

AN ABSTRACT OF THE THESIS OF

Jessica Grace Billings for the degree of Honors Baccalaureate of Science in Biology presented on December 2, 2008. Title: Bird Predation on the Garter Snake *Thamnophis elegans* near Eagle Lake in California.

Abstract approved: _____
Stevan J. Arnold

Previous studies have revealed distinctive ecotypic differences between garter snakes living in the meadow and lakeshore environments around Eagle Lake in California. Snakes from these contrasting environments have significantly different growth rates, litter sizes, adult body size, annual survival, and coloration. To try and explain these differences, bird predation was studied and compared between the two environments. Over a period of two years, snakes were collected and their wounds were photographed and analyzed. A bird survey was also conducted in the area.

The analysis of wounds revealed that a larger proportion of snakes were wounded in the meadow sites, but of these wounded snakes, a significantly larger proportion of smaller snakes displayed wounds in the lakeshore site. Furthermore, the bird survey suggested a much stronger bird predation pressure prevailed in the lakeshore environment. These results suggest that smaller birds may be preying on lakeshore snakes, injuring more of the smaller snakes. Additionally, birds may be more adept at killing the garter snakes in the lakeshore region, leaving fewer alive, injured snakes with visible wounds. These differences in bird predation may help promote the ecotypic differences between the lakeshore and meadow garter snakes.

Key Words: lakeshore, meadow, ecotypic differences, survival
Corresponding e-mail address: billinje@onid.orst.edu

©Copyright by Jessica Grace Billings
December 2, 2008
All Rights Reserved

Bird Predation on the Garter Snake
Thamnophis elegans near Eagle Lake in California

by

Jessica Grace Billings

A PROJECT

submitted to

Oregon State University

University Honors College

in partial fulfillment of
the requirements for the
degree of

Honors Baccalaureate of Science in Biology (Honors Scholar)

Presented December 2, 2008
Commencement June 2009

Honors Baccalaureate of Science in Biology project of Jessica Grace Billings
presented on December 2, 2008.

APPROVED:

Mentor, representing Biology

Committee Member, representing Biology

Committee Member, representing Biology

Chair, Department of Biology

Dean, University Honors College

I understand that my project will become part of the permanent collection of Oregon State University, University Honors College. My signature below authorizes release of my project to any reader upon request.

Jessica Grace Billings, Author

Acknowledgements

I would like to thank my mentor, Stevan Arnold, for introducing me to this project and guiding me throughout its process. You were always able to point me in the right direction when I couldn't figure out which way I should be going. Your knowledge on the topic was a huge help. Thank you for teaching me the difference between "putative" and "punitive" on one of the first days of recording data. I would also like to thank Anne Bronikowski and Amanda Sparkman for their ongoing research on the topic and especially for Amanda's very thorough bird survey. To everyone at snake camp, thank you for helping catch and process snakes and making it such a fun and welcoming place. I am extremely grateful to my family, especially my snake-phobic mom, who never did quite understand why I wanted to do a project on snakes, but still supported me. Thank you, Nick, for not minding when I spent hours in front of the laptop, mumbling to myself about snakes and birds. Finally, I would have never become involved in the project without the generous support from the NSF Research Experience for Undergraduates (REU) Award supplement to NSF grant DEB0323379 (to SJA and AMB).

TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION.....	1
METHODS.....	4
Wound and Scar Data.....	4
Bird Survey.....	6
RESULTS.....	8
Wound and Scar Data.....	8
Bird Survey.....	12
DISCUSSION.....	15
BIBLIOGRAPHY.....	18

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. The lakeshore environment.....	1
2. The meadow environment.....	2
3. Bill mark scar on a garter snake.....	5
4. Minor wound on snake.....	10
5. Major wound on snake.....	11
6. Comparison of different bird beaks.....	17

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Incidence of Bill Marks at Lakeshore Sites.....	8
2. Incidence of Wounds at Lakeshore Sites.....	8
3. Incidence of Bill Marks at Meadow Sites.....	9
4. Incidence of Wounds at Meadow Sites.....	9
5. Comparison of Wounded Snakes Between Ecotypes.....	9
6. Comparison of Wounded Snakes of Different Sizes Between Ecotypes..	10
7. Comparison of the Severity of Wounds Between Snakes of Different Ecotypes.....	11
8. Comparison of Snakes with Bill Marks Between Ecotypes.....	12
9. Comparison of Differently Sized Snakes With Bill Marks.....	12
10. Bird Species Found in the Eagle Lake Region Known to Eat Snakes ...	13
11. Comparison of Bird Pressure Between Environments.....	14

Bird predation on the garter snake *Thamnophis elegans* near Eagle Lake in California

Introduction:

For the terrestrial garter snakes *Thamnophis elegans* living in the Eagle Lake basin in California, life can take two very different directions. In this small area of around 100 square kilometers, located in Lassen Co., California, populations of snakes live in two contrasting environments: the rocky shores of the lake and the densely vegetated mountain meadow habitats (see Figures 1 & 2). Although these

populations began as one ancestral population, they have differentiated into two separate ecotypes (Manier et al., 2007). Across distances as small as a few kilometers, garter snakes in each of these



Figure 1: The lakeshore environment

environments vary in several dramatic ways. Based on thirty years of field data and six years of laboratory data, previous studies have shown a series of ecotypic differences between the two populations of snakes (Bronikowski & Arnold, 1999).

A striking difference between lakeshore and meadow snakes is in their growth rate and survival.

Snakes that inhabit the lakeshore environment have a much faster



Figure 2: The meadow environment

growth rate, mature at an

earlier age, have larger litters, and have a larger adult body size. However, they also have a low annual survival rate compared to the meadow snakes

(Bronikowski & Arnold, 1999). In addition, the two ecotypes differ in coloration.

The lakeshore snakes tend to have muted colors. They typically have dull yellow or tan stripes and a gray body, while the meadow snakes have yellow or orange stripes and a black body (Manier et al., 2007). Laboratory studies indicate that at least some of these ecotypic differences are heritable (Brownikowski & Arnold, 1999, Manier et al., 2007).

Several factors have been examined to determine why this ecotypic differentiation has evolved. The first factor is diet; the two ecotypes feed on different prey. In the lakeshore habitat, snakes feed primarily on fish while snakes in the meadow eat anuran tadpoles and metamorphs (*Bufo boreas*, *Pseudacris regilla*) (Kephart, 1982, Kephart & Arnold, 1982). Furthermore,

weather affects the availability of their food. Around 50% of the time, it does not rain enough for anurans to breed in the meadow, and the meadow snakes must find alternative sources for food (Bronikowski & Arnold, 1999). While this difference in food availability may explain why meadow snakes have a slower growth rate and smaller litters, it does not explain why they have a higher annual survival rate than the lakeshore snakes, which have a more dependable source of food. It also does not explain the coloration differences. Both of these differences suggest that other factors are involved.

The differences in coloration between the involved ecotypes may increase camouflage in their respective environments. The duller colors of the lakeshore snakes may blend in with the rocks and brush of the lakeshore environment, making the snakes harder to detect. The brighter contrast of the meadow snakes may promote resemblance with the grass and dead rushes scattered throughout the meadow environment (Manier et al., 2007). These differences would therefore be the result of selection for camouflage to hide from potential predators. Additionally, the ecotypic difference in survival rate could be due to a difference in predation rate or predation type in the two areas.

Because birds are thought to be one of the principal predators of snakes, a necessary first step is to study the birds in each area. In order to determine if there is an ecotypic difference in bird predation in, I examined the number and type of bill mark scars left on field-captured snakes, as well as the types and frequencies of snake-eating birds found in the meadow and lakeshore.

Methods:

The *T. elegans* in this study were collected in the Eagle Lake area in Lassen County, CA. Eagle Lake is California's second-largest natural lake and supports a wide range of wildlife. In this area, the meadow habitats have slightly cooler temperatures than the lakeshore environments, around 5^o-10^oC cooler. Additionally, the meadow tends to have variable prey and water availability, compared with the lakeshore, which has continuous availability of water and prey (Bronikowski & Arnold, 1999).

Wound and Scar Data

For several weeks during the summer of both 2005 and 2006, garter snakes were captured in a variety of meadow and lakeshore environments. During 2005, 5 lakeshore locations (Gallatin Shoreline, Pikes Point, Marina, Merrill, Rocky Point, and Stones) and 6 meadow locations (Colman, Mahogany Lake, Nameless Meadow, Papoose Meadows, Summit, and McCoy Flat Res.) were sampled. During 2006, 4 lakeshore locations (Gallatin Shoreline, Pikes Point, Marina, and Wildcat Shoreline) and 5 meadow locations (Colman, Mahogany Lake, Nameless Meadow, Papoose Meadow, and Summit) were sampled. Captured snakes were examined for wounds and scars, and if these were present, the snakes were then sexed, weighed, photographed, and had their length measured.

Later, the photographs were examined to document the number of wounds per snake, the size of the wound (in mm²), the severity of the wound (using a rating system from 1-4), and where the wound was located (using a numerical system where 1 represented the neck, 2 represented the midbody, and 3 represented the tail). The data was divided into two categories for analysis: scars that were clearly made by a bird's beak and other wounds from unknown origin. Bill mark scars were easily identified by a pair of thin, line-like impressions or scars on the snake (see Figure 3).

Using Chi-Square Tests, the incidence of bill marks and wounds was first compared on a location-to-location basis, within the meadow or lakeshore environment. In other words, the incidence of bill marks and wounds



Figure 3: Bill mark scar on a garter snake

were compared between each meadow location, then between each lakeshore location to see if the incidence varied between locations within each environment.

To further explore the data, Fisher's Exact Tests were used to compare the lakeshore and meadow ecotypes as a whole. Several questions were asked:

- 1) Are more snakes wounded in one environment than in the other?

- 2) Are smaller snakes wounded more often in one environment than in the other?
- 3) Are snakes wounded more severely in one environment than in the other?
- 4) Do more snakes have bill marks in one environment than in other?
- 5) Do smaller snakes have bill marks more often in one environment than in the other?

Bird Survey

To discover which birds are known to prey upon garter snakes, I conducted a survey of the literature. The resulting list of birds known to prey on snakes was then compared with a list of birds from the Eagle Lake region, compiled by an Audubon Society bird count (http://cbc.audubon.org/cbccurrent/current_table.html). Birds that have been documented to inhabit the area and are known to kill garter snakes were then identified as possible suspects. The prevalence of these suspects was compared between the meadow and lakeshore locations to see if there is a larger number of suspect bird species in one environment than in the other.

In the summer months of 2007, a collaborator (A. Sparkman) conducted a bird survey in three different meadow locations and three lakeshore locations and made her data available for inclusion in this report. Over a period of 1½ months, the locations were each sampled three times for time periods of two hours each from 9am-11am. During these time periods, birds were identified and tallied

every ten minutes. Because some birds could have been in the area for longer than ten minutes and were therefore counted twice, these numbers represent predation pressure, not the actual population numbers of birds.

Results:

Wound and Scar Data

The first step in analyzing the data was to see if the incidence of wounds and bill marks varied significantly between locations of the same environment. To do this, Chi-Square Tests were used. For all the following tests, a p-value of less than 0.05 was considered significant. For both 2005 and 2006, it was found that the incidences did not vary significantly between locations of the same environment (see Tables 1-4), suggesting that the data could be combined from all the locations of each environment to compare meadow data vs. lakeshore data.

Table 1: Incidence of Bill Marks at Lakeshore Sites			
Year: 2005			
	Bill Mark(s) Present	No Bill Marks	Total
Gallatin	6	55	61
Pikes	1	42	43
Marina	2	32	34
Total	9	129	138
	P<0.75	$X^2=2.3$	d.f.=2
Year: 2006			
	Bill Mark(s) Present	No Bill Marks	Total
Gallatin	5	33	38
Pikes	1	50	51
Wildcat	0	2	2
Total	6	85	91
	P<0.75	$X^2=4.6$	d.f.=2

Table 3: Incidence of Bill Marks at Meadow Sites			
Year: 2005			
	Bill Mark(s) Present	No Bill Marks	Total
Papoose	7	43	50
Nameless	9	124	133
Mahogany	8	32	40
Summit	12	82	94
Total	36	281	317
	P<0.50	$X^2=6.3$	d.f.=3
Year: 2006			
	Bill Mark(s) Present	No Bill Marks	Total
Papoose	5	48	53
Nameless	0	51	51
Mahogany	1	50	51
Total	6	149	155
	P<0.25	$X^2=7.0$	d.f.=2

Table 2: Incidence of Wounds at Lakeshore Sites			
Year: 2005			
	Wound(s) Present	No Wounds	Total
Pikes	7	36	43
Marina	7	27	34
Total	33	105	138
	P<0.75	$X^2=3.2$	d.f.=2
Year: 2006			
	Wound(s) Present	No Wounds	Total
Papoose	28	22	50
Nameless	57	76	133
Mahogany	15	25	40
Summit	42	52	94
Gallatin	10	28	38
Total	142	175	317
	P<0.75	$X^2=3.6$	d.f.=2
Wildcat	1	1	2
Total	25	66	91
	P<0.95	$X^2=0.5$	d.f.=2
Year: 2006			
	Wound(s) Present	No Wounds	Total
Papoose	31	22	53
Nameless	18	33	51
Mahogany	24	27	51
Total	73	82	155
	P<0.25	$X^2=5.6$	d.f.=2

To further compare the data from the two environments, I return to the questions asked earlier. The first issue is: Are more snakes wounded in one environment than in the other? To answer this question, I used a Fisher's Exact Test. With a p-value of less than 0.001, the findings were statistically significant that a larger proportion of the snakes have wounds from the meadow sites (see Table 5).

Table 5: Comparison of Wounded Snakes Between Ecotypes			
	Wounded	Not Wounded	% Wounded
Lakeshore	58	171	25.3%
Meadow	215	257	45.6%
	P < 0.001		

The next question I asked was: Are smaller snakes wounded more often in one environment than in the other? In order to answer this question, I grouped the snakes into two sets of data within each ecotype. Small snakes were defined as snakes with a snout-vent length (SVL) of less than 300mm. Medium-large snakes were defined as SVL \geq 300mm. Again, a Fisher's Exact Test was used and with a p-value of 0.001, the results suggest that a larger proportion of small snakes have wounds at lakeshore sites (see Table 6)

Table 6: Comparison of Wounded Snakes of Different Sizes Between Ecotypes

	Small	Medium-Large	% Small
Lakeshore	25	33	43.1%
Meadow	46	169	21.4%
	P = 0.001		

The third question I asked was: Are snakes wounded more severely in one environment than in the other? In order to judge how “severe” a wound is, a rating system was used where each wound is given a rating between 1 and 4, based on appearance at the time of capture. A rating of 1 would be a very minor wound, such as a snagged scale or small puncture. A rating of 4 would be a much more severe wound, such as a large scrape or scar that covered many scales (see Figures 4 & 5).



Figure 4: Minor wound on snake

For snakes with multiple wounds, an average was taken of the ratings. The snakes were then grouped into two categories, in which a snake with minor wounds was defined as having a rating between 1-1.5 and a



Figure 5: Major wound on snake

snake with moderate-severe wounds was defined as anything greater than that. Using another Fisher's Exact Test, the severity of the meadow snakes' wounds were compared with the severity of lakeshore snakes' wounds. A p-value of 0.769 was obtained, suggesting that snakes are not wounded more severely at either site (see Table 7).

Table 7: Comparison of the Severity of Wounds Between Snakes of Different Ecotypes			
	Minor	Moderate-Severe	% Minor
Lakeshore	31	27	53.5%
Meadow	110	105	51.2%
	P = 0.769		

Next, I focused on wounds that almost certainly were caused by birds, which appear as bill mark scars. The first step in analyzing these scars is to ask: Do more snakes have bill marks in one environment than in other? I used another Fisher's Exact Test to compare the proportion of snakes with bill marks in the meadow region to the proportion of snakes with bill marks in the lakeshore region. This test resulted in a p-value of 0.307, which is not a significant value.

Therefore, the same proportion of snakes from each site have bill marks (see Table 8).

	Bill Marks	No Bill Mark	% Bill Marks
Lakeshore	15	214	6.6%
Meadow	42	430	8.9%
	P = 0.307		

The last step in the analysis of bill marks was to ask: Do smaller snakes have bill marks more often in one environment than in the other? Again, the snakes were divided into two categories in which small snakes were defined as snakes with a SVL of less than 300mm and medium-large snakes were defined as SVL \geq 300mm. A final Fisher's Exact Test was used to compare these two sets of snakes, which resulted in a p-value of 0.062, which is not significant (see Table 9). Therefore, neither smaller nor larger snakes have more bill mark scars.

	Small	Medium-Large	% Small
Lakeshore	6	9	40.0%
Meadow	6	36	14.3%
	P = 0.062		

Bird Survey

To discover which species of birds are known to prey on snakes, a survey of the literature was conducted and compared with a bird count done by the Audubon Society (http://cbc.audubon.org/cbccurrent/current_table.html). Birds

that appeared on both lists became suspects that are both known to eat snakes and occur in the Eagle Lake region (see Table 10).

Table 10: Bird Species Found in the Eagle Lake Region Known to Eat Snakes	
Bird Species	Referenced to Eat Snakes
Osprey (<i>Pandion haliaetus</i>)	Wiley and Lohrer (1973)
Sandhill Crane (<i>Grus canadensis</i>)	Guthrie (1932)
Turkey Vulture (<i>Cathartes aura</i>)	Guthrie (1932)
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	Bent (1922)
Great Blue Heron (<i>Ardea herodias</i>)	Guthrie (1932), Manier et al. (2007); ‡
Black-crowned Night Heron (<i>Nycticorax nycticorax</i>)	Allen (1938)
Great Egret (<i>Ardea alba</i>)	Baynard (1912)
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	Grubb (1995), Haywood and Ohmart (1986), McEwan and Hirth (1980), Guthrie (1932); ‡
Northern Harrier (<i>Circus cyaneus</i>)	Guthrie (1932)
Sharp-shinned Hawk (<i>Accipiter striatus</i>)	Guthrie (1932)
Cooper's Hawk (<i>Accipiter cooperii</i>)	Rosenfield (1988)
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	Knight and Erickson (1976), Guthrie (1932), Errington (1933)
Rough-legged Hawk (<i>Buteo lagopus</i>)	McAtee (1935)
Golden Eagle (<i>Aquila chrysaetos</i>)	Guthrie (1932)
American Kestrel (<i>Falco sparverius</i>)	Guthrie (1932)
Mallard (<i>Anas platyrhynchos</i>)	Guthrie (1932)
Northern Shrike (<i>Lanius excubitor</i>)	Guthrie (1932)
Black-billed Magpie (<i>Pica hudsonia</i>)	Guthrie (1932)
Common Raven (<i>Corvus corax</i>)	Camp (1993)
American Crow (<i>Corvus brachyrhynchos</i>)	Guthrie (1932)
American Robin (<i>Turdus migratorius</i>)	Guthrie (1932), Jayne & Bennett (1990); ‡
Brewer's Blackbird (<i>Euphagus cyanocephalus</i>)	‡
‡ observed preying on garter snakes at Eagle Lake	

This list of known predators of snakes was then compared with the bird survey conducted at Eagle Lake. Counts of each bird species were tallied for the

meadow region and the lakeshore region. Known predators were totaled and compared between the lakeshore and meadow environments (see Table 11). The lakeshore had a total of 893 counts and the meadow had a total of 331 counts. It is important to remember that these numbers do not represent an accurate measurement of the bird populations in these areas, but they do represent how often potential bird predation is in the area. Therefore, it is clear there is a much higher bird predation pressure in the lakeshore environment.

Table 11: Comparison of Bird Pressure Between Environments		
	Lakeshore	Meadow
Osprey	24	0
Brewer's Blackbird	688	182
Bald Eagle	8	1
Double-crested Cormorant	48	0
Robin	117	84
Great Blue Heron	3	0
Mallard	1	0
Northern Harrier	0	41
Turkey Vulture	1	9
Red-tailed Hawk	0	2
Common Raven	3	4
Sandhill Crane	0	8
Total Suspect Predators	893	331

Discussion:

At first glance, the results of this study seem contradictory. Previous studies showed that the snakes in the lakeshore environment have a lower annual survival rate. Therefore, I expected that captured snakes in the lakeshore environment would have more wounds and bill mark scars. However, I found that a larger proportion of snakes in the meadow had wounds, and there was no significant difference between the proportion of snakes in either environment that had bill mark scars.

However, my study also revealed that a larger proportion of small snakes have wounds in the lakeshore environment. The data show that of all the snakes that were wounded in the lakeshore environment, almost half were small snakes, as opposed to less than a quarter in the meadow environment. This result suggests that predators in the lakeshore environment are attacking smaller snakes more often than predators in the meadow region. Previous studies also revealed what may be a long-term consequence of this higher predation on smaller snakes in the lakeshore region. Snakes in this area have a faster growth rate and a larger adult body size (Bronikowski & Arnold, 1999).

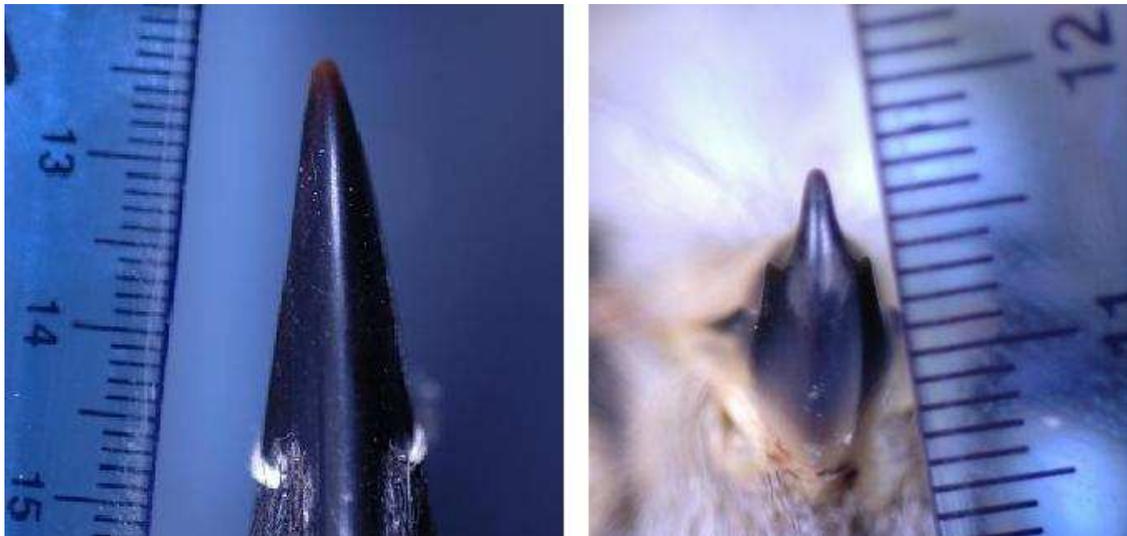
Because the smaller snakes are wounded so much more frequently in the lakeshore environment, it is possible that the predators in that area are smaller as well. The data from the bird study supports this idea. Smaller birds, such as Brewer's Blackbirds and Robins were more frequently observed in the lakeshore areas. Although the injuries classified as "wounds" cannot be identified as injuries

from a bird, as bill mark scars can, it is very possible some of these wounds are caused from the pecking motion of a bird's beak or the scraping of its claws.

It would be incorrect to assume that because a smaller proportion of wounded snakes were found in the lakeshore region, that a smaller proportion of them were killed by predators. It is also possible that a smaller proportion of wounded snakes were found in that area because lakeshore predators are more efficient killers and kill their prey more often than predators in the meadow region. If this were true, fewer wounded snakes would be captured at lakeshore sites, even though many more of the snakes were being killed by predators. This scenario is consistent with my impressions of vulnerability in the two habitats. Whereas the meadow environment is very thick with vegetation (Fig. 2) that would keep snakes hidden from potential predators, the lakeshore environment is rocky with far less vegetation (Fig. 1). Snakes might be easily spotted amongst the rocks because they do not have so many places to hide.

In order to further analyze the data, I suggest that the bill mark scar photos be compared with the bills of different species of birds (see Figure 6). By comparing the size and shape of the scars, it would be possible to determine what types of birds were leaving the scars. If there is a significant difference between the types of scars left on snakes in the meadow and lakeshore regions, that could help determine if there really is a difference in the species of birds preying on snakes in each area, especially between different sizes of snakes. If this information was compared with a more in-depth bird survey in which birds

were actually observed attacking snakes in the Eagle Lake area, it could show that birds have different success killing snakes in either one site or the other.



*Figure 6: Comparison of different bird beaks
On left: American Crow. On right: American Kestrel*

Clearly, there are alternative interpretations of the results of this study, but more information is needed in order to decide if they are correct or not. The bird survey suggests different species of birds are present and preying on the garter snakes in lakeshore and meadow environments. It is possible that this difference in predator identity causes a larger proportion of snakes to be wounded in the meadow area, but at the same time, causes smaller snakes to be wounded more often in the lakeshore area. These differences in predation could very well be a major driving force that promoted ecotypic differences between meadow and lakeshore garter snakes in the Eagle Lake region.

Bibliography:

- Allen, R.P. (1938). Black-crowned night heron colonies on Long Island. *Proceedings of the Linnaean Society of New York*. 49, 43-51.
- Baynard, O.E. (1912). Food of herons and ibises. *The Wilson Bulletin*. 24, 167-169.
- Bent, A.C. (1922). Life histories of North American petrels and pelicans and their allies. *U.S. Natl. Mus. Bull.*. 121.
- Bronikowski, A.M., & Arnold, S.J. (1999). The evolutionary ecology of life history variation in the garter snake *Thamnophis elegans*. *Ecology*. 80, 2314-2325.
- Camp, R.J., R.L. Knight, H.A.L. Knight, M.W. Sherman, and J.Y. Kawashima. (1993). Food habits of nesting common ravens in the eastern Mojave desert. *Southwest. Natur.* 38, 163-165.
- Errington, P.L. (1933). Food habits of southern Wisconsin raptors. *The Condor*. 35, 19-29.
- Grubb, T.G. (1995). Food habits of bald eagles breeding in the Arizona desert. *Wilson Bulletin*. 107, 258-274.
- Guthrie, J.E. (1932). Snakes versus birds; birds versus snakes. *Wilson Bulletin*. 44, 88-113.
- Haywood, D.D., & Ohmart, R.D. (1986). Utilization of benthic-feeding fish by inland breeding bald eagles. *The Condor*. 88, 35-42.
- Jayne, B.C., & Bennett, A.F. (1990). Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution*. 44, 1204-1229.
- Kephart, D.E. (1982). Microgeographic variation in the diets of garter snakes. *Oecologia*. 52: 287-292.
- Kephart, D.E. & Arnold, S.J. (1982). Garter snake diets in a fluctuating environment: a seven-year study. *Ecology*. 63: 1232-1236
- Knight, R.L., & Erickson, A.W. (1976). High incidence of snakes in the diet of nesting red-tailed hawks. *Raptor Research*. 10, 108-111.

- Manier, M.K., Seyler, C.M., & Arnold, S.J. (2007). Adaptive divergence within and between ecotypes of the terrestrial garter snake, *Thamnophis elegans*, assessed with Fst-Qst comparisons. *J. Evol. Biol.* 20, 1705-1719.
- McAtee, W.L. (1935). *Food habits of common hawks*. U.S. Dep. Agric., Circular 370, Washington, D.C.
- McEwan, L.C., & Hirth, D.H. (1980). Food habits of the bald eagle in north-central Florida. *The Condor*. 82, 229-231.
- National Audubon Society (2006). The Christmas Bird Count Historical Results [Online]. Available <http://www.audubon.org/bird/cbc> [September 3, 2007]
- Rosenfield, R.N. (1988). *Cooper's Hawk*. New Haven, CT: Yale Univ. Press.
- Wiley, J.W., & Lohrer, F.E. (1973). Additional records of non-fish prey taken by ospreys. *The Wilson Bulletin*. 85, 468-470.