

Population sex ratio in 3 species of eriophyid mites differing in degree of sex dissociation

KATARZYNA MICHALSKA¹ and DARIUSZ R. MAŃKOWSKI²

¹Department of Applied Entomology, Warsaw Agricultural University, 02-776 Warsaw, Nowoursynowska 159, Poland; katarzyna_michalska@sggw.pl;

²Laboratory of Seed Production and Plant Breeding Economics, Department of Seed Science and Technology, Plant Breeding and Acclimatization Institute, Radzików, Poland

(Received on 18 January 2006, accepted on 10 August 2006)

Abstract: Eriophyid males and females do not mate, as females are sexually independent in picking up sperm from spermatophores deposited by males (sex dissociation). However, species vary in the degree of male-male competition, and some temporary association of males with sexually independent females can be noted. We examined the sex ratio of *Aculus robiniae* (Nalepa), where males guard female quiescent nymphs (FQNs) and surround them with spermatophores; *Acalitus essigi* (Hassan), where males visit FQNs for a short time and rarely deposit spermatophores beside them; and *Cecidophyopsis hendersoni* (Keifer), where males do not associate with females. The proportion of males among adults (estimated for the whole observational period) reached 0.601 in *A. robiniae* (leaflets of black locust); 0.173 and 0.325 in *A. essigi* (current-year buds and fruiting shoots of blackberry, respectively); and 0.416 in *C. hendersoni* (apical leaves of yucca). Our results and those obtained by other authors indicate that a relatively high proportion of eriophyid males in a population (≈ 0.5), although intensifying male-male competition, is not a precondition for the occurrence of male interest in females and guarding. Other species-specific features, such as the degree of polyandry, can be key factors instead. The sex ratio of the 3 eriophyid species reported herein varied significantly between seasons, individual plants and/or plant organs. There were significant differences between proportions of *A. essigi* males at the base of fruiting shoots, on pedicels, and in fruits, and in the case of *C. hendersoni* between plants, but without differences between the first (the youngest) and fourth (much older) apical leaf.

Key words: *Aculus robiniae*, *Acalitus essigi*, *Cecidophyopsis hendersoni*, female re-mating, guarding, male-male competition, sex ratio, spermatophore deposition

INTRODUCTION

Knowledge about sex ratio can be useful both for applicative purposes, such as biological control and conservation, and in theoretical studies of life histories, population dynamics, or sexual selection (WEST & HERRE 2002, BESSA-GOMES et al. 2004). The operational sex ratio (OSR), i.e. the proportion of males to females ready to mate, is the central concept in predicting the intensity of mate competition

and which sex competes for which. For example, the greater the male bias, the more intense competition between males is expected. As direct measurement of OSR is often difficult or precluded, other proxy measurements of intensity of mating competition are used. These include factors strongly influencing OSR, such as: population sex ratios, female re-mating frequency, distribution of males and females, sexual differences in potential reproductive rates (PRRs), and costs of breeding (CLUTTON-BROCK & PARKER 1992, KOKKO & MONAGHAN 2001, MARKOW 2002).

Eriophyids are haplodiploids that reproduce by sex dissociation. Generally, under this mode of reproduction, males do not mate with females. Females actively search for spermatophores deposited by males and are independent in picking up sperm. Recent findings have revealed, however, that eriophyid males can temporarily associate with sexually independent females (female quiescent nymphs = FQNs) and intensity of male-male competition can be high (MICHALSKA & BOCZEK 1991, MICHALSKA 1999).

So far, no direct measurements of mating competition have been carried out in these mites. The possible impact of population sex ratios and other ecological factors on eriophyid male-male competition is also unknown.

In this paper we present data on proportions of males and females in 3 species of eriophyid mites that markedly differ in degree of sex dissociation: *Aculus robiniae* (Nalepa), where males guard FQNs and deposit several spermatophores beside them (MICHALSKA 1999); *Acalitus essigi* (Hassan), with sporadic visitations and depositions of spermatophores beside FQNs (MICHALSKA & BOCZEK 1991); and *Cecidophyopsis hendersoni* (Keifer), with increased spermatophore deposition rate in the presence of virgin females (MICHALSKA & SHI 2004). No physical interactions between males and females have been recorded so far. The study aimed to estimate the influence of seasons, individual plants and plant organs on eriophyid sex ratio and the role of the sex ratio in moulding the species-specific intensity of competition between males and the degree of their association with females.

MATERIALS AND METHODS

General methods and sex ratio assessment

Mites were collected from plants with the aid of a needle under a stereomicroscope and transferred into a drop of Heinze medium (EVANS 1992). Males and females were identified and counted on microscopic slides under a phase-contrast dissecting microscope.

Acalitus essigi

The mite was sampled in 1988 from a group of heavily infested wild blackberry bushes (*Rubus* sp.) growing in the Międzyborów woods near Skierniewice, Poland. The eriophyid sex ratio was examined in (1) current-year generative buds, which appeared in May-June on vegetative primary laterals ('primocanes'); (2) previous-year generative buds, which were formed on 'primocanes' in the year preceding the observation; and on (3) flowering and fruiting shoots (under scales of the basal part of the shoot, on pedicels, and in flowers and/or fruits), which developed from the previous-year buds. The sex ratio in current-year buds was monitored monthly, from

the end of blackberry blossoming until the fruit ripened and dried on shoots, while in previous-year buds every two weeks (from the initial stage of shoot internode elongation until the end of blackberry ripening). Each sample consisted of $N = 8$ buds, flowering or fruiting shoots. The sex ratio was estimated for all mites that were in individual buds or on shoots.

To determine whether the proportion of males and females is affected by the site of mite occurrence on a fruiting shoot and sampling date, 9 fruiting shoots were collected 3 times during the season: when blackberry fruits were pinkish, red and black. For each sample of $N = 3$ shoots, the sex ratio of adult eriophyids was assessed (1) under scales of the basal part of the shoots; (2) on pedicels; and (3) in fruits.

Aculus robiniae

This eriophyid species was collected in 1995 from a single black locust tree (*Robinia pseudoacacia* L.) growing on the campus of the Warsaw Agricultural University. On each date of mite collection, $N = 10$ leaflets were picked. The sex ratio was estimated for all adult eriophyids found on the underside of individual leaflets.

Cecidophyopsis hendersoni

The mite was mass-reared on potted *Yucca* plants in a growth room at 26°C and 16/8 h L/D photoperiod. Eriophyids were collected monthly in June–September 2005 from $N = 18$ randomly selected 1–4 apical unfolded leaves. To evaluate whether the sex ratio of the eriophyid is affected by leaf age, on 20 September we used 12 plants and compared the proportion of males on the first and fourth apical leaf of each plant by conducting $N = 2$ measurements per leaf area of ca. 0.6 cm in diameter, which was randomly sampled from an infested leaf patch. The proportion of males was estimated for the first 50 adult mites that were previously identified on microscopic slides.

Behavioural observations

Before collecting *A. essigi* from under scales or from blackberry fruits, as well as *C. hendersoni* from yucca leaves, additional behavioural observations were made to detect possible associations between sexes. We checked whether males visited FQNs and showed any particular interest in them (e.g. nymph body tapping, mounting, spermatophore deposition beside them, etc.), or paired with females terminating in spermatophore deposition and picking up of sperm by the females. Whenever such behaviours were observed, mites accompanying FQNs or females were sexed under a phase-contrast dissecting microscope.

Statistical analysis

The analysis was performed by using the software package SAS (SAS INSTITUTE 2004a, b). The sex ratio data was expressed as proportion of males in the total number of adults, and generalized linear models with binomial error structure and logit link function were applied (CRAWLEY 2002, WILSON & HARDY 2002). Analysis of deviance was conducted by using the PROC GENMOD procedure with the DSCALE option to correct for data over-dispersion (heterogeneity factor >1) and CONTRAST statement to test for pairwise differences. To limit the overall experiment-wise error rate, we additionally applied the sequential Bonferroni procedure for

multiple comparisons (see BOOSMA & NACHMAN 2002). To test the effect of leaves on proportions of *C. hendersoni* males, the plant variable was included as a block (plant \times leaf interaction was not investigated). Preliminary analysis of deviance (and model simplification) revealed the significant impact of site (i.e. the part of the fruiting shoot) on the proportion of *A. essigi* males. The heterogeneity factor, however, exceeded 4, indicating a serious over-dispersion of the data. The analysis of the effect of site and date on *A. essigi* sex ratio is, therefore, based on the general linear model with a normal error structure and arcsine-transformed data (GLM procedure in SAS) (WILSON & HARDY 2002). Means were compared by using the Tukey (HSD) test. Data were reported as back-transformed means and 95% confidence intervals (SOKAL & ROHLF 1995). Grand means were given as the proportion of total male counts and sum of adult samples (N) that were obtained during the whole observational period. The 95% confidence limits of the grand means were calculated from the binomial distribution.

RESULTS

Aculus robiniae

The grand mean proportion of males found on the black locust leaflets during the growing season in 1995 was 0.601 ($N = 1655$, CI: 0.570-0.630). The sex ratio was significantly influenced by the date of mite collection (date: $F_{3,36} = 9.93$, $P < 0.001$) (Fig. 1). In late spring (27 May), at the moment of development of the first mite generation, the sex ratio was markedly skewed towards females. It significantly differed from the proportion of sexes estimated in summer months, during which, by contrast, males outnumbered females on leaves.

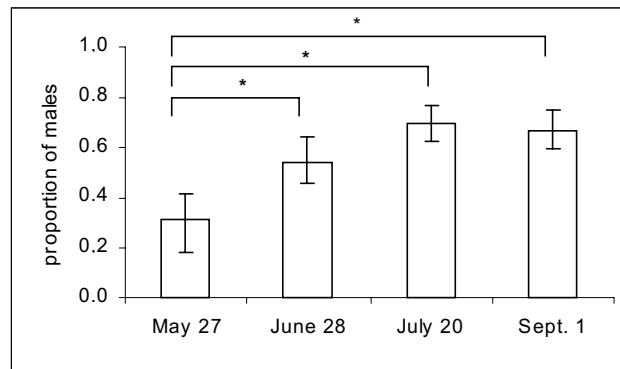


Fig. 1. Sex ratio of *Aculus robiniae* (Nalepa) on black locust leaflets during the growing season in 1995 (* $P < 0.05$)

Acalitus essigi

The date of mite collection had a significant impact on the sex ratio of this eriophyid species within current-year generative buds (date: $F_{4,35} = 23.55$, $P < 0.001$). On 16 June, at the beginning of development of the first mite generation within the

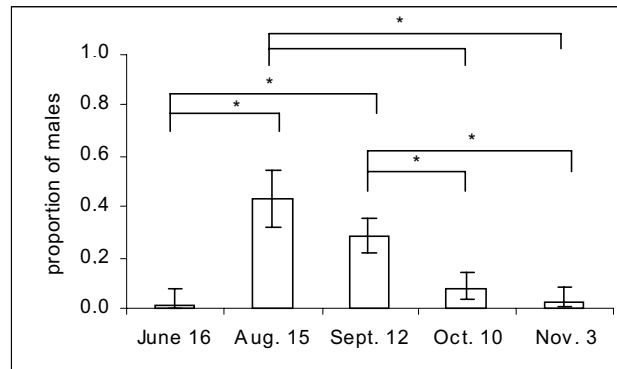


Fig. 2. Sex ratio of *Acalitus essigi* (Hassan) within current-year buds of blackberry during the growing season in 1988 (* $P < 0.05$)

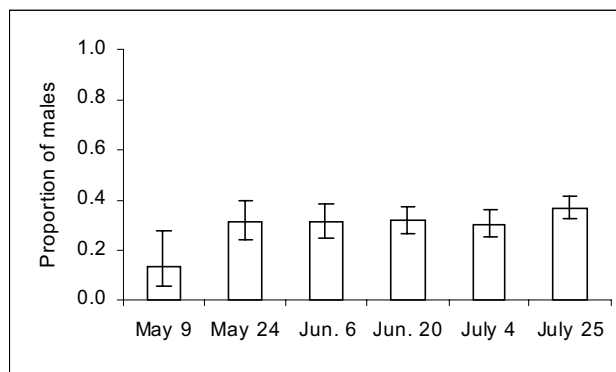


Fig. 3. Sex ratio of *Acalitus essigi* (Hassan) within previous-year buds, on flowering and fruiting shoots of blackberry during the growing season in 1988 (* $P < 0.05$)

buds, the proportion of males was very small (Fig. 2). It differed significantly from the sex ratios recorded in the following months, except those from October and November, when male numbers per bud were very small again. The proportions of males noted on 15 August and 12 September did not differ significantly from each other and were the greatest during the season. The grand mean proportion of males within current-year buds was 0.173 ($N = 923$; CI: 0.148-0.201).

As revealed by the analysis of deviance, sex ratio of this mite species within previous-year generative buds and on shoots that developed from the buds did not change significantly in May–July (date: $F_{5,42} = 2.4$, $P = 0.052$) (Fig. 3). The mean proportion of males calculated for the whole observational period was 0.325 ($N = 3860$, CI: 0.308-0.342).

The proportion of males on fruiting shoots was affected by 2 factors: shoot part (site: $F_{2,18} = 13.06$, $P = 0.0003$) and sampling date (date: $F_{2,18} = 12.79$, $P = 0.0003$). The interaction between site and date was non-significant (site \times date: $F_{4,18}$

= 0.64, $P = 0.6406$). The proportion of males was significantly smaller in fruits than under scales or on pedicels, while the differences between the latter 2 sites were non-significant (Fig. 4A). On 26 June, the overall proportion of males on fruiting shoots was significantly lower when fruits became pinkish than in the following months of fruit ripening (Fig. 4B).

During the growing season, males visiting FQNs under scales of fruiting shoots were frequently observed. Males did not pair with females but showed a marked interest in the FQNs, tapping their bodies with the forelegs, clinging tightly or mounting them. On 2 occasions, males depositing spermatophores beside FQNs were observed. By contrast, such male behaviours among drupelets of the aggregate fruits were not recorded.

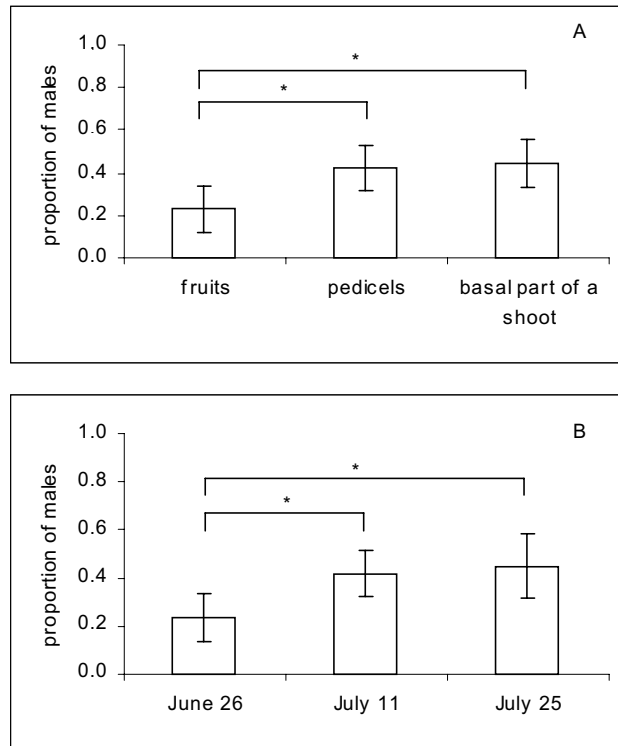


Fig. 4. Sex ratio of *Acalitus essigi* (Hassan) on fruiting shoots of blackberry in 1988: (A) effect of shoot part, (B) changes during shoot growth and fruit ripening ($*P < 0.05$)

Cecidophyopsis hendersoni

The date of mite collection had an effect on sex ratio ($F_{3,68} = 4.16$, $P = 0.0092$) (Fig. 5). On 20 September, the mean proportion of males was significantly lower than in the preceding months. The age of the apical leaf (first versus fourth) had no significant influence on the sex ratio of the mite (leaf: $F_{1,35} = 0.59$, $P = 0.4476$), while the plant had a significant effect (plant: $F_{11,35} = 5.49$, $P < 0.0001$). The proportion of

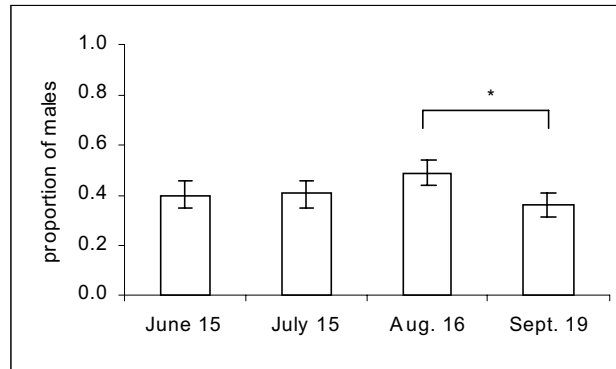


Fig. 5. Sex ratio of *Cecidophyopsis hendersoni* (Keifer) on potted yucca plants in June–September 2005 (* $P < 0.05$)

males calculated for the whole observational period was 0.416 ($N = 4998$, CI: 0.400–0.432).

Behavioural observations made on dozens of males directly within colonies did not reveal any physical interactions between sexes. Males neither visited FQNs, nor showed any particular interest in females.

DISCUSSION

If insect females are inseminated only once, or a few times but at long intervals in their lives, or they are receptive shortly after emergence, it can be beneficial for males to search for females in emergence sites and to be the first to copulate (THORNHILL & ALCOCK 2001). In eriophyids, the low frequency of female inseminations is presumably associated with asymmetrical sperm storage, which is a widespread phenomenon among species from dicot hosts and can also occur in some species that infest monocots (OLDFIELD 1999).

The frequency of female inseminations (= degree of polyandry) and the intensity of male-male competition appear to be key factors responsible for sex associations observed in some eriophyid species (Table 1). Rare inseminations by females can considerably intensify male-male competition due to a drop in the availability of receptive females (and male skew in OSR). *Aculus robiniae* females pick up sperm (and presumably become inseminated) from one, or, much more rarely, two spermatophores during their lifetime (MICHALSKA unpublished), which seems to favour guarding. The proportions of males and females in the field, however, could also affect male-male competition in this mite. Sex ratios of eriophyid mites, as of other haplodiploids, are usually female-biased (SABELIS & BRUIN 1996). In our study, males of *A. robiniae* made up nearly 60% of adults. Across eriophyid species, such a proportion of sexes can assure, relatively, the greatest supply of sexually active males in a population. As shown in Table 1, however, a proportion of males close to or above 0.5 is not a necessary precondition for the occurrence of male interest in females and guarding. For instance, in the polyandrous *Cecidophyopsis hendersoni*, males

Table 1. Sex associations, frequency of female inseminations, and population sex ratios of eriophyid mites

Mite species	Male associations with female quiescent nymphs	Frequency of inseminations by males	Proportion of males among adults
<i>Abacarus hystrix</i> (Nalepa)	guarding (A. SKORACKA unpubl. data)	probably single insemination (OLDFIELD 1999)	0.4, quack grass, Aug–Sep 2005 (A. SKORACKA unpubl. data)
<i>Aculus robiniae</i> (Nalepa)	guarding (MICHALSKA 1999)	no insemination recorded, only mounting 1–2 spermatophores (K. MICHALSKA unpubl. data)	0.60 black locust (this study)
<i>Aculops lycopersici</i> (Tryon)	no guarding (K. MICHALSKA unpubl. data)	probably single insemination (OLDFIELD 1999)	0.64 (tomato) (BAILEY & KIEFER 1943)
<i>Acalitus essigi</i> (Hassan)	visits (MICHALSKA & BOCZEK 1991)	?	0.17, current-year buds 0.33, fruiting shoots of blackberry (this study)
<i>Aculus fockeui</i> (Nalepa and Trouessart)	visits (PUTMAN 1938, MICHALSKA & BOCZEK 1991)	single insemination (OLDFIELD & NEWELL 1973a)	0.2–0.3 (plum) (PUTMAN 1938)
<i>Cecidophyopsis ribis</i> (Westwood)	visits (B. FENTON unpubl. data)	?	0.22, blackcurrant (from CSAPO 1992)
<i>Cecidophyopsis hendersoni</i> (Keifer)	no physical interactions with females or female quiescent nymphs (this study)	no insemination recorded, only mounting several spermatophores (K. MICHALSKA unpubl. data)	0.42, yucca (this study)

make up on average 40% of adults, but do not physically associate with females or FQNs (although the presence of virgins stimulates males for spermatophore deposition on infested leaves – MICHALSKA & SHI 2004); in *Aculops lycopersici* (Tryon), males outnumber females in a population (BAILEY & KEIFER 1943) but no guarding was observed (MICHALSKA unpublished); *Abacarus hystrix* (Nalepa) males guard FQNs, while field sex ratios appear to be female-biased (SKORACKA unpublished). It is likely that even slight inter-specific differences in frequency of female re-inseminations, male and female age at maturation, or potential reproductive rates, significantly differentiate OSRs across species, masking the effect of their overall sex ratios.

Although proportions of males and females in a population do not appear to correlate with the degree of sex dissociation across eriophyid species, this might not be true in the case of variation in male interest in females and male-male competition with-

in a species. Investigations on other taxa revealed that males can adjust their competitive behaviour to the current sex ratio (e.g. KVARNEMO et al. 1995). Also, marked discrepancy in sex ratio of *A. essigi* and male behaviour under scales and in fruits could account for such a correlation in these mites.

Possible explanations for the seasonal variation of the sex ratios could be: differential mortality and dispersal between males and females, changes in the viability of spermatophores, influenced by climatic conditions (STERNLICHT & GOLDENBERG 1972), or shifts in production of female offspring due to sperm depletion in once-inseminated eriophyid species (OLDFIELD & NEWELL 1973a). Generally, the female is the hibernating sex, which colonizes plants (LINDQUIST & OLDFIELD 1996). Thus, in spring, over-wintered females should prevail on plants, which may result in a strong female bias. Moreover, in species visiting spermatophores once or twice in their lifetimes, such as *A. robiniae* and also presumably *A. essigi*, as expected for most eriophyid species from dicot host plants (with asymmetrical sperm storage) (OLDFIELD 1999), the sex ratio of the first generation could be additionally skewed towards females due to a specific pattern of producing offspring of the two sexes. As revealed by OLDFIELD & NEWELL (1973a), *Aculus fockeui* produces predominantly females (female to male ratio 4:1) until sperm depletion, and then males only. Such a shift in production of offspring of the two sexes is also supported by field observations of another eriophyid that stores sperm asymmetrically, i.e. *Eriophyes emarginatae* (OLDFIELD 1969, 1999). This species produces one generation during the growing season and has initially female-skewed sex ratios (5.7:1), followed by the predominance of males in late reproductive life. Similarly, the outnumbering of males by over-wintered females, and then their daughters, may explain the female skew in the sex ratios of *A. robiniae* on leaves of the black locust in spring and *A. essigi* in current-year blackberry buds and fruits, after the summer migration of females to these sites from under scales and from pedicels of fruiting shoots.

One could also expect highly female-biased sex ratios of *A. essigi* at the beginning of the season within previous-year buds. However, the survey of the mite started when it already began to produce the second generation (9 May). The proportions of males at that time varied greatly among the buds and did not differ significantly from those found later in the season.

In autumn, as predicted, there was a gradual decrease in proportion of males in current-year buds due to male mortality. On the contrary, in *A. robiniae* one could expect male-skewed sex ratios at the end of the growing season because of the migration of deutogyne females to overwintering sites, as well as the possible 'overproduction' of males by last-generation protogynes (after sperm depletion). A significant male skew was found in autumn populations of the above-mentioned *Eriophyes emarginatae* (OLDFIELD 1969), as well as in *Aculus fockeui* on senescent peach leaves (OLDFIELD & NEWELL 1973b). Such a situation was also observed on 1 September on some black locust leaves. However, on the whole, we did not find any increase in the proportion of *A. robiniae* males at that time. Perhaps it was just the beginning of the deutogyne migration to crevices and/or 'overproduction' of males by protogynes, and a significant increase would be noted later in the season. Otherwise, the possible decrease in the number of deutogynes could be masked by a simultaneous increase in the mortality of males and protogynes on leaves.

The phenology of *Cecidophyopsis hendersoni* has not been investigated so far. When kept indoors, yucca plants usually curtailed all new growths after some months of eriophyid infestation, which resulted in a marked decline of the eriophyid population (K. MICHALSKA, unpubl. data). Also, on 20 September, more female-skewed sex ratios could have been connected with the beginning of the dormant period for yucca plants and an increased mortality of *C. hendersoni* males. Proportions of males significantly differed between the plants. This probably resulted from differences in the actual physiological state of the plants, as well as in the mortality and growth rate between sexes. Interestingly, *C. hendersoni* sex ratios were similar on the youngest (first) and the older (fourth) apical leaves. MICHALSKA & SHI (2004) found that the age of non-infested yucca leaves has a significant impact on spermatophore deposition by *C. hendersoni* males and mite settlement in general (with first apical leaves markedly preferred). When infested, however, all apical leaves are probably equally suitable for eriophyid survival. It is also likely that both sexes take part in migration to newly emergent leaves, which altogether makes the sex ratio of *C. hendersoni* similar within a plant.

It must be stressed that primary sex ratio and its shifts in response to external conditions (e.g. local mate or local resource competition) could also well explain the variation in proportions of males and females in populations (HARDY 2002). Haplodiploidy enables females to control the sex of their offspring through the process of fertilization. Such control has already been demonstrated in some arrhenotokous and pseudo-arrhenotokous mites (SABELIS et al. 2002). Females changed the primary sex ratio from female bias to equality, as the density (number of foundresses) increased or food availability decreased. Similarly, in eriophyids, one could expect less female-biased sex ratios in higher densities (e.g. later in the season) or on the less nutritive plant parts (e.g. senescent leaves, pedicels, and under scales of fruiting shoots). This aspect of eriophyid biology, however, still requires investigation.

Acknowledgements: We thank JAN BOCZEK for identification of the eriophyid species and PIOTR MATYJASIAK for his assistance in collecting *Acalitus essigi* and estimating its sex ratio. We are also indebted to GEORGE OLDFIELD and an anonymous referee for valuable comments on the manuscript.

REFERENCES

- BAILEY S. F., KEIFER H. H. 1943. The tomato russet mite, *Phyllocoptes destructor* Keifer: its present status. *J. Econ. Entomol.* 36: 706–712.
- BESSA-GOMES C., LEGENDRE S., CLOBERT J. 2004. Allee effects, mating systems and extinction risk in populations with two sexes. *Ecol. Lett.* 7: 802–812.
- BOOSMA J. J., NACHMAN G. 2002. Analysis of sex ratios in social insects. In: *Sex ratios, Concepts and Research Methods* (HARDY I. C. W., Ed.), pp. 93–111, Cambridge University Press, Cambridge.
- CLUTTON-BROCK T. H., PARKER G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Q. Rev. Biol.* 67: 437–456.
- CRAWLEY M. 2002. *Statistical Computing: An Introduction to Data Analysis using S-Plus*. J. Wiley, Chichester.
- CSAPO Z. 1992. Eriophyoid mites (Acarina, Eriophyoidea) on currants: morphology, taxonomy and ecology. PhD thesis, Warsaw Agricultural Univ., Warsaw, Poland.
- EVANS O. G. 1992. *Principles of Acarology*. C.A.B. International, Wallingford.

- HARDY I. C. W. 2002. Sex ratios, Concepts and Research Methods (HARDY I. C. W., Ed.), Cambridge University Press, Cambridge.
- KOKKO H., MONAGHAN P. 2001. Predicting the direction of sexual selection. *Ecol. Lett.* 4: 159–165.
- KVARNEMO CH., FORSGEN E., MAGNHAGEN C. 1995. Effects of sex ratio on intra- and inter-sexual behaviour in sand gobies. *Anim. Behav.* 50: 1455–1461.
- LINDQUIST E. E., OLDFIELD G. N. 1996. Evolution of eriophyid mites in relation to their host plants. In: *Eriophyoid mites: their biology, natural enemies and control* (LINDQUIST E. E., SABELIS M.W., BRUIN J., Eds), pp. 277–300, Elseviers Science Publ., Amsterdam, The Netherlands.
- MARKOW T. A. 2002. Perspective: female remating, operational sex ratio, and the arena of sexual selection in *Drosophila* species. *Evolution* 59: 1725–1734.
- MICHALSKA K. 1999. Spermatophore deposition and guarding in the free-living eriophyid mite *Vasates robiniae* (Acari). *Behaviour* 136: 899–918.
- MICHALSKA K., BOCZEK J. 1991. Sexual behaviour of males attracted to quiescent deutonymphs in the Eriophyoidea (Acari). In: *Modern Acarology* (DUSBABEK F., BUKVA V., Eds), Vol. 2, pp. 549–553, Academia, Prague, Checia, and SPB Academic Publishing bv, The Haque, The Netherlands.
- MICHALSKA K., SHI A. 2004. A first view on factors influencing spermatophore deposition by the eriophyid mite, *Cecidophyopsis hendersoni* (Keifer). In: *Acarine Biodiversity in the Natural and Human Sphere* (WEIGMANN G., ALBERTI G., WOHLTMANN A., RAGUSA S., Eds), Proc. V EURAAC Symposium, Berlin 2004, Phytophaga XIV, pp. 141–148, Tipolitografia Luxograph, Palermo, Italy.
- OLDFIELD G. N. 1969. The biology and morphology of *Eriophyes emarginatae*, a *Prunus* finger gall mite, and notes on *E. prunidemissae*. *Ann. Entomol. Soc. Am.* 62: 269–277.
- OLDFIELD G. N. 1999. Distribution of asymmetrical and symmetrical sperm storage in the Eriophyoidea and its phylogenetic implications. In: *Ecology and Evolution of the Acari* (BRUIN J., GEEST L. P. S., SABELIS M. W., Eds), pp. 157–161, Kluwer Academic Publishers.
- OLDFIELD G. N., NEWELL I. M. 1973a. The role of spermatophore in the reproductive biology of protogynes of *Aculus cornutus* (Acarina: Eriophyidae). *Ann. Entomol. Soc. Am.* 66: 160–163.
- OLDFIELD G. N., NEWELL I. M. 1973b. The spermatophore as the source of sperm for deutogynes of *Aculus cornutus* (Acari: Eriophyidae). *Ann. Entomol. Soc. Am.* 66: 223–225.
- PUTMAN W. L. 1939. The plum nursery mite (*Phyllocoptes fockeui* Nal. and Trt.). *Ann. Rept. Entomol. Soc. Ontario* 70: 33–40.
- SABELIS M. W., BRUIN J. 1996. Evolutionary ecology: life history patterns, food plant choice and dispersal. In: *Eriophyoid mites: their biology, natural enemies and control* (LINDQUIST E. E., SABELIS M. W., BRUIN J., Eds). Elseviers Science Publ., Amsterdam, The Netherlands.
- SABELIS M. W., NAGELKERKE J. C., BREEUWER J. A. J. 2002. Sex ratio control in arrhenotokous and pseudo-arrhenotokous mites. In: *Sex ratios, Concepts and Research Methods* (HARDY I. C. W., Ed.), pp. 235–253, Cambridge University Press, Cambridge.
- SAS INSTITUTE INC. 2004a. SAS 9.1 Companion for Windows. Cary, NC, USA, SAS Publishing, SAS Institute Inc.
- SAS INSTITUTE INC. 2004b. SAS/STAT 9.1 User's Guide. Cary, NC, USA, SAS Publishing, SAS Institute Inc.
- SOKAL R. R., ROHLF F. J. 1995. *Biometry*, 3rd ed. WH Freeman & Co., New York.
- STERNLICHT M., GOLDENBERG S. 1971. Fertilization, sex ratio and postembryonic stages of the citrus bud mite *Aceria sheldoni* (Ewing) (Acarina, Eriophyidae). *Bull. Ent. Res.* 60: 391–397.
- THORNHILL R., ALCOCK J. 2001. *The Evolution of Insect Mating Systems*. iUniverse.com, Inc. San Jose, New York.
- WEST S. A., HERRE A. E. 2002. Using sex ratios: why bother? In: *Sex ratios, Concepts and Research Methods* (HARDY I. C. W., Ed.), pp. 399–413, Cambridge University Press, Cambridge.
- WILSON K., HARDY I. C. W. 2002. Statistical analysis of sex ratios: an introduction. In: *Sex ratios, Concepts and Research Methods* (HARDY I. C. W., Ed.), pp. 48–92, Cambridge University Press, Cambridge.