TAXONOMIC VARIATION IN OVIPOSITION BY TAILED FROGS (*ASCAPHUS* SPP.)

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ABSTRACT—Tailed frogs (*Ascaphus* spp.) oviposit in cryptic locations in streams of the Pacific Northwest and Rocky Mountains. This aspect of their life history has restricted our understanding of their reproductive ecology. The recent split of *A. montanus* in the Rocky Mountains from *A. truei* was based on molecular differentiation, and comparisons of their ecology are limited. Our objectives were to provide a range-wide summary of information on *Ascaphus* oviposition, compare some aspects of the reproductive ecology of the 2 species, and examine geographic variation in their reproductive traits. Reproductive ecology of the 2 species differed. *Ascaphus truei* had smaller clutches, oviposited later in the summer, and had a longer duration of oviposition than *A. montanus.* A greater number of communal oviposition sites were attributed to *A. montanus.* These ecological differences support the recent taxonomic revision of *Ascaphus* and suggest that different management strategies may be necessary for each species where conservation is a priority.

Key words: coastal tailed frog, *Ascaphus truei,* Rocky Mountain tailed frog, *A. montanus,* reproduction, clutch size, oviposition, communal oviposition, geographic variation

The difficulty in detecting oviposition sites of tailed frogs (*Ascaphus* spp.) has limited our understanding of their reproductive ecology. *Ascaphus* are known to deposit eggs on the undersides of rocks in cold, fast-flowing mountain streams in northwestern North America (Nussbaum and others 1983). However, information on geographic variation in the reproductive ecology of these species is lacking. Given the recent taxonomic revision that split *A. truei* into 2 species (Nielson and others 2001) and the use of *A. truei* as an indicator of watershed condition (Welsh and Ollivier 1998), a bet-

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ter understanding of the reproductive ecology of *Ascaphus* is warranted.

The paucity of information on *Ascaphus* oviposition sites is not from lack of effort. Bury and others (2001) found only 6 sites in 1714 m of randomly selected 1-m (by variable width) search areas in 168 streams in Olympic National Park, Washington. Using the same methodology, 2 of us (DSP and EJH) found 3 sites in 1198 m in 41 streams in central Idaho and western Montana and 2 sites in 1036 m in 18 streams in southwest Oregon. In northern California, only 3 oviposition sites were found after searching under all large substrate pieces in seventeen 300- to 400-m reaches each year for 10 y (LVD, this study).

The association of *Ascaphus* with cold, high gradient streams has resulted in isolation and evolutionary divergence of the genus. Evidence from mitochondrial DNA suggests that inland and coastal populations of *Ascaphus* in North America were isolated from one another during the Miocene (28 to 10 mya) after the rise of the Cascade Range resulted in a drier climate in the rain shadow east of the Cascades (Nielson and others 2001). Nielson and others (2001) revised *Ascaphus* taxonomy, splitting *A. truei* into 2 species: the coastal tailed frog (*A. truei*), whose range extends from British Columbia through western Washington and Oregon and into northwestern California; and the Rocky Mountain tailed frog (*A. montanus*), whose range extends from southeastern British Columbia south through Idaho, western Montana, and into a few mountain ranges in eastern Washington and Oregon. Ritland and others (2000), reporting on a DNA assay of *A. truei* from 4 regions in British Columbia, suggested that the interior population (now attributed to *A. montanus*) could be designated as a separate species from *A. truei,* but cautioned that the genetic distance between interior and coastal populations was nearly equal to what would be predicted given the physical distance between them. Morphological differences between *A. truei* and *A. montanus* have also been found (Mittleman and Myers 1949). Yet, Metter (1967), comparing multiple morphological characteristics in 17 populations throughout the ranges of both species, indicated that differences did not warrant recognition of subspecies because adjacent populations often showed as much difference as those that were widely separated.

Both species of *Ascaphus* are listed in the United States as federal species of concern and are given special conservation status (for example, species of concern, vulnerable) in 1 state within their ranges. In Canada, *A. montanus* is listed as endangered, and *A. truei* is listed as a species of special concern. A number of studies on *A. truei* in British Columbia (Dupuis and Steventon 1999; Wahbe and Bunnell 2001; Wahbe and others 2004), Washington (Aubry 2000), Oregon (Corn and Bury 1989), and California (Welsh and Lind 1991) and on *A. montanus* in eastern Oregon (Bull and Carter 1996) appear to demonstrate that timber harvesting reduces abundances or limits movements of adults and larvae. Larval *A. truei* in streams on the north coast of California were not negatively affected by reductions in canopy cover or increases in water temperature associated with timber harvesting but were negatively associated with fine sediments (Diller and Wallace 1999). In light of the implications of timber management for both species of *Ascaphus,* developing a better understanding of their natural history, including their reproductive ecology, may permit identification of critical habitats or critical periods in the breeding season. This information can then be used in areas where conservation of *Ascaphus* is a priority or in the development of management plans for the species. The objectives of this research were to provide a range-wide summary of existing and new information on differences and geographic variation in the microhabitat characteristics of oviposition sites, clutch sizes, timing of oviposition, and frequency of communal oviposition in *A. truei* and *A. montanus.*

Methods

Data on oviposition sites were compiled from unpublished field research conducted at 59 sites from 1991 to 2003 (Fig. 1), and from published observations at 12 sites (Tables 1, 2). We summarized characteristics of oviposition sites, including type of substrate used for egg attachment and habitat in which oviposition sites were found. Habitat types included cascade, riffle, run, and pool (Platts and others 1983). Substrate sizes followed the Wentworth classification scheme (Platts and others 1983) and included sand (0.06 to 2 mm), gravel (2 to 64 mm), cobble (64 to 256 mm), and boulder (256 to 4096 mm) as measured across the lon-

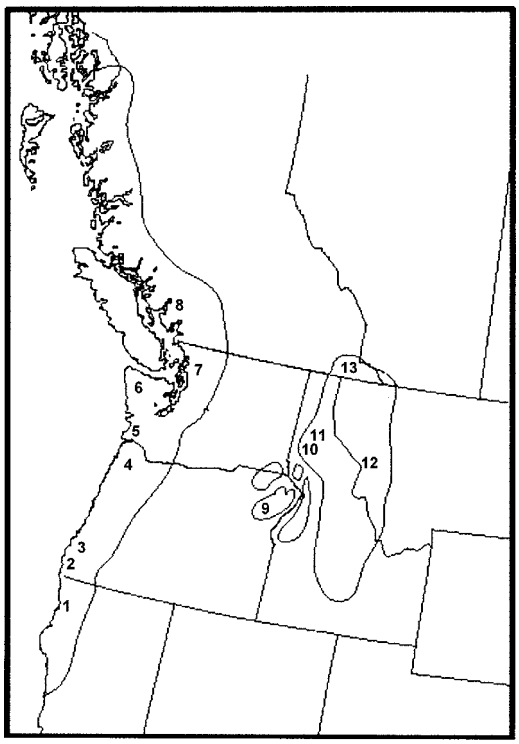

FIGURE 1. Approximate distributions of *A. truei* and *A. montanus* in the United States and Canada (modified from Nielson and others 2001), and general locations of oviposition sites reported in this study. Numbers refer to the following locations for *A. truei*: California: 1-Coast Range; Oregon: 2-Siskiyou Mountains, 3-Southern Coast Range, 4-Northern Coast Range; Washington: 5-Willapa Hills, 6-Olympic National Park, 7-Cascade Mountains; British Columbia: 8-Coast Range. Numbers refer to the following locations for *A. montanus*: Oregon: 9-Wallowa Mountains; Idaho: 10-Palouse Range, 11-St. Joe Mountains; Montana: 12-Bitterroot Range; British Columbia: 13-Flathead River.

gest diameter. A hand-held thermometer was used to record water temperatures at the time of egg observation. We compared water temperatures at oviposition sites of *A. truei* and *A. montanus* using a *t*-test.

Clutch sizes were based on field counts of eggs or determined from photographs. Clutches that appeared to have been fragmented when the attachment rock was turned or photographic counts that were ambiguous were not included in this analysis. We compared clutch sizes between the 2 species with a *t*-test, and used simple linear regression to examine variation in clutch size by elevation, latitude, and longitude for each species. Communal oviposition sites were determined based on the location and developmental stage of egg clusters on the same rock. For each species, we summarized the frequency of communal oviposition and the substrate types used at communal oviposition sites.

Information from Brown (1975) on development of *A. truei* at different temperatures was used to estimate timing of oviposition for each clutch. First, the time required for development of a given clutch from oviposition to hatching was estimated relative to the clutch site. Water temperature and incubation period data from Table 3 in Brown (1975) were then used to generate the regression equation ($y = 984.71x^{-1.5768}$), where x was temperature and y was the incubation period or duration of embryonic development. The regression $R^2 = 0.99$ indicated a strong relationship between water temperature and duration of development and good potential for use as a predictive equation. Based on this relationship, water temperature data were substituted for each of the clutches reported in this study into the equation, and duration of embryonic development was determined for each clutch. This approach assumed a constant water temperature during the developmental period and that the equation developed by Brown (1975) is broadly applicable to both species. There is likely both diel and seasonal variation in water temperature at oviposition sites.

Clutches for which developmental stage had been determined were grouped into 5 phases adapted from Gosner (1960): pre-cleavage (stages 1 to 2), cleavage (3 to 9), gastrulation (10 to 12), neurulation (13 to 16), and organogenesis (17 to 20). Information from Table 5 in Brown (1975) was used to determine the duration of each phase of development. We entered these data on water temperature (variable x) and time to complete each developmental phase (variable y) and generated regression equations for 4 of the 5 phases: cleavage ($y = 3064.7x^{-1.3668}$, $R^2 = 0.99$); gastrulation ($y = 3781.3x^{-1.4586}$, $R^2 = 0.98$); neurulation ($y = 2790.4x^{-1.5414}$, $R^2 = 0.93$); and organogenesis ($y = 18099x^{-1.8115}$, $R^2 = 0.99$). Because <1 h is required for completion of the pre-cleavage phase (Brown 1975), embryos found in pre-cleavage stage were considered to be found on

TABLE 1. Summary of clutch sizes and oviposition site characteristics for *Ascaphus* species. Data reported from California, Oregon, Washington, and British Columbia (except the Flathead River site) pertain to *Ascaphus truei*; all others pertain to *Ascaphus montanus*.

Species State area	Date observed	Estimated number of egg masses	Estimated clutch size(s)[a]	Substrate to which attached	Habitat	Water temperature (°C)	Source
Ascaphus truei							
California							
Coast Range	16 Aug. 1994	1	28	Boulder	Pool	15.9	Karraker and Beyersdorf (1997)
Coast Range	1 Aug. 1997	1	30–40	Cobble	Riffle	13.5	LVD (this study)
Coast Range	1 Aug. 1997	1	30–40	Cobble	Riffle	13.5	LVD (this study)
Coast Range	19 July 1997	1	39	Boulder	Riffle	14.0	LVD (this study)
Coast Range	11 Sept. 1996	1	45	Cobble	Riffle	12.2	LMO and GRH (this study)
Coast Range	28 July 1993	2	89	Boulder	Pool	13.0	BRN (this study)
Oregon							
Siskiyou Mtns.	1 Aug. 2002	1	15–20	—	Riffle	10.0	EJH (this study)
Siskiyou Mtns.	30 July 2002	1	20	Boulder	Riffle	8.5	EJH (this study)
Siskiyou Mtns.	13 Aug. 2002	—	—	—	Pool	11.0	EJH (this study)
Siskiyou Mtns.	19 June 2003	—	—	Boulder	Pool	12.0	EJH (this study)
Coast Range	19 July 1984	1	38	Cobble	Pool	13.0	PSC (this study)
Coast Range	7 Aug. 1996	1	50–80	Boulder	Run	12.0	CAP (this study)
Coast Range	12 Aug. 1991	1–2	60[b]	Boulder	Pool	14.5	Adams (1993)
Washington							
Olympic N.P.	4 Aug. 1998	1	40	Cobble	Pool	7.0	Bury and others (2001)
Olympic N.P.	4 Aug. 1998	1	46	Boulder	Pool	7.0	Bury and others (2001)
Olympic N.P.	15 Aug. 1996	1	52	Boulder	Pool	11.0	Bury and others (2001)
Olympic N.P.	31 July 1996	1	55	Cobble	Riffle	11.0	Bury and others (2001)
Olympic N.P.	8 July 1998	1	96	Cobble	Riffle	10.0	Bury and others (2001)
Olympic N.P.	6 Aug. 1996	—	182	Boulder	Pool	8.5	Bury and others (2001)
Cascade Mtns.	23 July 1972	2+	123	—	—	8.8	Brown (1975)
Cascade Mtns.	3 Sept. 2001	1	43	Boulder	Cascade	9.7–10.0	MPH (this study)
Willapa Hills	29 Aug. 2001	1	19	Cobble	Riffle	11.6–13.0	MPH (this study)
Willapa Hills	11 Aug. 2003	1	>17	Cobble	Riffle	11.1	MPH (this study)
Willapa Hills	18 Aug. 2003	2	39, 49	Cobble	Riffle	12.8	MPH (this study)
Willapa Hills	18 Aug. 2003	1	>7	On sand	Riffle	12.8	MPH (this study)
Willapa Hills	11 Aug. 2003	1	41	Cobble	Riffle	11.9	MPH (this study)
Willapa Hills	11 Aug. 2003	1	>2	Cobble	Riffle	12.1–12.6	MPH (this study)
Willapa Hills	28 Aug. 2003	1	35	Cobble	Riffle	12.9	MPH (this study)
Willapa Hills	28 Aug. 2003	1	43	Cobble	Riffle	12.7	MPH (this study)
Willapa Hills	27 Aug. 2003	1	>7	Cobble	Riffle	11.9	MPH (this study)
Willapa Hills	24 July 2003	1	39	Cobble	Cascade	9.7	MPH (this study)
Willapa Hills	28 July 2003	1	31	Gravel	Riffle	10.6	MPH (this study)

TABLE 1. Continued

Species State area	Date observed	Estimated number of egg masses	Estimated clutch size(s)[a]	Substrate to which attached	Habitat	Water temperature (°C)	Source
British Columbia							
Coast Range	Aug. 1995	—	~93	Cobble	Pool	9.0	LAD (this study)
Coast Range	22 Aug. 2002	—	160	Cobble	Pool	9.0	LAD (this study)
Coast Range	Aug. 1995	—	—	Boulder	Pool	—	LAD (this study)
Coast Range	21 Aug. 1995	—	—	—	—	6.0	LAD (this study)
Ascaphus montanus							
Oregon							
Wallowa Mtns.	24 Aug. 1993	—	—	—	Riffle	8.0	ELB (this study)
Idaho							
Palouse Range	9 July 2000	1	~45	Cobble	Riffle	8.0	KL (this study)
Palouse Range	9 July 1996	1	41	Boulder	Riffle	14.0	KL (this study)
St. Joe Mtns.	8 July 1997	1	75	Boulder	Riffle	9.0	BRH (this study)
St. Joe Mtns.	16 July 2002	1–2	102	Boulder	Riffle	9.4	CRP (this study)
Palouse Range	9 July 1996	2	53, 73	Cobble	Riffle	13.0	KL (this study)
St. Joe Mtns.	16 July 2002	2+	262	Boulder	Riffle	9.0	CRP (this study)
St. Joe Mtns.	2 July 1996	1	56	Boulder	—	10.0	CRP (this study)
St. Joe Mtns.	2 July 1996	1	62	Cobble	—	10.0	CRP (this study)
Montana							
Bitterroot Mtns.	12 July 2002	1	23[c]	Cobble	Riffle	—	DSP (this study)
Bitterroot Mtns.	28 July 1998	1	>26[b]	—	Riffle	20.2	Adams and Frissell (2001)
Bitterroot Mtns.	30 July 1997	1	>41	Boulder	Pool	17.4	Adams and Frissell (2001)
Bitterroot Mtns.	25 July 2003	1	80	Boulder	Riffle	10.0	DSP (this study)
Bitterroot Mtns.	23 July 2002	2	127	Boulder	Riffle	—	DSP (this study)
Bitterroot Mtns.	24 July 2002	2	130	Cobble	Riffle	—	DSP (this study)
Bitterroot Mtns.	20 July 1968	2	64, 86	Boulder	Cascade	11.0	Franz (1970)
Bitterroot Mtns.	11 July 2004	2	50, 50	Gravel	Riffle	9.0	DSP (this study)
Bitterroot Mtns.	11 July 2004	2	200	Boulder	Riffle	10.0	DSP (this study)
Bitterroot Mtns.	11 July 2004	1	150, 50	Boulder	Riffle	10.0	DSP (this study)
Bitterroot Mtns.	24 July 2004	—	30	—	Cascade	11.5	DSP (this study)
Bitterroot Mtns.	24 July 2004	1	7[c]	Boulder	Riffle	13.0	DSP (this study)
British Columbia							
Flathead River	8 Aug. 2003	—	—	—	—	12.0	LAD (this study)

[a] Individual clutch sizes given, when available, for communal oviposition sites.
[b] Combined eggs and newly hatched larvae.
[c] Incomplete clutch.

TABLE 2. Clutch sizes for dissected *Ascaphus* females or females in which ovulation was induced.

Species state	Number of females	Mean clutch size	Range of clutch sizes	Total number of eggs	Method of determination	Source
A. truei						
Oregon	7	49.3	39–61	345	Dissection	Metter 1967
	8	62.9	57–68	503	Dissection	Metter 1967
	7	56.0	41–73	392	Dissection	Metter 1967
	8	62.4	46–85	499	Dissection	Metter 1967
	10	58.0	47–77	580	Dissection	Metter 1967
Washington	2	42.0	35–49	84	Dissection	Gaige 1920
	5	36.6	28–47	183	Induced ovulation	Noble and Putnam 1931
	1	44.0	44	44	Dissection	Metter 1967
	10	55.1	44–69	551	Dissection	Metter 1967
	5	66.4	57–98	332	Dissection	Metter 1967
	22	59.0	37–82	1298	Induced ovulation	Brown 1975
A. montanus						
Oregon	7	55.4	48–62	388	Dissection	Metter 1967
Washington	10	68.2	50–85	682	Dissection	Metter 1967
Idaho	20	68.0	50–85	1360	Dissection	Metter 1964
	10	56.7	33–81	567	Dissection	Metter 1967
	10	67.8	56–81	678	Dissection	Metter 1967
	13	65.2	51–82	848	Dissection	Metter 1967
	11	63.7	49–88	701	Dissection	Metter 1967
Montana	7	74.6	57–97	522	Dissection	Metter 1967

the same day that oviposition occurred. For each clutch, water temperature was substituted into the appropriate equation, depending upon the developmental phase of the clutch when it was found, and was used to estimate how many days were required to reach that phase at that temperature. The number of days was subtracted from the date at which the clutch was found to determine an approximate date of oviposition for each clutch. We added the total number of days required for completion of development to the estimated date of oviposition and calculated an approximate date of hatching for each clutch. Timing of oviposition was compared between species using a *t*-test, and duration of timing was summarized for each species. We examined relationships between timing of oviposition and water temperature, elevation, latitude, and longitude using simple linear regression for each species. Statistical significance was based on alpha ≤ 0.05. All analyses were performed using SAS statistical software (Version 8.0, SAS Institute, Cary, NC).

Results

The general characteristics of oviposition sites varied between species. All egg masses were attached to cobble or boulder substrates (Fig. 2), with the exception of 1 attached to large gravel and 1 resting on sand (Table 3). Compared with *A. truei*, *A. montanus* oviposited more frequently on boulders than on cobbles. Oviposition sites of *A. montanus* were found predominantly in riffles, compared to cascade and pool habitats. *Ascaphus truei* oviposited commonly in riffles and pools, but infrequently in cascades and runs. Water temperatures at oviposition sites did not differ between species (combined $\bar{x} = 11.3$°C, $s = 2.5$, $n = 58$; $t = 0.34$, $df = 57$, $P = 0.75$; Table 4).

Mean clutch sizes observed in this study were larger in *A. montanus* than *A. truei* ($t = 3.71$, $df = 39$, $P < 0.001$; Table 3). Previous studies of dissected females or clutches obtained by injecting hormones (Table 2) found a similar trend of larger clutches in *A. montanus* ($\bar{x} = 65$, $n = 88$) than in *A. truei* ($\bar{x} = 57$, $n = 85$). Clutch size was not influenced by elevation, latitude, or longitude in *A. montanus* or in *A. truei* (Table 4).

The estimated oviposition period, or the period over which embryonic stages could be encountered in the field, was nearly 3 times longer in *A. truei* (81 d) than in *A. montanus* (30 d) (Table 3). Mean estimated timing of oviposition

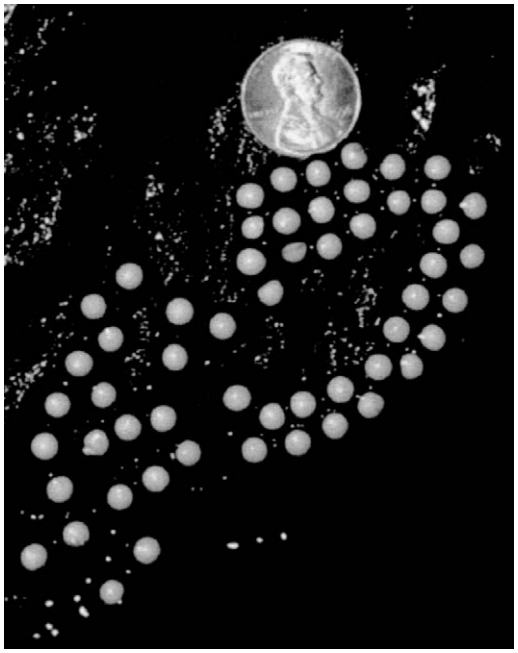

FIGURE 2. Eggs of *A. montanus* from Idaho. Photograph by C Peterson.

was earlier in *A. montanus* ($t = 4.90$, $df = 51$, $P < 0.001$). In *A. montanus,* nearly 25% of the variation in the timing of oviposition was explained by water temperature but timing was not strongly related to elevation, latitude, or longitude (Table 4). In *A. truei,* more than 25% of the variation in timing of oviposition was explained by elevation, but water temperature, latitude, and longitude were not important. Mean estimated hatching dates for *A. montanus* were earlier than for *A. truei* ($t = 4.43$, $df = 51$, $P < 0.001$; Table 3).

Communal oviposition sites were found for both species, including 7 of 17 (41%) sites for *A. montanus* (Franz 1970; this study) and 4 of 30 (13%) sites for *A. truei* (Brown 1975; Bury and others 2001; this study). In *A. montanus,* communal oviposition sites were found beneath boulder (57%), cobble (29%), and gravel (14%) substrates. For *A. truei,* communal sites were located beneath boulder (50%) and cobble (50%).

DISCUSSION

Overall, *A. montanus* and *A. truei* oviposit in cold (~11°C), fast-flowing, rocky streams. Average water temperature (11.3°C) at oviposition sites for both species was comparable to the optimum water temperature for development (12°C) reported by Wernz and Storm (1969). Water temperature was 12.0°C or lower at 67% of oviposition sites (n = 58). Water temperature was above the reported upper limit of 18.5°C for *Ascaphus* embryos (Brown 1975) at only 1 site (see Adams and Frissell [2001] for discussion of water temperature at that site). Both species deposit the majority of their egg masses on boulder or cobble substrates. Oviposition in both species occurs primarily in riffle habitats, although *A. truei* egg masses were also found relatively frequently in pools. Differences in use of substrates or habitats may reflect their relative abundance within the ranges of each

TABLE 3. Summary of differences in the reproductive ecology of *Ascaphus montanus* and *A. truei.*

Reproductive trait		*A. montanus*	*A. truei*
Clutch size	Mean ± *s*	66.6 ± 29.6	41.9 ± 16.3
	Range	41 to 150	20 to 96
Estimated timing of oviposition	Mean	7 July	24 July
	Range	24 June to 20 July	10 June to 29 August
Estimated timing of hatching	Mean	30 July	14 August
	Range	17 July to 14 August	30 June to 17 September
Water temperature	Mean ± *s*	11.4 ± 2.9	11.2 ± 2.2
	Range	8.0 to 20.2	6.0 to 15.9
Substrate (%)	Boulder	63	41
	Cobble	32	56
	Gravel	5	0
	Sand	0	3
Habitat (%)	Riffle	83	53
	Pool	6	38
	Cascade	11	6
	Run	0	3

TABLE 4. Relationships between reproductive traits and geographic and environmental variables in *Ascaphus montanus* and *A. truei.*

Reproductive trait Geographic or environmental variable	*A. montanus*			*A. truei*		
	R^2	*P*	*n*	R^2	*P*	*n*
Clutch size						
Elevation	0.06	0.40	15	0.02	0.52	24
Latitude	<0.01	0.95	15	0.09	0.15	24
Longitude	0.15	0.15	15	<0.01	0.98	24
Estimated timing of oviposition						
Elevation	0.15	0.06	24	0.26	<0.01	28
Latitude	0.06	0.25	24	0.03	0.37	28
Longitude	0.05	0.34	24	<0.01	0.88	28
Water temperature	0.22	0.02	24	0.12	0.07	28

species rather than an actual difference in preference.

Ascaphus montanus produce larger clutches than *A. truei* by an average number of approximately 14 eggs. A number of factors can affect clutch size in amphibians, including longevity of individuals, size at 1st reproduction, body size, phylogenetic differences, and geographic variation (Anderson 1967; Salthe and Duellman 1973; Licht 1975). A morphological basis for differences in clutch size may exist due to differences in the life histories of the 2 species. The length of the larval period in streams reported in this study is 1 to 2 y for *A. truei* (Wallace and Diller 1998) and 3 y for *A. montanus* (Metter 1967), and length of larval period is probably genetically controlled in *Ascaphus* (Metter 1967). There is a genetic basis for egg complement, but larger females generally produce larger clutches within a species (Stebbins and Cohen 1995). This suggests that females of *A. montanus* may be larger than those of *A. truei,* both at sexual maturity and throughout their reproductive stages. Metter (1964) suggested that *Ascaphus* might lay eggs every year in coastal areas and every other year at inland sites, whereas some female *A. montanus* may breed only once every 3 y (Daugherty 1979). Such a pattern would, in non-breeding years, permit females to allocate resources to growth rather than to egg production, possibly resulting in a larger body size and leading to the larger clutch sizes in *A. montanus.*

Differences in morphology are often correlated with geographic and associated climatic clines (Brown and Lomolino 1998). Positive correlations between body size or clutch size and latitude have been demonstrated in many species of endotherms and ectotherms (reviewed in Brown and Lomolino 1998), yet we found only weak relationships between clutch size and latitude in both species of *Ascaphus.* Bury and others (2001) suggested that inland populations of *A. truei* have 10 more eggs per clutch than coastal populations, but latitude was not important in explaining variation in clutch size for either *A. truei* or *A. montanus.* Elevation has been positively correlated with increases in body size in wood frogs (*Rana sylvatica*) (Berven and Gill 1983), but this pattern was not demonstrated in *Ascaphus.* Neither latitude nor elevation was important in explaining variation in clutch size in *A. montanus* or *A. truei.* In contrast, larval development in coastal populations of *A. truei* increased with latitude from 1 y in California and central Oregon to 2 y in northern Oregon and Washington (Bury and Adams 1999). We recommend further examination of the morphology of both species and environmental factors that might select for larger body size and correspond to larger clutch size, such as length of the winter period and winter minimum temperatures.

Ascaphus montanus oviposits earlier and over a shorter duration (June and July) than *A. truei* (June, July, and August). It is possible that an early and brief oviposition period in *A. montanus* permits larvae to reach a substantial size before the relatively colder and harsher winter period within its range. Attachment of eggs beneath larger substrate pieces, predominantly boulders, may help to protect the eggs from damage due to high flows. We caution that because much fieldwork is carried out in the summer, oviposition could occur at other times and not be observed.

Elevation explained more than 25% of the variation in timing of oviposition in *A. truei* compared with about 15% in *A. montanus.* Egg masses of *A. truei* have been found at sites ranging in elevation from 170 to 1700 m, or over a range of 1530 m, compared with egg masses of *A. montanus* at sites ranging from 980 to 1750 m, or over a range of 770 m. Both species may oviposit at lower or higher elevations than those that have been documented. Yet, timing of oviposition is probably a plastic trait, and, given the range of elevations over which *A. truei* is known to oviposit, timing may be highly variable due to the variability of environmental conditions across this elevational range. Adams (1993) suggested that stream temperature regimes might influence the timing of egg deposition for coastal *Ascaphus* (*A. truei*). We found that stream water temperature was more important in explaining the variation (22%) in oviposition timing in *A. montanus* than in *A. truei* (12%). It is apparent, however, that factors other than elevation and water temperature more strongly influence timing of oviposition in both species and that larger sample sizes may be needed to identify the factors regulating timing.

Communal oviposition may occur more frequently in *A. montanus* than in *A. truei.* However, this may reflect regional differences in stream geomorphology in the region, the types and accessibility of microhabitats used as communal oviposition sites, rather than differences in the propensity of each species to communally oviposit. Communal oviposition in both species may be more common than evidenced by the data, particularly if it occurs in well-protected places (25 of 51 sites were located under boulders) and thus is found less often by researchers.

Robertson and others (1998) proposed that communal nesting occurs when the benefits of communal nests outweigh the losses to individual reproduction, nesting sites are rare, and females have limited clutch sizes. Communal oviposition sites of *Ascaphus* species may increase an individual's fitness by reducing predation risk for a single clutch of eggs and distributing the risk among multiple clutches. *Dicamptodon* species (Nussbaum 1969) and probably fish and aquatic macroinvertebrates feed on the eggs of A*scaphus* species when they can gain access to oviposition sites. Although the quantity of suitable locations in the vicinity of the reported *Ascaphus* communal oviposition sites is not known, the locations used may represent oviposition sites that are continually stable within those streams. Stable, cryptic oviposition locations can be limiting in streams, creating conditions in which communal oviposition is favored for *Ascaphus,* which are highly philopatric to specific sections of a stream and can live at least 14 y in the wild (Daugherty and Sheldon 1982).

Molecular differences in *Ascaphus* populations have only recently been reported. Our results demonstrate divergences in the reproductive ecology of *A. montanus* and *A. truei* in the use of habitats and substrates, clutch size, frequency of communal oviposition, and timing and duration of oviposition. These differences lend support to the taxonomic revision, based on genetic differences, of *Ascaphus* by Nielson and others (2001). These ecological differences also suggest that different management actions for each species may be necessary where conservation is a priority. Most notably, the extended period of oviposition in *A. truei* potentially requires that timber management activities that increase fine sediment loads in streams, which may inhibit attachment of egg masses or gas exchange in embryos, would need to be limited over a 3-mo period rather than a 1-mo period for *A. montanus.* Oviposition periods may vary regionally in *A. truei* and could have a shorter duration at a local scale, but determining the oviposition period for an area would be difficult as oviposition sites are not easy to locate. One important similarity between the 2 species that was identified in this study is the requirement of cold water at oviposition sites. Remarkably, mean water temperature at oviposition sites was 11.4°C (median: 10.5°C) for *A. montanus* and 11.2°C (median: 11.4°C) for *A. truei.* Older forests are important for maintaining both larval and adult *Ascaphus* in some regions (Welsh 1990; Welsh, Hodgson, and Lind 2005), and this may be, in large part, related to the buffering capacities of these forests and in maintaining lower water temperatures (Welsh, Hodgson, and Karraker 2005). Our results and those of 1 laboratory study (Brown 1975) suggest that lower water temperatures may also be important for developing embryos. Conservation strategies aimed at maintaining viable populations of *Ascaphus*

should attempt to limit activities that increase sedimentation in streams during the oviposition periods of each species and activities that cause substantial increases in water temperatures.

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