Am. Midl. Nat. 147:145–152

Predation by Oregon Spotted Frogs (Rana pretiosa) on Western Toads (Bufo boreas) in Oregon

CHRISTOPHER A. PEARL[1]
USGS Forest and Rangeland Ecosystem Science Center 3200 SW Jefferson Way, Corvallis, Oregon 97333

AND

MARC P. HAYES
Washington Department of Fish and Wildlife, Habitat Program 600 Capitol Way North, Olympia, 98501

ABSTRACT.—Toads of the genus *Bufo* co-occur with true frogs (family Ranidae) throughout their North American ranges. Yet, *Bufo* are rarely reported as prey for ranid frogs, perhaps due to dermal toxins that afford them protection from some predators. We report field observations from four different localities demonstrating that Oregon spotted frogs (*Rana pretiosa*) readily consume juvenile western toads (*Bufo boreas*) at breeding sites in Oregon. Unpalatability thought to deter predators of selected taxa and feeding mode may not protect juvenile stages of western toads from adult Oregon spotted frogs. Activity of juvenile western toads can elicit ambush behavior by Oregon spotted frog adults. Our review of published literature suggests that regular consumption of toadlets sets Oregon spotted frogs apart from most North American ranid frogs. Importance of the trophic context of juvenile western toads as a seasonally important resource to Oregon spotted frogs needs critical investigation.

INTRODUCTION

Despite extensive overlap in aquatic habitat use, few observations have been reported suggesting that North American frogs of the genus *Rana* are important predators on toads of the genus *Bufo*. Throughout much of its range along the crest and eastern flank of the Oregon Cascade Range, the western toad (*Bufo boreas*) is sympatric with the Oregon spotted frog (*Rana pretiosa*) (Nussbaum *et al.*, 1983; Stebbins, 1985). Previous diet observations suggest that Oregon spotted frogs occasionally consume vertebrate prey (Licht, 1986). Cannibalism and predation on juvenile *R. a. aurora* and *Hyla regilla* (when provided in the field by the observer) have been described in Oregon spotted frogs (Licht, 1986), but no published references exist for predation on western toads. Herein we describe observations of predation on newly transformed western toads from localities across the range of the Oregon spotted frog in Oregon. We also report secondary evidence of predation by Oregon spotted frogs on western toad juveniles from analysis of garter snake (*Thamnophis* sp.) stomach contents, and include descriptions of a cryptic, ambush approach by Oregon spotted frog adults.

OBSERVATIONS

We directly observed Oregon spotted frog ambush behaviors and predation on western toad juveniles (hereafter 'bufivory') at three montane sites in the Oregon Cascade range. At Gold Lake Bog (Lane County; elevation 1460 m) on 18 July 1992, MPH observed one adult female Oregon spotted frog swim slowly and completely submerged except for the eyes toward an exposed peat shelf where ca. 20 juvenile western toads were active. Toadlets did not move in any way suggesting awareness of the frogs' approach. One toadlet moved

[1] Corresponding author: Telephone: (541) 754-4416; FAX: (541) 754-4326;
e-mail: christopher_pearl@usgs.gov

toward the concealed Oregon spotted frog, and was captured by the frog after the toadlet reoriented to face the opposite direction. In the ensuing 103 min, MPH observed 9 female (mean size 73 mm snout-vent length, SVL; range 68–77 mm SVL) and 1 male Oregon spotted frog (69 mm SVL) consume a total of 30 toadlets (range 1–7 toadlets per frog). Each Oregon spotted frog was captured and measured only after they were judged to have swallowed the last toadlet observed in the immediate area. Twenty juvenile toads similar in size with those that were consumed averaged 11.4 mm SVL (range 9–14 mm).

On 3 August 1993 at Big Marsh, MPH observed an 82 mm female Oregon spotted frog attempt to capture a juvenile western toad that also suggested ambush behavior by the spotted frog. When first observed floating in shallow water, the spotted frog maintained a typical, head-high position. Five to six toadlets were clearly visible on the sandy shoreline. The Oregon spotted frog depressed its head flush with the water surface and slowly approached the shoreline. From ca. 2 cm offshore, it lunged at the closest toadlet, which was located ca. 2 cm above the waterline. The toadlet evaded capture and quickly vacated the area.

Predation by two adult female Oregon spotted frogs was observed by CAP on 26 August 1999 near Mink Lake in the central Oregon Cascades (Lane County; elevation 1500 m). One 90 mm female consumed one juvenile western toad before it was captured, and ingested two additional toadlets during ca. 20 min of observation after release. Toadlets that were within 10–35 cm and had an unobstructed view of the adult Oregon spotted frog remained motionless throughout the ca. 20 min of observation. Toads farther away, or visually separated from the adult spotted frog by fallen logs continued hopping along the shore. After release, the same female hurdled two crouched, inactive toadlets to consume a moving individual immediately beyond them that could not directly see the frog. Movement of prey appeared important for detection, a cue that has been noted for other ranid frogs (Hamilton, 1948; Licht, 1986). Newly transformed American toads (*Bufo americanus*) exhibit crouching and inactivity in response to visual detection of predators (Hayes, 1989; Heinen, 1994), and a similar behavior was observed in these western toad juveniles.

When first encountered, the aforementioned and a second female were positioned in shallow water (3–6 cm deep, 15–25 cm from shore), facing the shoreline along which toadlets were moving. Twice during ca. 20 min of observation, the second female (87 mm SVL) sprang from a partially submerged position to capture moving toadlets, each time returning to her original location to complete ingestion. A similar aquatic approach is described in *Rana septentrionalis* (Hedeen, 1972) and *R. clamitans* (Hamilton, 1948), two eastern ranids that make similar use of aquatic habitats. The upright eyes of Oregon spotted frogs, a morphology thought to aid its aquatic microhabitat use (Dunlap, 1955; Licht, 1986), may also facilitate ambush predation of anurans.

Examinations of western toads eaten by adult Oregon spotted frogs that were subsequently consumed by garter snakes were made at three localities. On 3 August 1993, MPH captured an adult (860 mm SVL) common garter snake (*Thamnophis sirtalis*) at Big Marsh (Klamath County; elevation 1440 m). Juvenile western toads were abundant, in places exceeding 100 per square meter. The garter snake had recently ingested a large (88 mm SVL) female Oregon spotted frog, which itself contained three toadlets. At the same site, a 78 mm female Oregon spotted frog was captured with a 12 mm toadlet still alive in her buccal cavity. On 29 July 1997, along the Wood River (Klamath County; elevation 1263 m), MPH found a recently depredated Klamath garter snake (*Thamnophis elegans biscutatus*) that contained an 81-mm female adult Oregon spotted frog. Dissection of the Oregon spotted frog revealed 8 western toad juveniles that ranged from ca. 9 to 11 mm. Juvenile western toads were abundant where the snake was observed. On 15 August 1998, CAP captured an

adult common garter snake (*Thamnophis sirtalis*) near Mink Lake in the central Cascade Range. Palpation of the snake revealed a recently consumed male Oregon spotted frog (59 mm SVL). Dissection of the spotted frog revealed one juvenile western toad (15 mm SVL). Western toads (Gosner (1960) stages 43–46; 12–16 mm SVL) were abundant around the marsh, often exceeding 50 per square meter.

DISCUSSION

Our observations confirm that adult Oregon spotted frogs readily consume young juvenile western toads, and suggest that adults actively seek toadlets during the brief seasonal interval when they are abundant. Given the extensive co-occurrence of *Bufo* and *Rana* species at aquatic sites across their ranges and fairly well-studied diets of ranid frogs (especially *R. catesbeiana*), regular predation on juvenile western toads may make Oregon spotted frogs unique among North American ranids. Other researchers have speculated that *Bufo* are unfavorable food for ranid frogs. After finding one *Bufo* in 455 *R. catesbeiana* in Missouri, Korschgen and Moyle (1955; p. 340) stated, ''The question arises whether toads are less acceptable than are frogs for food.'' Perez (1951) found no *Bufo marinus* in 50 *R. catesbeiana* stomachs where they occur syntopically in their Puerto Rican introduced ranges, and concluded that declines in toads were not attributable to predation by bullfrogs. Hamilton (1948; p. 206) reported that ''repeated collecting of green frogs (*R. clamitans*) in areas that abounded with transforming toads showed no evidence of their feeding on small bufonids.'' Both Brown (1974) and Tucker and Sullivan (1975) concluded that adult *Bufo valliceps*, *B. americanus* and *B. woodhousei* are unpalatable and/or toxic after observing regurgitation and torpid behavior in adult *R. catesbeiana* after ingestion attempts.

Our review of published diet studies (Table 1) illustrates the rarity of detection of *Bufo* as prey in North American ranids. Among 10 published diet studies of pond-breeding northwestern ranids (*Rana a. aurora*, *R. luteiventris*, *R. pipiens*, *R. pretiosa* and introduced *R. catesbeiana*), only one *Bufo* was documented among stomach contents (Table 1). In that Montana study, juvenile *Bufo boreas* comprised only 4 of 373 identified food items in 52 *R. pipiens* (Miller 1978). One field observation has been made of *R. luteiventris*, the phylogenetic sister taxon of *R. pretiosa*, consuming juvenile *B. boreas* (Pearl, 2000). The diet of bullfrogs (*Rana catesbeiana*), the largest North American ranid and one documented to feed extensively on anurans, has been particularly well studied. Of 24 studies reviewed by Smith (1972), three (Korschgen and Moyle, 1955; Troyer, 1968; McCoy, 1969) documented *Bufo* in bullfrog diets in their native midwestern range. Brown (1974) reviewed 15 bullfrog diet studies, and of the 9 not included by Smith (1972), only one study documented *Bufo* as prey items. In at least two of the reviewed studies where no toads were detected in stomach contents (Lewis, 1962; Fulk and Whitaker, 1968), *Bufo woodhousei* was noted as common where bullfrogs were collected. Successful consumption of *Bufo* by bullfrogs has thus been documented only occasionally, and appears biased toward smaller toads: one 'young' *Bufo* in 99 young bullfrogs from New York (Munz, 1920; p. 39); one 46 mm *Bufo* in 52 bullfrogs from Oklahoma (McCoy, 1969); one *Bufo* (no size given) in 455 bullfrogs from Missouri (Korschgen and Moyle, 1955); one 42 mm *B. debilis* and one 70 mm *B. cognatus* in the same adult bullfrog in New Mexico (Stuart, 1995). Among other eastern ranids, we identified only one anecdotal observation of *Bufo* consumption. Hamilton (1948) reported *Rana palustris* consuming *Bufo* toadlets in New York, but specific data were not provided.

Most life stages of North American *Bufo* (including western toads) possess bufotoxins (bufodienolides and others) within granular glands of the skin, which afford protection from some predators (Licht and Low, 1968; Brodie *et al.*, 1978; Clarke, 1997). Selected

TABLE 1.—*Bufo* prey items reported in diet studies of North American *Rana*

	Locality		Frogs examined			Prey items[a]		
Rana species	Country	State or province[b]	Total	w/ *Bufo*	w/other Anura	Total	*Bufo* prey	Citation
a. aurora	CAN	BC	104	0	0	722	0	Licht, 1986
a. draytonii	USA	CA	35	0	1	190	0	Hayes and Tennant, 1985
catesbeiana		AR	139	0	9–11[c]	np	0	McKamie and Heidt, 1974
		CA	300	0	17–21[c]	np	0	Cohen and Howard, 1958
		IL	123	0	30	np	0	Lewis, 1962
		IN	442	0	17–32[c]	np	0	Fulk and Whitaker, 1968
		KS	2,763	0	Present	np	0	Smith, 1972
		MA, NY	98[d]	1	1	np	1	Munz, 1920
		MO	1,365	3	165	3,012	3	Corse and Metter, 1980
			408	0	19–26[c]	np	np	Korschgen and Baskett, 1963
			455	1	61–98[c]	np	1	Korschgen and Moyle, 1955
			52	1	1	np	1	McCoy, 1967
		NY	24	0	Present	np	0	Stewart and Sandison, 1972
		OH	158	0	5	np	0	Bruggers, 1973
		PR	50	0	np	np	0	Perez, 1951
		VA	138	0	11[c]	np	0	Brooks, 1964
clamitans		IL	475	0	2	np	0	Jenssen and Klimstra, 1966
		NY	434	0	16	np	np	Hamilton, 1948
			24	0	0	np	0	Stewart and Sandison, 1972
grylio		GA	122	0	0	177	0	Lamb, 1984
luteiventris[e]	CAN	AB	12	0	0	203	0	Moore and Strickland, 1955
	USA	MT	50	0	0	517	0	Miller, 1978
		OR	206	0	3	np	0	Whitaker *et al.*, 1983
		WY	178	0	0	802	0	Turner, 1959
pipiens		ID, UT	97	0	1	515	0	Knowlton, 1944
		MN	23	0	0	266	0	Hedeen, 1972
		MT	52	1–4	0	373	4	Miller, 1978
		NY	463	0	0	np	0	Linzey, 1967
	CAN	AB	20	0	0	184	0	Moore and Strickland, 1954

TABLE 1.—Continued.

	Locality		Frogs examined			Prey items[a]		
Rana species	Country	State or province[b]	Total	w/ *Bufo*	w/other Anura	Total	*Bufo* prey	Citation
pretiosa	CAN	BC	41	0	0[f]	307	0	Licht, 1986
pretiosa[g]	USA	OR, WA	37	0–1[h]	0–1[h]	159	0–1[h]	Schonberger, 1945
septentrionalis		MN	60	0	0	np	0	Hedeen, 1972
		NY	24	0	0	np	0	Stewart and Sandison, 1972
sphenocephala[i]		FL	497	0	14	1398[j]	0	Kilby, 1945
sylvatica	CAN	AB	36	0	0	440	0	Moore and Strickland, 1955

[a] np = data not provided in citation

[b] State or Province codes: Alberta (AB), British Columbia (BC), California (CA), Florida (FL), Georgia (GA), Idaho (ID), Illinois (IL), Indiana (IN), Kansas (KS), Massachusetts (MA), Minnesota (MN), Montana (MT), New York (NY), Ohio (OH), Oregon (OR), Puerto Rico (PR), Utah (UT), Virginia (VA), Washington (WA), Wyoming (WY)

[c] Calculations (upper and lower) from percentage data in original source

[d] Most smaller bullfrogs; 6 of 98 individuals >60 mm long

[e] Originally described as *Rana pretiosa*, subsequently revised to *Rana luteiventris* (Green *et al.*, 1997)

[f] Licht (1986) reports 3 observations of *R. pretiosa* capturing juvenile *R. aurora* in the field, and adults of *R. pretiosa* and *R. aurora* both consuming juveniles of the other in captivity

[g] May include a mix of what is now *R. pretiosa* and *R. luteiventris*

[h] Listed as "Amphibia, 1 tadpole" (Schonberger, 1945; p. 121)

[i] As *R. pipiens sphenocephala*

[j] Three items listed as "Other frogs (undetermined)"

predators are able to consume adult *Bufo*, relying either on avoidance of areas of toxin concentration (dorsal skin and parotoid glands) or some resistance to these compounds (Schaaf and Garton, 1970; Corn, 1993). Since Oregon spotted frogs seem undeterred in their predation on juvenile western toads, they are either unaffected by dermal granular glands and associated compounds or this defense is not fully developed in toadlets at this stage, or a combination of these factors occurs. Toxicity and unpalatability can vary through development, and metamorphic stages of several *Bufo* species are thought to be less palatable to vertebrate and invertebrate predators than premetamorphic larval stages (Brodie *et al.*, 1978; Brodie and Formanowicz, 1987; Lawler and Hero, 1997). Relative palatability of postmetamorphic stages of most *Bufo*, including western toads, has not been well studied. Duellman and Trueb (1986) speculated that *Bufo* immediately postmetamorphosis could be more palatable than peak metamorphic stages due to incomplete development of dermal granular glands. Licht (1967) found that complete formation of parotoid glands in three species of North American *Bufo* took between 18 and 29 d after metamorphosis. Formanowicz and Brodie (1982) suggested that continued development of granular glands in *Rana sylvatica* (which also possess some noxious dermal compounds) beyond metamorphosis would confer increased unpalatability and survival through the juvenile stages. That most of observed *B. boreas* western toad prey in our observations were less than 1 mo posttransformation suggest they had incompletely developed toxin-bearing dermal glands. In addition, unpalatable dermal compounds may not provide as effective a predation deterrent to nonmasticating, engulfing predators as to predators that chew skin directly (Wassersug, 1973; Heyer *et al.*, 1975). Further work is needed to examine phenology of dermal toxin glands in postmetamorphic *Bufo* to better understand their palatability to vertebrate predators.

Oregon spotted frogs occur at lentic sites where western toads reproduce, and occur from sea level to over 1550 m, where the active season is temporally limited (Nussbaum *et al.*, 1983; C. Pearl and M. Hayes, pers. obs.). At montane habitats in the Pacific Northwest, western toad metamorphosis generally peaks after mid-July, and localized aggregations of juveniles exceeding 100 per square m around breeding sites are not uncommon before dispersal (Arnold and Wassersug, 1978; Nussbaum *et al.*, 1983; C. Pearl, pers. obs.). Among the Oregon spotted frogs observed in predation episodes for which genders were confirmed, 16 were adult females and two were adult males. Besides being larger and able to accommodate larger prey (Licht, 1975), reproductive-age females may be taking advantage of this late-season food resource in preparation for extended winter inactivity (October–June) and development of ova, which is underway at this time (C. Pearl, pers. obs). Juvenile western toads are an abundant, readily captured food resource for Oregon spotted frogs during an important, but brief seasonal interval. Study is needed of how Oregon spotted frogs may exploit this resource.

Acknowledgments.—Reviews by R. Bruce Bury, Douglas P. Calvin, Alan D. St. John and Erik Jules improved early drafts of this manuscript. The U.S. Fish and Wildlife Service, Bureau of Land Management, Oregon Department of Fish and Wildlife and the Willamette and Winema National Forests provided support for portions of this work. All animals were handled under Scientific Collecting permits from the Oregon Department of Fish and Wildlife.

LITERATURE CITED

ARNOLD, S. J. AND R. J. WASSERSUG. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. *Ecology,* **59**:1014–1022.

BRODIE, E. D., JR. AND D. R. FORMANOWICZ, JR. 1987. Antipredator mechanisms of larval anurans: protection of palatable individuals. *Herpetologica,* **43**:369–373.

———, ——— AND E. D. BRODIE, III. 1978. The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. *Herpetologica,* **34**:302–306.

BROOKS, G. R. 1964. An analysis of the food habits of the bullfrog, *Rana catesbeiana*, by body size, sex, month, and habitat. *Virginia J. Sci.,* **15**:173–186.

BROWN, L. E. 1974. Behavioral reactions of bullfrogs while attempting to eat toads. *Southwestern Nat.,* **19**:335–337.

BRUGGERS, R. L. 1973. Food habits of bullfrogs in northwest Ohio. *Ohio J. Sci.,* **73**:185–188.

CLARKE, B. T. 1997. The natural history of amphibian skin secretions, their normal functioning and potential medical applications. *Biol. Rev.,* **72**:365–379.

COHEN, N. W. AND W. E. HOWARD. 1958. Bullfrog food and growth at the San Joaquin Experimental Range, California. *Copeia*, **1958**:223–225.

CORN, P. S. 1993. *Bufo boreas* (Boreal toad). Predation. *Herpetol. Rev.,* **24**:57.

CORSE, W. A. AND D. E. METTER. 1980. Economics, adult feeding and larval growth of *Rana catesbeiana* on a fish hatchery. *J. Herpetol.,* **14**:231–238.

DUELLMAN, W. E. AND L. TRUEB. 1986. Biology of amphibians. Johns Hopkins University Press, Baltimore, Maryland. 670 p.

DUNLAP, D. G. 1955. Inter- and intraspecific variation in Oregon frogs of the genus *Rana*. *Am. Midl. Nat.,* **54**:314–331.

FORMANOWICZ, D. R., JR. AND E. D. BRODIE, JR. 1982. Relative palatabilities of members of a larval amphibian community. *Copeia*, **1982**:91–97.

FULK, F. D. AND J. O. WHITAKER. 1968. The food of *Rana catesbeiana* in three habitats in Owen County, Indiana. *Proc. Indiana Acad. Sci.,* **78**:491–496.

GOSNER, N. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica,* **16**:183–190.

GREEN, D. M., H. KAISER, T. F. SHARBEL, J. KEARSLEY AND K. R. MCALLISTER. 1997. Cryptic species of spotted frogs, *Rana pretiosa* complex, in western North America. *Copeia*, **1997**:1–8.

HAMILTON, W. J. JR. 1948. The food and feeding behavior of the green frog, *Rana clamitans* Latrielle, in New York State. *Copeia*, **1948**:203–207.

HAYES, F. E. 1989. Antipredator behavior of recently metamorphosed toads (*Bufo a. americanus*) during encounters with garter snakes. *Copeia*, **1989**:1011–1015.

HAYES, M. P. AND M. R. TENNANT. 1985. Diet and feeding behavior of the California red-legged frog, *Rana aurora draytonii* (Ranidae). *Southwestern Nat.,* **30**:601–605.

HEINEN, J. T. 1994. Antipredator behavior of newly metamorphosed American toads (*Bufo a. americanus*), and mechanisms of hunting by eastern garter snakes (*Thamnophis s. sirtalis*). *Herpetologica,* **50**:137–145.

HEDEEN, S. E. 1972. Food and feeding behavior of the mink frog, *Rana septentrionalis* Baird, in Minnesota. *Am. Midl. Nat.,* **88**:291–300.

HEYER, W. R., R. W. MCDIARMID AND D. L. WEIGMANN. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica,* **7**:100–111.

JENSSEN, T. A. AND W. D. KLIMSTRA. 1966. Food habits of the green frog, *Rana clamitans*, in southern Illinois. *Am. Midl. Nat.,* **76**:169–182.

KILBY, J. D. 1945. A biological analysis of the food and feeding habits of two frogs, *Hyla cinerea cinerea* and *Rana pipiens sphenocephala*. *Quart. J. Florida Acad. Sci.,* **8**:71–104.

KNOWLTON, G. F. 1944. Some insect food of *Rana pipiens*. *Copeia*, **1944**:119.

KORSCHGEN, L. J. AND T. S. BASKETT. 1963. Foods of impoundment- and stream-dwelling bullfrogs in Missouri. *Herpetologica,* **19**:89–99.

———, AND D. L. MOYLE. 1955. Food habits of the bullfrog in central Missouri farm ponds. *Am. Midl. Nat.,* **54**:332–341.

LAMB, T. 1984. The influence of sex and breeding condition on microhabitat selection and diet in the pig frog *Rana grylio*. *Am. Midl. Nat.,* **111**:311–318.

LAWLER, K. L. AND J.-M. HERO. 1997. Palatability of *Bufo marinus* tadpoles to a predatory fish decreases with development. *Wildl. Res.,* **24**:327–334.

LEWIS, W. M. 1962. Stomach contents of bullfrogs (*Rana catesbeiana*) taken from a minnow hatchery. *Trans. Ill. State Acad. Sci.,* **55**:80–83.

LICHT, L. E. 1967. Initial appearance of the parotoid gland gland in three species of toads (Genus *Bufo*). *Herpetologica,* **23**:115–118.

———. 1975. Comparative life history features of the western spotted frog, *Rana pretiosa*, from low- and high-elevation populations. *Can. J. Zool.,* **53**:1254–1257.

———. 1986. Food and feeding behavior of sympatric red-legged frogs, *Rana aurora*, and spotted frogs, *Rana pretiosa*, in southwestern British Columbia. *Can. Field Nat.,* **100**:22–31.

———, AND B. S. LOW. 1968. Cardiac response of snakes after ingestion of toad parotoid venom. *Copeia*, **1968**:547–551.

LINZEY, D. W. 1967. Food of the leopard frog, *Rana p. pipiens*, in central New York. *Herpetologica,* **23**: 11–17.

MCCOY, C. J. 1969. Diet of bullfrogs (*Rana catesbeiana*) in central Oklahoma farm ponds. *Proc. Okla. Acad. Sci.,* **48**:44–45.

MCKAMIE, J. A. AND G. A. HEIDT. 1974. A comparison of spring food habits of the bullfrog, *Rana catesbeiana*, in three habitats of central Arkansas. *Southwestern Nat.,* **19**:107–111.

MILLER, J. D. 1978. Observations on the diets of *Rana pretiosa*, *Rana pipiens*, and *Bufo boreas* from Montana. *Northwest Sci.,* **52**:243–249.

MOORE, J. E. AND E. H. STRICKLAND. 1954. Notes on the food of three species of Alberta amphibians. *Am. Midl. Nat.,* **52**:221–224.

———, AND ———. 1955. Further notes on the food of Alberta amphibians. *Am. Midl. Nat.,* **54**:253–256.

MUNZ, P. A. 1920. A study of the food habits of the Ithacan species of Anura during transformation. *J. Entomol. Zool.,* **12**:33–56.

NUSSBAUM, R. A., E. D. BRODIE AND R. M. STORM. 1983. Reptiles and amphibians of the Pacific Northwest. University of Idaho Press, Moscow. 356 p.

PEARL, C. A. 2000. *Bufo boreas*. Predation. *Herpetol. Rev.,* **31**:233–234.

PEREZ, M. E. 1951. The food of *Rana catesbeiana* Shaw in Puerto Rico. *Herpetologica,* **7**:102–104.

SCHAAF, R. T. AND J. S. GARTON. 1970. Raccoon predation on the American toad, *Bufo americanus*. *Herpetologica,* **26**:334–335.

SCHONBERGER, C. F. 1945. Food of some amphibians and reptiles of Oregon and Washington. *Copeia*, **1945**:120–121.

SMITH, A. K. 1972. Feeding strategies and population dynamics of the bullfrog (*Rana catesbeiana*). Ph.D. Dissertation, Univ. of Kansas, Lawrence. 126 p + appendices.

STEBBINS, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston, Massachusetts. 279 p.

STEWART, M. M. AND P. SANDISON. 1972. Comparative food habits of sympatric mink frogs, bullfrogs, and green frogs. *J. Herpetol.,* **6**:241–244.

STUART, J. N. 1995. *Rana catesbeiana. Diet. Herpetol. Rev.,* **26**:33.

TROYER, D. R. 1968. Growth rate and movements of the bullfrog, *Rana catesbeiana*, in Kansas. M.S. Thesis, Dept. of Zoology, Univ. of Kansas. 89 p.

TUCKER, J. K. AND M. E. SULLIVAN. 1975. Unsuccessful attempts by bullfrogs to eat toads. *Trans. Ill. State Acad. Sci.,* **68**:167.

TURNER, F. B. 1959. An analysis of the feeding habits of *Rana p. pretiosa* in Yellowstone Park, Wyoming. *Am. Midl. Nat.,* **61**:403–413.

WASSERSUG, R. J. 1973. Aspects of social behavior in Anuran larvae, p. 273–297. *In:* J. L. Vial (ed.). Evolutionary biology of the Anurans. Univ. of Missouri Press, Columbia.

WHITAKER, J. O., JR., S. P. CROSS, J. M. SKOVLIN AND C. MASER. 1983. Food habits of the spotted frog (*Rana pretiosa*) from managed sites in Grant County, Oregon. *Northwest Sci.,* **57**:147–154.

SUBMITTED 12 SEPTEMBER 2000 ACCEPTED 28 JUNE 2001