CLUTCH AND OVUM SIZES OF THREE SPECIES OF WHIPSNAKES (*MASTICOPHIS*, COLUBRIDAE)

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Clutch size is an important component of fitness (Brockelman, 1975) and is one of the best documented aspects of reproduction in snakes (Seigel and Ford, 1987). Analyses of the relationship between offspring size and clutch size in snakes show that, when female body size is held constant, offspring size may decrease with increases in clutch size (Ford and Killebrew, 1983; Ford and Seigel, 1989). However, these analyses included heavy bodied snakes, such as *Elaphe, Thamnophis,* and *Trimeresurus.* This is the first such report for slender bodied snakes. We analyzed the relationship between clutch size and offspring size, as measured by egg volume, in *Masticophis taeniatus.* Data are presented on clutch and ovum sizes for *Masticophis bilineatus* and *Masticophis schotti* based on oviductal eggs from museum specimens and from freshly oviposited clutches.

Reproduction in *M. taeniatus* has been studied in a northern Utah population by Goldberg and Parker (1975) and Parker and Brown (1980). Other reports of clutch sizes include 2 clutches of 4 eggs each from Colorado (Maslin, 1947) and a single clutch of 5 eggs from Texas (Minton, 1959). The latter is the only report from the central Texas whipsnake, *Masticophis taeniatus girardi.* Little has been reported concerning reproduction in *M. schotti.* Gloyd and Conant (1934) reported 3 clutches of 3, 10, and 12 eggs, respectively, from *M. schotti* from southern Texas, and McCrystal and Dixon (1983) reported a single clutch of 5 eggs from Nuevo León, México. Reproductive cycles and clutch sizes in *M. bilineatus* were studied by Goldberg (1998). Van Denburgh (1922) reported a single clutch of 7 eggs, Vitt (1975) a single clutch of 6 eggs, and Rossi and Rossi (1995) a single clutch of 15 eggs from *M. bilineatus.*

Masticophis taeniatus, M. schotti, and *M. bilineatus* are parapatrically distributed (Camper and Dixon, 1994). *Masticophis taeniatus* is found in the Chihuahuan and Great Basin deserts, the Edwards Plateau of central Texas, and western portions of the Mexican Plateau. Populations on the Edwards Plateau and in the Chihuahuan Desert are assigned to *M. taeniatus girardi. Masticophis schotti* is found south of the Edwards Plateau and along eastern portions of the Mexican Plateau, east to the Gulf of Mexico. *Masticophis bilineatus* occurs in the Sonoran Desert of southern Arizona, along the west coast of México south to the state of Colima, and east to the Continental Divide. Narrow zones of sympatry exist between *M. taeniatus* and *M. schotti* along the Balcones Escarpment in central Texas, between *M. bilineatus* and *M. taeniatus* in central Arizona, and for all 3 in central México (Camper and Dixon, 1994).

Egg length and width were measured to the nearest 0.1 mm with dial calipers. Due to extensive variation in the condition of preserved specimens and the potential for mass increase of eggs in preservative (Vitt et al., 1985), clutch mass and female mass were not analyzed. How-

TABLE 1—Reproductive data for 3 species of whipsnakes (*Masticophis*). Egg length, width, and volume are averages per clutch and based on oviductal eggs only. Values in parentheses are number of clutches, whereas *n* is number of eggs. RF is relative fecundity (clutch size/female total length).

Parameter	*M. taeniatus*	*M. schotti*	*M. bilineatus*
SVL (mm)			
Mean (*SD*)	913.7 (104.9)	960.2 (81.1)	847.9 (64.5)
Range	688–1163	818–1041	768–965
Clutch size			
Mean (*SD*)	5.78 (1.89)	6.00 (1.67)	4.43 (1.40)
Range	3–10	4–8	3–6
n (clutches)	97 (27)	35 (7)	31 (7)
RF	0.041	0.045	0.037
Egg length (mm)			
Mean (*SD*)	54.57 (9.68)	51.67 (16.76)	51.63 (2.84)
Range	39.9–68.6	32.7–64.5	49.8–54.9
Egg width (mm)			
Mean (*SD*)	16.85 (2.54)	15.37 (3.70)	18.17 (2.84)
Range	14.4–22.5	11.6–19.0	15.3–19.6
n (clutches)	67 (10)	14 (3)	14 (3)
Egg volume			
Mean (*SD*)	8.25 (2.92)	9.52 (1.99)	9.08 (2.62)
Range	5.2–13.2	8.1–10.9	6.1–11.0
n (clutches)	67 (10)	9 (2)	14 (3)

ever, the relative fecundity (RF = clutch size/female total length) of Iverson (1987) was calculated for all gravid (containing enlarged follicles or oviductal eggs) females. Clutch and egg size were based on enlarged follicles, oviductal eggs, and freshly oviposited clutches. However, statistical analyses of egg size and volume are based on oviductal eggs and freshly oviposited clutches only. Data from oviposited clutches were gathered from eggs laid in captivity. Data from only 3 clutches, 1 from each species (*M. bilineatus*—TCWC 64842; *M. schotti*—TCWC 63774; *M. taeniatus*—TCWC 64841) were obtained this way. Mean egg volume (Vitt, 1983) for a clutch was used as a measure of offspring size where volume (V) = $4/3\pi$(½ egg length)(1.2 egg width^2). Partial correlation analysis, holding female SVL constant, was performed to test clutch size and offspring size relationships (Ford and Siegel, 1989). Data were log transformed prior to analysis. An alpha level of 0.05 was considered significant in all tests. Specimen locality information is listed in Appendix 1.

Gravid *M. bilineatus* had the smallest mean SVL, mean clutch size, and the lowest RF, whereas gravid *M. schotti* had the largest mean SVL, mean clutch size, and the highest RF (Table 1). Collection/oviposition dates for gravid *M. bilineatus* range from an undated May specimen to 9 July (n = 7). Collection/oviposition dates for gravid *M. schotti* range from 27 April to 5 May (n = 3). Because so little has been reported for *M. taeniatus girardi*, clutch sizes and collection/ovipositon dates will be reported separately for each *M. taeniatus* subspecies. Clutch size for *M. taeniatus girardi* ranged from 4 to 12 ($\bar{x}$ = 7.0, n = 8) and collection/ovipositon dates were 30 April to 1 July (n = 8). Clutch size for *M. taeniatus taeniatus* ranged from 3 to 8 ($\bar{x}$ = 5.6, n = 17) and collection/ovipositon dates were 30 April to 20 June (n = 15).

Dimensions and volume of oviductal eggs were similar for all 3 species (Table 1). *Masticophis bilineatus* had the shortest and widest eggs, whereas *M. taeniatus* had the longest eggs. The mean egg volume of *M. taeniatus* is smallest and that for *M. schotti* is the largest.

A significant positive relationship was found

TABLE 2—Linear regression results for the regression of 4 reproductive characteristics on SVL in 3 species of *Masticophis*. All data are log transformed.

Reproductive trait	Species	Y-intercept	Slope	*r*	*n*	*F*	*P*
Clutch size	*M. taeniatus*	−8.75	1.53	0.52	21	9.4	<0.005
	M. schotti	−7.16	1.30	0.41	6	0.8	<0.42
	M. bilineatus	6.13	−0.69	0.14	7	0.1	<0.74
Egg length*	*M. taeniatus*	5.60	−0.24	0.14	10	0.1	<0.72
Egg width*	*M. taeniatus*	0.11	0.39	0.28	10	0.7	<0.43
Egg volume*	*M. taeniatus*	−1.74	0.55	0.17	10	0.2	<0.64

* Only *M. taeniatus* were used due to insufficient sample sizes of oviductal eggs in the other 2 species.

between clutch size and female SVL for *M. taeniatus,* but not for the other 2 species (Table 2). Because this is common in snakes (Ford and Seigel, 1989), it is suspected that the other 2 species would show similar relationships had adequate sample sizes been available. Linear regression analyses of egg length, width, and volume on female SVL for *M. taeniatus* were not significant (Table 2). However, the interaction between egg size and clutch size may confound the detection of these relationships.

Due to the correlation of female size and clutch size, the former should be held constant in analyses of offspring size and clutch size relationships (Stewart, 1979; Ford and Seigel, 1989). A partial correlation analysis, holding female SVL constant, was conducted on the *M. taeniatus* data by regressing all 4 reproductive parameters on SVL and then conducting a partial correlation analysis on the resulting residuals. None of the coefficients, clutch size (CS) versus egg length (−0.31), CS versus egg width (0.56), and CS versus egg volume (0.28) were significant ($P > 0.05$). This may reflect a lack of linear relationships among these variables and SVL, from which the residuals were derived, or an inverse relationship between clutch size and egg length in accordance with Stewart's (1979) model.

Clutch size, gravid female SVL, and egg size reported here agree with the literature for *M. taeniatus* (Maslin, 1947; Minton, 1959; Parker and Brown, 1980) and for Mexican *M. schotti* (McCrystal and Dixon, 1983). However, egg width was considerably less than that reported by Gloyd and Conant (1934) for *M. schotti* from Texas. Clutch size was less than that reported by Van Denburgh (1922), Vitt (1975), Rossi and Rossi (1995), and Goldberg (1998) for *M. bilineatus.* Mean egg size was greater than Van Denburgh (1922) found and less than what Vitt (1975) reported for this species.

The RFs calculated here are lower than those calculated for terrestrial or arboreal snakes by Iverson (1987), who reported a relative fecundity of 0.057 for *M. taeniatus.* However, this was based on a mean clutch size of 7, greater than reported here (Table 1). Relative fecundities were not calculated for *M. schotti* or *M. bilineatus* by Iverson (1987). The relative fecundities presented here are low but still within the range of values obtained for 25 species of oviparous colubrines (Iverson, 1987).

Parker and Brown (1980) also reported a positive correlation between female SVL and clutch size in a northern Utah population of *M. t. taeniatus.* Even though the analysis of residuals was not significant, a negative relationship among clutch size and egg length may exist. The attenuate morphology of swift reptiles, such as *M. taeniatus,* may limit clutch and egg sizes (Vitt and Congdon, 1978). Ford and Seigel (1989) and Seigel and Ford (1991) reported no increase in egg width and reduction in egg length with increasing clutch size for 2 species of *Trimeresurus* and *Elaphe guttata.* However, meaningful comparisons with these taxa may be limited by the fact that they are much heavier bodied than *Masticophis.* This argument assumes that ovum size is proportional to offspring size and, as Ford and Killebrew (1983) stated, that offspring size is less variable than clutch size. Analyses from this study should be interpreted with caution, because data from different populations and from different years were combined.

Resumen—El tamaño de nidada y de óvulo

fueron registrados para *Masticophis bilineatus, M. schotti,* y *M. taeniatus.* Se encontró una relación positiva y significativa entre el tamaño de la nidada y la longitud hocico-cloaca para *M. taeniatus,* pero no para las otras dos especies. Análisis de correlación parcial, manteniendo constante la longitud hocico-cloaca, reveló que ninguno de los coeficientes parciales del tamaño de nidada versus longitud, anchura y volumen del huevo fue significativo. Los resultados del análisis de correlación parcial pueden reflejar una falta de relaciones lineales entre estas variables y la longitud hocico-cloaca o una relación inversa entre el tamaño de la nidada y el largo del huevo.

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APPENDIX 1

Specimens examined listed by county and state for United States specimens and state for Mexican specimens. See acknowledgments for definition of collection acronyms.

Masticophis bilineatus—ARIZONA: Graham Co.; ASU 7020, 7032; CM 70933. Maricopa Co.; ASU 3686. NEW MEXICO: Hidalgo Co.; TCWC 64842. MÉXICO: Nayarit; AMNH 74956. Sinaloa; CAS 120883.

Masticophis schotti—TEXAS: Comal Co.; UMMZ 74328. Frio Co.; TCWC 63774. Kleberg Co.; TAIC 4255. Uvalde Co.; TNHC 14581–14582. MÉXICO: Tamaulipas; TCWC 49933; UMMZ 101260.

Masticophis taeniatus—ARIZONA: Gila Co.; MVZ 6309. Graham Co.; SDNHM 62706. CALIFORNIA: San Bernardino Co.: MVZ 28565–28566. IDAHO: Fremont Co.; USNM 56018. NEW MEXICO: Catron Co.; UNM 32169. Quay Co.; UNM 19705. Socorro Co.: UNM 4154–4155. NEVADA: Humboldt Co.; MVZ 20622. Lander Co.; MVZ 12171. Nye Co.; MVZ 13082; UNM 463. Washoe Co.; MVZ 7546. White Pine Co.; MVZ 24583. TEXAS: Bexar Co.; AMNH 22743; CM 22850. Culberson Co.; SDNHM 25483. Kimble Co.; TCWC 65284. Llano Co.; TCWC 64841. Travis Co.; LACM 66801. Upton Co.; UTACV 14472–14473. UTAH: Grand Co.; LACM 103365. Iron Co.; KU 20907. Sevier Co.; SDNHM 38275. Tooele Co.; BYU 14823.