UNIVERSITY OF CALGARY

Colonization and extinction dynamics of Bank Swallow (*Riparia riparia*) colonies along the Sacramento River, California

by

Kerry C. Moffatt

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA

NOVEMBER, 2003

UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Colonization and extinction dynamics of Bank Swallow (*Riparia riparia*) colonies along the Sacramento River, California" submitted by Kerry C. Moffatt in partial fulfilment of the requirements for the degree of Master of Science.

Supervisor, Dr. E. E. Crone
School of Forestry, University of Montana

Dr. R. M. R. Barclay,
Department of Biological Sciences

Dr. Y. Martin,
Department of Geography

Dr. C. C. Gates,
Faculty of Environmental Design

8 Dec 2003

Date

Abstract

I analyzed existing monitoring data of Bank Swallows (*Riparia riparia*), a threatened bird species in California, within a metapopulation context. I tested the relative importance of several temporal and spatial factors to the probability of colonization and extinction of active sites. I found strong support for a temporal trend in the colonization rate and for the importance of river discharge, weather, and the number of burrows at a site the previous year to the extinction rates. I conclude that this is not a simple metapopulation, because the temporal trend in the colonization rate may reflect habitat change, and the importance of within-population indices illustrates a need to understand population dynamics of individual colonies. The importance of temperature and precipitation may reflect prey availability, and river discharge may reflect erosion of active sites. The viability of this population remains unclear because the confidence limits around the current rates of colonization and extinction illustrate both, equilibrium and non-equilibrium dynamics, as well as metapopulation extinction. Most climate change scenarios favour the continuing existence of Bank Swallows in California.

Acknowledgements

First and foremost, I owe a debt of gratitude to my supervisor Elizabeth Crone for continuing her mentorship through long-distance communication. I also thank her for helping to develop my critical thinking skills and for her expert editorial comments. I thank Robert Barclay for his support and guidance and the rest of my examining committee, Yvonne Martin, and Cormack Gates for valuable comments on this thesis.

I am grateful for the financial support I have received from my supervisor and her colleagues Karen Holl, Matt Kondolf, and Nadav Nur, through a National Science Foundation, Biocomplexity Grant. I also acknowledge financial support from the Government of Alberta and the Department of Biological Sciences at the University of Calgary. This research would not have been possible without the support and assistance of Ron Schlorff at the California Department of Fish and Game and thanks to both Ron and Barry Garrison for their knowledgeable input about the data and Bank Swallows in California. Thanks to Steve Greco at the University of California, Davis for use of bank revetment data. And special thanks to the Nature Conservancy of California for their warm welcome, accommodations, and the use of a kayak so that I might observe the wonderful creatures that are the focus of this research.

Kind thanks and thoughts go out to all of my fellow graduate students, especially Robyn Irvine and Erin Kinsella for their moral support, friendship, advice, and loads of laughs. Finally, I wish to thank Max Rioux for his many words of encouragement, his love, his enthusiasm, and for reminding me of my goals, aspirations, and attributes. We've come a long way baby!

Table of Contents

List of Tables

List of Figures

1. Introduction

Several factors have been implicated in the decline and extinction of bird species throughout the world. Habitat loss in North America has led to the decline of several species and to the extinction of the Ivory-billed Woodpecker (*Campephilus principalis*), the Carolina Parakeet (*Conuropsis carolinensis*), and, very likely, Bachman's Warbler (*Vermivora bachmanii*) (BirdLife International 2000, Askins 2002). Predation by introduced species has also had an impact on bird assemblages, especially on tropical islands (BirdLife International 2000). However, it is often difficult to determine the ultimate cause of decline and/or extinction in bird populations, especially when several proximate factors may be involved.

Population decline can be the result of several interacting factors. Much attention has been drawn to the decline of some Neotropical migrant populations in North America due to an increase in predation and/or cowbird parasitism at forest edges following fragmentation of the landscape (e.g. Gates and Gysel 1978, Wilcove 1985, Temple and Cary 1988, Yahner and Scott 1988, Paton 1994, Marini et al. 1995, Robinson et al. 1995). Other factors that have been linked to periods of decline and/or differences in abundance in bird populations include climate variables such as temperature and/or precipitation (e.g. Smith 1982, Elkins 1983, Holmes et al. 1986, Thompson et al. 1986, Sauer and Droege 1990, Greenwood and Baillie 1991, Blake et al. 1992, Faaborg and Arendt 1992, George et al. 1992, Madhusudan and Price 1996, Lusk et al. 2001, Moss et al. 2001, Benton et al. 2002), food resources (e.g. Lack 1966, Morse 1978, Holmes et al. 1986, Stuart Simons and Martin 1990, Rodenhouse and Holmes 1992, Madhusudan and Price

1996, Benton et al. 2002), competition from other species (e.g. Hunter 1988, Roy et al. 1998, Bowman et al. 1999, Copley et al. 1999, Kearvell et al. 2002), parasitism (other than cowbirds) (e.g. Hudson et al. 1992), as well as disease, accidental deaths, chemical contaminants and the exotic pet trade (see BirdLife International 2000, Youth 2003). A period of decline may also represent a small portion of a natural population cycle brought on by within-population regulation such as density dependent feedback (i.e. lower population growth rate at high density) (see Lack 1966, e.g. Greenwood and Baillie 1991, Ferrer and Donazar 1996, Fernandez et al. 1998). Although the preservation of essential habitat should be of primary importance in any conservation plan, it is important to consider all relevant factors of decline because many of them can and do act in concert. For example, while an abundant species may normally be able to cope with a sudden, temporary change in climate, a population already in decline due to habitat loss may have difficulty recovering losses due to a period of severe weather.

I investigated the decline of Bank Swallows (*Riparia riparia*) in California. Specifically, I analyzed the relative importance of several temporal and spatial factors for past population dynamics and, based on these results, assessed the persistence of this species within California under different ecological and management scenarios. Extensive population surveys for breeding colonies conducted in 1986 and 1987 (Humphrey and Garrison 1987) confirmed earlier reports that Bank Swallows had been extirpated throughout much of their historical breeding range in California (Remsen 1978); consequently, the species was listed as threatened in the state in 1989 (California Department of Fish and Game 1992). The primary cause of decline was habitat loss, mainly as the result of the channelization of rivers by the State Reclamation Board and the U.S. Army Corps of Engineers (Remsen 1978, Humphrey and Garrison 1987, California Department of Fish and Game 1992). Channelization involves limiting the natural meandering pattern of a river by using levees to control flooding and installing riprap, a form of bank revetment in which large boulder-sized rocks are placed from top to bottom along sections of a river's bank to minimize erosion.

The Bank Swallow is a colonial bird that requires eroded vertical banks in which to dig burrows for nesting; these are often found along meandering waterways or coastal cliffs (Garrison 1999). Therefore, any land use activity that involves bank stabilization and the curtailment of erosion limits available habitat for this species. Although Bank Swallows will use human-made sites such as sand and gravel quarries, especially in eastern North America (Garrison 1999), these artificial sites are rarely used by Bank Swallows in California (Humphrey and Garrison 1987). As long as their remaining nesting habitat is protected, the Bank Swallows that currently occupy several colonies along the Sacramento River represent the greatest chance that this species will continue to be a part of the California avifauna.

Bank Swallows along the Sacramento River make up over 70 percent of the remaining statewide distribution of this species (Schlorff 1997). Because of the location's obvious importance, the California Department of Fish and Game has monitored colonies along the Sacramento River since 1986. General trends of all colonies combined illustrate two distinct periods of decline followed by periods of increase. Overall, the total number of active burrows has declined by 36% between 1986 and 2002 (Figure 1).

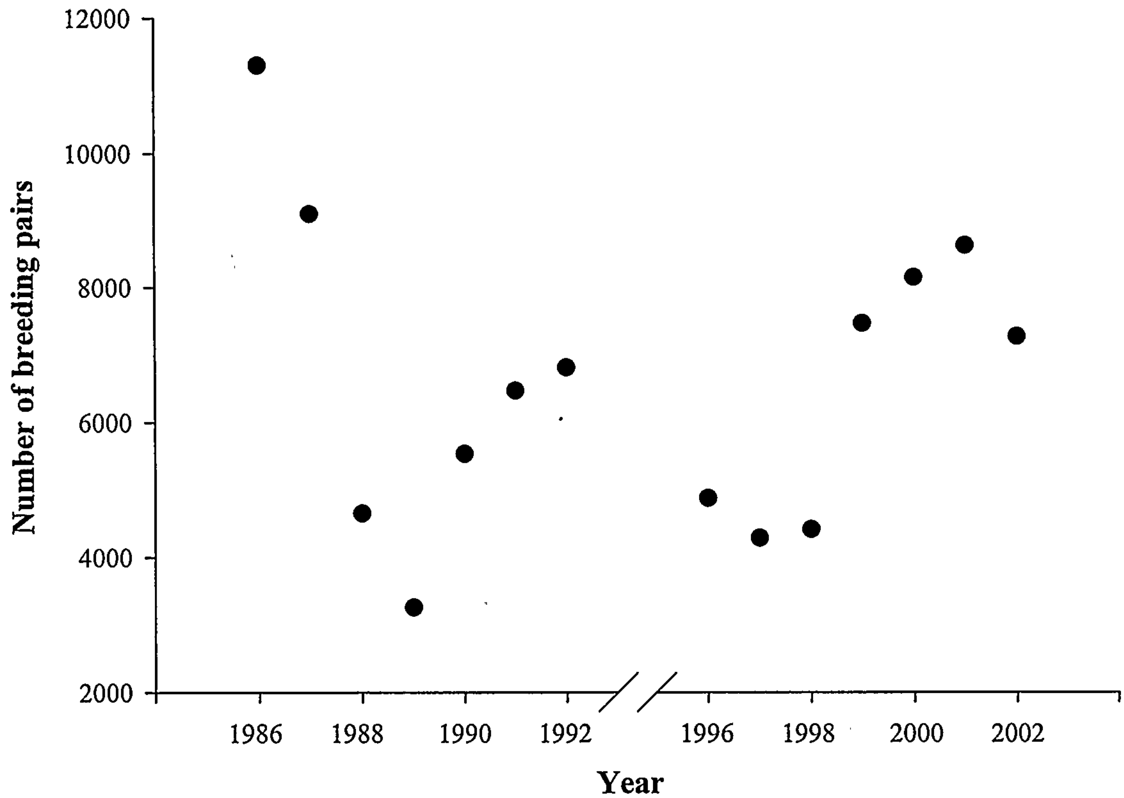


Figure 1. The number of Bank Swallow breeding pairs (calculated from the number of active burrows multiplied by a 45% occupancy rate) along the Sacramento River from river miles 144 to 243.

However, there was no significant linear trend in the data through time and it is unclear if 1986 and 1987 reflect historical abundances or particularly good breeding years. Declines in the early part of the period may be attributed to drought conditions in the mid-late 1980's and more recent increases may reflect a delayed response to the relief from drought stress, combined with changes in bank protection activities (Schlorff 2001). The construction and maintenance of bank stabilization projects during the breeding season were identified as a major source of mortality, due to the collapse of active banks and the complete loss of reproduction at several colonies; these activities have been curtailed during this sensitive period since 1986 (California Department of Fish and Game 1992). In the long term, riprap renders that portion of the river uninhabitable for Bank Swallow colonies. Although this habitat loss must be minimized to preserve Bank Swallows in California, other relevant factors that may affect the dynamics of this Sacramento River population have yet to be identified using the full period of monitoring.

Several temporal and spatial factors may be associated with trends observed within the Sacramento River Bank Swallow population. As this bird is intimately tied to erosional processes, river discharge likely plays an important role as well as the installation of riprap. Other potentially important temporal factors include weather variables such as temperature and precipitation. These factors have been associated with demographic change or population abundances of several bird species, including swallows (e.g. Bryant and Jones 1995, Szep 1995, McCarthy and Winkler 1999, and see Hoogland and Sherman 1976). Spatial factors may also be relevant if some of the colonies along the Sacramento River are located in less than optimum sites for breeding.

Bank Swallows prefer friable soils, characterized by small particle size (Garrison 1999). Ideally, however, soil should be sandy but not gravely, compact or high in organic matter (Peterson 1955, John 1991). Both Sharrock (1976) and Hjertaas (1984; as cited in Garrison 1999) state that Bank Swallows have a preference for sandy soils as opposed to clay or silts. Burrows in loose sand are generally deeper than those in compact soils and birds nesting in deeper burrows have greater breeding success (Sieber 1980; as cited in Garrison 1999). Presumably, protection from predators and climate increases, to some extent, with the depth of a burrow. Surrounding land use may also affect Bank Swallow population dynamics. Bank Swallow colonies along the Sacramento River are more often found adjacent to open areas such as sandy or grassy fields (Humphrey and Garrison 1987). However, foraging habitat may include wetlands, open water, grasslands, riparian woodlands, agricultural areas, shrublands and upland woodlands (Garrison 1999). Cliff Swallow *(Petrochelidon pyrrhonota)* colony size increased with land use diversity and varied inversely with the amount of cultivated cropland (Brown et al. 2002). Like Cliff Swallows, Bank Swallows are aerial insectivores that feed on a wide variety of flying insects, especially Hymenoptera, Diptera, and Coleoptera, (see Waugh 1979, Garrison 1999) and land use patterns may affect prey availability (Benton et al. 2002, Brown et al. 2002). Portions of the Sacramento River are currently undergoing restoration to native riparian forests. Thus, it is particularly important to determine if the surrounding habitat plays a role in the population dynamics of Bank Swallows.

I used a metapopulation framework to investigate factors influencing Bank Swallow population dynamics. Although Bank Swallows are migratory, they display a fairly strong affinity to breeding and natal sites while allowing for some interchange between colonies. Site fidelity among recaptured birds in several studies ranges from 55.6 to 92.0% (see Garrison 1999), and most colonies along the Sacramento River persist for less than seven years. Bank Swallows occupy habitat that is somewhat ephemeral in nature and may, therefore, persist through a balance between local extinction and recolonization of sites. Species that live in transient habitats have been described as archetypal metapopulations (Harrison and Taylor 1997). Examples include amphibians in small ponds, herbs on riverbanks, insects on weedy plants, snails on rocky outcrops and butterfly species vulnerable to bad weather or habitat change (Harrison and Taylor 1997). Metapopulation models have also been applied in the study of bird populations (e.g. Lahaye et al. 1994, Akçakaya et al. 1995, Akçakaya and Atwood 1997, Reed et al. 1998, McCarthy et al. 2000) including Neotropical migrants (e.g. Villard et al. 1992).

In this study, I used a combination of spatially implicit, discrete time, state-transition models to evaluate the relative importance of climate, river discharge, riprap, surrounding land use, soil, and year on the colonization and extinction dynamics of Bank Swallow colonies along the Sacramento River. In addition, I tested whether colonization-extinction dynamics depended on within-population dynamics, a key assumption of metapopulation models. Finally, I used models fit through statistical analyses to explore consequences of further change in environmental and habitat variables. This study is limited to proximate factors linked to the breeding ground. However, since the primary concern is the continued return of this species to the State of California, any relevant factors herein will have important implications for management.

2. Methods

2.1. Study system

The Sacramento River is the longest and one of the most important rivers in California; its drainage represents 17% of the state's land area and yields 35% of its water supply (Buer et al. 1989). The river runs for approximately 483 kilometres through California's Central Valley between the foothills of the Sierra Nevada and the Coast Mountain ranges. It winds its way from volcanic bedrock in the north to a more sinuous alluvial system and finally into delta mudflats in the south (Sacramento River Advisory Council 1998). The Sacramento/San Joaquin Delta is the interface between two meandering rivers and the San Francisco Bay estuary (Mount 1995). The Sacramento River drains 62,156 square kilometres and supplies approximately 80% of the delta in-flow (Nature Conservancy of California 1999).

Historically, bank erosion and lateral migration across the floodplain were natural processes (Buer et al. 1989). Currently, the watershed is intensely modified by dams, reservoirs, diversions, levees, flood control channels and land use change (CALFED Bay-Delta Program, 2000), which reduce the size and quantity of sediment supply, decrease peak and total discharges, and alter the timing and source of water released back into the river (Mount 1995). Levees now span approximately 2,092 kilometres along the Sacramento River (Sacramento River Advisory Council 1998).

Several initiatives have been undertaken since the 1980's to restore and enhance riparian habitat and associated wildlife along major sections of the Sacramento River. Management plans by both the Upper Sacramento River Fisheries and Riparian Habitat

Advisory Council, created in 1986 under Senate Bill 1086, and the CALFED Bay-Delta Program, a joint effort among state and federal agencies established in 1994, recognize the importance of restoring dynamic processes along the Sacramento River (Sacramento River Advisory Council 1998, CALFED Bay-Delta Program 2000). The Nature Conservancy, along with its partners, the United States Fish and Wildlife Service, California State University, Chico, and area farmers and ranchers, have also taken an active role by protecting over 8,094 hectares and restoring 1200 hectares of native riparian vegetation within the floodplain (Nature Conservancy of California 1999, D. Jukkola, pers. comm.).

2.2. Monitoring data

The California Department of Fish and Game has monitored the banks of the Sacramento River for the presence of Bank Swallow colonies in almost every year since 1986. The most consistent and uniform portion of the data involves the monitoring between river mile 243, just below the Red Bluff Diversion Dam and Colusa at river mile 144 (Figure 2). This area was surveyed in late May to early June in all years between 1986 and 1992, and between 1996 and 2002. In total, this research represents 263 Bank Swallow colonies and 14 years of monitoring.

Observations were made from a jet boat travelling downstream with the river current. When active colonies were located, the boat was positioned 10 to 20 metres from the site and two observers counted the number of active burrows (Schlorff 1997). The average of both counts was taken once they were within 10% of each other and then

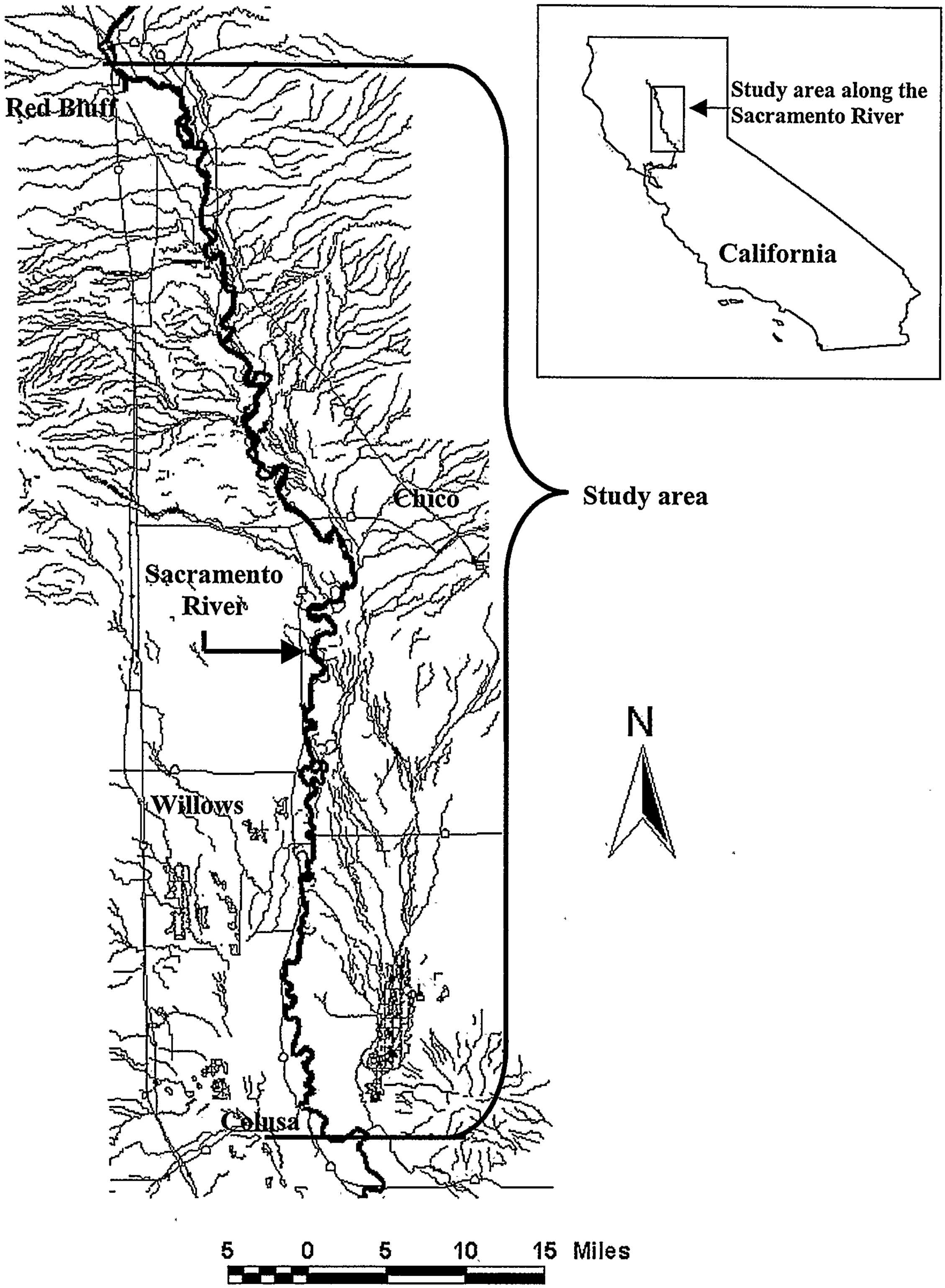


Figure 2. The location of monitoring for Bank Swallow colonies along the Sacramento River in California.

rounded to the nearest ten. Active burrows are described by the presence of nesting birds and indications of recent burrowing activity or occupancy such as scratch marks, lack of spider webs and sufficient depth to indicate that it was not an abandoned excavation (R. Schlorff, pers. comm.). This method has been used as an index of population in other Bank Swallow studies (Szep 1991, Bryant and Jones 1995). One of the observers, Ron Schlorff, has taken part in the monitoring in all years, minimizing, to some extent, the observation error encountered when using different observers. Burrow counts, which represent one breeding pair, are then multiplied by a 45% occupancy rate (Schlorff 1997). The occupancy rate is based on earlier studies in which a random sample of colonies was selected and the occupancy of active burrows was determined by investigating each burrow directly using a flashlight.

2.3. GIS analyses and landscape variables

2.3.1. Colony location and site positioning

During monitoring by the California Department of Fish and Game, the location of Bank Swallow colonies was determined to within one tenth of a river mile using aerial atlases and a river mile marker system assigned by the California Department of Water Resources-Northern District. Throughout my analyses, I referred to each 0.1 mile sighting as a "colony" or site. These counts represented what observers in the field deemed one interacting colony (R. Schlorff, pers. comm.). I assumed that each site that had a Bank Swallow colony for at least one year during the period of monitoring was available habitat during all years.

I assigned sites for GIS analyses onto ArcView landscape coverages by dividing the length of the river between two river mile markers by ten and placing the sites along the river bank to the nearest tenth of a mile, based on the California Department of Water Resources (CDWR) river mile markers (2000). I assumed that areas categorized as gravel and having the appearance of low sandbars immediately adjacent to the river would generally not have Bank Swallow colonies. Therefore, I positioned those sites adjacent to gravel further back onto the nearest vegetation (see Appendix A). For GIS analyses, I used points to represent the center of colonies, even though colonies can range between two and 336 metres in length (Humphrey and Garrison 1987). The length of the actual bank used in each year was not available.

The Sacramento River is an active, meandering and migrating channel; therefore, it is highly probable that a site located in 1986 may occupy a different location at that tenth of a river mile in 2002. To alleviate some of this displacement, I conducted two separate GIS analyses by placing all of the 263 sites on river channel maps from 1991 and 1999 for the early and late monitoring periods respectively. I used a 1991 river channel map (CDWR 2000) to locate available sites for the 1986 to 1992 period; this river was nearest in time to this subset of the monitoring data. I used the existing river channel digitized within the 1999 riparian vegetation coverage (discussed below) to locate sites for the 1996 to 2002 time period.

To test the accuracy of site placement, I used GPS data, which were available for 29 of the sites in 2001 and 40 of the sites in 2002. I measured the distance between these GPS locations and the placement of colonies using methods described above, and found that sites were displaced on average by 287 metres ± 200 SD but that the direction of displacement was not biased in any particular direction. To test how much this displacement might affect land use analyses, I conducted correlation analyses between the land use data calculated from these GPS sites and the land use data using my method of placement. All land use factors (described below) were positively and significantly correlated (riparian vegetation, $r=0.64$, $p<0.001$; developed land, $r=0.68$, $p<0.001$; and distance to nearest grassland, $r=0.53$ $p<0.001$). However, the correlation factors indicate that a high degree of variation remains unexplained. Therefore, my measures of the surrounding land-use within the foraging range are somewhat "noisy".

2.3.2. Land use analyses

I categorized the landscape as riparian (i.e. riparian forests, oak forests, and gravel), grassland, or developed land (i.e. crops, orchards, and urban) using two separate vegetation layers mapped by the Geographical Information Center at California State University in Chico in conjunction with the California Department of Water Resources and the California Department of Fish and Game (2000, 2001). The earlier GIS layer was digitized from various aerial photographs taken between 1991 and 1998 (the areas in my analyses were mostly from 1993 to 1995) and was used to represent the landscape surrounding burrows between 1986 and 1992. No earlier riparian vegetation coverages are available. The second layer was digitized from aerial photographs taken in 1999 and was used to represent the landscape surrounding burrows between 1996 and 2002.

I separated grasslands from other undeveloped land because they are structurally quite different from the riparian vegetation category and may be important for Bank

Swallows if they prefer to forage over open, natural areas (Humphrey and Garrison 1987, Schlorff 1997). I included all developed land in one category because transitions between crops and orchards were likely quite common during the study period (Greco 1999). Similarly, I included gravel bars with the riparian vegetation because the transition of gravel to riparian habitat can occur within the time frame that I assumed land use was stable (Greco 1999). Greco (1999) calculated the transitions among land cover types for a smaller reach of the river between river miles 196 and 219. He found that no riparian vegetation was converted to crops or orchards, or vice a versa, between 1987 and 1997, supporting my assumption that broad land use categories were constant during both 7-year time periods. To evaluate the broad habitat types surrounding each colony, I placed a circle with a 200-metre radius around each site; Bank Swallows tend to forage within 50-200 metres of the colony when feeding nestlings (Garrison 2002). Grassland habitat was limited within the foraging area itself so I calculated the distance to grassland as a measure of its role in Bank Swallow population dynamics, instead of the area within the foraging range.

To align river channel and land cover maps for the 1986 to 1992 data, I subtracted any land from the riparian vegetation layer that fell within the 1991 river channel and extrapolated from the remaining land the amount of land that would have been present in areas where the river channel on the riparian vegetation coverage was not contained within the 1991 river channel (see Appendix A). For example, if after removing the amount of land taken up by the 1991 river channel, the land remaining within the 200-metre radius was comprised of an equal proportion of riparian and developed, I assumed that the land which eroded away (as indicated by the 1995 river channel on the riparian vegetation file) was comprised of equal proportions of riparian and developed. The only exception occurred when a site was located adjacent to a riparian forest where the river simply migrated laterally. I assumed that the eroded area consisted of riparian vegetation in the past since a small patch of agriculture is not likely to have been present on the river side of a riparian patch (see Appendix A).

I converted developed areas undergoing restoration to the land type that was planted (mixed riparian or grassland) three years after the initial planting to allow for a more accurate representation of the surrounding vegetation. I grouped restoration sites with disturbed lands during their first three years because restoration sites are actively managed for three years following planting and management practices may include herbicide spraying (Griggs and Golet 2002).

2.3.3. Bank revetment

To test the importance of riprap (or rock revetment), I used the Sacramento River Bank Revetment Inventory from the Center for Design Research at the University of California, Davis (Greco and Tuil 2002). Because the date of installation is not available for any rock revetment installed after 1983, I placed the riprap into two separate categories: old for installations prior to 1983 and new for any installed after this date. Old riprap would have definitely been in place prior to the Bank Swallow monitoring period, whereas new riprap may have been installed during the monitoring period. Riprap was categorized as present when it was located along the same bank and within

287 metres of a site (287 metres was used because this is the average displacement of sites using my methods when compared to the GPS sites, see above).

2.3.4. Soil analyses

To characterize the soil at each colony, I used a GIS coverage mapped by the Natural Resources Conservation Service in which aerial photos were overlain with soil type as determined by soil surveys conducted by the U.S. Department of Agriculture. I placed soil into four categories based on previous studies of soil used by Bank Swallows: clay and silty soils, strictly loam soils, all sandy soils (including four gravely loam sites) and strictly sand and gravel soils.

I measured the soil along the bank, following the outline of the river, from each of the sites to 100 meters on either side. Since the average colony length was 66 metres ± 12 SD in a previous study (Humphrey and Garrison 1987), 100 metres should be a good representation of the majority of colonies. The depth of an average burrow is approximately 62 cm and all sites had consistent soil classifications that extended at least twenty metres back from the bank, justifying the use of a length measurement (as opposed to area) to categorize the soil. Since the soil surveys represented only the first stratum of deposited material, they may not represent the entire vertical face of the habitat. However, the prime location for burrows is near the tops of banks (Petersen 1955, Sieber 1980 as cited in Jones 1987) where reproductive success is greatest (Hoogland and Sherman 1976). Burrows typically occupy only 15% of a bank's vertical face with 20% of the bank above and 65% of the bank below the colony (Humphrey and Garrison 1987). Therefore, the top portion of a bank's soil composition may play a relevant role in the quality of a site, as long as the sedimentary layer is consistent throughout the bank.

Soils were mapped using aerial photos taken from 1967 to 1996, so the river channel did not always align with the assigned colony sites. If the bank from one of my sites was located in water on the soil coverage, I extrapolated from whatever soil was present on the nearest bank on the same side of the river as the colony (see Appendix A).

2.3.5. Correlation and Principal Components analyses

To alleviate the problems incurred by correlations among landscape variables during the interpretation of the results, and to potentially reduce the number of variables, I conducted correlation and principal component analyses (Manly 1994). Since the models and the data that I used to predict the probability of colonization are different from those that I used to predict the probability of extinction (see Statistical Analyses), I analyzed the landscape variables for each data set separately. Landscape variables were often correlated, particularly between different kinds of land use ($p<0.001$) and different soil variables ($p<0.0001$), using both the colonization data set (Table 1a) and the extinction data set (Table 1b). This was expected between the soil variables since these variables represent the entire range of possible soil textures for the area. This is also true of the riparian and developed variables since most of the surrounding land use was of either one or the other type. The negative and positive relationships between distance to grass and riparian and developed, respectively, are also not surprising since you would expect natural grasslands to be in closer proximity to natural riparian areas than to developed agricultural lands. The location of old riprap was not significantly correlated

Table 1. Correlation coefficient (r) between landscape variables in the colonization (n=2697) and extinction (n=459) data sets.

	riparian area	dev. area	dist. to grass	old riprap	new riprap	clay-silty	loam	sandy	gravely
a. colonization data									
riparian area	1.00	-0.71	-0.10	-0.16	-0.18	-0.24	0.03	-0.09	0.32
developed area	-0.71	1.00	0.37	0.20	0.19	0.25	0.01	0.06	-0.33
dist. to grass	-0.10	0.37	1.00	-0.02	0.08	0.12	0.08	-0.10	-0.14
old riprap	-0.16	0.20	-0.02	1.00	0.02	0.05	0.05	0.11	-0.19
new riprap	-0.18	0.19	0.08	0.02	1.00	0.09	0.10	-0.01	-0.18
clay-silty	-0.24	0.25	0.12	0.05	0.09	1.00	-0.35	0.37	-0.46
loam	0.03	0.01	0.08	0.05	0.10	-0.35	1.00	-0.24	-0.28
sandy	-0.09	0.06	-0.10	0.11	-0.01	-0.37	-0.24	1.00	-0.27
gravely	0.32	-0.33	-0.14	-0.19	-0.18	-0.46	-0.28	-0.27	1.00
b. extinction data									
riparian area	1.00	-0.68	-0.16	-0.10	-0.16	-0.16	-0.01	-0.07	0.28
developed area	-0.68	1.00	0.44	0.07	0.19	0.22	0.10	-0.05	-0.33
dist. to grass	-0.16	0.44	1.00	-0.05	0.17	0.17	0.13	-0.18	-0.21
old riprap	-0.10	0.07	-0.05	1.00	-0.07	-0.03	-0.06	0.19	-0.10
new riprap	-0.16	0.19	0.17	-0.07	1.00	0.04	0.05	0.08	-0.18
clay-silty	-0.16	0.22	0.17	-0.03	0.04	1.00	-0.41	-0.45	-0.39
loam	-0.01	0.10	0.13	-0.06	0.05	-0.41	1.00	-0.23	-0.22
sandy	-0.07	-0.05	-0.18	0.19	0.08	-0.45	-0.23	1.00	-0.25
gravely	0.28	-0.33	-0.21	-0.10	-0.18	-0.39	-0.22	-0.25	1.00

with the location of new riprap. However, both riprap categories were positively associated with developed land and negatively associated with riparian land. This simply reflects the propensity to riprap agricultural land. The most significant trends and strongest correlations between land use and soil texture illustrated a negative relationship between clay-silty soils and riparian areas and a positive relationship between gravely soils and riparian areas. The opposite trends were found between the same soil variables and developed areas and probably reflect a selection of clay-silty sites, as opposed to gravely sites, for agriculture. All other correlations, whether significant or not, likely do not make biological sense and were conducted simply to indicate any problematic correlations in the interpretation of the results.

Principal components analyses indicated that I could explain more than 95% of the variation in the nine variables using seven principal components. I decided reduction from nine to seven variables was not sufficient to justify analyzing complex principal components over untransformed variables. However, I repeated PCA analyses, within land use and soil variables separately, to test whether interpretable patterns emerged. I did not succeed in reducing the number of variables in a principal component analysis of the three land use types in either the colonization or extinction data; the proportions explained by the third principal component were 0.0790 and 0.0854, respectively. However, I reduced the four soil factors to three principal components that cumulatively explained 99.87% of the variance in the original variables for the colonization data (Table 2a) and 99.75% of the variance in the extinction data (Table 2b). Thus, I used the three soil PCA variables, in subsequent analyses.

Table 2. The eigenvectors for the first three principal components in analyses including all four soil variables.

Soil type	**PC1**	**PC2**	**PC3**
a. colonization data			
clay-silty	-0.7956	-0.2158	-0.0262
loam	0.1590	0.5196	0.7056
sandy	0.2155	0.4931	-0.7072
gravely	0.5435	-0.6636	0.0356
b. extinction data			
clay-silty	-0.8039	-0.0888	0.0107
loam	0.3328	0.1139	0.8168
sandy	0.4262	-0.6761	-0.3521
gravely	0.2476	0.7225	-0.4569

2.4. Temporal environmental variables

2.4.1. Year and river discharge

I used several temporal factors as predictors in most of the models. I added year as a parameter in case a temporal trend is currently affecting Bank Swallow population dynamics. I also used the maximum river discharge before and during the breeding season, and weather variables such as temperature and precipitation.

River discharge has a direct effect on erosional processes and, therefore, available habitat. High flows are beneficial before the breeding season (August 1 to February 28) because Bank Swallows prefer freshly eroded, vertical banks (Garrison 1999); the accumulation of scree can provide access to predators (Mead 1979a). However, high flows during the breeding season (March 1 to July 31) would be detrimental since undercutting may lead to the sloughing off of an active colony (Humphrey and Garrison 1987) and bankfull flows (approximately 2406 cms) could potentially drown nestlings. Since hydrographs of river discharge throughout the year are characterized by distinct periods of high flows and because one day of exceptionally high flow can have a significant impact on both the habitat and nesting Bank Swallows directly, I used the maximum river discharge (cms) during each of these two time periods, rather than a measure of average discharge over each period. Average discharge may mask the importance of peak events represented by maximum discharge and lead to less variation in river dynamics among years. Both rainfall and snowmelt contribute to the hydrology of the Sacramento River with greater importance likely placed on the former. Peak floods during the snowmelt are much smaller than peak floods during winter storms and have been attributed to the fact that the Sacramento River watershed is at a lower elevation than adjacent rivers that drain higher elevations (CALFED Bay-Delta Program 2000).

I obtained the river discharge data from the USGS Water Resources-California website. I used the river discharge data from the Sacramento River Bend Bridge station because it is located upstream of all the study sites and downstream of the Shasta Dam, and because available data covered the period of the present study. Several water diversion areas for irrigation and flood control located south of this monitoring station have an obvious impact on discharge downstream. However, discharge from the Bend

Bridge station should at least reflect yearly variations in flow for the entire monitoring area.

2.4.2. Weather

Survival and fecundity are both likely to decline during years with colder (or warmer) than average temperatures and/or higher (or lower) than average rainfall. One of the major inferences made in the literature for this relationship is the effect of weather on food resources (Lack 1966, Elkins 1983). Aerial insectivores are especially limited by poor weather conditions because cold, wet weather, for example, not only decreases the number of flying insects but also compromises the birds' foraging ability (Elkins 1983). The direct effect of extreme cold (or heat) and drought on survival also cannot be overlooked. I chose the average of the maximum daily temperatures during the breeding season (i.e. March 1 to July 31) to avoid the inclusion of nightly temperature readings included in average daily temperatures. Bank Swallows feed from dawn until dusk and nightly temperatures would not be relevant, especially since burrows would likely provide relief from colder temperatures. Nightly temperatures may also be more "forgiving" and may not accurately represent the level of heat stress experienced by birds during the day in this area of North America. The precipitation data includes precipitation for the entire twenty-four hour period and may, therefore, not reflect changes in behaviour for either birds or insects if most of the recorded precipitation occurred at night. However, the total amount of precipitation will have an affect on insect populations (i.e. if conditions are too dry, insect larvae may desiccate). The precipitation data represent monthly totals, averaged over the five months when the birds are present. I obtained the weather data from the Northern California Climate Summaries posted on the Western Regional Climate Centre-Desert Research Institute website. I used the weather stations along the river that were closest to each site and had records for the entire monitoring period; they include, from north to south, the stations at Red Bluff, Chico, Willows and Colusa.

2.4.3. Correlation and Principal Components analyses

I included temperature, precipitation and river discharge during the breeding season in the extinction models only (these factors did not apply to the colonization models since colonization implied the colonization of a previously unused site; weather variables cannot have an impact on a non-existent population). Year and river discharge before the breeding season, the only two temporal factors in the colonization models, were significantly, positively correlated ($p=<0.0001$) (Table 3a); it's possible that flows during the months of August and February have been regulated to run at a higher level over the course of the monitoring period. This trend was also present in the extinction data ($p<0.0001$). The only other temporal trend in the extinction data was a decrease in temperature through time ($p<0.0001$), although the strength of the correlation was fairly weak (Table 3b). River discharge before and during the breeding season was significantly correlated ($p=0.006$), which is not surprising since the regulation of flow at one point during the year is likely related to the regulation of flow later in the year. The significant correlation ($p=0.0003$) between river discharge before the breeding season and precipitation during the breeding season is likely spurious since precipitation measured

Table 3. Correlation coefficient (r) between temporal variables in the colonization (n=2697) and extinction (n=459) data sets.

	Year	River discharge (B)	River discharge (D)	Temperature	Precipitation
a. colonization data					
Year	1.00	0.52	NA	NA	NA
River discharge (B)	0.52	1.00	NA	NA	NA
b. extinction data					
Year	1.00	0.54	-0.00	-0.22	-0.02
River discharge (B)	0.54	1.00	-0.13	0.07	-0.17
River discharge (D)	-0.00	-0.13	1.00	-0.19	0.22
Temperature	-0.22	0.07	-0.19	1.00	-0.69
Precipitation	-0.02	-0.17	0.22	-0.69	1.00

B = before the breeding season, D = during the breeding season after the discharge has occurred should be irrelevant. River discharge during the breeding season was negatively related with temperature ($p<0.0001$) and positively related with precipitation ($p<0.0001$). Since temperature and precipitation were negatively related ($p<0.0001$) (as is often the case since it's generally colder on rainy days), the relationships between each of the weather variables and river discharge are self-evident. The strength of the correlation is greatest for an increase in river discharge before the breeding season through time and the negative relationship between temperature and precipitation (Table 3).

I conducted principal components analyses with the temporal variables in the extinction data set only. I did not succeed in reducing the number of variables. In the first analysis, with all five temporal variables, the fifth principal component explained 5.25% of the variance in all variables. In a second analysis, in which I removed year as a factor, the fourth principal component explained 7.69% of the variance in all variables. I decided to include all of the original variables, regardless of correlations, and discuss the implications in analyzing the results.

2.5. Within-population indices

To test the potential importance of within-population dynamics, I tested whether colonization and extinction probabilities depended on the number of burrows (an index of population size) the previous year, at three different distances: within-site, one kilometre and the entire monitoring area. The within-site variable applied to the extinction models only since sites available for colonization would be empty the previous year. For the colonization models, I used the number of burrows within one kilometre; this distance has sometimes been suggested as representing one active colony (Humphrey and Garrison 1987). The importance of this variable may indicate a high level of dispersal within this range. I used the total of all active burrows within the monitoring area in both sets of models in case birds are exchanged along this entire length of river. Because the river is a meandering system, I used radial distances as opposed to an "as the crow flies" along the river distance. Although both variables were significantly correlated in both sets of analyses (Table 4), I chose not to run principal components analyses on these variables since there were only two of them in each set. The strength of the correlation was fairly weak, therefore, there still exists a fair amount of unexplained variation between these two variables to justify using both in my analyses.

Table 4. Correlations between population indices.

	number of burrows within the entire monitoring area
number of burrows within one kilometre (colonization only)	0.22
number of burrows at individual colonies (extinction only)	0.16

2.6. Statistical analyses

I analyzed the colonization and extinction dynamics of Bank Swallow colonies using logistic regression models (SAS LOGISTIC Procedure, 2000). Logistic regression models quantify the colonization and extinction rates as a function of the spatial, temporal, and population variables described above (Morris and Doak 2002). I used the turnover of sites to mark both colonization and extinction events.

Before proceeding with model selection, Burham and Anderson (1998) suggest testing the fit of the "global" model, which is the most parameterized model in the candidate set. I analyzed the fit of the global model, as well as the selected "best" models, using logistic regressions of the observed versus the fitted values for that particular model (McCarthy et al. 2000). Specifically, if a model provides a good fit, the slope of the logistic regression should be equal to one and the intercept should be zero.

2.6.1. Model selection using the information theoretic approach

I used the information theoretic approach to test the importance of suites of variables for extinction and colonization rates. I grouped the variables into 7 categories: temporal trend, land use, bank revetment, soil, river discharge, weather, and population indices (Table 5). Since my objective was to understand Bank Swallow population dynamics with regard to these general categories, testing each variable separately, and in every possible combination, would likely be confusing and futile. Rather, I looked at all of the possible combinations among these "groups" of factors. The 64 models that I fitted to the colonization data and the 128 models that I fitted to the extinction data are listed in Tables 6 and 7, respectively. Variables were normalized to a mean of zero and a variance of one to allow comparison of coefficients and to obtain an average rate of colonization and extinction from the intercepts of the models.

Table 5. The broad categories and the individual variables included in them for both the colonization and extinction models.

Category	**Variables in colonization models**	**Variables in extinction models**
temporal trend	year	year
land use	riparian area developed area distance to grassland	riparian area developed area distance to grassland
bank revetment	old riprap new riprap	old riprap new riprap
soil texture	principal component 1 principal component 2 principal component 3	principal component 1 principal component 2 principal component 3
river discharge	max. cms before breeding	max. cms before breeding max. cms during breeding
weather		avg. max. temp-breeding avg. mo. precip-breeding
population	burrows within 1 km total number of burrows	burrows at site total number of burrows
Total in global model (plus intercept)	**13**	**16**

Table 6. The models that were fit to the data to predict the probability of colonization using logistic regression.

Groups of variables included	**Number of parameters**
NULL-Intercept only	1
soil PCs, land use, year, discharge, riprap, burrows	13
soil PCs, land use, year, discharge, riprap	11
soil PCs, land use, year, discharge, burrows	11
soil PCs, land use, year, riprap, burrows	12
soil PCs, land use, discharge, riprap, burrows	12
soil PCs, year, discharge, riprap, burrows	10
land use, year, discharge, riprap, burrows	10
soil PCs, land use, year, discharge	9
soil PCs, land use, year, riprap	10
soil PCs, land use, discharge, riprap	10
soil PCs, year, discharge, riprap	8
land use, year, discharge, riprap	8
soil PCs, land use, year, burrows	10
soil PCs, land use, discharge, burrows	10
soil PCs, year, discharge, burrows	8
land use, year, discharge, burrows	8
soil PCs, land use, riprap, burrows	11
soil PCs, year, riprap, burrows	9
land use, year, riprap, burrows	9
soil PCs, discharge, riprap, burrows	9
land use, discharge, riprap, burrows	9
year, discharge, riprap, burrows	7
soil PCs, land use, year	8
soil PCs, land use, discharge	8
soil PCs, year, discharge	6
land use, year, discharge	6
soil PCs, land use, riprap	9
soil PCs, year, riprap	7
land use, year, riprap	7
soil PCs, discharge, riprap	7
land use, discharge, riprap	7
year, discharge, riprap	5
soil PCs, land use, burrows	9
soil PCs, year, burrows	7
land use, year, burrows	7
soil PCs, discharge, burrows	7
land use, discharge, burrows	7

cont…

Table 6. The models that were fit to the data to predict the probability of colonization using logistic regression.

Groups of variables included	**Number of parameters**
year, discharge, burrows	5
soil PCs, riprap, burrows	8
land use, riprap, burrows	8
year, riprap, burrows	6
discharge, riprap, burrows	6
soil PCs, land use	7
soil PCs, year	5
soil PCs, discharge	5
soil PCs, riprap	6
soil PCs, burrows	6
land use, year	5
land use, discharge	5
land use, riprap	6
land use, burrows	5
year, discharge	3
year, riprap	4
year, burrows	4
discharge, riprap	4
discharge, burrows	4
riprap, burrows	5
soil PCs	4
land use	4
year	2
discharge	2
riprap	3
burrows	3

Table 7. The models that were fit to the data to predict the probability of extinction using logistic regression.

Groups of variables included	Number of parameters
NULL-Intercept only	1
soil PCs, land use, year, discharge, riprap, weather, burrows	16
soil PCs, land use, year, discharge, riprap, weather	14
soil PCs, land use, year, discharge, riprap, burrows	14
soil PCs, land use, year, discharge, weather, burrows	14
soil PCs, land use, year, riprap, weather, burrows	14
soil PCs, land use, discharge, riprap, weather, burrows	15
soil PCs, year, discharge, riprap, weather, burrows	13
land use, year, discharge, riprap, weather, burrows	13
soil PCs, land use, year, discharge, riprap	12
soil PCs, land use, year, discharge, weather	12
soil PCs, land use, year, riprap, weather	12
soil PCs, land use, discharge, riprap, weather	13
soil PCs, year, discharge, riprap, weather	11
land use, year, discharge, riprap, weather	11
soil PCs, land use, year, discharge, burrows	12
soil PCs, land use, year, riprap, burrows	12
soil PCs, land use, discharge, riprap, burrows	13
soil PCs, year, discharge, riprap, burrows	11
land use, year, discharge, riprap, burrows	11
soil PCs, land use, year, weather, burrows	12
soil PCs, land use, discharge, weather, burrows	13
soil PCs, year, discharge, weather, burrows	11
land use, year, discharge, weather, burrows	11
soil PCs, land use, riprap, weather, burrows	13
soil PCs, year, riprap, weather, burrows	11
land use, year, riprap, weather, burrows	11
soil PCs, discharge, riprap, weather, burrows	12
land use, discharge, riprap, weather, burrows	12
year, discharge, riprap, weather, burrows	10
soil PCs, land use, year, discharge	10
soil PCs, land use, year, riprap	10
soil PCs, land use, discharge, riprap	11
soil PCs, year, discharge, riprap	9
land use, year, discharge, riprap	9
soil PCs, land use, year, weather	10
soil PCs, land use, discharge, weather	11
soil PCs, year, discharge, weather	9

cont...

Table 7. The models that were fit to the data to predict the probability of extinction using logistic regression.

Groups of variables included	**Number of parameters**
land use, year, discharge, weather	9
soil PCs, land use, riprap, weather	11
soil PCs, year, riprap, weather	9
land use, year, riprap, weather	9
soil PCs, discharge, riprap, weather	10
land use, discharge, riprap, weather	10
year, discharge, riprap, weather	8
soil PCs, land use, year, burrows	10
soil PCs, land use, discharge, burrows	11
soil PCs, year, discharge, burrows	9
land use, year, discharge, burrows	9
soil PCs, land use, riprap, burrows	11
soil PCs, year, riprap, burrows	9
land use, year, riprap, burrows	9
soil PCs, discharge, riprap, burrows	10
land use, discharge, riprap, burrows	10
year, discharge, riprap, burrows	8
soil PCs, land use, weather, burrows	11
soil PCs, year, weather, burrows	9
land use, year, weather, burrows	9
soil PCs, discharge, weather, burrows	10
land use, discharge, weather, burrows	10
year, discharge, weather, burrows	8
soil PCs, riprap, weather, burrows	10
land use, riprap, weather, burrows	10
year, riprap, weather, burrows	8
discharge, riprap, weather, burrows	9
soil PCs, land use, year	8
soil PCs, land use, discharge	9
soil PCs, land use, riprap	9
soil PCs, land use, weather	9
soil PCs, land use, burrows	9
soil PCs, year, discharge	7
soil PCs, year, riprap	7
soil PCs, year, weather	7
soil PCs, year, burrows	6
soil PCs, discharge, riprap	8
soil PCs, discharge, weather	8

cont…

Table 7. The models that were fit to the data to predict the probability of extinction using logistic regression.

Groups of variables included	Number of parameters
soil PCs, discharge, burrows	8
soil PCs, riprap, weather	8
soil PCs, riprap, burrows	8
soil PCs, weather, burrows	8
land use, year, discharge	7
land use, year, riprap	7
land use, year, weather	7
land use, year, burrows	7
land use, discharge, riprap	8
land use, discharge, weather	8
land use, discharge, burrows	8
land use, riprap, weather	8
land use, riprap, burrows	8
land use, weather, burrows	8
year, discharge, riprap	6
year, discharge, weather	6
year, discharge, burrows	6
year, riprap, weather	6
year, riprap, burrows	6
year, weather, burrows	6
discharge, riprap, weather	7
discharge, riprap, burrows	7
discharge, weather, burrows	7
riprap, weather, burrows	7
soil PCs, land use	7
soil PCs, year	5
soil PCs, discharge	6
soil PCs, riprap	6
soil PCs, weather	6
soil PCs, burrows	6
land use, year	5
land use, discharge	6
land use, riprap	6
land use, weather	6
land use, burrows	6
year, discharge	4
year, riprap	4
year, weather	4

cont…

Table 7. The models that were fit to the data to predict the probability of extinction using logistic regression.

Groups of variables included	Number of parameters
year, burrows	4
discharge, riprap	5
discharge, weather	5
discharge, burrows	5
riprap, weather	5
riprap, burrows	5
weather, burrows	5
soil PCs	4
land use	4
year	2
discharge	3
riprap	3
weather	3
burrows	3

Parameter estimates in the logistic regression analyses were obtained by maximum likelihood. I compared the models using AIC_c, an extension of AIC adjusted for small sample sizes (Burham and Anderson 1998). AIC is based on maximum log-likelihood values and the number of parameters in the model and, therefore, discriminates against over-parameterized models:

$$AIC_c = -2 \log (\mathscr{L}(\theta)) + 2K + [2K(K+1)/n-K-1]$$

where $(\mathscr{L}(\theta))$ is the likelihood of the parameters given the data, K is the number of parameters in the model, and n is the number of data points (Burham and Anderson 1998). The model with the lowest AIC (or AIC_c) value is best supported by the data. One of the great advantages of using AIC is that it allows you to rank models from best to worst using the difference in AIC values and gives you an indication of the relative support for different models. No such formal framework to compare multiple models exists using classical hypothesis tests. Models that may be equally valid using hypothesis testing, where models are individually compared to a null model, can be ruled out based on their AIC rankings. However, models may be equally valid using AIC values as well. If the difference between a candidate model and the "best" model is two or less, both models must be considered as the "best" approximating models. Models with AIC values within two to four of the best model show weak evidence that they are not the best models, whereas models with AIC values within four to ten of the best model show increasingly strong evidence that they are not the best models. If the AIC difference is greater than ten, there is very strong evidence that that model is not the best model (Burnham and Anderson 1998).

I estimated both model selection uncertainty and the contribution of each category of factors to the models using Akaike weights (Burham and Anderson 1998). Akaike weights describe the relative likelihood of a model, or the weight of evidence in favour of a model being the actual best model (Burham and Anderson 1998); basically, it is the relative likelihood of a model given the data and the set of candidate models. I assessed the relative contribution of each group of factors by adding the Akaike weights for all of the models containing that group of variables (Burham and Anderson 1998). For example, to assess the contribution of the weather factors, I added the Akaike weights of all the models that had both temperature and precipitation as variables. If a group of variables had a combined weight of more than 0.25, I assumed that it was an important group. This is an arbitrary cut off; since these numbers represent a relative weight, readers may draw their own conclusions.

To assess the contribution of each individual variable, I multiplied the standardized coefficients, obtained in each logistic regression model, by the weight of that model and summed these values over all candidate models within ten AIC_c of the best model. I applied the same principle to the standard error of each coefficient and multiplied this model-averaged standard error by two to obtain a confidence limit around the coefficient. I used these model-averaged coefficients to make predictions under different ecological and management scenarios. If model-averaged confidence limits for a factor did not overlap zero, I concluded that there was support for a positive or negative relationship with colonization or extinction. Otherwise, I concluded that a factor's effect could not be determined, even if it was part of a well-supported category of factors.

To test the importance of error in linking colonies and landscape data, I created reduced data sets in which I removed all of the most questionable sites (i.e. sites in areas of active meandering, or where factors such as land use or soil had to be extrapolated; see Appendix B for the location and reason behind the removal of each site). I ran all of the above analyses a second time using these reduced data sets in case any signal from the land use, soil or riprap factors would be made clearer when the more questionable sites were removed. Since the importance of these groups of factors did not increase appreciably, and because their influence on the colonization and extinction dynamics is undetermined in either case (see Results), I chose to present the results from the full data set only. In addition, the reduced data set was biased towards the later years of the data because most of the sites that I found questionable to place onto the GIS layers were from the earlier part of the data set. Therefore, the full data set depicts a clearer representation of the temporal variability. I present relevant exceptions in the Results section.

2.7. Metapopulation model

I used model-averaged colonization and extinction parameters to model metapopulation dynamics using an internal colonization model (Levins 1969):

$$\Delta f_t = i f_t(1-f_t) - p_e f_t$$

where f_t is the fraction of sites that are occupied in year t, i is a constant that measures how the probability of local colonization of empty sites increases with the number of available sites ($i = p_c/f$), p_c is the probability of local colonization and p_e is the probability of local extinction. Setting the equation to zero, the fraction of occupied sites at equilibrium, F*, becomes:

$$F^* = 1 - p_e/i$$

I then used exploratory models of statistically supported factors to assess the fraction of occupied sites under various conditions of climate change.

3. Results

3.1. Model fit

The global colonization model fit the data reasonably well. In a logistic regression analysis of the observed versus expected values from the global model, the parameter estimate and confidence limits for the intercept and the slope were -0.0674 (-0.8498, 0.715) and 0.9995 (0.6375, 1.3615), respectively. The global extinction model also fit the data. The estimate and confidence interval of the intercept was 0.00308 (-0.2123, 0.2185) and the estimate and confidence interval of the slope was 0.9891 (0.7171, 1.2611). All of the intercepts overlapped zero and all of the slopes overlapped one for the selected best models, the models within ten AIC_c, for both the colonization and extinction data.

3.2. Colonization model selection

Overall, I found strong support only for increased colonization probability over time. The "best" model, the model with the lowest AIC_c value, indicated that the probability of colonization increased over time and with maximum river discharge before the breeding season. Since the model with just year as the predictor variable was within two AIC_c of the best model it could not be ruled out as the best model. The AIC_c values and Akaike weights of all the models within ten AIC_c of the best model are listed in Table 8.

Table 8. The results of the logistic regression models predicting the probability of colonization, including the number of parameters, the AIC_c value, the Akaike weight, and the AIC_c difference between each model and the "best" model.

Model	**Parameters**	**AIC_c**	Δ_i	w_i
year, discharge	3	1671.558	0.000	0.2993
year	2	1672.360	0.802	0.2003
year, discharge, land use	6	1674.078	2.520	0.0849
year, discharge, riprap	5	1674.530	2.972	0.0677
year, burrows	4	1674.939	3.381	0.0552
year, discharge, burrows	5	1675.032	3.474	0.0527
year, riprap	4	1675.329	3.771	0.0454
year, land use	5	1675.397	3.839	0.0439
year, discharge, land use, riprap	8	1676.737	5.179	0.0225
year, discharge, soil PCs	6	1677.231	5.673	0.0175
year, discharge, land use, burrows	8	1677.597	6.039	0.0146
year, land use, burrows	7	1677.893	6.335	0.0126
year, burrows, riprap	6	1677.943	6.385	0.0123
year, soil PCs	5	1678.015	6.457	0.0119
year, discharge, burrows, riprap	7	1678.045	6.487	0.0117
year, land use, riprap	7	1678.071	6.513	0.0115
year, discharge, land use, soil PCs	9	1679.795	8.237	0.0049
year, discharge, riprap, soil PCs	8	1680.144	8.586	0.0041
year, discharge, land use, riprap, burrows	10	1680.290	8.732	0.0038
year, land use, riprap, burrows	9	1680.589	9.031	0.0033
year, burrows, soil PCs	7	1680.603	9.045	0.0033
year, discharge, burrows, soil PCs	8	1680.714	9.156	0.0031
year, riprap, soil PCs	7	1680.923	9.365	0.0028
year, land use, soil PCs	8	1681.060	9.502	0.0026

Δ_i=AIC_c difference between model i and the best model, w_i=Akaike weight for model i.

The Akaike weights for the individual models were not exceptionally strong. The best model, with year and discharge as predictor variables, was only about one and half times as likely as the next best model with just year as the predictor variable. However, the best model was over one hundred times more likely than the last of the twenty-four models selected. The summed Akaike weights for groups of variables supported the importance of a temporal trend (0.9970) and perhaps river discharge (0.5927) with less emphasis on the surrounding land use (0.2088), riprap (0.1893), the number of burrows at different distances (0.1763) and soil (0.0556). The value of the weighted standardized coefficient for year (Table 9) further illustrated the importance of a temporal trend in the colonization dynamics. However, the role of river discharge before the breeding season and of all the other variables in the analyses, were not strongly supported because all of their confidence intervals overlapped zero.

Table 9. The weighted standardized coefficients and their confidence limits in order of their influence on the colonization rate calculated from the best models. The 95% confidence limits were calculated from the weighted standard errors of the variables.

Variable	**coefficient**	**lower C. L.**	**upper C. L.**
Intercept	-2.2851	-2.4214	-2.1488
Year	0.3003	0.1514	0.4493
Max. river discharge (before)	0.0703	-0.0135	0.1540
Distance to grass	0.0284	-0.0021	0.0588
New riprap	-0.0110	-0.0364	0.0143
Number of burrows (m)	-0.0108	-0.0371	0.0156
Developed land	-0.0076	-0.0544	0.0391
Old riprap	0.0072	-0.0170	0.0314
Number of burrows (1 km)	0.0070	-0.0159	0.0298
Soil PC1	-0.0019	-0.0086	0.0048
Riparian land	-0.0008	-0.0430	0.0413
Soil PC3	-0.0005	-0.0071	0.0062
Soil PC2	0.0002	-0.0066	0.0070

m represents the entire monitoring area used in these analyses

3.3. Extinction model selection

I found strong support for relationships between river discharge, the number of burrows, and weather and extinction. Out of the one hundred and twenty eight models that I fit to the extinction data, nineteen cannot be entirely ruled out as the selected "best" model (Table 10). There was strong support for the first three models, all of which included river discharge, the number of burrows, and weather factors as predictor variables. The Akaike weights indicated that the best model, with river discharge, the number of burrows, weather, and riprap was only a little over one and half times more likely than the second model without riprap, and over twice as likely as the third model that included the additional variable of year. However, the best model was almost one hundred times more likely than a model that did not include the number of burrows (third last model selected in the group of nineteen) and over one hundred times more likely than a model with just discharge and the number of burrows (second last model selected) or discharge and weather (last model selected). Therefore, I concluded that all three groups of variables, river discharge, weather, and population indices, in combination, are important to the extinction dynamics of Bank Swallow colonies along the Sacramento River.

I explored the role of these variables further by examining their summed Akaike weights and the weighted standardized coefficients. The Akaike weight for river discharge (0.9966), the number of burrows (0.9866), weather (0.9753), riprap (0.6312) and year (0.3023), are all fairly high and indicated a strong influence on the extinction rate. The summed Akaike weights for soil (0.1502) and land use (0.0568) showed that

Table 10. The results of the logistic regression models predicting the probability of extinction, including the number of parameters, the AIC_c value, the Akaike weight, and the AIC_c difference between each model and the "best" model.

Model	**Parameters**	**AIC_c**	**Δ_i**	**w_i**
discharge, burrows, weather, riprap	9	582.019	0.000	0.3433
discharge, burrows, weather	7	583.130	1.111	0.1970
discharge, burrows, weather, riprap, year	10	583.806	1.787	0.1405
discharge, burrows, weather, year	8	584.700	2.681	0.0898
discharge, burrows, weather, riprap, soil	12	585.417	3.398	0.0628
discharge, burrows, weather, soil	10	586.554	4.535	0.0356
discharge, burrows, weather, riprap, year, soil	13	587.450	5.431	0.0227
discharge, burrows, weather, riprap, land use	12	587.593	5.574	0.0212
discharge, burrows, weather, year, soil	11	588.486	6.467	0.0135
discharge, burrows, weather, land use	10	588.880	6.861	0.0111
discharge, burrows, weather, riprap, year, land use	13	589.264	7.245	0.0092
discharge, burrows, riprap, year	8	589.987	7.968	0.0064
discharge, burrows, riprap	7	589.999	7.980	0.0064
discharge, burrows, weather, year, land use	11	590.484	8.465	0.0050
discharge, burrows, year	6	591.021	9.002	0.0038
discharge, burrows, weather, riprap, soil, land use	15	591.074	9.055	0.0037
discharge, weather, riprap	7	591.159	9.140	0.0036
discharge, burrows	5	591.691	9.672	0.0027
discharge, weather	5	591.940	9.921	0.0024

Δ_i=AIC_c difference between model i and the best model, w_i=Akaike weight of model i.

these factors are of less importance. The weighted standardized coefficients, and the confidence limits for the variables within these groups, are listed in Table 11. Individually, temperature appeared to have the greatest effect on the extinction rate, indicating that the probability of extinction increased with colder temperatures during the breeding season. The extinction rate also appeared to increase with maximum river discharge before the breeding season and decreased with the number of burrows present at a site the previous year and with the average amount of precipitation during the breeding season in the previous year. The confidence limits of all other variables overlapped zero, which made their contribution to the extinction rate ambiguous.

Table 11. The weighted standardized coefficients and their confidence limits in order of their influence on the extinction rate, calculated from the best models.

Variable	coefficient	lower C. L.	upper C. L.
Intercept	0.3496	0.1494	0.5498
Temperature	-0.5163	-0.8317	-0.2009
River discharge (before)	0.4932	0.2497	0.7366
Number of burrows (site)	-0.3705	-0.5904	-0.1506
Precipitation	-0.3503	-0.6424	-0.0582
Old riprap	0.1079	-0.0255	0.2413
Number of burrows (m)	0.0972	-0.1929	0.3873
New riprap	-0.0921	-0.2175	0.0333
River discharge (during)	0.0535	-0.2090	0.3161
Year	0.0223	-0.0508	0.0954
Soil PC2	0.0220	-0.0077	0.0518
Soil PC1	0.0096	-0.0186	0.0379
Riparian land	0.0067	-0.0084	0.0218
Distance to grass	0.0041	-0.0076	0.0158
Soil PC3	-0.0037	-0.0343	0.0270
Developed land	-0.0023	-0.0185	0.0138

m represents the entire monitoring area used in these analyses

3.4. Full versus reduced data sets

I obtained very similar results using both data sets to predict the probability of colonization with one notable exception. The importance of the number of burrows increased substantially (0.6592), leading to a decrease in the probability of colonization with an increase in the number of active burrows within the entire monitoring area the previous year. It may be reasonable to assume that when the overall number of active burrows is up, colonizing birds are very likely more attracted to some of these larger colonies than they are to empty, available sites. However, since the reduced data is biased towards the later years of the data and therefore, towards lower abundances, this relationship likely levels off at high abundances and may explain why the signal deteriorated in the full data set.

The general findings were also similar for both data sets predicting the probability of extinction. The only notable exception was a decrease in the importance of riprap (0.2190). However, since the confidence intervals for both of the riprap variables overlapped zero, using either the full or reduced data set, I could not determine the effect of these variables on the extinction dynamics.

3.5. Exploratory models to depict changes in metapopulation dynamics

This population did not represent a stable metapopulation. Although the average colonization rate exceeded the average extinction rate, the confidence intervals for the two rates overlapped (Table 12). I calculated a 95% confidence interval using model-averaged standard errors for the intercept. It is possible, under current conditions, that the extinction rate could exceed the colonization rate, driving the entire population to extinction. The equilibrium fraction of sites occupied predicted from the average rates (0.06) is less than what was actually observed during monitoring (0.15). Thus, the metapopulation has not yet reached equilibrium, there were fluctuations in the rates, or I have not accurately captured the average rates. However, when I explored all combinations within the confidence limits of the average rates, the fraction of occupied sites varied between -0.15 and 0.24, overlapping the average occupancy rate observed during the study.

Table 12. The estimate and confidence limits of the average maximum colonization and extinction rate using the weighted coefficients and their weighted standard errors.

	Maximum colonization rate	Extinction rate
average coefficient	0.624	0.587
lower confidence limit	0.551	0.537
upper confidence limit	0.706	0.634

In addition, I explored the consequences of changes in statistically-supported factors that are at least partially under human control: river discharge, controlled at Shasta Dam, and temperature and precipitation, both predicted to change due to anthropogenic climate change. Although it is extremely difficult to predict the exact course of future weather conditions, it is possible to examine the effect of various scenarios on the equilibrium metapopulation. I used the predictions of global climate change models (Gleick 1987, Walther et al. 2002) to examine the effects of shifts in precipitation and temperature patterns on the equilibrium metapopulation. Global climate models consistently predict a general increase in the overall temperature for California (Gleick 1987, U. S. Environmental Protection Agency 2000, Intergovernmental Panel on Climate Change 2001, Krotz 2002, Snyder et al. 2002, Walther et al 2002, Union of

Concerned Scientists 2003). Changes will be greatest during the winter months and could range between a 0.3 to a 1.0 degree Celsius increase per decade in the Central Valley (Walther et al. 2002). Precipitation predictions are more variable, but most models predict that precipitation will increase in the winter, leading to more frequent flooding along the river, and will decrease in the summer, leading to an increase occurrence of drought (Gleick 1987, U. S. Environmental Protection Agency 2000, Intergovernmental Panel on Climate Change 2001, Krotz 2002, Snyder et al. 2002, Walther et al 2002, Union of Concerned Scientists 2003).

I used various combinations of a zero, 0.3, 0.7 and 1.0 degree Celsius increase per decade in temperature, a zero, ten and twenty percent decrease in summer precipitation per decade, and a zero, ten and twenty percent increase per decade in river discharge before the breeding season. After adjusting colonization and extinction rates for these changes, I calculated the equilibrium metapopulation ten and twenty-five years into the future. At ten years into the future, most scenarios (22 out of 31) predicted a larger fraction of occupied sites at equilibrium than that predicted from the average rates, but nine scenarios predicted a lower fraction. Conditions appeared to deteriorate slightly twenty-five years into the future as eleven of the scenarios predicted a lower fraction of sites, seven of which predicted extinction (fractions equal to zero or less) (Table 13). At the lowest predicted temperature change of 0.3 Celsius per decade, the negative effects of changes in river discharge and/or precipitation begin to outweigh the positive effects of a change in temperature.

Table 13.. The fraction of occupied sites at equilibrium ten and twenty-five years into the future using the average weighted coefficients and different combinations of predicted trends in climate variables.

Conditions			fraction of sites occupied	
actual average from data			0.15	
predicted from models			0.06	
Temperature (°C)	**Precipitation**	**River discharge**	**10 years**	**25 years**
same	down 10%	same	0.03	-0.01
same	down 20%	same	0.01	-0.07
same	same	up 10%	0.03	-0.02
same	same	up 20%	0.00	-0.09
up 0.3	same	same	0.12	0.19
up 0.3	down 10%	same	0.09	0.12
up 0.3	down 20%	same	0.06	0.05
up 0.3	same	up 10%	0.08	0.11
up 0.3	same	up 20%	0.05	0.03
up 0.3	down 10%	up 10%	0.06	0.04
up 0.3	down 20%	up 10%	0.03	-0.03
up 0.3	down 10%	up 20%	0.03	-0.04
up 0.3	down 20%	up 20%	0.00	-0.10
up 0.7	same	same	0.17	0.34
up 0.7	down 10%	same	0.14	0.27
up 0.7	down 20%	same	0.11	0.20
up 0.7	same	up 10%	0.13	0.26
up 0.7	same	up 20%	0.10	0.18
up 0.7	down 10%	up 10%	0.11	0.19
up 0.7	down 20%	up 10%	0.08	0.12
up 0.7	down 10%	up 20%	0.07	0.11
up 0.7	down 20%	up 20%	0.05	0.04
up 1.0	same	same	0.22	0.46
up 1.0	down 10%	same	0.19	0.39
up 1.0	down 20%	same	0.16	0.33
up 1.0	same	up 10%	0.18	0.38
up 1.0	down 10%	up 10%	0.15	0.31
up 1.0	same	up 20%	0.16	0.32
up 1.0	down 20%	up 10%	0.13	0.24
up 1.0	down 10%	up 20%	0.12	0.23
up 1.0	down 20%	up 20%	0.10	0.16

4. Discussion

Bank Swallows along the Sacramento River in California did not conform to a simple metapopulation structure. Simple models assume that all patches are equal and that the probabilities of colonization and extinction are constant through time and space (Hanski 1997). In my study, the colonization rate tended to increase over time and the extinction rate depended on the number of burrows at the site the previous year, indicating the possibility of ecological differences among sites. The probability of extinction also varied with weather and river discharge. These fluctuating rates may explain why this metapopulation may not be at equilibrium. Below, I discuss possible mechanisms for different correlates of colonization and extinction dynamics.

4.1. Temporal trend

The cause for a temporal increase in the probability of colonization is unknown, but could be related to a decrease in available habitat, leading to a greater number of smaller colonies. For example, in assuming that a site occupied in one year was available in all years, I also assumed that sites did not change from one year to the next. If half of an existing site were riprapped, the length of available bank at that site would be shorter, thereby accommodating a smaller number of burrows. If this were to occur at a number of sites, and if the number of birds in one year along the entire Sacramento River were to return the next year, following such habitat change, they would need to distribute themselves across a greater number of smaller colonies. However, simple regression analyses of the number of colonies through time and the size of colonies through time showed no significant trends (p=0.85 and p=0.86, respectively). Alternatively, this temporal trend in the probability of colonization may simply reflect unrecorded changes in site quality such as the removal of accumulated scree at the bottom of banks by natural hydrological processes, meaning that a bank which became colonized later in time might not have been attractive in previous years, contrary to my assumption that all sites were equally attractive in all years of the monitoring period. The number of colonizations that occurred on "new" sites, as opposed to sites that had been occupied at some time in the past, did show a significant linear increase in time (p=0.05, r=0.63).

4.2. Weather variables

The effect of temperature and precipitation on bird populations has been well documented (Lack 1966, Elkins 1983). Weather factors have been linked to several demographic variables as well as overall population abundance. Cold, wet weather caused increased mortality of Tanagers (*Piranga* sp.) and other aerial-foraging species in New Hampshire (Holmes et al. 1986), and a decrease in hatching success of Greenshanks (*Tringa nebularia*) in North-west Scotland (Thompson et al. 1986). Also in Scotland, hens (*Capercaillie* sp.) reared more chicks during years of warmer spring temperatures with fewer rain days (Moss et al. 2001), while in the grasslands of North America, Vesper Sparrows (*Pooecetes gramineus*), Horned Larks (*Eremophila alpestris*) and Western Meadowlarks (*Sturnella neglecta*) abandoned nests during a period of extremely hot weather (George et al. 1992). Since my study was purely correlative, processes are strictly inferred based on general knowledge about bird populations. Nonetheless, I will speculate about possible mechanisms by which temperature and precipitation could affect colonization and extinction rates.

High or low temperatures could plausibly lead to an increase in extinction rates through direct effects on individual birds. The temperature range over which normal activities can be maintained without an increase in metabolic energy is called the thermoneutral zone (Gill 1990). At temperatures above or below this thermoneutral zone, animals must spend energy to maintain their body temperature. For example, in cold weather, birds may achieve this by shivering. Alternatively, an animal may seek refuge, such as roosting in burrows, and, thereby, suspend other activities, such as feeding, until conditions improve. Whether a response to temperature conditions outside the thermoneutral zone is behavioural or physiological in nature, cold and heat stress generally cost energy. Over the course of this study, Bank Swallows may have experienced periods of unfavourable temperatures leading to an overall decrease in the survival rates of either or both adults and fledglings, resulting in an increase in the probability of extinction at lower temperatures.

Lower than average temperatures would also have implications for the physiological requirements of invertebrate prey, and colder temperatures may have led to a decrease in their abundance in certain years. Insect activity increases with increasing temperature (Haskell 1966, Taylor 1963) and trap catches show an increase in insect abundance and species richness with temperature (Taylor 1963, Turner 1983). These studies were conducted in temperate climates and may not be as relevant to the Mediterranean climate of the Central Valley of California, where it is generally hot and dry in the summer. However, insects are adapted to local conditions and extreme fluctuations in weather have the potential to affect the level of insect activity. Therefore, not only would Bank Swallows require a greater amount of food to maintain normal metabolic requirements due to colder temperatures, but they may also need to spend additional energy in acquiring it if food resources are reduced. Bank Swallows tend to make longer foraging trips when food conditions are poor, and foraging distances have been negatively correlated with both insect abundance and temperature (Bryant and Turner 1982). It is possible that adults must forage greater distances or for longer periods during bad weather at a cost to both themselves and developing fledglings. Bank Swallows spend more metabolic energy in poor weather, likely related to changes in foraging strategy and food supply (Westerterp and Bryant 1984). High stress during cold spring weather, when insects have not yet accumulated, may be the reason that mortality declines over the breeding period (Mead 1979b).

Bank Swallows also delay breeding during periods of bad weather (Cowley 1979). Svensson (1986) detected a critical temperature range below which temperatures deterred the onset of egg-laying and suggested that the abundance of flying insects was likely the critical factor. This could lead to declines in overall population growth rate since productivity also declines during the breeding season (Hjertas et al. 1988) and the survival of juveniles is often linked to the date of fledging (Cowley 1979, Persson 1987). However, even though Turner (1982) found that foraging rates were depressed during bad weather, to the point where females could not meet their daily energy requirements, she suggested that Bank Swallows may be less likely to delay breeding, compared to some swallow species, since both the male and female Bank Swallow share in the incubation duties.

Variation in precipitation can also lead to fluctuations in bird population size. Dry years during the monitoring period may have reduced population size, increasing the probability of extinction. Some of the studies described above link productivity to both temperature and precipitation (Westerterp and Bryant 1984, Holmes et al. 1986, Thompson et al. 1986, Moss et al. 2001). Additionally, breeding is often delayed after dry winters in Mediterranean areas while wet winter and spring conditions lead to an increase in populations (Elkins 1983). The annual variation in abundance of several bird species in Wisconsin and Michigan were correlated with a period of severe drought (Blake et al. 1989), while the density of six common bird species declined significantly during a period of drought in North Dakota (George et al. 1992). In examining the long-term declines of winter resident warblers in Puerto Rico, Faaborg and Arendt (1989) found that the period with the lowest recorded populations corresponded to severe drought conditions on the breeding grounds. Located along a constant water source, Bank Swallows are not likely to experience the effects of low precipitation directly. However, the region has experienced a period of drought over the course of the study, which may have had an impact on the insect prey community. In warmer climates, insect development is often limited by high temperatures and moisture stress. For example, hot, dry conditions in the summer reduce populations of aphids (Drake 1994). Several studies have linked population declines of European Bank Swallows (Sand Martins) to drought conditions on their wintering grounds in Africa, although, the direct mechanism of decline was not determined (Cowley 1979, Persson 1987, Bryant and Jones 1995, Szep 1995).

Bird populations can be limited by prey availability (Lack 1966, Elkins 1983, Martin 1987, Boutin 1990, Stuart Simons and Martin 1990, Rodenhouse and Holmes 1992), and a relationship to food resources is often inferred from correlations between weather conditions and population fluctuations or demographic parameters (Lack 1966, Elkins 1983, Holmes et al. 1986, Thompson et al. 1986, Greenwood and Baillie 1991). More elaborate studies have measured both the abundance of prey as well as recorded climate conditions and related them to variation in bird populations. The density of farmland birds in Scotland was significantly related to insect abundance, agriculture and climate (Benton et al. 2002). In a study of over-wintering warblers in India, rainfall affected both vegetation and arthropod production, which were then associated with differences in body mass and population density of warblers (Madhusudan and Price 1996). At times, it is likely impossible to separate the effects of food and weather due to the strong interaction between the two (Rodenhouse and Holmes 1992). It is also difficult to separate the effects of precipitation and temperature since these variables are often correlated. The general pattern of all of these studies also illustrates that populations appear to be limited by cold, wet weather in temperate climate, and hot, dry weather in arid and Mediterranean climates.

4.3. River discharge

Assuming that maximum river discharge is positively correlated with erosion, it is not surprising that the probability of extinction increased with river discharge. Sites used the previous year may wash out, and returning birds may choose to join nearby colonies or establish new colonies nearby. However, if the latter were true, maximum river discharge should have influenced the probability of colonization as well as extinction. Perhaps some banks used the previous year simply slough off in the first year of high discharge and it is not until this accumulated scree is washed away during consecutive years of erosion that a bank becomes suitable once more for colonization. Sites with an accumulation of scree at the base are generally avoided by Bank Swallows (Ghent 2001) as it provides easy access to predators from below (Mead 1979a).

4.4. Within-population indices

Although the number of burrows the previous year did not play a major role in colonization dynamics, larger colonies were less prone to extinction. This may either reflect a greater probability of one bird returning to an existing site when more birds occupy it, or it could be indicative of greater site fidelity to more favourable areas. Bank Swallows return more consistently to successful breeding sites (Freer 1979). Alternatively, these results may indicate that within-site dynamics are important to understanding the dynamics of this threatened population. For example, larger colonies would be less susceptible to extinctions through demographic, genetic, and environmental stochasticity. Also, population growth rates within these smaller colonies may be lower, compared to larger colonies, due to inefficiencies related to group foraging and predator defense at smaller colonies.

4.5. Land use

I have shown that the surrounding land use within the foraging range is not appreciably relevant to colonization and extinction dynamics. Although the data for these factors were somewhat noisy due to the displacement of sites, these findings reflect the general consensus of researchers in the area. Bank Swallows nest adjacent to a variety of vegetation types (Humphrey and Garrison 1987, Garrison et al. 1987). However, the importance of the surrounding land use cannot be ruled out based solely on these analyses. It is possible that responses to surrounding land use extend beyond the 200 metre foraging range that I used in my analyses. In addition, data to conduct finer grain analyses that would include transitions within the broad land use groups that I used (i.e. crops vs. orchards vs. fallow within the developed category and gravel vs. willow vs. mature forest within the riparian category) were not available.

4.6. Soil

I was surprised that soil did not play a larger role in the colonization process. It could be that soil would differentiate more between used and unused sites. As I only looked at sites that have had colonies at some point in time, the variation within these colonies may not be great enough to make an overall difference on colonization and extinction processes. It is also possible that soil analyses conducted for agricultural purposes (<0.5 metres deep) are not indicative of soil conditions for the entire site since the average height of banks where colonies are found is 3.3 m ± 1.7 SD and the average distance of the top burrow to the bank top is 0.7 m ± 0.1 SD (Humphrey and Garrison 1987). In my general observations of the river, the soil at the top of most colonies looked fairly consistent throughout the bank. There is also the issue of the displacement of sites. However, the soil classification should have been fairly accurate; although soil texture differed among sites, it was uniform across large areas of the landscape.

4.7. Riprap

I was also surprised that riprap did not play a larger role in both colonization and extinction rates. Again, it is possible that the displacement of sites may have introduced a level of noise to these data. I included all riprap within 287 metres of a site to ensure that, if riprap were installed at a site, it would be included, even if the placement of the site was inaccurate. This may have had the effect of including riprap on sites when in actuality it was placed over two hundred metres away. It is also possible that, even though riprap has destroyed colonies along the Sacramento River since the 1960s (Schlorff 1997) and was instrumental in the reduction of habitat and population loss across the state (see Introduction), it has not had a detectable effect on the Sacramento River population within this period of monitoring. Colonies were lost due to bank protection between 1986 and 1988 (Garrison 1991, as cited in Schlorff 1997), but most new bank protection projects in the early to mid nineties were installed downstream of major colonies (Schlorff 1997). More accurate data of the exact timing of the installation of riprap would increase the efficiency of these analyses.

4.8. Other factors

Other factors, not measured in this study, could also be important to the probability of colonization, although some of these may be difficult to measure, at least on a regular basis. For example, if an activity requiring heavy machinery occurred along the bank at the time of arrival, a potential colonizer may chose to keep looking, regardless of the physical conditions of the bank itself. Perhaps one of the greatest attractors for a colonial species is the presence of other birds. However, that still leaves the question of what attracted those initial colonizers to that particular site along the river. Bank height and slope have been positively correlated with the number of burrows (Humphrey and Garrison 1987) and are likely important factors in the colonization process, but data were not available for my analyses.

5. Management implications

It is difficult to determine whether this population is viable based on my results. The confidence limits around the average rates of colonization and extinction indicate the possibility of metapopulation extinction, a system that is at equilibrium, and a system that is not at equilibrium. Overall, climate change models suggest the continuing existence of Bank Swallows in California. However, the risk of extinction due to climate cannot be dismissed, especially since current temperature trends seem to be opposite to those predicted from most climate change models. A regression analysis using temperature data over the past 97 years (Northern California Climate Summaries posted on the Western Regional Climate Centre-Desert Research Institute website) indicated a significant decline in spring/summer temperature (i.e. temperature over the breeding season; $p=0.0007$, $r=0.34$).

The only potential Bank Swallow management directives related to this study involve riprapping of the riverbank, changing river flow, and altering the surrounding land use. Although the presence or absence of riprap did not appear to play a significant role in the colonization and extinction of Bank Swallow colonies over the course of this monitoring period, it could not be entirely ruled out based on these analyses. Also, common sense suggests that there is a limit as to how much of the existing river can be covered up and still maintain a healthy Bank Swallow population. If no eroding banks are exposed for colonization, Bank Swallows cannot occupy the river. There is currently approximately 102 km of riprap within the Bank Swallow monitoring area (derived from GIS layers) and Schlorff (2001) claims that if all planned new bank protection sites were riprapped, the habitat could be severely affected. As proposed in a 1992 Bank Swallow Recovery Plan, it would be extremely beneficial to investigate where along the river this riprap has been proposed and whether or not it will affect sites used over the course of the monitoring period:

> "In order to accomplish the goals of Bank Swallow habitat protection and species recovery, the Department recommends that a critical review and analysis of existing and proposed bank stabilization projects be initiated. The heart of Bank Swallow conservation and recovery strategy must include the option to avoid impacts to habitat. An important step in this process will be the critical evaluation of all proposed projects that will impact known Bank Swallow colonies and potential habitat" (California Department of Fish and Game 1992, p.9).

Earlier studies indicated that there is a surplus of habitat so that not all available banks are occupied every year (Garrison 2002). It would be worthwhile to determine the role of this surplus by documenting the available versus the used habitat each year. Metapopulations require a surplus of habitat and if this surplus disappears, it may become necessary to create habitat more quickly than natural erosion rates allow. Presumably, if most land adjacent to agricultural areas is eventually riprapped and becomes unavailable (worst case scenario), natural, protected areas will have to provide the bulk of Bank Swallow habitat. If these natural areas do not consistently provide habitat every year, due to the sloughing of banks, increasing river discharge before the breeding season could wash away scree along banks in these areas (alternatively, it could just create more sloughing). Hopefully, this would ensure that steep, vertical banks are available in all natural areas year after year. This would put excessive strain on riprap along agricultural areas, but this may be negated by more upkeep of the bank revetment itself.

Another potential problem would involve an increase in the repeated use of sites, leading to an increase in parasite load within the burrows. In two separate studies, on the effect of parasites on Bank Swallows, ectoparasites, in general, decreased the body mass of nestlings (Santos Alves 1997), while ticks, in particular, reduced the reproductive success of adults (Szep and Møller 1999). However, sometimes blood loss is not sufficient to actually kill nestlings (Whitworth and Bennett 1992) and the cost of parasitism in colonial species may be countered by an increased investment in antiparasite defenses (Møller et al. 2001). Also, although burrows are reused, the actual nesting material is replaced at the start of each breeding season (Garrison 1999), which may reduce the potential increase in parasite loads if burrows are used year after year. Generally, a better understanding of the processes of erosion along the Sacramento River and how quickly new banks are created would help elucidate long term habitat needs. Plans to restore natural processes will undoubtedly benefit these Bank Swallows but it would be valuable to link any current studies of erosional processes to population trends.

With respect to the surrounding land use, it does not appear that restoration of natural habitat will interfere with the current population or that planting herbland cover as opposed to riparian tree species is warranted at this time. However, the importance of the surrounding land use also cannot be ruled out based solely on my analyses.

In addition to the re-introduction of natural hydrological processes and the maintenance of existing sites (or at least the number of available sites), further, in-depth study of this population is warranted. It would be beneficial to determine exactly how weather factors affect this population. Because temperature and precipitation were highly correlated, I could not separate these effects. However, given the climate of the area, it is likely that precipitation and the occurrence of drought played a greater role than a decline in temperature. As precipitation predominantly occurs before the breeding season, including precipitation data during this time period (as opposed to simply when the birds are present) may better reflect the effect of drought conditions on invertebrate prey. Obtaining Bank Swallow demographic data from a few key sites, along with data on insect availability and weather would be ideal, given personnel time and adequate funding. Based on such findings, alterations in pesticide use may be important in years of drought in order to maintain prey populations.

Determining the extent to which colonies interact by measuring dispersal would help validate whether or not this population is actually a metapopulation or simply reflects a population in a patchy habitat. Return rates (barring mortality) would likely be high given the level of site fidelity in other studies, but determining them would depend on capturing most birds along the entire 160 km stretch of the river where most colonies are located. Mist netting along a flowing river has inherent difficulties. Most demographic studies of Bank Swallows are conducted in sand quarries where researchers are able to capture birds as they exit burrows at first light.

In the meantime, determining what influences within-population dynamics, the number of breeding pairs within a colony (determined from burrow counts), is a valuable avenue for future research. For example, models that describe trends at individual colonies may help explain why there are yearly fluctuations in the entire population. One could examine the relative importance of density independent, density dependent with a time lag, and random noise models (with and without temporal variables) using the number of burrows at individual sites that have been active for three consecutive years or more.

References

Akçakaya, H. R., M. A. McCarthy, and J. L. Pearce. 1995. Linking landscape data with population viability analysis: management options for the helmeted honeyeater, *Lichenostomus melanops cassidix*. Biological Conservation **73**:169-176.

Akçakaya, H. R., and J. L. Atwood. 1997. A habitat-based metapopulation model of the California Gnatcatcher. Conservation Biology **11**:422-434.

Askins, R. A. 2002. Restoring North America's Birds, Lessons from Landscape Ecology. Second Edition. Yale University Press, New Haven.

Benton, T. G., D. M. Bryant, L. Cole, and Q. P. Crick-Humphrey. 2002. Linking agricultural practice to insect and bird populations: A historical study over three decades. Journal of Applied Ecology **39**:673-687.

BirdLife International. 2000. Threatened birds of the world. Lynx Edicions and BirdLife International, Barcelona and Cambridge, UK.

Blake, J. G., G. J. Niemi, and J. M. Hanowski. 1992. Drought and annual variation in bird populations. Pages 419-430 in J. M. Hagan and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C.

Boutin, S. 1990. Food supplementation experiments with vertebrates: patterns, problems, and the future. Canadian Journal of Zoology **68**:203-220.

Bowman, R., D. L. Jr. Leonard, L. K. Backus, and A. R. Mains. 1999. Interspecific interactions with foraging Red-cockaded Woodpeckers in south-central Florida. Wilson Bulletin **111**:346-353.

Brown, C. R., C. M. Sas, and M. Bomberger Brown. 2002. Colony choice in Cliff Swallows: effects of heterogeneity in foraging habitat. The Auk **119**:446-460.

Bryant, D. M., and A. K. Turner. 1982. Central place foraging by swallows (Hirundinidae): the question of load size. Animal Behaviour **30**:845-856.

Bryant, D. M. and G. Jones. 1995. Morphological changes in a population of Sand Martins *Riparia riparia* associated with fluctuations in population size. Bird Study **42**:57-65.

Buer, K., D. Forwalter, M. Kissel, and B. Stohler. 1989. The middle Sacramento River: Human impacts on physical and ecological processes along a meandering river. USDA Forest Service Gen. Tech. Rep. PSW-110: 22-32.

Burnham K. P., and D. R. Anderson. 1998. Model Selection and Inference, A Practical Information-Theoretic Approach. Springer-Verlag, New York, NY.

CALFED Bay-Delta Program. 2000. Flow regime requirements for habitat restoration along the Sacramento River between Colusa and Red Bluff. Sacramento, California.

California Department of Fish and Game. 1992. Recovery Plan: Bank swallow *(Riparia riparia)*. Prepared by the Nongame Bird and Mammal Section, Wildlife Management Division, Report 93.02.

California Department of Water Resources. 2000. The Sacramento River GIS data. Northern District, Red Bluff, California.

California State University-Chico, California Department of Water Resources, and California Department of Fish and Game. 2000. Sacramento River riparian Vegetation GIS data. Chico, California.

California State University-Chico, California Department of Water Resources, and California Department of Fish and Game. 2001. Sacramento River riparian Vegetation GIS data. Chico, California.

Copley, D., D. Fraser, and J. C. Finlay. 1999. Purple Martins, *Progne subis*: A British Columbian success story. Canadian Field Naturalist **113**:226-229.

Cowley, E. 1979 Sand Martin population trends in Britain, 1965-1978. Bird Study **26**:113-116.

Drake, V. A. 1994. The influence of weather and climate on agriculturally important insects: an Australian perspective. Australian Journal of Agricultural Research **45**:487-509.

Elkins, N. 1983. Weather and bird behaviour. T. & A. D. Poyser, Carlton.

Faaborg, J., and W. J. Arendt. 1992. Long-term declines of winter resident warblers in a Puerto Rican dry forest: which species are in trouble? Pages 57-63 in J. M. Hagan and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C.

Fernandez, C., P. Azkona, and J. A. Donazar. 1998. Density-dependent effects on productivity in the Griffon Vulture *Gyps fulvus*: the role of interference and habitat heterogeneity. IBIS **140**:64-69.

Ferrer, M., and J. A, Donazar. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. Ecology **77**:69-74.

Freer, V. M. 1979. Factors affecting site tenacity in New York Bank Swallows. Bird-Banding **50**:349-357.

Garrison, B. A. 1999. Bank Swallow. No. 414 in A. Poole and F. Gill, editors. The Birds of North America. Cornell Laboratory of Ornithology and The Academy of Natural Sciences.

Garrison, B. A. Bank Swallow, California Partners in Flight Riparian Conservation Plan. Available at: http://www.prbo.org/calpif/htmldocs/species/riparian/bansacct.html Accessed April 22, 2002.

Garrison, B. A., J. M. Humphrey, and S. A. Laymon. 1987. Bank swallow distribution and nesting ecology on the Sacramento River. Western Birds **18**:71-76.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology **59**:871-883.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of severe drought on grassland birds in Western North Dakota. Ecological Applications **2**:275-284.

Ghent, A. W. 2001. Importance of low talus in location of bank swallow (*Riparia riparia*) colonies. American Midland Naturalist **146**:447-449.

Gill, F. B. 1990. Ornithology, Second Edition. W. H. Freeman and Company, New York, NY.

Gleick, P. H. 1987. Regional hydrologic consequences of increases in atmospheric CO_2 and other trace gases. Climatic Change **10**:137-161.

Greco, S. E. 1999. Monitoring riparian landscape change and modeling habitat dynamics of the Yellow-billed Cuckoo on the Sacramento River, California. Ph.D. thesis, University of California at Davis, Davis, California.

Greco, S. E., and J. Tuil. 2002. Sacramento River Bank Revetment Inventory. University of California at Davis, Davis, California.

Greenwood, J. J. D., and S. R. Baillie. 1991. Effects of density-dependence and weather on population changes of English passerines using a non-experimental paradigm. IBIS **133** (supp. I):121-133.

Griggs, F. T., and G. H. Golet. 2002. Riparian Valley Oak (*Quercus lobata*) forest restoration on the middle Sacramento River, California. USDA Forest Service Gen. Tech. Report.

Hanski, I. 1997. Metapopulation Dynamics, From Concepts and Observations to Predictive Models. Pages 69-91 in I. A. Hanski, and M. E. Gilpin, editors. Metapopulation Biology. Academic Press, San Diego, California.

Harrison, S. and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27-42 in I. A. Hanski, and M. E. Gilpin, editors. Metapopulation Biology. Academic Press, San Diego, California.

Haskell, P. T. 1966. Insect Behaviour. Adlard and Son, Ltd. Bartholomew Press, Dorking, Surrey.

Hjertaas, D. G., P. Hjertaas, and W. J. Maher. 1988. Colony size and reproductive biology of the Bank Swallow, *Riparia riparia*, in Saskatchewan. The Canadian Field Naturalist **102**:465-470.

Holmes, R. T., T. W. Sherry, and F. W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs **56**:201-220.

Hoogland, J. L. and P. W. Sherman. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. Ecological Monographs **46**:33-58.

Hudson, P. J., D. Newborn, and A. P. Dobson. 1992. Regulation and stability of a free-living host-parasite system: *Trichostrongylus tenuis* in red grouse. I. Monitoring and parasite reduction experiments. Journal of Animal Ecology **61**:477-486.

Humphrey, J. M. and B. A. Garrison. 1987. The status of bank swallow populations on the Sacramento River, 1986. Sacramento, California: State of California, The Resources Agency, Department of Fish and Game, Wildlife Management Division, Administrative Report 87-1.

Hunter, L. A. 1988. Status of the endemic Atitlan Grebe of Guatemala is it extinct? Condor **90**:906-912.

Intergovernmental Panel on Climate Change. 2001. Summary for Policy Makers, A Report of Working Group I. Available at: htttp://www.energy.ca.gov/global_climate_change/documents/IPCC_Summary_Report.pdf Accessed August 2003.

John, R. D. 1991. Observations on soil requirements for nesting Bank Swallows, *Riparia riparia*. The Canadian Field Naturalist. **105**:251-254.

Jones, G. 1987. Colonization patterns in Sand Martins *Riparia riparia*. Bird Study **34**:20-25.

Kearvell, J. C., J. R. Young, and A. D. Grant. 2002. Comparative ecology of sympatric orange-fronted parakeets (*Cyanoramphus malherbi*) and yellow-crowned parakeets (*C. auriceps*), South Island, New Zealand. New Zealand Journal of Ecology **26**:139-148.

Krotz, D. 2002. Berkeley Science Beat, New Study Projects Climate Change's Impacts on California Watersheds, Berkeley Lab. Available at: http://www.lbl.gov/Science_Articles/Archive/ESD_climate_change_miller.html Accessed August 2003.

Lack, D. 1966. Population Studies of Birds. Oxford University Press, Oxford.

LaHaye, W. S., R. J. Gutiérrez, and H. R. Akçakaya. 1994. Spotted owl metapopulation dynamics in Southern California. Journal of Animal Ecology **63**:775-785.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237-240.

Lusk, J. J., F. S. Guthery, and S. J. DeMaso. 2001. Northern bobwhite (*Colinus virginianus*) abundance in relation to yearly weather and long-term climate patterns. Ecological modelling **146**:3-15.

Madhusudan, K. and T. Price. 1996. Effects of climate on palaearctic warblers over-wintering in India. Journal of the Bombay Natural History Society **93**:411-427.

Manly, B. F. J. 1994. Multivariate Statistical Methods, a primer. Second edition. Chapman & Hall, London.

Marini, M. A., S. K. Robinson, and E. J. Heske. 1995. Edge effects on nest predation in the Shawnee National Forest, Southern Illinois. Biological Conservation **74**:203-213.

Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual Review of Ecology and Systematics **18**:453-487.

McCarthy, J. P. and D. W. Winkler. 1999. Relative importance of environmental variables in determining the growth of nestling Tree Swallows *Tachycineta bicolor*. IBIS **141**:286-296.

McCarthy, M. A., D. B. Lindenmayer, and H. P. Possingham. 2000. Testing spatial PVA models of Australian Treecreepers (Aves: Climacteridae) in fragmented forest. Ecological Applications **10**:1722-1731.

Mead, C. J. 1979a. Colony fidelity and interchange in the Sand Martin. Bird Study **26**:99-106.

Mead, C. J. 1979b. Mortality and causes of death in British Sand Martins. Bird Study **26**:107-112.

Møller, A. P, S. Merino, C. R. Brown, and R. J. Robertson. 2001. Immune defense and host sociality: A comparative study of swallows and martins. American Naturalist **158**:136-145.

Morris, W. F. and D. F. Doak. 2002. Quantitative Conservation Biology, Theory and Practice of Population Viability Analysis. Sinauer Associates, Inc., Sunderland Massachusetts.

Morse, D. H. 1978. Populations of Bay-breasted and Cape May warblers during an outbreak of the spruce budworm. Wilson Bulletin **90**:404-413

Moss, R., J. Oswald, and D. Baines. 2001. Climate change and breeding success: Decline of the capercaillie in Scotland. Journal of Animal Ecology **70**:47-61.

Mount, J. F. 1995. California Rivers and Streams, The Conflict between Fluvial Process and Land Use. University of California Press, Berkeley, California.

Nature Conservancy of California. 1999. Central Valley Ecoregion, Sacramento River Project Update.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence. Conservation Biology **8**:17-26.

Persson, C. 1987. Age structure, sex ratios and survival rates in a south Swedish Sand martin (*Riparia riparia*) population, 1964 to 1984. Journal of the Zoological Society of London Series B. **1**:639-670.

Petersen, A. J. 1955. The breeding cycle in the Bank Swallow. Wilson Bulletin **67**:235-286.

Reed, J. M., C. S. Elphick, and L. W. Oring. 1998. Life-history and viability analysis of the endangered Hawaiian Stilt. Biological Conservation **84**:35-45.

Remsen, J. V. 1978. Bird species of special concern in California. Sacramento, California: California Department of Fish and Game, Wildlife Management Branch, Administrative Report, No. 78-1.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**:1987-1990.

Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated blue warblers. Ecology **73**:357-372.

Roy, M. S., Torres, M. J. C., and F. Hertel. 1998. Evolution and history of hummingbirds (Aves: Trochilidae) from the Juan Fernandez Islands, Chile. IBIS **140**:265-273.

Sacramento River Advisory Council. 1998. Draft Sacramento River Conservation Area Handbook. Department of Water Resources, Sacramento California.

Santos Alves, M. A. 1997. Effects of ectoparasites on the Sand Martin *Riparia riparia* nestlings. IBIS **139**:494-496.

SAS Institute Inc. 2000. SAS Version 8.1. SAS Institute, Cary, North Carolina.

Sauer, J. R., and S. Droege. 1990. Recent population trends of the Eastern Bluebird. Wilson Bulletin **102**:239-252.

Schlorff, R. W. 1997. Monitoring Bank Swallow populations on the Sacramento River: A decade of decline. Transactions of the Western Section of the Wildife Society **33**:40-48.

Schlorff, R. W. 2001. Bank Swallow population survey, Sacramento River. California Department of Fish and Game, Habitat Conservation Planning Branch.

Sharrock, J. T. R. 1976. The Atlas of Breeding Birds in Britain and Ireland. T. & A. D. Poyser, Carlton.

Smith, K. G. 1982. Drought-induced changes in avian community structure along a montane sere. Ecology **63**:952-961.

Snyder, M. A., J. L. Bell, L. C. Sloan. 2002. Climate responses to a doubling of atmospheric carbon dioxide for a climatically vulnerable region. Geophysical Research Letters **29**:9.1-9.4.

Stuart Simons, L., and T. E. Martin. 1990. Food limitation of avian reproduction: an experiment with the Cactus Wren. Ecology **71**:869-876.

Svensson, S. 1986. Number of pairs, timing of egg-laying and clutch size in a subalpine Sand Martin *Riparia riparia* colony 1968-1985. Ornis-Scandinavica **17**:221-229.

Szep, T. 1991. Number and distribution of the Hungarian Sand Martin. Aquila **98**:111-124.

Szep, T. 1995. Survival rates of Hungarian Sand Martins and their relationship with Sahel rainfall. Journal of Applied Statistics **22**:891-904.

Szep, T., and A. P. Møller. 1999. Cost of parasitism and host immune defense in the sand martin *Riparia riparia*: A role for parent-offspring conflict? Oecologia **119**:9-15.

Taylor, L. R. 1963. Analysis of the effect of temperature on insects in flights. Journal of Animal Ecology **32**:99-117.

Temple, S. A., and J. R. Cary. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology **2**:340-347.

Thompson, D. B. A., P. S. Thompson, and D. Nethersole-Thompson. 1986. Timing and breeding performance in a population of Greenshanks (*Tringa nebularia*). Journal of Animal Ecology **55**:181-199.

Turner, A. K. 1982. Timing of laying by Barn Swallows *Hirundo rustica* and Sand Martins *Riparia riparia*. Journal of Animal Ecology **51**:29-46.

Turner, A. K. 1983. Time and energy constraints on the brood size of swallows, *Hirundo rustica*, and sand martins, *Riparia riparia*. Oecologia **59**:331-338.

Union of Concerned Scientists. 2003. Global Environment-Climate Change in California. Available at: http://www.ucsusa.org/climatechange/california.html Accessed August 2003.

U. S. Environmental Protection Agency. 2000. Global Warming Impacts-State Impacts-California. Available at: http://yosemite.epa.gov/oar/globalwarming.nsf/content/ImpactsStateImpactsCA.html. Accessed August 2003.

USGS Water Resources, Daily Streamflow for California. Available at: http://waterdata.usgs.gov/ca/nwis/discharge/?site_no=11377100 Accessed September 2001 to March 2003.

Villard, M.-A., K. Freemark, and G. Merriam. 1992. Metapopulation theory and Neotropical migrant birds in temperate forests: an empirical investigation. Pages 474-482 in J. M. Hagan and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D. C.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Waugh, D. R. 1979. The diet of Sand Martins during the breeding season. Bird Study **26**:123-128.

Western Regional Climate Centre-Desert Research Institute. Northern California Climate summaries. Available at: http://www.wrcc.dri.edu/summary/climsmnca.html.

Westerterp, K. R., and D. M. Bryant. 1984. Energetics of free existence in swallows and martins, Hirundinidae, during breeding. A comparative study using doubly labeled water. Oecologia **62**:376-381.

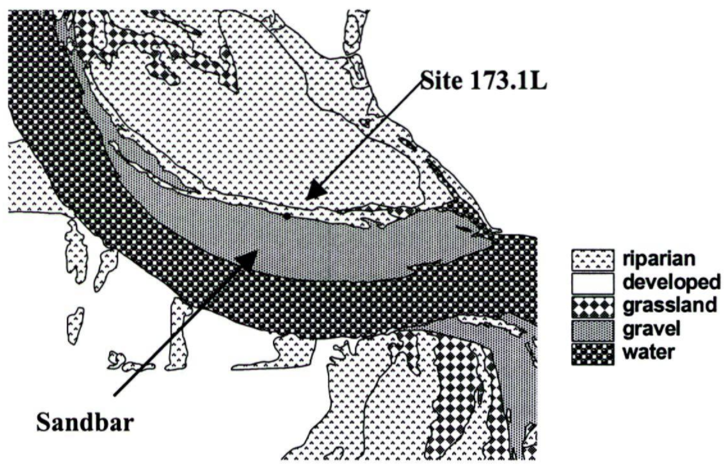
Whitworth, T. L., and G. F. Bennett. 1992. Pathogenicity of larval Protocalliphora (Diptera:Calliphoridae) parasitizing nestling birds. Canadian Journal of Zoology **70**:2184-2191.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66**:1211-1214.

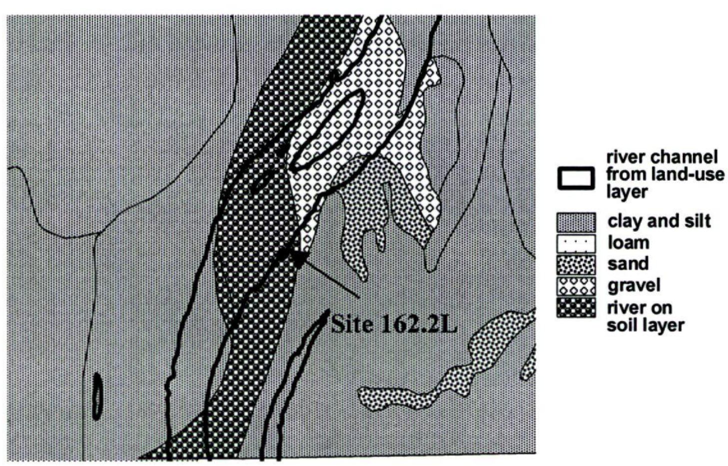
Yahner, R. H., and D. P. Scott. 1988. Effects of forest fragmentation on depredation of artificial nests. Journal of Wildlife Management **52**:158-161.

Youth, H. 2003. Winged Messengers, The Decline of Birds. Worldwatch Paper 165, Worldwatch Institute, Washington.

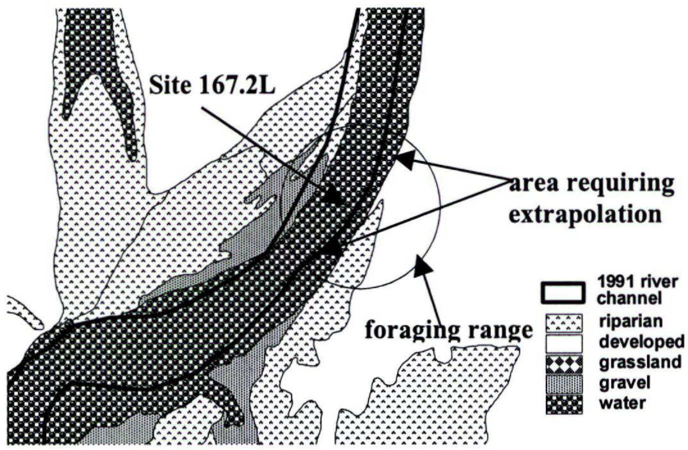
Appendix A. Illustrations of GIS site placement and extrapolations.



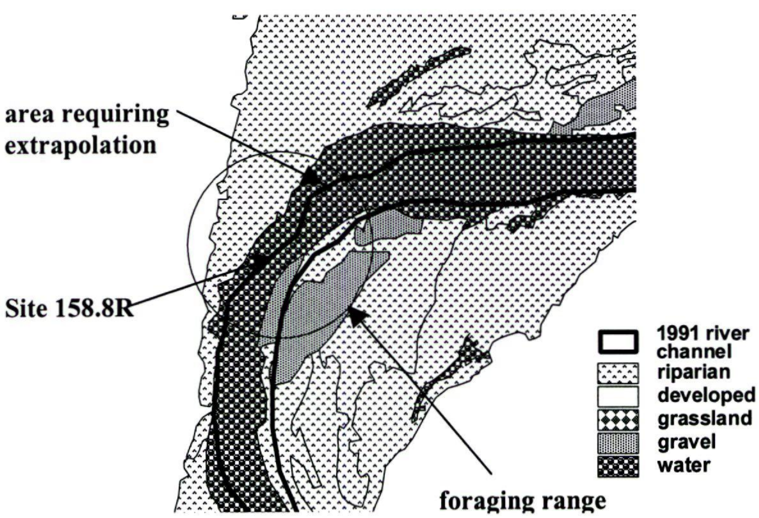
a. Example illustrating the placement of a site behind what I assumed was a sandbar.



b. Example of a site located in the river on the soil GIS. I used the nearest bank for the soil measurement.



c. Example of the extrapolation of the land that has eroded away since 1991. I assumed that the eroded land consisted of both riparian and developed since both are adjacent to the river on the GIS land use file.



d. This example is similar to example c. with the exception that I assumed that the surrounding land-use that eroded away consisted of riparian only since there is no developed land adjacent to the river bank on the GIS land use file.

Appendix B. List of sites that were removed (due to difficulties in extrapolating GIS information) to create the reduced data set.

River mile	Years	Major meander or cutoff	Sandbar	Landscape extrapolation	Soil extrapolation
144.1L	‘86-’92			X	
144.3L	‘86-‘92			X	
144.3L	‘96-’02		X		
144.9R	‘86-‘02				X
145.4R	‘86-‘92			X	
146.4L	‘86-‘92			X	
146.5L	‘86-‘92			X	
147.0L	‘86-‘92			X	
147.2L	‘86-‘92			X	
147.2L	‘96-‘02				X
147.2R	‘86-‘92			X	
147.4R	‘86-‘92			X	
150.5L	‘86-‘92			X	
154.0L	‘86-‘92			X	
154.6L	‘86-‘92			X	
154.7L	‘86-‘92			X	
155.0L	‘86-‘92			X	
155.1L	‘86-‘92			X	
155.7R	‘86-‘02				X
155.9R	‘86-‘02				X
156.3L	‘86-‘92				X
156.3L	‘96-’02	X			
156.4R	‘86-‘92			X	
156.5R	‘86-‘92			X	
156.6L	‘86-’92		X		
156.6L	‘96-‘02				X
156.8L	‘86-‘92			X	
156.9L	‘86-‘92			X	
157.0L	‘86-‘92			X	
157.0R	‘86-‘92			X	
157.1L	‘86-‘92			X	
157.3L	‘86-’92		X		X
157.3L	‘96-’02		X		
157.6L	‘86-‘02		X		
162.2L	‘86-’02				X
164.8L	‘86-’92			X	

cont…

River mile	Years	Major meander or cutoff	Sandbar	Landscape extrapolation	Soil extrapolation
165.5L	‘86-‘92			X	
165.7L	‘86-‘92			X	
165.8L	‘86-‘92			X	
166.5R	‘86-‘92			X	
166.6R	‘86-‘92			X	
167.2L	‘86-‘92			X	
167.9L	‘86-‘92			X	
168.5R	‘86-‘92			X	
168.6R	‘86-‘92			X	
168.8L	‘86-’92		X		
169.9R	‘86-‘92			X	
171.2R	‘86-‘92			X	
171.4R	‘86-‘92			X	
171.5R	‘86-‘92			X	
171.8L	‘86-‘92			X	X
171.8L	‘96-‘02		X		X
172.0L	‘86-‘92			X	
173.1L	‘86-’02		X		
173.6L	‘86-‘92			X	
173.6L	‘96-’02		X		
173.8R	‘86-‘92	X		X	
173.8R	‘96-’02	X			
174.0L	‘86-‘92	X	X	X	
174.0L	‘96-’02	X	X		
174.0R	‘86-’02	X			
174.2L	‘86-‘92			X	
174.2R	‘96-’02	X			
174.4L	‘86-‘92			X	X
174.4L	‘96-‘02				X
174.5L	‘86-‘92			X	X
174.5L	‘96-‘02				X
177.0L	‘86-‘92			X	
177.5L	‘86-‘92			X	X
177.6L	‘86-’92			X	
179.0R	‘86-’02		X		
179.4R	‘86-‘92			X	
182.5L	‘86-‘92			X	
182.6R	‘96-’02		X		

cont…

River mile	Years	Major meander or cutoff	Sandbar	Landscape extrapolation	Soil extrapolation
182.8L	‘86-‘92			X	
183.0L	‘86-’02		X		
185.0L	‘86-‘92			X	
185.1L	‘86-‘92			X	
185.1R	‘96-‘02		X		
185.5L	‘86-‘92			X	
185.5L	‘96-’02		X		
185.5R	‘86-‘92			X	
185.7R	‘86-‘92			X	
186.2R	‘86-’02		X		X
186.5R	‘86-‘02				X
187.4R	‘86-’02		X		X
187.6R	‘86-’02				X
189.8R	‘86-‘92			X	
191.2L	‘86-’92				X
191.2L	‘96-‘02		X		X
191.5L	‘86-’02		X		
191.8R	‘86-‘92			X	
192.0L	‘86-‘92			X	
192.4L	‘86-‘92			X	
193.0R	‘86-’02		X		
194.5L	‘96-’02		X		
194.5R	‘86-’02		X		
195.2L	‘86-‘92				X
195.5R	‘86-’02				X
195.6L	‘86-’92			X	
196.0L	‘86-’02				X
200.8L	‘86-’92			X	
201.0R	‘86-‘92			X	
201.3R	‘86-‘92			X	
201.4R	‘86-‘92			X	
201.5L	‘86-’02		X		
201.5R	‘86-‘92			X	
202.3R	‘86-‘92				X
202.5R	‘86-‘92			X	X
203.0L	‘96-’02		X		
203.4L	‘86-‘92	X		X	
203.4L	‘96-‘02	X			X

cont…

River mile	Years	Major meander or cutoff	Sandbar	Landscape extrapolation	Soil extrapolation
205.5R	‘86-‘92		X	X	
205.7R	‘86-‘92			X	
205.8L	‘86-’92		X		
205.8L	‘96-‘02				X
207.2R	‘86-‘92			X	
207.5R	‘86-‘92			X	
208.9L	‘86-‘92			X	
208.9L	‘96-’02		X		
209.5L	‘86-’02		X		
209.8R	‘86-‘92			X	
210.0R	‘86-’92		X		
211.0L	‘86-’92				X
211.4R	‘86-‘92			X	
212.0L	‘86-‘02				X
213.0L	‘86-’92			X	
213.5L	‘86-‘02	X			
217.2L	‘86-’92			X	
218.3R	‘86-‘92			X	
218.4L	‘86-‘92		X	X	
218.4L	‘96-’02		X		
219.8R	‘86-‘92			X	
221.0L	‘86-‘92			X	
221.0R	‘86-‘92			X	X
221.4L	‘96-’02		X		
221.5L	‘86-‘92		X		
223.0R	‘86-’92			X	
225.1L	‘86-‘92			X	
225.5R	‘86-‘92			X	
226.0L	‘86-’02		X		
226.1L	‘86-’02		X		
226.2L	‘86-’02		X		
228.8L	‘86-‘92			X	
230.9L	‘86-‘02		X		
231.2R	‘86-’92			X	
231.3L	‘86-’92		X		
231.9R	‘96-’02		X		
232.0R	‘86-’02		X		
232.2L	‘86-‘92		X	X	
232.2L	‘96-’02		X		

cont...

River mile	Years	Major meander or cutoff	Sandbar	Landscape extrapolation	Soil extrapolation
232.4R	‘86-‘92			X	
232.8L	‘86-‘92		X	X	
232.8L	‘96-’02		X		
232.8R	‘86-‘92			X	
233.4L	‘86-‘92			X	
233.5R	‘86-‘92		X	X	
233.5R	‘96-’02		X		
234.1L	‘86-‘92	X	X		
234.1L	‘96-’02				X
234.3L	‘86-’02	X	X		
234.3R	‘86-‘92	X	X		X
234.3R	‘96-’02	X	X		
234.9R	‘86-’92		X		
235.0R	‘86-’92		X		
235.1R	‘86-‘92		X	X	
236.4R	‘86-’92			X	
236.5R	‘86-‘92			X	
236.6R	‘86-‘92			X	
236.9R	‘86-‘92		X	X	
236.9R	‘96-‘02				X
237.2R	‘86-‘92		X	X	
237.2R	‘96-’02		X		
238.0R	‘86-‘92			X	
238.5R	‘86-‘92			X	
239.0R	‘86-‘92			X	
239.2R	‘86-‘92			X	
239.5L	‘86-‘92		X	X	
239.5R	‘86-‘92		X	X	
241.5L	‘86-‘92			X	
241.6L	‘86-‘92			X	
242.8L	‘86-‘92			X	

R = right side of river travelling downstream, L = left side of river travelling downstream