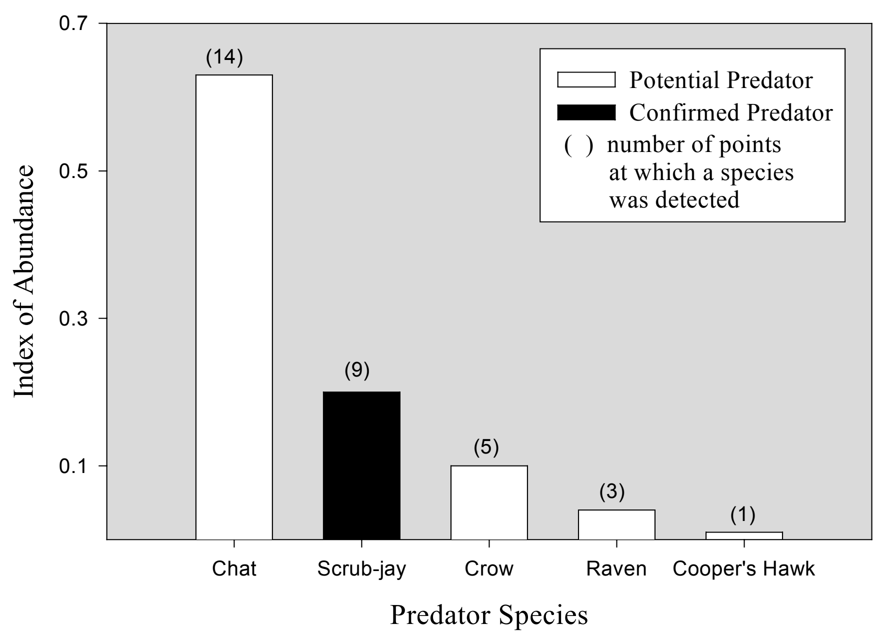

Figure 3: Index of abundance (number of occurrences per species/total number of station days) of predators identified on point counts. Confirmed predator observed by camera.

Confirmed Nest Predators

Twelve depredation events were recorded from a total of 25-videotaped nests, including eight by the Western Scrub-Jay (67%), two by Virginia opossum (17%), one by a gopher snake (8%) and one by Argentine ants (*Linepithema humile*) (8%) (Table 1). Cameras placed at the nest did not affect the outcome of the nest (χ^2_1 =0.958, P=0.33).

Most of the nests depredated by the Western Scrub-Jay were in the egg stage but one had progressed to the nestling stage (Table 1). The two nests depredated by Virginia opossum included one in the nestling stage. The second nest may have hatched but was probably in the late stages of incubation. The gopher snake ate all four eggs from one nest. The Argentine ant depredation occurred on hatch day. There were two nestlings in the nest and one egg that had not yet hatched.

The time of day at which depredation events occurred varied between predators The Western Scrub-Jay was recorded depredating nests in the morning between 08:00 and 10:00, and then again in the afternoon between 14:00 and 18:00. Both Virginia opossum

Table 1: Data collected from video review of Least Bell's Vireo nests that were depredated.

Nest predator	Date Depredated	Time Depredated	Nest Condition	Stage Depredated
Western Scrub-Jay	27-Apr	8:15	intact	egg
	14-May	9:51	intact	egg
	15-May	13:46	intact	egg
	17-May	7:54	intact	egg
	19-May	17:24	intact	egg
	23-May	9:15	intact	egg
	2-Jun	14:55	intact	nestling
	18-Jun	15:41	intact	egg
Virginia Opossum	4-Jun	23:20	torn	nestling
	5-Jun	0:00	torn	egg or nestling
Gopher Snake	30-Apr	15:58	intact	egg
Argentine Ants	7-Jul	14:10	intact	nestling

depredations occurred close to midnight. The one gopher snake predation event occurred in the late afternoon, and the ant predation in early afternoon.

Three of the 25 nests with cameras were abandoned. Review of the tapes indicated a Western Scrub-Jay visited one nest prior to egg laying. The reasons for the other two abandonments are unknown. In one case, the birds did not visit the nest after camera set-up. The vireos were not observed incubating the nest prior to camera set-up, but the birds were in the vicinity of the nest. At the other nest, the birds returned to the nest for several days prior to abandonment. The female appeared to be incubating but no egg was ever deposited in the nest cup. The female was not seen in the territory after this event.

No partial predation of nest contents was observed. However, two nests were missing individual eggs or nestlings prior to fledging. At one nest, an adult removed a single egg that had not hatched five days after the others hatched. In the other nest, a nestling fell out of the nest prior to fledge date. Videotape review also showed one successful nest fledging early because Argentine ants were attacking the nestlings in the nest cup. No partial predations were recorded.

Depredation Descriptions and Condition of Nest

The Western Scrub-Jay, when depredating a nest, would land beside the nest and remove an egg, disappear from view and return within 1-3 minutes and remove the next egg until the nest was empty. Only once was a scrub-jay observed consuming an egg at the nest. In that case, the bird ate the first egg and then removed the remaining eggs one at a time. The remains of the consumed egg were left in the nest and removed later by the vireo. Nests depredated by Western Scrub-Jay were left intact.

The gopher snake climbed the tree supporting the nest, consumed all four eggs, and returned down the tree the same way it had ascended. This is the only time the Least Bell's Vireo was observed trying to protect the nest, which it did by flying near the nest. It never actually attacked the snake. The nest was left intact.

Argentine ants were observed attacking nestlings as soon as they hatched. Over a period of at least three hours, the ants entered the nest, gradually building in numbers from a few ants to a dense trail leading into the nest. They killed the nestlings by biting them, until the nestlings finally stopped moving. The nestlings were observed jumping every time they were bitten. The adults were actively trying to remove the ants until the ants' numbers became overwhelming. One adult even brought food to the nest for the nestlings, but was unable to remain on the branch due to ant movement. This nest was also left intact.

The Virginia opossum depredations occurred at night, making it difficult to piece together the entire chain of events. It appears that they located the nest, tore the side and allowed the contents to fall to the ground, at which point the predator disappeared from view. At one nest, the opossum returned to the nest and appeared to be consuming further contents. In both cases, the opossums remained at the nest after it had been depredated and appeared to be searching the surrounding area. Both nests depredated by Virginia opossum were torn down.

Parental Behavior

The average number of trips to and from nests by adults did not differ between successful and depredated nests (paired t_8=1.34, P=0.34). Vireo males that sang at the nest did not have higher nest predation that those that never sang (Fisher's exact test, P=0.64).

DISCUSSION

Point counts and tracking stations did not identify nest predators in a manner that would enable these methods to determine the active predators within the riparian community. Coyotes and Yellow-breasted Chats were the most abundant potential predators detected by these methods, but were not documented as actual nest predators.

The Yellow-breasted Chat has been recorded as a nest predator of other species (Paradzick et al. 2000), but it does not appear to be a predator of Least Bell's Vireo nests at this site. Yellow-breasted Chats were recorded in high abundance throughout the study area and their territories overlap those of the Least Bell's Vireo; however, no predation events by Yellow-breasted Chats were observed.

Coyotes are common throughout the area but were not documented in this study as a nest predator. Donovan et al. (1997), using artificial nests, had several nests depredated by coyote, and it therefore should be considered a potential predator. The coyote can also have an indirect effect on nest predation by controlling the populations of smaller mammals, or mesopredators, such as opossum, skunk and raccoon (Soule et al. 1988, Rogers and Caro 1998, Crooks and Soule 1999). It is possible that this is occurring along the San Luis Rey River where coyotes were recorded in high abundance and mesopredators in very low numbers on the tracking stations. Coyotes were recorded consistently throughout the site, while mesopredators were recorded in low numbers.

Virginia opossums were detected at tracking stations in low abundance, but were recorded within the home range of nests they depredated. Raccoons were not detected at any of the tracking stations, but were observed in the area (B. Sharp, pers.comm.). The failure of tracking stations to detect raccoons is probably due to the placement of the tracking stations. Tracking stations were placed along the riparian/upland transition to avoid attracting potential predators to areas where Least Bell's Vireos were nesting. The use of chemical attractants, therefore, made it difficult to sample the river corridor commonly used by raccoons. Virginia opossums may have been underrepresented for the same reason; both Virginia opossum depredations occurred within a few meters of the river. The avoidance of nesting areas when setting up tracking stations may have been the reason these results differed from those of Conner et al. (1983), who found that scent-stations were a good measure of raccoon abundance and a poor indicator of Virginia opossum abundance.

Ant depredation was more frequent than expected given the sample size of predation events. In this study, Argentine ants were responsible for both depredating a nest as well as causing one nest to fledge early. Early fledging could increase the chances of mortality in the post-fledging stage.

The Western Scrub-Jay was the primary nest predator at this site, but was not recorded in high abundance on the point counts and was recorded in lower abundance than expected based on familiarity with the site. Unlike the constantly vocal Yellow-breasted Chat, Western Scrub-Jays vocalized less frequently, and were occasionally observed visually but not heard. This could have lead to undercounting the number of scrub-jays present at the site because dense vegetation could limit their view from the observer. This also holds true for the greater roadrunner. Greater Roadrunner tracks were observed on the ground in areas where point counts were being conducted, but roadrunners were not observed during the counts. They were, however, detected on the tracking stations.

The results clearly demonstrate that it is not possible to ascertain nest predators using point counts and tracking stations. These are, however, methods that could be useful in measuring changes in relative abundance and distribution of known predators. Placement of tracking stations and point counts for monitoring purposes can be improved by knowing the identities of nest predators and how they forage.

Video cameras were an excellent method of determining actual nest predators. Four nest predators of the Least Bell's Vireo were identified, and it is now known that the Western Scrub-Jay is the major nest predator on the San Luis Rey River. This method was implemented with minimal disturbance to the Least Bell's Vireo and did not cause an increase in nest predation.

Nest condition after predation allowed for a crude classification of the type of predators active at this study site. In every case, it correctly differentiated nests that were depredated by mammals from those depredated by birds or snakes. This information is useful in establishing classes of nest predators, but does not aid in the identification to species. Even when used in conjunction with information from point counts and tracking stations, it would be difficult to establish the actual nest predators.

Least Bell's Vireo behavior at the nest prior to depredation did not affect predation rates. Similar results were found by Martin et al. (2000), who demonstrated that parental activity (number of adult trips to the nest) increased between incubation and nestling stage but nest predation did not.

Knowledge of the actual nest predators of a particular species, at each specific site, would enhance both nest predation studies and management efforts. Studies on nest predation often concentrate on nest concealment, habitat edge and habitat fragmentation, producing varying results. Differences in nest searching techniques and life histories among specific nest predators could explain some of the variation in these results. Nest predators vary between systems, sites, and the species studied, requiring specific knowledge of nest predators at the study site. Increased knowledge of actual nest predators can also enhance management efforts. Examining the active nest predators at a site allows for increased understanding of the process of nest predation. This understanding of nest predators and searching techniques could allow for alterations to habitats and surrounding areas that improve reproductive success of an endangered species or a community of species.

EFFECTS OF ADJACENT LAND USE, HABITAT EDGE AND NEST-SITE CHARACTERISTICS ON NEST PREDATION OF THE LEAST BELL'S VIREO

Nest predation is the major cause of nest failure in open nesting birds (Ricklefs 1969, Martin 1992, Martin 1993). With nest predation accounting for an average of 80% of all nest losses (Martin 1992, Best and Stauffer 1980), it is thought to be an important process in the evolution of habitat selection and reproductive strategies in birds (Gates and Gysel 1978, Martin 1993). Human alterations of the landscape may influence the process of nest predation by causing increased habitat fragmentation as well as changes in the land use surrounding breeding habitat. Habitat fragmentation can lead to increased habitat edge and changes in habitat or vegetative composition. Alterations in the surrounding land use can cause changes in predator composition and density. This is of special interest in areas such as Southern California where natural habitats are being altered at a phenomenal rate to accommodate a rapidly increasing human population.

Observed patterns of predation result from a complex interplay of processes occurring at several scales. At fine scales (meters), placement of the nest and vegetation immediately surrounding the nest may influence visibility of the nest to predators. At broad scales (tens of meters) vegetation structure, gaps and edges may influence both movement and behavior of nest predators. At even broader scales (hundreds of meters), land use surrounding breeding habitat may influence the composition, density and the behavior of nest predators.

Nest concealment is thought to be an important determinant of nest success in avian species (Martin and Roper 1988, Martin 1992). Nests that are well concealed are predicted to be more difficult to locate by nest predators, particularly opportunistic predators. Studies relating nest success to nest concealment have produced varying results. A number of papers found some measure of nest concealment important to increasing reproductive success, such as vertical (above and below) concealment (Hoover and Brittingham 1998) and minimum side cover (Martin and Roper 1988). Other studies found no difference in nest concealment between depredated and successful nests (Howlett and Stutchbury 1996, Burhans and Thompson 1998, Braden 1999, Ricketts and Ritchison 2000). Howlett and Stutchbury (1996) performed a manipulative study of active Hooded Warbler (*Wilsonia citrina*) nests and removed vegetation around half the nests in their study. Manipulated nests were about 86% more visible than control nests, but there was no measurable difference in nest predation between the two types of nests.

At an intermediate scale, changes along the edge of a habitat, or increased edge due to fragmentation, can have an effect on nest success. The edge between adjacent habitat types has traditionally been thought of as an area of increased wildlife density and diversity. This idea dates back to Leopold's (1933) "law of interspersion", which suggested that habitat edge enhances diversity because it increases the numbers of animals that can forage in an area where two habitats meet. Increases in habitat fragmentation have led biologists to reassess the impacts of habitat edge on the reproductive success of birds (Gates and Gysel 1978). Increased predator diversity or density, particularly in a restricted area such as a habitat edge, can have a negative effect on the reproductive success of birds. Nest predators may be attracted to edges, increasing nest predation. This attraction could be due to increased nest density (Gates and Gysel 1978, Martin 1988), ease of movement (Bidder 1968, Yahner 1988), or foraging overlap between one habitat and another (Yahner 1988). Martin (1993) suggested that an increase in forest edges, not representative of the natural habitat in which a species evolved, could result in individuals selecting nest sites in ways that no longer protect their nests against predation.

There have been many studies of the effects of habitat edge on nest predation, with varying results. Some studies focus on a single edge bordering another habitat type (Gates and Gysel 1978, Heske et al. 1999), some on "interior" edges or large gaps within a forest system (Suarez et al. 1997), and others on predation in relation to patch or fragment size (Wilcove 1985, Donovan et al. 1997). Although many studies found no increase in predation near habitat edges relative to forest interiors (Keyser et al. 1998, Best 1978), those that did indicate that the increase occurs within about 50 meters of the habitat edge (Gates and Gysel 1978, Paton 1994). Paton (1994) reviewed 14 studies on the effects of edge on nest predation of both artificial and natural nests, and found that even though there was great variation in experimental design, ten of them demonstrated some variation in nest predation as a function of distance to edge. In contrast, Lahti (2001) reviewed papers on edge effects published between 1978 and 1998, including many reviewed by Paton, and found that 58% demonstrated no significant edge effects, while a further 18% had varying results.

Part of the debate concerning the importance of edge centers on the definition of edge itself. Some studies use the transition between two habitat types as the definition of edge, ignoring spatial variation within a habitat. Paton (1994) expressed the need to define edge in studies that examine edge effects on nest outcome. He suggested that openings in the forest canopy with a diameter three or more times the height of the adjacent trees should be considered "edges" and be included in edge analyses. It has also been suggested that an abrupt change in habitat structure best describes an edge (Harris 1988, Yahner 1988).

Natural landscapes are altered and fragmented through urban development and agriculture, resulting in an increase in edge habitat often surrounded by altered and degraded land. At the landscape scale, urbanization, agriculture, grazing and other land uses encroach on native habitat and have an effect on both the composition of the predator community and rates of nest predation (Wilcove 1985, Danielson et al. 1997). Wilcove (1985) found that nest predation varied with surrounding land use. Predation rates were higher in suburban woodlots than in isolated rural woodlots. Contrary to these findings, Danielson et al. (1997) found that rural-edged woodlots experienced a higher rate of predation than those in urban areas. These conflicting results appear to be due to differing predator composition in the study areas. Both of these studies were in eastern woodlots and used artificial nests, which may not sample the whole suite of predators (Paton 1994, Willebrand and Marcstrom 1988, Haskell 1995).

Nest predation in a given area can be caused by a wide variety of predators, including birds, mammals and snakes. Each type of predator utilizes its habitat and searches for prey in a different manner. Changes in landscape dynamics can complicate the understanding of predator composition by causing changes in foraging strategies (Harrison 1997) and affecting predator density and community composition (Soule et al. 1988, Rogers and Caro 1998, Crooks and Soule 1999). Adjacent land use can also affect predator composition in an area, with some nest predators being eliminated and others increasing. In highly fragmented areas, large mammals are often absent, disrupting community dynamics and food chains. This phenomenon is known as mesopredator release, whereby the absence of large mammals allows an increase in the population density and composition of smaller mammals such as raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginiana*), and skunks (*Mephitis mephitis*) (Soule et al. 1988, Rogers and Caro 1998, Henke and Bryant 1999). These smaller mammals, or mesopredators, are known to be active nest predators. Rogers and Caro (1998) demonstrated that mesopredator abundance and predation rates on artificial nests were positively related.

An explicit understanding of scale is important (Levin and Pacala 1997) in understanding nest predation. As with all ecological systems, the observed results depend on the scale at which the system is studied (Weins 1989, Levin 1986). Often processes, such as nest predation, which appear variable (or random) at one scale can be predictable at another scale; therefore, examining nest predation at multiple scales can aid in detecting where these patterns are emerging (Weins et al. 1986).

Some of the important factors thought to influence nest predation actually span these multiple scales, but are seldom combined in one study. This study was designed to examine factors, described in the literature as being important to the reproductive success of birds, at various scales within the landscape. These factors include fine-scale or nest-site characteristics such as nest height and nest concealment. Habitat edge, on the intermediate scale, has often been described as having a negative effect on the reproductive success of birds. On the broad scale, the land use adjacent to the breeding habitat can have an effect on the process of nest predation, directly or indirectly, through changes in the habitat structure and predator composition. This study was designed to answer the following questions: (1) What are the effects of nest concealment, edge and surrounding land use on nest predation? (2) What model best describes nest predation in the study area? (3) What is the spatial distribution of nest predation?

This study examined nest predation of Least Bell's Vireo (*Vireo bellii pusillus*) nests at several scales in order to understand key determinants of nest predation within a southern willow riparian habitat, a habitat of special concern because it supports many resident birds and neotropical migrants.

METHODS

This study was conducted along the San Luis Rey River and one of its tributaries, Pilgrim Creek, in San Diego County, California. The study included a 16-kilometer stretch of the San Luis Rey River west of Highway 15 winding southwest towards the ocean at Oceanside. The San Luis Rey River is a linear, willow riparian corridor that ranges in width from approximately 50 to 500 meters. It consists of areas of early- to mid-successional willow riparian interspersed with open areas of deposited debris and sand washes caused by natural disturbance. Anthropogenic disturbances such as roads, trails and stands of exotic grasslands increase fragmentation within this riparian system. A mosaic of urban, rural, and agricultural lands, as well as some native and disturbed upland habitat, surrounds the riparian corridor. The Pilgrim Creek riparian corridor included a 2-kilometer stretch between Camp Pendleton Marine Corp Base to the east and Oceanside Golf Course to the west. It is approximately 50 to 400 meters in width and is surrounded by native coastal sage scrub and urban development.

Study Species

The Least Bell's Vireo is an endangered, migratory songbird that breeds exclusively in willow riparian woodlands. This species nests in the dense understory near open patches, placing its nest about one meter from the ground. Nest construction usually takes about four days, with egg laying starting a day or two after nest completion. Least Bell's Vireos lay one egg per day until a full clutch of three or four is achieved, and begin incubating with the penultimate egg. The eggs hatch about twelve days later, and nestlings remain in the nest for about twelve more days prior to fledging. The entire nesting cycle takes approximately one month from start to finish. Least Bell's Vireos may attempt several (1-4) nests in a season, particularly if earlier nests are lost due to nest predation.

Monitoring

For the duration of this study, the riparian area was monitored for reproductive success of the Least Bell's Vireo by several field monitors under the direction of Dr. Barbara Kus, USGS, Biological Resources Division at San Diego State University. Least Bell's Vireo territories were located and monitored throughout the breeding season (April through August). This study includes data from the 1999 and 2000 breeding seasons.

Each Least Bell's Vireo territory was visited every 5-7 days to locate nests and assess their status. Visits were kept to a minimum in order to limit disturbance and to prevent increased nest predation in keeping with the U. S. Fish and Wildlife Service protocol. Nests were classified as successful if, at the expected time of fledging, the nest was intact and evidence indicated that at least one nestling had fledged. Such evidence included feather dust in the nest, fledgling droppings below the nest, or fledglings seen or heard within the territory. Unsuccessful nests included nests that were depredated, abandoned, or failed as a result of some other cause such as inviable eggs or the death of nestlings. The goal of this study was to assess nest predation; therefore, only successful nests and unsuccessful nests presumed to be depredated were included in the analysis. Depredation was presumed based upon the disappearance of all eggs or nestlings from active, monitored nests prior to their expected date of fledging.

Information recorded at each nest including year (1999 or 2000), site (San Luis Rey River or Pilgrim Creek) and lay date (the date on which the first egg was laid). Nests were categorized as early or late based on the median lay date in each year. Stage at depredation and condition of the nest after depredation were recorded. Stage of depredation was categorized as egg or nestling. Nests for which the stage at the time of depredation was unknown were omitted from analysis. Nest condition after depredation were categorized as intact if the nest was left undisturbed or torn if the nest was torn on one side or dislodged from the host branch. Nests left intact were thought to have been depredated by avian or snake predators, and torn nests by mammals (see the first section).

Fine-scale Measurements

Several measurements were made to characterize the environment immediately surrounding the nest. These included nest height, species of host plant, and several measures of nest concealment. Measurements were made at the end of the breeding season. For nests that were torn down, measurements were recorded only when it could be determined where the nest had been located. This could be done when remnants of the nest remained on the branches of the host plant.

Nest height was defined as the distance from the ground to the top of the nest cup. Host species was recorded as the plant species used to support a specific nest. For analysis, host species was assigned to one of four categories: the three most common species: arroyo willow (*Salix lasiolepis*), mule fat (*Baccharis salicifolia*), sandbar willow (*Salix exigua*), and all others. Nest concealment within one meter of each nest was quantified by recording whether vegetation cover was present (=”hit”) or absent at ¼-meter intervals along a 1-m transect in all four cardinal directions as well as above and below the nest. Hits per transect were averaged over the six transects to give a nest concealment index, ranging between 0 and 4.

In order to determine the importance of gaps within the riparian habitat, percent cover within a 15-meter radius of each nest was recorded. Fifteen meters was chosen to relate to the ability of nest predators to navigate through the vegetation and observe both adult vireos and their nests. In order to relate open space to both ground and aerial predators, two measurements of vegetation were visually assessed: vegetation below two meters (% cover) and vegetation above two meters to the top of the canopy (% canopy). A four-point range scale was used: category 1: <40%, 2: 41-60%, 3: 61-80% and 4: 81-100%. Percent cover was rarely less than 40% (category 1); therefore, data from this category were combined with the data from category 2. This formed three category classes for % cover, while % canopy remained at four categories.

Intermediate-scale Measurements

The outermost edge of the riparian forest was used in this study as the definition of "edge". The outermost edge is the area where the vegetation changes from willow riparian to some other natural form of vegetation (such as grassland or coastal sage scrub) at the wetland/upland transition, or to an anthropogenic feature (such as a paved road, housing development or golf course). The distance to the closest edge of the riparian habitat was measured for each vireo nest. Nests that were less than 100 meters from the edge were measured in the field, but due to movement constraints, distances over 100 meters were more accurately measured from maps in ArcView, using GPS coordinates.

Paton (1994) suggested that the definition of forest edge should include gaps that are three times the width of the adjacent trees. Using this method, distance to the edge was measured to analyze whether these internal gaps were acting as edges (adjusted edge). Distance was measured to the closer edge of either the outer riparian edge or a large gap within the riparian habitat system.

Broad-scale Measurements

The coordinates of all nests were recorded using a Global Positioning System (GPS) unit. In order to examine the effect of adjacent land use on nest predation, all Least Bell's Vireo nests were mapped onto aerial photographs (flown in 1995) in ArcView. Land uses surrounding the study area were then identified and recorded in ArcInfo (Imagine) as polygons. The land use assigned to each area was adjusted for any changes in land use since the aerial photographs were taken by assessing actual use on the ground. Thirteen land use categories were identified for this study as listed and described in Table 2. These land use polygons were then transferred back to ArcView and a circle with a 400-meter radius drawn around each nest. The number of pixels in each land use category was calculated for each polygon within the 400-meter radius area and converted to percent cover of each land use type. A 400-meter radius was chosen to ensure that the measurements for interior nests in the wider riparian areas would incorporate some type of adjacent land use. The land use category 'trails/dirt roads' was calculated using a 200-meter radius circle in order to incorporate trails and dirt roads thought to be close enough to a nest to affect it by providing potential travel lanes for predators.

Table 2: Description of each surrounding land use cover type in this study.

Land Use	Description
Willow Riparian	All areas within the riparian system including the river, washes and areas of disturbed and restored riparian.
Disturbed Upland	Areas that contain a combination of shrub species and disturbed grasslands.
Urban Housing	Areas with >1 house/acre, shopping malls, business areas, schools, etc.
Grassland	Areas of non-native grasslands and grazed land.
Coastal Sage Scrub	Areas of intact or relatively intact habitat. Areas that are highly disturbed are included in disturbed upland category.
Wetland	Both fresh water marshes and brackish areas containing salt marsh species. Standing water may or may not be present.
Golf Course/Park	Golf courses and manicured parks.
Agriculture	Usually, but not exclusively, tomato fields.
Roads	Highways, major and paved rural roads. Roads occurring in urban housing were recorded as urban unless they were major roads.
Cleared	Areas completely cleared of vegetation for development. Large equipment periodically active at site.
Orchards	Areas planted in groves whether they are actively farmed or not. Could include citrus, avocado or walnut groves.
Dirt Roads/Trails	Single lane dirt roads with low traffic usage, and manicured or worn dirt trails.
Rural Housing	Areas with <1 house/acre. Included all areas with buildings and what appeared to be the borders of the yard.

Listed in descending order based on of percent cover.

Statistical Analysis

Least Bell's Vireo territories are often fairly close together, with an average territory size of 0.63 hectares (Newman 1992), and there are typically multiple nests per territory because one pair can attempt more than one nest in a season. Using a distance of 400 meters from each nest within which to characterize adjacent land use could result in overlap of circular land use measurement areas for multiple nests and could even include several territories. As a result, the explanatory variables are not spatially independent, and the large scale variables in particular may be highly correlated spatially and may violate the assumption of independence of nests. This possibility was tested using several methods by assessing the independence and spatial distribution of nest predation across each site. Nests were placed in numerical order along the landscape for each year of the study. They were then assessed for patterns in runs of nest predation and nest success across each site using Wald Wolfowitz Runs, a test of autocorrelation for binary data. In this study, nests are treated as the unit of observation because of their separation through space and time, but because the reference variables occur on several scales, independence is unclear.

The distributions of the data for many of the land use types were right-skewed, with a large number of zeros and a long tail. Land use types that exhibited this type of distribution were those that were found at fewer than 70% of the nests. To better analyze these land use types, the land use variable was expressed in terms of presence or absence, whereby < 5% cover was considered absent. Five percent was chosen because it eliminated nests with only a small amount of cover, which was predicted to have little or no effect on nest outcome. The land use types transformed in this manner were urban, grassland, coastal sage scrub, wetland, golf course/park, agriculture, cleared, rural housing and orchards. Percent cover of willow riparian, disturbed upland, roads and trails/dirt roads was analyzed as a continuous variable (Table 3).

Logistic regression was used to estimate the relationships among individual nest site and land use variables and nest predation. This method was selected because it is appropriate for data in which the response variable is binary (successful/depredated; Hosmer and

Lemeshow 1989). Both year and site were kept in all individual and multivariate models to control for any broad difference between year and site.

Results of the logistic regression analysis are presented as odds ratios with 95% confidence intervals and their P values. The odds ratio is the increase or decrease in the odds that a nest will be depredated as a function of the independent variable. If the odds ratio is below one, the independent variable is associated with a decrease in nest predation. On the other hand, if the odds ratio is above one, the independent variable is associated with an increase in nest predation. Unless otherwise specified, significance will mean $\alpha=0.05$.

For continuous variables, odds ratios were calculated for incremental increases in the independent variable that were considered biologically meaningful. Odds ratios were calculated for a 5% change in surrounding land use cover, a 5-meter change in distance to edge, a 0.1-meter change in nest height, and an increase of 0.5 in the nest concealment index.

Two multiple logistic regression models were constructed using all fine-scale, intermediate-scale and broad-scale variables in this study. The first model (best fit model) contained the variables that best explained increases or decreases in nest predation across the sites, balancing parsimony and explanatory power. A second model (expanded model) expanded on the best fit model to include variables that were significant when analyzed as individual variables, as well as variables that were found to be correlated with nest predation in other published studies. These variables included presence of coastal sage scrub and agriculture, % cover of trails/dirt roads, index of nest concealment, and distance to edge.

χ^2 analysis was used to compare the stage (egg or nestling) of the nest when depredated and the condition (torn or intact) of the nest after depredation.

RESULTS

Data were collected from 231 of the 315 monitored Least Bell's Vireo nests: 108 in 1999 and 123 in 2000. The outcome of nests was evenly divided between nests that were depredated (50.3%) and nests that were successful. The observed rate of nest predation was similar in both years (53% vs. 48%, χ_1^2=0.532, P=0.47) and between sites, Pilgrim Creek and San Luis Rey River (χ_1^2=0.201, P=0.65, both years combined). The area surveyed on the San Luis Rey River included 79% of the total number of nests used in this study.

The division between early and late lay dates differed between years. Least Bell's Vireo nests were initiated between April 27 and July 5 in 1999 and had a median lay date of June 6. Nests in 2000 were initiated between April 16 and June 30 and had a median lay date of May 14. Nests that were initiated early over the entire study area had a tendency to have a higher predation rate with an odds ratio (OR) of 1.64 ([0.97 – 2.77], P=0.06). The timing of nest predation was different at each site. Nests along the San Luis Rey River (n=184) were more likely to be depredated early in the season than late in the season (OR=2.22, [1.2-4.0], P=0.008). The opposite appeared true at Pilgrim Creek (n=47), where nest predation was higher late in the season as opposed to early, although this differences was not significant (OR=0.51, [0.15-1.66], P=0.26) (Figure 4).

Seventy-two ± 3.7 percent of all nests that were depredated in this study were left intact. The percent of intact nests varied between sites (χ_1^2=15.9, P<0.001). Forty percent (n=25) of the nests at Pilgrim Creek were left intact after predation in contrast to 80% (n=92) at San Luis Rey River (Figure 5).

Sixty-nine ± 5 percent of all nests were depredated in the egg stage and 31 ± 8 % in the nestling stage (n=107, χ_1^2=10.2, P=0.001). Nine nests were omitted because the stage was unknown. There was no significant difference between sites in the stage at which nests were depredated (χ_1^2=2.6, P=0.11) (Figure 6).

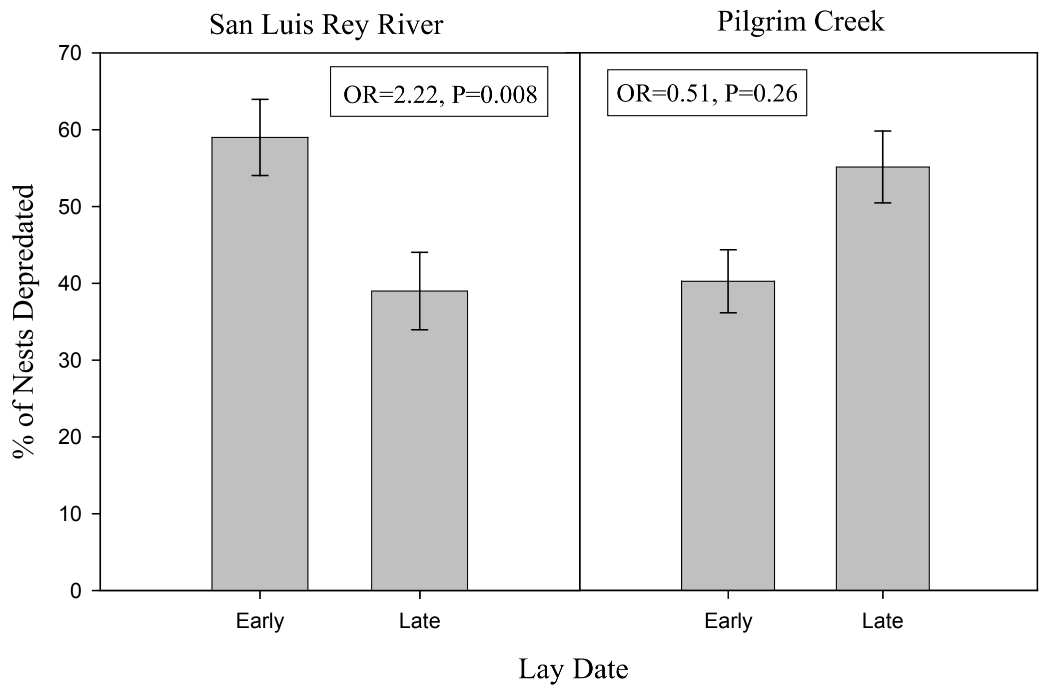

Figure 4: Percent of early and late (± 95% confidence interval) Least Bell's Vireo nests that were depredated at the San Luis Rey River and Pilgrim Creek, 1999 and 2000.

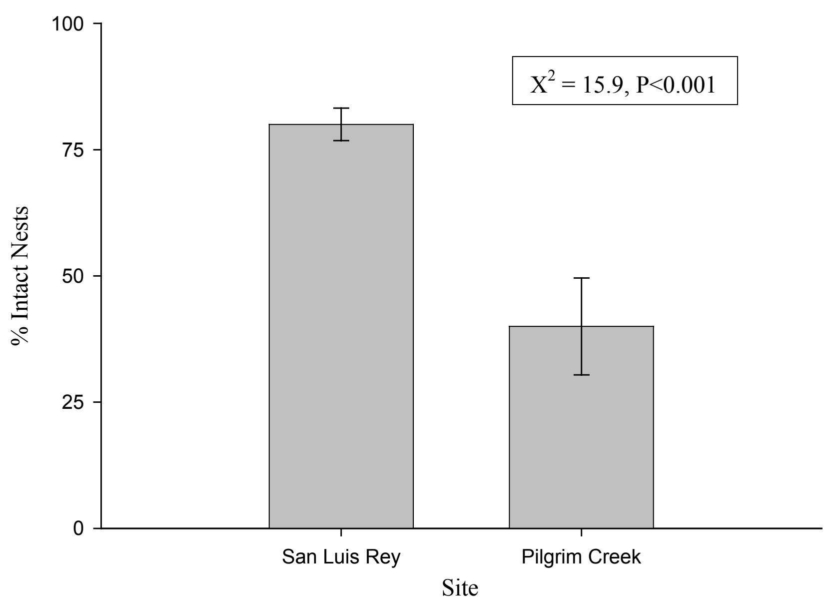

Figure 5: Percent of Least Bell's Vireo nests left intact after depredation (± 95% confidence interval) at the San Luis Rey River and Pilgrim Creek, 1999 and 2000.

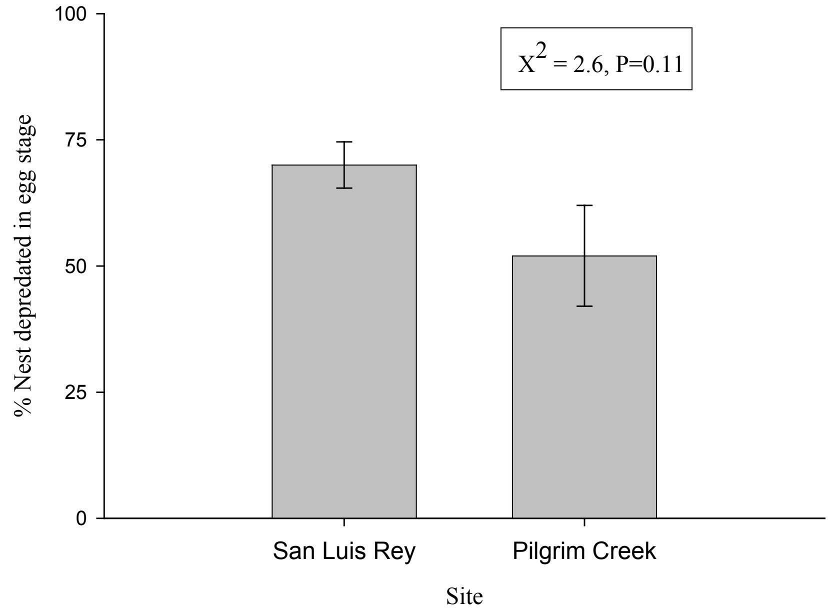

Figure 6: Percent of nests depredated during the egg stage (± 95% confidence interval) at the San Luis Rey River and Pilgrim Creek. Nests in which stage was unknown at the time of depredation were excluded.

Fine-scale Measurements

Nest height ranged from 0.22 to 1.85 meters, with an average height of 0.85 ± 0.28 meters (n=219). Nest height did not differ between nests that were depredated and those that were successful (OR=0.99 [0.89 – 1.09], P=0.87) (Figure 7). Least Bell's Vireos used eighteen different host species for placement of their nests. The three host species most frequently used were arroyo willow (36%, n=84), mule fat (20%, n=47), and sandbar willow (17%, n=39). Host plants of the remaining nests (27%, n=61) included black willow (*Salix gooddingii*), white alder (*Alnus rhombifolia*), Fremont's cottonwood (*Populus fremontii*), elderberry (*Sambucus mexicana*), tamarisk (*Tamarix* sp.), wild rose (*Rosa californica*), and various other native and non-native shrubs and herbs. The host species chosen by the Least Bell's Vireo did not have an effect on nest predation rates (χ^2_3=3.5, P=0.32; Figure 8).

The index of nest concealment within one meter of the nest was not related to outcome (OR=1.15, [0.94 – 1.41], P=0.17), (Figure 7). Neither % cover below 2 meters (χ^2_2=1.4, P=0.50) nor % canopy above 2 meters (χ^2_3=4.3, P=0.23) were related to nest predation (Figure 9).

Intermediate-scale Measurements

Nests ranged in distance to the nearest riparian edge from 1 to 265 meters. Forty-eight percent (n=110) of all nests were within 50 meters of the edge. Distance from the edge of the riparian did not affect outcome of the nest (OR=1.01, [0.99 – 1.03], P=0.43) (Figure 10). Visual assessment of the nests on maps in ArcView suggested that many nests far from the riparian edge were close to inner gaps in vegetation. Distance to edge was re-calculated to incorporate these inner gaps, as defined by Paton (1984), by measuring to the nearest riparian edge or large gap (adjusted edge). This adjusted measurement of edge produced little change in the effect of distance to edge on outcome (OR=0.98, [0.95 – 1.02], P=0.40). Sixty-five percent of the nests were within 50 meters of some type of edge (Figure 10).

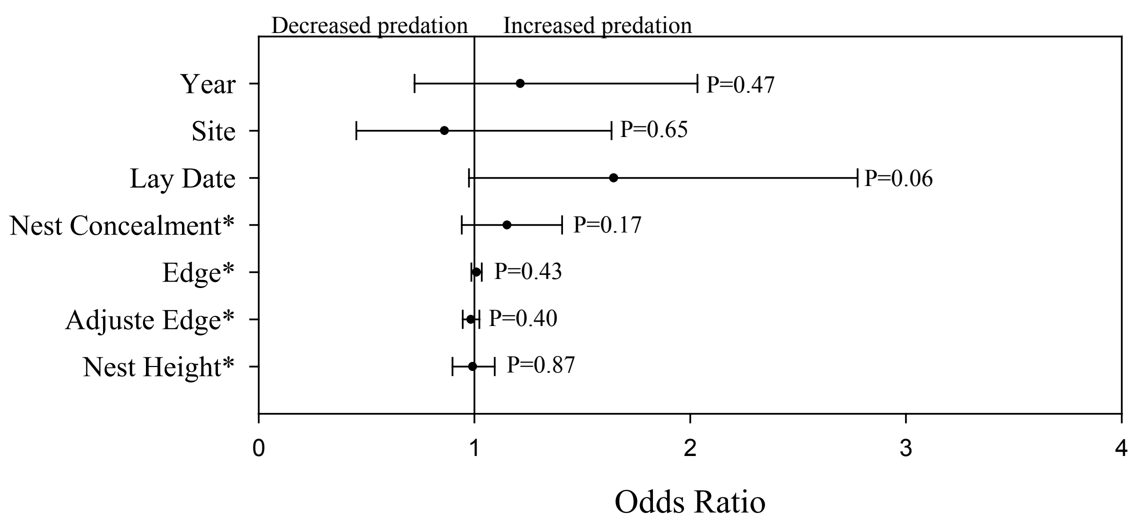

Figure 7: Odds ratios and their 95% confidence intervals for each individual variable. Each variable is controlled for year and site. Those variables that are marked with * are continuous and the odds ratios are calculated for a varying amount of change (edge=5m, nest height=0.1m, and nest concealment index=0.5). All others are categorical.

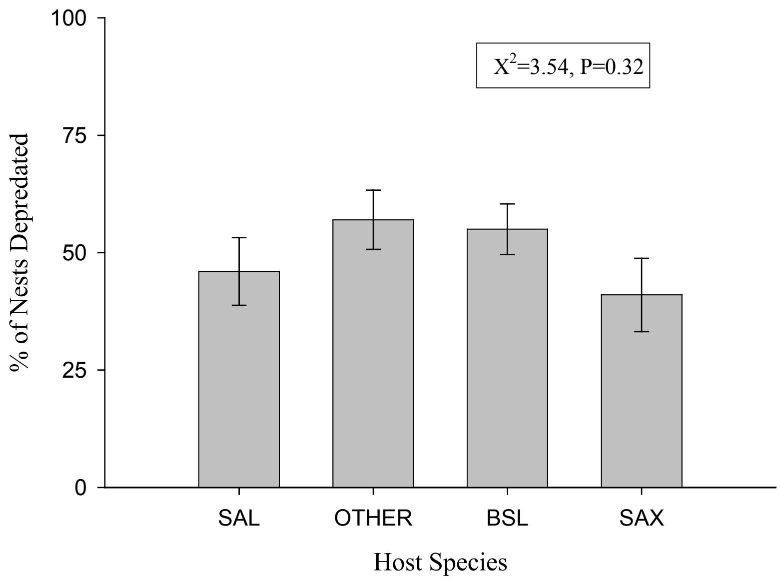

Figure 8: Percent of nests depredated (± 95% confidence interval) in each category of host plant, placed in descending order of use by the Least Bell's Vireo (SAL=*Salix lasiolepis*, BSL=*Baccharis salicifolia*, and SAX=*Salix exigua*)

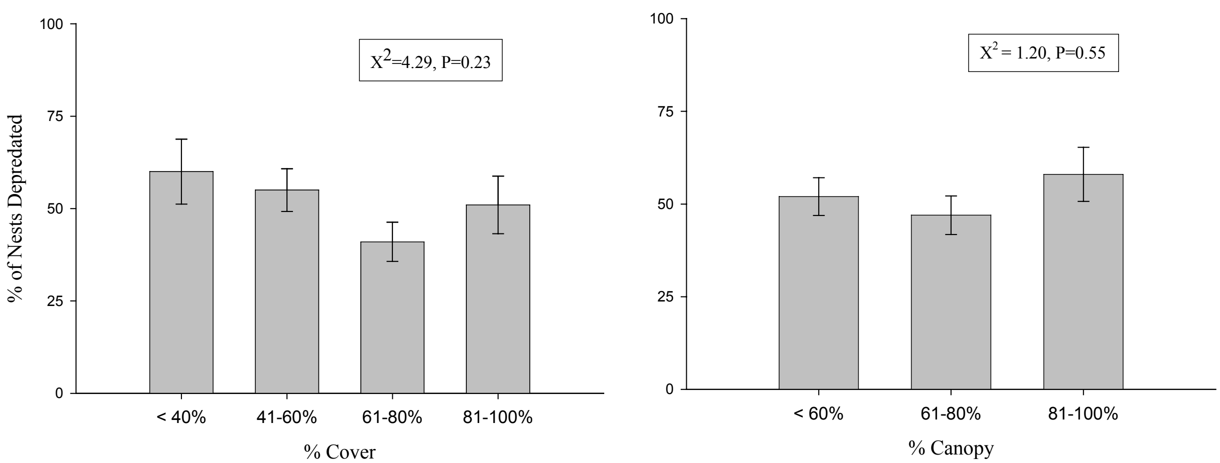

Figure 9: Percent of nests depredated (± 95% confidence interval) for percent cover below 2 meters and percent canopy from 2 meters to the top of the canopy.

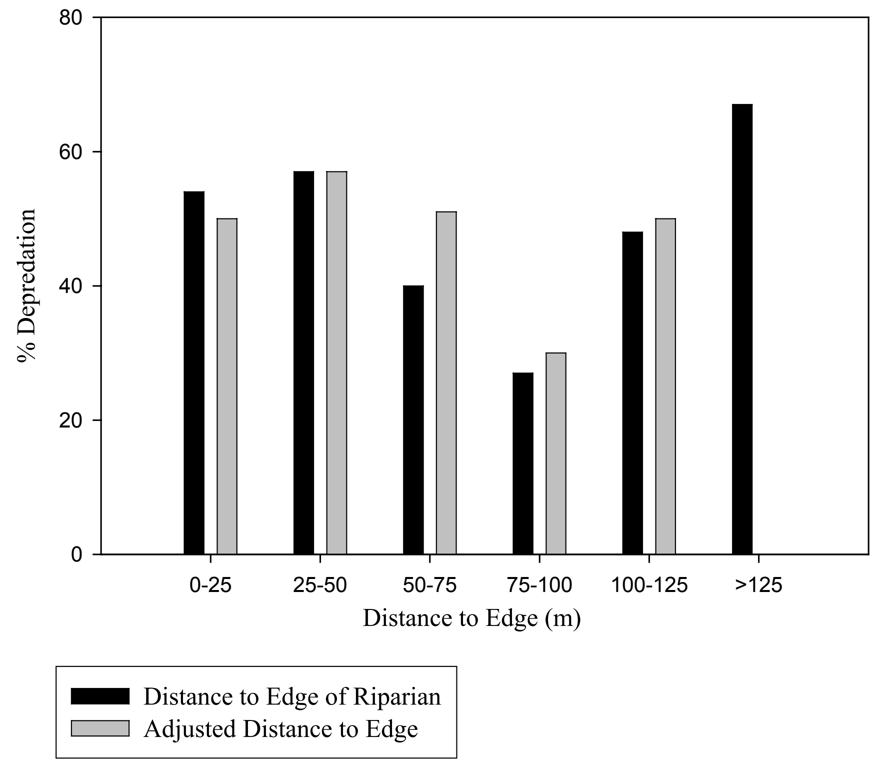

Figure 10: Distance from Least Bell's Vireo nests to the edge of the riparian habitat and to the adjusted edge (including large gaps within the riparian habitat). No nests were >125 meters from the adjusted edge.

Broad-scale Measurements

The thirteen surrounding land uses were distributed throughout the site (Table 3). The number of land use types, including riparian around each nest averaged 6.7 and ranged from three to nine. When analyzed individually using logistic regression, only two land use variables were significant predictors of nest predation (Figure 11). The presence of both golf course/parks and coastal sage scrub increased the odds of nest predation when they were located within 400 meters of a nest. Nests located near golf courses and manicured parks were 2.7 times [1.2 – 5.7], P=0.01) more likely to be depredated than nests distant from these land uses. Nests located near coastal sage scrub were 1.8 ([1.0 – 3.1], P=0.048) times more likely to be depredated (Figure 11). No other lands use variables significantly affected nest predation (Figure 11).

Table 3: Surrounding land use categories, percent of total land use cover (range of percent cover at each nest), number of nests represented in each surrounding land use cover, and the data type.

Land Use	% of Total Land Use Cover (Range)	% of Nests Adjacent to Land Use	Data Type
Willow Riparian	50.2% (11.6 - 91.1%)	100%	Continuous
Disturbed Upland	13.5% (0.0 - 46.0%)	95%	Continuous
Urban Housing	8.5% (0.0 - 56.9%)	64%	Discrete
Grassland	5.2% (0.0 - 36.0%)	59%	Discrete
Coastal Sage Scrub	5.0% (0.0 - 35.5%)	50%	Discrete
Wetland	4.3% (0.0 - 54.0%)	17%	Discrete
Golf Course/Park	2.6% (0.0 - 35.9%)	24%	Discrete
Agriculture	2.4% (0.0 - 69.3%)	23%	Discrete
Roads	2.3% (0.0 - 7.6%)	93%	Continuous
Cleared	1.8% (0.0 - 20.0%)	31%	Discrete
Orchards	0.6% (0.0 - 14.5%)	15%	Discrete
Dirt Roads/Trails*	0.5% (0.0 - 9.6%)	71%	Continuous
Rural Housing	0.4% (0.0 - 32.5%)	30%	Discrete

Note: Ordered by descending cover. All land uses were calculated within a 400m radius of each nest except * which was calculated at a 200m radius. Land use variables that were represented in <70% of the nests were converted to presence/absence data from continuous data in all logistic regression analyses to ensure better representation of the results.

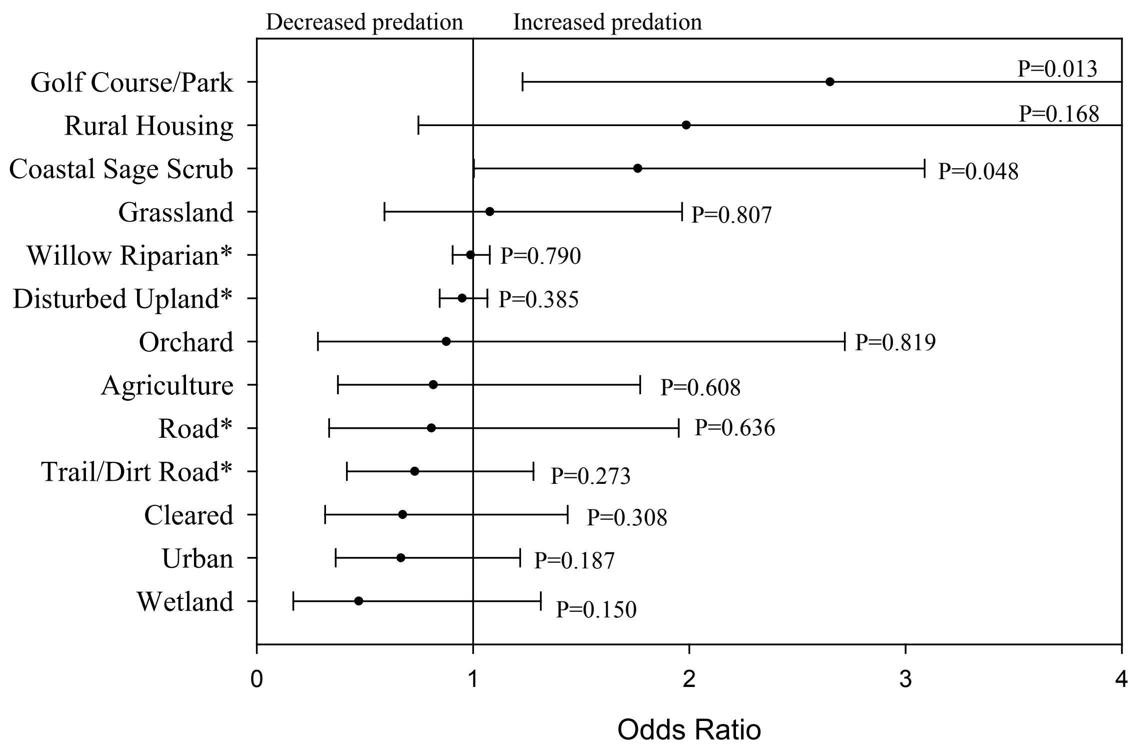

Figure 11: Odds ratios and their 95% confidence intervals for each individual surrounding land use variable. Each variable was controlled for year and site. Those variables marked with * are continuous and the odds ratio was calculated for a 5% change in percent cover. All others were calculated as categorical variables (presence/absence).

Models

The variables retained in the predictive model included year (P=0.45), site (P=0.04), golf course/park (P<0.001), an interaction between site and lay date (P=0.009), and an interaction between golf course/park and urban (P=0.007) (Table 4). Lay date (P=0.17) and urban (P=0.67) were retained in the model due to their interactions but do not, by themselves, influence nest predation. This model was derived using data combined from 1999 and 2000, with year forced into the model to control for any differences between the two years. To assess whether this model adequately captured year-to-year differences, the model was run separately for each year and individual parameter estimates compared with a two-tailed z score (Table 5). There was no difference between years for each variable retained in the model (largest deviation was golf course/park, Z= -0.38, P=0.70).

Table 4: Odds ratio (± 95% confidence interval) and Pvalues for all variables used in models as well as individual variables for comparison.

Variable	Individual Variables		Best-Fit Model		Expanded Model	
	OR (95%CI)	Pvalue	OR (95%CI)	Pvalue	OR (95%CI)	Pvalue
Site	0.86 (0.45 - 1.64)	0.65	0.28 (0.09 - 0.91)	0.04	0.22 (0.05 - 0.90)	0.04
Year	1.21 (0.72 - 2.03)	0.47	1.24 (0.71 - 2.15)	0.45	1.09 (0.59 - 2.06)	0.77
Laydate	1.64 (0.97 - 2.77)	0.06	0.42 (0.12 - 1.45)	0.17	0.37 (0.10 - 1.41)	0.15
Laydate*Site	0.22 (0.06 - 0.84)	0.03	0.15 (0.04 - 0.62)	0.009	0.14 (0.03 - 0.64)	0.01
Golf Course/Park	2.65 (1.23 - 5.72)	0.01	13.55 (2.95 - 62.23)	<0.001	32.6 (3.75 - 283.3)	0.002
Golf Course/Park*Urban	0.08 (0.01 - 0.53)	0.009	0.06 (0.009 - 0.46)	0.007	0.03 (0.002 - 0.41)	0.009
Urban	0.67 (0.37 - 1.22)	0.19	0.85 (0.41 - 1.77)	0.67	0.88 (0.38 - 2.06)	0.77
Edge	1.01 (0.99 - 1.03)	0.43	-	-	1.02 (0.99 - 1.06)	0.15
Nest Concealment	1.15 (0.94 - 1.41)	0.17	-	-	1.02 (0.97 - 1.07)	0.45
Coastal Sage Scrub	1.76 (1.00 - 3.09)	0.048	-	-	1.54 (0.70 - 3.37)	0.28
Trail/Dirt Roads	0.73 (0.42 - 1.28)	0.27	-	-	1.61 (0.72 - 3.61)	0.25
Agriculture	0.82 (0.38 - 1.77)	0.61	-	-	1.35 (0.48 - 3.86)	0.57

Note: Changes for continuous variables are calculated for the following changes: edge (5m), nest concealment (0.1), trail/dirt roads (5%). All significant variables are highlighted.

Table 5: Z test (two-tailed) comparing the estimate (β) of each variable or interaction included in the best fit model to determine if there were any differences between years.

	1999		2000				
Variable	Estimate	S.E.	Estimate	S.E.	% Change	Z score	P value
Site	-1.19	0.88	-1.33	0.83	12%	0.08	0.94
Lay Date	-0.77	0.87	-1.07	0.96	39%	0.16	0.88
Site*Lay Date	1.74	1.00	2.08	1.05	19%	-0.17	0.87
Golf Course/Park	2.51	1.11	2.70	1.09	8%	-0.09	0.93
Golf Course/Park*Urban	-3.20	1.45	-2.28	1.43	29%	-0.38	0.70

Within the model, only site and golf course/park were significant main effects. The interaction between lay date and site revealed that more nests were depredated early in the nesting season along the San Luis Rey River than late in the nesting season, while the opposite appeared to be true at Pilgrim Creek as presented earlier (Figure 4). Urban development, like lay date, was not by itself a significant factor, but interacted significantly with golf course/park. This means that in non-urban areas, the presence of golf course/parks within 400 meters of nests significantly increased nest predation, but in urban areas, the effect of golf course/parks on nest predation was not elevated (Figure 12)

The expanded model contained an additional five independent variables. The addition of these variables did not alter the model appreciably and yielded an expanded model that did not differ qualitatively from the best fit model (Table 4). Coastal sage scrub was the only variable that changed in importance when added to the expanded model. When analyzed as an individual variable, its presence was associated with increased predation of nearby nests, but in the expanded model it was no longer significant (OR=1.5, [0.7 - 3.4], P=0.28) (Table 4).

Spatially, nest predation appeared random throughout the site. A Wald Wolfowitz Runs test detected no significant patterns in nest predation in 1999 (runs = 48, Z= -1.325, P=0.19) or in 2000 (runs = 61, Z= -0.25, P=0.80). The runs were also inspected to identify any localized clustering of depredated or successful nests. Run length did not differ from expected except for one group of 11 depredated nests. This occurred in an area of high predation along a single golf course (Figure 12).

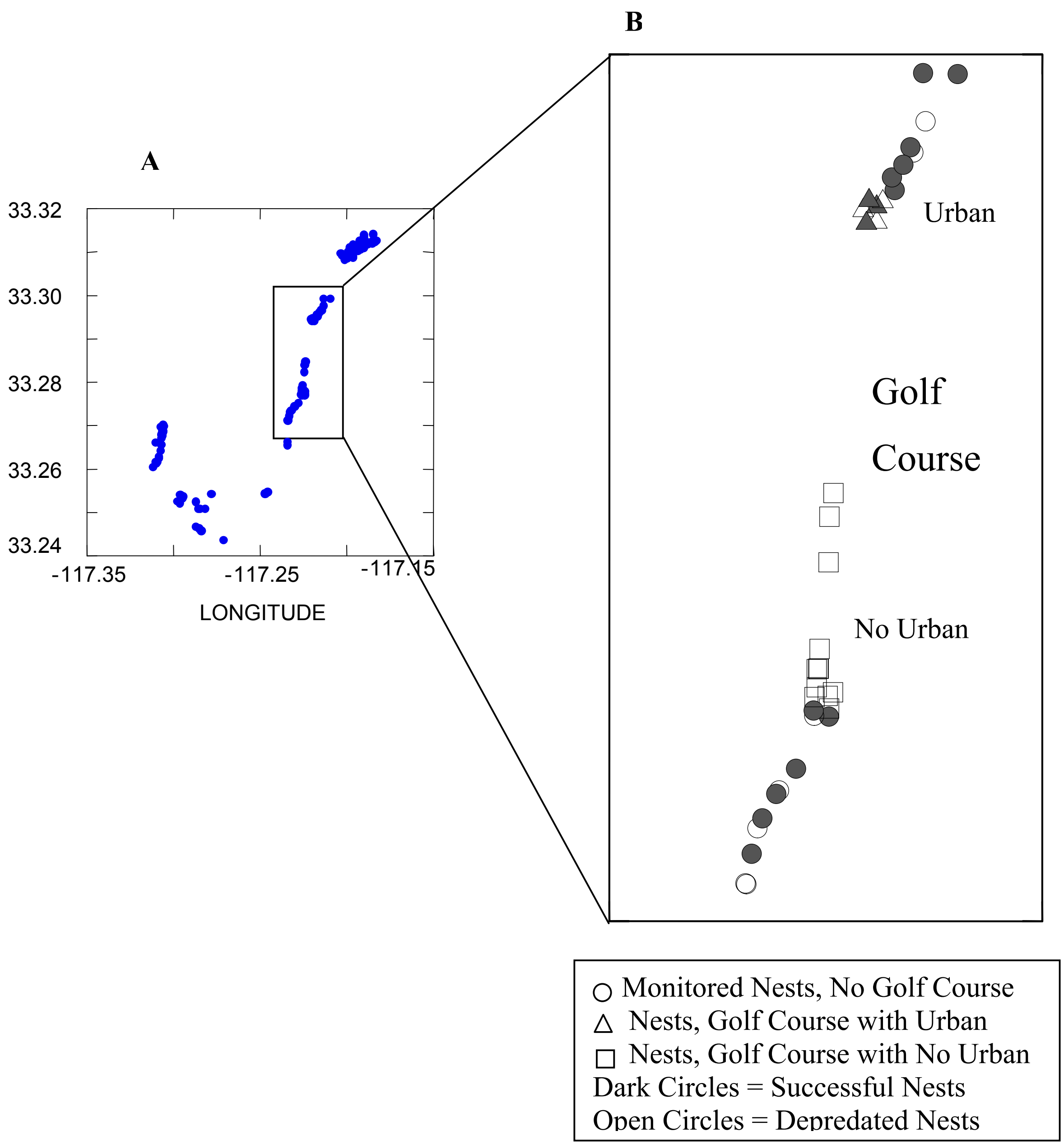

Figure 12: (A): all monitored nests included in the study from both Pilgrim Creek and the San Luis Rey River in 2000. (B): enlargement of the area around the golf course where nest predation was elevated. □ = nests within 400m of golf course not not urban development. △ = nests within 400m of golf course and urban development.

DISCUSSION

The results of this study demonstrate that habitat and landscape variables, at a range of scales, are not strongly related to nest outcome. Placement of the nest was measured in the form of nest height, host species, nest concealment, % cover, % canopy and distance from the edge. None of these variables were significant predictors of nest outcome. On a broader scale, land use surrounding the riparian habitat did not affect the likelihood of nest predation with the exception of increased predation on nests located adjacent to a golf course.

This unpredictability in nest predation was further demonstrated when the spatial distribution of successful and depredated nests was examined. The results of the runs test confirms that the pattern of depredation of Least Bell's Vireo nests cannot be distinguished from random across the study site. This pattern was observed in both years of the study. The apparent random pattern of nest predation, even when considering variables at a very broad scale such as land use adjacent to the riparian, leads to the conclusion that nest predation is largely a random event. This was also concluded in several other studies (Filliater et al. 1994, Wilson and Cooper 1998) even though their studies on Northern Cardinals (*Cardinalis cardinalis*) and Acadian Flycatcher (*Empidonax virescens*), respectively, were limited to habitat characteristics. It may be that the Least Bell's Vireo has evolved to increase reproductive success by having multiple broods rather than selecting for specific habitat characteristics.

Nest concealment, at two scales (1 meter and 15 meters from the nest), was not found to be an important factor influencing nest predation in this study. This is consistent with many other studies that measured concealment and related it to nest predation (Howlett and Stutchbury 1996, Burhans and Thompson 1998, Braden 1999, and Ricketts and Ritchison 2000). A wide array of nest predators, particularly opportunistic predators, could make it difficult for birds to select nest sites with particular characteristics that protect the nest from depredation. At this site, the Western Scrub-Jay (*Aphelocoma californica*) is the major nest predator. Visibility around the nest may allow the Least Bell's Vireo to observe approaching nest predators. The incubating bird could be relying on a balance between two factors to reduce nest predation: visibility of approaching predators, allowing detection time for an appropriate response, and concealment to protect their nests from being observed by predators(Wiebe and Martin 1998, Burhans and Thompson 2001*)*.

Nest predation did not decrease with distance from the edge of the riparian habitat. This was confirmed when the edge measure was adjusted to include large gaps within the riparian system. The hypothesis that nest predation decreases with distance from the edge has been debated since Gates and Gysel (1978). A large number of papers have been devoted to edge effects and have been reviewed by Paton (1994) and Lahti (2001). Their reviews found that there are conflicting results on this subject. Almost all of the studies from North America are of eastern forests, which are different in structure from western riparian forests. Instead of monotypic stands of forest with very few gaps, western riparian forests are linear and patchy in nature. There is no evidence of an edge effect in this type of habitat. This could occur because there is no edge effect or because this linear system is all edge.

Paton (1994) found, based on the papers he reviewed, that decreased nest predation generally occurs within 50 meters of the habitat edge. Although about half of all Least Bell's Vireo nests are within 50 meters of the edge (48% riparian edge and 65% adjusted edge), there was no indication of increased nest predation of edge nests, even though Least Bell's Vireo nest density was higher near edges.

In this study, nest predation was significantly increased near golf course/parks. No other land use variables affected nest outcome. This site has a wide variety of land use types spread throughout the site rather than having monotypic areas of each land use (Table 3). It is possible that the heterogeneous mixture of land use types at this site interacts with nest predation in a way that could not be fully detected in this study.

Golf course/manicured parks was the most important surrounding land use in this study in that its presence or absence within 400 meters of a nest was associated with a 10-fold increase in nest predation. Although there were two golf courses and one manicured park within the study site, high predation at one particular golf course was driving these results. This golf course runs for about 1.8 kilometers along the riparian corridor. The southern section does not have urban development within 400 meters and the nests were much closer to the golf course, incorporating an average of 30% cover of golf course. Along the northern section of this golf course the nests are further from the golf course (average cover is 8%) and also had urban development occurring within 400 meters. Nest predation in this section was not elevated (Figure 12). With most of the nest predation around just one major golf course, it is impossible to rule out some other factor acting to increase nest predation; therefore, the results that golf courses increased nest predation cannot be considered conclusive.

Coastal sage scrub, when analyzed individually, appeared to be associated with elevated nest predation at this site. Coastal sage scrub is found throughout the site and within 400 meters of half the Least Bell's Vireo nests monitored (Table 3). Although coastal sage scrub was significant as an individual variable, the nests that experienced high predation that included this land use within 400 meters also occurred near the golf course. When combined with other variables in the model, the contribution of coastal sage scrub was not significant.

Even though other studies have demonstrated increased nest predation at forest/agriculture edges, this study demonstrated that proximity to agricultural areas did not affect nest outcome. The results for urbanization were similar in that nest predation was unaffected by the presence of this land use. Proximity to trails and dirt roads did not have an effect on nest predation rates as found in other studies (Heske et al. 1999, Miller and Thompson 2000). It is possible that the riparian system in this study is acting as a corridor through a mosaic of land use types that contain a single suite of predators that is enhanced by the variety of land use types.

Habitat and availability of prey usually dictate the predator community within a system. When the system is a narrow, linear riparian system, predators can easily be supported or enhanced by the adjacent land use, increasing foraging and breeding areas. Urban, orchard and agricultural areas may act to increase food supplies that enhance the activity and inflate the numbers of many generalist predators, both avian and mammalian. Lahti (2001) expressed a need know what the major predators are within an area prior to examining the importance of edge and adjacent land use to nest outcome. Until we understand more about how these predators utilize their surroundings, it may be difficult to identify areas where nest predation can be managed for increased reproductive success.

Site differences between Pilgrim Creek and the San Luis Rey River include differences in both the timing of nest predation (lay date) and condition of the nest after nest predation. Nests at the San Luis Rey River were more likely to be depredated early in the nesting season, and 80 % of nests were left intact. At Pilgrim Creek, nest predation appeared to increase late in the season, and only 40% of all nests were left intact. These differences did not have an effect on the overall nest predation rate at the two sites, but do have some implications for the composition of the actual predator community. The predator composition appears to be similar at both sites with one exception. At Pilgrim Creek, one major nest predator, the Western Scrub-Jay, is not present. This nest predator is present all along the San Luis Rey River and has been documented as the major predator in the area by using video cameras (n=23) on Least Bell's Vireo nests in the 2000 breeding season (see the first section). Ritter (1983) studied the nesting ecology of the Western Scrub-Jay in northern California and found that 92% of this species' nests are initiated at the end of March and the beginning of April, which is consistent with Unitt (1984) for this species in San Diego County. This means that Western Scrub-Jay nests typically fledge during the first two weeks in May, and therefore the majority of Western Scrub-Jays complete their nesting cycle during the early nesting period of the Least Bell's Vireo. It is possible that nestlings and particularly eggs provide a source of nutrition that enhances the reproductive success of the Western Scrub-Jay. Once the Western Scrub-Jay nestlings leave the nest, adults may rely on other food sources.

Further evidence of differences in predator composition between the two sites was provided by the condition of nests after depredation. The large number of nests that were left intact on the San Luis Rey River suggests that most nests were depredated by either snakes or birds. The use of video cameras on the San Luis Rey River to identify nest predators showed that 81% (n=11) of all nests were depredated by either snakes or birds, and 100% of those nests were left intact. This is consistent with the overall data at the San Luis Rey River (n=185), where 80% of all depredated nests were left intact. Data from Pilgrim Creek (n=47) demonstrated very different results. At this site, only 40% of all nests were left intact, suggesting that the main nest predators are mammals.

The Least Bell's Vireo has evolved specific requirements for territory and nest-site selection, such as dense cover at nest height and a stratified canopy for foraging (Fish and Wildlife Service 1998). These habitat requirements were identified by examining occupied and unoccupied sites and comparing differences in vegetation structure. Once these specific requirements are met, it appears that there are no further habitat characteristics that protect against nest predation. This is demonstrated by the fact that the Least Bell's Vireo, in this study, did not select habitat features that affected nest outcome. With a large number of nest predators using a variety of search tactics, it may be difficult for Least Bell's Vireos to protect their nests beyond this point.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Nest predation of Least Bell's Vireo nests, both spatially and in terms of habitat variables at a range of scales, appears to be unpredictable. Differences between sites found in this study, such as timing of nest predation and condition of the nest after depredation, were related to predator composition, which varied between sites. Patterns of nest predation and predator composition can change between and within sites as well as from year to year.

The unpredictability of nest predation found in this paper does not mean that nest predation cannot be managed to improve the reproductive success of birds. The clumping of nest predation around a single golf course indicates that areas of concern can be identified through the examination of the spatial distribution of nest predation. If clumping of predation occurs repeatedly, in the same area, over a period of years, this could indicate that the cause needs to be examined on the landscape or broad scale.

Identifying the actual predators in a particular area can increase the understanding of nest predation. Indications of the type of predator occurring in the area can be determined by examining the nest condition after depredation, but this can only be used to determine the type of predator. The use of video cameras is highly recommended for identifying actual predators. In this study, one major predator of the Least Bell's Vireo was confirmed, the Western Scrub-Jay. Once the major predator is identified, the process of examining how to control its abundance, change its foraging behavior, or alter the landscape to decrease their abundance can be examined. Understanding predators and how they forage appears to be critical in managing for nest predation.

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ABSTRACT

ABSTRACT

Nest predation is the major cause of nest loss for the Least Bell's Vireo (*Vireo bellii pusillus)*. Two approaches were used to examine predation risk for this species including monitoring predation events and the predator community, as well as examining habitat correlates of predation at two sites in San Diego County, California: San Luis Rey River and Pilgrim Creek.

Three methods were used: point counts and tracking stations to determine the potential predator community, and videophotography of active nests to determine actual nest predators. These methods were then compared for their ability to determine nest predators. Nest condition (torn, intact) after depredation was examined to determine its ability to identify predators. Parental behavior at depredated nests was quantified and compared to that at successful nests to determine whether activity (trips to and from the nest) and singing at the nest affected outcome.

Yellow-breasted Chats (*Icteria virens*) were the most abundant potential avian predator, followed by Western Scrub-Jay (*Aphelocoma californica*), which occurred less frequently and in lower abundance. Coyote (*Canis latrans*) was both common and abundant within the site, with smaller mammals such as striped skunk (*Mephitis mephitis*), opossum (*Didelphis virginiana*), and long-tailed weasel (*Mustela frenata*) occurring in low numbers. Cameras placed at 25 nests recorded 12 predation events, documenting the Western Scrub-Jay as the major nest predator at this site, responsible for 67% of predation events. Opossum (17%), gopher snake (8%, *Pituophis melanoleucus*) and Argentine ants (8%, *Linepithema humile*) were also confirmed as nest predators.

Identification of potential predators from tracking stations and point counts showed only moderate correspondence with the actual nest predators confirmed by videocameras. All nests depredated by birds and snakes were left intact while nests depredated by mammals were torn. Parental behavior at the nest prior to depredation was not related to nest outcome.

Factors influencing nest predation of the Least Bell's Vireo were examined to determine what nest-site, habitat or landscape characteristics affected the likelihood of nest predation and to determine the spatial distribution of nest predation. Fine scale characteristics included nest concealment within 1 and 15 meters of the nest. Edge (intermediate scale) was measured as the distance from each nest to the edge of the riparian habitat. On the broad scale, percent cover of landscape features was quantified within 400 meters of each nest. Simple and multiple logistic regression was used to analyze nest predation at the study sites. The spatial distribution of nest predation was examined to determine spatial autocorrelation as well as any spatial pattern.

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The results of this study demonstrated that habitat variables, at a range of scales, were not strongly related to nest outcome, with the exception that nest predation was elevated in areas adjacent to a single golf course. No other significant spatial patterns in nest predation were detected, suggesting that nest predation is unpredictable and appears to be largely random. This may be a consequence of a diverse predator community that changes through time and across space. Management decisions must respect the tremendous variability in nest predation.