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Female Reproductive Characteristics of Three Species in the *Orconectes* Subgenus *Trisellescens* and Comparisons to Other *Orconectes* Species

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Abstract.— In streams of Mississippi and southwest Tennessee, *Orconectes* females with eggs or hatchlings are not commonly encountered while sampling. This paper reports on fecundity, egg size, and aspects of reproductive timing for small samples of female *Orconectes chickasawae*, *Orconectes etnieri*, and *Orconectes jonesi* carrying eggs or hatchlings and discuss the results in the context of the subgenus and genus. Ovigerous *O. jonesi* females, collected in March, had the fewest eggs of the three species. Ovigerous *O. chickasawae* and *O. etnieri* were collected in March and April, with fecundity not significantly different between the two species. *Orconectes etnieri* had the largest eggs of the three species. Results are compared to data for other species within the subgenus and genus. [Keywords.— egg size; fecundity; *Orconectes chickasawae*; *Orconectes etnieri*; *Orconectes jonesi*; reproduction].

INTRODUCTION

Several species in the *Orconectes* (*Trisellescens*) subgenus occur in Mississippi or western Tennessee. *Orconectes etnieri* Bouchard and Bouchard occurs in southwestern Tennessee and extreme northern Mississippi. *Orconectes jonesi* Fitzpatrick is known only from the Sucarnoochee River drainage in extreme east-central Mississippi and west-central Alabama. *Orconectes chickasawae* Cooper and Hobbs was described from western tributaries of the Tombigbee River in eastern Mississippi (Cooper and Hobbs 1980), and in this paper, closely allied forms in the Yazoo and Noxubee river basins, Mississippi, have been assigned to *O. chickasawae*. Although *O. jonesi* was not included in the list of species originally placed in the subgenus *Trisellescens* (Bouchard and Bouchard 1995), it does belong in that subgenus (Bouchard 2007, personal communication).

For most species in the *Orconectes* (*Trisellescens*) subgenus, the only published life history information is what is noted in the species descriptions. For several species, including *O. chickasawae* and *O. jonesi*, no records of females with eggs or hatchlings are published. For such species, oviposition timing typically has been inferred from ratios of adult males to females in populations over time or from dates of appearance of free-swimming juveniles. Better life history information is useful for interpreting how environmental factors influence populations, for modeling population dynamics, and for planning research and monitoring.

Because collecting ovigerous *Orconectes* females can be difficult in the southern USA, it is useful to present data on ovigerous females collected incidentally during other studies, as is the case with the data presented here.

METHODS

Female *Orconectes* with attached eggs or hatchlings were captured during several recent studies. Sampling was conducted by backpack electrofishing or seining. Prior to 2007, seining was only conducted immediately after electrofishing. In 2007, seining was used alone. Most locations were in Mississippi, but two were in southwestern Tennessee (Table 1).

Most crayfish were placed into 70% or 95% ethanol after capture, although three were frozen and three were kept alive in the laboratory (Table 2). Female postorbital carapace lengths (POCL) and carapace lengths (CL) were measured with calipers. Eggs were counted and their diameters were measured with calipers under a dissecting microscope in May 2007. Up to 20 eggs per female were measured, or fewer when 20 were not present. Empty, soft eggshells (the embryonic envelope of Tack 1941) were also counted when still attached to pleopods and included in "total egg" counts. Freezing caused many eggs to burst, making counting more difficult and measuring eggs impossible for two specimens. For the *O. etnieri* females captured with hatchlings, the CL of five hatchlings each were measured. Live females were kept in aquaria at about 15°C and their eggs were not counted; the females were measured after their post-hatchling-release molt. Stage 2 or 3 (Reynolds 2002) hatchlings from one female were counted, but for the others, substantial mortality from various sources occurred before hatchlings could be counted.

From 2004 – 2007, *O. chickasawae* were maintained in 946 L outdoor tanks at the laboratory. Wild-caught individuals from several locations and captive-reared individuals commingled in the tanks. The crayfish were examined intermittently to observe reproductive condition. Although they reproduced annually, fecundity was low and fungus infected many eggs.

RESULTS

Of more than 800 *Orconectes* crayfish captured in streams in March and early April over three years (2004, 2005, and 2007), 20 were females carrying eggs or hatchlings. Combining years, female *Orconectes* with eggs or hatchlings were encountered from

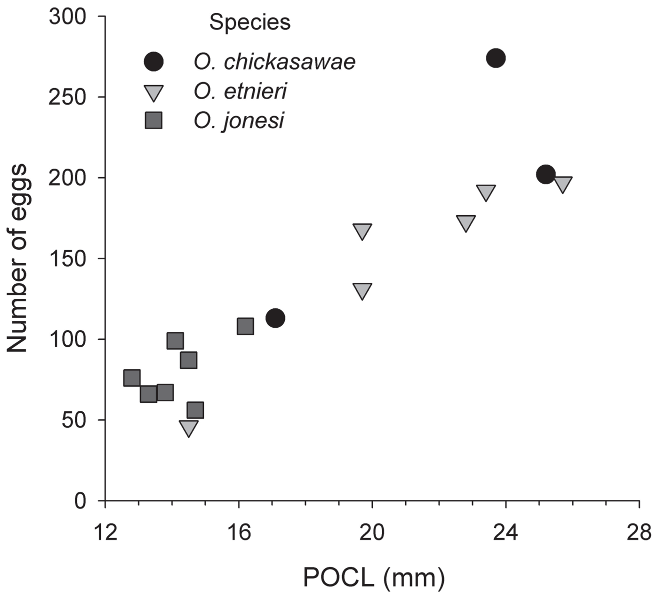

Figure 1. Relationship between postorbital carapace length (POCL) and total egg counts. Total egg counts included both intact eggs and empty eggshells attached to pleopods and, thus, did not necessarily reflect realized fecundity.

9 March to 16 April (Table 2). Ovigerous females in outdoor tanks were observed as early as 27 February.

From 12 March to 6 April 2007, six ovigerous *O. etnieri* females were collected, one of which was kept alive in the laboratory (Table 2). Total egg counts for the five individuals preserved or frozen ranged from 46 – 197. The female kept alive in the laboratory had free-swimming hatchlings by 20 April. Two additional females with hatchlings were collected from a stream on 6 April 2007. One of the females collected with hatchlings had six eyed eggs remaining, two of which were preserved mid-hatch, and both females had empty eggshells still attached to their pleopods. Their hatchlings were stage 1 and averaged 3.0 mm CL (SE ± 0.02 mm) on the smaller female and 3.2 mm CL (SE ± 0.04 mm) on the larger female.

Ovigerous *O. chickasawae* females were collected from 9 March to 16 April (Table 2). A single female with eyed eggs was found on 23 March 2007 in the Noxubee River drainage, the southern extent of the species' range. The two females kept alive in aquaria had free-swimming hatchlings by 26 April. Egg counts ranged from 113 – 274. In the outdoor tanks, ovigerous female *O. chickasawae* were observed on 25 March and 15 April 2005, 27 February and 10 April 2006, and 27 February and 19 March 2007.

These collections indicate that ovigerous *O. jonesi* females are relatively common in March, and based on egg developmental stage, presumably into early April (Table 2). The smallest ovigerous female collected had a POCL of 12.8 mm. The largest ovigerous *O. jonesi* was smaller than the smallest ovigerous *O. chickasawae* and smaller than six of eight *O. etnieri* with eggs or hatchlings (Table 2).

Three of the seven ovigerous *O. jonesi* females had empty eggshells attached to their pleopods, and on the largest female, over 40% of the total egg count consisted of empty shells. It appears unlikely that this was due to successful hatching of those eggs because the remaining eggs appeared viable (Reynolds 2002) and not fully developed (no eye pigment was visible).

Total egg counts differed significantly among species and were related to female size. *Orconectes etnieri* and *O. chickasawae* had significantly higher total egg counts than *O. jonesi* (ANOVA, $F_{2,13}$ = 7.0, $P = 0.009$; LSD pairwise comparisons between *O. jonesi* and the other two species, $P < 0.025$). Total egg counts were correlated with crayfish size (POCL) across the three species (Pearson's r = 0.916, n = 16, $P < 0.001$, Figure 1). Within species, female size and total egg count were correlated only in *O. etnieri* (Pearson's $r = 0.94$, n = 6, $P = 0.005$), but statistical power was low for all species due to small sample sizes.

Mean egg diameter per female also differed significantly among species (ANOVA $F_{2,11} = 27.9$, $P = 0.000$) with *O. etnieri* having significantly larger eggs than *O. chickasawae* and *O. jonesi* (LSD pairwise comparisons between *O. etnieri* and the other two species, $P = 0.000$). Mean egg diameter per female was correlated with female POCL across the three species (Pearson's $r = 0.642$, n = 14, $P < 0.013$), but no significant correlations between crayfish size and egg size were observed within species (all $P > 0.36$), possibly due to small sample sizes.

DISCUSSION

The findings of ovigerous females from late February to April are consistent with expectations based on limited literature for the three species and the subgenus. Two ovigerous *O. etnieri* females were reported from 1 and 15 March in different years (Bouchard and Bouchard 1976). Cooper and Hobbs (1980) found first form *O. chickasawae* males from October and April, but no females carrying eggs or hatchlings have been reported. Likewise, nothing has been reported about female *O. jonesi* carrying eggs or hatchlings; however, based on seasonal presence of form I males and on male:female ratios, Fitzpatrick (1992) inferred that the breeding period of *O. jonesi* begins in early fall (October) and that females become ovigerous in January.

Within the subgenus *Trisellescens, Orconectes immunis* (Hagen) is the only species for which abundant female life history information is available. Although *O. immunis* is widespread, it does not occur south of extreme northwestern Tennessee (Taylor and Schuster 2004); therefore, its life history timing likely differs substantially from that of closely related species occurring farther south. For example, ovigerous *O. immunis* occurred from January to April in Illinois (Page 1985), and at least some individuals oviposited as early as September (Rach and Dawson 1991) or October (Tack 1941) in Wisconsin and New York, respectively, and retained eggs over the winter (Table 3). In more southerly latitudes, females from the subgenus are most commonly ovigerous in March and April, with *Orconectes alabamensis* (Faxon) ovigerous from February to May (Table 3). This timing is likely explained by warmer water temperatures, and thus, shorter incubation periods in the southern latitudes of the U.S. (Reynolds 2002). More extensive sampling will likely extend the known egg incubation period for some species.

Table 1. Location information for *Orconectes* collections. Collection numbers correspond with the portion of the catalog numbers preceding the dashes in Table 2. Subbasins correspond to US Geological Survey 6-digit hydrologic unit codes. Latitude and longitude are in decimal degrees.

Species	Collection	Stream	Subbasin	County	State	Lat	Long
O. chickasawae	SA91	Potts Cr.	Little Tallahatchie	Marshall	MS	34.5919	-89.3425
O. chickasawae	SA161	Jones Cr.	Noxubee	Winston	MS	33.2658	-88.9004
O. chickasawae	SA11	Lee Cr.	Little Tallahatchie	Lafayette	MS	34.4978	-89.4572
O. chickasawae	SA189	Big Cr.	Yalobusha	Calhoun	MS	33.9212	-89.3894
O. chickasawae	SA167	Houlka Cr.	Tibbee	Clay	MS	33.7415	-88.7656
O. etnieri	SA145	Houston Branch	Tennessee-Beech	Hardin	TN	35.0486	-88.2515
O. etnieri	SA154	Dry Cr.	Upper Hatchie	Prentiss	MS	34.6770	-88.7149
O. etnieri	SA178	Blind Tiger Cr.	Wolf	Benton	MS	34.9462	-89.1633
O. etnieri	SA180	Keith Branch	Hatchie-Obion	McNairy	TN	35.1983	-88.7025
O. jonesi	SA159	Running Tiger Cr.	Sucarnoochee	Kemper	MS	32.8174	-88.7010
O. jonesi	SA157	Sucarnoochee Cr.	Sucarnoochee	Kemper	MS	32.7830	-88.6030

Table 2. Data on *Orconectes* females, eggs, and hatchlings collected in Mississippi and Tennessee, USA. Postorbital carapace length (POCL) and carapace length (CL) are both given unless rostrum was broken. Measurements are in mm. Empty eggshells were counted if still attached to pleopods. NC means not counted. Catalog numbers are individual crayfish identification numbers in the USFS Center for Bottomland Hardwoods Research crayfish collection (see Table 1 for collection site locations).

Species	Date Collected	PO CL	CL	# eggs	Shells	# hatch-lings	Mean egg diam. (± SE)	Comments	Catalog #
O. chickasawae	29-Mar-05	17.1	23.2	113			1.61 (0.02)		SA91-1
O. chickasawae	23-Mar-07	23.7	31.9	274			1.76 (0.02)	eyed eggs	SA161-12
O. chickasawae	09-Mar-04	25.2		202			1.68 (0.02)		SA11-06
O. chickasawae	16-Apr-07	21.9[a]	29.5[a]	NC		NC	—	hatched in lab	SA189-11
O. chickasawae	29-Mar-07	23.8[a]	30.9[a]	NC		NC	—	hatched in lab	SA167-2
O. etnieri	12-Mar-07	22.8	29.3	173			1.89 (0.03)		SA145-2
O. etnieri	12-Mar-07	23.4	31.2	192[b]			1.86 (0.02)	frozen	SA145-26
O. etnieri	12-Mar-07	25.7	32.7	197			1.92 (0.01)		SA145-5
O. etnieri	21-Mar-07	24.6[a]	31.9[a]	NC		> 130	—	hatched in lab	SA154-20
O. etnieri	06-Apr-07	14.5	20.2	46[b]				frozen	SA180-19
O. etnieri	06-Apr-07	19.7	26.8	168[b]				frozen	SA180-18
O. etnieri	06-Apr-07	15.5	20.1		~ 41	10	—		SA178-3
O. etnieri	06-Apr-07	19.7	25.3	6	~ 125	48	2.00 (0.00)		SA178-1
O. jonesi	22-Mar-07	12.8	18.1	76			1.56 (0.01)		SA159-13
O. jonesi	22-Mar-07	13.3	18.8	66			1.70 (0.02)		SA159-14
O. jonesi	22-Mar-07	13.8	19.5	63	4		1.70 (0.01)		SA157-5
O. jonesi	22-Mar-07	14.1	19.4	99			1.66 (0.02)		SA157-4
O. jonesi	22-Mar-07	14.5	19.4	84	3		1.68 (0.01)		SA157-2
O. jonesi	22-Mar-07	14.7	20.7	56			1.66 (0.01)		SA157-3
O. jonesi	22-Mar-07	16.2	22.3	76	32		1.65 (0.01)		SA157-6

[a] Lengths measured after post-hatching molt by female.
[b] Many eggs burst from freezing - count includes eggshells.

Although in *Orconectes* as a whole, ovigerous females occur most commonly from March to May (Table 4), some notable variations exist. Similar to *O. immunis,* individuals or populations of several other species oviposit in the fall and incubate eggs through the winter (Table 4). In several populations, including some cave crayfish, at least a portion of the females in a population release juveniles in mid- to late-summer (e.g., *Orconectes inermis inermis* Cope, Taylor and Schuster 2004; *Orconectes propinquus* (Girard), Simon et al. 2005; Table 4).

Fecundity and female size were correlated across the three species in this study, as is typical of crayfish in general (Reynolds 2002) and of many *Orconectes* species in particular (e.g., Tack 1941; Corey 1988a; Stechy and Somers 1995). *O. jonesi* appears to be among the smallest species in the *Trisellescens* subgenus, and that was reflected in reproductive characteristics. The smallest mature *O. jonesi* previously reported was a form I male with a POCL of 13.6 mm (Fitzpatrick 1992), and I found two ovigerous females that were even smaller. Fitzpatrick (1992) also noted that

Table 3. Summary of reproductive timing, fecundity (abdominal egg counts), egg diameter, and female size data for various species in the *Orconectes* subgenus *Trisellescens*. Measurements are in mm. POCL is postorbital carapace length.

Species	Months ovigerous	# of eggs: mean; range	Egg diam. range (mode)	POCL (range)	N	Source
O. alabamensis	Feb – May	99; 40 – 154	1.5 – 2.1 (1.6)	13.2 – 21.4	5	Cooper and Hobbs 1980
O chickasawae [a]	Mar – Apr	196; 113 – 274	1.6 – 1.9 (1.7)	17.4 – 25.2	5	This study
O. cooperi	Mar	—	—	—	—	Cooper and Hobbs 1980
O. etnieri	Mar	—	—	—	2	Bouchard and Bouchard 1976
O. etnieri [b]	Mar – Apr	155; 46 – 197	1.5 – 2.1 (1.9)	14.5 – 25.7	8	This study
O. immunis	Sep – Apr	126; 5 – 529		25 – 43[c]	64	Rach and Dawson 1991
O. immunis	Oct – May	102; 4 – 289		22 – 34[c]	37	Tack 1941
O. immunis	Jan – Apr	169; 102 – 285	(1.7[d])	21.8 – 35.9[c]	7	Page 1985
O. immunis	Mar – Apr	173; 12 – 423		45.7 – 68.6[e]	10	Pfleiger 1996
O. immunis	Apr	191; 33 – 372	1.0 – 2.1	13 – 32	15	Simon et al. 2005
O. jonesi	Mar	74; 63 – 99	1.5 – 1.8 (1.7)	12.8 – 16.2	7	This study
O. mississippiensis	Mar	162; 77 – 289	1.4 – 1.9 (1.8 – 1.9)	17.9 – 21.6	3	Cooper and Hobbs 1980
O. validus	Apr	144; 62 – 206[f]	1.5 – 2.1 (1.8 – 1.9)	14.8 – 21.8	12	Cooper and Hobbs 1980

[a] egg counts and mean diameters based on 3 of the 5 females

[b] egg counts based on 5 of 8 and mean egg diameters on 4 of 8 females

[c] carapace length

[d] mean

[e] total length

[f] some eggs loose in jar, so mean is accurate but both lower and upper ends of range may have been undercounted.

the species appeared to be smaller than *O. chickasawae*. Based on the limited data available, *O. jonesi* and *O. alabamensis* are on the low end of the fecundity scale in the subgenus, whereas *O. immunis* is at the higher end, and *O. chickasawae* and *O. etnieri* are in the middle. Fecundity also varies greatly within several other *Orconectes* subgenera, including *Crockerinus*, *Gremicambarus*, and *Procericambarus* (Table 4). The range of fecundities observed in the *Triscellescens* subgenus approximates the range observed in the genus as a whole, with several species in other subgenera having higher or lower mean fecundities. However, comparisons are tentative because of the very limited sample sizes of ovigerous females for most species.

For each series of ovigerous *Orconectes* reported on by Cooper and Hobbs (1980), the largest female had the largest eggs, as is the general pattern for crayfishes (Reynolds 2002). In the small collections in the present study, the smallest females of two species had the smallest eggs for the species, but relationships between female size and egg size were not evident within species. Egg developmental stage appeared to confound the relationship (Table 2), but even for *O. jonesi*, all of which were collected the same day, a positive relationship between female size and egg size was not evident. However, egg size was correlated with female size across the three species.

Egg diameters for the three species studied were lower than average for Cambarid crayfishes (Reynolds 2002) but within the range reported for other species in the subgenus (Tables 2 and 3). Mean or modal egg diameters for two species in this study, *O. chickasawae* and *O. jonesi*, were smaller than those reported for most *Orconectes* populations (Tables 2 and 4), whereas egg diameters for *O. etnieri* were within the range reported for most *Orconectes* species. Relative to the genus as a whole, species in *Trisellescens* tend to have small to moderate sized eggs, whereas species in *Procericambarus* tend to have large eggs. Again, sample sizes limit the strength of comparisons.

It is not known why several *O. jonesi* carried numerous empty eggshells. Reynolds (2002) noted that small females are less likely to carry eggs to hatching, and even the largest female *O. jonesi* in the present study was small relative to mature crayfish of many other species in the subgenus. All three female *O. jonesi* with empty eggshells were from the same site (SA157, Table 1), so it is possible that environmental factors contributed to egg loss. One of the three form I males collected from the same site had deformed gonopods, further suggesting the possibility of an environmental factor influencing reproduction. Corey (1987b, 1988a) noted that internal parasites appeared to reduce fecundity in some populations of two *Orconectes* species, but she did not report empty egg shells attached to pleopods. Specimens were not examined for internal parasites.

Of the three species studied, *O. jonesi* has the most restricted distribution (limited to the Sucarnoochee River drainage),

Table 4. Summary of reproductive timing, female size, fecundity (abdominal egg counts), and egg diameter data for a sampling of *Orconectes* species organized by subgenera (excluding *Trisellescens*). Ranges of means and sample sizes from multiple studies or populations are given for some species. All measurements in mm. TL = total body length; CL = carapace length; POCL = post-orbital carapace length.

Species	Months ovigerous	Number of eggs: means; ranges	Mean egg diam.	Size range of ovigerous females	N	Sources
Buannulafictus						
O. p. palmeri	late Feb – Apr	1 – 354	2.0	43.2 – 58.4 TL	4 – 12	Payne and Price 1983; Pflieger 1996
Crockerinus						
O. bisectus	Mar, May	140; 134 – 146		57.7 – 60.1 TL	2	Taylor and Schuster 2004
O. eupunctus	Mar – May	79; 53 – 103	2.0	38.1 – 53.34 TL	7	Pflieger 1996
O. illinoiensis	Mar – Apr	123; 84 – 175		21.5 – 31.3 CL	3	Page 1985
O. jeffersoni	Apr					Taylor and Schuster 2004
O. marchandi	Mar – Apr	71; 26 – 112	1.5 – 1.8		3 – 26	Pflieger 1996; Flinders and Magoulick 2005
O. margorectus	Mar – Apr	278; 156 – 400	1.9	63.3 – 77.0 TL	2	Taylor and Schuster 2004
O. obscurus	Apr – May					Fielder 1972
O. propinquus	Mar – Jun, Aug	72 – 220; 4 – 277	1.9 – 2.3	12.8 – 26.1 POCL, 16 – 32 CL	2 – 116	Fielder 1972; Page 1985; Page 1985 citing VanDeventer 1937; Corey 1987a, b, 1988a; Simon et al. 2005
O. rafinesquei	Mar – Apr	312	1.9	68.2 TL	1	Taylor and Schuster 2004
O. sanbornii	Apr – May		< 2.3			Fielder 1972
O. stannardi	May	154; 124 – 184	1.9	20.7 – 28.9 CL	2	Page 1985
O. tricuspis	Apr	99; 70 – 128	1.8 – 1.9	50.0 – 55.8 TL	2	Taylor and Schuster 2004
Faxonius						
O. indianensis	Mar – May	149 – 184; 121 – 209	1.8	22 – 23 POCL, 26.3 – 32.2 CL	2 – 3	Page 1985; Simon et al. 2005
O. limosus	Mar – Jun	309; 57 – 440	2.0			Hamr 2002
Gremicambarus						
O. compressus	Mar – Apr	47; 38 – 57	1.8	29.3 – 43.1 TL	3	Taylor and Schuster 2004
O. virilis	Mar – Jul, Nov	108 – 449; 20 – 707	2.1	13.9 – 29.6 POCL, 18.4 – 49.7 CL, 50.8 – 99.1 TL	5 – 12	Page 1985; Corey 1987a; Mitchell and Smock 1991; Pflieger 1996; Hamr 2002; Reynolds 2002
Orconectes						
O. i. inermis	Jun, Aug	45	2.0 – 2.5			Taylor and Schuster 2004
O. pellucidus	Sep – Nov					Taylor and Schuster 2004
Procericambarus						
O. cristavarius	Mar – Apr	58; 43 – 74	2	37.0 – 42.6 TL	2	Taylor and Schuster 2004
O. hylas	Apr – May	166; 96 – 240		20.1 – 29.9 CL	13	DiStefano et al. 2002
O. juvenilis	Apr	141	2.1	60.2 TL	1	Taylor and Schuster 2004
O. luteus	Mar – Jun	139; 20 – 286	1.7 – 2.4	11.2 – 29 CL	28	Pflieger 1996; Muck et al. 2002b
O. macrus	Mar	39; 23 – 63		20.3 – ? TL	9	Pflieger 1996
O. neglectus	Mar – Jun	245; 54 – 505	1.6 – 2.0	40.6 – 78.7 TL	18	Pflieger 1996
O. ozarkae	late Feb – May	103; 30 – 353	1.8 – 2.4	35.6 – 78.7 TL	23	Pflieger 1996; Muck et al. 2002a
O. peruncus	Mar – May	61; 15 – 123		35.6 – ? TL	7	Pflieger 1996; Riggert et al. 1999
O. placidus	Mar – Apr	78-250; 12 – 514	1.9 – 2.1	15.7 – 27.2 CL; 41.8 – 49.1 TL	2 – 3	Page 1985; Walker et al. 2002; Taylor and Schuster 2004
O. putnami	Mar – May	154; 134 – 175	1.8 – 1.9	52.4 – 55.6 TL	2	Taylor and Schuster 2004
O. quadruncus	Mar – May	43; 21 – 78		33.0 – 45.7 TL	5	Pflieger 1996; Riggert et al. 1999
O. rusticus	Feb – Jun, Oct	143 – 162; 35 – 575	2.4	13.9 – 38.7 POCL, 17 – 38 CL	43 – 170	Page 1985 citing Prins 1968; Corey 1987a, 1988b; Hamr 2002
O. ronaldi	late Mar	199; 142 – 256	1.9 – 2.1	53.7 – 69.7 CL	2	Taylor and Schuster 2004
Rhoadesius						
O. kentuckiensis	Mar – May	110; 49 – 248	1.9		15	Boyd and Page 1978; Page 1985
Tragulicambarus						
O. lancifer	Feb	570	1.5	40 CL	1	Page 1985

the smallest body size and lowest fecundity, and possibly an environmental factor influencing egg survival in at least one site. Together, these factors suggest that *O. jonesi* may be of conservation concern and that further research on distribution, population size, habitat conditions, and life history is warranted.

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