The Butterfly Agamid Lizard (*Leiolepis belliana*) remains locally abundant in remnant natural forests in peninsular Malaysia.

Battle of the Sexes: Asexuality versus Sexuality

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Photographs by the author.

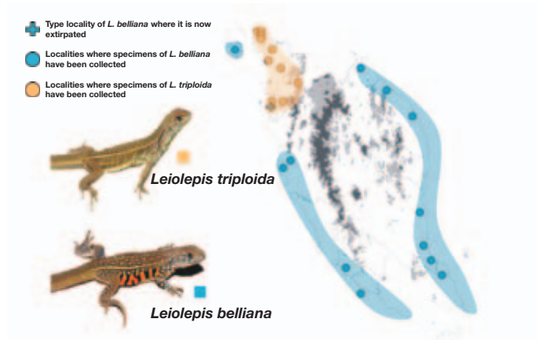
From the time of Aristotle, naturalists and evolutionary biologists have been intrigued with the origins of species and their life histories. The discovery of asexual lineages opened the door to a new chapter of evolutionary biology that is still not completely understood. The evolution of this unique reproductive lifestyle has perplexed biologists for years. Among vertebrates, lizards contain the highest number of asexual species. Two major pathways have been proposed for the origins of asexuality in lizards: (1) a genetic mutation (usually within a single egg clutch) results in individuals that have the ability to clone themselves, and (2) two sexual (or sometimes a sexual and an asexual) species hybridize to create a polyploid (multiples of the "normal" number of chromosomes), all-female population that has the ability to clone itself (Cole 1975; Cole et al. 1983, 1988; Dessauer and Cole 1989; Reeder et al. 2002). However, only the second pathway has been supported by empirical evidence. Although asexuality is rare among lizards, one of the best-studied cases concerns North America teiids of the genus *Aspidocelus* (Racerunners or Whiptails), in which two sexual species hybridized at the intersection of two major habitat types. This resulted in a polyploid, all-female, asexual population in what is usually a relatively narrow ecotone (boundary between habitats). However, one plum remaining to be picked from the tree of herpetological sexuality deals with a group of relatively understudied lizards from southeastern Asia.

The Southeast Asian Butterfly Lizard genus *Leiolepis* contains seven species comprising the monotypic family Leiolepididae (Townsend et al. 2004). *Leiolepis* has a wide, continuous distribution ranging from Myanmar and China south through the Malay Peninsula (Peters 1971). *Leiolepis* is the only acrodont lizard group in which parthenogenesis (production of a viable embryo without an egg being fertilized) has evolved, with three species consisting of all-female populations. All *Leiolepis* are large (snout-vent length to 18 cm) diurnal omnivores that generally inhabit coastal vegetation, but will follow riverbanks and flood plains into continental interiors.

What is it about the evolutionary history of Butterfly Lizards that predisposed them to switch to an asexual mode of reproduction, and does parthenogenesis have an advantage over sexuality in certain habitats? Given the disjunct distribution of the three asexual species (*L. guentherpetersi* from central Vietnam, *L. boehmei* from southern Thailand, and *L. triploida* of northwestern peninsular Malaysia), parthenogenesis probably evolved independently in each species. Schmitz et al. (2001) addressed the maternal origin of the triploid asexual *L. guentherpetersi* and demonstrated that it had arisen through a hybridization event in central Vietnam involving the two bisexual species *L. reevesii* and *L. guttata*. However, the origins of *L. boehmei*, a diploid (Aranyavalai et al. 2004, Darevsky and Kupriyanova 1993), and *L. triploida*, a triploid (Peters 1971), are still mysteries.

The only species of *Leiolepis* in peninsular Malaysia are *L. triploida* (found in disturbed habitat) and *L. belliana* (in disturbed and natural habitats). Data from museum specimens and the literature indicate that, prior to 1920, *L. belliana* was the only *Leiolepis* in peninsular Malaysia. After 1920, however, *L. triploida* appeared at various localities in northwestern peninsular Malaysia and no new records for *L. belliana* were recorded.

In 2007 and 2008, I visited each of the localities from which *L. belliana* had been reported prior to 1920 and confirmed that the species was no longer present, and *L. triploida* is the only species to be found. More interestingly, I realized that *L. triploida* occurred only in highly disturbed habitats. On a hunch, I looked at the history of



The current distributions of *Leiolepis belliana* and *L. triploida* in peninsular Malaysia.

An oil palm plantation in the karst formations of northwestern peninsular Malaysia. *Leiolepis triploida* occurs only in this type of habitat.

A female *Leiolepis belliana*, a "normal" diploid species largely displaced from disturbed habitats by asexual *L. triploida*.

A male *Leiolepis belliana*; unlike asexual *L. triploida*, males consume resources without contributing offspring.

Leiolepis triploida is an all-female, asexually reproducing species.

agriculture in the area and discovered that Malaysia underwent an agricultural boom in the late 1920s, during which large tracts of natural vegetation were cleared to plant oil palms and rubber trees. Suspiciously, this agricultural expansion occurred at the same time that *L. triploida* began appearing in museums, and it encompassed the same localities from which *L. triploida* was being collected.

My hypothesis is that, following the agricultural boom of the late 1920s, *L. triploida* was able to expand its range, largely displacing *L. belliana* from disturbed habitats. In fact, *L. belliana* can occasionally be found in disturbed habitats — but only where *L. triploida* is absent. This is in accord with current research on other groups that has demonstrated that asexual species can colonize an environment with just a single individual, and that they tend to flourish in habitats that are unsuitable for sexual species to which they are closely related (e.g., Kearney 2005, Wright and Lowe 1968). The first of these attributes clearly reflects their two-fold reproductive advantage over sexual species. None of their progeny are males that use resources but do not produce offspring. Instead, they produce only females that can clone themselves. The underlying explanation for their success in apparently marginal habitats remains more elusive, but might, as in the American Whiptails, be attributable to an ecological diversity emanating from an ancestry of two species occupying different ecological niches. The next pieces of this puzzle and the focus of my current research are to identify the parental species of *L. triploida* and to investigate whether or not the species' origin may have played a role in its ability to colonize disturbed areas and displace competitors.

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