Evidence for adaptive sex allocation in *Tamalia coweni* (Hemiptera: Aphididae) in response to nutrient variability in *Arctostaphylos patula*

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**ABSTRACT**

**Question:** Do animal species with facultative sex allocation invest adaptively according to local environmental conditions?

**Hypothesis:** The Trivers-Willard hypothesis can explain maternal sex allocation patterns in response to experimental manipulations in the field.

**Organisms:** A galling aphid, *Tamalia coweni*, and its host plant, *Arctostaphylos patula*.

**Field site:** Lassen National Forest, Butte County, California, USA, 1700 m above sea level.

**Methods:** Using a randomized block design we enriched host plants with various concentrations of nitrogen (urea), then recorded sex ratios and mass of developing male and female offspring, as well as female fecundity.

**Conclusions:** Aphid foundresses respond to nitrogen enrichment by skewing brood sex ratios towards daughters. We observed no changes in *T. coweni* body mass or its number of presumptive ova.

**Keywords:** aphid, gall, nitrogen, parental investment, sex ratio, Trivers-Willard hypothesis.

**INTRODUCTION**

Fisher (1930) used straightforward logic to explain why sex ratios tend to be equal in many species, a conundrum bedevilling Darwin some 60 years earlier (Darwin, 1871). Fisher gained his insights by considering sex ratio patterns across multiple generations, suggesting that negative frequency-dependent selection can favour parents investing in the sex in shortest supply. However, biased population-wide sex ratios have been characterized both empirically and theoretically, especially among invertebrates (Craig and Mopper, 1993; West, 2009). More precisely, patterns of parental investment in sons and daughters (i.e. sex allocation) are frequently skewed away from equilibrium, owing to a multitude of factors including selection. Manipulating sex ratios can be advantageous when differential payoffs on
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