

## REPRODUCTIVE BIOLOGY OF THE VIVIPAROUS SEA SNAKE *EMYDOCEPHALUS IJIMAE* (REPTILIA: ELAPIDAE: HYDROPHIINAE) UNDER A SEASONAL ENVIRONMENT IN THE NORTHERN HEMISPHERE

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Reproductive traits of *Emydocephalus ijimae* were examined on the basis of specimens from shallow waters around the central Ryukyus, Japan. Sampling was carried out from December 1979 until November 1980 (with the exception of September), and yielded a total of 240 specimens. Gonadal examinations revealed that males and females mature at 550–600 mm and 500–550 mm snout-vent length (SVL), respectively. We therefore regarded female snakes > 550 mm SVL and male snakes > 500 mm SVL as adults. Mean length of the largest ovarian follicles in the monthly adult female sample increased gradually from July to March, and rapidly from March to April, and then swiftly decreased from April to June. Oviducal eggs occurred only in samples from May to November, although the occurrence of one gravid female in early January was recently reported. Possible neonates (i.e. juveniles as large as the largest embryos [280–320 mm in SVL]) were found from November to January. These data suggest that ovulation occurs from May to June and parturition from November to January after 6–8 months of gestation. Of 19 adult females collected in June, ten (52.6%) were gravid, whereas the remainder had neither oviducal eggs nor enlarged ovarian follicles close to ovulation. Likewise, both gravid and non-gravid females were observed in each of the July–November samples, although their sample sizes were much smaller (4–8) and frequencies of gravid individuals varied considerably (0–50%). It is likely that the overall frequency of reproduction in individual females is biennial or even less frequent. Clutch size varied from 1 to 4 eggs, and showed no significant correlation with maternal body size (as represented by SVL or BW). In adult males, on the other hand, gonadal index (total mass of gonads × 100/body mass) increased from May to November, and largely decreased from November to April. Present results indicate that the reproductive activities of both male and female *E. ijimae* are synchronized and seasonal, as in some other lower latitude marine snakes.

*Key words:* biennial reproduction, clutch size, reproductive cycle, Ryukyu Archipelago

### INTRODUCTION

The venomous sea snakes of the family Elapidae (sensu McDowell, 1987) consist of two distinct clades that most likely represent independent marine invasions (Keogh *et al.*, 1998; Heatwole, 1999). Of these clades, one consisting of so-called sea kraits (the subfamily Laticaudinae) is characterized by oviparous reproduction, whereas members of the other clade (the subfamily Hydrophiinae) are invariably viviparous (Heatwole, 1999).

The elapid sea snakes have been considered as interesting subjects for studying the process and mechanism of adaptations to the marine life by ectothermic amniotes, and a number of research projects have thus been carried out in this context (see reviews by Dunson, 1975; Heatwole, 1999). Nevertheless, relatively little is known of the ecology of this group of sea snakes. With respect to reproductive biology, most studies have been carried out on populations from low latitudes in the

Southern Hemisphere and equatorial region (Voris & Jayne, 1979; Lemen & Voris, 1981; Burns, 1985; Ward, 2001; Fry *et al.*, 2001). For the reproduction of sea snakes in the distinctly seasonal region of the Northern Hemisphere, quantitative data are available only for one oviparous species, *Laticauda semifasciata* (Kuwabara *et al.*, 1990; Tu *et al.*, 1990).

*Emydocephalus ijimae* is a viviparous hydrophiine species inhabiting coral reefs in the East China Sea (Nakamura & Ueno, 1963; David & Ineich, 1999), an area with distinct seasonal fluctuations in water temperature (Fig. 1) and representing the northernmost extremity of a range of coastal-water dwelling sea snakes (Toriba, 1994). Along with its congener (*E. annulatus*) and another species of a different genus from Australasian and South-east Asian waters (*Aipysurus eydouxi*), *E. ijimae* is known to feed exclusively on fish eggs (Voris, 1966; Voris & Voris, 1983; Heatwole, 1999). This suggests that this sea snake plays a peculiar role in the coral ecosystem (Voris, 1972). Nevertheless, very little is known of other ecological aspects of *E. ijimae*. With respect to reproduction, published information is limited to records of three females collected

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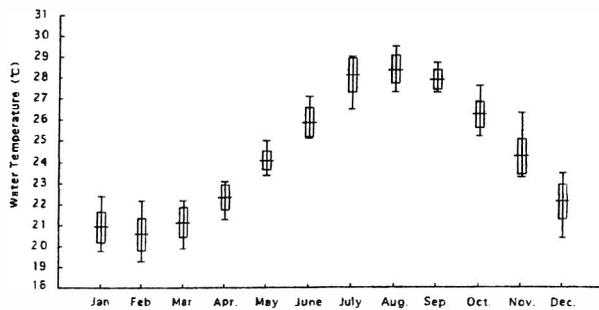


FIG. 1. Monthly averages of water temperature in Okinawajima, the central Ryukyus, measured at a depth of 1 m. Data obtained from 1978 to 1996 by the National Sea Level Monitoring Centre of Japan were used. Horizontal and vertical lines, and vertical bars represent means, ranges, and standard deviations, respectively.

from the central Ryukyus in October, November, and January that had 3–4 embryos (Moriguchi, 1991; Uehara, 1993).

In this study, we analyse the reproductive traits of *E. ijimae* from the central Ryukyus on the basis of samples obtained from almost a complete year of study. We then compare the reproductive pattern of this species with those of other sea snakes hitherto studied.

#### MATERIALS AND METHODS

Sampling was carried out in all months from December 1979 until November 1980, except for September. Sea snakes found in shallow waters (<10 m) around Sesokojima (26°37–39'N, 127°51–53'E) and Zamamijima Islands (26°13–15'N, 127°17–20'E) of the central Ryukyus, were captured by hand and euthanized in the laboratory.

Specimens were then measured for snout-vent length (SVL) to the nearest 5 mm, using a flexible tape measure for individuals greater than 400 mm SVL, or to the nearest 1 mm by rigid ruler for individuals less than 400 mm SVL. Body weight (BW) was taken to the nearest 0.5 g using an electronic balance for each individual. After these measurements, ovaries and oviducts (fe-

male), or testes and epididymides (male), were extracted from each specimen by abdominal autopsy, and were fixed in the Bouin's solution (Lee, 1950).

For each male, gonads were weighed to the nearest 0.01 g by electronic balance, and gonadal index, defined as total mass of gonads  $\times$  100/total body mass, was calculated accordingly. Male gonads were then dehydrated, embedded in paraffin, and sectioned at 8–10  $\mu$ m. Sections were stained with Delafield haematoxylin-eosin, and were observed under a light microscope.

For each female, diameter of the largest ovarian follicle was measured to the nearest 0.1 mm with dial calipers. Oviducal eggs, when present, were counted and embryos, when evident, were also measured for SVL to the nearest 1 mm using a bar scale. Developmental stages of embryos followed definitions by Hubert & Dufaure (1968).

#### RESULTS

##### SIZE AT MATURITY

Some females between 550 and 600 mm SVL showed signs of sexual maturity, but others exhibited none (Fig. 2). In the following analyses, we therefore treated females greater than 550 mm (SVL) as adults. Of the ten females collected in April, seven, with a SVL larger than 600 mm had ovarian follicles larger than 18 mm in length. Another female measuring 575 mm SVL, had two distinctly enlarged ovarian follicles (greater than 44 mm in length), whereas the two remaining specimens, 545 and 585 mm (SVL) respectively, had follicles less than 12 mm length. In the other monthly samples, all females greater than 600 mm (SVL) also had ovarian follicles greater than 12 mm in length, oviducal eggs or embryos, or flaccid oviducts (an indication of recent embryos), whereas those less than 550 mm (SVL) exhibited none of these features.

Microscopic examination of gonadal sections revealed that most males greater than 500 mm (SVL) had distinct seminiferous tubules with sperms, spermatids, or large hollows that had most likely been occupied by

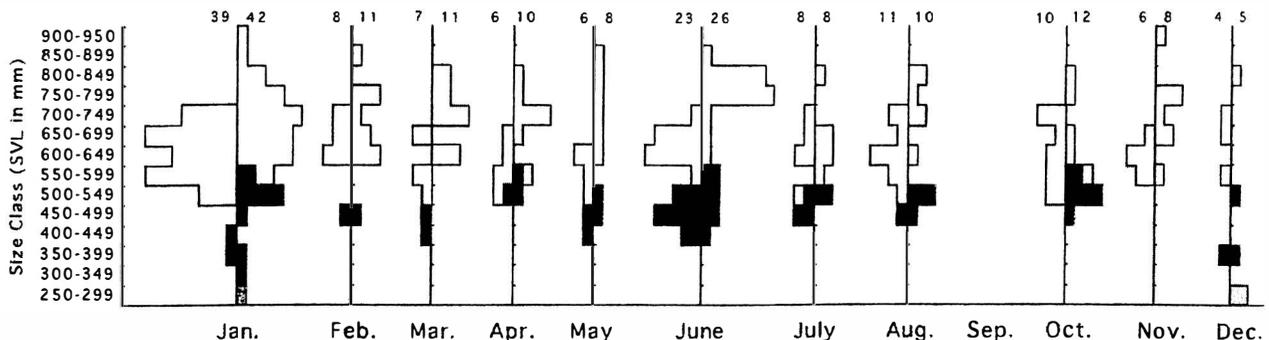


FIG. 2. Size distribution, based on snout-vent length (SVL, in mm), in monthly samples of male (left) and female (right) *Emydocephalus ijimae* from the central Ryukyus, Japan. Individuals were categorized as mature (open), immature (filled), and possible neonates (stippled). The numbers to the left and right above each month's column are male and female sample sizes, respectively.

recently ejected sperms. In contrast, in testes of all males less than 500 mm (SVL) seminiferous tubules were not recognized, or were recognized but with no evidence of spermatogenesis (Fig. 2). These suggest that male *E. ijimae* mature at around 500 mm (SVL). In the following analyses, we thus treated males greater than 500 mm (SVL) as adults.

#### OVARIAN FOLLICLES IN ADULT FEMALES

The monthly fluctuation in the length of the largest follicle (LFL) in adult females is shown in Fig. 3. The monthly mean was smallest in July (6.83 mm), increasing gradually to March (29.50 mm), and rapidly to April (47.38 mm). The value dropped rapidly in May (17.50 mm), more slowly to June (9.71 mm) and finally to July (see above). The standard deviation of LFL varied extensively among the monthly samples, being low in the July–November samples (0.96–1.72 mm), moderate in the January–March and June samples (3.41–6.60 mm), and largest in the April (15.84 mm) and May (16.14 mm) samples. In the latter two samples, the LFL ranged from 11.5 to 60.5 mm and from 4.5 to 52.5 mm, respectively (Fig. 3).

Gravid females were found only in the samples from May (42.8%), June (52.6%), July (50%), August (50%) and November (28.6%). All four adult females collected in October were not gravid. No significant differences were recognized in mean of LFL (mean±SD; range) between the gravid (14.17±2.52 mm; 11.5–16.5 mm;  $n=3$ ) and non-gravid adult females (20.00±22.29 mm; 4.5–52.5 mm;  $n=4$ ) in the May sample (Student's  $t$ -test using log-transformed values:  $t=0.16$ ,  $P>0.05$ ; two tailed variances ratio test:  $F=35.94$ ,  $P>0.05$ ). In the June sample, no significant differences were found in mean of LFL between the gravid (9.10±5.56 mm; 4.5–20.5 mm;  $n=10$ ) and the non-gravid adult females (10.39±4.76 mm; 5.5–20.5 mm;  $n=9$ ;  $t=1.43$ ,  $P>0.05$ ;  $F=1.36$ ,  $P>0.05$ ). Differences were not evident in either the mean or the variance of LFL between the gravid and non-gravid adult females in each of the July, August, and

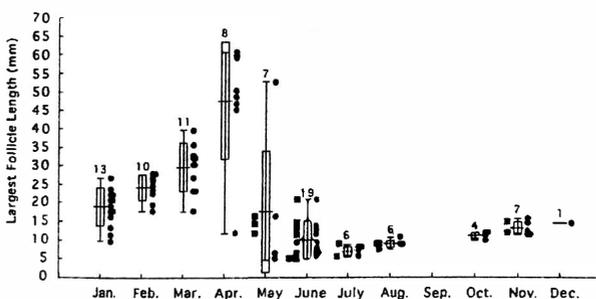


FIG. 3. Annual pattern of largest follicle length in adult female *Emydocephalus ijimae* from the central Ryukyus, Japan. Horizontal and vertical lines and vertical bars represent means, ranges, and standard deviations, respectively. The numbers above are sample sizes. Rectangles and circles represent individual data for gravid and non-gravid females, respectively.

November samples, although their sample sizes were too small for statistical analyses (Fig. 3).

#### OVIDUCAL EGGS AND EMBRYOS

The clutch size in gravid females (see above) varied from 1 to 4 (mean=2.74, SD=0.75,  $n=20$ ). This range covers the values previously reported for three gravid females from the central Ryukyus (3–4; Moriguchi, 1991; Uehara, 1993). Analysis of pooled data from our specimens and those from previous reports of Moriguchi (1991) and Uehara (1993) revealed that the clutch size was unrelated to female body size as represented by body weight ( $t=1.69$ ,  $P>0.05$ ; Fig. 4) or SVL ( $t=0.60$ ,  $P>0.05$ ).

Of a total of eight oviducal eggs from the three gravid females in the May sample, four had blastoderms, but the remaining four, including three comprising a single clutch, did not show any evidence of development. A total of 28 oviducal eggs were obtained from the ten gravid females in the June sample, of which six (two clutches) were not fixed well and thus were not examined in detail. Of the remaining 22 eggs, 16 showed embryos at stages 26–30 of Hubert & Dufaure (1968), whereas the remaining six did not show any evidence of development at all. The three gravid females collected in July had a total of five oviducal eggs, all possessing embryos at stages 34–38. Of a total of ten oviducal eggs from the three gravid females in the August sample, four – all in the same clutch – had embryos at stages 39–41, whereas five others were at stages 36–38. The remaining egg showed no evidence of development at all. All five eggs from the two gravid females in the November sample seemed to have fully developed embryos with SVLs ranging from 310 to 322 mm (mean=315.4, SD=4.72).

#### GONADAL CYCLE IN MALES

The gonadal index in adult males showed a considerable monthly fluctuation, with a minimum in June and a maximum in November. Values in the remaining months varied between these extremes. Gonadal indices

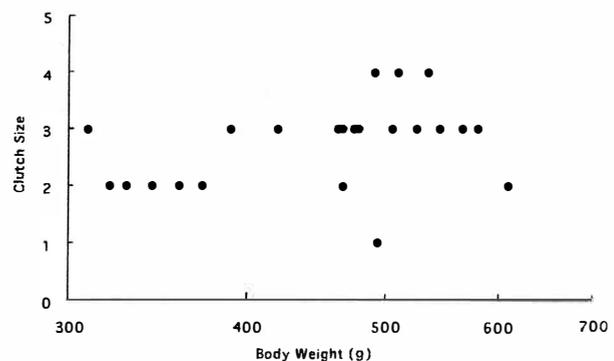


FIG. 4. Relationship between body size (represented by body weight in log scale) and clutch size of gravid female *Emydocephalus ijimae* from the central Ryukyus, Japan.

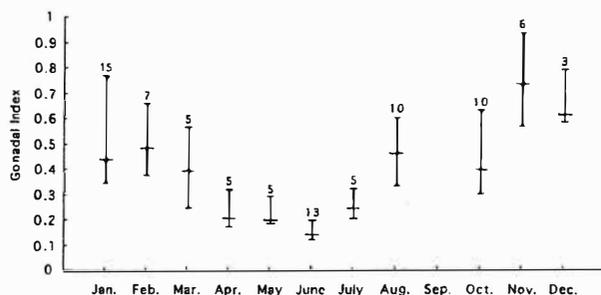


FIG. 5. Annual pattern of male gonadal index (percentage of body weight). Horizontal and vertical lines represent medians and ranges, respectively.

in October and January were slightly smaller than the values in August and February, respectively (Fig. 5).

Microscopic examinations of sections showed that the seminiferous tubules of testes were filled with sperm (characterized by distinct tails) in all adult males collected in December and three of the six adult males in November. In males collected from January to March, the seminiferous tubules also contained sperm but in decreasing densities. The tubules in all adult males from April to October and in the remaining three of the November males lacked sperm. Seminiferous tubules in all August and October males, as well as in the three November males that lacked sperm, were filled with dense spermatocytes and spermatids medially. In contrast, the tubules in adult males collected from April to July exhibited more or less prominent voids and many fewer cells in lumens.

#### APPEARANCE OF JUVENILES IN MONTHLY SAMPLES

Juveniles smaller than 400 mm (SVL) were collected only in the winter months of December and January. These samples included one and two juveniles whose respective SVLs did not reach 300 mm (i.e. 280 mm, and 280 and 297 mm; Fig. 2). These values are smaller than those of the well-developed embryos possessed by the two gravid November females (see above). They are within the range of SVLs of six neonates reported by Moriguchi (1991) and Uehara (1993) (266–342 mm; mean=301.5; SD=30.6).

## DISCUSSION

#### SEXUAL SIZE DIMORPHISM AND ANNUAL REPRODUCTIVE OUTPUTS

Greer (1997) listed the maximum SVL of *E. ijimae* as 750 mm. Our results, though, indicate that females of this species very often exceed 750 mm, and sometimes even reach 900 mm (Fig. 2). Heatwole (1999), on the other hand, suggested that there was no sexual size dimorphism (SSD) in *E. ijimae*. However, because the minimum (555 mm), mean (726.2 mm), and maximum (900 mm) SVLs in adult females were larger than in males (510 mm, 626.5 mm, and 745 mm; Fig. 2), it is obvious that this sea snake exhibits a SSD like the majority of other sea snake species (Heatwole, 1999; Fry et

al., 2001; Ineich & Laboute, 2002) or of snakes in general that have been studied to date (Shine, 1993).

For snakes, such SSD is often considered a consequence of selection that favours larger females due to their greater fecundity (review by Shine, 1993, 1994). Indeed, a majority of snakes – including more than two thirds of the marine species – are known to show statistically significant correlations between female body size and clutch size (Lemen & Voris, 1981; Seigel & Ford, 1987; Greer, 1997). In *E. ijimae*, however, no significant correlation was recognized between these variables. Moreover, of the adult females collected in June (a post-ovulation season), gravid individuals (SVL: mean=750.5 mm, 605–835 mm;  $n=10$ ) were even smaller than the non-gravid females (mean=810.0 mm, 765–885 mm;  $n=9$ ) (ANOVA:  $F=5.07$ ,  $P<0.05$ ). It is, therefore, likely that the observed SSD in the present species is not a direct consequence of selection for greater fecundity. Patterns of SSD in the other congeneric species, *E. annulatus*, remain uncertain, although Guinea (1996) mentioned that in one observed mating pair of this species the female was larger in SVL than the male. Since most other hydrophiine sea snakes – including a species of *Aipysurus* (the putative sister group of *Emydocephalus*: Voris, 1977; Rasmussen, 2002) – also have larger females (Heatwole, 1999; Burns & Heatwole, 2000), it is probable that the observed SSD in *E. ijimae* actually represents phylogenetic conservatism rather than the consequence of proximate selection (Shine, 1994). Further population studies, using the mark-recapture technique, are needed to verify this conclusion, especially by examining the influence of body size upon the survivorship of gravid females (Shine, 1993, 1994). Mark-recapture studies are also needed to clarify the proximate mechanisms responsible for the observed SSD (e.g. Burns & Heatwole, 2000).

Lemen & Voris (1981), based on the analyses of various reproductive parameters in hydrophiines and other marine snakes from Malaysia, recognized several reproductive patterns that are considered in the context of r- and K-selection. Such a divergence in the reproductive pattern seems to be prominent also in the hydrophiines of Australia (Ward, 2001; also see pertinent tables in Greer, 1997). The mean clutch size in gravid females of *E. ijimae* (2.74) is one of the smallest of the hydrophiines so far examined (Greer, 1997; Ward, 2001; Fry et al., 2001). Furthermore, considering that only 16 adult females (45.7%) out of 35 collected during the gestation period (i.e. from June to October: see below) were gravid, it is highly likely that an adult female reproduces biennially or even less frequently like a few other hydrophiine species (Burns, 1985; Ward, 2001). Thus, the mean annual reproductive output of an adult female *E. ijimae* seems to be even less than 1.4, and this suggests that this seasnake is a typical K-strategist. Mean relative reproductive effort per embryo (10.3%: sensu Lemen & Voris, 1981), calculated from data for two females and their neonates in Moriguchi (1991) and

Uehara (1993), is close to the highest known value for hydrophiines (10.9% for *Hydrophis fasciatus*: Lemen & Voris, 1981), and this further supports the hypothesis of *E. ijimae* being a K-strategist.

#### ANNUAL REPRODUCTIVE PATTERN IN FEMALES

Rapid reduction in mean length of the largest ovarian follicles from April to May, along with the complete absence of oviducal eggs in the April sample and their presence in a part of the May sample, indicates that ovulation commences in May. Furthermore, the presence of a non-gravid female with large ovarian follicles in the May sample – and the complete absence of such females in the June and subsequent samples – suggest that, in all females scheduled to breed in a given year, ovulation is completed no later than June (Fig. 3). On the other hand, the largest follicle lengths in non-gravid females are significantly greater in the February–April samples than in the June–August samples, with a very slight range overlap (ANOVA:  $F=17.68$ ,  $P<0.001$ ). This, as well as the absence of apparent differences in this variable between gravid and non-gravid females in each of the latter (Fig. 3), suggests that in spring, vitellogenesis in ovarian follicles occurs almost in all adult females, and that in non-reproductive females, vitellogenic follicles are subjected to yolk re-absorption, instead of ovulation, from April to June.

Aldridge (1979) recognized two seasonal patterns in the secondary vitellogenesis of ovarian follicles in temperate zone snakes: type I, as characterized by a rapid secondary vitellogenesis only in the spring; and type II, by commencement of secondary vitellogenesis shortly after ovulation. A seasonal pattern of secondary vitellogenesis in the central Ryukyu population of *E. ijimae*, illustrated by an increase in ovarian follicle length shortly after ovulation (i.e., in July: Fig. 3), seems to belong to type II. However, it differs from the typical type II pattern in lacking an apparent cessation of vitellogenesis during the cold season (from December to March: see Fig. 1), unlike many temperate zone terrestrial snakes (Aldridge, 1979) and another sea snake, *Aipysurus laevis*, from subtropical Australian waters (22°–22°10'S) (Burns, 1985). *Aipysurus laevis* studied by Burns (1985) also differs from *E. ijimae* of the central Ryukyus in showing a clear dichotomy of adult females into reproductive and non-reproductive individuals in a given year (indicated by a marked difference in the largest follicle length), more than one month before commencement of ovulation. Considering that nutrition condition usually plays a crucial role in the commencement or cessation of vitellogenesis in snakes (Aldridge, 1979; Saint Girons, 1982; Seigel & Ford, 1987), it is probable that the differences in vitellogenic patterns between the two subtropical reef-dwelling sea snakes may be attributable to differences in seasonal energetic patterns resulting from those in their feeding habits (Voris & Voris, 1983). Rapid increase of spawning by coral reef fishes with an increase in water

temperature in spring (Thresher, 1984) may account for the “delayed decision” regarding ovulation by female *E. ijimae*.

Our data, and those from the literature (Moriguchi, 1991; Uehara, 1993) indicate that in *E. ijimae* of the central Ryukyus parturition occurs from November to January. This, along with the timing of ovulation, suggests that the gestation period ranges from six to eight months. This value is similar to those estimated for other sea snakes also showing biennial or less frequent reproduction (*Aipysurus laevis*: six months; and *Hydrophis elegans*: seven months [Burns, 1985; Ward, 2001]), and is larger than those for sea snakes that reproduce annually (*Lapemis curtus*: five months; *Enhydrina schistosa*: three months [Voris & Jayne, 1979; Ward, 2001]), as well as for most terrestrial live-bearers (3–4 months: Shine, 1977; Tinkle & Gibbons, 1977). This may support the idea that a decrease in frequency of reproduction in some aquatic snakes involves an extension of gestation period, which necessitates a female having a long non-breeding interval after breeding to restore nutrition (e.g. Burns, 1985; Ward, 2001). In *E. ijimae*, however, the success of spring food intake may be crucial, as mentioned above, to the occurrence of an individual's ovulation in a given year, rather than the presence or absence of gestation in the preceding year.

#### ANNUAL REPRODUCTIVE PATTERN IN MALES

Spermatogenic cycles in male temperate snakes are usually classified into two types, post-nuptial and pre-nuptial, on the basis of timing of maximum spermatogenic activity in relation to the ovulation season (Volsoe, 1944). Of these, the post-nuptial type, showing testicular weight peak in autumn, is much more common than the pre-nuptial type in which maximum testis mass is achieved in early spring, just before ovulation in conspecific females (Seigel & Ford, 1987). In tropical snakes, on the other hand, spermatogenesis is generally aseasonal or essentially pre-nuptial (Saint Girons & Pfeffer, 1971; Fitch, 1982; Vitt, 1983), and Seigel & Ford (1987) doubted the presence of the post-nuptial tropical cycle.

Of the elapid sea snakes, members of *Ladicauda* so far studied, including subtropical East Asian populations of *L. semifasciata*, exhibited no significant seasonal variation in testis mass (Gorman *et al.*, 1981; Bacolod, 1983; Tu *et al.*, 1990). In contrast, testis mass in three hydrophiines from tropical waters (*Enhydrina schistosa* from Malaysia, and *Lapemis curtus* and *Hydrophis elegans* from northern Australia: Voris & Jayne, 1979; Ward, 2001) showed a typical pre-nuptial pattern with its peak appearing in 2–3 months before ovulation.

*Emydocephalus ijimae* from the subtropical Ryukyus showed a prominent seasonal variation in testis mass like these three tropical hydrophiines. Even so, the peak of testis mass in *E. ijimae* (November: Fig. 5) precedes ovulation (May to June: Fig. 3) by no less than six

months, suggesting that the spermatogenic pattern in this species is post-nuptial. Considering that the two northern Australian species showed the testis mass peak in May (a month corresponding to late autumn in the higher latitude of the Southern Hemisphere) and ovulation in August (late winter), it is probable that the annual reproductive pattern of *E. ijimae* has been formed under the influence of an extended cold season upon females as a result of dispersal from the tropical region to higher latitudes. This scenario is comparable to that hypothesized for the evolution of a seasonal reproductive pattern in some viperid snakes in North America (Aldridge & Duvall, 2002).

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