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Stomach contents from invasive American bullfrogs *Rana catesbeiana* (= *Lithobates catesbeianus*) on southern Vancouver Island, British Columbia, Canada

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Abstract

Invasive alien American bullfrog populations are commonly identified as a pernicious influence on the survival of native species due to their adaptability, proliferation and consequent ecological impacts through competition and predation. However, it has been difficult to determine conclusively their destructive influence due to the fragmentary and geographically dispersed nature of the historical database. An expanding meta-population of invasive American bullfrogs, *Rana catesbeiana* (= *Lithobates catesbeianus*), became established on southern Vancouver Island, British Columbia, Canada in the mid- to late 1980s. An on-going bullfrog control program begun in 2006 offered a unique opportunity to examine the stomach contents removed from 5,075 adult and juvenile bullfrogs collected from 60 sites throughout the active season (April to October). Of 15 classes of organisms identified in the diet, insects were numerically dominant, particularly social wasps and odonates (damselflies and dragonflies). Seasonality and site-specific habitat characteristics influenced prey occurrence and abundance. Native vertebrates in the diet included fish, frogs, salamanders, snakes, lizards, turtles, birds, and mammals, including some of conservation concern. Certain predators of bullfrog tadpoles and juveniles are commonly preyed upon by adult bullfrogs, thereby suppressing their effectiveness as biological checks to bullfrog population growth. Prey species with anti-predator defences, such as wasps and sticklebacks, were sometimes eaten in abundance. Many prey species have some type of anti-predator defence, such as wasp stingers or stickleback spines, but there was no indication of conditioned avoidance to any of these. Results from this study reinforce the conclusion that, as an invasive alien, the American bullfrog is an opportunistic and seemingly unspecialized predator that has a uniquely large and complex ecological footprint both above and below the water surface.

Keywords

Bullfrog, *Rana catesbeiana*, *Lithobates catesbeianus*, predation, diet, invasive species

Introduction

The American bullfrog, *Rana catesbeiana* (= *Lithobates catesbeianus*), is widely considered one of the most ecologically destructive of invasive alien vertebrate species (Lowe et al. 2000, Kraus 2009, CABI 2011). Conservation concerns arise from its adaptability to a wide variety of environmental conditions, extraordinarily rapid population growth and distributional expansion rates, and most particularly to its presumed rapacious unspecialized carnivory. However, documentation of its full impact as an invasive remains regionally fragmentary. Numerous studies from around the world have examined bullfrog stomach contents, but these have tended to sample relatively few bullfrogs from a very few sites in a narrow time frame (Table 1).

From previous studies, a number of commonalities emerge. Bullfrogs consume a large number and variety of prey species (Bury and Whelan 1984) with insects usually numerically dominant (Korschgen and Moyle 1955, Cohen and Howard 1958, McCoy 1967, Bruggers 1973, Werner et al. 1995, Hirai 2004, Laufer 2004, Barrasso et al. 2009, Hothem et al. 2009, Silva et al. 2009). Certain insect groups are eaten more frequently, and many studies have found beetles (Coleoptera) to be most often consumed (Cohen and Howard 1958, McCoy 1967, Bruggers 1973, Laufer 2004, Diaz De Pascual and Guerrero 2008, Hothem et al. 2009). Other invertebrates, such as isopods (Irwin 1994, Krupa 2002) and crayfish (Bruggers 1973, Carpenter et al. 2002, Hirai 2004) are common prey. Adult bullfrogs are known to eat larger prey (Bruneau and Magnin 1980), and this is often vertebrates–frequently frogs (Korschgen and Moyle 1955, Stuart and Painter 1993, Werner et al. 1995, Govindarajulu et al. 2006, Diaz De Pascual and Guerrero 2008).

Populations of alien, invasive bullfrogs, geographically isolated and arising independently, are scattered along the southeast coast of Vancouver Island–their origins are often obscure. However, in the mid-1980s, a population of American bullfrogs became established just north of the City of Victoria at the extreme southern end of Vancouver Island (Orchard 1999). Subsequently, the population expanded unchecked and, consequently, invaded dozens of lakes and ponds throughout regional Victoria (Saanich Peninsula). Previous studies on bullfrogs in regional Victoria have included diet (Irwin 1994, Govindarajulu et al. 2006), but the sites sampled and bullfrogs examined were limited in number (Table 1). Differences in seasonality, site variation, and age-class could not therefore be reliably inferred on either a population or regional scale. An on-going bullfrog eradication program on southern Vancouver Island got underway in 2006 (Orchard 2011) which presented a rare opportunity to thoroughly examine and compare the stomach contents of all, or a majority of, post-metamorphic size-classes from entire populations taken from a diversity of lakes and ponds and collected throughout the 6-month active season. The results presented here are derived from the stomach contents of 5,075 bullfrogs caught and euthanized during the course of the eradication program. The data explores the scope of bullfrog predation on the native fauna, as well as site and seasonal variation in prey species composition. All this is relevant to the fundamental question and discussion of whether or not control or eradication efforts are warranted for invasive alien populations of the American bullfrog.

Table 1. Stomach contents analyses from both native and invasive alien populations.

Location	Invasive alien status	Sample size	Number of sites	Reference
Argentina: Buenos Aires	Non-native	35	3	Barrasso et al. 2009
Brazil: Minas Gerais	Non-native	113	1	Silva et al. 2009
Canada: British Columbia	Non-native	13	1	Irwin 1994
Canada: British Columbia	Non-native	150	4	Govindarajulu et al. 2006
China: Daishan Island	Non-native	121	1	Wu et al. 2005
Germany: Baden Wuerttemberg	Non-native	44	1	Laufer 2004
Japan: Kyoto	Non-native	128	1	Hirai 2004
USA: California	Non-native	5	1	Jennings and Cook 1998
USA: California	Non-native	30	1	Carpenter et al. 2002
USA: California	Non-native	107	2	Hothem et al. 2009
USA: Michigan	Native	166	2	Werner et al. 1995
USA: Missouri	Native	455	1	Korschgen and Moyle 1955
USA: Missouri	Native	4	1	Beringer and Johnson 1995
USA: Nebraska	Non-native	1	1	Bomberger Brown and Brown 2009
USA: Nevada	Non-native	28	2	Cross and Gerstenberger 2002
USA: New Mexico	Non-native	138	1	Stuart and Painter 1993
USA: New Mexico	Non-native	85	1	Krupa 2002
USA: Ohio	Native	158	1	Bruggers 1973
USA: Ohio	Native	1	1	Spetz and Spence 2009
USA: Oklahoma	Native	52	1	McCoy 1967
Venezuela	Non-native	338	1	Diaz De Pascual and Guerrero 2008
Total for all locations		2172	29	

Methods

Study sites

The term "site" is used here, as in Orchard (2011), to mean a discrete body of standing water–generally a lake, pond, or pool–where some or all life stages of bullfrogs are present. All bullfrogs examined came from 60 lakes and ponds spread across the coastal lowlands of southeastern Vancouver Island, 44 (73%) of which are clustered in peninsular regional Victoria (Figure 1, Table S1). All of these lakes and ponds are situated between the latitudes 49.8047 and 48.3867 (Figure 1) and range in surface area from lakes as large as 61 ha^2 (Langford Lake: 48.4484, -123.5296) with perimeter distances of almost 5 km down to very small ponds of less than 1 ha^2. Most of the sites were florally complex with thick patches of floating aquatic and emergent vegetation, often with surrounding riparian thickets of willow (*Salix* spp.) and hardhack (*Spiraea douglasii*). Conversely, many of the smaller ponds were highly disturbed and modified habitats such as at farm ponds or golf course ponds with relatively little vegetation either in the water or around the shoreline.

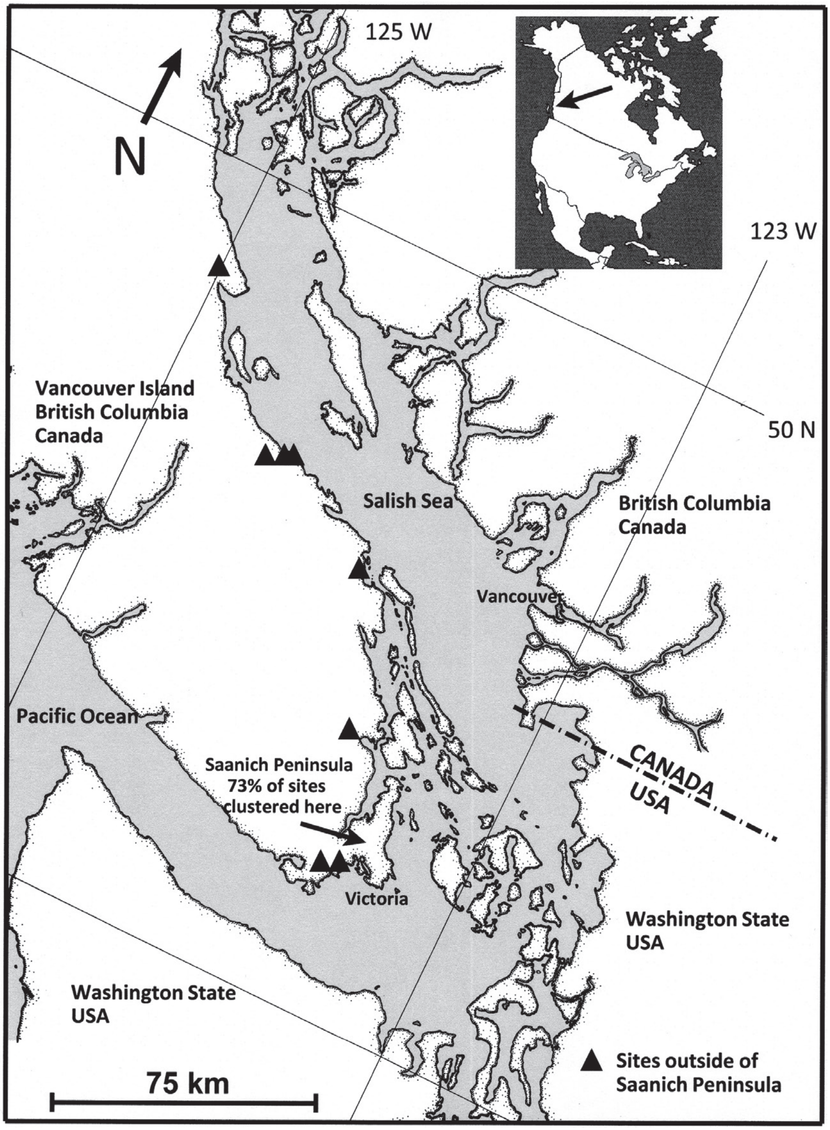

Figure 1. Latitudinal range of study sites on southeastern Vancouver Island, British Columbia, Canada.

Collecting and processing

All fieldwork was carried out by one 2-person team working full-time, approximately 125 nights per season (April-September). Adult and juvenile bullfrogs were captured live using a patented manual "electro-frogger" technique that stuns them momentarily in the water so that they can be netted. They were later euthanized in a two-stage process that cooled them to torpor below 2^0 C before being quick frozen (Orchard 2011). After at least 48 hours in a deep freeze, the bullfrogs were thawed and body lengths measured with Vernier calipers (BL; snout to anus) recorded to the nearest 0.1 mm. The alimentary canal of each bullfrog was incised at the anterior and posterior sphincters of the stomach. All contents were removed and examined. Vegetation and other non-animal material were not included in this analysis. Size-classes were grouped according to body length and categorized as "juvenile" (< 80 mm; includes metamorphs but excludes tadpoles), "young adult" (80–120 mm), and "mature adult" (> 120 mm) (Table 2). "Metamorph" is a transitional stage whose morphology is primarily that of a juvenile but exhibiting some residual larval (tadpole) characteristics. We classed metamorphs as juveniles. Tadpoles did not figure in this study. The terms juvenile, young adult, and mature adult generally correspond to age-class cohorts, e.g. bullfrogs at this latitude spend their first year post-metamorphosis as a juvenile, their second year as a young adult, and their third year as a mature adult. Gender was determined by dissection for all specimens greater than or equal to 80 mm.

Six calendar months were available for fieldwork (April to September, inclusive) but only one site was sampled in all six calendar months (Florence Lake, 48.4589, -123.5127). This site provided 33% (*n* = 1,681) of the total sample. Conversely, 58% (*n* = 35) of the total sites sampled were each visited in only one calendar month of each

Table 2. A. Numbers of bullfrog stomachs with contents (91% of total examined), (**B**) without stomach contents (9% of total examined), and (**C**) with stomach contents as a percentage of monthly totals (with contents + without).

A.

Body length (mm)	April	May	June	July	August	September	Totals	% of Total
Juveniles < 80	338	496	212	224	397	453	2120	46
Young males 80-120	70	113	182	214	313	102	994	22
Mature males > 120	7	74	95	41	53	31	301	6
Young females 80-120	110	111	111	139	242	212	925	20
Mature females > 120	3	60	61	35	67	36	262	6
Totals	528	854	661	653	1072	834	4602	100
% of Total with contents	12	19	14	14	23	18	100	

B.

Body length (mm)	April	May	June	July	August	September	Totals	% of Total
Juveniles < 80	44	19	15	67	52	90	287	61
Young males 80-120	8	9	8	7	3	3	38	8
Mature males > 120	3	19	19	10	7	8	66	14
Young females 80-120	14	4	2	5	6	10	41	8.5
Mature females > 120	2	9	6	9	10	5	41	8.5
Totals	71	60	50	98	78	116	473	100
% of Total	15	13	11	21	16	24	100	

C.

	April	May	June	July	August	September	Total Sample
Total sample (with contents + without)	599	914	711	751	1150	950	5075
% with contents	88%	93%	93%	87%	93%	88%	91%

of the 6 months available but these collectively produced only 10% (n = 516) of the total sample. Most of the total bullfrog sample (68%, n = 3,455) came from 8 sites that were visited in at least 4 of the 6 months (Table S1, Table S2).

Results

The range of organisms found in the stomachs of adult and juvenile bullfrogs spans 15 taxonomic classes (Table 3). The overall sample included 350 (7%) metamorphosed bullfrogs taken between 2006 and 2008; the entire 3,835 caught in 2009 (76%); and 890 (17%) selected from a much larger sample from 2010. Contents from a total of 5,075 bullfrog stomachs, collected over a five-year span, were ultimately examined (Tables 2A, 2B). Of all stomachs, 473 were found to be empty and were removed from the subsequent analyses of the remaining 4,602 (Table 2A). A total of 18,814 identifiable individual prey remains were recovered: 15,081 (80%) of these from the 2009 series, 2,612 (14%) from the 2010 series, and the remaining 1,121 (6%) from 2006 to 2008.

Insects

Out of 18,814 instances of identifiable remains, 84% were insects. Insects were also found in 93% of bullfrog stomachs and were consumed at 95% of the 60 sites sam-

Table 3. Prey remains identified to class.

Class	Total number of instances	% of total prey remains	% of bullfrog stomachs with contents	% of sites
Insecta	15,827	84.1	93.0	95
Arachnida	874	4.6	12.4	51
Malacostraca	770	4.1	10.9	50
Gastropoda	644	3.4	10.3	62
Amphibia	247	1.3	4.2	72
Actinopterygii	166	0.9	2.8	32
Clitellata	107	0.6	1.4	25
Diplopoda	59	0.3	0.9	20
Mammalia	40	0.2	0.9	32
Aves	25	0.1	0.6	27
Chilopoda	20	0.1	0.3	17
Reptilia	12	0.06	0.2	15
Chelonia	12	0.06	0.2	2
Bivalvia	8	0.04	0.1	5
Gordioidea	3	0.02	0.06	2
Totals	18,814	100		

pled. The range in types of insects consumed is highly variable. Most insect parts were not identifiable to species but were at least attributable to one of 47 broader categories of variable taxonomic resolution (Table 4, Table S3).

At least 87% of adult and juvenile bullfrogs had food in their stomachs irrespective of month (Table 2C), although the species composition and densities of available prey change from month to month (Table 4). For example, dragonflies and damselflies were a dietary staple except in April, whereas social wasps were a dominant prey item but only in the late summer. Aphids were similarly important in the late summer but at only 20% of sites (Table 4). Late-summer prey also included brachyceran flies (par-

Table 4. Occurrence of individual prey remains identifiable as insect. The 21 most abundant insect prey categories are shown (See Table S3 for other insects identified).

Insect group (adults unless specified)	Total # of instances	% of total prey items	% of bullfrog stomachs	% of sites	Seasonality: % cases / month					
					Apr	May	June	July	Aug	Sept
Social Wasp	2,674	14.0	16.0	50	< 1	< 1	1	13	64	22
Aphid	1,982	10.0	4.9	20	1	2	1	2	71	24
Damselfly	1,947 (17% nymph)	10.0	23.0	68	2	18	35	13	25	7
Dragonfly	1,415 (27% nymph)	7.5	22.0	87	1	21	25	17	23	13
Water Strider	1,259	6.7	12.0	41	42	13	17	12	11	5
Unidentified Beetle	1,157	6.1	18.0	67	13	27	16	13	15	16
Brachycera fly	726 (61% larvae)	3.8	8.9	42	4	3	7	10	21	55
Ground Beetle	675	3.6	9.6	67	20	26	15	7	19	13
Nematocera fly (not crane flies)	472	2.5	6.9	30	8	34	7	14	24	13
Ant	415	2.2	6.3	42	7	16	11	21	39	6
Predaceous diving beetle	399	2.1	6.8	67	12	31	18	9	23	7
Butterfly/ Moth	365 (55% larvae)	1.9	5.4	55	5	14	36	12	28	5
Weevil	324	1.7	4.6	28	6	12	4	13	18	47
Other bee	257	1.4	3.4	18	4	2	7	50	18	19
Honey bee	254	1.4	2.5	11	1	< 1	8	70	16	5
Unidentified insect	234	1.2	4.6	47	13	19	16	11	20	21
Back-swimmer	225	1.2	3.4	50	2	30	25	9	8	26
Caddisfly	206 (10% larvae)	1.1	2.8	28	38	45	6	1	5	5
Non-social wasp	124	0.7	2.4	31	3	6	13	22	41	15
Click beetle	108	0.6	2.0	27	23	52	19	3	3	0
Giant water bug	96	0.5	1.9	37	1	43	24	9	14	9
Ladybird beetle	87	0.5	1.6	18	3	5	3	12	33	44

ticularly hoverfly larvae) (September), honey bees and other bees (July), and ladybird beetles (August-September) (Table 4). Water striders were especially significant at the start of the active season in mid-April (Table 4). They peaked in the diet of bullfrogs 60-70 mm in body length and then gradually dropped to zero in those over 140 mm. Giant water bugs were found in 27% of stomachs from one site (Filberg Marsh, May 27, 2010) but were relatively uncommon at most other sites.

Non-insect invertebrates

Collectively, non-insect invertebrates made up just over 13% of prey remains with spiders and mites (Arachnida) at 4.6%, isopods and crayfish (Malacostraca) at 4.1%, and snails and slugs (Gastropoda) at 3.4% (Table 5). These three non-insect invertebrate classes all follow immediately behind Insecta (84%) in number of prey instances (Table 3). Gastropods had been eaten at 62% of sites, followed by Arachnida (52%), and Malacostraca (50%) (Table 3).

Spiders (Arachnida) were the most frequently encountered non-insect invertebrate group (Table 5) but still ranked seventh overall behind the six dominant categories of insect. Unlike the seasonal and transient nature of many of the insect groups, spiders remained common prey throughout the active season (Table 5). After spiders, the next arthropod groups were isopods, in eleventh place overall, and crayfish (Malacostraca) in twenty-second. Crayfish figured in the diet at only 22%, of sites and their importance varied from site to site. For example, at one site they were found in 62% of stomachs, but these were taken from a relatively small series of only 16 bullfrogs. Aquatic snails ranked tenth in overall frequency while terrestrial slugs were in twenty-fifth place and found in 1.6% of bullfrog stomachs (Table 5).

Table 5. Non-insect invertebrate prey remains.

Non-insect invertebrate group	Total # of cases	% of total prey remains	% of bullfrog stomachs	% of sites	Seasonality: % of cases / month					
					Apr	May	June	July	Aug	Sept
Spiders	873	4.6	8.9	52	7	24	24	25	10	10
Snails	533	2.8	8.1	58	12	12	12	11	15	20
Isopods	481	2.6	5.3	40	22	17	17	6	9	26
Crayfish	174	0.92	2.8	22	2	17	17	18	52	6
Amphipods	115	0.61	0.24	2	0	62	62	9	1	0
Slugs	108	0.57	1.60	38	22	10	10	20	23	3
Earthworms	83	0.44	0.37	12	76	0	0	0	2	2
Millipedes	59	0.31	0.91	20	22	5	5	5	10	12
Leeches	24	0.13	0.48	20	17	8	8	0	13	37
Centipedes	20	0.11	0.33	17	0	33	33	20	7	7
Clams	8	0.04	0.11	5	0	25	25	0	0	12
Mites	1	0.01	0.02	2	0	0	0	100	0	0

Vertebrates

Fish (Actinopterygii) and amphibians (Amphibia) were the dominant vertebrate prey, occurring in 2.8% and 4.2% of the stomachs, respectively (Table 3). Three-spined stickleback fish (*Gasterosteus aculeatus*) was the most common vertebrate prey species, but found in only 1.5% of bullfrogs stomachs and at just 27% of sites (Table 6). Their frequency in the diet varied from place to place, but at one site they were found in 26% of stomachs.

Cannibalism of bullfrog juveniles and tadpoles collectively made up only 0.43% of total prey remains (Table 6). In one extraordinary instance, they were found in 48% of bullfrog stomachs from a single site. However, when all other records of amphibian predation [Pacific treefrogs, red-legged frogs, rough-skinned newts, ambystomatid salamanders (2 species), and plethodontid salamanders (2 species)] are combined ($n = 159$), they amount to almost exactly twice the number of instances of bullfrog cannibalism ($n = 81$) (Table 6, Table S4). Individual bullfrog stomachs were found to contain as many as 4 adult Pacific treefrogs and 3 adult rough-skinned newts. At one location, treefrogs were in the stomachs of 31% of bullfrogs sampled.

Table 6. The top 14 vertebrate prey categories in the bullfrog diet (See Table S4 for other vertebrates identified).

Vertebrate Group or Species	Total # of cases	% of total prey remains	% of bullfrog stomachs	% of sites	Seasonality: % instances/month					
					Apr	May	June	July	Aug	Sept
Three-spined stickleback (*Gasterosteus aculeatus*)	97	0.52	1.5	27	3	30	19	11	6	31
Pacific treefrog (*Hyla regilla*)–including tadpoles	74	0.39	1.2	33	12	39	19	25	4	1
Bullfrog juveniles (*Rana catesbeiana*)	51	0.27	0.96	33	2	6	2	10	10	70
Rough-skinned newt (*Tarchica granulosa*)	50	0.26	0.87	21	0	36	18	8	26	12
Bullfrog tadpoles	30	0.16	0.43	15	0	7	33	30	27	3
Sculpin (*Cottus* sp.)	25	0.13	0.46	3	20	8	8	0	40	24
Shrew (*Sorex* sp.)	24	0.13	0.48	18	4	17	17	4	54	4
Unidentified fish	18	0.10	0.39	6	28	11	6	22	22	11
Townsend's vole (*Microtus townsendi*)	16	0.08	0.35	13	0	25	31	0	25	19
Pumpkinseed sunfish (*Lepomis gibbosus*)	14	0.07	0.30	18	0	21	29	14	29	7
Western painted turtle (*Chrysemys picta*)	12	0.06	0.17	2	81	19	0	0	0	0
Red-legged frog (*Rana aurora*)	10	0.05	0.21	9	0	10	10	20	60	0
Northwestern salamander (*Ambystoma gracile*)	10	0.05	0.20	5	0	60	40	0	0	0
Coho salmon (*Oncorhynchus kisutch*)	9	0.05	0.13	2	0	0	0	100	0	0

The majority (60%) of the 40 individual mammals consumed were shrews, while the rest were all Townsend's voles (Table 6). There were eight passerine bird species represented by 25 records from 27% of the sites (Table S4). Of reptiles, three species of garter snakes (11 total snakes) were found in the diet along with a single northern alligator lizard (Table S4). Of special conservation concern were the 12 western painted turtle hatchlings (Class Chelonia) that equaled all reptile species combined as a percentage of total bullfrog prey (0.06%, Table 6, Table S4).

Discussion

The approach used here is to focus primarily on instances of predation rather than on ingested volume or nutritional quality in the diet. We accept that one vertebrate is the nutritional equivalent of many insects or other invertebrates, but quantifying and analyzing the relative nutritional significance of each prey instance was beyond the scope of this study.

Insects are the main prey group

Insects were found in 93% of the 4,602 bullfrog stomachs with contents, which is consistent with Korschgen and Moyle's (1955) 83.5% from a much smaller sample (n = 455). Of total identifiable remains 84% were insects, whereas Cohen and Howard (1958) found only about 67% insects in a sample of 300 from California's San Joaquin Valley. The differences in these figures likely reflect lower latitude, seasonality, sample size, and size-class mix; however, the conclusions are all fundamentally the same, e.g. insects are consistently the most numerous organisms in the bullfrog diet. Certain insect groups, such as odonates and beetles, have frequently been identified as predominate (Bruggers 1973, Werner et al. 1995, Hothem et al. 2009).

This study found that early in the bullfrog active season, Odonata (dragonflies and damselflies; May: 45% adults; June: 81% adults) were a consistently important prey for all size-classes of bullfrogs, and this has also been reported by Werner et al. (1995). Water striders (Gerridae) were most frequently consumed by juvenile bullfrogs and were of particular importance during the first few weeks after spring emergence. On the other hand, Hothem et al. (2009) found a greater frequency of water striders in adult bullfrogs (21.5%) than in juveniles (6.5%), but from a much smaller series of only 107 bullfrogs (11 had no stomach contents), 31 of which were juveniles.

Immunity from various natural defenses

Bullfrogs are seemingly immune to many natural predator defenses. Previous studies have alluded to the toxic or potentially repellent effects of natural prey defense mechanisms on predatory bullfrogs. For example, Brodie (1968) found that northern rough-skinned newts from Oregon were lethally toxic to bullfrogs. Later, it was determined that newts from Vancouver Island were at least 1,000 times less toxic than those from Oregon (Brodie and Brodie 1991). Of the 50 northern rough-skinned newts removed from bullfrogs, we recovered as many as three partially to well-digested newts from a single bullfrog stomach. It appears, therefore, that bullfrogs routinely ingest and safely digest rough-skinned newts on southern Vancouver Island with no apparent lethal effects. This situation likely makes northern rough-skinned newts on Vancouver Island exceptionally vulnerable to bullfrog predation.

Krupa (2002) examined bullfrog stomach contents from New Mexico and noted that wasps were commonly consumed. He posed the question: Are bullfrogs immune to the effects of wasp stings or do individuals consume wasps until they develop a conditioned avoidance? For example, in our results 35 bullfrogs had each eaten at least 10 social wasps and as many as 19 without any apparent conditioned avoidance to the wasp sting. Wasps and bees were eaten throughout the active season. Govindarajulu et al. (2006), in examining a small sample of stomach contents from Vancouver Island, also reported wasps as being important in sub-adult bullfrogs. Similarly, Diaz De Pascual and Guerrero (2008) discovered hymenopterans to be the most important dietary item for juvenile bullfrogs in Venezuela; however, it is not stated what type of hymenopterans. Interestingly, the bullfrog's close relative, the green frog (*Rana clamitans*), showed the same seasonal pattern in terms of wasp and bee consumption in Michigan (Werner et al. 1995).

Sticklebacks were the most numerous vertebrate prey and were also one of the most defensively armed. Bullfrogs, however, were seemingly immune to the discomfort of stickleback spines, and we recovered as many as five of these fish from a single stomach. Bullfrogs are reported to have eaten both scorpions and rattlesnakes along the lower Colorado River (Clarkson and de Vos 1986), so their powers of overcoming or withstanding highly evolved, mechanical and chemical, prey defenses are known to be impressive.

Bullfrog survival may be facilitated by bullfrog predation

Dragonfly nymphs are known to prey on bullfrog tadpoles (Hunter et al. 1992), but, conversely, adult and juvenile bullfrogs are major predators of adult and nymphal dragonflies (Table 4). It is fair to speculate that increasing densities of invasive predatory bullfrogs could create a corresponding decline in the densities of dragonfly nymphs. In some previous studies, dragonflies and damselflies are spoken of collectively as odonates (Korschgen and Moyle 1955, Werner et al 1995, Diaz De Pascual and Guerrero 2008), whereas in this study the two groups are reliably separated. Of damselflies, 83% consumed were adult; and of dragonflies, 73% were adult (Table 4). Other studies have found adult odonates to be important in the bullfrog diet (Werner et al 1995), but Hothem et al. (2009) in California and Korschgen and Moyle (1955) in Missouri found that the nymphal stage was more frequently consumed.

In 2011, we observed an adult common garter snake (*Thamnophis sirtalis*) eating a juvenile bullfrog, and this aquatic-foraging snake when at full adult size should be easily able to eat at least half-grown bullfrogs. Smith (1977) considered larger *T. sirtalis* as a likely bullfrog predator but also reported smaller *T. sirtalis* in bullfrog stomachs. All three native garter snake species found on Vancouver Island (*T. elegans, T. ordinoides, T. sirtalis*) were recorded in the bullfrog diet (Table S4). Taken together, the 11 garter snakes of three species reported here would rank just above red-legged frogs in total number of instances. It seems unlikely that the two aquatic foragers, *T. sirtalis* and *T. elegans*, would be able to avoid falling prey to adult bullfrogs. Seigel (1994) found that *Thamnophis atratus,* not native to British Columbia, is an ineffective predator of bullfrog tadpoles, and only the largest snakes can eat them.

A giant water bug (Belostomatidae) was observed killing a bullfrog tadpole in captivity (K. Jancowski, personal observation), and they are known predators of other anurans including ranids (Toledo 2005). At one site, Filberg Marsh (49.8047, -125.0594; May 27, 2010), 43% of the 44 adult bullfrogs captured had consumed one or more giant water bugs. Consequently, predation of giant water bugs by adult bullfrogs may be just one more example of adult bullfrog predation facilitating the survival of bullfrog tadpoles.

Another organism found in the adult bullfrog diet, and also a predator of bullfrogs (Hunter et al. 1992) is the predacious diving beetle, which was found in almost 7% of bullfrog stomachs and had been consumed at 67% of sites (Table 4).

Terrestrial prey

Bullfrogs routinely leave the water and migrate overland as adults and juveniles, presumably feeding as they travel. This may account for species turning up in the bullfrog diet that are strictly terrestrial, e.g. Townsend's voles, terrestrial shrews, northern alligator lizards, western red-backed salamanders (*Plethodon vehiculum*), and Oregon ensatina salamanders (*Ensatina eschscholtzii*).

Indirect predation?

Aphids, because they are tiny, would seem to be an unlikely temptation to bullfrogs. However, aphids ranked second only to social wasps in number of instances of insect predation (Table 4). One probable explanation for this is that in late-summer aphids aggregate in large numbers to feed on the floating leaves of the yellow pond-lily (*Nuphar polysepalum*). The aphids, in turn, attract the attention of predatory wasps, dragonflies, damselflies, brachyceran flies, lacewings, and ladybird beetles, which also attract the interest of predatory bullfrogs. In the process of catching or attempting to catch these larger insects, bullfrogs are inadvertently picking up aphids on their sticky tongues. Approximately 55% of bullfrogs containing aphids had also eaten one or more of these associated species. Consequently, pond-lily leaves can be important feeding stations for bullfrogs as aphids gather on them in late summer.

Cannibalism

Cannibalism, though well known to occur in bullfrogs, has not been very comprehensively studied (Bury and Whelan 1984). Cannibalism in this study was of minor significance overall (0.43% of total prey remains) on south Vancouver Island, with 80% consumed in August and September (Table 6). Similarly, in Brazil, Silva et al. (2009) sampled 79 "adult bullfrogs" but found only one case of cannibalism in 49 cases of anuran predation. By contrast, Govindarajulu et al (2006) reported bullfrogs in the stomachs of almost half (44%) of a sample of 68 "large" (≥ 130 mm) bullfrogs from southern Vancouver Island. One study from New Mexico (Stuart and Painter 1993) found evidence of cannibalism in 56 (40.6%) of 138 stomachs examined. In Venezuela, another study looked at 338 bullfrogs and reported cannibalism in 5% of sub-adults and 32% in adults (Diaz De Pascual and Guerrero 2008).

We sampled 448 bullfrogs that were greater than or equal to 130 mm in body length, or comparable in body size to the "large" category in Govindarajulu et al (2006). Of our 448, only 35 (7.8%) had conspecifics in their stomachs. We sampled throughout the bullfrog active season (April to September) rather than just in the latter half of summer and we sampled 56 more sites than Govindarajulu et al (2006). The smallest cannibalistic bullfrog that we found was 85 mm in body length, one of 25 cases involving bullfrogs less than 130 mm body length. Overall, we recorded 240 instances of bullfrog predation on amphibians with cannibalism accounting for only 34%.

In the absence of alternative prey, cannibalism remains an option for this species that would be of variable importance from site to site, season to season, and year to year. In the long-term, unmanaged bullfrog populations might conceivably drive down native species numbers to the point where cannibalism becomes increasingly important to bullfrog population sustainability.

Phenology and its relation to diet and sampling

Of native amphibians, the Pacific treefrog was the most frequently eaten by bullfrogs (Table 6). Treefrogs peaked in the bullfrog diet in May (39%) as male treefrogs migrate into the water to set up a mating chorus closely followed by females. At least 30% of treefrogs eaten in April and May were females, and 53% of these were gravid. Although bullfrogs are eating more adult males than adult females during this spawning period, the numerical loss of eggs to persistent (April to July) bullfrog predation could be substantial. Male treefrogs are likely in the water for a much longer interval than the females and they are making themselves more conspicuous by vocalizing (Smith 1977), which may account for their higher rate of mortality. Mid-summer predation of treefrogs is primarily attributable to the mass transformation of treefrog tadpoles and their subsequent migration to land (Table 6).

Second to treefrogs are rough-skinned newts. Predation on newts peaked in May (36%) and then rose again in August (26%) (Table 6). These peaks coincide with the May migration of gravid adult female newts to the water to reproduce and the late-summer transformation of larval newts into terrestrial juveniles migrating away from the water (Oliver and McCurdy 1974).

Krupa (2002) has also noted a mid-summer increase in the consumption of social wasps, rising steeply in August then dropping slightly in September (Table 4). Social wasps (Vespidae) become more accessible to bullfrogs in August as the wasps prey upon aphids that aggregate on pond-lily leaves. This wasp-aphid association is an annually recurring phenomenon that may account for the extraordinary abundance of aphids in the bullfrog diet.

Included in this study were the four sites sampled over 5 years by Govindarajulu et al. (2006). We documented more species overall, which included additional vertebrate species. Our early-spring sampling of Beaver Lake Pond (48.5102, -123.3991) on April 24 and May 5, 2010 undoubtedly accounts for our records of recently hatched red-listed western painted turtles. This species would have certainly been missed entirely if fieldwork had been carried out at any other time. Similarly, timing may have been a factor in our discovery of coho salmon at Prior Lake (48.4764, -123.4672) on July 3, 2010.

Sites and sampling

The bullfrogs that figured in this study were not collected primarily for the purpose of examining their stomach contents. They were captured and euthanized as part of a research and development program exploring the feasibility and practicality of bullfrog eradication. This was carried out while testing and refining the electro-frogger technique on a regional scale. Most of the 60 sites included in this study (86%) were only visited in three or less of the six months available within the bullfrog's active season, resulting in only 32% of the overall sample (Table S2). This is because, for the most part, they were smaller ponds where all of the adult and juvenile bullfrogs present could be removed in one or two evenings. In addition, there were a few single-evening reconnaissance missions to sites of interest. The remaining 14% of sites were the larger and more difficult ones where bullfrog densities, immigration rates, and problematical habitats required more effort to bring bullfrog numbers down. The most demanding (Florence Lake, 48.4589, -123.5127) was the only site visited in each of all six months (April to September) and produced 33% of the overall sample (Table S1, Table S2). Consequently, stomach contents from most sites are snapshots of what bullfrogs were eating at that particular site on a specific evening or over a few nights. The database compiled for this analysis is, therefore, a blend of a few sites sampled many times throughout the summer coupled with many sites visited only a few times each in a much more restricted time-frame. The regional database is comprehensive in terms of including samples collected nightly during the entire field season, but is fragmentary in terms of providing seasonally comparative datasets for most of the sites.

Prey species of special concern

American bullfrogs have been identified as, or are suspected to be, a threat to the survival of various vertebrates world-wide, including native fish (Mueller et al. 2006), amphibians (Fisher and Shaffer 1996, Hecnar and M'Closkey 1997, Adams 2000, Kats and Ferrer 2003, Lannoo et al. 1994, Moyle 1973, Hammerson 1982), aquatic turtles (Spetz and Spence 2009), and island endemic birds (Pitt et al. 2005).

In British Columbia, three species of conservation concern relate to this study: the red-listed western painted turtle (*Chrysemys picta bellii*), the blue-listed northern red-legged frog (*Rana (Lithobates) aurora*), and, the aquatic-foraging and red-listed, American water shrew (*Sorex palustris brooksi*). Bullfrogs were found to be consuming hatchling western painted turtles as they entered the water. This was clear from the average carapace length of only 3 cm and the timing of these instances in late April and early May (Table 6). Any loss of hatchling painted turtles is a serious threat to turtle survival because the females produce few eggs and survivorship to recruitment is low (Gregory and Campbell 1996). Hatchling painted turtles are easily swallowed by bullfrogs and will remain vulnerable for at least the first few weeks post-hatching until their shell dimensions exceed a bullfrog's maximum gape. Red-legged frogs were consumed primarily as fully metamorphosed juveniles and eaten mostly in the month of August (Table 6). American water shrews have not been recorded in the bullfrog diet, but they are flagged because the historical database for this shrew lists localities, such as Hamilton Marsh on Vancouver Island (49.3159, -124.4625), that are now thoroughly invaded by bullfrogs. The presence of shrews (at least some were *S. vagrans*), as well as the larger Townsend's voles, demonstrate that bullfrogs will take small mammals, and the habits and habitat preferences of the American water shrew should make them especially vulnerable to bullfrog predation. The Pacific water shrew (*Sorex bedirii*) has also been recorded in the bullfrog diet (Campbell and Ryder 2004).

It is of economic interest that coho salmon (*O. kisutch*) juveniles were found in 16% of bullfrogs sampled from Prior Lake in early July (Table 6, Table S1). Most of these were about 8 cm long, though bullfrogs have been documented eating trout up to 15 cm in length (Bury and Whelan 1984). It is not known whether coho salmon are being preyed upon locally in lotic habitats. However, many streams on southern Vancouver Island become intermittent in late summer and in shallow isolated pools salmon fry could be more vulnerable to bullfrog predation. Garwood et al. (2010) recently documented an adult bullfrog from a stream in California with an 11.6 cm long coho salmon in its stomach. Lotic habitats were not sampled in our study because bullfrogs aggregate and reproduce locally only in the warmer standing water of lakes and ponds. Salmonids, such as coho salmon, tend to prefer cooler and better oxygenated flowing waterways.

Empty stomachs

An organism that lies dormant for almost six months of the year must replenish its fat reserves during the relatively brief six-month active season. Mature adults, in particular, should have the life experience to be proficient hunters. They also have energy demanding roles that include vocalizations, territorial defense, egg production, spawning, and may include overland migrations. Then they must end the season with sufficient reserves to overwinter for another six months. The percentage of mature adults of both genders with empty stomachs was, therefore, remarkably high (Table 2B).

Govindarajulu et al. (2006) also found empty stomachs but only in mature males and newly metamorphosed bullfrogs. The so-called "metamorph" is a brief transitional stage at the end of the tadpole stage and at the very beginning of the juvenile stage. During this interval, the frog displays combined morphological characteristics of a larva and a juvenile. Feeding in juveniles is not possible until the mouth and internal organs of the tadpole stage are fully resorbed and reformed into a completely metamorphosed morphology. An indeterminate number of the juveniles with empty stomachs (Table 2B) exhibited tail vestiges and so their empty stomachs may be attributed to this transitional "metamorph" morphology that is not yet fully, or has only just become, operational in the predator mode.

Conclusions

1 As an "invasive alien" the American bullfrog is a highly adaptable, opportunistic, and seemingly unspecialized predator that has a uniquely large and complex ecological footprint both above and below the water surface.
2 Insects were the dominate prey group found in 84% of prey instances and 93% of stomachs with food, but seasonality influenced the relative importance of any one insect group over another at any given time period.
3 Cannibalism was found to be a minor component of the diet in terms of relative instances and accounted for approximately 34% of all instances of predation on amphibians.
4 Bullfrog control measures should be routinely factored into management plans for rare and endangered species, such as the western painted turtle on southern Vancouver Island, which are particularly vulnerable to bullfrog predation.

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Appendix

Supplementary tables. (doi: 10.3897/neobiota.16.3806.app) File format: Microsoft Excel Document (xls).

Explanation note: Table S1: Sites where bullfrogs were collected on Vancouver Island, British Columbia, Canada. **Table S2:** Sampling frequency by month per site and its relation to catch. **Table S3:** Occurrence of individual prey remains identifiable as insect. The remaining 26 insect prey categories not given in Table 4. **Table S4:** The remaining 19 vertebrate prey groups in the bullfrog diet not shown in Table 6.

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