

Local mate competition model alone cannot predict the offspring sex ratio in large and dense populations of a haplodiploid arthropod

Nuwan Weerawansa^{a,b}, Qiao Wang^a, and Xiong Zhao He^{a,*}

^aSchool of Agriculture and Environment, Massey University, Private Bag 11222, Palmerston North 4442, New Zealand and

^bFaculty of Animal Science and Export Agriculture, Uva Wellassa University of Sri Lanka, Passara Road, Badulla 90000, Sri Lanka

*Address correspondence to Xiong Zhao He. E-mail: x.z.he@massey.ac.nz.

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Sex ratio in animals has profound impacts on the fitness of mothers and their offspring. When the local competition intensity is sex-specific, selection favors the sex that may mitigate such negative impacts (West 2009). This may occur under 1) local mate competition (LMC)—in a discrete population established by one or a few foundresses, they tend to produce female-biased offspring sex ratio to reduce the LMC between related males (Hamilton 1967); 2) local resource competition (LRC)—in a dense population where related individuals compete for resources, mothers are selected to produce more offspring of dispersive sex to decrease resource competition (Clark 1978; Wild and Taylor 2004; Iritani et al. 2021), and 3) local resource enhancement (LRE)—when one sex helps one another rather than compete with one another, selection favors an excess production of the more helpful sex (Taylor 1981). These scenarios may take place simultaneously in the same species (West 2013). However, theoretical models for prediction of sex ratio only consider LMC (Hamilton 1967, 1979; Herre 1985; West 2009).

Under the assumption that mated females disperse to found new colonies, Hamilton (1967) proposes the first theoretical model to predict the evolutionary outcome of offspring sex ratio (proportion of male offspring, s) for diploid species under LMC: $s = (N-1)/(2N)$ (Equation 1), where N is the number of females in a population whose offspring develop and mate on the patch. The model predicts that an increase of LMC (i.e., decrease of foundress population size) reduces the proportion of sons from 50% for a large population to 0% for a single foundress, and the 0% of sons could be interpreted as the minimum proportion of sons needed for fertility insurance even though this minimum is unknown. In haplodiploid species, however, inbreeding is common and females can control the sex of their offspring in response to the social environment through arrhenotoky (fertilized eggs give rise to diploid female offspring and unfertilized eggs to haploid male offspring) (West 2009). The LMC with

intensive inbreeding in small local populations will promote a female-biased sex ratio (Herre 1985). Therefore, the effect of inbreeding should be incorporated into Hamilton's (1967) model when predicting sex ratio in this group of animals. If the probability of inbreeding in a population of constant size (N) is fixed, that is, $k = 1/N$ ($1 \leq k \leq 0$) (West 2009), then $s = [(N-1)(2N-1)]/[N(4N-1)]$ (Equation 2). If N varies across patches in a population and there is an average level of inbreeding k ($1 \leq k \leq 0$) (Herre 1985; West 2009), then $s = [(N-1)(2-k)]/[N(4-k)]$ (Equation 3) (when $k = 0$, Equation 3 is the same as Equation 1).

In numerous haplodiploid taxa, including many wasps, beetles, thrips, and mites, females may produce extremely female-biased offspring sex ratios (West 2009) which cannot be explained by LMC theory alone, probably because of impacts from LRC and/or LRE (Iritani et al. 2021). However, it is still not clear how LMC, LRC, and LRE affect sex allocations in haplodiploid animals. Here, we used a haplodiploid mite *Tetranychus ludeni* Zacher to test 1) how females adjusted the sex allocation strategies in response to different levels of LMC and LRC and 2) whether the LMC theoretical models could predict the offspring sex ratio under different levels of LMC and LRC. *Tetranychus ludeni* is an invasive pest of horticultural crop and inhabits discrete patches of various population sizes and densities with varying inbreeding intensity. We designed a factorial experiment by keeping each of the three test population sizes constant but allowing the population density to alter at three levels, and *vice versa* (Table 1) and recorded the sex ratio.

The sex ratio of *T. ludeni* under all tested social environments was low (0.13–0.21) (Figure 1 and Table 1). Results show that when population size was large (5 or 10 females), offspring produced were significantly more female biased at higher population densities (1 and 2 females/cm²) than at lower population density (0.67 female/cm²) ($F_{2,60} = 13.55$, $P < 0.0001$ for 5 females; $F_{2,52} = 26.95$, $P < 0.0001$ for

Table 1. Comparisons of observed sex ratios (proportion of male offspring) at different social environments with predictions of LMC models

Leaf area (cm ²)	Population size (females)	Population density (females/cm ²)	Observation <i>n</i> mean (SE)	Prediction (Equation 2)	Prediction (Equation 3)		
					<i>k</i> = 0 (Equation 1) ^a	<i>k</i> = 0.5	<i>k</i> = 1
				0.2143	0.2500 ^b	0.2142	0.1667
1.5	1	0.67	25 0.1497 (0.0144)	4.47 ^{c***}	6.94 ^{****}	4.46 ^{***}	1.18 ^{ns}
1	1	1	18 0.1544 (0.0193)	3.11 ^{**}	4.96 ^{****}	3.10 ^{**}	0.64 ^{ns}
0.5	1	2	24 0.1534 (0.0067)	9.14 ^{****}	14.51 ^{****}	9.13 ^{****}	1.99 ^{ns}
				0.3789	0.4000	0.3429	0.2667
7.5	5	0.67	25 0.2065 (0.0080)	21.54 ^{****}	24.18 ^{****}	17.05 ^{****}	7.53 ^{****}
5	5	1	22 0.1484 (0.0106)	21.83 ^{****}	23.83 ^{****}	18.42 ^{****}	11.21 ^{****}
2.5	5	2	16 0.1520 (0.0089)	25.36 ^{****}	27.72 ^{****}	21.43 ^{****}	12.82 ^{****}
				0.4385	0.4500	0.3857	0.3000
15	10	0.67	18 0.1934 (0.0086)	28.36 ^{****}	29.69 ^{****}	22.25 ^{****}	12.33 ^{****}
10	10	1	16 0.1325 (0.0086)	35.76 ^{****}	37.11 ^{****}	29.59 ^{****}	19.58 ^{****}
5	10	2	21 0.1482 (0.0126)	23.20 ^{****}	23.93 ^{****}	18.83 ^{****}	12.04 ^{****}

ns indicates no significant difference between the observed and predicted sex ratios.

^aWhen *k* = 0 (i.e., no inbreeding) in Equation (3), the predicted sex ratios are the same as that in Equation (1).

^bWhen *N* = 1 in Equations (1) and (3), the sex ratio *s* = 0 which is logically incorrect, thus the predicted sex ratio *s* = 0.25 when *N* = 2.

^c*t*-Value for the one-sample *t*-test.

, *, and **** indicate a significantly lower observed sex ratio than the predicted ones at *P* < 0.01, *P* < 0.001, and *P* < 0.0001, respectively.

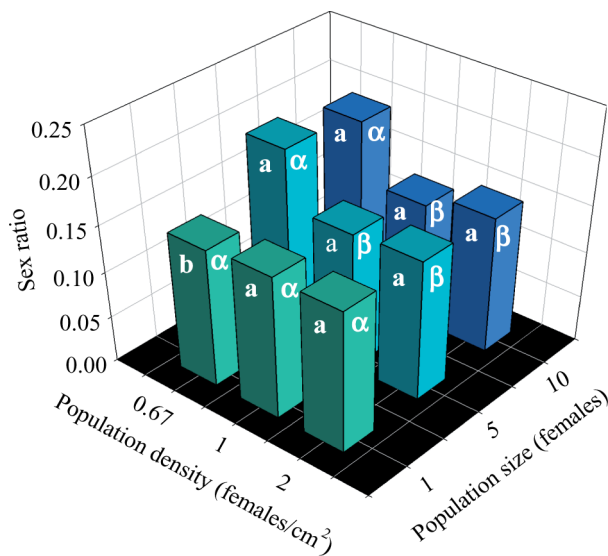


Figure 1. Sex ratio (proportion of male offspring) of *T. ludeni* under various social environments. For a given population density, columns with the same English letters are not significantly different between population sizes; for a given population size, columns with the same Greek letters are not significantly different between population densities (Tukey–Kramer test: *P* > 0.05).

10 females). However, when population size was small (1 female), population density had no effect on offspring sex ratio ($F_{2,64} = 0.01$, $P = 0.9879$) (Figure 1). Furthermore, we detected a significantly lower sex ratio at the small population size of 1 female than at large population sizes (5 and 10 females) with a low population density (0.67 female/cm²) ($F_{2,65} = 3.17$, $P = 0.0488$) but population size had no significant effect on sex ratio when population density was high (1 or 2 females/cm²) ($F_{2,53} = 1.35$, $P = 0.2689$ for 1 female/cm²; $F_{2,58} = 0.15$, $P = 0.8609$ for 2 females/cm²) (Figure 1). When

comparing the observed sex ratios with the predictions of the three LMC models, we found that the predictions of LMC models only fitted the observed sex ratios when the population size was 1 female with intensive inbreeding (*k* = 1, in Equation 3), but the observed sex ratio in the larger populations was significantly lower than that predicted by LMC models (Table 1).

Our results only support LMC theory (Hamilton 1967) when population size is small where mated mothers produce more daughters to reduce LMC between their sons (Figure 1). Regardless of population size, females may be selected to produce more dispersing daughters in the dense populations (Figure 1) to reduce resource competition in the local populations, agreeing to the LRC prediction (Clark 1978; Wild and Taylor 2004; Iritani et al. 2021). We suggest that females change their sex allocation strategies in response to social environment. In small populations, they produce more daughters to reduce mate competition between sons while in large and dense populations they give birth to more dispersing daughters to reduce resource competition.

The extremely female-biased sex ratio in *T. ludeni* may be attributed to the life history characteristics of spider mites. First, if the increase in fitness return per unit investment is greater in daughters than in sons, an optimal sex allocation is expected to be female-biased (Seeger and Stubblefield 2002). In *T. ludeni*, females are larger in size than males, thus investing more resources to daughters is advantageous for the mothers. Second, although daughters are more likely to compete for local food due to their large body size, they usually disperse from the dense conditions after mating. Thus, production of more dispersing daughters will eventually reduce LRC as well as LMC. Third, spider mite females may cooperate as a form of LRE in spinning silk webs which are crucial for dispersal and protection against environmental hazards, and group-living females produce more silks per mite than single females (Le Goff et al. 2010). In

the scenario of LRE, females are the helpers and thus production of more daughters may reduce both local mate and resource competition. Although production of more mates or helping and dispersing daughters may potentially intensify LRC, the benefit gained from more daughters produced under LMC, LRC, or LRE outweighs the costs of resource competition among females. We suggest that under varying social environments, LMC, LRC, and LRE could be the main mechanisms leading to the extremely female-biased sex ratio in *T. ludeni*.

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Authors' Contribution

N.W., X.Z.H., and Q.W. conceived and designed the study. N.W. collected the data. N.W. and X.Z.H. analyzed the data. All authors contributed to manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest to any other institutions.

Supplementary Material

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

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