

Precocious maturation and semi-multivoltine lifecycle in a subtropical grass lizard, *Takydromus toyamai*

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Abstract

There are many short-lived animals, but those displaying a lifecycle with more than one generation per year (multivoltine lifecycle) are rare among terrestrial vertebrates. The multivoltine lifecycle requires rapid growth and maturation and a long active season. Thus, small lizards in humid tropical or subtropical areas are candidates for multivoltine lifecycles. To test this prediction, we conducted a capture-mark-recapture study of a subtropical grass lizard, *Takydromus toyamai*, endemic to Miyako Islands, Japan. Juveniles grew very quickly, averaging 0.3 mm/day in the warm season, and attained sexual maturity at 2.5 months post-hatching. The breeding season was very long, and hatchlings emerged from May to November. The prolonged breeding season and rapid growth to maturity allowed some individuals to produce a second generation in their first year. Estimates of hatching date from growth rates indicated that many females that hatched in May–June became gravid 76–120 days after hatching and 122–165 days after oviposition of the eggs from which they hatched. Analyses of juvenile survivorship and month of hatching suggest that nearly half of breeding adults were members of multivoltine generations, although the 2 generations were not discrete. The species is short-lived, with only 16% of individuals surviving beyond 12 months, and few individuals reproduced in a second year. We refer to this condition as a “semi-multivoltine lifecycle.” Individuals that hatch late in the season defer reproduction until the following year and become founders of the next season’s cohort. This putative advantage of late-hatching individuals may have driven the evolution of this lifecycle.

Key words: capture-mark-recapture, fast growth, Lacertidae, prolonged breeding season, short-lived, subtropical climate.

Life history traits of animals vary depending on many extrinsic factors, such as ambient temperature (Hart 2004; McNutt et al. 2019), precipitation (Lampo and Medialdea 1996; Madsen and Shine 1999), seasonality (Wikelski et al. 2000; Varpe 2017), and resource abundance (Tinney et al. 2001; Rubenstein and Wikelski 2003), as well as some intrinsic physiological factors. Age at maturity in relation to lifespan is one of the fundamental variables in life history traits, directly affecting individual fitness. There are two extremes in this respect: early maturation with fast growth and late maturation with slow growth (Stearns 1983; Promilow and Harvey 1990). The former strategy is generally related to high mortality rate under high predation pressure, by which selection favors individuals that allocate energy intake to near-term reproductive output, rather than to greater, but uncertain future success (Scharf et al. 2015). Early maturation is also associated with climate and seasonality: A prolonged warm, mesic season facilitates constant growth and rapid maturation in species. Thus, animals with this strategy tend to be found in tropical regions (Cabezas-Cartes et al. 2018; Žák et al. 2021).

Age at maturity is known to correlate with lifespan, which in turn correlates with body size (Speakman 2005; Healy et al. 2014). Therefore, species that mature quickly are more common among invertebrates than vertebrates. For example, many insects attain sexual maturity much less than a year.

Nonetheless, some vertebrates do mature in less than 1 year. Žák et al. (2021) reviewed lifespan and age to mature among ray-finned fishes and listed some 60 species in 13 orders that start reproduction earlier than 1 year, in addition to some 350 annual species of the killifish, in which adults spawn in ephemeral pools, and their eggs spend the harsh dry season lying dormant in the muddy bottom of dried-up pools. In the most extreme case, some schindleriid gobies start breeding at 1 or 2 months old (Kon and Yoshino 2002). Maturation within a few months is also known for many small mammals (rodents and voles) (e.g., Oh and Mori 1998; Lambin and Yoccoz 2001).

Such early maturation potentially allows animals to complete more than one generation per year, which is referred to as a multivoltine lifecycle (Southgate 1981; Corbet et al. 2006). One of the schindleriid gobies mentioned above was estimated to have up to 9 generations per year (Kon and Yoshino 2002). Many insects are also known to have multivoltine lifecycles, and some exhibit seasonal polymorphism, with plasticity in ecological, physiological, and/or morphological features between generations in different seasons (e.g., Shapiro 1976; Brakefield 1996; Larsdotter Mellström et al. 2010).

In reptiles, a few dozen species have been reported to exhibit maturation within several months after the hatching (Fitch 1973; Karsten et al. 2008). One is Labord’s chameleon,

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Furcifer labordi, in the tropical dry forest of Madagascar. This chameleon matures at less than 2 months after hatching (Karsten et al. 2008). However, all adults die before 6 months of age, and only dormant eggs remain to survive the dry season, as in most species of the killifish. Therefore, Labord's chameleon is univoltine, despite their rapid maturation. It is obvious that a species must mature in less than half a year to accomplish 2 generations per year, that is minimum requirement to be multivoltine. It is also considered that the species must not have long dormant phase, and thus live in a mild climate that allows the animal to be active for much of the year.

In this respect, we predict that small lizards in tropical rainforests or mesic subtropical regions may have multivoltine lifecycles, but for several reasons, no studies have explicitly demonstrated that. First, life history studies of tropical lizards are relatively few (Brown and Shine 2002). Second, although a study may reveal the presence of vitellogenic females year round like many previous studies (e.g., Mojica et al. 2003; Goldberg 2010), additional life history parameters must also be known, including growth rate, age at maturity, and incubation/gestation period, in order to document a multivoltine lifecycle. To verify the above prediction, we conducted a capture-mark-recapture (CMR) study on an insular species of humid subtropical grass lizard, *Takydromus toyamai*. The CMR method, in which each free ranging animal is uniquely marked and then recorded again with certain interval, is one of the most effective methods for collecting life history data at both population and individual levels. Detailed life history data have also been provided by this method in other *Takydromus* species (Takeishi 1987; Lin et al. 2020). Using CMR data over multiple years, our results provided evidence of a semi-multivoltine lifecycle, in which a considerable proportion of the population experiences 2 generations within a year, with precocious maturation. Life history traits of several species within the genus *Takydromus* have been reported (e.g., Takenaka 1980; Huang 1998; Du and Shou 2008; Norval et al. 2012; Lin et al. 2020), and we conclude with a discussion of how the semi-multivoltine lifecycle evolved in *T. toyamai*.

Materials and Methods

Study species and sites

Takydromus toyamai is endemic to the Miyako Islands Group of the Ryukyu Archipelago, Japan, and is listed as an endangered and critically endangered species in the International Union for Conservation of Nature and Natural Resources and Japanese Red Lists, respectively (Kidera and Ota 2017; Ministry of the Environment of Japan 2020). In our preliminary surveys, this species was found at many sites in central and western Miyakojima, although only one or a few individuals were found in most of these places, suggesting very low population densities. Takenaka (2014) and Kidera and Ota (2017) pointed out the recent severe population decline in this species, most probably due to predation by invasive species, land development, pesticide pollution, and illegal collection for pet trade. Nonetheless, we finally found several places where many individuals could be found through repeated field surveys since 2014 covering almost the entire area of the Miyako Islands Group, as well as taking a hint from sighting records of this species provided by local residents (Saiki et al. 2018; Toda and Takahashi 2018). We chose 2 sites in western Miyakojima for our field surveys, but we do not report

detailed locality information, to prevent the illegal collection of this protected grass lizard for the pet trade (Janssen and Shepherd 2019).

This species is usually found in grassy environments, including forest edges, abandoned agricultural fields, and areas surrounding villages (Saiki et al. 2018; Toda and Takahashi 2018). There is a report of predation on *T. toyamai* by the Ruddy Kingfisher, *Halcyon coromanda* (Uemura and Hamachi 2020). Predation by *Bubulcus ibis*, *Falco tinnunculus*, and *Lanius cristatus* have been reported to be an important source of mortality on a Taiwanese congener (Lin et al. 2017), and these birds are common in Miyakojima, so avian predation is assumed to be a major cause of mortality on *T. toyamai*. In addition, the Japanese weasel (*Mustela itatsi*), an introduced predator on Miyakojima, has been documented to preying upon *T. toyamai* (Kawauchi et al. 2018).

Miyakojima Island has a humid subtropical climate (average air temperatures of the hottest and lowest months are 28.9 °C in July and 18.3 °C in January) with monthly precipitation of 119.8–259.3 mm and total annual precipitation exceeding 2,000 mm (Japan Meteorological Agency 2020). The flat terrain of this island makes it easy to cultivate, and approximately 50% of the island's total area is in agriculture (Miyakojima City Office 2022). Secondary forests of broad-leaved trees and *Casuarina equisetifolia* remain along rock terraces of uplifted Quaternary limestones, and grassy environments beside such forests serve as important habitat for *T. toyamai*. We chose 2 different sites, Site A and Site B, near rock terraces, because relatively large numbers of grass lizards were found there. Site A is surrounded by secondary forest, park, and the garden of a social facility; Site B is surrounded by secondary forest, sugarcane fields, and a meadow with a cowshed.

We set 5 survey routes (2 in Site A and 3 in Site B) along grassy zones that grow between the forest edge and small roads or trails. Two survey routes in Site A are 120 m and 85 m in lengths and located along a secondary forest with approximately 5.9 hectares in area. Three survey routes in Site B are 138 m, 136 m, and 88 m in lengths and located along another secondary forest with approximately 9.2 hectares in area. The grasses at both study sites, mainly consisting of Gramineae and *Bidens pilosa*, were sometimes cut by local people for roadside maintenance or for pasture harvest, on an irregular basis. The grasses regrow very quickly, and the original grassy environment usually recovers within a few months after cutting.

CMR survey

The CMR survey of *T. toyamai* was conducted from June 2016 to December 2021. Initially, we conducted field surveys 1 or 2 nights per month along 2 routes at Site A and 1 route at Site B, during period from June 2016 to July 2017. This annual survey provided basic knowledge regarding recruitment and growth of individuals. However, we discovered even denser populations at Site B, and thus we initiated long-term CMR surveys there, to study survival and reproduction, in addition to growth and recruitment. CMR surveys along 3 routes at Site B were conducted 1 to 5 nights per month from March 2019 to December 2021. The surveys at Site A continued to be conducted until December 2021 but on an irregular basis. There were periods when public access to Miyakojima was almost closed due to COVID-19, and this sometimes compelled us to discontinue monthly surveys from August 2017

to February 2019. As a result, our field surveys occurred at intervals of 1 to 6 months during this period.

We conducted the classical transects survey with CMR (Lovich et al. 2012). For the census, we walked very slowly at night and searched for grass lizards sleeping on the grasses along the survey routes with the aid of a flashlight. All individuals encountered were captured by hand whenever possible and temporally held in plastic bags with small air holes and pieces of paper. The captured lizards were weighed to the nearest 0.01 g using an electronic balance, and their snout-vent lengths (SVL) and tail lengths (TL) were measured to the nearest 1 mm using a plastic ruler. In many species of squamate reptiles, including lacertid lizards, the male exhibits a hemipenial bulge in the base of tail (Norval et al. 2016; Lin et al. 2020). Sex was determined according to the presence or absence of that bulge. The females were checked for gravidity by abdominal palpation, and we counted the number of eggs when possible. Our preliminary survey showed that the smallest SVL at which females contained eggs was 46 mm, so individuals smaller than this size were tentatively treated as juveniles. The hemipenial bulge in males, as a secondary sexual character, could be recognized in individuals with SVL 46 mm or larger, and thus, individuals smaller than 46 mm were treated as juveniles in males as well. We recorded the numbers of bite scars, which typically remain as paired marks in the dorsal abdominal region of females after copulation (Sasai et al. 2016). We scored no, one, or more than one bite scar as representing low, medium, or high levels of reproductive activity, respectively. All individuals were uniquely marked by toe clipping and were released at the point of capture after processing. This marking method is commonly used for small lizards and has been shown to have little effect on survival and stress (Langkilde and Shine 2006; Perry et al. 2011). The data obtained from Site A and Site B were pooled for further analyses because of the sample size. SVL of both male and female showed no significant difference between the sites (Student *t*-test, $P > 0.05$).

Data analyses

Growth rates for SVL (mm/day) were calculated for individuals that were recaptured in successive monthly surveys (Table 1), using the formula of $SVL(t1) - SVL(t0) / \text{number of days}$, where $SVL(t0)$ is SVL of a lizard at a given capture and $SVL(t1)$ is its SVL at the capture in the next month. We used data from a single individual multiple times if the lizard was captured in more than 2 successive months. The average growth rates were calculated separately for 4 seasons (spring: March–May; summer: June–August; autumn: September–November; winter: December–February). The data from

different years were pooled in these calculations. We compared growth rates between juveniles and adults in each season and between the warm seasons (spring and summer) and the cool seasons (autumn and winter). For adults, we modeled the effects of climate variables and sex on individual growth rates using generalized linear mixed models. Growth rates were assessed by linear regression, and we used 4 variables as fixed effects (sex, temperature, precipitation, and $SVL(t0)$) and individual ID as random effects. Data for monthly averages of air temperature and precipitation were taken from Japan Meteorological Agency (2020). $SVL(t0)$ was included to assess the effect of size at initial capture, as growth rates are expected to decrease when approaching asymptotic size.

To estimate the lifespan of this species, the periods between the first and last captures were calculated for individuals that were recaptured once or more. For the individuals that were juveniles at the time of the first capture, the hatching date was estimated from the date of the first capture, SVL at that time, and the juvenile's growth rate obtained by the method described above. Saito (2023) reported incubation periods of this species as 40–50 days in captivity. We thus further estimated the date of oviposition by calculating back 45 days from the day of hatching.

We used the program MARK 9.0 (White and Burnham 1999) to estimate survival rate of the adult males and females. Since juveniles' life history parameters and capture rates would be different from those of adults, non-adult records were removed from the analysis. We fitted a full set of 16 Cormack-Jolly-Seber (CJS) models in which survival (ϕ) and recapture rates (p) were either held constant, varied between sexes, varied over time, or varied over time differently for each sex. We assessed the fits of the 16 CJS models by comparing their Akaike's Information Criterion (AICc) values.

Results of our field survey revealed that *T. toyamai* attains sexual maturity within a few months and that at least some females lay eggs in the year in which they hatch (see Results). To calculate the proportion of breeding females and males that hatched in the year of oviposition, we estimated the hatching month of the adult lizards based on capture–recapture records and SVL data. Males and females of adult size (regardless of whether or not the females were confirmed to be gravid) that were captured late in the breeding season (July to September) were classified into either the “precocious” group, which were estimated to have hatched in the spring of the same year, or the “overwintered” group, which had hatched in the previous year, based upon the capture–recapture records or on SVL (See Results for the threshold for SVL). Next, adult-sized males and females captured early in the breeding season (March to April) were classified into either summer/

Table 1. Average growth rates of juveniles, adult males, and adult females of *Takydromus toyamai* during the 4 seasons. The rate is indicated as mm/day in SVL. The scores were calculated for individuals that were recaptured in successive months. The data from different years were pooled before the calculations.

	Winter	Spring	Summer	Autumn
Juveniles	0.07 ± 0.04 (<i>n</i> = 13, 0–0.16)	0.29 ± 0.08 (<i>n</i> = 3, 0.18–0.36)	0.30 ± 0.08 (<i>n</i> = 61, 0.10–0.47)	0.17 ± 0.09 (<i>n</i> = 60, 0–0.37)
Males	0.01 ± 0.03 (<i>n</i> = 16, –0.03–0.06)	0.04 ± 0.05 (<i>n</i> = 9, 0–0.12)	0.05 ± 0.07 (<i>n</i> = 112, –0.10–0.30)	0.05 ± 0.08 (<i>n</i> = 35, –0.12–0.29)
Females	0.05 ± 0.06 (<i>n</i> = 11, 0–0.21)	0.05 ± 0.05 (<i>n</i> = 11, 0–0.18)	0.06 ± 0.07 (<i>n</i> = 70, –0.10–0.28)	0.06 ± 0.08 (<i>n</i> = 34, –0.11–0.29)

autumn-hatched or spring-hatched (or earlier) in the previous year, according to the capture-recapture records or SVL (see Results for details). These analyses were primarily based on data from Site B, from 2019 to 2021, because we conducted our surveys there during that period in almost every month without missing periods.

Results

Body size and growth

During the 5.5-year survey, 2694 records representing 1635 unique individuals were obtained over 46 monthly surveys. Of those, 934 were from Site A, and the remaining 1760 were from Site B. The number of captured individuals fluctuated on an annual cycle, being lowest in February and highest from July to September (Supplementary Figure S1). Adult individuals accounted for 1879 records, of which 1103 were males and 776 were females. The sex ratio was male-biased throughout most of the year. The combined sex ratio was 1.42:1 (male: female), which is significantly skewed toward males (Chi square test, $\chi^2 = 56.21$, $P < 0.05$).

On average, males had significantly larger SVL than females (Welch's t -test, $t = 1.98$, $P < 0.05$); the mean SVL was 55.1 ± 5.4 mm for males ($n = 560$), 54.3 ± 5.6 mm for females ($n = 397$). The maximum SVL was 71 mm in 1 male and 2 females. The smallest individuals ($n = 2$) were 25 mm in SVL, both at initial capture. These small individuals were considered to be recent hatchlings, because SVL of *T. toyamai* at hatching is reported to range from 24.57 mm to 25.92 mm (Mochida et al. 2013). In juveniles, the growth rate was much greater in the warm period than the cool period, and these rates were significantly larger than the adults in both periods (Wilcoxon rank sum test, $P < 0.05$; Table 1). Juveniles grew very quickly, and their mean growth rates in spring and summer were 0.30 mm/day. The growth rate of small juveniles, up to 40 mm, was 0.33 mm/day ($n = 29$) and was significantly higher than juveniles larger than 40 mm (0.28 mm/day, $n = 33$) (Welch's t -test, $t = 2.35$, $P < 0.05$). Growth rates during the warm season for males and females at the juvenile stage (< 46 mm in SVL), whose sexes were determined by subsequent recapture records, were 0.30 mm/day ($n = 24$) and 0.31 mm/day ($n = 29$), respectively, and the difference was not statistically significant (Welch's t -test, $t = -0.22$, $P > 0.05$). The growth rates of adults were significantly correlated with sex, temperature, and SVL(t_0) ($P < 0.05$). The growth rate of males was greater than that of females. Temperature had a significantly positive effect, and SVL(t_0) significantly negative effect on the growth rate.

Annual breeding cycle and clutch size

The smallest gravid female in this study was 47 mm, although a single female of 46 mm had been confirmed to be gravid in our preliminary survey. Reproduction in females followed an annual cycle. In monthly samples from March to August, approximately half of the females exhibited mating bite scars. The proportion began to decline from September and became low (9.7–26.5%) between October and February (Figure 1A). The proportion of gravid females increased from January and exceeded 40% from February through August. Almost no gravid females were recorded from October to December (Figure 1B).

The clutch size ranged from 1 to 3. Among 244 gravid females whose eggs could be accurately counted, 56 (23.0%)

had 1 egg, 182 (74.6%) had 2 eggs, and 6 (2.5%) had 3 eggs. The mean SVLs of females with 1, 2, or 3 eggs were 54.39 mm (range: 47–68 mm), 58.40 mm (49–71 mm), and 63.17 mm (60–67 mm), respectively, and those differences were statistically significant (Tukey test, $P < 0.05$). In the monthly comparison, the number of females with 2 eggs peaked in May–September (Supplementary Figure S2). However, a large proportion of females with one egg was recorded in September, and all gravid females from October to December bore one egg.

Annual cycle of demographic structure

Size distributions of captured lizards in monthly samples are shown in Figure 2. Juveniles of the smallest size class (< 30 mm in SVL) first appeared in May, indicating that recruitment of hatchlings began that month. Recruitment continued until November. Hatchlings < 30 mm did not appear from December to April, and the size of the smallest size class in these months increased to 41–45 mm until April. In May, the size distribution of the lizards was clearly bimodal, with the first peak consisting of recent hatchlings < 30 –35 mm in SVL and the second peak consisting of older lizards 51–65 mm. This suggests that yearlings (individuals overwintered after hatching) reach 51+ mm SVL by May of the second year, regardless of which month they hatched. This bimodal pattern, corresponding to new hatchlings and older individuals, was discernable until July, with the smaller peak becoming larger each month due to juveniles' growth. The size distribution became unimodal in August, as the smaller peak merged with the larger one.

In adult lizards less than 60 mm SVL, there was no bias in sex ratio during most months, whereas large lizards (> 60 mm) included a higher proportion of males. The total sex ratio of adult lizards less than 60 mm SVL and that for adult lizards > 60 mm SVL were 1.23:1 and 2.44:1 (male: female), respectively, and this difference was statistically significant (Fisher's exact test, $P < 0.05$). No significant sexual differences were found in growth rates at the juvenile stage nor in the recapture rate of adults (see result of CJS models below), suggesting that the observed bias in sex ratio is due to the shorter lifespan of the females.

Gravidity in the year of hatching

The surprisingly rapid growth of juveniles during the warm season (0.3 mm/day) allowed them to reach adult size within a few months. Of 92 individuals that were first captured as juveniles and then recaptured as adult females, 18 were confirmed to bear eggs in the same year that they hatched. For instance, individual B4034 was first captured as a juvenile and was 38 mm SVL on 23 June 2021. She was recaptured 33 days later (26 July 2021) as an egg-bearing female, at 52 mm SVL (Table 2). With an SVL much less than 51 mm on 23 June, this female clearly had hatched in the same year (see above). We calculated that she had hatched around 10 May, based on the average size at the hatching (25 mm) and her size at first capture (38 mm on 23 June), using a juveniles growth rate of 0.3 mm/day. We further estimate that the egg from which she hatched was laid around 26 March, assuming an incubation period of 45 days. Thus, this female was found to be gravid about 77 days after hatching and about 122 days after her own egg had been laid. The period from the time an egg was laid until the hatched individual was found to be gravid, for 18 females, (Table 2) was approximately 4–5 months (122–165

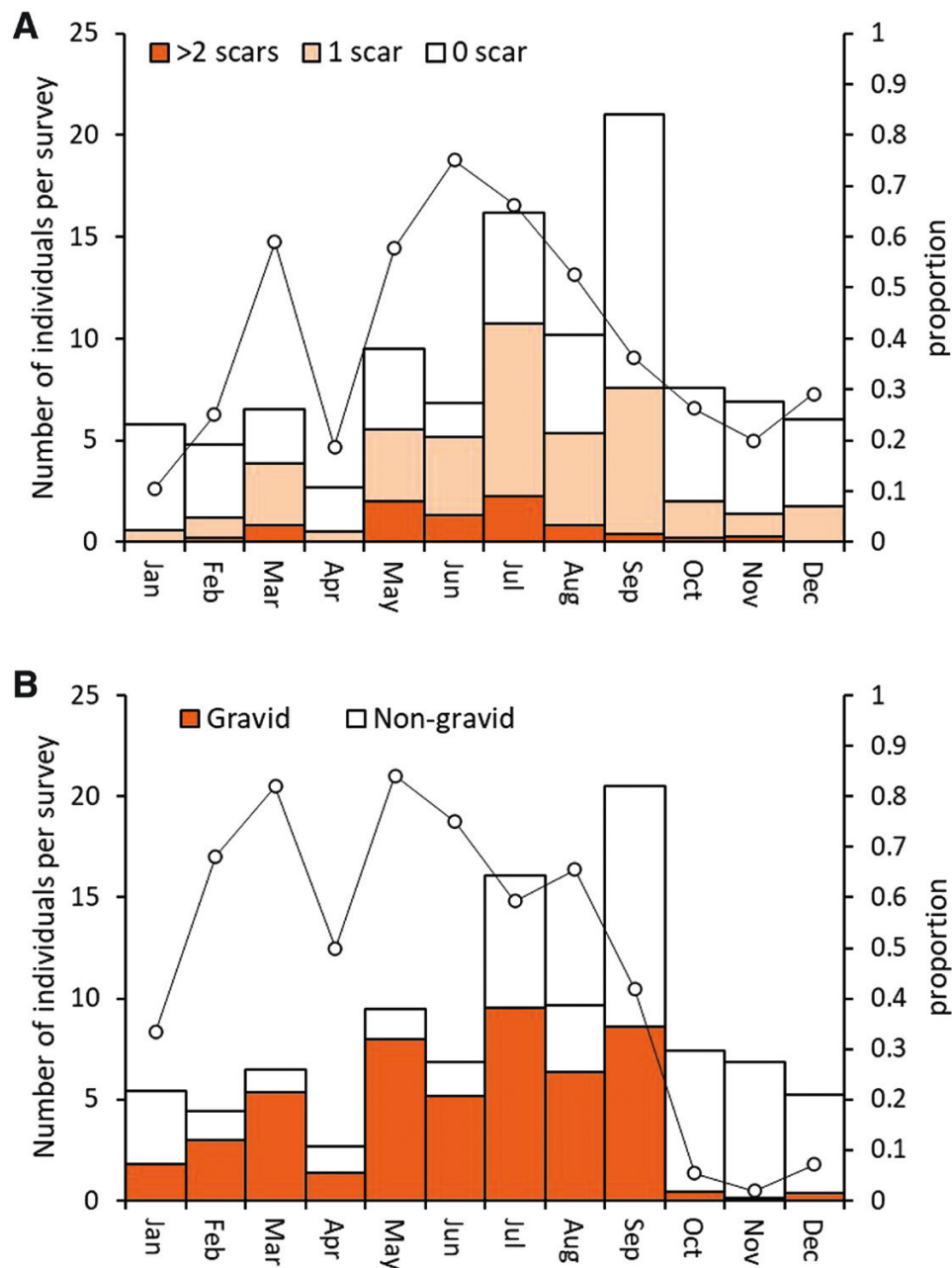


Figure 1. Annual cycle of (A) number and proportion of females with mating bite scars and (B) number and proportion of gravid females of *Takydromus toyamai* based on capture data from 2016 to 2021. The scores for each month are based on pooled data for the 6 years.

days). In addition, at least 34 out of 134 adult females that were recorded for the first time between July and October at less than 53 mm in SVL (indicating that they had hatched that year; see below) were also found to be gravid.

Short lifespan and semi-multivoltine lifecycle

Among the 574 individuals with one or more recapture records, only 52 (9.1%) were recaptured over 12 months after the first capture, and only 5 (0.9%) were recaptured over 24 months after the first capture. Twelve of the 574 recaptured lizards (2.1%) were recorded over 2 winters, and the longest capture interval was 32 months (970 days). Based on estimated hatching dates for 160 individuals that were juveniles at their first capture and were recaptured at least one time, 27 (16.9%) survived more than 12 months from the estimated

hatching dates, and only two (1.3%) survived more than 24 months (Figure 3).

The fit of the top 5 CJS models is shown in Table 3. In this analysis, the top 2 models were far better supported than the rest of the models, according to the AICc. The model $\phi(t)$, $p(t)$ was ranked most highly among the candidate models. In that model, survival and recapture were time-dependent. Estimated monthly survival rate during the breeding season (March to October, $\phi = 0.697 \pm 0.184$) was lower than during the non-breeding season (November to February, $\phi = 0.902 \pm 0.174$). In the other fitting model, $\phi(\text{sex})$, $p(t)$, survival was sex-dependent, and the probability of recapture was time-dependent; that is, survival of males was higher ($\phi = 0.825$, $\text{SE} = 0.012$) than survival of females ($\phi = 0.754$, $\text{SE} = 0.019$).

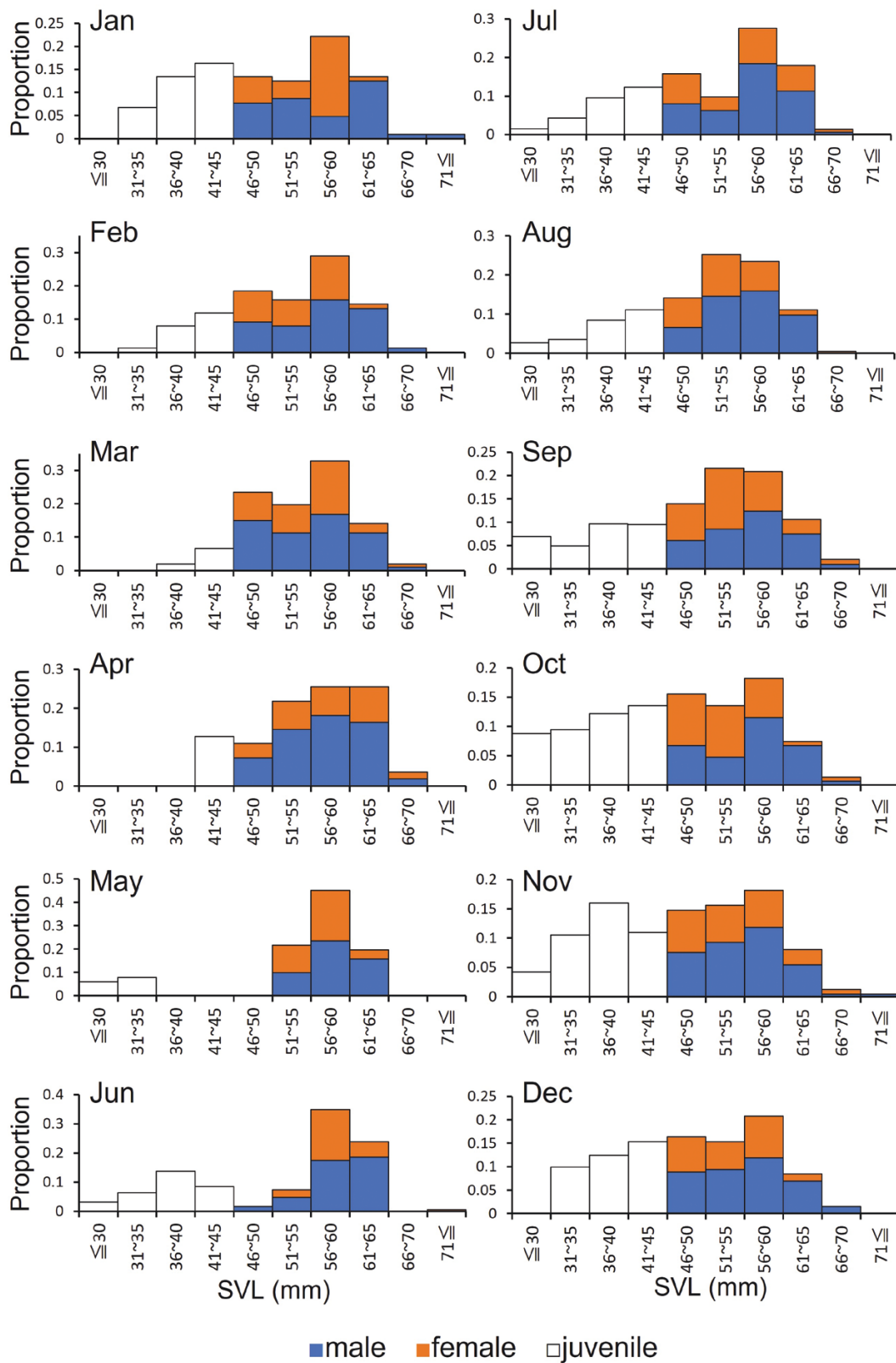


Figure 2. Body size distribution of captured lizards in each month based on the 6-year survey, from 2016 to 2021. The scores are based on pooled data for the 6 years. Note that lizards of both sexes smaller than 46 mm in SVL were tentatively considered to be juveniles (see text for details).

As spring-hatched individuals (hatched in April–June) begin laying eggs in July (Table 2), these individuals would typically spend up to 4 months of the breeding season as adults (July to October), and their survival rate for this period

was calculated as $0.6974^4 = 0.236$ based on the results of CJS analyses mentioned above. In contrast, summer-hatched individuals (hatched in July–August) would only spend the non-breeding season (November to February) as adults, and

Table 2. A list of the females that were recorded as gravid within the year in which they hatched. The hatching date was estimated from the date of first capture as juvenile, SVL at that time, and the average juvenile growth rate (0.3 mm/day). The date on which the egg was laid was estimated by tracing back 45 days, the standard incubation period (Saito, 2023), from the estimated hatching date.

	Estimated date of the egg laid	Estimated hatching date	The first captured as juvenile		The first record as gravid female			Estimated period from it was laid as an egg to becoming a gravid (days)
			Date	SVL (mm)	Date	SVL (mm)	No. eggs	
B1510	4-Mar-2020	18-Apr-2020	2-Jun-2020	38	10-Jul-2020	51	2	128
B1530	13-Mar-2020	27-Apr-2020	4-Jun-2020	36	11-Aug-2020	52	1	151
B3323	14-Mar-2017	28-Apr-2017	1-Jul-2017	44	27-Jul-2017	53	1+	135
B4044	16-Mar-2021	30-Apr-2021	23-Jun-2021	41	26-Jul-2021	51	2	132
B4240	18-Mar-2021	2-May-2021	25-Jun-2021	41	28-Jul-2021	53	2	132
B4054	19-Mar-2021	3-May-2021	23-Jun-2021	40	26-Jul-2021	53	1+	129
B5221	20-Mar-2020	4-May-2020	10-Jul-2020	45	11-Aug-2020	53	1+	144
A4510	21-Mar-2019	5-May-2019	24-Jun-2019	40	2-Sep-2019	51	1+	165
B4034	26-Mar-2021	10-May-2021	23-Jun-2021	38	26-Jul-2021	52	2	122
B5011	27-Mar-2020	11-May-2020	4-Jun-2020	32	13-Aug-2020	52	2	139
B5212	3-Apr-2020	18-May-2020	10-Jul-2020	41	11-Aug-2020	50	2	130
B3530	6-Apr-2017	21-May-2017	27-Jul-2017	45	18-Sep-2017	55	1	165
A4033	14-Apr-2019	29-May-2019	21-Jul-2019	41	2-Sep-2019	55	1	141
B4225	14-Apr-2019	29-May-2019	21-Jul-2019	41	8-Sep-2019	55	2	147
B4210	17-Apr-2019	1-Jun-2019	21-Jul-2019	40	2-Sep-2019	53	1	138
B4430	17-Apr-2019	1-Jun-2019	24-Jul-2019	41	2-Sep-2019	51	1	138
A4032	20-Apr-2019	4-Jun-2019	21-Jul-2019	39	2-Sep-2019	52	1	135
B3125	20-Apr-2019	4-Jun-2019	27-Jul-2019	41	2-Sep-2019	51	1	135

their survival rate until next breeding season should be much higher (simply calculated as $0.9024^4 = 0.662$). This suggests that the breeding population in the early period of the next breeding season would chiefly consist of individuals that hatched during the second half of the previous breeding season. To test this prediction, we examined the survivorship of individuals according to their month of hatching. Among the 65 individuals that were first captured as juveniles in May to July (the early season of recruitment) and recaptured at least once as females of mature size, only 8 (12.3%) were recaptured after the beginning of the next breeding season, in March. On the other hand, among 40 juveniles first captured in August to September (the middle season of recruitment) and 34 in October to November (the late season of recruitment), 17 (42.5%) and 16 (47.1%), respectively, were recaptured after the beginning of next breeding season. The differences in survivorship until the next season between individuals from early recruitment and those from middle or late recruitment were statistically significant (Fisher's exact test, $P < 0.05$).

We also examined the proportions of “precocious” adults that were estimated to have hatched in the spring of the same year and “overwintered” adults that had hatched in the previous year, by tracing back to their hatched month or year. In the late breeding season (July to September), the hatching month of recaptured adult lizards could be estimated from capture-recapture records. For lizards without sufficient capture-recapture records, separation of cohorts by the threshold of 53 mm SVL is effective, as SVL distribution until July is bimodal, bordering the 51–55 mm size class (Figure 2). Our recapture data indicated that all individuals that hatched in the previous year (except one extremely small male of 52 mm

SVL) reached 54 mm or more in females and 55 mm or more in males by July of the second year. For 83 recaptured females that were recorded in the late breeding season, 39 were estimated to have hatched in the same year, and 44 had hatched in the previous year. In addition, among 99 adult females that had not been recaptured, 53 were estimated to have hatched in the same year and 46 in the previous year. Thus, in total, among 182 adult females captured during the late breeding season, 92 (50.5%) were estimated to be precocious, and 90 (49.5%) had overwintered. For 87 recaptured males that were recorded during the late breeding season, 27 were estimated to have hatched in the same year and 60 in the previous year. Among 114 adult males that had not been recaptured, 50 were estimated to have hatched in the same year and 64 in the previous year. Thus, in total, among 201 adult males captured during the late breeding season, 77 (38.3%) were precocious and the remaining 124 (61.7%) had overwintered. In summary, about 40–50% of the breeding lizards in the late breeding season had hatched in the spring of the same year.

Adult lizards recorded during the early breeding season (March to April) were classified into either summer–autumn-hatched or spring-hatched (or earlier) in the previous year, according to their capture-recapture records. For the lizards with insufficient capture-recapture records, separation of cohorts divided by the threshold of 54 mm SVL was used, as all females and males hatched in the spring of the previous year reached 55 mm by March. Of the adult females that were recaptured during the early breeding season, 7 were estimated to have hatched in the summer–autumn months of the previous year and 9 in the spring months of the previous year or earlier. Of the adult females without any recapture records, 10 were estimated to have hatched in summer–autumn of the

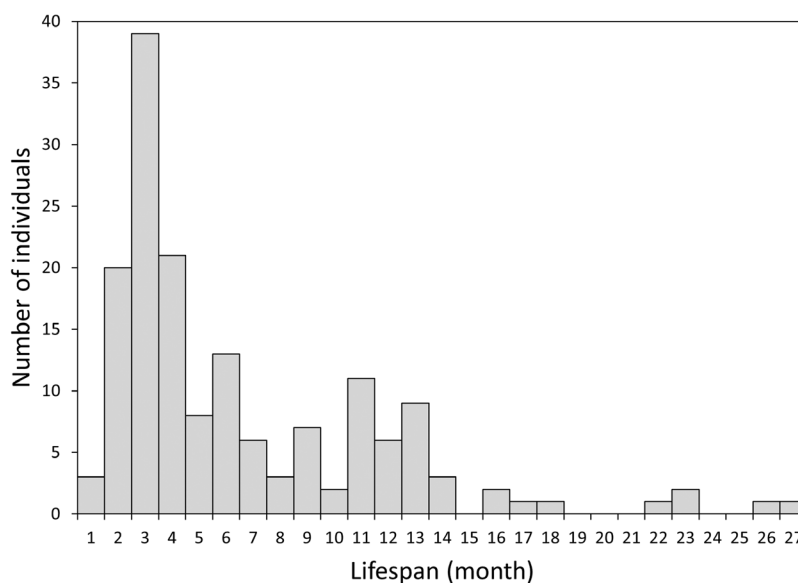


Figure 3. Estimated lifespan of 160 individuals that were first captured as juveniles and recaptured at least once. The hatching date was estimated by back-calculating from the SVL at first capture as a juvenile, applying the average growth rate of juveniles in each season (Table 1). Lifespan is the period from the estimated hatching date to the date of last recapture. Note that the small numbers of individuals in the “1 month” and “2 months” categories reflect that very young juveniles, immediately after hatching, were rarely collected.

Table 3. Model selection of candidate models to estimate survival (ϕ) and recapture rate (p) for adults of *Takydromus toyamai*.

	AICc	Δ AICc	Weight	Likelihood	Parameters	Deviance
$\phi(t) p(t)$	2,236.033	0.000	0.530	1.000	51	872.102
$\phi(\text{sex}) p(t)$	2,236.295	0.262	0.465	0.888	28	922.512
$\phi(.) p(t)$	2,246.377	10.344	0.003	0.006	27	934.717
$\phi(\text{sex}) p(\text{sex} \times t)$	2,247.553	11.520	0.002	0.003	54	876.891
$\phi(t) p(\text{sex} \times t)$	2,258.625	22.592	0.000	0.000	77	834.816

sex: males and females; t = month; $.$ = constant.

previous year and 10 in the spring of the previous year. Thus, almost half of the adult females (17 females, 47.2%) in the early breeding season were estimated to be summer–autumn-hatched. For the males that were recaptured during the early breeding season, 11 were estimated to have hatched in summer–autumn of the previous year and 13 in the spring of the previous year or earlier. For the males without any recapture records, 19 were estimated to have hatched in the summer–autumn of the previous year and 21 in the spring of the previous year. A total of 30 adult males (46.9%) recorded during the early breeding season were estimated to have hatched in summer–autumn in the previous year. Together, our analyses show that nearly half of the adult lizards in the early breeding season hatched during the summer–autumn months of the previous year, and almost half of the adult lizards in the late breeding season had hatched during the spring months of the same year, corroborating that a large proportion of lizards are involved in a 2-generation lifecycle within a single year.

Discussion

Our investigation clarified the life history traits of the subtropical grass lizard *T. toyamai*, from both the individual and population perspectives. First, the lifecycle of this species is

extremely fast. It is clear from the CMR records that juveniles of *T. toyamai* grow very quickly, at 0.3 mm/day in the warm season (Table 1). Second, this species has a prolonged breeding season, and thus also a prolonged period of juvenile recruitment, from May to November, although recruitment ceases during the remaining 5 months. Third, the rapid growth of juveniles and the prolonged recruitment period allow some females that hatch in the spring to produce a second generation within the same year. Fourth, analyses of the survivorship of juveniles during both the early and the middle–late recruitment periods and estimation of the hatching months of breeding adults suggested that nearly half of breeding adults are involved in a lifecycle with 2 generations per year. Nonetheless, the 2 generations are not completely separate, unlike a typical multivoltine lifecycle in invertebrates, in which individuals belonging to successive generations do not overlap in time. Female *T. toyamai* have been reported to produce multiple clutches within a single reproductive season under captive conditions (Saito 2023). Considering that the lizards occasionally survived more than 1 year, and thus a number of females can reproduce for the entire breeding season, or even 2 successive seasons, they are not obligately involved in the multivoltine lifecycle. We here refer to this mixed condition as a “semi-multivoltine” lifecycle (Figure 4).

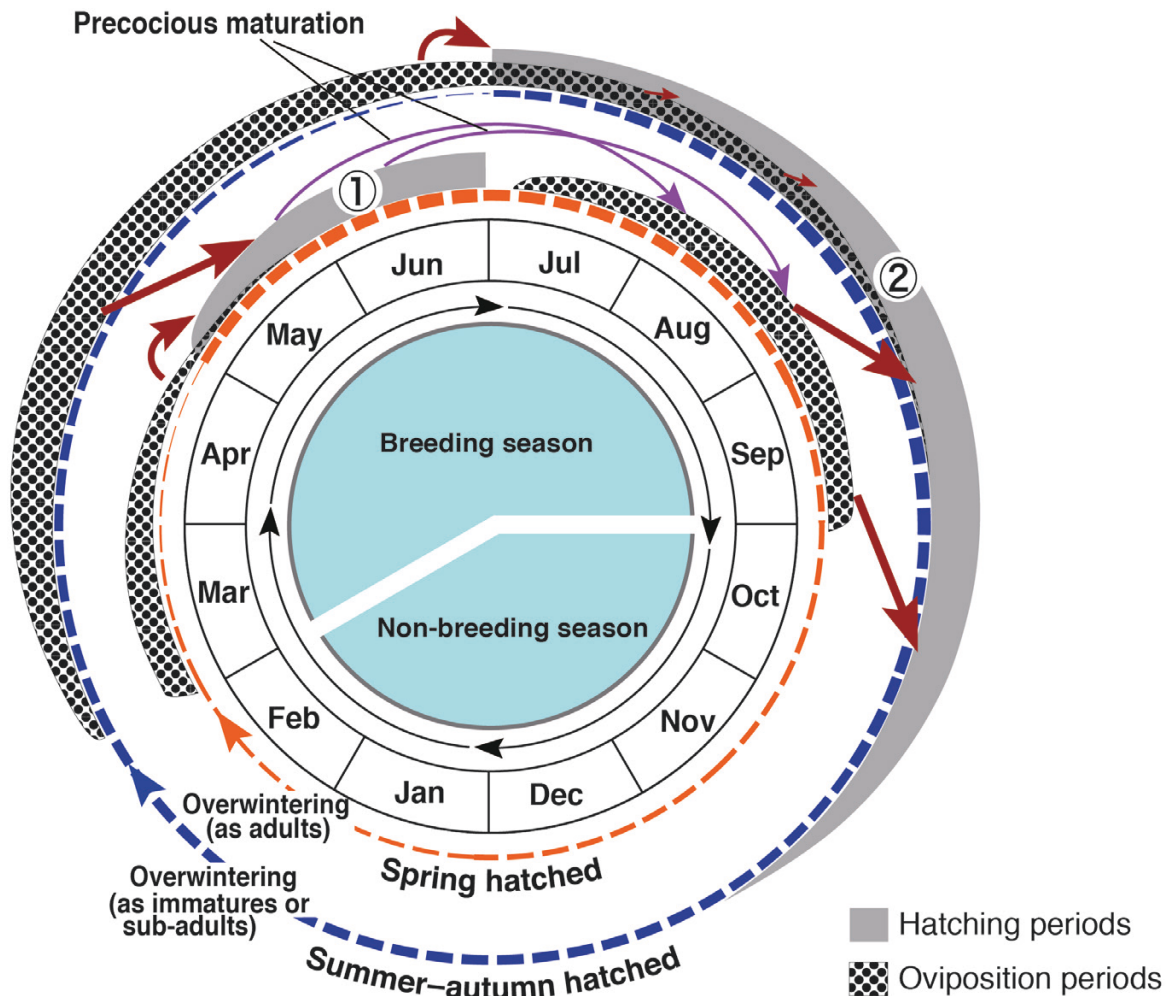


Figure 4. A schematic explanation of the semi-multivoltine lifecycle of *Takydromus toyamai*. The dashed orange line and dashed blue line indicate life histories of spring-hatched and summer-autumn-hatched individuals, respectively. The narrowing of the orange and blue dashed lines indicates possible decrease in numbers of individuals through natural mortality. The gray and dotted areas along the orange and blue dashed lines indicate putative hatching and oviposition periods, respectively, and their width indicates relative abundance of hatched individuals or laying individuals. Note that the long duration of the oviposition period in the summer-autumn-hatched group reflects the long period of hatching and recruitment. The summer-hatched lizards seldom survive until mid-summer of the next year. On the other hand, autumn-hatched lizards typically defer oviposition until April of the next breeding season or later and have a higher probability of survival until mid-summer. Red arrows crossing between the inner and outer circles indicate multivoltine lifecycles.

Labord's chameleon in Madagascar is a fast-maturing lizard but has univoltine life cycle as we mentioned earlier (Karsten et al. 2008). Another short-lived lizard is the Mexican high-elevation phrynosomatid *Sceloporus bicanthalis*. This small lizard is semelparous, and the mean generation time was reported to be 7 months (Rodríguez-Romero et al. 2011), but the authors did not comment on age at maturity and the possibility of multiple generations per year. Some tropical Costa Rican lizards reportedly reach size at maturity within a few months after hatching, and they are reproductively active all year in tropical rainforest (Fitch 1973). Thus, they are likely to produce more than one generation per year, although there is no direct evidence of that. Technically, voltinism refers to the number of generations per year (Corbet et al. 2006). Therefore, a rapid generation cycle independent of the annual seasonal cycle, if applied to any of the Fitch's (1973) Costa Rican lizards that may complete more than one generation in less than 12 months, is somewhat mismatched with this concept. Therefore, to the best of our knowledge, this study

represents the first demonstrated case of a semi-multivoltine lifecycle in a lizard living under a seasonal climate.

Compared with other lacertid lizards studied to date, the growth rate of juvenile *T. toyamai* is very fast and is comparable to another subtropical species, *T. viridipunctatus*, which occurs in Taiwan (Table 4; Lin et al. 2020). The life history of the latter species was studied in detail by Lin et al. (2020), and they demonstrated a long period of recruitment, from July to November, but did not mention instances where individuals bred within the same year in which they had hatched. In *T. toyamai*, the proportion of females with mating bite scars begins to increase in February, and the proportion of gravid females begins to increase in March (Figure 1). Recruitment is first observed in May and ends in November (Figure 2), indicating that the breeding season is 2 months longer than that of *T. viridipunctatus*. Compared to Lin et al.'s (2020) study site in northern Taiwan, the temperature in Miyakojima Island is 1.5–2 °C higher in the early spring (February–May) (Japan Meteorological Agency 2020). This warmer climate

Table 4. Growth rates of juvenile lacertid lizards studied to date.

Species	Growth rate (mm/day)	Notes	Reference
<i>Takydromus toyamai</i>	0.3		This study
<i>T. tachydromoides</i>	0.11/0.15	Hatchlings/yearlings	Takeishi (1987)
<i>T. tachydromoides</i>	0.06–0.22		Takenaka (1980)
<i>T. smaragdinus</i>	0.2		Takenaka (1981)
<i>T. viridipunctatus</i>	0.3		Lin et al. (2020)
<i>T. septentrionalis</i>	0.03	Data for a yearling in captivity	Ji et al. (1993)
<i>Podarcis muralis</i>	0.157–0.198	Data for first 20 days after hatching	Brana and Ji (2000)
<i>P. bocagei</i>	0.186/0.142	Juveniles of males/females	Galán (1999)
<i>P. lilfordi</i>	0.066/0.027	Hatchlings/yearlings	Rotger et al. (2016)

allows *T. toyamai* to begin breeding earlier and to grow over a longer period, which may have facilitated evolution of the semi-multivoltine lifecycle. Other a few species of Lacertidae, such as *Psammotromus hispanicus* and *Ichnotropis squamulosa*, are also known to grow fast considerably and have short lifespans, but they do not achieve multiple generations within a year due to shorter summer (e.g., Jacobsen 1987; Carretero and Llorente 1991; Carretero 1992).

It is well known that some multivoltine species of invertebrates show seasonal polymorphism in their ecological and morphological traits (e.g., Shapiro 1976; Brakefield 1996; Larsdotter Mellström et al. 2010). Although the 2 generations are not separated completely in *T. toyamai*, differences in the month of hatching appear to cause differences the resultant life history pattern (Figure 4). Our data suggest that lizards that hatch in spring enjoy more rapid growth during the spring and summer months, as well as precocious breeding within the year (Table 2). Lizards that hatch in summer also grow rapidly during the late summer, but they defer breeding until the beginning of the next breeding season. Lizards that hatch in autumn grow relatively slowly during autumn and winter and attain reproductive size by the following April, when they initiate reproduction. In univoltine species in general, individuals that hatch in spring may enjoy advantages in intraspecific competition due to greater hatching success, better post-hatching survival, and/or larger body size (Olsson and Shine 1997; Uller and Olsson 2010). In the case of *T. toyamai*, the summer–autumn-hatched lizards may incur an advantage by having a higher probability of becoming the founders of a cohort in the following year, due to the lower survival rate of the spring-hatched lizards until the next breeding season. The mild climate allows the summer–autumn-hatched lizards to grow moderately even in winter, and the higher survival rate during the non-breeding season may afford a benefit in becoming founders in the next breeding season. These possible advantages of the summer–autumn-hatched individuals are considered to have driven the evolution of the semi-multivoltine lifecycle in this species. The existence of a non-breeding season in the subtropical climate on Miyakojima may have hastened the onset of breeding in *T. toyamai* because selection would favor females that lay as many clutches as possible within a breeding season, given the relatively low survival rate of individuals until the following season.

It has repeatedly been pointed out that seasonality may also influence the quality and quantity of progeny evolutionarily (e.g., Nussbaum 1981; Williamson and Bull 1995; Mitchell et al. 2018). Although the clutch size of *T. toyamai*

was most frequently 2, as in *T. viridipunctatus* (Lin et al. 2020), the proportion of females bearing one egg increased from September to winter (Supplementary Figure S2). Small rodents with multivoltine lifecycles regulate the quality and quantity of their progeny to adjust to seasonally different demands, with more frequent litters in spring and larger litters in autumn (Dobson and Myers 1989). *Takydromus toyamai* may produce higher quality offspring by reducing clutch size in autumn, or the smaller clutches may simply reflect insufficient caloric intake to produce 2 eggs in autumn. Laboratory studies of *T. septentrionalis* indicated that clutch size late in the breeding season is smaller than the earlier clutches, even when the lizards are fed ad libitum (Ji et al. 2007; Du and Shou 2008). In a population of *T. septentrionalis* in East China that experiences a seasonally fluctuating climate, there is also a seasonal shift in egg size, suggesting that they regulate not only egg quantity but also egg quality (Ji et al. 2007). With respect to clutch size in *T. toyamai*, the hypotheses mentioned above should be tested by examining whether a correlation exists between the quality of the eggs (and offspring) and clutch size.

T. toyamai is short-lived, with only 16% of individuals surviving over 12 months, implying that there is little overlap of generations from year to year. Although the semi-multivoltine lifecycle might reduce the impact of this circumstance (Figure 4), there is no doubt that the breeding population in early spring consists almost entirely of individuals that hatched in the previous year and successfully overwintered. That means that a reduction in the number of individuals that overwinter in any given year may pose a risk of severe population decline. Participation in breeding by the second generation in the last half of the breeding season is believed to play an important role in generating a sufficient number of overwintering lizards to establish a new cohort the following year. Thus, the semi-multivoltine lifecycle of *T. toyamai* may have contributed to the persistence of local populations and is important from a conservation perspective.

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Authors' Contributions

All authors contributed to funding, project design, field work, and manuscript writing. H.A. carried out data analysis.

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Conflict of Interest

None declared.

Ethics Statement

Handling of animals in this study was conducted under permission from the Japan Ministry of the Environment, the Okinawa Prefectural Board of Education, and the Environment Policy Division of the Miyakojima City Government.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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