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Author(s): David L. Schaub and John H. Larsen, Jr.

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THE REPRODUCTIVE ECOLOGY OF THE PACIFIC TREEFROG (*HYLA REGILLA*)

DAVID L. SCHAUB AND JOHN H. LARSEN, JR.

ABSTRACT: Breeding activities, population levels, movements, and pond preferences were investigated for the Pacific treefrog, *Hyla regilla*, during two breeding seasons at five small ponds in northern Idaho. The number of males declined from approximately 360 in 1976 to approximately 160 in 1977. Individual males spent more time at the ponds in 1976 than in 1977, and the average snout-vent length for both sexes was less in the first year than in the second. The dominant coloration of males shifted from nongreen in 1976 to green in 1977.

Key words: Anura; Breeding; Idaho

FEW North American anurans exploit such a variety of habitats as does the Pacific treefrog, *Hyla regilla*. Occurring from Baja California to British Columbia, it inhabits deserts, grasslands, mountains, and rain forests (Stebbins, 1966). Because of the ubiquity of this species, its temperature tolerances and relationship to water have been investigated by several workers (Brown, 1975; Claussen, 1973; Jameson, 1966). In addition, studies of morphology, including color polymorphism, have examined the adaptations of populations to local environments (Calhoun and Jameson, 1970; Jameson et al., 1966, 1970; Resnick and Jameson, 1963; Vogt and Jameson, 1970). Geographic variation in mating calls of *H. regilla* has been established (Snyder and Jameson, 1965), and behavioral responses to different patterns of vocalization have been observed by Allan (1973).

Relatively few field studies have been conducted on the ecology and behavior of *Hyla regilla*. Brattstrom and Warren (1955) and Cunningham and Mullally (1956) investigated populations of *H. regilla* in southern California. Temperature preferences of frogs in California populations have been discussed by Brattstrom (1963). Feeding habits of treefrogs in northern California were analyzed by Johnson and Bury (1965). Growth, population structure, and movements of *H. regilla* were studied by Jameson (1956, 1957) in western Oregon. Spacing and calling behavior

of *H. regilla* near Vancouver, B. C., were observed by Whitney and Krebs (1975a, b). Information regarding the ecology of *H. regilla* in the northern, inland part of its range is extremely limited. To provide such information, the current study examined treefrogs in northern Idaho during two consecutive breeding periods to determine population size, structure, movements, pond preferences, and breeding activities.

STUDY AREA

The study area, located 10 km E of Moscow, Latah County, Idaho, is densely forested with conifers, predominantly ponderosa pine (*Pinus ponderosa*) and grand fir (*Abies grandis*). Nonforested areas support a variety of shrubs, including snowberry (*Symphoricarpos albus*), thimbleberry (*Rubus parviflora*), ninebark (*Physocarpus capitatus*), red twinberry (*Lonicera utahensis*), ocean spray (*Holodiscus discolor*), black nightshade (*Solanum nigrum*), service berry (*Amelanchier alnifolia*), common wild rose (*Rosa nutkana*), and dwarf rose (*Rosa gymnocarpa*). Grasses dominate areas unoccupied by shrubs or trees. This region is in turn surrounded by agricultural land, primarily wheatfields.

Five permanent, man-made ponds were monitored from March 1976 through June 1977. The ponds (labelled A-E) extend from west to east along the north base of a hill at an elevation of approximately 850

m. The hill rises southward to crest 100 m above the ponds. Except for ponds A and B which are 20 m apart, distances between ponds are approximately 200 m. The surface areas of the ponds are 100–300 m². A, B, and C are located in relatively open areas, whereas D and E are closely surrounded by trees. Because D and E are more shaded, ice melts in spring 1–2 wk later than at A, B, and C. An underwater photometer indicated that D and E are considerably more turbid than the other three ponds.

Other species of amphibians which breed in these ponds include the northern long-toed salamander (*Ambystoma macrodactylum*), the western toad (*Bufo boreas*), and the spotted frog (*Rana pretiosa*). Cattails (*Typha latifolia*) and spikerush (*Eleocharis palustris*) are abundant at all ponds. Floating mats of duckweed (*Lemna* sp.) and various forms of algae are particularly abundant at A and B during the summer months.

A small, intermittent stream normally flows through the area from the time of snowmelt (March) to mid-summer. However, in 1977 water flow was greatly decreased due to reduced winter snowfall.

MATERIALS AND METHODS

Air temperature and relative humidity were recorded in the shade with a recording hygrothermograph placed near pond B. Local precipitation was recorded to 0.1 mm with a rain gauge. Water temperatures, recorded to 0.5°C, were taken from three points spaced evenly around each pond at a depth of 2.5 cm.

Numbered stakes were placed at 10-m intervals around each pond so that locations of captured frogs could be recorded. Sampling was usually carried out in the afternoon, and each frog captured by hand or with a dip net was marked for individual identification by toe-clipping. Snout-vent length, sex, dominant coloration (green or nongreen), and time of capture were recorded for each individual. Each frog was then released at its point of cap-

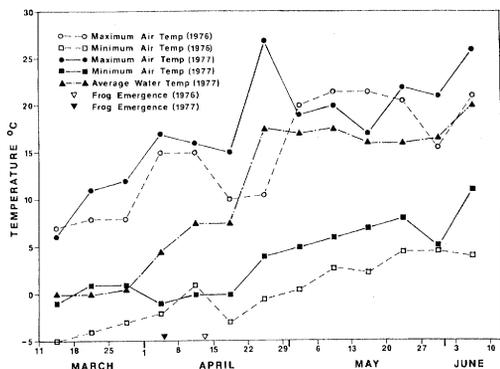


FIG. 1.—Air and afternoon water temperatures during spring, 1976 and 1977. Each point represents the average for 1 wk.

ture, with no individual being removed from the area during the course of the study.

RESULTS

Average maximum and minimum air temperatures for 1976 and 1977 are given in Fig. 1. Temperatures for 1977 were slightly warmer than during the previous year. This factor was reflected in an earlier ice-melt at the ponds in 1977 than in 1976.

Water temperatures correlated well with maximum air temperatures. The average afternoon water temperatures for 1977 for all five ponds are present in Fig. 1. Ponds A, B, and C were consistently warmer than D and E (Fig. 2).

Relative humidity was similar in 1976 and 1977. In the evening, it would approach 100% and remain near saturation throughout the night. At sunrise the humidity would start to drop rapidly until it reached the 15–50% range where it would stabilize until sunset.

Precipitation data for the period June 1975 through May 1976 are compared with those for June 1976 through May 1977 (Fig. 3). There was a severe drought throughout the Pacific Northwest from September 1976 to April 1977. Where 50–100 cm of snow accumulated at the ponds during most previous years, there were

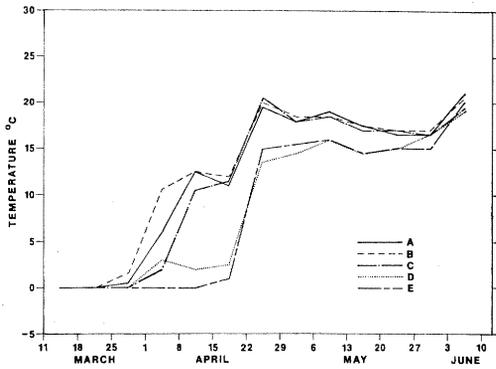


FIG. 2.—Afternoon water temperatures for 1977 at each pond (A–E). Temperatures are averaged for each week.

only a few centimeters of snow during the winter of 1976–1977. Because the ponds are largely dependent on snowfall for their water supply, water levels were noticeably lower during the spring of 1977 than during the same season of the previous year.

Breeding activities of *Hyla regilla* and *Rana pretiosa* for 1976 and 1977 are compared in Fig. 4. Although *H. regilla* lay eggs later than *R. pretiosa*, hatching occurs at approximately the same time, due to a longer incubation period for *R. pretiosa*. In 1976, *H. regilla* tadpoles underwent metamorphosis from mid-July to mid-September. *Rana pretiosa* tadpoles began metamorphosis in late September, and individuals continued to transform until the ponds were frozen over (mid-November).

In late spring, a marked reduction in the number of treefrogs heard chorusing, day or night, suggests that the adults vacate the ponds at this time. No adult treefrogs were found during daytime examinations of the ponds from mid-June (1976) to early April (1977).

In 1976, both the valley garter snake (*Thamnophis sirtalis*) and the wandering garter snake (*Thamnophis elegans*) were active near the ponds throughout the breeding season and into late September (Fig. 4).

Early in the study, it was observed that the number of treefrogs varied during the

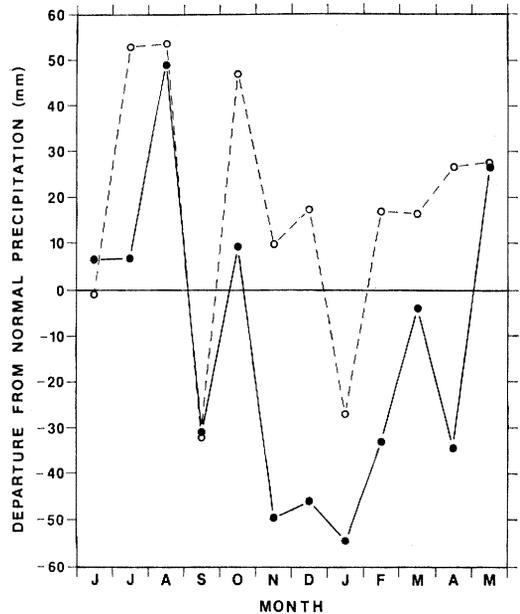


FIG. 3.—Departure from normal precipitation. Dashed line indicates June 1975 through May 1976. Solid line indicates June 1976 through May 1977.

breeding period. In addition, some frogs arrived early and left early, whereas other individuals arrived later. Due to dispersal and mortality, recapture success decreased as the interval between release and recapture increased (Fig. 5). Females appeared to have a higher turnover rate than males and few were caught (15 in 1976; 4 in 1977). Because of these differences, females are excluded from the discussion below concerning population size.

For males that were recaptured within 3 d of marking, recapture success was 0.10 in 1976 and 0.12 in 1977. From these data, initial capture efficiency was estimated to be 0.12 in 1976 and 0.15 in 1977. The average time a male spent at the ponds was estimated from the capture data to be 13 d in 1976 as compared to 10 d in 1977.

Capture records for *Hyla regilla* are given in Fig. 6. From these data and an assumed capture efficiency for males of 0.12 in 1976 and 0.15 in 1977, it is possible to estimate the population levels for the study area

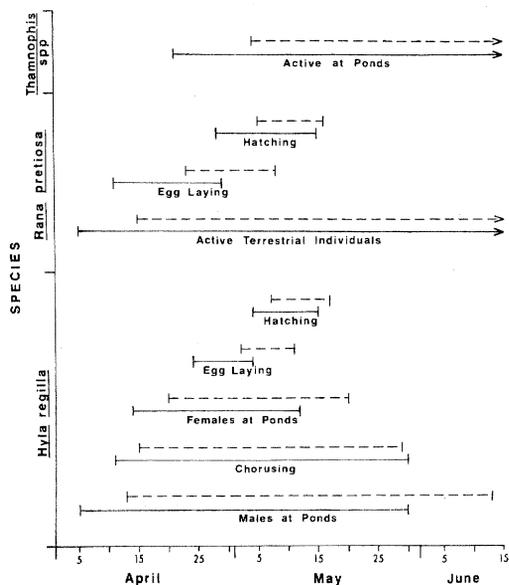


FIG. 4.—Comparison of times of various breeding activities for *Hyla regilla* and *Rana pretiosa*. Note periods of activity for the amphibian predator *Thamnophis* spp. Dashed lines = 1976; solid lines = 1977.

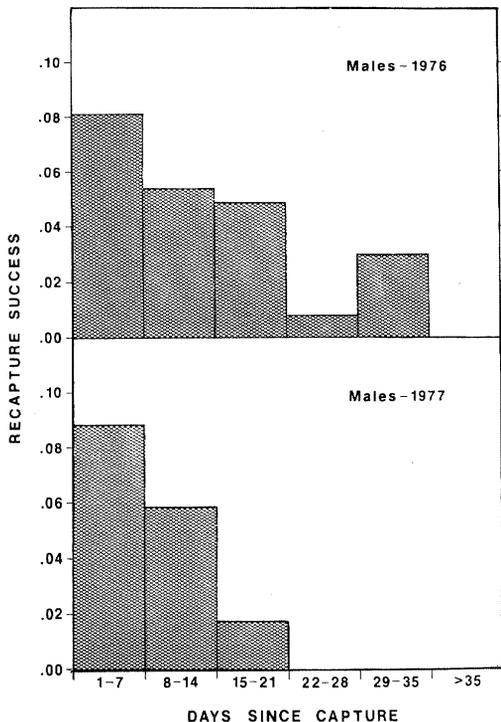


FIG. 5.—Success in recapturing male *Hyla regilla*.

(Fig. 6). Knowing the population level at any point in time and the average length of time a male stays at the ponds, it is possible to determine roughly the total number of males using the ponds. Such estimations indicate that approximately 360 males came to the ponds in 1976, whereas only 160 used the ponds in 1977. Admittedly, these estimates are crude, but a drastic drop in the 1977 population level is indicated.

Hyla regilla appeared to be relatively sedentary while they were at the ponds. Of 25 recaptures in 1976, 5 (20%) were within 10 m of the previous site of capture and 18 (72%) were at the same pond. Of 31 recaptures in 1977, 6 (19%) were within 10 m of the previous capture-site and 28 (90%) were at the same pond. However, individuals are capable of moving relatively long distances. One male moved from pond C to pond B (230 m) within a 48 h period. Another male moved from pond C to pond E (400 m) in no more than

4 d. Of the 10 wandering individuals observed during 1976 and 1977, 9 (90%) moved to an adjacent pond. The stimulus responsible for this pond-switching behavior is unknown. While it is possible that handling some frogs may have provided a sufficient incentive for them to move from the location of initial capture, most individuals remained in place even after repeated recaptures.

Of the 65 *Hyla regilla* captured in 1977, 9 (13.8%) had been marked in 1976. Only 2 (22%) of the recaptured frogs were found at the same pond at which they were last captured in 1976. Of the 7 individuals that switched ponds, 6 (86%) migrated to adjacent ponds and one male moved from D to B.

From the beginning of the breeding period to its peak, males often chorused during the day. However, as the season progressed, chorusing became restricted to

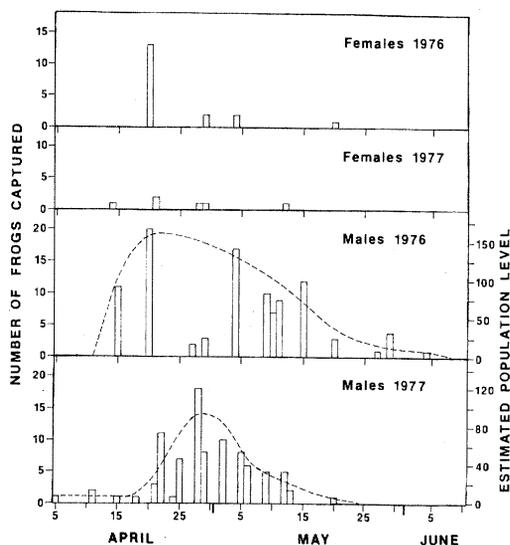


FIG. 6.—Capture record (bars) and estimated population size (dashed line).

hours of darkness. Chorusing was monitored at pond C for a full 24-h period on 8–9 May 1977. During the daylight hours calling was extremely limited, and usually involved only 2–4 individuals. Chorusing increased after sunset and by the end of civil twilight had reached a maximum which was maintained for the next 1–2 h. This period was followed by gradually decreasing bouts of calling until chorusing became very infrequent. Two hours after sunrise, calling increased again and continued for an additional 1–2 h.

Minor changes in the weather did not appear to influence calling behavior. Several males were observed calling when the water temperature was as low as 2.0°C. Also, males were heard chorusing when the air temperature was 0.5°C. Although the environmental temperature does not necessarily represent the body temperature of an amphibian (Brattstrom, 1963), calling behavior of the treefrogs of our northern population did not appear to be limited by the same minimum temperature as reported in earlier studies in California (Brattstrom and Warren, 1955; Cunningham and Mully, 1956).

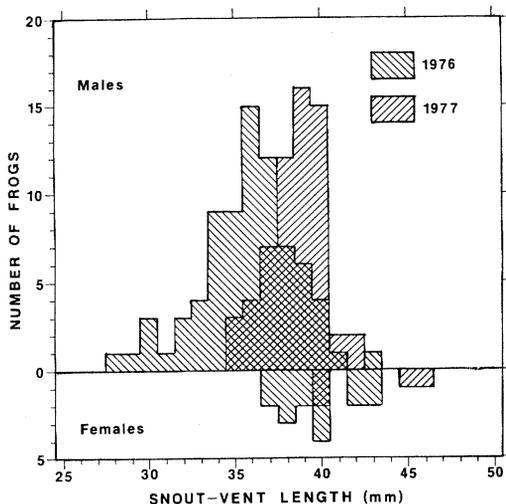


FIG. 7.—Distribution of size for males and females captured during 1976 and 1977.

The size distribution of treefrogs for this investigation is given in Fig. 7. In both years, females were significantly larger than males. In 1976, females averaged 39.6 mm snout-vent length, whereas males averaged 35.7 mm (one-tailed t -test, $t = 5.18$, $df = 90$, $P < .001$). In 1977, females averaged 42.9 mm, whereas males averaged 38.5 mm (one-tailed t -test, $t = 3.75$, $df = 63$, $P < .001$). The snout-vent length of females in 1977 was significantly larger than in 1976 (one-tailed t -test, $t = 2.64$, $df = 17$, $P < .01$), a difference also apparent for males (one-tailed t -test, $t = 6.95$, $df = 136$, $P < .001$). No male under 35 mm was captured in 1977, whereas a sizable proportion of males in 1976 were under this size (Fig. 7).

In 1976, 60.2% of treefrogs captured were nongreen (brown or gray) and 39.8% were green. In 1977, 45.3% were nongreen and 54.7% were green. Males exhibited a significant shift in the color ratio during the two years; in 1976 there were 61.5% nongreen, whereas in 1977 there were 56.7% nongreen ($\chi^2 = 4.56$, $df = 1$, $P < .05$). No significant difference in color ratio was detected between females in 1976

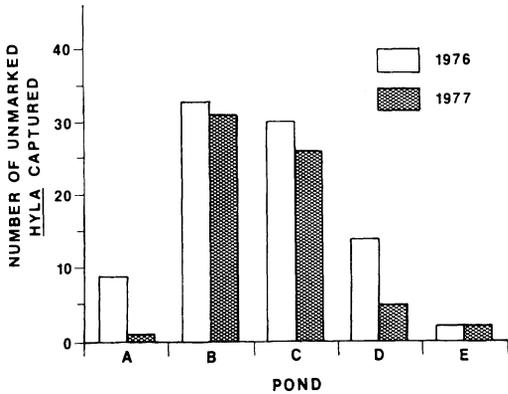


FIG. 8.—Number of *Hyla regilla* captured at ponds A-E.

and 1977, or between males and females in either year.

Jameson and Pequegnat (1971) reported a significant increase in frequency of green individuals and a decrease of brown and gray individuals as the breeding season progressed. Similarly, our 1976 data indicate a proportional increase of green individuals (and a concomitant decrease of nongreen individuals) during the spring (weighted regression analysis, $F = 5.52$, $df = 1, 11$, $P < .05$). A similar trend could not be detected in 1977 ($F = 1.36$, $df = 1, 16$, $P > .10$). This discrepancy may have resulted from inadequate sample sizes and/or the short time period when breeding frogs were abundant in 1977 (Fig. 6).

Capture data suggest that *Hyla regilla* do not utilize the five ponds equally (Fig. 8). Their apparent preference for ponds B and C was also evident from the number of frogs chorusing at each pond.

DISCUSSION

The treefrog population associated with this complex of ponds differed in several important ways between the two years of this study. Breeding activities were earlier in 1977 than in 1976. The size of the male population in 1977 was less than half that of 1976. The average period of time an individual male remained at the pond area

was shorter in 1977 than in 1976. The snout-vent length of both sexes was significantly greater in 1977 than in 1976. Finally, while the nongreen phase was the predominant color morph in 1976 (60.2%), there was a shift to the green phase in 1977 (54.7%). This shift in color frequency was statistically significant for males.

Brattstrom (1963) has reported thermal preferences for many amphibian species, including *Hyla regilla*. Licht (1969) suggested that a temperature threshold must be reached before breeding activities are initiated by *Rana aurora* and *Rana pretiosa*. A temperature threshold probably exists for *H. regilla* also, since the precocious emergence of these frogs from hibernation in 1977 seems to correlate well with the early spring warming trend that year (Fig. 1).

Ectothermic organisms that are subject to desiccation can be greatly affected by climatic conditions. Therefore, the uncharacteristic weather during late 1976 and early 1977 could be responsible for the decline in the size of the breeding population and the increase in the average snout-vent length. Various studies (e.g., Farrell and MacMahon, 1969) have demonstrated that small amphibians have a higher rate of water loss than large ones due to the greater ratio of surface area to volume. When drought conditions are serious, as they were from September 1976 to April 1977 (Fig. 3), small treefrogs apparently suffer higher mortality than large ones as a result of their more rapid desiccation. Therefore, the larger individuals would probably be in better condition to migrate to the ponds and breed successfully. Selection against smaller treefrogs is suggested by the data on size distribution which indicate a noticeable reduction in numbers of such individuals in 1977 (Fig. 7). Poor breeding conditions could be a factor responsible for the decreased amount of time each male spent at the ponds.

A severe reduction in the insulating blanket of snow during the winter of 1976-77 may have resulted in a ground freeze of greater depth even though the tempera-

tures were relatively mild. This factor could have contributed directly to an increase in mortality by eliminating individual treefrogs that chose shallow, subterranean locations for hibernation.

Predation appears to be another important element involved in regulating the population size of *Hyla regilla*. White and Kolb (1974) found that this frog was an important food item in the diet of the snakes *Thamnophis elegans* and *Thamnophis sirtalis*, and Wassersug and Sperry (1977) reported that the latter species was highly successful in capturing transforming frogs. Jameson (1956) attributed a rapid increase in a population of *H. regilla* to the removal of two species of *Thamnophis* (including *T. sirtalis*) and bullfrogs (*Rana catesbeiana*) from the study area.

Garter snakes were abundant at all of the ponds during the spring and summer months (Fig. 4), and they were apparently important predators on the *Hyla regilla*. Of 6 *Thamnophis sirtalis* and 2 *Thamnophis elegans* palpated to cause regurgitation during the spring of 1977, 2 of the *T. sirtalis* had recently fed on treefrogs. Any fluctuation in snake populations probably would directly influence the number of treefrogs. It seems likely that predation and climatic conditions, as well as other unknown factors, interacted to produce the observed population reduction.

Although yearly fluctuations in color frequencies have been reported for *Hyla regilla* by Resnick and Jameson (1963), the causes are unknown. Possibly the factors which adversely affected population size in our study during 1977 also selected against the nongreen individuals. Jameson and Pequegnat (1971) attributed changes in color frequencies during the spring in Oregon to differential mortality among the color morphs. However, data on males from our investigation suggest another possible interpretation. The shift from predominantly nongreen to green could result from green animals preferring a later breeding season. Perhaps green frogs require warmer temperatures for emergence and

breeding than nongreen individuals. Since some populations exhibit several nongreen color types (Resnick and Jameson, 1963), it is also possible that animals of each color phase have different emergence and breeding temperatures.

Our observations on the mode of dispersal of frogs from the ponds after breeding agree with those of Jameson (1956). Females remain at the breeding sites for a shorter period of time than the males (Fig. 4). Young frogs of the year leave the ponds soon after transformation (mid-summer to early fall). Treefrog populations are probably most vulnerable to predation when adults are congregated together at the ponds and chorusing, and when tadpoles are metamorphosing. Therefore, it would seem to be adaptively advantageous for the adults to disperse from the pond area as soon as breeding is terminated and for the young to leave as soon as they complete metamorphosis.

Jameson (1957) described strong homing responses in *Hyla regilla*. Our study indicates that in a situation where several ponds are close together, individuals usually remain at the same pond during a single breeding season. Individuals probably home to the same general area every year and then migrate to the nearest pond or to the pond with the loudest chorusing.

With the exception of pond A, there was a definite preference for the warmer, more open ponds. Warmer temperatures are known to accelerate developmental rates for embryos and tadpoles (see Brown, 1975). This factor would promote earlier metamorphosis and provide a longer post-transformation growth period before hibernation, thus resulting in larger individuals less susceptible to starvation and desiccation.

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Department of Zoology, Washington State University, Pullman, Washington 99164, USA