Volume 33 (October 2023), 115–118

Herpetological Journal

SHORT NOTE

https://doi.org/10.33256/33.4.115118

Published by the British Herpetological Society

Intensive and efficient egg-laying tempo of the parthenogenesis mourning gecko *Lepidodactylus lugubris*

Tsui-Wen Li[1], Jhan-Wei Lin[2] & Si-Min Lin[1]

[1]School of Life Science, National Taiwan Normal University, No. 88, Sec. 4, Tingzhou Rd., Taipei, Taiwan

[2]Department of Biology, National Museum of Natural Science, No. 1, Guanqian Rd., Taichung, Taiwan

Although suffered from many evolutionary disadvantages, asexual species benefit from their high efficiency to build clonal populations in a novel habitat. Here we report that a parthenogenetic mourning gecko *Lepidodactylus lugubris* continuously laid 12 clutches within two years. The egg-laying period lasted from mid-April to late October, and the egg-laying interval ranged between 24 and 73 days with a mean of 34.4 days. Referring to this fecundity, a female gecko could reproduce up to 24 clonal female offspring every year, and expand the population size in an efficient way much faster than most bisexual species. The intensive and efficient egg-laying tempo, associated with the parthenogenetic breeding mode, are crucial factors which facilitated their successful colonisation into many islands.

Keywords: clonal population, cost of sex, invariant clutch size, invasive species

From a long-term aspect, parthenogenetic species were regarded as an evolutionary deadend (Burt, 2000; Barraclough et al., 2003). Asexual species usually suffered from many disadvantages such as losing the opportunity of recombination, lack of the ability to adapt fluctuating environment and accumulation of deleterious mutations (Normark et al., 2003; Otto, 2009). However, asexual species are free from the "cost of sex" (Maynard Smith, 1971; Lehtonen et al., 2012). In addition to the advantages of saving time and energy in courtship behaviours, a straightforward benefit is the two-fold breeding efficiency because only daughters are produced. This advantage facilitates their clonal colonisation to new environments, especially on the islands (Baker, 1955; Cuellar, 1977; Ineich, 1999).

The mourning gecko *Lepidodactylus lugubris* (Duméril & Bibron, 1836) is the most well-known parthenogenetic Squamata which has increasingly expanded its range during the last century. This gecko was deduced to have a hybrid origin, while the central Micronesia is where two putative parental species overlap their distributional ranges (Radtkey et al., 1995; Ineich, 1999; Karin et al., 2021). It has been reported from multiple tropical and subtropical countries; most of which were colonised in recent years. For example, the species has reached several central and south American countries (Nania et al., 2020) during the last decades, established new invasive populations in Thailand (Lapwong & Juthong, 2018), and is continuing to spread (Hoogmoed & Avila-Pires, 2015). In the islands off the coast of east Asia (except the endemic populations on Daito islands), populations of *L. lugubris* occurred after WWII, including islands of Taiwan, Ryukyu and adjacent islets (Yamashiro et al., 2000; Ota et al., 2004; Lee et al., 2019).

Figure 1. The mourning gecko *Lepidodactylus lugubris* collected from Guishan Island in this study, photographed in 2021.

The breeding ecology of *L. lugubris* has been studied in different aspects. For example, Brown & Murphy-Walker (1996), Yamashira & Ota (1998) and Röll & von

Correspondence: Si-Min Lin (lizard.dna@gmail.com)

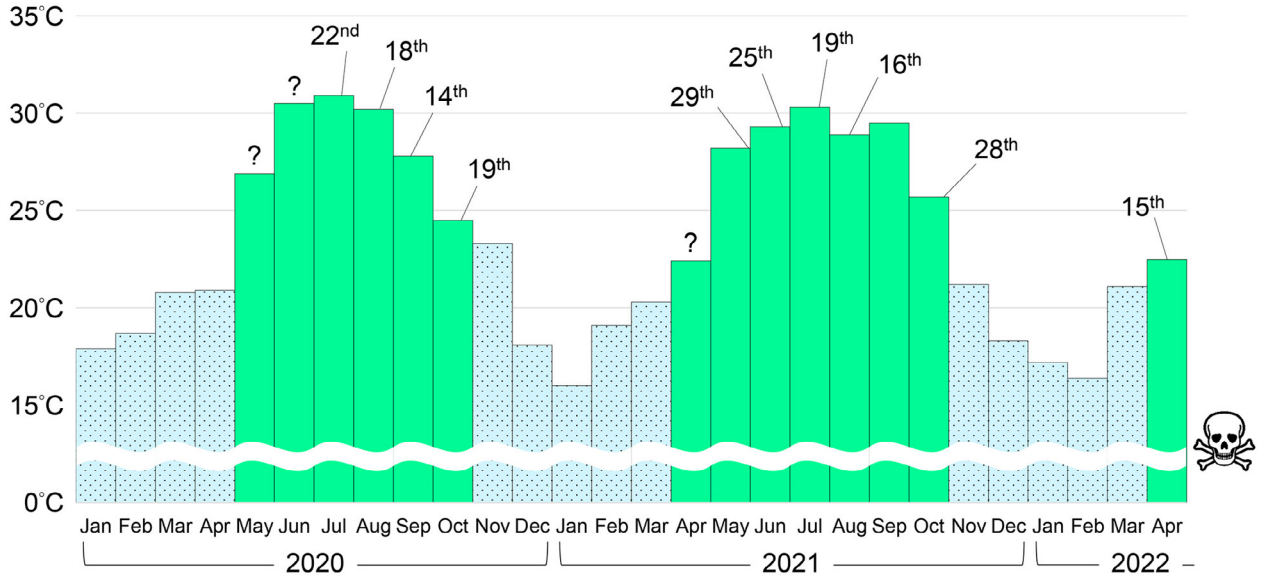

Figure 2. Month and date of the thirteen clutches produced by a young captive mourning gecko *Lepidodactylus lugubris* from 2020–2022. The green bars indicate the potential breeding season in Taiwan, and the question marks indicate that the date of the clutch were not confirmed. The gecko died of dystocia (egg-binding) on the last clutch on 15 April 2022.

Düring (2008) reported the rare cases of sterile males in this species. Brown & Sakai (1988) compared the impact of social experience on egg development; and Brown & O'Brien (1993) further compared the growth rate and fecundity of dominant versus subordinate females. The hatching success was evaluated under the influence of temperature and salty water (Brown & Duffy, 1992; Ota, 1994). In recent years, this gecko is further applied as a model species which contributes to a variety of fields of embryological research, including developmental morphology, sexual development or clutch size variation (Griffing et al., 2019a; 2019b; Sakai, 2021). However, most of these experiments were conducted in Hawaii or Okinawa, and their fecundity in other subtropical regions has never been studied.

Here we report a case of a captive mourning gecko which laid 12 clutches (24 eggs) within 2 years. This record helps to roughly estimate the fecundity of this parthenogenetic species under a subtropical environment.The young *L. lugubris* (snout-vent length = 24.6 mm; Fig. 1) was collected on 14 July 2019 from Guishan island (24.84167 N, 121.95315 E) (research permission No. 1110072285). Based on measurements from Brown & O'Brien (1993), the mean snout-vent length of newly hatched *L. lugubris* is 18.7 mm, and the growth rate is 3 mm per month in the first two months. Therefore, the gecko was deduced to be less than two months old which was hatched during middle to late May of 2019.

The individual was transferred to the laboratory in National Taiwan Normal University (25.00678 N, 121.53564 E) in Taipei and was kept in an acrylic enclosure (30 × 15 × 20 cm). The floor of the enclosure was covered with 2 cm of humic soil mixed with coco chip and coco fibre, and a pottery pot was provided as shelter. Because we did not use an air conditioner in the enclosure which housed the gecko, the room temperature and humidity were identical to the outdoor ambient environment with light and dark cycles following natural conditions. The climate of Taipei City (the captive site) and Guishan Island (the collection site) represented congruent temperature fluctuation (open data from the Central Weather Bureau, Taiwan; 2019–2022). In the breeding season, four to five newly hatched crickets *Gryllus bimaculatus* or cockroaches *Shelfordella lateralis* (mean mass = 0.0218 g each) were consumed every day, with calcium and vitamins provided once a week. Collection and husbandry of the gecko was approved by Institutional Animal Care and Use Committee (IACUC) of National Taiwan Normal University (license No. 110038).

The individual reached sexual maturity (> 40 mm snout-vent length) in spring of 2020 and laid the first and second clutches (both 2 eggs) in May and June, respectively. Since July, we started to record the precise egg-laying date. During 2020–2021, it produced 12 clutches (Fig. 2); 6 clutches per year and 2 eggs per clutch. Under the climate of Taipei, the egg-laying period lasted from mid-April to late October, only in months when the mean temperature was higher than 22.4 °C. The egg-laying interval (N = 7) ranged between 24 and 73 days, with a mean of 34.4 days. Among these eggs, two clutches hatched in 2020, but others failed because we did not maintain enough moisture in the enclosure. On 15 April 2022 the gecko died during its 13th clutch from dystocia (egg-binding).

As a member of Gekkonidae, *L. lugubris* exhibits an invariant clutch size (ICS): usually two eggs are laid in each clutch (occasionally one in some cases), which is a common phenomenon in the Gekkonidae, *Anolis* spp., some skinks and some *Takydromus* lizards (Kluge, 1967; Andrews & Rand, 1974; Shine & Greer, 1991; Vitt

& Caldwell, 2014; Lin et al., 2020). In these cases, the lizards could compensate their fitness by producing repetitive and continuous clutches, as shown from this gecko.

Based on records in Hawaii, the time for egg development (the period from eggs > 1 mm to the egg-laying day) was usually 25–26 days (Brown & Sakai, 1988). However, the inter-clutch interval was more than 40 days (Brown & O'Brien, 1993). In this study, we did not record the egg development period; whereas the inter-clutch interval could be as short as 24 days, and more frequently to be 27 to 28 days (N = 4). Compared to Hawaii, the climate of northern Taiwan represents a much higher temperature oscillation among seasons, i.e. a hotter temperature in summers (mean maximum temperature 34 °C vs. 30 °C in July), and a cooler temperature in winters (mean minimum temperature 14 °C vs. 20 °C in January) (data source: https://tw.weatherspark.com/). In two previous works, Ota (1994) and Sakai (2016) indicated the temperature limitation of egg development in cooler climate condition. This might explain why the mourning gecko in Taiwan was not able to breed all year round. We suspect that the high seasonal variation in Taiwan might shrink the breeding season of the gecko, and the higher temperature in summer may accelerate the development of the eggs in the females' body.

Because *L. lugubris* could reach reproductive age in the second year (Brown & O'Brien, 1993; this study), they have the potential to build a clonal population soon after they arrive in a new habitat. In order to provide a simplified speculation on how fecund a parthenogenetic gecko could be, we estimated the upper bound of the gecko (although it could not be reached in a realistic situation). Assuming the most extreme situation that all the eggs successfully hatched and all offspring successfully survived, two females could expand the population size to 26 in the second year, and reach 338 in the third year. At the same time, a pair of bisexual gecko with the same fecundity (6 clutches per year) could only reach the population size of 98; only half of them are females if the sex ratio of the species is 1:1.

As one of several fastest spreading geckos in the world, the occurrence of *L. lugubris* in many tropical and subtropical regions seems inevitable. We conclude that the intensive and efficient egg-laying tempo, associated with the parthenogenetic breeding mode, have facilitated the colonisation of this gecko in many tropical and subtropical islands. Although suffered from many disadvantages under a long-term evolutionary aspect, the asexual breeding system has undoubtedly acquired advantages in this age with frequent human-mediated dispersal events.

ACKNOWLEDGEMENTS

This work was funded by Ministry of Science and Technology, Taiwan (MOST 110-2311-B-178-001-MY3). Thanks to Chung-Wei You for the photograph in Figure 1.

REFERENCES

Andrews, R. & Rand, A.S. (1974). Reproductive effort in anoline lizards. *Ecology* 55(6), 1317–1327.

Baker, H.G. (1955). Self-compatibility and establishment after 'long-distance' dispersal. *Evolution* 9(3), 347–349.

Barraclough, T.G., Birky Jr., C.W. & Burt, A. (2003). Diversification in sexual and asexual organisms. *Evolution* 57(9), 2166–2172.

Brown, S.G. & Duffy, P.K. (1992). The effects of egg-laying site, temperature, and salt water on incubation time and hatching success in the gecko *Lepidodactylus lugubris*. *Journal of Herpetology* 26(4), 510–513.

Brown, S.G. & Murphy-Walker, S. (1996). Behavioural interactions between a rare male phenotype and female unisexual *Lepidodactylus lugubris*. *The Herpetological Journal* 6(3), 69–73.

Brown, S.G. & O'Brien, J. (1993). Pseudosexual and dominance behaviour: their relationship to fecundity in the unisexual gecko, *Lepidodactylus lugubris*. *Journal of Zoology* 231(1), 61–69.

Brown, S.G. & Sakai, T.J.Y. (1988). Social experience and egg development in the parthenogenic gecko, *Lepidodactylus lugubris*. *Ethology* 79(4), 317–323.

Burt, A. (2000). Perspective: sex, recombination, and the efficacy of selection - was Weismann right? *Evolution* 54(2), 337–351.

Cuellar, O. (1977). Animal parthenogenesis: a new evolutionary-ecological model is needed. *Science* 197(4306), 837–843.

Griffing, A.H., Sanger, T.J., Daza, J.D., Nielsen, S.V., Pinto, B.J., Stanley, E.L. & Gamble, T. (2019a). Embryonic development of a parthenogenetic vertebrate, the mourning gecko (*Lepidodactylus lugubris*). *Developmental Dynamics* 248(11), 1070–1090.

Griffing, A.H., Sanger, T.J., Matamoros, I.C., Nielsen, S.V. & Gamble, T. (2019b). Protocols for husbandry and embryo collection of a parthenogenetic gecko, *Lepidodactylus lugubris* (Squamata: Gekkonidae). *Herpetological review* 49(2).

Hoogmoed, M.S. & Avila-Pires, T.C. (2015). *Lepidodactylus lugubris* (Duméril & Bibron 1836) (Reptilia: Gekkonidae), an introduced lizard new for Brazil, with remarks on and correction of its distribution in the New World. *Zootaxa* 4000(1), 90–110.

Ineich, I. (1999). Spatio-temporal analysis of the unisexual-bisexual *Lepidodactylus lugubris* complex (Reptilia, Gekkonidae). In *Tropical island herpetofauna.* Ota, H. (Ed.). Current Diversity and Conservation, Elsevier. 199–228 pp.

Karin, B.R., Oliver, P.M., Stubbs, A.L., Afirin, U., Iskandar, D.T., Arida, E., Oong, Z., Mcguire, J.A., Kraus, F., Fujita, M.K. et al. (2021). Who's your daddy? On the identity and distribution of the paternal hybrid ancestor of the parthenogenetic gecko *Lepidodactylus lugubris* (Reptilia: Squamata: Gekkonidae). *Zootaxa* 4999(1), 87–100.

Kluge, A.G. (1967). Higher taxonomic categories of gekkonid lizards and their evolution. *Bulletin of the American Museum of Natural History* 135, 1–60.

Lapwong, Y. & Juthong, W. (2018). New records of

Lepidodactylus lugubris (Duméril and Bibron, 1836) (Squamata, Gekkonidae) from Thailand and a brief revision of its clonal composition in southeast Asia. *Current Herpetology* 37(2), 143–150.

Lee, K.H., Chen, T.H., Shang, G., Clulow, S., Yang, Y.J. & Lin, S.M. (2019). A check list and population trends of invasive amphibians and reptiles in Taiwan. *ZooKeys* 829, 85.

Lehtonen, J., Jennions, M.D. & Kokko, H. (2012). The many costs of sex. *Trends in Ecology & Evolution* 27(3), 172–178.

Lin, J.W., Chen, Y.R., Li, T.W., Shaner, P.J.L. & Lin, S.M. (2020). Long-term monitoring reveals invariant clutch size and unequal reproductive costs between sexes in a subtropical lacertid lizard. *Zoological Letters* 6(1), 1–12.

Maynard Smith, J. (1971). What use is sex? *Journal of Theoretical Biology* 30(2), 319–335.

Nania, D., Flecks, M. & Rödder, D. (2020). Continuous expansion of the geographic range linked to realized niche expansion in the invasive Mourning gecko *Lepidodactylus lugubris* (Duméril & Bibron, 1836). *PloS ONE* 15(7), e0235060.

Normark, B.B., Judson, O.P. & Moran, N.A. (2003). Genomic signatures of ancient asexual lineages. *Biological Journal of the Linnean Society* 79(1), 69–84.

Ota, H. (1994). Female reproductive cycles in the northernmost populations of the two gekkonid lizards, *Hemidactylus frenatus* and *Lepidodactylus lugubris*. *Ecological Research*, 9, 121–130.

Ota, H., Toda, M., Masunaga, G., Kikukawa, A. & Toda, M. (2004). Feral populations of amphibians and reptiles in the Ryukyu Archipelago, Japan. *Global Environmental Research* 8(2), 133–143.

Otto, S.P. (2009). The evolutionary enigma of sex. *The American Naturalist* 174(S1), S1–S14.

Radtkey, R.R., Donnellan, S.C., Fisher, R.N., Moritz, C., Hanley, K.A. & Case, T.J. (1995). When species collide: the origin and spread of an asexual species of gecko. Proceedings of the Royal Society of London. Series B: *Biological Sciences* 259(1355), 145–152.

Röll, B. & von Düring, M.U.G. (2008). Sexual characteristics and spermatogenesis in males of the parthenogenetic gecko *Lepidodactylus lugubris* (Reptilia, Gekkonidae). *Zoology* 111(5), 385–400.

Sakai, O. (2016). Size distribution suggests a seasonal effect on reproduction of *Lepidodactylus lugubris* on Okinawajima Island, Japan, the northernmost distributional area. *Current Herpetology* 35(1), 59–63.

Sakai, O. (2021). One or two eggs: what underlies clutch size variation within a gecko species? *Zoology* 146, 125911.

Shine, R. & Greer, E. (1991). Why are clutch sizes more variable in some species than in others? *Evolution* 45(7), 1696–1706.

Vitt, L.J. & Caldwell, J.P. (2014). *Herpetology: an introductory biology of amphibians and reptiles (4th Edition)*. Academic press, London: UK. 757 pp.

Yamashiro, S. & Ota, H. (1998). Discovery of a male phenotype of the parthenogenetic gecko, *Lepidodactylus lugubris*, on Ishigakijima Island of the Yaeyama Group, Ryukyu Archipelago. *Japanese Journal of Herpetology* 17(4), 152–155.

Yamashiro, S., Toda, M. & Ota, H. (2000). Clonal composition of the parthenogenetic gecko, *Lepidodactylus lugubris*, at the northernmost extremity of its range. *Zoological Science* 17(7), 1013–1020.

Accepted: 8 April 2023