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Temperature and sex allocation in a spider mite

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Abstract Although temperature is the most important environmental factor regulating arthropod development and reproduction, its influence on sex allocation in haplodiploid arthropods remains largely unexplored. We investigated under laboratory conditions how maternal age and temperature mediate offspring sex ratio of the spider mite *Tetranychus mcdanieli* (Acari: Tetranychidae). Over nine temperature regimes, female-biased sex ratios were consistently observed, varying from 57 to 87% among progeny produced over lifetime. Spider mite sex ratio was affected by maternal age: more male progeny were produced at both the beginning and the end of the female lifespan, yielding a dome shaped curvilinear relationship. This pattern of variation with age probably results from constraints on using sperm at young ages and sperm depletion or viability at older ages. We found a significant curvilinear relationship between temperature and sex ratio. The proportion of female offspring was lowest at intermediate temperatures and highest at extreme temperatures. We suggest that increased female-biased sex ratio at extreme temperatures is an evolutionary response of spider mites to deteriorating habitats as, in the Tetranychidae, females have better capacities than males to disperse and survive under harsh conditions.

Keywords Haplodiploidy · Maternal age · Sex allocation · Temperature · Tetranychidae

Introduction

An important aspect of the study of sex allocation in haplodiploid arthropods is to explore selective factors leading to a biased sex ratio. Two main forms of selection have been generally identified. First, sex allocation is a typical case of frequency-dependent selection where the value of one sex changes with its frequency of occurrence in a population. The best documented case concerns the evolution of female-biased sex ratios in species where mating frequently occurs between siblings. In this instance, local mate competition models predict that females should overproduce daughters when their brothers compete for mates (Hamilton 1967; Charnov 1982). Second, sex allocation is affected by individual selection, which arises whenever the value of one sex varies under particular ecological conditions. For example, in parasitoids, host quality models predict that female eggs should be laid in relatively large hosts when individual fitness increases with size more sharply in females than in males (Charnov 1979; Waage 1986).

Sex ratio is a phenotypic trait that is likely to be affected by abiotic factors such as temperature, humidity, photoperiod, and light conditions (Pianka 1988; Wrensch 1993). Temperature is the most important environmental factor regulating arthropod development and reproduction. Variation in temperature can also be a reliable indicator of habitat quality and trigger the production of individuals with differential abilities to reproduce, disperse, or enter dormant stages (Wellington et al. 1999). The influence of temperature on sex allocation in haplodiploid insects and mites remains largely unexplored (King 1987; Wrensch 1993). Detailed studies are too few to reach conclusions and describe patterns about the relative importance and adaptive significance, if any, of temperature as a determinant of sex allocation.

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For colonizing species which inhabit ephemeral and heterogeneous resources, Wrensch (1993) hypothesized that a female should adjust her sex ratio to produce more males when facing stressful environments. She argued that haploid males are a significant advantage for colonizing species because they increase the group's ability to respond to selection. A critical assumption is that haploid males provide a faster rate of evolution than diploid males as shown theoretically by Griffing (1982). As a result, sex allocation could provide a mechanism to accelerate evolutionary responses of an organism to harsh conditions. An alternative hypothesis would be that females are selected to maximize the production of the sex better adapted to cope with deteriorating habitats and extreme weather conditions. Biased sex ratios might therefore reflect differential abilities of males and females to disperse or survive under extreme environmental conditions (Pianka 1988).

In this study we examined how the sex ratio of the spider mite, *Tetranychus mcdanieli* McGregor (Acari: Tetranychidae) changes in response to temperature. Distributed throughout North America, the McDaniel spider mite is the most important pest of red raspberry, *Rubus idaeus* L. in Quebec (Roy et al. 1999), where it damages canes from late spring to early fall. Spider mites develop through egg, larva, protonymph, deutonymph and adult stages. In the temperate zones, females may undergo a facultative reproductive diapause during winter. They are typical colonizing species characterized by short generation time, a high capacity for population growth, and cyclic dispersal (Sabelis 1985). Spider mites form colonies which vary in size and longevity from a few individuals breeding for one generation to thousands that exploit the resource for extended periods. Outbreaks are characterized by exponential population growth, immoderate damages to the host plant, rapid decline of spider mite populations, and dispersal to new resources. Tetranychid mites are arrhenotokous and females can determine the sex of each offspring by choosing whether or not to fertilize the egg (Helle and Pijnacker 1985). They usually live in colonies and mating occurs between siblings. Typically, spider mites exhibit moderate to extreme female-biased sex ratios (Sabelis 1991; Wrensch 1993). *T. mcdanieli* is a multivoltine species that shows strong developmental and reproductive responses to temperature; it develops to maturity and reproduces in the 14–36°C range (Roy et al. 2002, 2003). In the present study, sex allocation patterns in *T. mcdanieli* were determined under laboratory conditions over temperatures covering the full range of constant temperatures allowing complete development of the species. We also investigated the relationship between maternal age and offspring sex ratio as influenced by temperature.

Material and methods

The experiment was conducted using *T. mcdanieli* from a 1-year-old laboratory culture. Spider mites were originally collected from

a raspberry field near Quebec City, Canada (46°59'N, 71°29'W) and were maintained on red raspberry, cultivar Killarney, at 24°C and 50–70% relative humidity with a 16:8 (L:D) photoperiod.

Spider mites were reared on raspberry leaf discs (2.0 cm in diameter) placed upside down on submerged cotton wool in individual petri dishes. Synchronized eggs were obtained by introducing adult mites (ca. 100 for each temperature) on leaf discs for 5 h. Newly laid eggs were then placed individually on leaf discs and reared in growth chambers at 12, 14, 16, 20, 24, 28, 30, 32, 34, 36 or 38±0.5°C, under the same photoperiod and humidity conditions as described above. Sixty individuals were tested per temperature regime.

Females in their quiescent stage prior to adulthood (teleiochrysalis) were provided with a newly emerged male. Males were replaced regularly (2–4 days) depending on temperature. On the onset of reproduction, females were transferred every day to fresh leaf discs. For each temperature, eggs were collected daily, pooled per female age, and transferred to new arenas. The progeny were kept at 24°C until the adult stage. Sex ratio was then determined for each cohort. Additional details on rearing methods and experimental procedures are described in Roy et al. (2002).

As sexing of the offspring was performed after rearing to adulthood, our data refer to secondary sex ratio. This measure may not be a reliable indicator of sex allocation if one sex suffers higher mortality during development. In *T. mcdanieli*, although juvenile mortality varied from 10 to 30% at temperature between 16°C and 36°C (the range of temperature suitable for *T. mcdanieli* development and reproduction), mortality did not differ significantly between temperatures (Roy et al. 2002). We therefore assume that secondary sex ratio (sex ratio hereafter) accurately reflects temperature-dependent sex allocation in this species. Sex ratio was calculated as the proportion of females in the progeny of cohorts of females of similar age and reared under the same temperature regime. Temperature and female age, and their interactions were tested for significant effects on sex ratio by fitting a binomial regression model to the sex ratio data following logit transformation (Agresti 1990). To complete the analysis, linear and quadratic effects of temperature on overall (lifetime) sex ratio were similarly tested for significance by fitting a binomial regression model to data pooled across all cohorts for each temperature. Statistical analyses were performed using the SAS system GENMOD procedure (SAS Institute 1999).

Results

Tetranychus mcdanieli successfully developed to adulthood at temperatures from 14 to 36°C, but failed at 12°C and 38°C. The percentage of females that reproduced was over 83% at each temperature (14–36°C). The duration of the preoviposition and oviposition periods are shown in Fig. 1. The preoviposition period shortened at a decreasing rate as temperature increased, whereas the oviposition period lengthened between 14 and 20°C but shortened at higher temperatures. A 5-fold difference in the time required to lay a first egg was observed between temperature extremes. Similarly, oviposition periods were 29 days at 14°C and 5.4 days at 36°C. Roy et al. (2003) more fully analyzed the effects of temperature on both developmental and reproductive parameters of *T. mcdanieli*.

McDaniel spider mite sex ratio was a function of maternal age. An increase of male progeny at both the beginning and at the end of the reproductive period yielded a dome shaped curvilinear relationship (Fig. 1). Statistical analysis confirmed that age had both linear

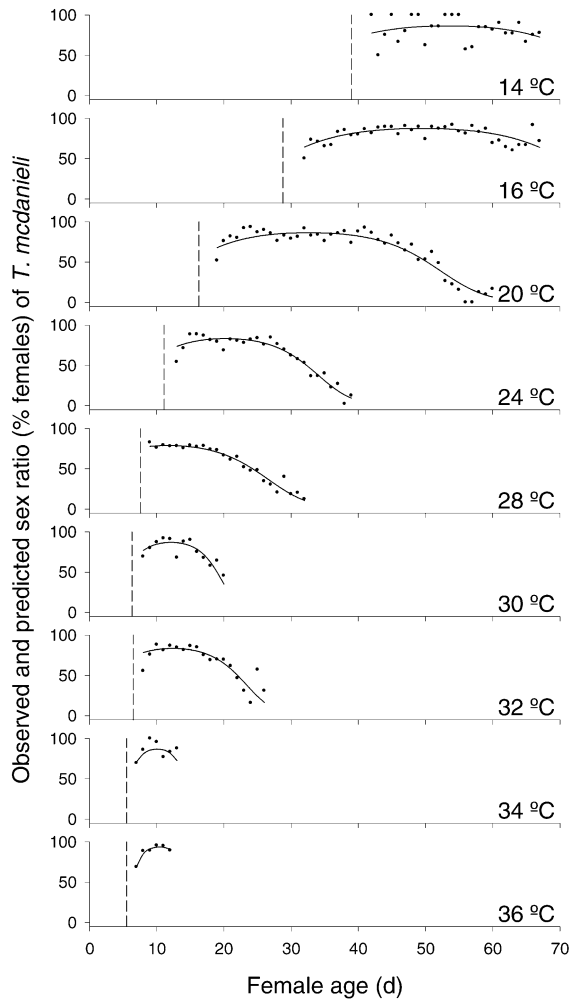


Fig. 1 Effect of female age on sex ratio (% females) of *Tetranychus mcdanieli* reared at different constant temperatures; lines show predicted values based on a binomial regression model; curvilinear relationships are all significant at $P < 0.0001$. The dashed vertical lines indicate age at the end of the preoviposition period

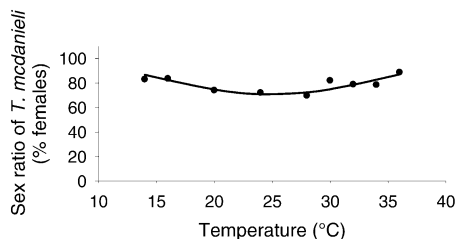


Fig. 2 Lifetime sex ratio (% females) of *Tetranychus mcdanieli* reared at nine constant temperatures; line shows predicted values based on a binomial regression model; curvilinear relationship significant at $P < 0.0001$

($\chi^2_{1df} = 14.82$, $P < 0.0001$) and quadratic ($\chi^2_{1df} = 8.38$, $p = 0.0038$) effects on sex ratio. Temperature affected sex ratios directly ($\chi^2_{7df} = 33.71$, $p < 0.0001$), and interacted with age both linearly ($\chi^2_{7df} = 14.91$, $P = 0.0372$) and quadratically ($\chi^2_{8df} = 36.84$, $P < 0.0001$). Thus temperature had a

strong modulating effect on the maternal age pattern of sex ratio, although the above curvilinear trend was observed even at the highest temperatures (34 and 36 °C), when reproduction was greatly compressed in time (6–7 days). (Fig. 1).

Over the range of temperatures tested, lifetime sex ratios were consistently female biased, varying from 56.7% at 28 °C, to 87.3% at 34 °C (Fig. 2). Regression analysis showed that linear ($\chi^2_{1df} = 17.03$, $P > 0.0001$) and quadratic ($\chi^2_{1df} = 17.06$, $P < 0.0001$) effects of temperature on lifetime sex ratio were both significant, a quadratic effect confirming that sex ratios were lowest at intermediate temperatures and highest at extremes.

Discussion

Our results provide experimental evidence of the effect of maternal age and temperature on sex allocation in a tetranychid mite. The following discussion first examines age-specific patterns and identifies potential physiological constraints of sex allocation. Next, we suggest that temperatures are instrumental in determining optimal sex ratios because they are correlated with ecological conditions that influence the actual and future reproduction of an individual. We suggest that the increased female-biased sex ratio observed in *T. mcdanieli* at extreme temperatures is an adaptive response to cope with deteriorating habitats.

Several studies have shown that female age influences sex allocation in tetranychid mites (Shih 1979; Hamilton et al. 1986; de Moraes and McMurtry 1987; Krainacker and Carey 1988). In some cases, patterns are incomplete and therefore difficult to interpret mainly because data sets cover only a fraction of the reproductive period. In *T. mcdanieli*, we observed an increased proportion of males produced towards the beginning and the end of the oviposition period. This pattern does not vary with temperature.

The dome-shaped relationship between female age and sex ratio is likely due to constraints on using sperm at young ages and sperm depletion or inviability at older ages. In tetranychid mites, sperm cannot fertilize the first mature oocytes. These eggs are formed during the quiescent deutonymph stage and are impenetrable by sperm by the time copulation occurs (Feiertag-Koppen and Pijnacker 1985). The amount of sperm stored in the female's spermatheca depends on the length of copulation (Overmeer 1972) and females are known to mate only once (Helle 1967). In *T. cinnabarinus*, females were incapable of accepting a second insemination, even when they began to lay only haploid eggs (Potter 1978). The production of mostly sons by aging females could therefore result from sperm depletion (Wrensch 1993). In a cohort, we might expect some females who run out of sperm to show a switch from a 'normal' sex ratio to producing only males, while other females who are not sperm depleted would show no such switch. At the level of the whole cohort, this would produce a gradual

decrease in female production as observed in Fig. 1. Male-biased sex ratios at the end of the oviposition period could also arise either from reduced sperm viability over time (de Moraes and McMurtry 1987), from a physiological degradation of the female's ability to fertilize eggs (Krainacker and Carey 1989), or from a decrease in overall quality of eggs produced by aging females.

Male-biased sex ratios late in the reproductive period probably do not modify substantially the realized sex ratio of a female or the demographic parameters of the population. Massive early breeding is favored in colonizing species of spider mites (Sabelis 1991). For example, in *T. urticae*, most of the reproductive effort is made by younger females which produce over 90% of the offspring during a period of 9 days early in their life, when sex ratio is highly biased towards females (Young et al. 1986). As first demonstrated by Lewontin (1965) and further validated by numerous studies (see Sabelis 1991; Krainacker and Carey 1988 and references therein), daughters produced early in life are the ones which contribute the most to population growth rates. In spider mites, the inability of aging females to fertilize eggs does not appear to significantly impair their overall reproductive potential.

Our results are original as very few studies have explicitly explored, testing a sufficiently large range of temperatures, how temperature influences sex allocation in haplodiploid arthropods. Most of the information found in the literature is derived from studies primarily designed to examine life-history parameters related to population dynamics. As a consequence, some of the inferences drawn on sex allocation can be misleading. A good example is the work of Carey and Bradley (1982): this study was nicely conducted and provided accurate life tables for three species of tetranychid mites reared at two temperatures on cotton. However, data on sex ratio were less reliable. An average of only 24 eggs of each species were reared at five temperatures and used to determine the offspring sex ratio. The data were not statistically analyzed, no clear pattern emerged within and among species, and the authors themselves did not draw conclusions about temperature-dependent sex ratio. Nevertheless, this work is regularly cited by other researchers to describe relationships between temperature and sex ratio in tetranychid mites.

The observed pattern of sex ratio in *T. mcDanieli* is likely to reflect a direct effect of constant temperature on sex allocation rather than differences in female reproductive capacity at various temperatures. Reviewing the literature on spider mites, Sabelis (1991) and Sabelis and Janssen (1996) did not find significant correlation between sex ratio and either the mean rate of oviposition or the peak rate of oviposition. For example, although female *T. urticae* produced varying numbers of offspring per day during their peak oviposition period, the proportions of sons and daughters remained relatively constant (Young et al. 1986). Similarly, Margolies and Wrensch (1996) concluded that fecundity in *T. urticae* is not correlated with sex ratio.

Wrensch (1993) proposed that extreme temperatures should trigger an increase in the relative proportion of males in the progeny of haplodiploid species, thereby increasing the rate of evolution in local populations under intense selection pressure. This hypothesis was supported by Margolies and Wrensch (1996) who reported that sex ratio of *T. urticae* females exposed to a high temperature (32°C) was more male biased (0.536) than for females exposed to a low temperature (22°C; 0.727). In contrast, our results showed the opposite pattern with *T. mcDanieli*. Testing sex allocation within the wide range of temperatures generally prevailing in natural conditions, we found the greatest female-biased sex ratios at both the lowest and highest temperatures. De Moraes and McMurtry (1987) observed an almost identical pattern in *T. evansi* reared at temperatures ranging from 15 to 35°C.

Female-biased sex ratios under extreme temperatures may be an evolutionary response of spider mite to harsh conditions. Coping with an environment which is unfavorable and predictably declining requires appropriate life-history strategies (Horn and Rubenstein 1984), and one potential adjustment would be through reproduction and the allocation of sex. For instance, it may be adaptive for females to vary offspring sex ratios seasonally if the relative reproductive success of males and females differs in time (Werren and Charnov 1978). Accordingly, seasonal variations in offspring sex ratios have been observed in haplodiploid parasitic wasps (see King 1987 and references therein).

Distinctive biological attributes of spider mites could favor the production of females rather than males at extreme temperatures. Local populations of spider mites are typically transient and selection favors the sex having a higher capacity for dispersal and finding new resources (Sabelis 1991). In the Tetranychidae, only the females disperse. They do so after being fertilized to cope with the risk of not finding a mate when colonizing new resources (Wrensch and Young 1975; Potter 1978). Regular extreme temperatures are a reliable indicator of unfavorable habitats and could therefore influence the female decision to produce more female offspring to escape from local conditions. A similar strategy was reported by Wrensch and Young (1978) in response to a different stimulus. They observed that females of *T. cinnabarinus* responded to leaves of poor nutritional quality by producing a maximum of daughters, the potential emigrants.

Male and female spider mites also show differential abilities to survive prolonged adverse weather conditions. In *Tetranychus* species, only adult females are known to overwinter as diapausing individuals in temperate areas (Veerman 1985). Likewise, aestivation allows spider mite females to survive periods of excessive heat and dryness while males die (Veerman 1985). Regular extreme temperatures are used by arthropods as cues to predict the onset of autumn or drought period (Wellington et al. 1999). They are likely to influence the female decision to minimize the production of male eggs, the sex less adapted to detrimental environmental conditions.

We do not emerge from this discussion with a definite understanding of the relation between temperature and sex allocation. Major gaps exist in our knowledge of the natural history of spider mites in natural environments. Do females finely adjust offspring sex ratios? Even this simple question remains open. This is due to the obvious experimental difficulties of studying sex ratio under field conditions (King 1987; Stoks 2001). Nevertheless, laboratory experiments and analytical models indicate that Hamilton's (1967) theory of local mate competition is a convincing explanation for the evolution of female-biased sex ratio in the Tetranychidae (Charnov 1982). However, other determinants such as maternal age and environmental factors may shape sex allocation in spider mites and other haplodiploid arthropods.

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References

- Agresti A (1990) Categorical data analysis. Wiley, New York
- Carey JR, Bradley JW (1982) Developmental rates, vital schedules, sex ratios, and life tables for *Tetranychus urticae*, *T. turkestanii* and *T. pacificus* (Acarina: Tetranychidae) on cotton. *Acarology* 23:333–345
- Charnov EL (1979) The genetical evolution of patterns of sexuality: Darwinian fitness. *Am Nat* 113:465–480
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton, N.J.
- Feiertag-Koppen CCC, Pijnacker LP (1985) Oogenesis. In: Helle W, Sabelis MW (eds) Spider mites, their biology, natural enemies and control. Elsevier, Amsterdam, pp 117–127
- Griffing B (1982) A theory of natural selection incorporating interactions among individuals. X. Use of groups consisting of a mating pair together with haploid and diploid caste members. *J Theor Biol* 95:199–223
- Hamilton A, Botsford LW, Carey JR (1986) Demographic examination of sex ratio in the two-spotted spider mite, *Tetranychus urticae*. *Entomol Exp Appl* 41:147–151
- Hamilton WD (1967) Extraordinary sex ratios. *Science* 156: 477–488
- Helle W (1967) Fertilization in the two-spotted spider mite (*Tetranychus Urticae*: Acari). *Entomol Exp Appl* 10:103–110
- Helle W, Pijnacker PL (1985) Parthenogenesis, chromosomes and sex. In: Helle W, Sabelis MW (eds) Spider mites, their biology, natural enemies and control. Elsevier, Amsterdam, pp 129–139
- Horn HS, Rubenstein D I (1984) Behavioural adaptations and life history. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell, London, pp 279–298
- King BH (1987) Offspring sex ratios in parasitoid wasps. *Q Rev Biol* 62:367–396
- Krainacker DA, Carey JR (1988) Maternal heterogeneity in primary sex-ratio of three tetranychid mites. *Exp Appl Acarol* 5:151–162
- Krainacker DA, Carey JR (1989) Reproductive limits and heterogeneity of male twospotted spider mites. *Entomol Exp Appl* 50:209–214
- Lewontin RC (1965) Selection for colonizing ability. In: Baker HG, Stebbins GL (eds) The genetics of colonizing species. Academic Press, San Diego, Calif. pp 79–94
- Margolies DC, Wrench DL (1996) Temperature-induced changes in spider mite fitness: offsetting effects of development time, fecundity, and sex ratio. *Entomol Exp Appl* 78:111–118
- Moraes GJ de, McMurtry JA (1987) Effect of temperature and sperm supply on the reproductive potential of *Tetranychus evansii* (Acari: Tetranychidae). *Exp Appl Acarol* 3:95–107
- Overmeer WPJ (1972) Notes on the mating behaviour and sex ratio of *Tetranychus urticae* (Koch) (Acarius: Tetranychidae). *Entomol Ber* 32:240–244
- Pianka ER (1988) Evolutionary ecology, 4th edn. Harper & Row, New York
- Potter DA (1978) Functional sex ratio in the carmine spider mite. *Ann Entomol Soc Am* 71:218–222
- Roy M, Brodeur J, Cloutier C (1999) Seasonal abundance of spider mites and their predators on red raspberry in Quebec. *Environ Entomol* 28:735–747
- Roy M, Brodeur J, Cloutier C (2002) Relationship between temperature and developmental rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). *Environ Entomol* 31:177–187
- Roy M, Brodeur J, Cloutier C (2003) Effect of temperature on intrinsic rates of natural increase (r_m) of a coccinellid and its spider mite prey. *BioControl* 48:57–72
- Sabelis MW (1985) Reproductive strategies. In: Helle W, Sabelis MW (eds) Spider mites, their biology, natural enemies and control. Elsevier, Amsterdam, pp 237–278
- Sabelis MW (1991) Life history evolution of spider mites. In: Schuster R, Murphy PW (eds) The Acari. Reproduction, development and life-history strategies. Chapman & Hall, New York, pp 23–49
- Sabelis MW, Janssen A (1996) Evolution of life-history patterns in the Phytoseiidae. In: Houck MA (ed) Mites: ecological and evolutionary analyses of life-history patterns. Chapman & Hall, New York, pp 70–98
- SAS Institute (1999) SAS/STAT User's Guide, Version 8. SAS Institute, Cary, N.C.
- Shih CT (1979) The influence of age of female *Tetranychus kanzawai* on sex ratio and life cycle of its progeny. In: Rodriguez JG (ed) Recent advances in acarology, vol 1. Academic Press, San Diego, pp 511–517
- Stoks R (2001) Male-biased sex ratios in mature damselfly populations: real or artefact? *Ecol Entomol* 26: 181–187
- Veerman A (1985) Diapause. In: Helle W, Sabelis MW (eds) Spider mites, their biology, natural enemies and control Elsevier, Amsterdam, pp 279–316
- Waage JF (1986) Family planning in parasitoids: Adaptive patterns of progeny and sex allocation. In: Waage JK, Greathead D. (eds) Insect parasitoids. Academic Press, New York, pp 63–95
- Wellington WG, Johnson DL, Lactin DJ (1999) Weather and insects. In: Huffaker CB, Gutierrez AP (eds) Ecological entomology. Wiley, New York, pp 313–353
- Werren JH, Charnov EL (1972) Facultative sex ratios and population dynamics. *Nature* 272: 349–350
- Wrench DL (1993) Evolutionary flexibility through haploid males or how chances favors the prepared genome. In: Wrench DL, Ebbert MA (eds) Evolution and diversity of sex ratio in insects and mites. Chapman & Hall, New York, pp 118–149
- Wrench DL, Young SSY (1975) Effects of quality of resource and fertilization status on some fitness traits in the two-spotted spider mite, *Tetranychus urticae* Koch. *Oecologia* 18:259–267
- Wrench DL, Young SSY (1978) Effects of density and host quality on rate of development, survivorship, and sex ratio in the carmine spider mite. *Environ Entomol* 7:499–501
- Young SSY, Wrench DL, Kongchuensin M (1986) Control of sex ratio by female spider mites. *Entomol Exp Appl* 40:50–60