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Habitat associations and nest survival of Yellow Warblers in California

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HABITAT ASSOCIATIONS AND NEST SURVIVAL OF
YELLOW WARBLERS IN CALIFORNIA

A Thesis

Presented to

The Faculty of the Department of Biological Sciences
San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

Matthew Strusis-Timmer

May 2009

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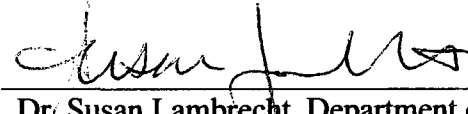
HABITAT ASSOCIATIONS AND NEST SURVIVAL OF
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by

Matthew Strusis-Timmer

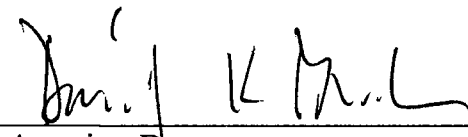
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ABSTRACT

HABITAT ASSOCIATIONS AND NEST SURVIVAL OF YELLOW WARBLERS IN CALIFORNIA

by Matthew Strusis-Timmer

Yellow Warblers have experienced population declines in California, earning them special status as a Species of Special Concern. The causes are thought to be habitat loss, nest predation, and Brown-headed Cowbird parasitism. In order to effectively conserve their remaining populations it is imperative to understand their specific habitat requirements and susceptibility to predation and parasitism. Ecological factors that best explained the distribution of Yellow Warblers were investigated by conducting point counts and recording stream and landscape, vegetation, and predator and parasite characteristics along streams in Santa Cruz County, California. In addition, predation and parasitism pressures were examined by monitoring nests and determining reproductive success. Yellow Warblers were highly associated with agriculture on the landscape scale. On the patch scale, willow (*Salix* sp.) shrubs and stream characteristics that are conducive to willow growth were the best predictors of Yellow Warbler presence at a site. A notably large portion of the Yellow Warblers breeding in the study area was found along the Pajaro River, a stream that is leveed and managed for flood control through annual vegetation-reduction regimes. However, the Yellow Warbler's partiality to this heavily disturbed system was met with very low nesting success due to high predation rates and cowbird parasitism, indicating that this scenario may be an ecological trap.

ACKNOWLEDGEMENTS

I thank my advisor S. Bros-Seemann, committee members S. Lambrecht and D. Suddjian, and good friend W.S. Smithson for guidance and suggestions on this project. I am grateful to S. Gerow and C. Strusis-Timmer for assistance in the field and the private landowners who granted me permission to access streams via their property. Financial assistance was provided by San Jose State University through an Arthur and Karin Nelson and Evelyn Gerds Research Fellowship and an Arthur and Karin Nelson Scholarship. The San Lorenzo Valley Water District contributed with an Education Program Grant.

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INTRODUCTION

In California, the Yellow Warbler (*Dendroica petechia*) is a species that has been identified as in need of conservation action through the California Wildlife Action Plan (California Dept. of Fish and Game: <http://www.wildlifeactionplans.org/california.html>). According to long-term California Breeding Bird Survey data, Yellow Warblers have experienced broad-scale population declines: an average of 1.4% yearly between 1966 and 2004 and 2.0% yearly between 1980 and 2004 (Sauer et al. 2005). It is estimated that Yellow Warbler populations have decreased 40-80%, and their breeding range in California has been reduced 20-40% in the last 65 years (Shuford and Gardali 2008). As a result, this species has been listed on all three Species of Special Concern lists in California (1978, 1992, and 2008). Yellow Warblers are listed at the Priority 2 level, defined as “population or range size greatly reduced *or* population or range size moderately reduced and threats projected to greatly reduce the taxon’s population in California in the next 20 years” (Shuford and Gardali 2008:12).

In order to develop an effective conservation plan for Yellow Warblers, it is critical to understand the basis for their decline. It is likely that there will not be a single approach to conserving Yellow Warblers because their populations are widely distributed in the varied Californian landscape, and they differ in their life-history traits (Heath 2008). In many situations, the primary reason for their decline is likely habitat loss. While Yellow Warbler habitat use varies by geographic region in California, most breeding populations occupy riparian forests during the breeding season. For example, widespread destruction of already scarce riparian habitat to accommodate agriculture

caused Yellow Warblers to be nearly extirpated in the central valley of California. In fact, over 20 years ago, Franzreb (1987) claimed that only 11% of original riparian habitat remained in California; undoubtedly, this has caused hardship for riparian-associated birds like Yellow Warblers.

Habitat destruction may not be the reason for population reductions of riparian obligatory Yellow Warblers in coastal California because they have declined *despite* available riparian habitat. For instance, in Monterey County, regular counts of singing Yellow Warblers along a stretch of suitable riparian habitat showed a 50% decline during the 1980s (Roberson 1993). In addition to numerical declines, Yellow Warblers' breeding range has contracted in neighboring Santa Cruz County (D. Suddjian, pers. comm.). Santa Cruz County, on the central coast of California, is characterized by high human population density mixed with both coniferous forests in the mountains and intensive agriculture in the valleys. Although not pristine, most streams in the region still contain some elements of riparian vegetation, and minimal riparian habitat destruction has taken place away from the Pajaro River in the last thirty years. However, there are several possible reasons why coastal Yellow Warbler populations have declined despite available riparian habitat.

First of all, although still present, fine scale habitat characteristics of riparian systems may be altered to the point where they are no longer attractive to Yellow Warblers. In most parts of their continent-wide distribution, Yellow Warblers are found in shrubby, recently disturbed vegetation often consisting of willows. Removing or reducing natural disturbance regimes from streams may make riparian habitat less

attractive by creating structurally simple and uniform forests (e.g., tall canopy, little shrub or undergrowth), which may be no longer useful for shrub-nesting species like Yellow Warblers. In coastal montane riparian systems, encroachment of coniferous and evergreen forest tree species may have also occurred in the absence of flooding, fire, and other natural disturbances. In the valleys, streams have been channelized and riparian forests have been narrowed for agricultural and flood control purposes.

Nest predation is a second factor that may also contribute to Yellow Warbler population declines in the coastal riparian habitat. Birds breeding in areas near suburban and human-altered upland landscapes can have lowered reproductive success because predator densities and predation pressure are higher (Wilcove 1985, Andren 1992, Michaud et al. 2004). Therefore, land use adjacent to streams appears to be important. However, studies in naturally patchy western ecosystems have demonstrated nest predation to be higher for Yellow Warblers in predominantly forested landscapes rather than in landscapes fragmented by agriculture, mainly due to mammalian (sciurid rodents) predators (Tewksbury et al. 1998, Cain et al. 2003).

Third, brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) may be an important factor in reducing reproductive success in the coastal habitats. Agriculture and human habitation, interspersed with natural habitats, can attract cowbirds. Although commonly cited as a cause for Yellow Warbler population declines (e.g., Gaines 1974, Garrett and Dunn 1981), it has typically not been supported by regional data on parasitism and nest success rates (Heath 2008). However, unlike other parts of California, cowbirds are relatively recent additions to the coastal avifauna (arriving in the

last century). Therefore, it is possible that the resident breeding Yellow Warbler subspecies, *D. p. brewsteri* (Grinnell and Miller 1944), haven't evolved defense mechanisms, like egg burial, to cope with cowbirds, unlike inland Rocky Mountain and eastern U.S. subspecies.

Another possibility is a disruption to the metapopulation dynamics in the region. In a landscape, habitat patches differ in quality, resulting in source and sink populations (Pulliam 1988). This leads to a stable population given the fact that there is enough source habitat in the landscape (Pulliam and Danielson 1991). Nevertheless, human disturbance in a system can result in fewer patches of high quality source habitat and a slow decline in range and total population size. This assumes that the animal will choose the optimal habitat in which to breed. However, Yellow Warblers may be choosing nesting sites based on certain characteristics, but experiencing low reproductive success in these habitats. This scenario, where there is a decoupling of attractiveness and suitability in human-altered systems, is an ecological trap (Delibes et al. 2001, Battin 2004, Robertson and Hutto 2006).

In this study, I examined the distribution and habitat characteristics associated with *D. p. brewsteri*, the resident breeding Yellow Warbler sub-species found along the central coast of California, because they are unreported for this sub-species. To define habitat associations, I compared habitat characteristics between sites with and without Yellow Warblers; I chose vegetation factors based on the known preference of Yellow Warblers for willow shrubs in other parts of their range and I also measured abiotic stream factors that may create early successional willow habitat. I developed a model to

predict occurrence of Yellow Warblers as a function of these habitat characteristics. In order to better interpret and corroborate the habitat association model, I measured characteristics of the vegetation at warbler nest sites.

Since mere presence, abundance, or density of individuals at a site are not necessarily good indicators of habitat quality (Van Horne 1983), it is critical to measure productivity. I measured reproductive success and examined the effects of nest predation and Brown-headed Cowbird parasitism to assess the viability of the Pajaro River population of Yellow Warblers.

METHODS

I studied Yellow Warblers May through August 2008 in Santa Cruz County, California, just south of the San Francisco Bay area. The six streams that were surveyed varied in size, topography, seasonality, level of disturbance, and adjacent land use (Table 1). Riparian vegetation at these streams varies slightly; but, in general, Black Cottonwood (*Populus trichocarpa*), Red Alder (*Alnus rubra*), or willow (*Salix spp.*) dominated the canopy with lesser amounts of sycamore (*Platanus racemosa*), Big-leaf Maple (*Acer macrophyllum*), Coast Redwood (*Sequoia sempervirens*), Box-elder (*Acer negundo*), California Bay (*Umbellularia californica*), eucalyptus (*Eucalyptus spp.*), and Coast Live Oak (*Quercus agrifolia*). The understory was dominated by willow (*Salix spp.*), Red Alder (*Alnus rhombifolia*), California Blackberry (*Rubus ursinus*), dogwood (*Cornus sericea*), or poison-oak (*Toxicodendron diversilobum*). For consistency, I conducted all bird and vegetation surveys.

Table 1. General characteristics of the six streams surveyed to determine the current breeding distribution and habitat associations of Yellow Warblers in Santa Cruz County, CA, in 2008.

Stream	Size	Gradient	Seasonality	Disturbance Level	Adjacent Land Use
Wilder Creek & Moore Creek	small	low	persistent	low	parkland
San Lorenzo River	large	high	persistent	medium	residential rural, parkland
Soquel Creek	medium	high	persistent	medium	residential rural, urban
Corralitos Creek	medium	medium	intermittent	high	agriculture
Pajaro River	large	low	both	high	agriculture

I censused 53 km (33 mi.) of streamside habitat in order to determine the distribution of Yellow Warblers along the six streams. I restricted my sampling to streams and sections of streams that have been known historically to support breeding Yellow Warblers. Using streams as line transects, I placed 176 point count stations (Figure 1) at randomly chosen distances between 200 m and 400 m apart to avoid sampling bias that would occur if territories were uniformly spaced. I conducted 5 min point count surveys between 2 May and 11 June, the time period suggested by Ralph et al. (1993). I started the surveys 3 weeks after the first documented Yellow Warbler spring-arrival, to minimize counting singing migrants. Each point was surveyed twice, at least 16 days apart. The surveys were begun at 0-15 minutes before sunrise and ended no later than 4 h after sunrise. To avoid time-of-day bias, I changed the order in which points were surveyed by surveying in both upstream and downstream directions.

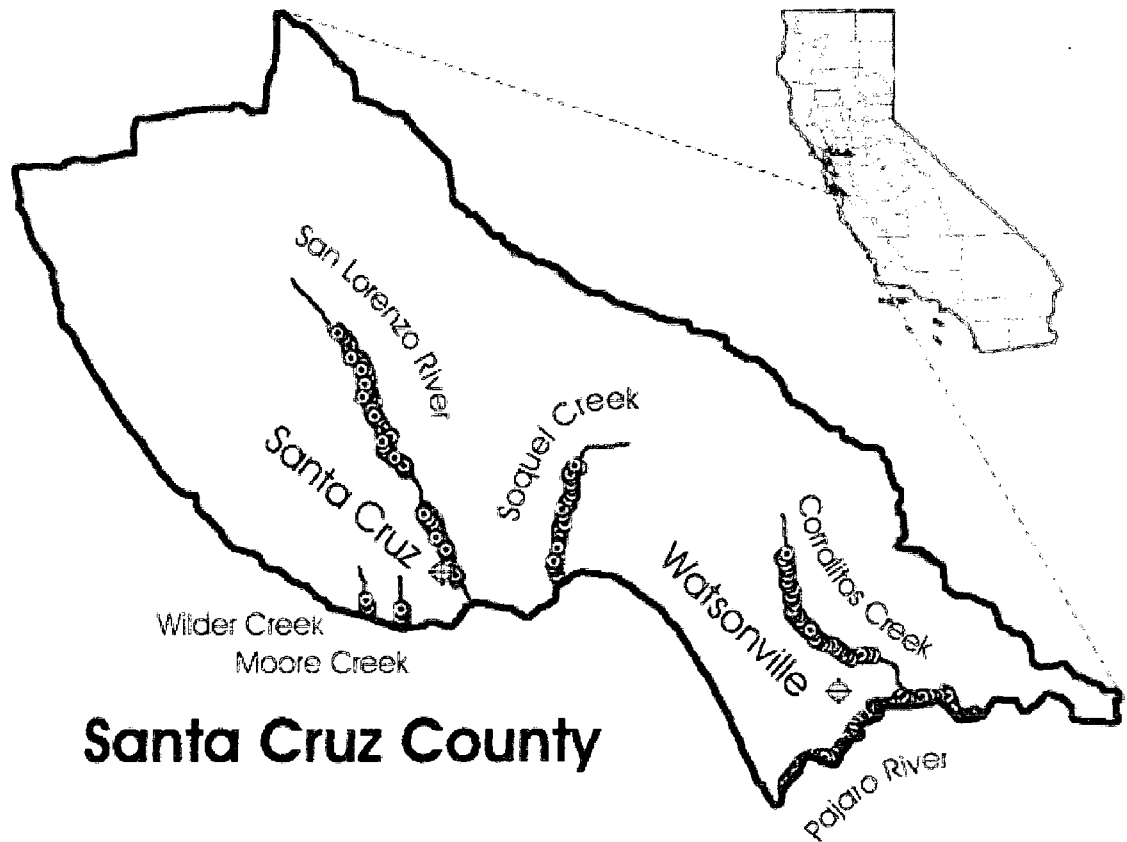


Figure 1. Map showing the study area with labeled streams and point count locations.

To examine the influence of patch and landscape-scale ecological factors on the distribution of Yellow Warblers along streams on the central coast of California, I measured factors relating to the stream and landscape, vegetation composition and structure, and predators and brood parasites at each of the 176 point count stations (Table 2). For logistical reasons of working in streams that flow mostly through private property and to maximize the range of inference, I developed a rapid habitat assessment method that used discrete data measurements to assess the stream and landscape and vegetation characteristics. I measured components of the vegetation within a 25 m radius circle, centered on the point count station. Dominant plant species in the canopy (≥ 5 m) and

shrub (50 cm \geq 5 m) layers were assigned based on abundance. I used the Braun-Blanquet Cover Abundance Scale (Mueller-Dombois and Ellenberg 1974) to estimate cover in each of the layers. I measured stream width by either pacing the distance or using a rangefinder. I surveyed for nest predators and Brown-headed Cowbirds concurrently with Yellow Warblers during the point counts.

Table 2. Habitat factors measured at each of the 176 survey points in order to determine habitat associations of the Yellow Warbler in coastal California, 2008.

A-Stream and Landscape	B-Vegetation: canopy layer	C-Vegetation: shrub layer	D-Predators and Parasites
<i>Stream width (m):</i>	<i>Ave. canopy height (m):</i>	<i>Shrub layer:</i>	<i>Mammalian predator:</i>
0-5		present or absent	present or absent
5-10	5-10	<i>Shrub dominance:</i>	<i>Mammal abundance:</i>
10-20	10-15	shrub species	average
20-40	15-20	<i>Salix:</i>	<i>Corvid^b species:</i>
>40	>20	present or absent	present or absent
<i>Direction of flow:</i>	<i>Percent canopy cover:</i>	<i>Ave. Salix height (m):</i>	<i>Corvid species abundance:</i>
to nearest 45°			average
<i>Channel shape:</i>	BBCAS ^a	0-2	<i>Cowbird:</i>
both banks <2 m	<i>Canopy dominance:</i>	2-4	present or absent
both banks 2-4 m	tree species	4-6	<i>Cowbird abundance:</i>
both banks >4 m	<i>Canopy type:</i>	6-8	average
one bank <2 m and	Deciduous or	>8	
one bank >2 m	evergreen	<i>Percent Salix cover:</i>	
<i>Flood evidence:</i>		BBCAS	
present or absent		<i>Exotic species:</i>	
<i>Adjacent land use:</i>		present or absent	
ag.-row crop			
ag.-orchard			
res.-urban			
res.-suburban			
res.-exurban open			
res.-exurban forest			
park-open			
park-forest			
<i>Agriculture:</i>			
present or absent			
<i>House:</i>			
present or absent			

^a Braun-Blanquet Cover Abundance Scale (Mueller-Dombois and Ellenberg 1974)

^b Corvid refer to ravens, crows, and jays

I used stepwise backward elimination hierarchical log-linear analysis to test whether the biotic and abiotic habitat factors measured at each survey point were associated with the distribution of Yellow Warblers. Log-linear analysis is a technique that investigates potential relationships between categorical or grouped data by analyzing all levels for possible interaction and main effects. It finds the most parsimonious model by comparing saturated models with reduced models. Reduced, lower-order two-way interactions are desired, as they suggest a simpler system where relationships can be more easily visualized between warblers and their surroundings. In order to clearly identify these relationships, I grouped similar factors together for the analyses. The four groups of factors were those pertaining to: (A) stream and landscape characteristics; (B) the canopy layer of vegetation; (C) the shrub layer of vegetation; and (D) predators and parasites (refer to Table 2). Each of these groups of factors was analyzed with Yellow Warbler presence/absence. Also, since the landscape can influence predator and brood parasite loads, I investigated potential relationships between these two groups (A and D) by analyzing them independently of Yellow Warbler presence/absence.

I used all of the vegetation factors to build a predictive habitat association model of Yellow Warbler occurrence using backward stepwise binary logistic regression (Quinn and Keough 2003). Logistic regression allows the prediction of a discrete outcome (Yellow Warbler presence or absence) from a set of independent factor variables. In order to create a balanced model, one that was equally capable of accurately predicting Yellow Warbler presence and absence, I selected a random subset of 86 points to include in the model construction: 43 points where at least one singing male Yellow Warbler

was detected and 43 points where warblers were not detected. Before running the analysis, factor levels with very low frequencies were collapsed together to prevent instability in the model. I used the Last Step method to select the final model, where adding another variable would not improve the model significantly (most parsimonious), providing it met the following criteria: Hosmer and Lemeshow chi-square test of goodness-of-fit statistic (Hosmer and Lemeshow 2000), an overall high percent correct for the model, and similar accuracy in predicting absence and presence. The Hosmer and Lemeshow test is the most robust test for overall fit of a logistic model; a finding of non-significance indicates that the model was not significantly different from observed values and, thus, adequately fits the data. Logistic coefficients (B) are assigned to the levels of each independent factor variable and are used to predict the log odds (logit) of the dependent variable. They are weighted relative to the highest level, which acts as a reference category. These coefficient values may be used to compare the relative strength of the independent variables on the probability of detecting Yellow Warblers at a given point. The odds ratio ($\text{Exp}(B)$) values shows the impact of each coefficient on the overall model. An odds ratio of 1 corresponds to an explanatory variable which has no effect on the dependent variable (Yellow Warbler). An odds ratio > 1 increases the logit and, therefore, increases the odds of Yellow Warblers being present while an odds ratio < 1 decreases the logit and the odds of Yellow Warblers being present (or, put another way, increases the odds of Yellow Warblers being absent). Therefore, high positive values are strong predictors of presence, whereas very low values (at or near zero) are strong predictors of absence in the system.

I tested the effectiveness of the logistic regression model to predict presence or absence of Yellow Warblers at locations that had not been used for the creation of the model. I measured the habitat characteristics and assessed the presence or absence of Yellow Warblers at 32 randomly selected survey points in potential warbler habitat along streams. I used SPSS 16.0 (SPSS, Chicago, Illinois) to predict presence or absence of the birds using the logistic regression model and compared the predicted values to the actual values. I used a membership cutpoint value of 0.5; probabilities greater than or equal to 0.5 were assigned “presence” and those less than 0.5 “absence”. I used $\alpha = 0.05$ for all statistical tests, unless stated otherwise.

At the conclusion of the breeding season, I recorded the species, height, and diameter at breast height of the tree or shrub containing the nest. I measured the height of the nest off the ground, the distance from the stream, and the distance from the riparian vegetation edge to assist in interpreting the results of the habitat association model for Yellow Warblers. All means are presented as \pm SE.

In order to determine reproductive success, I searched for nests 25 April through 29 July along the Pajaro River using guidelines described by Martin and Guepel (1993). I selected the Pajaro River alone to search for nests because of the sheer abundance and concentration of Yellow Warblers at this site (est. 100-120 pairs) and the paucity of Yellow Warblers breeding along the other streams (the San Lorenzo River had the second most, an estimated eight pairs, which was insufficient for comparisons). Nests were monitored every 1-4 days until fledging or failure (Ralph et al. 1993, Martin et al. 1997) using a digital camera mounted to the end of a telescoping aluminum pole to accurately

observe the contents. Care was taken to minimize observer effects on nest survival by using a GPS unit to mark nest sites, and, if necessary, placing a flag at a distance and recording the distance and bearing to the nest. Flagging nest trees was avoided altogether. I followed all other precautions described in Ralph et al. (1993) to minimize sample bias.

A nest was considered successful if it fledged at least one Yellow Warbler young, even if the nest also fledged a cowbird. Fledging was determined based on visual and audible detections of dependent young in the proximity of an intact nest near the expected fledging date. A nest was considered unsuccessful if: all of the Yellow Warbler eggs or nestlings disappeared prior to the expected fledging date, a nest was torn from its supporting branches, an adult was found dead on the nest midway through the nesting cycle, or some other cause such as inviable eggs or the death of nestlings. Nests were considered parasitized if they contained a cowbird egg or nestling at any stage in the nesting cycle. I considered nests to have failed from cowbird parasitism if only cowbird eggs or nestlings were present in the nest after Yellow Warbler eggs or young had been observed; or, if only cowbird eggs or young were observed during the entire monitoring period of a nest. When feasible, I probed nests after they fledged or failed for the presence of buried cowbird eggs.

Nest survival rates were calculated using the Mayfield (1975) method with a standard error estimator (Johnson 1979). This approach to nest success minimizes the bias that results from finding nests at different periods in the nesting cycle. The Mayfield method is based on the concept of “nest days” or “exposure days,” which is the

probability that a nest will survive a 24-hour period. The probability a nest will survive one day (the daily survival rate) can then be extrapolated to figure out the probability of a nest surviving a stage of the nest cycle and the entire nest cycle. Nest survival probabilities were calculated individually for each stage (laying, incubation, and nestling) and across a 25-day nesting cycle (4 egg-laying days, 11 incubation days, and 10 nestling days), which was based on the best available breeding biology literature for the species. For all nests, I started counting exposure days when at least one Yellow Warbler egg or nestling was present. To calculate exposure days for nests with known fates, I used the midpoint between the last observed active date and the first observed inactive date as the terminal date; for nests with unknown fates, I used the last active date to count exposure days (Last-Active B method in Manolis et al. 2000).

RESULTS

Breeding Yellow Warblers are most abundant at the Pajaro River. I detected at least one singing male Yellow Warbler at 87% of the point count stations (n=52) on this stream, compared to very low occupancy rates on the other streams (Figure 2). In fact, using the average number of singing males per point for the two counts, 84% of all detections county-wide were at the Pajaro River, obviously making it the site of highest breeding activity in Santa Cruz County.

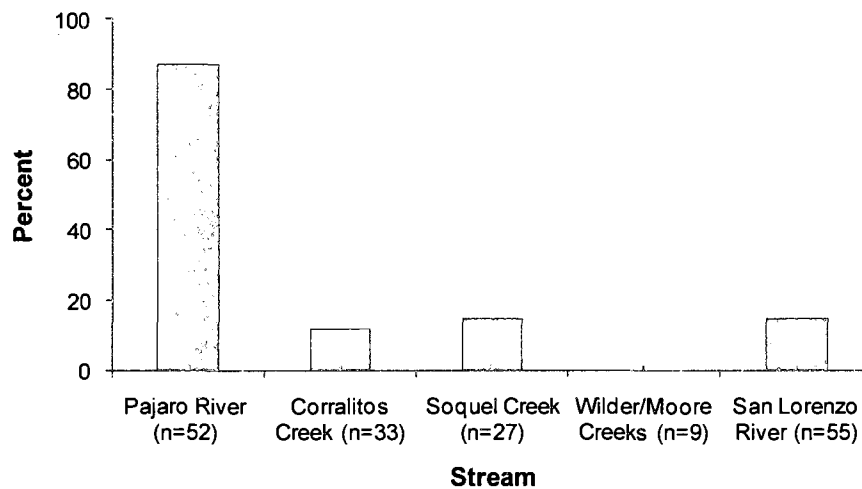


Figure 2. Occupancy rates of Yellow Warblers among streams in Santa Cruz County resulting from censuses conducted during the 2008 breeding season. Rates are expressed as the percentage of point count stations with at least one singing male detected during one or more of the surveys.

The log-linear analysis indicated that stream and landscape characteristics were associated with Yellow Warblers (Table 3). The significant interaction between Yellow Warbler presence and Yellow Warbler absence and stream flow direction showed that warblers were present proportionately more often at points in streams that flowed in south, southwest, and west directions than in other directions (Figure 3). The significant three-way interaction between Yellow Warbler presence and Yellow Warbler absence, flood evidence, and adjacent land use suggested that the proportion of warblers present at points with adjacent agriculture was significantly greater than those without, especially if there was evidence of high water present (Figure 4). The significant interaction between Yellow Warbler presence and Yellow Warbler absence and the presence or absence of

agriculture showed warblers to be in much higher proportions at points where agriculture was present (Figure 5). The significant three-way interaction between Yellow Warbler presence or absence, channel shape, and the presence or absence of a house indicated that when houses were absent, the warblers tended to occupy areas with at least one low stream bank; but when houses were present, warblers were rarely present (Figure 6).

Table 3. Results of the log-linear analysis showing significant ($p < 0.05$) two and three-way interactions between Yellow Warbler presence or absence (YWAR) and stream and landscape, canopy and shrub vegetation, and predator and parasite factors at 176 points located along streams in Santa Cruz County, CA, in 2008.

Groups	Factors	X²	df	(p)
A. Stream and Landscape	YWAR*flow direction	21.733	7	0.003
	YWAR*adj. land use*flood evidence	10.965	2	0.004
	YWAR*agriculture	8.937	1	0.003
	YWAR*channel shape*house	13.951	3	0.003
B. Vegetation: Canopy	YWAR*canopy dominant species	53.418	8	<0.001
	YWAR*canopy cover	22.875	7	0.002
C. Vegetation: Shrub	YWAR* <i>Salix</i> cover	30.356	7	<0.001
D. Predators and Parasites	YWAR*CORV ^a ave.*BHCO ^b abundance	5.426	1	0.020
	YWAR*ave. CORV abundance*BHCO	6.840	2	0.033
E. Other Relationships	BHCO*agriculture	31.998	1	<0.001
	CORV*agriculture	82.084	1	<0.001

^a CORV= Corvid presence/absence

^b BHCO= Brown-headed Cowbird presence/absence

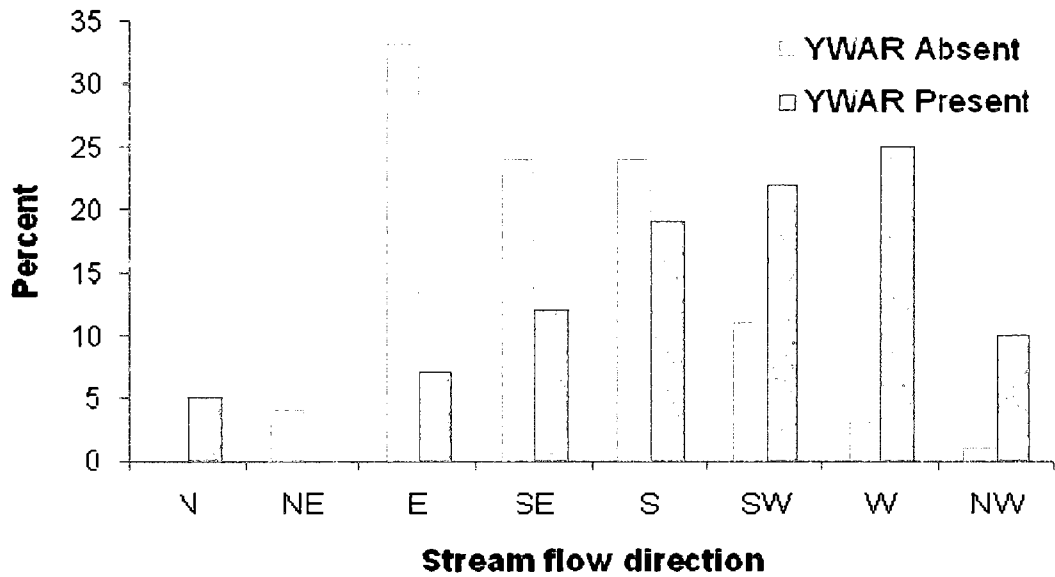


Figure 3. Relationship between Yellow Warblers (YWAR) and stream flow direction at 176 points along streams in Santa Cruz County, CA, in 2008; shown as the percentage of survey points where Yellow Warblers were present and absent. A point was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys.

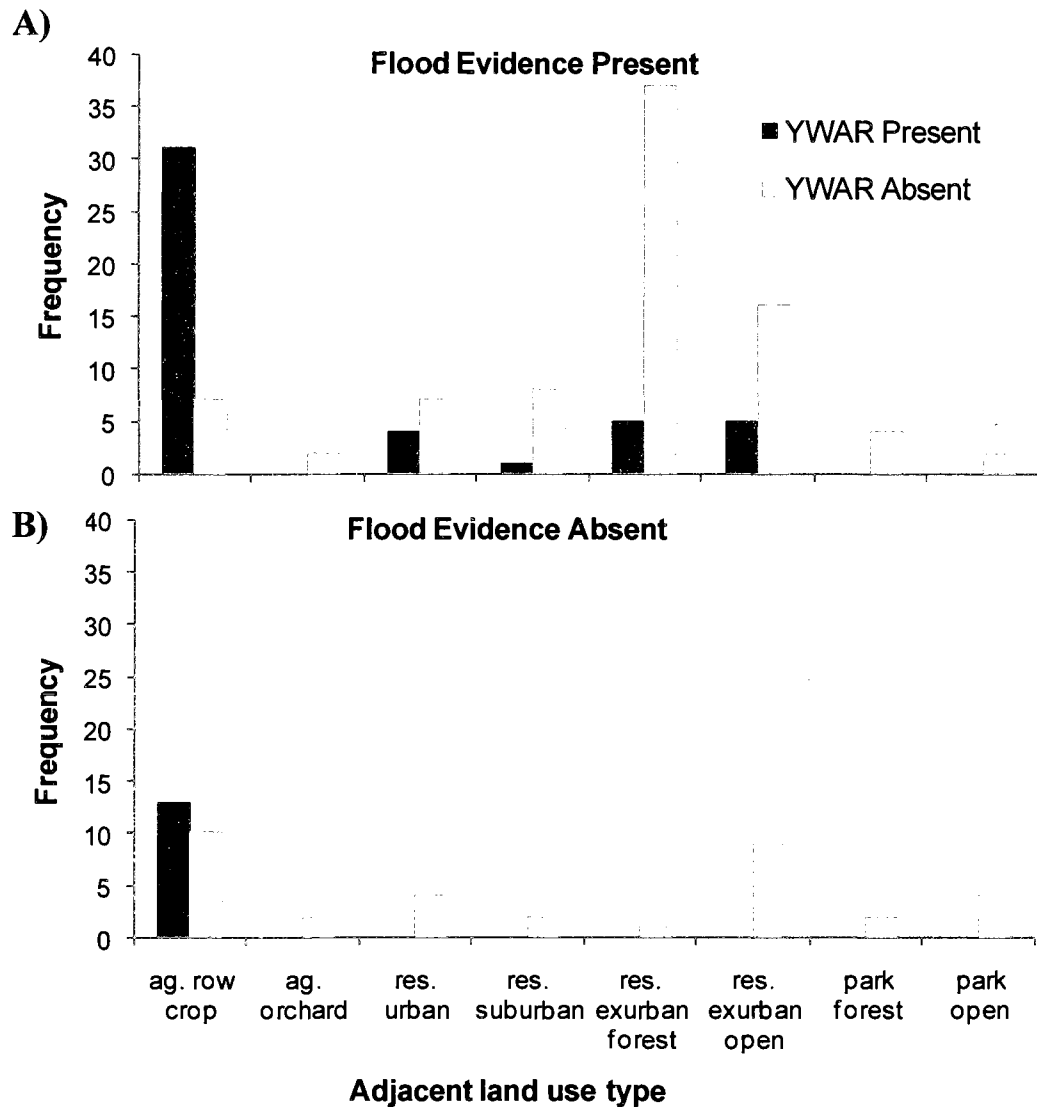


Figure 4. Significant three-way interaction between Yellow Warblers (YWAR), adjacent land use, and evidence of flooding at 176 points along streams in Santa Cruz County, CA, in 2008. Frequency refers to the number of points where warblers were present or absent. A point was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys. Figure 4-A illustrates the case when flood evidence was present and Figure 4-B illustrates the case when flood evidence was absent.

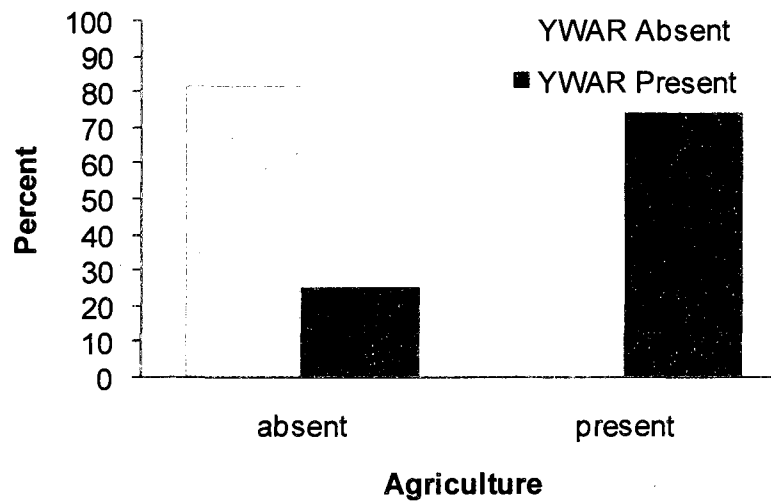


Figure 5. Percentage of survey points with Yellow Warblers present and absent in relation to points with and without adjacent agriculture along streams in Santa Cruz County, CA, in 2008. A site was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys.

The log-linear analysis suggested that vegetation composition and structure also affected Yellow Warblers. The significant interaction between Yellow Warbler presence and Yellow Warbler absence and tree species showed that most of the points where warblers were detected were dominated by *Salix* (Figure 7). The significant interaction between canopy cover and Yellow Warbler presence or absence indicated that warblers were present more often in cover levels less than 50% (Figure 8). The strong relationship between *Salix* shrub cover and Yellow Warbler presence and Yellow Warbler absence showed that warblers were present mainly at sites with 25-50% cover and 50-75% cover (Figure 9).

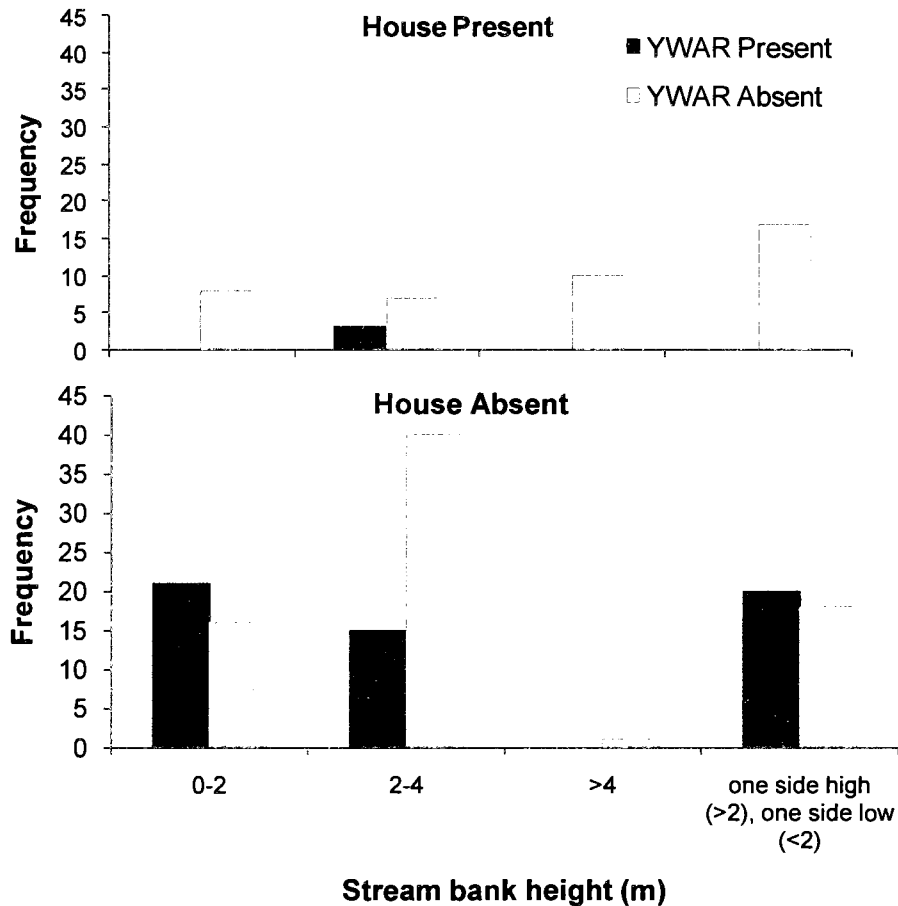


Figure 6. Significant three-way interaction between Yellow Warblers, channel shape, and streamside houses at 176 points along streams in Santa Cruz County, CA, in 2008. Frequency refers to the number of points where warblers were present or absent. A point was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys. Figure 6-A illustrates the case when a house was present and Figure 6-B illustrates the case when a house was absent.

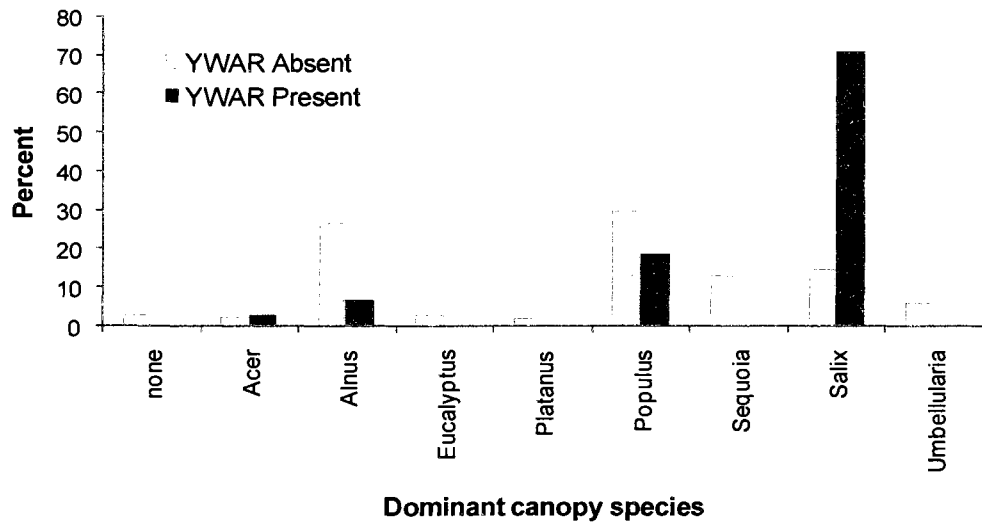


Figure 7. Relationship between Yellow Warblers (YWAR) and dominant canopy species at 176 points along streams in Santa Cruz County, CA in 2008; shown as the percentage of survey points where Yellow Warblers were present and absent. A point was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys.

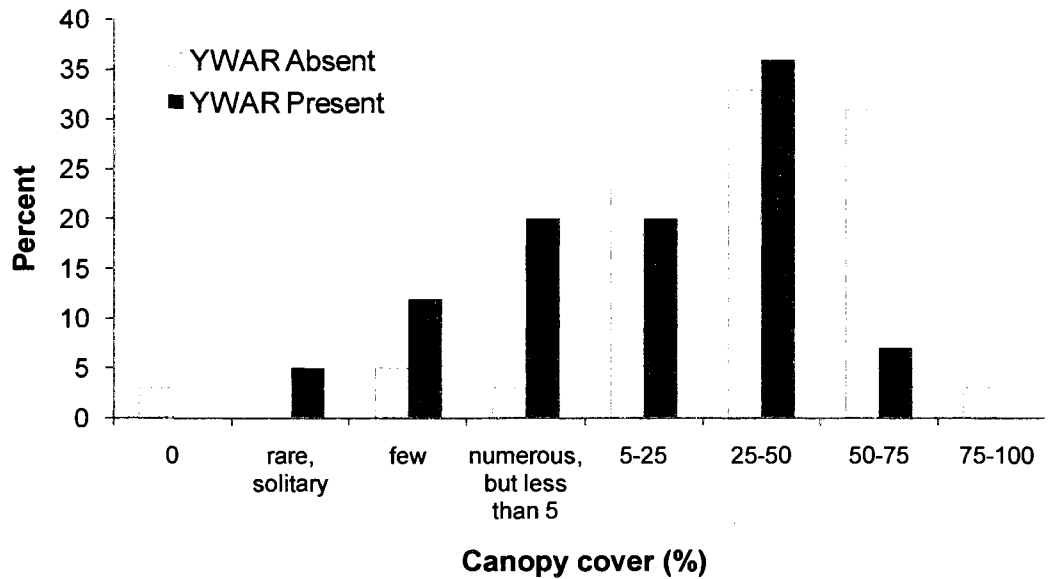


Figure 8. Relationship between Yellow Warblers and canopy cover at 176 points along streams in Santa Cruz County, CA in 2008; shown as the percentage of survey points where Yellow Warblers were present and absent. A point was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys.

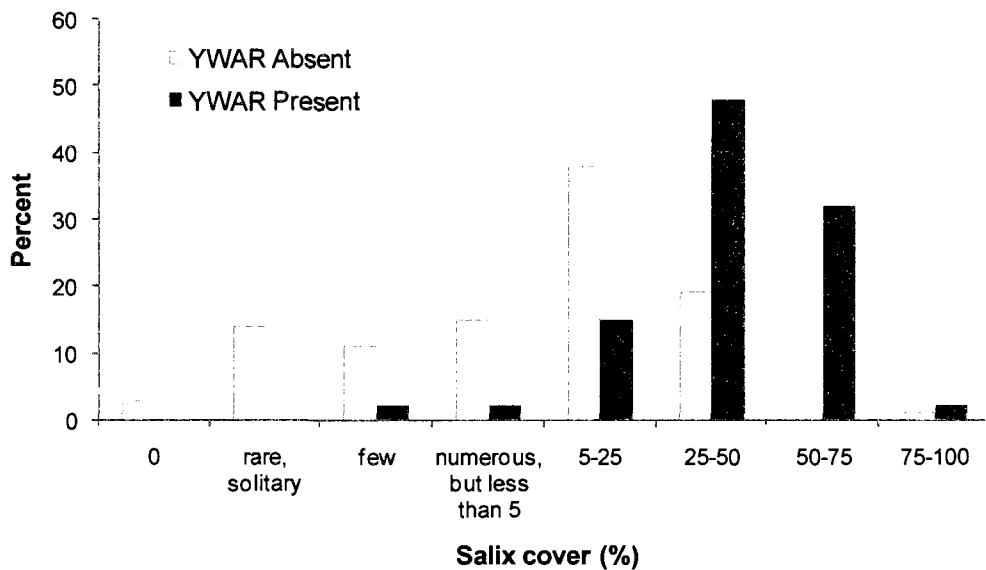


Figure 9. Relationship between Yellow Warblers and percent *Salix* cover at 176 points along streams in Santa Cruz County, CA in 2008; shown as the percentage of survey points where Yellow Warblers were present and absent. A point was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys.

The log-linear analysis also indicated relationships between Yellow Warblers, cowbirds, and corvids. The significant three-way interaction between Yellow Warbler presence and Yellow Warbler absence, corvid presence or absence and average cowbird abundance showed that warbler presence was positively associated with cowbird abundance and both of these species were negatively associated with corvids (Figure 10). The significant three-way interaction between the presence or absence of Yellow Warblers, average corvid abundance, and cowbird presence or absence showed that warblers were often present at points with cowbirds but without corvids (Figure 11).

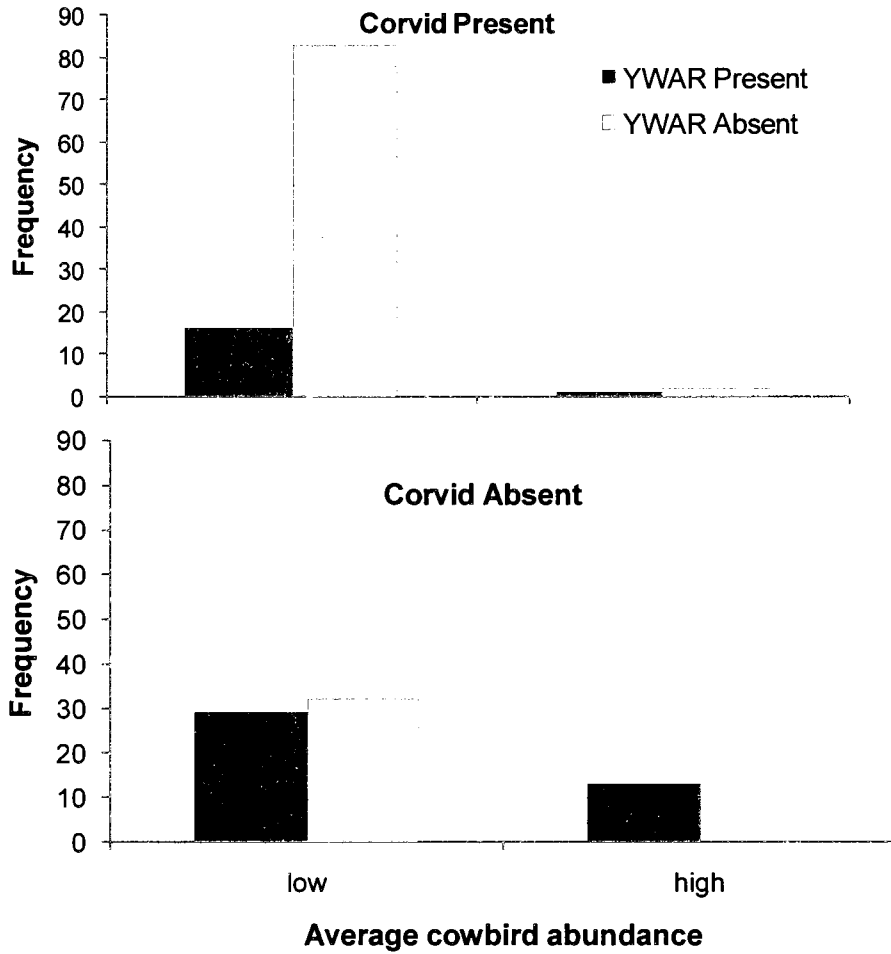


Figure 10. Significant three-way interaction between the presence or absence of Yellow Warblers, average cowbird abundance, and presence or absence of corvids at 176 points along streams in Santa Cruz County, CA, in 2008. Frequency refers to the number of points where Yellow Warblers were present or absent in relation to average cowbird abundance (low=0-1.25; high=1.25-2.5). A point was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys. Figure 10-A illustrates the case when corvids were present and Figure 10-B illustrates the case when corvids were absent.

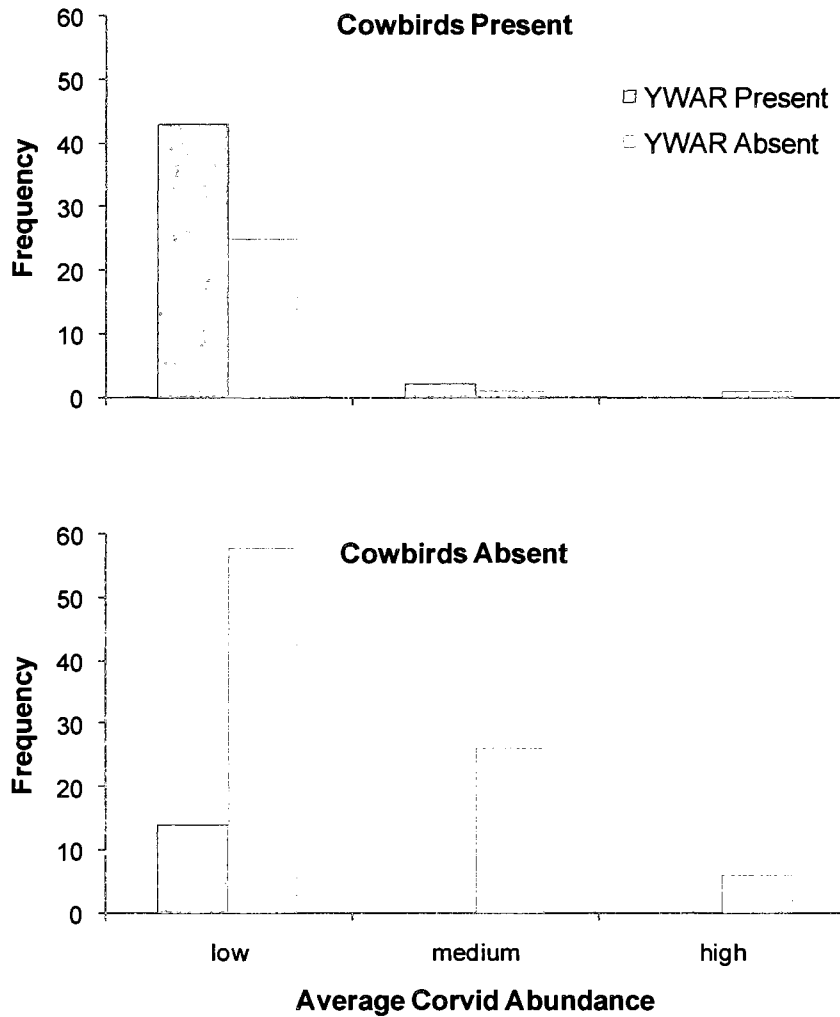


Figure 11. Significant three-way interaction between the presence or absence of Yellow Warblers, average corvid abundance, and presence or absence of cowbirds at 176 points along streams in Santa Cruz County, CA, in 2008. Frequency refers to the number of points where Yellow Warblers were present or absent in relation to average corvid abundance (low=0-1.5; medium=1.5-3.0; high=3.0-4.5). A point was considered to have Yellow Warblers present if at least one singing male was detected during one of the surveys. Figure 11-A illustrates the case when cowbirds were present and Figure 11-B illustrates the case when cowbirds were absent.

Lastly, log-linear analysis into relationships between corvids and cowbirds and landscape factors demonstrated significant interactions between both cowbirds and corvids and agriculture. As expected, cowbirds were positively associated with agriculture (Figure 12), whereas corvids were negatively associated with agriculture (Figure 13).

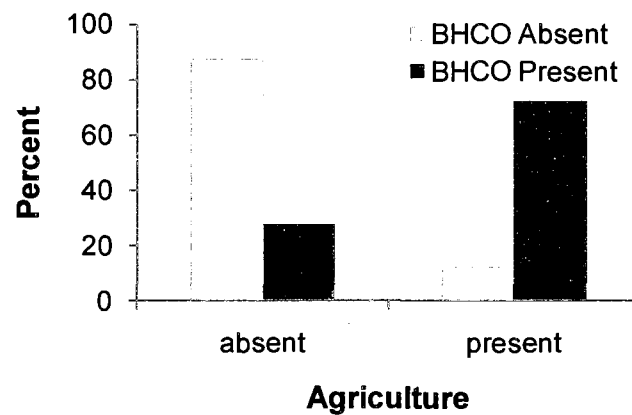


Figure 12. Relationship between the presence or absence of Brown-headed Cowbirds and whether or not there were agricultural fields nearby at 176 points along streams in Santa Cruz County, CA, in 2008. A site was considered to have Brown-headed Cowbirds present if at least one individual was detected on one of the surveys.

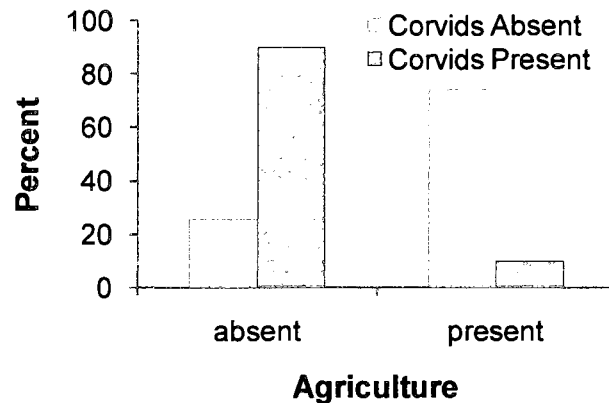


Figure 13. Relationship between the presence or absence of Corvid predators and whether or not there were agricultural fields nearby at 176 points along streams in Santa Cruz County, CA, in 2008. A site was considered to have Corvids present if at least one individual was detected on one of the surveys.

The final logistic regression model strongly fit the data (Hosmer and Lemeshow chi-square goodness-of-fit test statistic (p) = 1.00) and was correct a combined 94% of the time in predicting Yellow Warbler presence or absence at a survey point (Figure 14). The model retained four vegetation factors in the equation: average canopy height, dominant canopy species, *Salix* cover, and *Salix* height (Table 4). The 4-6 m and 6-8 m categories of *Salix* height had high logistic coefficients and odds ratios and were the strong predictors of Yellow Warbler presence at a site (Figure 15-A). In general, as the average height of willows increases, the probability of Yellow Warblers increases until the trees become over 8 m tall, whereupon the likelihood drops back down. The reference level for *Salix* cover (>50%) was the highest relative to the other levels that had negative coefficients (Figure 15-B). This result can be interpreted that lower amounts of *Salix* cover increases the probability that warblers will be absent. Canopy dominant

species cottonwood and alder were strong predictors of Yellow Warbler presence at a site (Figure 15-C), as was an average canopy height of 5-10 m (Figure 15-D). All combined, the model predicts that a very high probability site would have a 5-10 m cottonwood or alder-dominated canopy coupled with greater than 50% cover of 4-6 m tall willow shrub layer. The model performed well in predicting presence or absence of Yellow Warblers in sites other than those used to develop the model. When evaluated for accuracy at the 32 test sites, the model was 81% correct in predicting that Yellow Warblers would be present and 69% correct in predicting absence (Figure 16).

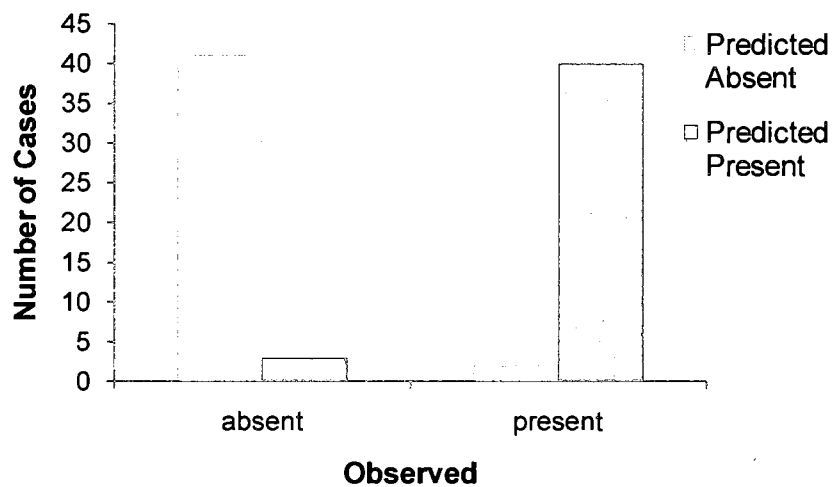


Figure 14. The final logistic regression habitat association model was correct in predicting Yellow Warbler presence or absence a combined 94% of the time (n=86). The cut value used for membership was 0.5.

Table 4. The final logistic regression habitat-association model resulting from riparian vegetation data collected at 86 survey points during the breeding season 2008.

Factor	Logistic coefficient (B)	S.E.	Odds ratio (Exp(B))
<i>Ave. canopy height (m)</i>			
None	-3.471	24352	0.031
5-10	34.078	5037	6.310E14
10-15	-83.079	7605	0.000
15+	reference		
<i>Dom. canopy spp.</i>			
<i>Sequoia</i>	-2.143	12795	0.117
<i>Salix</i>	28.724	4955	0.413
<i>Umbellularia</i>	-.885	26041	2.984E12
<i>Alnus</i>	50.413	5501	7.836E21
<i>Populus</i>	64.929	6212	1.579E28
<i>Acer/Platanus</i>	reference		
<i>Salix cover (%)</i>			
0, rare, solitary	-69.649	17663	0.000
Few, small cover	-48.934	8205	0.000
Numerous, but <5	-48.934	8205	0.000
5-25	-84.836	9628	0.000
25-50	-16.636	6781	0.000
50+	reference		
<i>Salix height (m)</i>			
0-2	-14.488	2819	0.000
2-4	17.316	2835	3.312E7
4-6	133.798	11248	1.282E58
6-8	119.003	10063	4.812E51
8+	reference		
<i>constant</i>	-17.395	7952	0.000

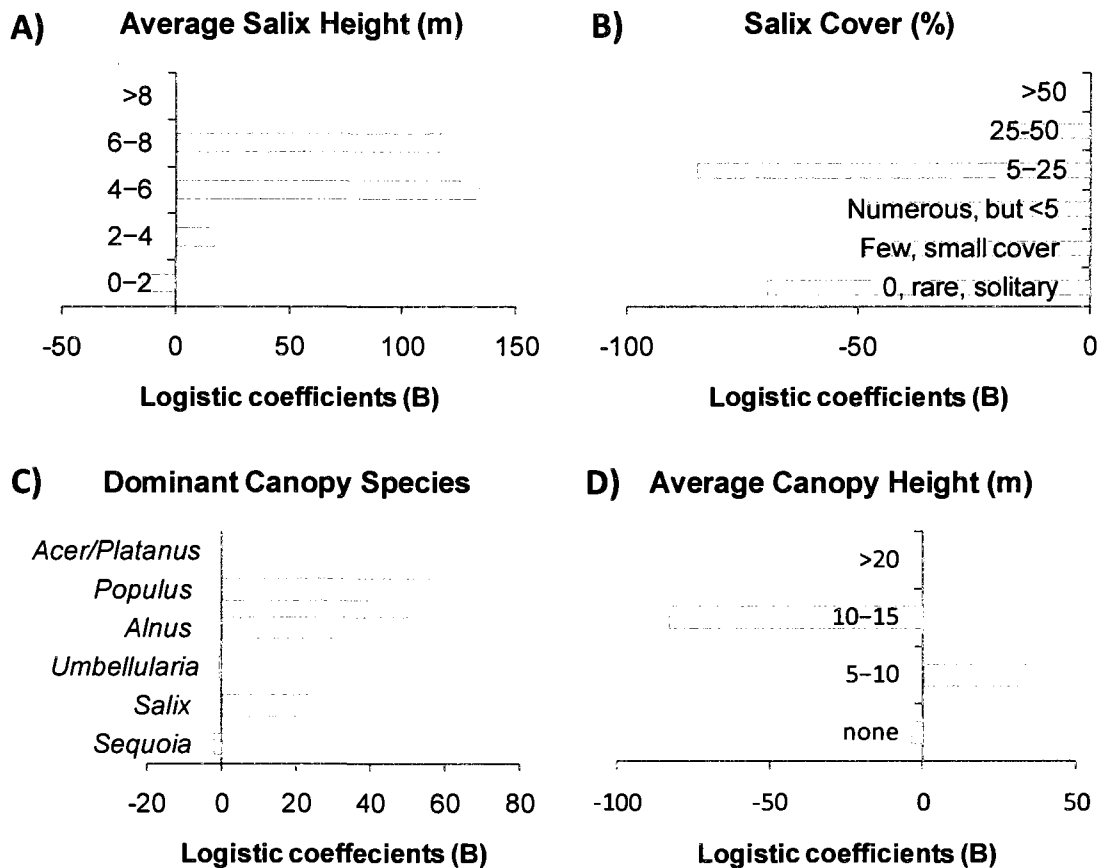


Figure 15. The relative strength of the logistic coefficients for vegetation factors included in the final logistic regression habitat association model. In each graph, the top level is the reference category. Figure 15-A shows the logistic coefficients for height classes of *Salix*, Figure 15-B shows the logistic coefficients for *Salix* cover, Figure 15-C shows the logistic coefficients for dominant canopy species, and Figure 15-D shows the logistic coefficients for average canopy height.

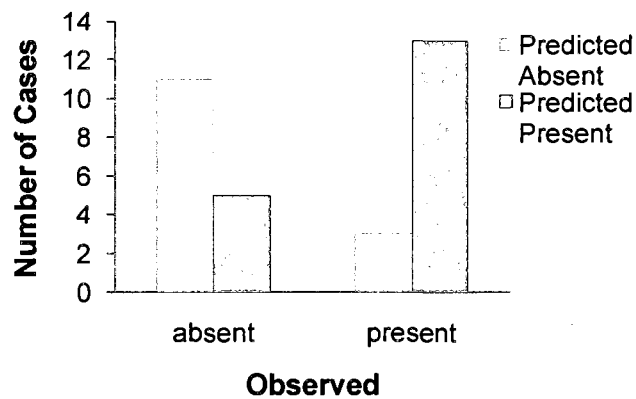


Figure 16. The results of the logistic regression model test; evaluated at 32 randomly selected stream-side points. The cut value used for membership was 0.5.

All 26 of the nests that were monitored were located in willows, which was by far the most abundant plant in the study plot. Four nests were in Arroyo Willow (*Salix lasiolepis*) and 22 in Red Willow (*Salix laevigata*). Mean nest tree height was 6.9 ± 0.5 m (range 2.4-13.2 m). Mean nest height was 3.8 ± 0.3 m (range 1.5-6.6 m). On average, the nests were located closer to the stream (5.4 ± 1.1 m, range 0-25.7 m) than the outer edge of the riparian vegetation (10.0 ± 1.4 m, range 0.4-23.0 m).

I located and monitored 26 Yellow Warbler nests over the course of the breeding season. The earliest nest initiation date (based on the first egg laid) for the nests that I monitored was 3 May. Only two (8%) nests were successful and produced young while 24 nests (92%) failed to produce young. The daily survival rate for all nest periods combined was 0.912 ± 0.019 (Table 5). The Mayfield (1975) estimate of overall nest success was 10.0%. There appears to be little difference in nest success between periods,

although daily survival rates were lower during the laying period than the incubation and nestling periods.

Table 5. Daily survival and total nest success (Mayfield 1975) for Yellow Warblers breeding in riparian habitat along the lower Pajaro River, California, 2008.

Period	Exposure Days	Daily survival (SE, 95% CI)	Nest success (95% CI)
Laying	39	0.821 (0.061, 0.698-0.943)	0.453 (0.237-0.792)
Incubation	112.5	0.929 (0.024, 0.880-0.977)	0.444 (0.246-0.777)
Nestling	63.5	0.937 (0.030, 0.876-0.998)	0.522 (.0266-0.980)
All	216	0.912 (0.019, 0.874-0.950)	0.100 (0.035-0.276)

Nest predation directly caused 48% of the nest failures (11/23) (Table 6). In fact, when including nests that had already failed due to cowbirds, 83% (20/24) of nests that reached egg-laying were eventually depredated. Depredation events resulted in either intact empty nests or nests that were destroyed after being torn from the supporting branches. Of the 20 nests that were eventually depredated, seven were destroyed, 11 were emptied but left intact, and two contained dead adults. Of the seven destroyed nests, all but one occurred prior to the nestling stage, and five of the seven were not yet parasitized. No depredated nests were found destroyed past 12 June. Two nests were abandoned and one nest had an unknown fate (depredated before the contents were identified).

Brown-headed cowbirds parasitized 61% (14/23) of known active Yellow Warbler nests, and were directly responsible for at least 43% (10/23, excluding abandoned nests) of the nest failures. Of the 10 nests that failed due to cowbird parasitism, two fledged cowbird young, and the remaining eight were depredated. No instances of cowbird egg burial were observed.

Table 6. Nest outcome and causes of failure for Yellow Warblers breeding at the Pajaro River, Santa Cruz County, California, 2008. BHCO refers to Brown-headed Cowbird parasitism.

	All nests	Parasitized nests	Unparasitized nests	Unknown
Nest Outcome				
Total number of nests	26	14	11	1
Successful ^a	2	1	1	0
Unsuccessful	24	13	10	1
Percent successful	8%	7%	9%	0
Causes of nest failure				
Depredated	12	3	8	1
BHCO ^b	10	10	-	-
Abandoned (unknown)	2	-	2	-

^aNests from which at least one Yellow Warbler fledged.

^bIncludes two nests fledging BHCO and eight lost to predation subsequent to parasitism.

DISCUSSION

Habitat loss *per se* does not seem to be the reason for the declines in Yellow Warbler populations on the central coast of California. In this study, Yellow Warblers were most abundant in valley riparian systems at the Pajaro River, where habitat loss has been greatest over the years because of agricultural and flood control pressures. By comparison, Yellow Warblers were scarce along streams where there has been minimal destruction of riparian forests.

On the landscape scale, Yellow Warblers were most abundant along streams with adjacent agricultural fields. In fact, 84% Yellow Warblers in Santa Cruz County were breeding along the lower main stem Pajaro River, bordered almost entirely by row crop agriculture. These findings were similar to a study in Idaho, where Saab (1999) found

Yellow Warblers to be associated with increased agriculture and decreased upland natural vegetation. Saab (1999) also found Yellow Warblers to be associated with areas of high landscape heterogeneity. Although not measured in this study, the ongoing but irregular vegetation removal (for maintenance of the levee benches) along the Pajaro River has created an abundance of patchy, early successional vegetation with high structural heterogeneity. Saab (1999) speculated that this association may be reminiscent of pre-dam conditions when flooding was more frequent.

At the patch scale, willow shrubs appeared to be the primary characteristic with which Yellow Warblers are associated in coastal riparian forests. Yellow Warblers were mainly found in areas with a short, sparse riparian deciduous canopy and extensive willow shrub cover. They were also associated with stream characteristics like flow direction (aspect) and channel shape, which can influence conditions that are conducive to the growth of willows. These findings are similar to those in other parts of the country, where Yellow Warblers were highly associated with increasing shrub cover and density and high amounts of edge (Saab 1999), and positively correlated with average willow height (Olechnowski and Debinski 2008). Likewise, in northern California, willow cover was an important predictor of high Yellow Warbler abundance (Heath 2008). The most obvious explanation for this association is their frequent use of willow shrubs for nest substrate.

Habitat degradation may be partly to blame for range contraction of this species on the central coast of California. The *lack* of disturbance appears to degrade the habitat in a riparian system to a point where it is no longer appealing to Yellow Warblers,

probably due to the paucity of shrubs for nesting and foraging. The Pajaro River contains the most disturbed riparian system of the six streams in the study, but hosts most of the breeding population. In 1995, after a catastrophic flood in the Pajaro Valley, much of the riparian vegetation was removed by bulldozers for future flood control, including many of the mature trees that made up the canopy. Since then, there have been annual vegetation reduction regimes to control flooding. This activity has resulted in extensive willow thickets with which Yellow Warblers are highly associated. Perhaps this management partly mimics cycles of disturbance that would occur in a naturally functioning hydrologic system. Many of the other streams surveyed had the correct vegetation *composition*, but not the necessary vegetation *structure*. For instance, willows may have been present, but offered too little cover or were too short or tall to be attractive for nest sites. Likewise, tall alders and cottonwoods with thick canopies line several of the streams where Yellow Warbler abundance was low, creating shady, poor growing conditions for willows.

However, Yellow Warblers nesting in high-probability (predictive model) habitat on the Pajaro River had very low reproductive success, due in part to high predation rates. Tewksbury et al. (1998) compared nesting productivity between non-fragmented forested sites and fragmented agricultural sites in Montana and found that the forested sites had high predation and low parasitism whereas the agricultural sites had low predation and high parasitism that, in the end, resulted in equally low nesting success. Similarly, in the northern Sierra Nevada, Cain et al. (2003) found that nests further away from forest edges or trees experienced lower predation rates. A study conducted in

coastal Marin County, California, just north of the San Francisco Bay, found high (73%) predation rates of Wilson's Warblers, which also nest in shrubs, nesting in riparian woodland, especially near human-use areas (Michaud et al. 2004). I predicted that predation rates would be low at the Pajaro River, which is bordered mainly by agriculture and has no adjacent forested habitat and minimal adjacent residential areas.

Unfortunately, overall predation rates were comparably high to the Marin County and Sierra Nevada studies, and brood parasitism rates were high.

Brown-headed Cowbird parasitism, in conjunction with high predation rates, poses a real threat to the largest concentration of Yellow Warblers in the study area. On the landscape scale, cowbirds were positively associated with agriculture, as were Yellow Warblers. As a result, parasitism rates were high and the parasitized nests almost always resulted in failure. I suspect that the cowbirds also played a role in depredating and destroying the warbler nests early in the season during egg-laying. Interestingly, there were no nests destroyed during a depredation event after 12 June, and most of those that were destroyed did not yet carry a cowbird egg. This activity may have accounted for the lower daily survival rates during the laying period. In other parts of the country, Yellow Warblers have adopted anti-parasite strategies such as nest abandonment or burying cowbird eggs with another layer of nest material, sometimes producing multi-tiered nests (Clark and Robertson 1981, Lowther et al. 1999). Inland California populations (*D. p. morcomi*) on the eastern side of the Sierra Nevada mountain range regularly bury cowbird eggs (S. Heath, pers. comm.). No egg burial was observed in the studied coastal population, and only two nests were abandoned (both prior to containing eggs). Perhaps

the coastal California Yellow Warbler population (*D. p. brewsteri*), which hasn't evolved with cowbirds for as long as inland populations, are more susceptible to cowbird pressure.

Effectively recovering and managing declining populations of coastal Yellow Warblers relies on the knowledge of their specific breeding habitat requirements, its availability in the landscape, and high productivity and recruitment at these breeding locales. The predictive habitat association model will be useful for conservation and management of Yellow Warbler populations on the central coast of California. First, it can be used to identify potential habitat, even in the non-breeding season when the birds are on their wintering grounds. Second, it can be used to guide restoration projects that attempt to enhance or create habitat to facilitate population expansion. However, its usage must be coupled with demographic and nest survival data.

Simply employing the habitat-association model without demographic data may result in the creation of a sink, or even worse, an ecological trap and lead to the further demise of the population. No doubt source-sink dynamics play a role in the health of the central coast metapopulation. The Pajaro River contains the largest breeding population and has likely been a source for other breeding locales in the region in the past. Flood control management of the vegetation along this river may have turned this source population into a sink by facilitating access to nest predators and parasites. Even worse, the highly disturbed riparian amidst agricultural fields at the Pajaro River may constitute an "attractive sink", otherwise known as an ecological trap, where the habitat is highly attractive to Yellow Warblers but of very low quality.

It will take creative biologists and land managers to reconcile the problems of predation and nest parasitism with the Yellow Warblers preference for disturbed habitat. How does one manage for a species that is attracted to marginal “edgy” habitat, where there are potentially inflated numbers of native and non-native nest predators? High predation and parasitism rates of Yellow Warblers in the Mono Basin of eastern California have resulted in low daily survival rates for nests. Yet, the population seems to be stable (Heath 2008). Perhaps low nest survival and low nesting success from predation is the norm for this species. Fortunately, Yellow Warblers seem to respond quickly and favorably to habitat restoration and cowbird trapping by recolonizing sites (Heath 2008). However, warbler presence at these restored sites may not necessarily be indicative of population success if met with high predation and parasitism rates.

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