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Basic and Applied Ecology xxx (2017) xxx–xxx

Basic and
Applied Ecology

www.elsevier.com/locate/baae

ORIGINAL PAPERS

Biased parasitoid sex ratios: *Wolbachia*, functional traits, local and landscape effectsZoltán László^{a,*}, Avar-Lehel Dénes^{a,b}, Lajos Király^{a,b}, Béla Tóthmérész^c^aHungarian Department of Biology and Ecology, Babeş-Bolyai University, str. Clinicilor nr. 5–7, 400006 Cluj-Napoca, Romania^bInterdisciplinary Research Institute on Bio-Nano-Sciences of Babes, Bolyai University, Treboniu Laurian 42, 400271 Cluj-Napoca, Romania^cMTA-DE Biodiversity and Ecosystem Services Research Group, Egyetem tér 1, 4032 Debrecen, Hungary

Received 9 June 2017; accepted 27 May 2018

Abstract

Adult sex ratio (ASR) is a key demographic parameter, being essential for the survival and dynamics of populations. Biased ASRs are adaptations to the environment on different scales, resulting from different mechanisms such as inbreeding, mating behaviour, resource limitations, endosymbionts such as *Wolbachia*, and changes in density or spatial distribution. Parasitoid ASRs are known to be strongly biased, but little information is available on how they are affected by large-scale variables such as landscape composition or fragmentation. We examined whether landscape scale variables affect the ASR of several parasitoid species belonging to the same tritrophic gall inducer community. We examined the effects of various explanatory variables on parasitoid ASR: the ovipositor length (a species level functional trait), resource amount (gall size) and density (local scale) as well as habitat amount, land use and landscape history (landscape scale). We controlled for the incidence and prevalence of *Wolbachia* infections. We found that parasitoid ASR is best explained by and positively correlated with ovipositor length and gall diameter. The interaction of functional traits with habitat availability also significantly explained parasitoid ASRs. Our results support the hypothesis that large-scale environmental characteristics affect parasitoid ASRs in addition to intrinsic and local characteristics.

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Keywords: ASR; Chalcidoidea; Rose galls; *Diplolepis*; Endosymbionts**Introduction**

The adult sex ratio (ASR), or the ratio of adult males to females in a population, has critical effects on the ecology and population dynamics of insects and animals (Pipoly et al., 2015). ASR for many species approaches 1:1, as outlined

by Fisher (1930). However, ASR ranges from populations that are heavily male-biased to those composed only of adult females (Xu et al. 2016). Understanding the causes and consequences of this variation is important in population biology and biodiversity conservation because it affects the fitness of populations through breeding systems (Pipoly et al., 2015).

Biased ASRs may be adaptations to conditions on various scales, such as inbreeding due to small population sizes, resource limitations, changes in density, or spatial distri-

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<https://doi.org/10.1016/j.baae.2018.05.014>

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bution (Kraft & Van Nouhuys 2013). Factors leading to biased ASRs include sex-differential mortality of immatures and adults or sex-differential dispersal and migration patterns (Székely, Liker, Freckleton, Fichtel, & Kappeler 2014). Biased ASRs may also be caused by reproductive parasites (endosymbionts) such as *Wolbachia* or *Cardinium* in many arthropod species (Floate & Kyei-Poku 2013) as they kill males (Werren 1997) and cause parthenogenesis (Provencher, Morse, Weeks, & Normak 2005; Duploux, Couchoux, Hanski, & Van Nouhuys 2015).

Several related population level factors may alter parasitoid ASR such as female wasp density and host density (King 1987). The local resource competition (LRC) theory (Clark 1978) explains male-biased ASR through the reduction of competition between daughters with small dispersal distances for local limiting resources (West 2009). Local mate competition (LMC) (Hamilton 1967) occurs when male relatives with low dispersal ability compete for mating opportunities, favouring female-biased sex allocation over time (Rodrigues & Gardner 2015), because they are originally more numerous than females (Herre 1985).

Parasitoid ASRs are known to be mostly female-biased (Hamilton 1967; Charnov, Hartogh, Jones, & van den Assem 1981). Egg-laying females control their offspring's sex in response to host quality, including host size. Haplodiploid sex determination provides parasitoid females a physiological mechanism for this control (Charnov et al. 1981). A population level mechanism is based on the prediction that the rarer sex in a population may have higher fitness, i.e. isolated females produce primarily daughters (Frank 1986). As the number of females increases, the number of sons has to increase as they become rarer (King 1987). Another population level mechanism is based on host density: at low host density brood size and sex ratio are strongly positively correlated, while at high density there is no such relationship (Kraft & Van Nouhuys 2013).

Functional traits such as ovipositor length of parasitoids are also adaptations to suboptimal conditions which may have significant effect on ASR (Sivinski & Aluja 2001; Sivinski, Vulinec, & Aluja 2001). For species with short ovipositors, host finding is difficult and therefore they may show low population densities and aggregated distributions (Alvarenga, Dias, Stuhl, & Sivinski 2016). Species with low population sizes and aggregated distributions are more likely to avoid LMC through female-biased ASRs (Alvarenga et al. 2016), while species with large population sizes tend to have male-biased (West 2009) or 1:1 ASRs.

Large-scale effects on parasitoid ASR are virtually unknown. Studies at this scale have usually targeted vertebrates (Amos et al., 2013; Amos et al., 2014; Reid & Peery 2014), while ASR in parasitoids (for a review see (King 1987)) has usually been explored at the individual (*Wolbachia* presence, genetic variability) or local scale (population size effects). In this study, we aimed to analyse large-scale variables affecting parasitoid ASR such as landscape composition, configuration and landscape history.

We used the community of common parasitoids inhabiting rose bedeguar galls (*Diplolepis rosae*) occurring on wild roses as a model system. We hypothesize that parasitoid ASRs are affected by large-scale variables as well as individual and local scale variables. Our predictions were as follows: (i) ovipositor length as a functional trait is positively related to parasitoid ASR: longer ovipositors may be regarded as adaptations to limited resources; (ii) available resource amount (=gall diameter, a small-scale variable) is negatively related to parasitoid ASR, since limited resources increase female bias; (iii) landscape characteristics (large-scale variables) are indirectly related to parasitoid ASR, since changes in available habitat are related to resource availability.

Materials and methods

Study area

Data were collected in three consecutive years (2004–2006) in seven landscapes (Fig. 1) located along a South-East–North-West axis of 328 km length from the Transylvanian Plateau (Romania) to the Great Hungarian Plain (Eastern Hungary). Surveyed habitats were semi-dry grasslands used as pasture along the axis. Galls were collected from randomly chosen 50 × 50 m area plots (N = 65) in habitats of the Robin's pincushion or rose bedeguar gall (*D. rosae*). Plot locations within the sites (each site is located in the center of a landscape) varied between the measurement years, thus, each plot was sampled only once. Usually 3 plots per year per site were surveyed (Appendix A: Table 1).

Study system

The Robin's pincushion induced by females of *D. rosae* has a Holarctic distribution, and is one of the most abundant cynipid galls in the Carpathian Basin and Eastern Europe. Gall wasp females produce multi-chambered galls on wild rose species, without a preference for a given rose species (Kohnen, Wissemann, & Brandl 2011). The most abundant primary solitary specialist parasitoid species of the *D. rosae* gall community in the Carpathian Basin are *Orthopelma mediator* (Ichneumonidae), *Pteromalus bedeguaris* (Pteromalidae), *Torymus bedeguaris* (Torymidae) and *Glyptomerus stigma* (Torymidae) (László, Rákossy, & Tóthmérész 2014). We chose these species to analyse various scale effects on parasitoid ASR. *O. mediator* and *P. bedeguaris* emerge early in the spring (early-flying species), when galls are small and have just begun to grow. *T. bedeguaris* and *G. stigma* emerge late in the spring (late-flying species), when galls are large and close to maturation (László & Tóthmérész 2011). Late-flying species have significantly longer ovipositor sheaths than early-flying species:

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