

Avian Predation and the Evolution of Life Histories in the Garter Snake *Thamnophis elegans*

Author(s): A. M. Sparkman and A. M. Bronikowski J. G. Billings ,
D. Von Borstel and S. J. Arnold

Source: The American Midland Naturalist, 170(1):66-85. 2013.

Published By: University of Notre Dame

URL: <http://www.bioone.org/doi/full/10.1674/0003-0031-170.1.66>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Avian Predation and the Evolution of Life Histories in the Garter Snake *Thamnophis elegans*

A. M. SPARKMAN¹ AND A. M. BRONIKOWSKI

Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames 50011

AND

J. G. BILLINGS, D. VON BORSTEL AND S. J. ARNOLD

Department of Zoology, Oregon State University, Corvallis 97331

ABSTRACT.—Predation pressure has often been postulated as a major selective force for the evolution of life histories, with high predation (particularly on small sizes) resulting in a fast-living strategy characterized by fast growth, early maturation, and short lifespan. However, due to the difficulty of assessing actual predation pressure in the wild, evidence for a role of predation in life-history evolution is rare. We examined the relationship between avian predation and life-history strategy in replicate populations of fast and slow-living garter snake ecotypes. To assess avian predation, we first compiled a list of known and suspected predators based on direct observations of predation events recorded in our long term detailed field notes from 1978 – present. Furthermore, we added to this list with published records of snake predation involving avian species known to occur in our study site, and a novel method of inferring predator identity via analysis of bill marks on live snakes. Using this list of candidate predators, we conducted surveys quantifying predator incidence in replicate habitats of both ecotypes. We found that known and suspected predators are more abundant in habitats of the fast-living ecotype than in those of the slow-living ecotype. We also show a higher incidence of bill marks on slow-living snakes, which may indicate an increased effectiveness at escaping predation attempts. In general, we provide evidence to suggest that predation pressure may indeed have been an important selective force in the evolution of fast growth and early maturation in the fast-living ecotype and may continue to constitute an important source of extrinsic mortality leading to differences in lifespan between the two ecotypes.

INTRODUCTION

Predator activity can induce both plastic and evolutionary change in the behaviour, morphology, development, and life history of prey species (*e.g.*, Warkentin, 1995; Crowl and Covich, 1990; Janzen *et al.*, 2000; Eggers *et al.*, 2006; Swain *et al.*, 2007). Furthermore, prey responses to predators can be a complex function of such factors as foraging risk, availability of refugia, strength and consistency of predation pressure, and life-history trade-offs (*e.g.*, Werner and Gilliam, 1984; Williams, 1957). Compelling examples of life-history evolution in response to predation abound, and the direction of change appears to be highly contingent on predator size preference (*e.g.*, Jennions and Telford, 2002; Vonesh and Warkentin, 2006; Basolo, 2008). For instance *Daphnia* populations in alpine Sierra lakes have evolved earlier maturation at smaller sizes in response to the introduction of nonnative salmonids that prey preferentially on larger size groups (Fisk *et al.*, 2007). Similarly, the Trinidadian guppy, *Poecilia reticulata*, has evolved delayed maturation at large sizes in the presence of gape limited predators and early maturation at small sizes in the presence of predators targeting all sizes (Reznick, 1982; Reznick *et al.*, 1990).

¹Corresponding author present address: Department of Biology, Westmont College, Santa Barbara, California 93108; e-mail: sparkman@westmont.edu; fax: 515-294-1337

While numerous studies have demonstrated how profoundly and variously prey species can be influenced by predator activity, documenting evolutionary response of life histories to predation in the wild remains a daunting task. In particular, to understand how predation contributes to intraspecific life-history differences among populations, it is important to distinguish between short term plastic responses and longer term evolutionary responses. Furthermore, phylogenetic constraint and lability, population density, resource availability, climate, and parasite abundance may act in conjunction with predation pressure to shape life-history strategy (e.g., Stearns, 1992; Norris and Evans, 2000; Arendt and Reznick, 2005). Because of these complications, understanding of the role of predation in the evolution of life histories, particularly in long-lived species, must be built on long term research that details genetic, physiological, behavioural, population, community, and landscape dynamics of wild populations.

The western terrestrial garter snake, *Thamnophis elegans*, presents an ideal system in which to study how predation affects the evolution of life-history traits. Lakeshore and meadow ecotypes in northeastern California have been studied for over 30 y and exhibit two distinct life-history strategies (Bronikowski and Arnold, 1999; Sparkman *et al.*, 2007). The lakeshore ecotype, consisting of multiple populations along the shore of Eagle Lake, California, grows fast to larger asymptotic size, matures early, gives birth to larger and more frequent litters, and has low annual survival rates across the entire lifespan. The meadow ecotype, consisting of multiple populations that inhabit montane meadows surrounding Eagle Lake, grows slowly to small asymptotic size, matures late, has low reproductive output and high annual survival rates relative to the fast growth ecotype. Neonates from both ecotypes, raised in a laboratory common environment, exhibit fixed differences in growth trajectory between ecotypes, indicating a genetic basis for life-history differences between the two ecotypes (Bronikowski, 2000).

Lakeshore snakes experience more consistent prey availability than meadow snakes, a difference that has probably contributed to, or at least facilitated, the evolution of a “fast” lifestyle (Bronikowski and Arnold, 1999; Miller *et al.*, 2010). Nevertheless, in spite of frequent years with little or no prey, as well as widespread infection by the tail trematode *Alaria* (present only in meadow habitats), meadow snakes live longer on average than lakeshore snakes. These results suggest that lakeshore snakes may incur an intrinsic cost to fast growth even though they experience relatively favourable conditions. Alternatively, extrinsic sources of mortality may be greater in lakeshore than in meadow habitats. Whether the higher adult mortality of lakeshore snakes is due primarily to intrinsic costs (e.g., a more rapid rate of senescence) or higher rates of extrinsic mortality is as yet unknown. However, the apparent absence of reproductive senescence even at late ages in either lakeshore or meadow snakes, suggests that a higher rate of extrinsic mortality on the lakeshore may be the predominant factor contributing to overall mortality rate differences between the two ecotypes (Sparkman *et al.*, 2007).

We hypothesize that avian predation has been a potent agent of selection in the evolution of life histories in Eagle Lake *T. elegans*, by selecting for faster growth to larger sizes and high early life reproduction in lakeshore snakes. Two major lines of evidence support this hypothesis. First, lakeshore snakes exhibit higher juvenile mortality than meadow snakes (Bronikowski and Arnold, 1999; Miller *et al.*, 2010). Thus, faster growth rates in the lakeshore ecotype may facilitate escape from predators that specialize on small prey or may represent an evolutionary response to high predation on all sizes. Second, lakeshore and meadow ecotypes exhibit dramatic adaptive divergence in colouration, suggesting that highly visual predators, such as birds, have been important agents of selection in this system (Manier *et al.*, 2007).

Direct observation of predation is difficult in open ended natural systems with intricate trophic relationships. Predation on snakes is especially difficult to quantify because specialization on snakes is rare in temperate communities and the incidence of snakes in the diets of generalists is poorly known. Nevertheless, there are several ways of assessing: (1) which species eat snakes, (2) how abundant those predators are in a given habitat, and (3) the relative effectiveness of those predators in different habitats. To identify potential avian predators at Eagle Lake, we compiled a list of all avian species occurring in the region. We combined observations of actual predation events at Eagle Lake with published reports of avian snake predation to create a short list of species occurring in the region that are both known and suspected predators. We also devised a computerized procedure for comparing marks on snakes with the dimensions of bird bills and evaluated the ability of that procedure to identify bird predators. Using this information on the identity of avian predators, we conducted replicate bird surveys in three lakeshore and three meadow habitats, to quantify the incidence of potential predators as an index of relative predation pressure. Finally, we examined snakes for marks and assorted wounds to determine whether incidence of snakes with bill marks or other wounds varied between lakeshore and meadow habitats, which may indicate differences in predator effectiveness.

METHODS

DIRECT OBSERVATIONS OF AVIAN PREDATION ON SNAKES

Over the course of 30 y of field work in our study system, we and our collaborators observed birds preying on snakes on several occasions. We describe these predation events in detail as direct evidence for avian predation on snakes in our system.

CANDIDATE SNAKE EATING AVIAN SPECIES

Because predation on snakes is rarely observed, we expanded our list of candidate snake-eating species first by enumerating the bird species found in our study system from a systematic search of our database of long term field notes and then by searching the literature for records of snake predation by those species. A list of avian species occurring in the Eagle Lake region was obtained from the Audubon Society Christmas Bird Count historical results (http://cbc.audubon.org/cbccurrent/current_table.html). A literature search was then conducted to determine which of these species have been known to prey on snakes in general and garter snakes in particular. We also compiled a list of web photos and amateur videos that documented avian predation on snakes (see <http://people.oregonstate.edu/~arnoldst/>). Finally, published predation reports were combined with observations of actual predation events at Eagle Lake (40°33'N, 120°46'W) to create a short-list of known and suspected avian predators in the region.

IDENTIFICATION OF PREDATORS FROM MARKS ON LIVE SNAKES

To identify potential snake eating species, marks that resembled bill impressions on snake venters were quantitatively compared with the bills of snake eating birds found at Eagle Lake. These marks (pairs of impressions or scars) came in a variety of sizes and angles, suggesting that recognition of particular species of bird predators might be possible. High resolution photographs of 74 marks on the venters of 47 *T. elegans* were taken while the snakes were stretched and held in place against a metric ruler (Fig. 1). All of the snakes were captured in Jun. 2005 at three lakeshore (L1–L3) and four meadow sites (M1–M5) and marks were photographed within 2 d of capture. To facilitate comparison to bird bills, marks were converted to trapezoids by overlaying lines on the putative bill impressions on each

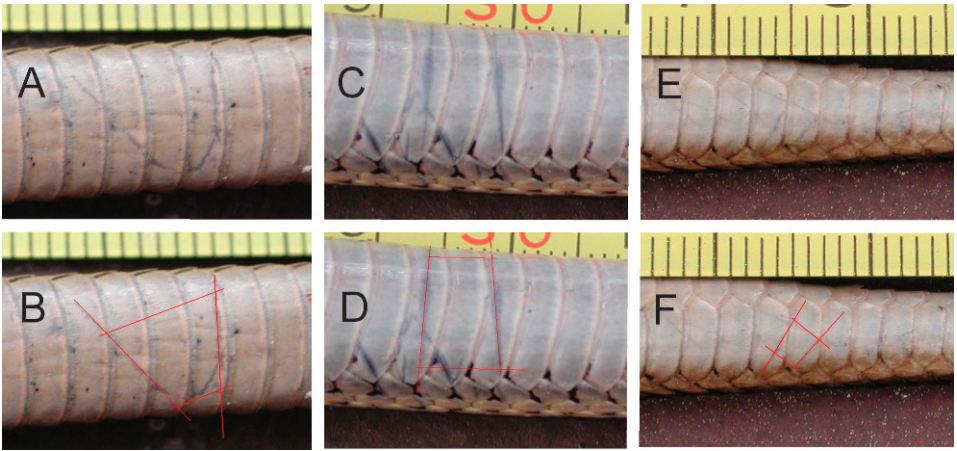


FIG. 1.—Three examples of bill marks on the venters of *T. elegans*. The upper panel shows the marks; the lower panel shows the trapezoids fitted to those marks. The mark shown in (A) gave at top best match (0.940) to the bill of a Bald eagle. The mark shown in (C) gave top best match (0.984) to the bill of a Great Blue Heron. The mark shown in (E) gave a top best match (0.994) to the bill of a Brewer's Blackbird. See Supplementary Materials for definition of terms. Please see online version for color figures

image (Fig. 1) to form the sides of a trapezoid. The tops and bottoms of a trapezoid were then drawn, using the maximum visible extents of the impressions. Finally, using the metric scale available on each image, the four sides of the trapezoid were measured to the nearest 0.1 mm.

A similar procedure was used to photograph bird bills and convert their dimensions to trapezoids (Fig. 2). Bills of 21 of the 25 snake predator species listed in Table 1 were compared to marks. The upper bills of these 21 species were photographed using avian study skins and mounted specimens. In each case a high resolution photograph was taken that included a metric ruler for scale. Trapezoids were drawn on the image of each bill following a procedure similar to that used for trapezoid-conversion of marks (Fig. 3).

We made computerized comparisons between the 74 marks and the bills of 21 species of birds, for a total of 1554 comparisons, each evaluated at an average of 136 positions. Details of this approach and statistical methods are presented in Appendix A. An R program for implementing our comparison procedure, output from that program, statistical analyses, as well as all mark and bill images are available on SJA's website (<http://people.oregonstate.edu/~arnoldst/>).

AVIAN PREDATOR SURVEYS

To estimate the incidence of known and suspected avian predators (see *Results* for species names), three replicate bird surveys were conducted at three lakeshore (L1–L3) and three meadow sites (M1–M3) (habitat IDs in accordance with those described in Bronikowski and Arnold, 1999). All 18 surveys were conducted in Jun. and Jul. from 900–1100 a.m. on a clear, mild, mornings with little wind. The surveyor (AMS) conducted the surveys from a sheltered vantage point with minimal movement so as to remain as inconspicuous as possible. All known or suspected predators that passed within approximately 100 m of the observer were tallied in each of 12 consecutive 10 min time intervals. Raptors flying or perched within

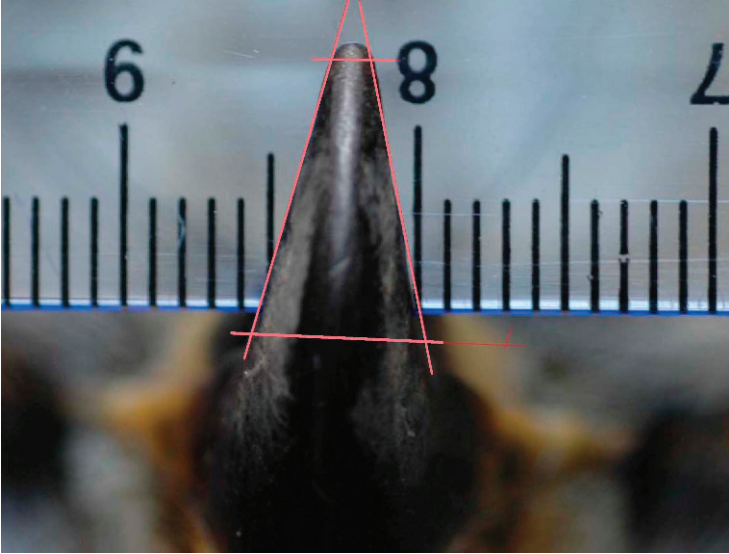


FIG. 2.—The upper bill of a rough-legged hawk showing the trapezoid that was fitted to this image. Please see online version for color figures

approximately 300 m, over areas in which snakes are known to reside, were also counted. Some individuals may have passed through the survey area multiple times throughout the morning and were therefore counted more than once. The relative incidence of predator species in different habitats was, therefore, intended as an index of relative predation pressure rather than the actual number of individual birds.

Tallies for each species were summed to obtain a total that reflected their incidence over the 2 h survey period. Predator incidences were then summed into two major size groups, small and large. Analysis of large predator incidence was conducted in two ways: first, considering only the incidence of large predators known to prey on garter snakes at Eagle Lake; and second, the total incidence of all large predators, both known and suspected in light of published reports. Thus, analyses of variance (ANOVAs) were performed with three separate response variables—small predators, large known predators, and large known and suspected predators—with habitat type and population nested within habitat type as the main effect. All statistical analyses were conducted using JMP 6.0.0 (SAS Institute Inc.)

NUMBER, SIZE, AND LOCATION OF PREDATORY WOUNDS

Predatory wounds were scored on *T. elegans* were captured in 2005 and 2006 at two lakeshore (L1–L2) and four meadow (M1–M3, M4) sites. All wounds on individual snakes were photographed and each snake was then sexed, weighed, measured, and palpated to establish gravidity. Images were later examined to document the number of wounds per snake and the area of each wound in mm^2 .

Wound data were divided into two categories for analysis: (1) marks that resembled bird bill impressions, and (2) other wounds of unknown origin. Bill marks were identified by a pair of thin lines so superficial that they did not break the surface (Fig. 1). Two logistic regression analyses were performed with presence/absence of wounds as the categorical response variable: one using frequency of individuals with bill marks, and one using

TABLE 1.—Candidate avian predators on snakes in the Eagle Lake study system, based on published records. Numbers in parentheses after Guthrie 1932 and Sherrod 1978 refer to the number of references they contain regarding predation events for a given species. P1-7 and V1-8 refer to amateur online pictures and videos of predation events

Avian Snake Predators at Eagle Lake	Eats Snakes	Eats <i>Thamnophis</i>
American Crow (<i>Corvus brachyrhynchos</i>)	Guthrie 1932 (3); Smith <i>et al.</i> 2002; P1	Shine <i>et al.</i> 2001
American Kestrel (<i>Falco sparverius</i>)		Guthrie 1932 (1)
American Robin (<i>Turdus migratorius</i>)	P6; V8; Central American robin, <i>Turdus greyi</i> --Fedulucci 1971	Guthrie 1932 (4); Kilham 1950; Gullition 1950; Davis 1969; Richmond 1975; Erickson 1978; Jayne & Bennett 1990
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	Guthrie 1932 (1); Haywood & Ohmart 1986; McEwan & Hirth 1980; Grubb 1995	
Black-billed Magpie (<i>Pica hudsonia</i>)	Guthrie 1932 (1)	
Black-crowned Night Heron (<i>Nycticorax nycticorax</i>)	Guthrie 1932 (1)	Allen 1938
Common Raven (<i>Corvus corax</i>)	Murray 1949; Camp 1993	
Cooper's Hawk (<i>Accipiter cooperii</i>)	Rosenfield 1988	
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	Guthrie 1932 (1); V1; Florida cormorant, <i>Phalacrocorax auritus</i> --Guthrie 1932 (1)	
Golden Eagle (<i>Aquila chrysaetos</i>)	Guthrie 1932 (3)	
Great Blue Heron (<i>Ardea herodias</i>)	Guthrie 1932 (3); Sutton 1940; V2-3	P2
Great Egret (<i>Ardea alba</i>)	Guthrie 1932 (1); V4-6	
Mallard (<i>Anas platyrhynchos</i>)	Guthrie 1932 (3)	other duck species--Guthrie 1932 (2)
Northern Harrier (<i>Circus cyaneus</i>)	Fisher 1893; Guthrie 1932 (3); Sherrod 1978 (1); Tolland 1985; Collopy & Bildstein 1987;	Wilhelm 1960; Sherrod 1978 (x) Tolland 1985
Northern Shrike (<i>Lanius excubitor</i>)	Guthrie 1932 (1); Loggerhead Shrike, <i>Lanius ludovicianus</i> --Guthrie 1932 (2)	<i>L. ludovicianus</i> --Guthrie 1932 (2)
Osprey (<i>Pandion haliaetus</i>)	Wiley & Lohrer 1973	
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	Guthrie 1932 (2); Fitch <i>et al.</i> 1946; Hensley 1959; Sherrod 1978 (1); van Heest & Hay 2000; V7	Errington 1933; Trauth & Klotz 2002; Knight & Erickson 1976; Sherrod 1978 (x) P4
Ring-billed Gull (<i>Larus delawarensis</i>)	Herring Gull, <i>Larus argentatus</i> --Goldman 1971	
Rough-legged Hawk (<i>Buteo lagopus</i>)	McAtee 1935; Sherrod 1978 (1)	
Sandhill Crane (<i>Grus canadensis</i>)	Guthrie 1932 (1); whooping crane, <i>Grus americana</i> --Guthrie 1932 (1); P7	
Sharp-shinned Hawk (<i>Accipiter striatus</i>)	Guthrie 1932 (1); Sherrod 1978 (1)	
Great Horned Owl (<i>Bubo virginianus</i>)	P3; other owl species--Guthrie 1932 (1)	van Damme 2005; other owl species--Guthrie (2)
Turkey Vulture (<i>Cathartes aura</i>)	Guthrie 1932 (1)	
Western bluebird (<i>Sialia mexicana</i>)	Eastern Bluebird, <i>Sialia sialia</i> --Flanigan 1971	

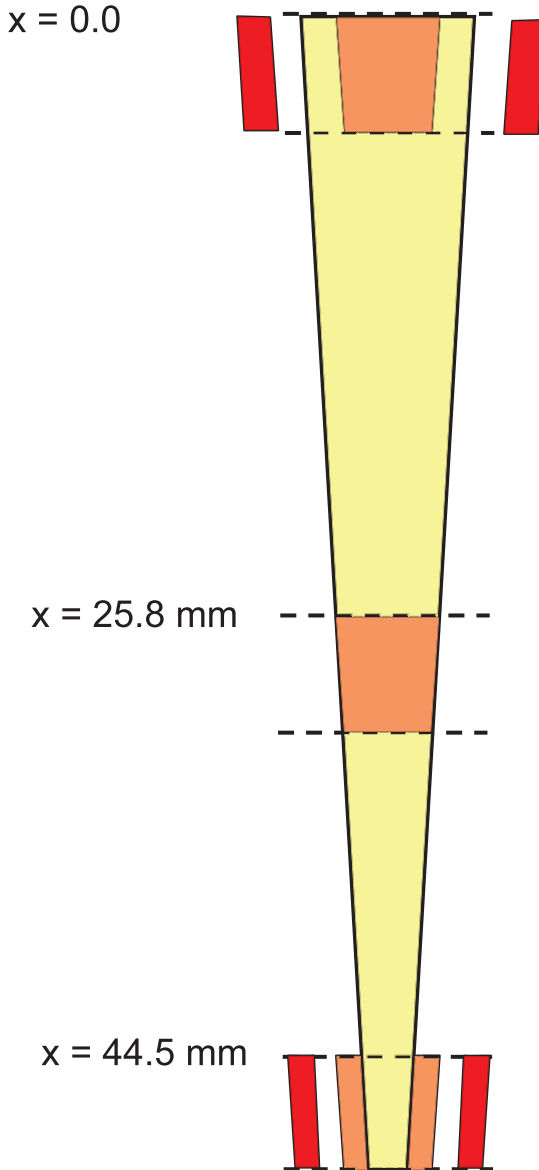


FIG. 3.—Diagram illustrating the procedure for evaluating the match between mark (medium shading) and bill (light shading) trapezoids. The match is shown at three positions of mark trapezoid and sections of the bill trapezoid (bounded by dashed lines). At each position the area of discrepancy is shown in dark shading. At the middle position, 25.8 mm from the base of the bill trapezoid, the best match was obtained (the area of discrepancy is minuscule) out of comparisons at 445 positions. This figure is based on a Great Blue Heron trapezoid and the mark trapezoid shown in Figure 1D. The match obtained at position 25.8 mm (0.984) was the best of comparisons with bills from 21 other species of snake-eating birds. Please see online version for color figure

frequency of individuals with any type of wound. Ecotype and population nested within ecotype were both treated as main fixed effects because population-specific heterogeneity of potential predators had been observed. Since wounds of unknown cause were present in all but three wounded individuals (that had only bill marks), and analyses considering the frequency of individuals any type of wound versus those with wounds of unknown cause were virtually identical, only the former data are presented.

The number of wounds per snake (both of presumed and unknown origin) and average area of wounds in wounded snakes were used as response variables in two separate ANCOVAs, with ecotype, population(ecotype), and sex as main effects (sex being divided into three categories: male, non-gravid female, and gravid female) with SVL (snout-vent length in mm) as a covariate. Both response variables were log transformed to achieve normality. All interactions were nonsignificant ($P > 0.1$) and thus were excluded from the final models.

The location of each wound was also recorded as occurring in one of three major regions: 1 = neck, 2 = midbody, or 3 = tail. Where more than one wound was present on an individual, locations of wounds were averaged and rounded to the nearest 0.5, resulting in five regional categories: 1, 1.5, 2, 2.5 and 3. A multinomial test was used to determine whether the distribution of the observed frequency of wounds in the five regions specified differed from a hypothetical distribution with an equal probability of wounds occurring in each region.

RESULTS

DIRECT OBSERVATIONS OF AVIAN PREDATION ON SNAKES

Four bird species have been directly observed to prey on snakes at Eagle Lake. A great blue heron on the lakeshore was seen attacking and flying off with a large, gravid *T. elegans* in its bill (C. Cox, pers. obs.), and an American robin was seen carrying a juvenile common garter snake, *Thamnophis sirtalis* (Jayne and Bennett, 1990). Two predation events on adult garter snakes by bald eagles have also been observed (AMS, pers. obs.). One predation event occurred when an eagle, perched on a small rock on the lakeshore, jumped on a snake a few feet away from the shore and flew away with it in its talons. Another bald eagle was seen feeding a snake to its nestling at a nest approximately 300 m from the lakeshore. An osprey was also seen flying along the lakeshore with an adult (>400 mm) snake in its talons (AMS, pers. obs.). Furthermore, several local residents and long term anglers at Eagle Lake also report having seen osprey carrying snakes (communicated to AMS).

CANDIDATE SNAKE EATING AVIAN SPECIES

According to the Audubon Society Christmas Bird Count, approximately 132 species of birds occur in the Eagle Lake region. A large proportion of these species are small songbirds and a variety of other birds not known to prey on snakes. However, we found published reports of 25/132 of these species preying on snakes. We confirmed sightings of these potential predators within our long term field notes. Guthrie (1932) provided a list of invaluable references for avian snake predation reports prior to 1932, and Sherrod (1978) provided a very thorough and detailed list of references describing falconiform birds consuming snakes. Identities of avian predator species and references for predation reports—divided into those that involve predation particularly on *Thamnophis* sp. and those that involve predation on other snake species—are given in Table 1. In a few instances, we also indicate when a close relative has been known to prey on snakes.

TABLE 2.—Candidate avian predators on snakes in the Eagle Lake study system. Direct observation of predation events on *T. elegans*, published records, and promising matches with bill marks are indicated. Predators included in the survey are also indicated. In the “bill marks” column, crosses indicate a lack of a match between bills and scars, or an unlikely match due to low abundance of the species in question. In the “surveyed” column, crosses indicate species that did not appear during the survey period and are rarely seen in the study area. Blank entries indicate categories for which no information is available. Note that the direct observation of predation by a robin involved *T. sirtalis*

Candidates	Direct observation	Published record	Bill Marks	Surveyed
American Crow (<i>Corvus brachyrhynchos</i>)		✓	✓	✓
American Kestrel (<i>Falco sparverius</i>)		✓	x	x
American Robin (<i>Turdus migratorius</i>)	✓	✓	✓	✓
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	✓	✓	✓	✓
Black-billed Magpie (<i>Pica hudsonia</i>)		✓	x	x
Black-crowned Night Heron (<i>Nycticorax nycticorax</i>)		✓	x	x
Brewer's Blackbird (<i>Euphagus cyanocephalus</i>)			✓	✓
Common Raven (<i>Corvus corax</i>)		✓	✓	x
Cooper's Hawk (<i>Accipiter cooperii</i>)		✓	x	x
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)		✓	x	x
Golden Eagle (<i>Aquila chrysaetos</i>)		✓	x	x
Great Blue Heron (<i>Ardea herodias</i>)	✓	✓	✓	✓
Great Egret (<i>Ardea alba</i>)		✓		x
Mallard (<i>Anas platyrhynchos</i>)		✓	x	x
Northern Harrier (<i>Circus cyaneus</i>)		✓	✓	✓
Northern Shrike (<i>Lanius excubitor</i>)		✓	x	x
Osprey (<i>Pandion haliaetus</i>)	✓	✓	✓	✓
Red-tailed Hawk (<i>Buteo jamaicensis</i>)		✓	x	✓
Ring-billed Gull (<i>Larus delawarensis</i>)		✓		✓
Rough-legged Hawk (<i>Buteo lagopus</i>)		✓	✓	x
Sandhill Crane (<i>Grus canadensis</i>)		✓	✓	✓
Sharp-shinned Hawk (<i>Accipiter striatus</i>)		✓	✓	x
Great Horned Owl (<i>Bubo virginianus</i>)		✓		x
Turkey Vulture (<i>Cathartes aura</i>)		✓	x	x
Western bluebird (<i>Sialia mexicana</i>)		✓		x

IDENTIFICATION OF PREDATORS FROM MARKS ON LIVE SNAKES

Four species are known to be predators on *T. elegans* in our system by direct observation and those results were confirmed by our analyses of marks: robin, great blue heron, osprey, and bald eagle (see Appendix A for details). From our analyses of bill marks, we can also be confident that at least six other bird species are also predators on *T. elegans* in our study system (see Table 2): Brewer's blackbird, raven, common crow, sharp-shinned hawk, harrier or rough-legged hawk, and sandhill crane. Cooper's hawk and golden eagle may also be predators, but the evidence implicating them is more equivocal.

AVIAN PREDATOR SURVEYS

Out of the 25 avian snake predators known to occur at Eagle Lake, 10 species were observed and counted during the predator surveys (indicated in Table 1). These 10 predators are those that have been most commonly observed in these habitats over 30 y of study (S.J. Arnold, field notes), suggesting that the species exerting the most predation pressure on these snake populations were likely accounted for already. Two small predator

TABLE 3.—ANOVA models testing for habitat type (lakeshore or meadow) and population nested within habitat differences in predator incidence. Asterisks denote significant effects

Predator Group	Source	d.f.	SS	F	P
Small known	Habitat	1	6160.50	9.703	0.0089*
	Population(habitat)	4	3661.78	1.442	0.2798
	Error	12	7618.67		
Large known	Habitat	1	43.56	2.915	0.1135
	Population(habitat)	4	75.56	1.264	0.3370
	Error	12	179.33		
Large known & suspected	Habitat	1	854.22	37.402	<0.0001*
	Population(habitat)	4	740.22	8.124	0.0021*
	Error	12	273.33		

species (American robin and Brewer's blackbird), four large known predator species (osprey, bald eagle, sandhill crane, and great blue heron), and four large suspected predators (red-tailed hawk, northern harrier, common crow, and ring-billed gull) were encountered during the surveys. Bill-mark matches (see above) provided additional justification for identifying all of these species as potential predators, with the exception of the ring-billed gull (which was not examined) and the red-tailed hawk. The red-tailed hawk bill did not match up well with any bill marks, but as it is a widely known snake predator that may well be able to capture and kill snakes without leaving survivors, we included it in analyses of large suspected predators.

In general surveys of avian predators showed that lakeshore habitats had the highest incidence of known and suspected avian predators both large and small. Avian surveys showed a significant difference in the incidence of small predators between the two habitats, with the lakeshore habitat having more than twice as many sightings of small predators than the meadow habitat (Table 4, Fig. 4A). While there were more large known predators present in the lakeshore, this trend was not significant (Fig. 4B). However, when the incidence of suspected large predators was added to that of known large predators, there was a significant habitat difference, with the lakeshore exhibiting approximately three times as many large known and suspected predators than the meadow habitat (Fig. 4C). There was no significant population heterogeneity within habitat types for either small or large known predators. However, there was significant population heterogeneity for large known and suspected predators within habitat types (Table 3).

TABLE 4.—Incidence of wounded individuals in lakeshore/meadow

ecotype	population ID	bill marks	no bill marks	wounded	not wounded	total individuals
Lakeshore	L1	11	88	32	67	99
	L2	3	125	31	97	128
Meadow	M1	12	91	62	41	103
	M2	9	175	79	105	184
	M3	9	82	45	46	91
	M5	12	82	50	44	94

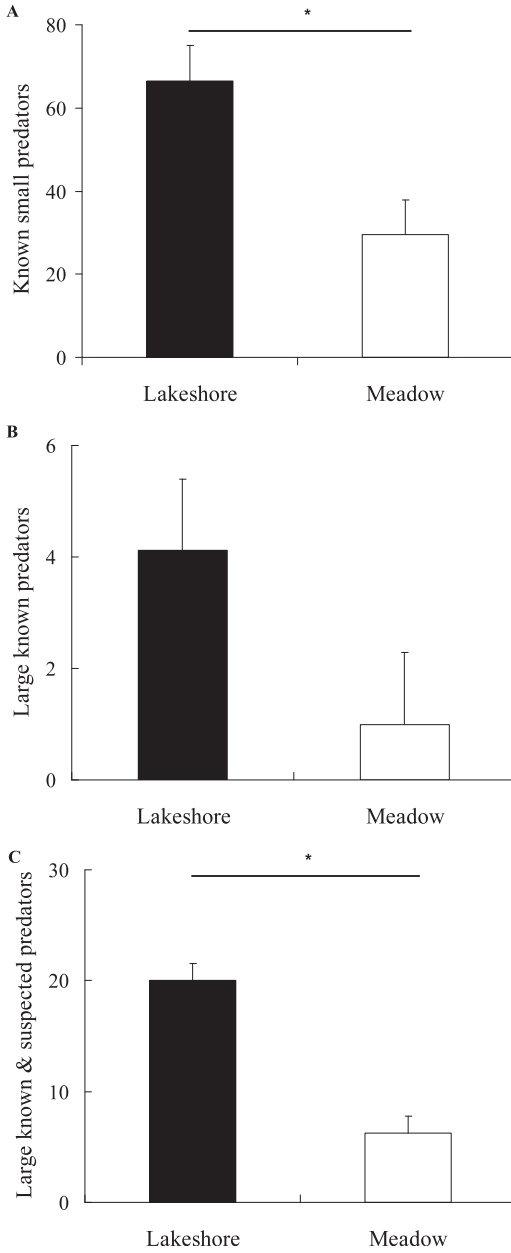


FIG. 4.—Least square means and standard errors of the means of the incidence of different avian predator groups in lakeshore and meadow habitats. Asterisks denote significant differences

TABLE 5.—ANCOVA of number of wounds and average wound area for lakeshore and meadow snakes. Asterisks denote significant effects

Response	Source	d.f.	SS	F	P
Number of wounds	Habitat	1	0.00	0.03	0.874
	Population(habitat)	4	1.60	3.91	0.004*
	Sex	2	0.04	0.22	0.807
	SVL	1	0.65	6.35	0.012*
	Error	295	30.27		
Average wound area	Habitat	1	0.01	0.06	0.808
	Population(habitat)	4	1.12	2.03	0.090
	Sex	2	0.10	0.35	0.706
	SVL	1	1.15	8.31	0.004*
	Error	295	40.68		

NUMBER, SIZE AND LOCATION OF PREDATORY WOUNDS

Individuals with wounds of both known (bill mark) and unknown origin were found more often in slow living meadow than in fast living lakeshore ecotypes (*unknown origin*: ecotype: $\chi^2 = 27.28$, $P < 0.0001$; population(ecotype): $\chi^2 = 21.18$, $P = 0.0370$; *bill mark*—ecotype: $\chi^2 = 3.24$, $P = 0.0717$; population(ecotype): $\chi^2 = 14.43$, $P = 0.0060$; Table 4). The difference in incidence of snakes with bill marks was marginally nonsignificant ($P < 0.1$), but exhibited a trend in the same direction as that of wounds of unknown origin.

There were weak but significant relationships between SVL and both number of wounds per snake and average area of wounds per snake (Table 5). In general larger snakes had greater number of wounds and greater average wound areas than smaller snakes. The observed frequency of wounds in the five body regions differed significantly from the expected frequency of an equal distribution across the body ($\chi^2 = 316.75$, $P < 0.001$), with by far the highest frequency of wounds occurring in the mid-body region (Fig. 5).

DISCUSSION

IDENTITY AND INCIDENCE OF AVIAN PREDATORS

Using a combination of direct observations in the field, published sources, and predatory mark analyses we were able to identify 10 avian predator species for *T. elegans*: American robin, Brewer's blackbird, osprey, bald eagle, sandhill crane, great blue heron, red-tailed hawk, northern harrier, common crow, and ring-billed gull. Importantly, our surveys of these known and suspected avian snake predators suggest that predation pressure is higher overall in lakeshore habitats, where fast-living populations of garter snakes reside, than in meadows. In particular lakeshore habitats showed a higher incidence of avian predators than meadow habitats for both small and large known and suspected predators (Table 3, Fig. 4). Thus, these data support the hypothesis that avian predation may have played a major role in the evolution of life histories in this system of differentiated *T. elegans*.

Higher incidence of large known and suspected predators in the lakeshore habitat supports the prediction of greater predation pressure; however, this difference was partially driven by the presence of gulls and osprey at the lakeshore sites, both of which were *not* present at the meadow sites. The fact that predator suites are different is not unexpected, but can pose challenges in comparing predation pressure between the two habitat types. Specifically, though we have observed osprey predation on *T. elegans*, and predation on similar sized snakes has been reported elsewhere for gulls, we do not know how frequently

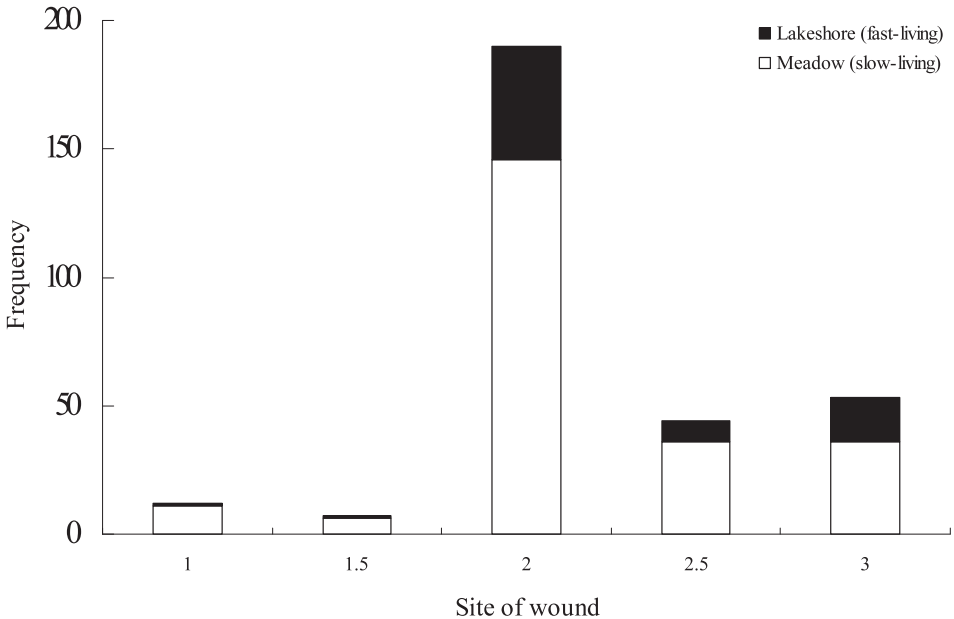


FIG. 5.—Frequency of wounds occurring at different body sites in lakeshore and meadow snakes. Site values were averaged for each individual and rounded to the nearest 0.5 (1 = head; 2 = mid-body; 3 = tail)

these and other species prey on snakes. Therefore, it is difficult to evaluate the ramifications of a higher incidence of large predators in the lakeshore habitat. It is straightforward, however, to compare incidences of small predators, constituted by the American robin and Brewer's blackbird, which are present in both habitats. The greater incidence of the same small predators in the lakeshore habitat suggests that small, fast living lakeshore snakes may experience higher predation pressure than small, slow living meadow snakes. And indeed, this finding is consistent with known differences in juvenile mortality between the two ecotypes, with lakeshore snakes having higher juvenile mortality than meadow juveniles (Bronikowski and Arnold, 1999).

On a number of occasions, American robins have been reported to prey on small snakes, including *Thamnophis*, which they kill via repeated pecking, and may carry away to feed nestlings (references in Table 1). Robins have been observed preying on snakes in the 200–330 mm size range (Guthrie, 1932). Thus, it appears that robins, and probably blackbirds, are predators that can handle only very small snakes, such as newborn and juvenile *T. elegans* not exceeding 350 mm SVL. Consequently, high avian predation pressure early in life in lakeshore habitats may constitute both historical and contemporary selective pressure for fast growth to larger, less vulnerable sizes. Interestingly, lakeshore snakes do not commence reproduction until they exceed approximately 425 mm in size, while meadow snakes have a lower bound for reproduction of 400 mm SVL (Bronikowski and Arnold, 1999; Sparkman *et al.*, 2007). This disparity suggests that maturation of lakeshore snakes is restricted by age rather than size, as they commence reproduction at an earlier age than meadow snakes, but at a larger size—in other words, the rapidity of their growth rate is such that it overshoots the size required for maturation before maturation is developmentally feasible. Thus early maturation in lakeshore relative to meadow snakes may or may not be attributable to higher predation rates by small predators in

the same way that may be growth and size. If maturation at 2 y is an insurmountable physiological constraint, high predation pressure by small predators may select for accelerated maturation only indirectly through selection on fast growth to the safety of large size.

In addition to avian predation, other forms of predation on *T. elegans* occur in our study system. For instance one snake was seen being eaten by a long-tailed weasel (*Mustela frenata*) on the lakeshore (T. Rickman, *pers. comm.*), while another snake was found under a rock near the lakeshore bearing teeth marks of an unidentified rodent (K. Robert, *pers. comm.*). We have also found several headless snakes in meadow habitats, which may have lost their heads either by twisting out of bird bills, or been bitten by a mammal, as suggested by fresh coyote (*Canis latrans*) tracks next to one carcass. Finally, while there have been no observations of predation on snakes by native fish in Eagle Lake, either by researchers or long time anglers interviewed, fish are also a possible source of mortality on the lakeshore. Nevertheless, the readily apparent adaptive differences in colouration between the two ecotypes suggest that avian predation is one of the most important sources of extrinsic mortality between the two ecotypes (Manier *et al.*, 2007).

PREDATORY WOUNDS

A few recent studies have presented evidence for a relationship between predation pressure and injury in different habitats. For example, aquatic snakes, *Natrix maura*, living on a fish farm and protected from aerial attack by a wire mesh have a lower frequency of tail breakage than populations in more natural settings (Santos *et al.*, 2001), and mainland *Thamnophis sirtalis* in Michigan have higher rates of tail breakage than island populations, which may be related to local differences in predator communities (Placyk and Burghardt, 2005). It has long been recognized that interpretation of predatory wound frequency is not straightforward, because the proportion of wounded animals that died is typically unknown (Schoener, 1979; Jaksic and Greene, 1984; King, 1987; Mushinsky and Miller, 1993). However, in some cases, predatory wound data can broaden our understanding of interactions between predators and prey, and lead to hypotheses testable by methods less subject to interpretive ambiguity. The first question that arises is whether the majority of the wounds we documented on *T. elegans* individuals were due to interactions with predators or other nonpredator related accidents. Some wounds were clearly the result of bill marks and enumerated as such; others, of unknown origin, may have been the result of being pecked or scraped or pierced with claws. It is likely that the majority of wounds were due to predatory encounters because the highest incidence of wounds by far was in the mid-body region (Fig. 5). This result suggests that wounds were inflicted by predators that preferentially targeted the mid-body, as is known to occur with corvid predation on *T. sirtalis* (Shine *et al.*, 2001).

We found a higher incidence of individuals with wounds in slow living meadow populations than in fast living lakeshore populations (Table 4). This relationship was significant for incidence of individuals with wounds of both unknown and known origin and nearly significant for those carrying wounds due to bill marks. Given that we do not know how many predation attempts were actually successful, because the victims of such attacks do not live to show their scars, this finding has two possible interpretations: (1) meadow snakes experience a higher number of predation attempts overall, both successful and unsuccessful, or (2) meadow snakes are more likely to survive predation attempts. Option (1) would suggest higher predation pressure in meadow populations, which is unlikely, given that both juvenile and adult survivorship are substantially higher in meadow populations than in lakeshore populations (Bronikowski and Arnold, 1999; unpublished data), and that both large and small avian predators appear to be more actively present in the lakeshore habitat (this study). The second interpretation is more plausible, and in turn suggests four alternative (but not mutually exclusive) possibilities: (a) meadow avian predators are less effective at killing snake prey, (b) the

meadow habitat is more conducive to escape from avian predators, (c) meadow snakes are more skilled at escape, or (d) the two snake ecotypes differ in the degree of risky foraging behaviour.

With regard to (a), while gulls and osprey are absent in the meadow habitat, sandhill cranes and northern harriers are common in the meadows but not along the lakeshore. Thus, it is unlikely that the higher incidence of predatory wounds in meadow populations is due to significant disparities in the snake handling skills of predators, since both cranes and harriers are large birds and likely to be quite effective with even the largest of meadow snakes (~600 mm). Possibility (b) has greater explanatory potential, because meadow grass and rushes, both on the periphery of the meadows and in conjunction with loose mud in standing water, provide a means for rapid cover and camouflage from predators. Garter snakes can twist and spin violently in order to escape a predator's bill, and if successful at freeing themselves, will quickly seek cover to evade recapture. In contrast to grassy meadow areas, rocky areas are the predominant retreat sites in the lakeshore habitat. A spatial analysis of both retreat site and garter snake distributions, as well as behavioural trials examining escape behaviour, could help determine whether meadow habitats do indeed offer more potential for escape than lakeshore habitats, and distinguish this hypothesis from the two remaining possibilities, (c) and (d): that meadow snakes are better escapists, and/or take more (or fewer) risks.

A number of studies, particularly in fish, have suggested a performance trade off with fast growth (*e.g.*, Arendt, 1997; Billerbeck *et al.*, 2001; Metcalfe and Monaghan, 2003), and others have suggested that fast growing organisms may be more likely to spend time foraging, which can place them at greater risk (*e.g.*, Arendt, 1997; Lankford *et al.*, 2001; Stamps, 2007; Chiba *et al.*, 2007; Biro and Dingemanse, 2009). Our results are in accord with the former scenario, if we assume that fast living lakeshore snakes have fewer predatory wounds because they are more likely to be killed than merely wounded. It is possible that fast growth produces a cost to neurological and/or muscular development in lakeshore snakes that makes them less efficient at escaping predator bills or moving quickly away from a predator provided they do manage an initial escape.

ON IDENTIFICATION OF PREDATORS FROM MARKS ON LIVE SNAKES

Although we succeeded in identifying avian predators from marks on live snakes, the procedural system we devised is not foolproof: (1) In particular, among-species similarities in the bill dimensions lead to errors in identification. Ecological considerations helped correct some of these errors, but even apparently unambiguous cases of identification need to be viewed with caution. (2) It is important to consider the fact that snakes with bill marks escaped from a predatory encounter. The frequency of predator encounters and the probability of escape given encounter both contribute to the proportional representation of bill marks by a particular bird species. This dual contribution frustrates attempts to translate mark frequency into predation intensity. (3) We matched marks to the dimensions of upper bills, but it seems likely that some of the marks we scored were produced by the lower bill, especially because they occurred on the snake's ventral surface. Although, the shapes of the two bills are very similar, the consequences of any discrepancy should be evaluated in future studies. (4) We used a single trapezoid to represent the bill of each bird species. In some cases (*e.g.*, great blue heron), however, the angular aspect of the bill changes from the proximal to the distal portion. In such cases, multiple trapezoids could be used in matches to marks. (5) Most of the marks that we scored were blackish impressions on the venter (Fig. 1) rather than wounds that broke through the surface. Marks of this kind are commonly observed in *T. elegans*, but they are not present on *T. sirtalis* found at the same localities. By keeping *T. elegans* with such superficial marks in captivity, we found that the

marks disappeared after one or two skin-sheddings. In contrast, some of the marks we scored were actual scars, marks of this kind probably persist long enough to increase in size and perhaps in shape as the snake grows. These possibilities need to be explored in future work. By recognizing and correcting some of the limitations that we have just enumerated it should be possible to devise a more robust procedure for identifying avian predators, especially in systems with a relatively small list of avian candidates.

CONCLUSION

In this study we present a comprehensive list of potential avian predators of Eagle Lake *T. elegans*, develop a novel approach for identifying avian predators via predatory marks, and provide evidence that known and suspected predators are more active in lakeshore habitats, where fast living snakes reside, than in meadow habitats. These results suggest that higher mortality rates in the lakeshore ecotype may be largely mediated by extrinsic rather than intrinsic sources of mortality *per se*. Furthermore, our results suggest that faster growth rates, larger body sizes, and early age at maturation in lakeshore snakes may have evolved as a result of selection by avian predators, both large and small. Analysis of interactions with predators via predatory wound data suggest furthermore that meadow snakes may be more effective at escaping predators—though whether this ability is due to an intrinsic trade-off between growth and performance in fast growing lakeshore snakes, relative ease of finding refuge in the meadow habitat, or a complex interaction between foraging behaviour and habitat features, remains to be tested.

Acknowledgments.—Our analyses relied in part on long term data collection made possible by grants from the National Institutes of Health (R01-GM-35492 and K04-HD-00392), the National Science Foundation (DEB-7812560, BSR-8111489, BSR-8918581, BSR-9119588, DEB-9520694, DEB-0323379, DEB-0710158), and NSF REU supplements. This research was conducted with permission from the State of California Department of Fish and Game. Observations of bald eagles were facilitated by U.S.F.S. Wildlife biologist Tom Rickman. We also thank R.T. Mason for access to bird specimens in the J.C. Braly Natural History Collection at Oregon State University.

LITERATURE CITED

- ALLEN, R. P. 1938. Black-crowned night heron colonies on Long Island. *Biol. J. Linnean Soc.*, **49**:43–51.
- ARENDT, J. D. AND D. N. REZNICK. 2005. Evolution of juvenile growth rates in female guppies (*Poecilia reticulata*): predator regime or resource level? *Proc. R. Soc. B-Biol. Sci.*, **272**:333–337.
- BASOLO, A. L. 2008. Evolution of pleiotropic alleles for maturation and size as a consequence of predation. *Bio. Lett.*, **4**:200–203.
- BILLERBECK, J. M., T. E. LANKFORD, AND D. O. CONOVER. 2001. Evolution of intrinsic growth and energy acquisition rates. I. Trade-offs with swimming performance in *Menidia menidia*. *Evolution*, **55**:1863–1872.
- BRONIKOWSKI, A. M. 2000. Experimental evidence for the adaptive evolution of growth rate in the garter snake *Thamnophis elegans*. *Evolution*, **54**:1760–1767.
- AND S. J. ARNOLD. 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. 1933. Food habits of nesting common ravens in the eastern Mojave desert. *Southwest Nat.*, **38**:163–165.
- CHIBA, S., S. A. ARNOTT, AND D. O. CONOVER. 2007. Coevolution of foraging behavior with intrinsic growth rate: risk-taking in naturally and artificially selected growth genotypes of *Menidia menidia*. *Oecol.*, **154**:237–246.
- COLLOPY, M. W. AND K. L. BILDSTEIN. 1987. Foraging behavior of Northern Harriers wintering in southeastern salt and freshwater marshes. *Auk*, **104**:11–16.
- CROWL, T. A. AND A. P. COVICH. 1990. Predator-induced life-history shifts in a fresh-water snail. *Science*, **247**:949–951.
- DAVIS, W. F. 1969. Robin kills snake. *Wilson Bull.* **81**.

- EGGERS, S., M. GRIESSER, M. NYSTRAND, AND J. EKMAN. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. *Proc. R. Soc. B-Biol. Sci.*, **273**:701–706.
- ERICKSON, D. B. 1978. Robin Feeding upon Snake. *Murrelet*, **59**:26.
- ERRINGTON, P. L. 1933. Food habits of southern Wisconsin raptors. *Condor*, **35**:19–29.
- FSK, D. L., L. C. LATTA, R. A. KNAPP, AND M. E. PFRENDER. 2007. Rapid evolution in response to introduced predators I: rates and patterns of morphological and life-history trait divergence. *BMC Evol.*, **7**.
- FLANIGAN, A. B. 1971. Predation on snakes by Eastern bluebird and Brown thrasher. *Wilson Bull.*, **83**.
- GOLDMAN, P. 1971. Herring gull predation on common water snake in Lake Erie. *Wilson Bull.*, **83**:196–197.
- GRUBB, T. G. 1995. Food habits of bald eagles breeding in the Arizona desert. *Wilson Bull.*, **107**.
- GREGORY, P. T. AND L. A. ISAAC. 2005. Close encounters of the worst kind: patterns of injury in a population of grass snakes (*Natrix natrix*). *Herpetol. J.*, **15**(4):213–219.
- GULLION, G. W. 1950. Robin feeds fledgling a snake. *Condor*, **46**:52.
- GUTHRIE, J. E. 1932. Snakes versus birds; birds versus snakes. *Wilson Bull.*, **44**:88–113.
- HAYWOOD, D. D. AND R. D. OHMART. 1986. Utilization of benthic-feeding fish by inland breeding bald eagles. *Condor*, **88**.
- HENSLEY, M. M. 1959. Notes on the nesting of selected species of birds of the Sonoran Desert. *Wilson Bull.*, **71**:86–92.
- JAKSIC, F. M. AND H. W. GREENE. 1984. Empirical-evidence of non-correlation between tail loss frequency and predation intensity on lizards. *Oikos*, **42**:407–410.
- JANZEN, F. J., J. F. TUCKER, AND G. L. PAUKSTIS. 2000. Experimental analysis of an early life-history stage: avian predation selects for larger body size of hatchling turtles. *J. Evol. Biol.*, **13**:947–954.
- JAYNE, B. C. AND A. F. BENNETT. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution*, **44**:1204–1229.
- JENNIONS, M. D. AND S. R. TELFORD. 2002. Life-history phenotypes in populations of *Brachyrhaphis episcopi* (Poeciliidae) with different predator communities. *Oecol.*, **132**:44–50.
- KILHAM, L. 1950. A snake-eating robin. *Auk*, **72**:375.
- KING, R. B. 1987. Color pattern polymorphism in the Lake Erie water snake, *Nerodia sipedon insularum*. *Evolution*, **41**:241–255.
- KNIGHT, R. L. AND A. W. ERICKSON. 1976. High incidence of snakes in the diet of nesting red-tailed hawks. *J. Raptor Res.*, **10**:108–111.
- LANKFORD, T. E., J. M. BILLERBECK, AND D. O. CONOVER. 2001. Evolution of intrinsic growth and energy acquisition rates. II. Trade-offs with vulnerability to predation in *Menidia menidia*. *Evolution*, **55**:1873–1881.
- NATIONAL AUDUBON SOCIETY. 2006. Christmas Bird Count Historical Results.
- MANIER, M. K., C. M. SEYLER, AND S. J. ARNOLD. 2007. Adaptive divergence within and between ecotypes of the terrestrial garter snake, *Thamnophis elegans*, assessed with F_{ST}-Q_{ST} comparisons. *J. Evol. Biol.*, **20**:1705–1719.
- MCATEE, W. L. 1935. Food habits of common hawks. U.S. Department of Agriculture Circular 370.
- MC EWAN, L. C. AND D. H. HIRTH. 1980. Food habits of the bald eagle in north-central Florida. *Condor*, **82**:229–231.
- METCALFE, N. B. AND P. MONAGHAN. 2003. Growth versus lifespan: perspectives from evolutionary ecology. *Exp. Gerontol.*, **38**:935–940.
- MURRAY, J. J. 1949. Nesting habits of the raven in Rockbridge County, Virginia. *Raven*, **20**:40–43.
- MUSHINSKY, H. R. AND D. E. MILLER. 1993. Predation on water snakes - ontogenic and interspecific considerations. *Copeia*, 660–665.
- PLACYK, J. S. AND G. M. BURGARDT. 2005. Geographic variation in the frequency of scarring and tail stubs in eastern gartersnakes (*Thamnophis s. sirtalis*) from Michigan, U.S.A. *Amphibia-Reptilia*, **26**:353–358.
- REZNICK, D. 1982. The impact of predation on life-history evolution in Trinidadian guppies - Genetic basis of observed life-history patterns. *Evolution*, **36**:1236–1250.
- REZNICK, D. A., H. BRYGA, AND J. A. ENDLER. 1990. Experimentally induced life-history evolution in a natural population. *Nature*, **346**:357–359.
- RICHMOND, M. L. 1975. American robin feeds garter snake to its nestlings. *Wilson Bull.*, **87**:552.

- ROSENFELD, R. N. 1988. Cooper's hawk. Yale University Press, New Haven, CT.
- SANTOS, X., M. FERICHE, R. LEÓN, A. FILIPAKOPOULOU, M. VIDAL-GARCÍA, G. A. LLORENTE, AND J. M. PLEGUEZUELOS. 2011. Tail breakage frequency as an indicator of predation risk for the aquatic snake *Natrix maura*. *Amphibia-Reptilia*, **32**(3):375–383.
- SCHOENER, T. W. 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology*, **60**.
- SHERROD, S. K. 1978. Diets of North American falconiformes. *J. Raptor Res.*, **12**.
- SHINE, R., M. P. LEMASTER, I. T. MOORE, M. M. OLSSON, AND R. T. MASON. 2001. Bumpus in the snake den: Effects of sex, size, and body condition on mortality of red-sided garter snakes. *Evolution*, **55**:598–604.
- SPARKMAN, A. M., S. J. ARNOLD, AND A. M. BRONIKOWSKI. 2007. An empirical test of evolutionary theories for reproductive senescence and reproductive effort in the garter snake *Thamnophis elegans*. *Proc. R. Soc. B-Biol. Sci.*, **274**:943–950.
- STAMPS, J. A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol. Lett.*, **10**:355–363.
- STEARNS, S. C. 1992. The Evolution of Life Histories. Oxford, Oxford University Press.
- SUTTON, G. M. 1940. Great blue heron swallows large snake. *Auk*, **63**:97.
- SWAIN, D. P., A. F. SINCLAIR, AND J. M. HANSON. 2007. Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc. B-Biol. Sci.*, **274**:1015–1022.
- TOLAND, B. 1985. Northern harrier predation on greater prairie chickens in Southwest Missouri. *J. Raptor Res.*, **19**:146–148.
- VAN DAMME, L. M. 2005. Diet of the great horned owl in the Creston Valley, British Columbia, 1998–2005. *Wildlife Afield* 2.
- VONESH, J. R. AND K. M. WARKENTIN. 2006. Opposite shifts in size at metamorphosis in response to larval and metamorph predators. *Ecology*, **87**:556–562.
- WARKENTIN, K. M. 1995. Adaptive plasticity in hatching age - A response to predation risk trade-offs. *Proc. Natl. Acad. Sci.*, **92**:3507–3510.
- WERNER, E. E. AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size structured populations. *Annu. Rev. Ecol. Syst.*, **15**:393–425.
- WILEY, J. W. AND F. E. LOHRER. 1973. Additional records of non-fish prey taken by ospreys. *Wilson Bull.*, **85**.
- WILLIAMS, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. *Evolution*, **11**:398–411.

SUBMITTED 16 MARCH 2012

ACCEPTED 6 SEPTEMBER 2012

Appendix A: Analysis of Bill Marks on *T. elegans*

For each comparison, our computer algorithm found the best match between mark and bill trapezoids by exhaustive search. As a beginning position for comparison, the base of the mark trapezoid was positioned at the base of the bill trapezoid. Additional positions for comparison were then incremented by 0.1 mm along the entire height of the bill trapezoid, until the bases of both trapezoids were in the same position. At each position, we computed the area of discrepancy (Da) between those the mark trapezoid and a section of the bill trapezoid with the same height. We expressed this area (Da) as a fraction of the total area of the mark trapezoid, Da/Ma , where Ma is the area of the mark trapezoid. Finally, we assessed the *match* between mark and bill trapezoids at each position as $1-(Da/Ma)$ and determined the *best match* for the entire series of positions using this measure. Occasionally, when $Da > Ma$, yielding a negative value for the match, we set the value of the match to zero. Using these procedures, we compiled a mark by bill comparison table in which each entry was the best match obtained for each mark and bill (bird species) combination. All of our statistical analyses were then based on this table. For example, we computed Pearson product-moment correlations between columns in the table (vectors of best matches for each bill type) and did a principal components analysis of the resulting correlation matrix. In these and other statistical analyses we dropped one species from our list (mallard), because nearly all of the best matches for this species were zero.

For each mark we determined the *top best match* (*t_{bm}*, the best match with the highest value among all bird species) and, corresponding to it, the identity of the predator that yielded that top best match. Similarly, for each mark, we determined the second best or runner up to the top best match (*s_{bm}*). For each mark we also calculated a *reliability index* (*RI*) which took into account the absolute value of the best match, as well as the distinction between that top best match (*t_{bm}*) and the second best match (*s_{bm}*): $RI = t_{bm} + (t_{bm} - s_{bm}) = 2t_{bm} - s_{bm}$. In other words, this index places a premium on a high value for the best match and on a value that stands above the next highest match.

We conducted some additional analyses to assess the reliability of our procedures. For these analyses we focused on a subset of rows in the comparison table that included only those cases in which we scored multiple marks from the same snake and compared them with all the bills. This subset of the table consisted of 11 snakes with a total of 38 marks. For each mark in this subset we used the first four principal component (PC) scores in data analysis. In particular, we conducted a one-way analysis of variance for each PC score, extracted the among-snake components of variance from the corresponding mean squares (Sokal & Rohlf 1995), and computed the repeatability of each PC (among-snake component of variance/sum of variance components).

Our quantitative analysis of bill marks helped narrow the list of actual avian predators on snakes at Eagle Lake. Because this type of identification method does not seem to have been tried before, we present our results in detail. First, we were able to exclude a few species from the pool of those contributing to beak marks in our sample of snakes: American kestrel, northern shrike, and red-tailed hawk. None of these species provided top best matches to marks on snakes or runners up to best matches. Turning to the species that did provide top best matches, not surprisingly, related or similar bird species sometimes produced high correlations in their matches to marks (*e.g.*, golden and bald eagle, $r = 0.997$; American crow and black-billed magpie, $r = 0.987$), although such high correlations were not always the case (*e.g.*, rough-legged and red-tailed hawk, $r = 0.806$). More surprising, several pairs of dissimilar birds produced high correlations in their matches to marks (*e.g.*, osprey and black-crowned night heron, $r = 0.999$; Brewer's blackbird and double-crested cormorant, $r = 0.967$). In these cases, high correlations arose not because of overall similarity in the bill dimension of the two species, but because the entire bill of one species was similar to part of the bill of the other species (*e.g.*, the entire bill of the Brewer's blackbird closely resembled the terminal portion of the cormorant's bill). The consequence of high correlations of both kinds was that multivariate analysis using principal components was largely unsuccessful in identifying the bird species responsible for marks.

We were able to use principal component scores to test the reliability of our scoring procedure. In particular, by focusing on the subset of snakes with multiple marks, we were able to assess the repeatability of our scoring procedure. The first four principal components of the sample of 74 marks accounted for 96% of the variance in best matches. One-way ANOVAs of scores from these four PCs revealed statistically significant differences between snakes in their marks (significance level ranged between 0.01 and 0.001) with repeatabilities ranging from 0.46–0.78. Although these measures of reliability are reasonably high, examination of our main data table revealed that in 10 out of 11 cases, marks on the same snake were attributed to more than one bird species. Although it is conceivable that more than one bird species actually attacked each of these snakes (see *Discussion*), misidentification is a more likely explanation. Our best example is the snake with the largest sample of scored marks ($n = 15$) in which top best matches were attributed to great blue herons (8 times), sandhill crane (4 times), and Black-crowned night heron (3 times). These identifications clearly implicate a heron or crane as the attacker, but which one? In this particular case, our avian survey results help us achieve an identification, because cranes

have never been seen at the lakeshore locality where the snake was captured, and night herons are extremely rare; the predator producing all 15 marks was almost certainly a great blue heron. This approach suggested a conservative use of these analyses. Therefore, instead of pursuing identification on a snake-by-snake basis, we tried summarizing our data bird-by-bird to ask which species were implicated across the entire sample of snakes and marks.

A summary of our mark analysis categorized by bird species is presented in Suppl. Table 1. This table shows that 12 of 14 species implicated in best matches with marks produced especially reliable matches in the senses that their average top best matches were high (≥ 0.95) with small standard errors (< 0.02), and their average reliability indices were high (> 0.95). In other words, the last two species on the list (bald eagle and Cooper's hawk) are less reliably implicated in failed predation attempts than the other 12 species. Although the tabulations of second best top matches suggest that misidentifications are possible with 1–3 other species, these numbers are considerably lower when we take into account our survey and observational results. On that basis, four species in Suppl. Table 1 are less likely predators than other candidates (*i.e.*, magpie, night heron, vulture, and cormorant). These species are either so rare as to be undetectable in our surveys and the 20 most recent years of field work (magpie, night heron, and crane on lakeshore), or are so rare in the actual habitats of snakes that encounters must be infrequent (vulture and cormorant).

SUPPLEMENTARY TABLE 1.—Summary of predator identifications based on marks found on live snakes. The 'top best match mean' column reports the average value of all those marks in which the predator in question was the top best match. *RI* is the reliability index, described in the text. The 'Marks' column reports the number of marks for which the predator in question scored the top best match. The 'Snakes' columns report the total number of individual snakes bearing marks for which the predator in question scored best matches; L and M report subtotals for lakeshore and meadow snakes, respectively. The 'second best to top matches' column reports the identities of predators that scored as runner up to the predator in question for top best match. In that column 15, 16, and 17 denote, respectively, Turkey vulture, Double-crested cormorant, and Rough-legged hawk. Entries indicated in parentheses are likely to be misidentification of predators for reasons discussed in the text.

Code	Predator	Top best match	Top best match	RI	Marks n	Snakes			Second best to top matches
		mean	s.e.	mean		total	L	M	
1	raven	0.994	0.0065	1.04	2	2	0	2	5,(11)
2	ss_hawk	0.989	-	1.011	1	1	1	0	-15
3	bbb	0.994	0.0011	1.001	3	3	1	2	-16
4	crow	0.996	0.0005	1.001	6	6	1	5	-10
5	robin	0.997	0.0004	1	4	4	2	2	4
6	harrier	0.998	-	1	1	1	0	1	17
7	osprey	0.995	-	1	1	1	0	1	3
8	gbh	0.967	0.005	0.983	14	6	2	4	9
9	crane	0.97	0.0101	0.979	8	5	-2	3	(11),8
-10	magpie	0.964	0.0176	0.979	4	4	1	3	4
-11	n_heron	0.96	0.0067	0.962	16	14	4	10	7
12	g_eagle	0.955	0.0119	0.957	3	3	1	2	(10),13,17
13	b_eagle	0.879	0.0352	0.903	8	8	2	6	(15),12
14	c_hawk	0.869	0.1117	0.885	3	3	0	1	13,(15)
total =					74	61	17	42	