

Geographic parthenogenesis and the common tea-tree stick insect of New Zealand

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Abstract

Worldwide, parthenogenetic reproduction has evolved many times in the stick insects (Phasmatidae). Many parthenogenetic stick insects show the distribution pattern known as geographic parthenogenesis, in that they occupy habitats that are at higher altitude or

common in marginal habitats, parthenogenetic lineages may replace sexual ones due to inbreeding depression suffered within small sexual populations.

Selective advantage of parthenogenetic individuals might also rest in their potential for long distance colonization. Thus geographic parthenogenesis may result from differential ability to colonize areas following climate warming of interglacial cycles, because a single individual or egg can give rise to a new population following dispersal. For example, the stick insect, *Argosarchus horridus*, is a facultative parthenogen that has probably expanded its range in New Zealand since the last glacial maximum (Buckley et al. 2009), and a population on the geologically young Chatham Islands are all-female (Trewick et al. 2005). The New Zealand tea-tree stick insect, *Clitarchus hookeri* (White) was accidentally introduced to the United Kingdom where all-female populations have established in the Scilly Isles (Brock 1987). Parthenogenetic reproduction is common in stick insects (Phasmida) where many independent lineages have evolved the ability to reproduce without males (Bullini 1994). Some lineages are obligate parthenogens (with males entirely absent) but many other species are facultative parthenogens and have the ability to reproduce with or without males. The term facultative parthenogen is applied to a species when both sexual and asexual reproduction has been observed, although the ability of individual females to reproduce in both ways has rarely been tested (see Bedford 1978). It is possible that once lost to a lineage, sexual reproduction is not retrievable, in which case parthenogenetic females would be genetically isolated from their sexual siblings.

The theoretical reproductive output per individual for asexual species is twice that for sexual species where a male-female pair produce the same number of offspring as a single asexual female, hence the twofold

of the alternative strategies, focusing on the key issue of whether *C. hookeri* is a true facultative parthenogen. Do females from bisexual populations employ a mixed mating strategy? Can females from parthenogenic populations reproduce sexually if a male becomes available? We consider whether these alternative reproductive strategies confer short-term fitness advantages by comparing development time of eggs, and fertility.

Materials and methods

Common New Zealand tea-tree stick insect

Clitarchus hookeri



Fig. 1 Phylogenetic relationships of mtDNA haplotypes of the New Zealand common tea-tree stick insect *Clitarchus hookeri*. (a) Maximum Likelihood analysis of 1350 bp COI–COII DNA sequence. Stick insects from putative-parthenogenetic populations are part of a single clade (double female symbols), with two exceptions (single female symbols). Node support shown where Maximum Likelihood bootstraps are above 70 (above branches) and Bayesian Posterior Probabilities above 0.96 (below branches). Tree was rooted with three outgroup taxa (*Pseudoclitarchus sentus*, *Acanthoxyla prasina*, *Argosarchus horridus*). (b) New Zealand sampling locations of *Clitarchus hookeri* and regions referred to in the text are shown. Both Auckland and Wellington are regions represented by many sample sites (see Appendix S2).

Bayesian posterior probabilities and PHYML (Guindon & Gascuel 2003) bootstrap values (1000 replicates) for the major lineages. A minimum spanning network for a subset of haplotypes was constructed without the need of computer software. We used three New Zealand species as the outgroup; the sexual species *Pseudoclitarchus sentus* that is sister to *Clitarchus hookeri*, the obligate parthenogen *Acanthoxyla prasina*, and the facultative parthenogen *Argosarchus horridus* (Trewick et al. 2005, 2008).

We used absolute pairwise sequence differences to examine the mismatch distributions among haplotypes within *Clitarchus hookeri*. Time since expansion was not estimated due to lack of information about mutation rate in these insects and the likelihood that time depen-

dency of estimates of the rate of nucleotide substitution would make any inference of unknown value (lazy-j-shaped curve; Ho et al. 2005; Burrridge et al. 2008).

Fertility

Fertility was estimated from hatching rates of eggs laid by females from a number of populations. A comparison of fertility of virgin and mated females used *C. hookeri* females collected from a single location (Lake Karapiro, Waikato). Each adult was held with either zero, one or two males from the same location, for the same 6 week period (Table 1). Copulation was observed where males were present. After 6 weeks all



Fig. 2 Reproductive and genetic variation in the New Zealand common tea-tree stick insect *Clitarchus hookeri*. (a) Distribution of sexual and putative-parthenogenetic populations reveal a pattern of geographic parthenogenesis.

(Posada 2008) selected GTR+I+G model of DNA evolu-

of unfertilized eggs, there was no evidence that the proportion of female nymphs changed at this time (Fig. 4). Eggs resulting from sexual reproduction, on average

females from parthenogenetic populations produce only a few male offspring after copulating. A single male offspring hatched from the egg of a virgin mother (1 of 315 parthenogenetic offspring). This male may have arisen by the loss of an X chromosome during cell division (non-disjunction), a mechanism recorded for other stick insect species with the same XO/XX sex-determination mechanism seen in *C. hookeri* (Parfitt 1980; Morgan-Richards & Trewick 2005). Such fatherless males might have the capacity to restore sexuality to parthenogenetic diploid populations (as suggested for *Bacillus rossius*) but males of virgin-birth of the triploid, hybrid species *Carausius morosus* have all been sterile due to abnormal sperm and failure to transfer sperm during copulation (Pijnacker 1987).

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