Sex-biased Predation on Newts of the Genus Taricha by a Novel Predator and its Relationship with Tetrodotoxin Toxicity

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ABSTRACT.—Newts of the genus *Taricha* have long been studied in regards to their skin toxin, tetrodotoxin (TTX). It has been shown that the TTX levels across populations of *Taricha* are highly variable, and this has been mostly attributed to the interaction between *Taricha* and their only documented predators, garter snakes of the genus *Thamnophis*. Here we show that predators other than *Thamnophis* prey extensively on some newt populations. Ledson Marsh in Annadel State Park in Santa Rosa, CA is a breeding ground for both the California newt (*Taricha torosa*) and the rough-skinned newt (*Taricha granulosa*). Predation on these newts was tracked from 1998–2009 and was most often in the form of evisceration and significantly male-biased. As TTX seems to have been developed as an antipredator defense in *Taricha*, we used Fluorometric High Phase Liquid Chromatography (HPLC) analysis to quantify TTX levels in the skin of ten male and ten female newts of each species to determine the influence that TTX levels may have on sex-biased predation in this population. We found *Taricha* females were not significantly more toxic than males. Also, we found that *T. torosa* were significantly more toxic than *T. granulosa*, which is in contrast with other newt toxicity studies.

INTRODUCTION

Unlike many prey species, adult *Taricha* are highly toxic (Mosher *et al.*, 1964; Wakely *et al.*, 1966; Brodie, 1968; Brodie *et al.*, 1974; Daly *et al.*, 1987; Hanifin *et al.*, 1999, 2002). Early studies of *Taricha granulosa* (Brodie, 1968) showed that virtually all potential predators were susceptible to tetrodotoxin (TTX), the deadly neurotoxin found in the newts' skin. Tetrodotoxin acts by blocking sodium channels (Narahashi *et al.*, 1967) and death from exposure is usually the result of respiratory failure (Brodie, 1968). The only known predators that do not die from ingesting adult *Taricha* were garter snakes of the genus *Thamnophis* (Brodie and Brodie, 1990, 1991). Garter snakes have varying levels of resistance to TTX that apparently coevolved with newt toxicity (Brodie *et al.*, 2002; Hanifin *et al.*, 2008).

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Hanifin *et al.* (2008) have shown that there is great geographic variation in the toxicity of newts throughout their range. Populations of newts throughout the Pacific coast of the United States and Canada have an average range of whole skin toxicity from 0.000 mg TTX to 4.695 mg TTX. These results suggest that predation on *Taricha* in some localities along their range is possible, although successful predation has almost never been documented by predators other than *Thamnophis*. Anecdotal accounts of predation attempts on *Taricha* by various birds usually report the subsequent death of the predator (McAllister *et al.*, 1997; Mobley and Stidham, 2000). However, recently, successful predation on *Taricha,* whereby the entire newt was consumed whole with no apparent ill effects by great blue herons (Fellers *et al.*, 2008) and bullfrogs (*Rana catesbeiana;* Jennings and Cook, 1998), has been reported, although other studies found both species susceptible to TTX (Brodie, 1968). The reports of predation by great blue herons and bullfrogs are from areas where newts have very little or no TTX (Hanifin *et al.*, 2008). Additionally, predation attempts on *Taricha* by a skunk have been observed, but the fate of the skunk is unknown (M. Edgehouse, pers. comm.). The outcome of these individual predator-prey interactions may be highly influenced by variations in newt toxicity.

Not only is there variation in toxicity geographically, but there is variation within a population and between the sexes (Hanifin *et al.*, 2002). Female *Taricha* have been found to be more toxic in some populations than male *Taricha*, likely as a maternal investment to protect eggs. This type of investment could lead to phenomena such as sex-biased predation where a predator selectively preys on the sex with lower toxicity. Sex-biased predation is common in predator/prey systems; however, the causes of such sex differences in predation as well as the direction of bias (*i.e.*, male-biased vs. female-biased) vary depending on the habits or life-history traits of both predator and prey species (*e.g.,* Dickman *et al.*, 1991; Norrdahl and Korpimäki, 1998; Christe *et al.*, 2006; Boukal *et al.*, 2008). Christe *et al.* (2006) investigated sex-biased predation as a source of extrinsic mortality, which may be a possible cause for differences in the lifespan of males and females in various species. They found that sex-biased predation, especially by birds, was common and directed toward male prey. However, Boukal *et al.* (2008) found that when combining data from a literature review and theoretical modeling to investigate predator-prey relationships, avian predators more often exhibited female-biased predation. Nevertheless, the results from Boukal *et al.* (2008) also indicate that when considering all of the taxa studied together, male-biased predation is approximately two times as common as female-biased predation.

There are several possible reasons that a species might experience sex-biased predation, and these often influence the direction of bias. Females often have specific traits resulting from fecundity selection that may increase vulnerability to predation (Hairston *et al.*, 1983). For example, females of some species may be larger than males due to selection for increased offspring number. Females may also experience reduced performance during reproductive periods that results in higher mortality by predators (*e.g.*, Seigel and Fitch, 1984; Seigel *et al.*, 1987; Brodie, 1989). Male-biased predation may result from sexual dimorphism (*e.g.,* Andersson, 1994; Christe *et al.*, 2006). In many cases males are much more visible than females due to conspicuous plumage, coloration, size, etc. Males and females often exhibit different behaviors, which may place one sex at a higher risk for predation (*e.g.,* Estes, 1969; Burk, 1981; Christe *et al.*, 2006; Samelius and Alisauskas, 2006). Behavioral differences are often seen in animals that have parental care, wherein the female parent stays close to the nest or burrow while the male parent travels in search of food, exposing the male to higher predation risk.

Breeding episodes, phenology and associated activities may also contribute to a differential predation risk for males and females (*e.g.,* Burk, 1982; McCauley *et al.*, 2000;

Christe *et al.*, 2006; Boukal *et al.*, 2008). In many cases, communal breeding may decrease the individual risk of predation due to the benefits of having many individuals to watch for predators and/or help defend against predators, as well as associated dilution effects (*e.g.*, Smith and Graves, 1978; Robinson, 1985; Brown and Brown, 1987). However, Burk (1982) discusses the mating behaviors of insects and the male-biased costs associated with some of these behaviors. Burk found that male insects often swarm to attract mates, which results in high-energy gain with little energy expenditure for feeding bats. Many species of amphibians explosively breed, a behavior thought to be driven by the limited availability of suitable breeding habitats (*i.e.*, vernal pools or seasonal marshes), appropriate climactic conditions (Wells, 1977; Sullivan, 1982), increased predation pressures (Woodward and Mitchell, 1990; Lucas *et al.*, 1996; McCauley *et al.*, 2000), or as a means of decreasing cannibalism on eggs and tadpoles (Wells, 1977; Petranka and Thomas, 1995). Newts of the genus *Taricha* may be either explosive breeders or prolonged breeders depending on the breeding site (Twitty, 1942; Stebbins, 1951; Pimentel, 1960; Neish, 1971; Petranka, 1998). Explosive breeding in amphibians may be expected to lead to sex-biased predation as in other taxa.

Our study documents extensive predation on the adult *Taricha* population in Annadel State Park in Santa Rosa, CA between 1998 and 2009. Field observations of predation on adult *Taricha* indicated substantial attacks and/or predation on adult newts during the winter breeding period resulting in injuries and/or death that are inconsistent with *Thamnophis* or bullfrogs and great blue herons. Furthermore, the observed predation appeared to be male biased. As newts at this site are explosive breeders, we investigated whether predation was in fact sex-biased. Additionally, because these observations contradict the general lack of predation seen on *Taricha* adults, we further investigated whether local newts were defended by the neurotoxin TTX. In some populations, female *Taricha granulosa* are more toxic than conspecific males (Hanifin *et al.*, 2002), so we also explored whether sex differences in toxicity might contribute to the observed patterns of predation.

METHODS

Study site.—All work was conducted at Ledson Marsh in Annadel State Park in Santa Rosa, ca. The park is over 2000 ha and includes a variety of habitat types including oak woodland, fir forest, marshland, chaparral, grassland and meadow (Cook and Jennings, 2007). A low dam was built in 1930 in what is now known as Ledson Marsh to retain water in an area of the park that may have once been a vernal pool and wet meadow. The marsh is seasonal and is approximately 11 ha in size when at capacity with water during the winter season. Ledson Marsh serves as a breeding ground for many local amphibians, including California red-legged frogs (*Rana draytoni*), California newts (*Taricha torosa*) and rough-skinned newts (*T. granulosa*).

Taricha mortality.—We collected *Taricha* mortality data from Ledson Marsh during the active breeding season (Nov.–Mar.) from 1998 to 2009. We visually searched for newts by wading through the marsh haphazardly at approximately weekly intervals. One to two researchers were present during each survey. Surveys began with the onset of heavy winter rains that were sufficient to completely or nearly fill the marsh (usually Dec. or Jan.). Subsequently, weekly surveys were conducted until the end of the breeding season (usually Feb. or Mar.). During heavy breeding periods, the marsh was sometimes surveyed multiple days during the week. The cold waters during the winter season allowed newts to be recovered during weekly surveys with limited decomposition. Newt carcasses were collected,
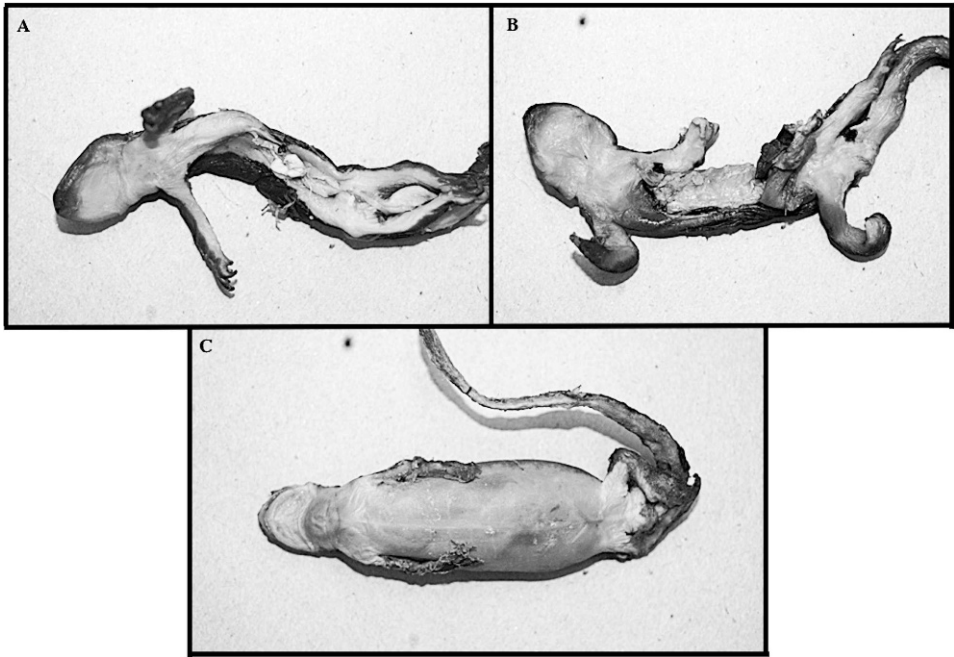
FIG. 1.—Typical mortality seen in Ledson Marsh. (A) Punctured male newt. (B) Eviscerated male. Intestines are visible. (C) Gravid female with no injury

sexed and assigned one of three injury types—none, punctured or lacerated, and eviscerated. Carcasses categorized as ''none'' showed no damage to the skin or other external physical injuries (Fig. 1). Newts that were eviscerated and had another injury type were classified as eviscerated. Newt carcasses that had an injury were considered ''killed,'' whereas those without injury were considered ''dead.'' In some cases, newts were collected that had decayed or been torn apart to the point that sex, species, and/or injury were unable to be assigned. These unknown newts comprised 12.4% of the total newts collected, and were excluded from all analyses. Gravidity was recorded for female newts. During the years 2007 through 2009, species identifications (*Taricha torosa* or *T. granulosa*) were also made. All newt carcasses collected were preserved.

Quantification of TTX.—Forty live adult newts (10 of each sex and species) were collected from Ledson Marsh in Santa Rosa, CA in Feb. 2007 for quantification of TTX levels. Specimens were frozen within three days of collection at −80 C. Procedures for collection of skin tissue as well as extraction and quantification of TTX were performed as in Hanifin *et al.* (2002) with minor modifications. Extracts of the tissue were prepared by homogenizing a 5 mm diameter skin punch in 600 μl of 0.1 M acetic acid using a tissue sonicator (550 Sonic Dismembrator, Fisher Scientific). Standards for flourometric High Phase Liquid Chromatography (HPLC) were prepared from tetrodotoxin with citrate buffer available from Sigma (product number T8024-1MG).

Analyses.—All comparisons between newt species, sex or injury type were assessed using Pearson's chi-squared analysis. Comparisons of toxicity levels between species of newts were analyzed using a two-way ANOVA. Comparisons within species and within sex were analyzed

TABLE 1.—Total numbers of dead male and female *Taricha* collected each year according to injury type. Injury designations are N = none, L = laceration and E = evisceration. Gravid is the total number of the female carcasses collected that were also gravid

| | Male *Taricha* | | | | Female *Taricha* | | | | |
| | Injury type | | | | Injury type | | | | |
Year	N	L	E	Total	N	L	E	Gravid	Total
1998	0	5	5	10	22	0	1	23	23
1999	1	6	7	14	1	4	0	4	5
2000	6	6	4	16	45	3	5	53	53
2001	0	0	0	0	0	0	0	0	0
2002	0	2	1	3	16	0	2	18	18
2003	2	2	2	6	11	0	2	13	13
2004	3	107	111	221	37	7	3	46	47
2005	0	16	16	32	11	1	2	10	14
2006	0	77	78	155	10	0	0	10	10
2007	2	0	3	5	18	1	2	16	21
2008	1	12	101	114	12	0	2	12	14
2009	0	1	20	21	1	0	0	1	1
Total	**15**	**234**	**348**	**597**	**184**	**16**	**19**	**206**	**219**

using a one-way ANOVA. All toxicity data were log transformed to meet the assumptions of normality and homoscedasticity. Because toxicity data included zeros, 0.00001 was added to each individual value before log transformation. All analyses were performed using SAS/ STAT version 9.1 (SAS Institute).

RESULTS

Taricha mortality.—A total of 932 *Taricha* (116 of these were unassigned due to decomposition) carcasses were collected between 1998 and 2009 (Table 1). Of those assigned, 597 were male and 219 were female. Few of the females had been killed (*i.e.*, punctured or eviscerated; 16.0%), whereas 97.5% of the males had been killed (Fig. 2). Of those that were killed, males were eviscerated slightly more often than females (59.8% and 54.3%, respectively). Significantly more male than female *Taricha* carcasses were found (χ^2 = 175.81, df = 1, P < 0.0001) over the course of the study. From 2007–2009, the vast majority of newt carcasses found were *Taricha torosa. Taricha granulosa* represented less than 8% of the newt carcasses collected during those years, which represents a significant difference in mortality between the two newt species (χ^2 = 119.05, df = 1, P < 0.0001).

Whereas the total number of *Taricha* carcasses collected varied across years (Fig. 3), overall mortality was male-biased. Moreover, there was either no sex-biased mortality or female biased mortality through 2003, followed by a substantial increase in male mortality starting in 2004. The frequency of injury types between the two sexes was also significantly different (Table 1, Fig. 2). Male *Taricha* were killed significantly more often than females (laceration χ^2 = 287.36, df = 1, P < 0.0001; evisceration χ^2 = 439.51, df = 1, P < 0.0001). Conversely, there was a significantly larger number of female newt carcasses found with no injury than there were of male newts (χ^2 = 92.11, df = 1, P < 0.0001). These females with no injury (n = 184) consisted of primarily gravid individuals (92.4%), indicating that they died before egg laying.
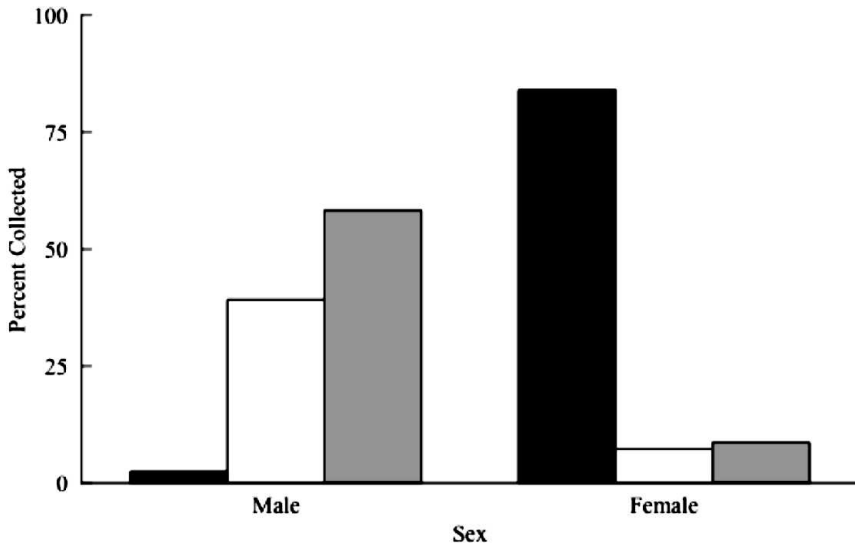
Fig. 2.—Percentage of dead male and female *Taricha* collected with no injury (black bars), laceration (white bars) or evisceration (grey bars)

Quantification of TTX.—HPLC analysis showed a diversity of TTX levels in both species of newts. *Taricha torosa* had a range of TTX levels from 0.0003–0.0143 mg TTX/cm^2, whereas *T. granulosa* had TTX levels from none to 0.0612 mg TTX/ cm^2 (HPLC analysis was done twice on this high toxicity *T. granulosa* female to confirm the result) (Fig. 4, Table 2). There were only two newts without any TTX and both were *T. granulosa* males. We did not find any
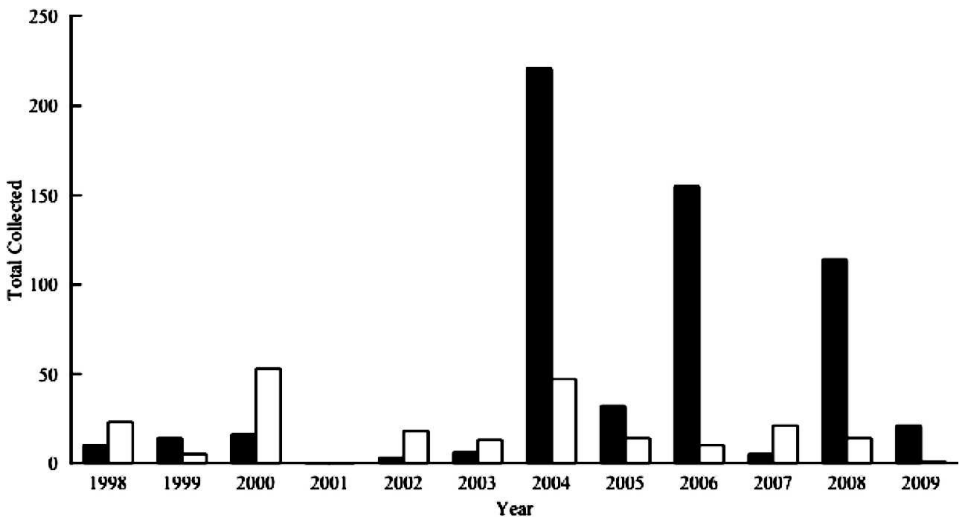

Fig. 3.—Total numbers of dead male (black bars) and female (white bars) newts collected from 1998 to 2009
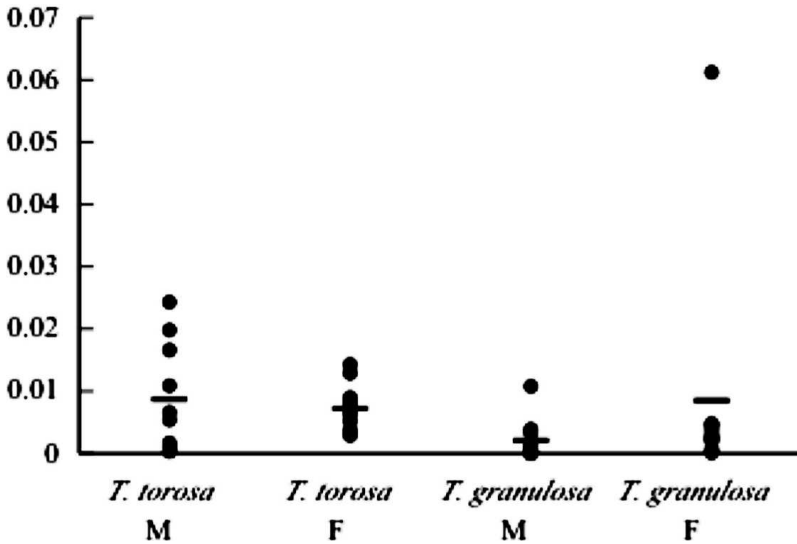
FIG. 4.—Plot of individual values of TTX (mg)/cm^2 for each individual within each species and sex. The letters M and F indicate males and females, respectively. Horizontal lines represent the mean value for each group

significant differences in the levels of TTX between males and females of *T. torosa* (F = 0.79, df = 1, P = 0.3845), and only moderate non-significance between males and females of *T. granulosa* (F = 3.60, df = 1, P = 0.0738). Although *T. torosa* males had a greater mean toxicity than females, males also had a much larger standard error than that of the females (Table 2, Fig. 4). In contrast, the standard error for *T. granulosa* was much larger for females than for males. Additionally, *T. torosa* were significantly more toxic than *T. granulosa* (F = 8.48, df = 1, P = 0.0061). It was also found that there were no significant differences in toxicity between *T. torosa* and *T. granulosa* females (F = 2.79, df = 1, P = 0.1119); however, *T. torosa* males were significantly more toxic than those of *T. granulosa* (F = 5.74, df = 1, P = 0.0276).

DISCUSSION

Previous work by Hanifin *et al.* (2003) found that levels of TTX in *Taricha granulosa* eggs are highly correlated with TTX levels in the dorsal skin of the mother. This suggests that

TABLE 2.—Comparison of levels of TTX mg/cm^2 in *Taricha torosa* and *T. granulosa* males and females. Sample sizes within each group were equivalent, with N = 10 for each sex

Species/Sex	TTX/cm^2 (mg, mean ± SE)	Predicted whole newt toxicity (mg, mean ± SE)	Range TTX/cm^2 (cm)
T. torosa			
Male	0.00871 ± 0.00278	0.3266 ± 0.10606	0.0003–0.0243
Female	0.00724 ± 0.00124	0.2203 ± 0.04745	0.0029–0.0143
T. granulosa			
Male	0.00211 ± 0.00106	0.0583 ± 0.02911	0.0000–0.0108
Female	0.00852 ± 0.00587	0.2285 ± 0.15813	0.0001–0.0612

females invest TTX into their eggs, presumably as a source of protection from predation, and that females may be more toxic than males both internally and externally. As an explosively breeding species, male-biased predation rates for *Taricha* species and sexes at this locality are likely influenced by breeding migration patterns. Migration patterns for *Taricha* have been found to vary depending on the species and sex of individuals (Twitty, 1942; Stebbins, 1951; Pimentel, 1960; Neish, 1971; Petranka, 1998), which affects the length of time that each is exposed to predators. When migrating to a pond, males often arrive before females and typically stay longer following breeding (Twitty, 1942; Stebbins, 1951). Given this scenario, there should be a higher ratio of males to females in the marsh, which would increase the chances of predation on male *Taricha*. Studies on explosively breeding anurans also have shown that there are higher abundances of males in breeding locations than females (*e.g.,* Turner, 1960; Calef, 1973). Relative abundances for this breeding location are unknown at this time.

The few females that were found killed (*i.e.*, laceration) during the course of this study, were usually not eviscerated. It is possible that while handling newts, the predator responds to the toxin level and releases more toxic individuals. Garter snakes, *Thamnophis sirtalis,* limit exposure time to *Taricha granulosa* based on the toxicity of the newt as well as the snake's own resistance (Williams *et al.*, 2003). Newts are also toxic internally, however, this may be of little impact to a predator as visceral TTX levels are extremely low (0.5 to 0.1 μg/g) as are liver TTX levels (<0.1 ug/g) (Wakely *et al.*, 1966). Numbers of male and female newts found dead and without injury may be due to the courting process. In both species, several males simultaneously attempt to mate with one female (Smith, 1941; Janzen and Brodie, 1988; pers. obs.). It is possible that males competing to mate with a female accidentally drown the female in the process of breeding (Briggs and Storm, 1970; Kargarise Sherman, 1980). The few males found with no injury may also have been drowned in this struggle (Kargarise Sherman, 1980). There were not differences in the amount of search effort at the marsh each year contributing to the inter-annual variation in deaths observed. This variation may be due to predator presence during migration patterns of newts, variation in rainfall patterns, variation in migration patterns or availability of alternate food sources for predators.

Despite efforts to observe predation on newts during the study, predation attempts were not observed and the predator was not identified. Although we were unable to witness an attack, the common raven is likely one of the dominant predators of newts at Ledson Marsh. We frequently observed or heard ravens in the forest surrounding the marsh, but never foraging in the marsh. However, ravens are known to eviscerate other amphibians with toxic skin (Olson, 1989; Brothers, 1994). Ravens will quickly abandon foraging and depart if disturbed (Olson, pers. comm.; Hayes and Price, 2009), so it is not surprising that we did not observe attacks. Most newt carcasses that we found were eviscerated through an abdominal puncture wound or laceration that would require a predator with dexterity consistent with a raven's ability. Also, we found several newt carcasses lying on the top of floating aquatic vegetation [*i.e.*, aquatic fern (*Asola* sp.)] indicating the carcass was either dropped by a bird or placed there by a predator of light weight. In many cases the newts were found freshly killed, in which case they were still moving, indicating that they were preyed upon rather than scavenged. It is unlikely that the predator was a great blue heron (Fellers *et al.*, 2008) or bullfrog (Jennings and Cook, 1998) as newts preyed upon by these species were swallowed whole and not eviscerated, as we observed.

Other species of birds may also contribute to newt predation. There are examples of evisceration and/or consumption on other amphibian species by Corvids such as gray jays,

Stellar's jays, and Clark's nutcrackers (Turner, 1960; Tordoff, 1980; Beiswenger, 1981; Pilliod, 2002; Murray *et al.*, 2005). Stellar's jays and American crows are Corvids in addition to the raven that are found in Sonoma County and may contribute to the observed newt mortality in Ledson Marsh. Also, we cannot rule out small mammals as potential predators. We observed a few dead newts with gnaw marks suggesting a small carnivorous mammal predator. There have been multiple descriptions of attacks on toxic toads by skunks and raccoons in which the toads are often eviscerated (Hanson and Vial, 1956; Wright, 1966; Schaaf and Garton, 1970; Groves, 1980; Woodward and Mitchell, 1990), and both of these species occur at Annadel State Park (DGC, pers. obs.).

Taricha in Annadel state park are preyed upon by a predator that, although unidentified, is novel. Other accounts of successful *Taricha* predation have involved consumption of whole newts (Jennings and Cook, 1998; Fellers *et al.*, 2008). This study, however, found that newts were often eviscerated, which requires a substantial amount of dexterity. It is likely that given the geographical variation in newt toxicity (Hanifin *et al.*, 2008), there are other locations such as Ledson Marsh where there is a significant amount of predation on *Taricha* occurring by species other than *Thamnophis*. It seems possible that the predator in the case of this study is responding to a cue that we have yet to identify or understand as males are killed significantly more often than females, but toxicity is not the clear driver of sex-biased predation in this system.

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