NOTE / NOTE

Using effects of parasitoid size on fitness to test a host quality model assumption with the parasitoid wasp *Spalangia endius*

B.H. King and M.E. Napoleon

Abstract: How body size affects fitness of males relative to females is relevant to understanding the evolution of sexual size dimorphism and maternal sex-ratio manipulation. In most parasitoid wasps, mothers oviposit a greater proportion of daughters in larger hosts. The host-quality model describes how this may be adaptive. A major assumption of the model is that host size has a greater effect on the fitness of daughters than of sons. The assumption has often been tested indirectly by examining the effects of parasitoid size on fitness, because a parasitoid's size generally increases with the size of the host on which it develops. The validity of this indirect method is examined here for the parasitoid wasp *Spalangia endius* Walker, 1839 parasitizing *Musca domestica* L., 1758. If the method is valid, effects of parasitoid size on fitness should match the effects of host size on fitness that were shown in a previous study. The effects matched in that both parasitoid size and host size affected the fitness of females but not of males. However, the aspects of female fitness that were affected differed. That female size but not male size affected fitness was consistent with the female-biased sexual size dimorphism of *S. endius*.

Résumé : L'effet de la taille corporelle sur la fitness des mâles par rapport à celle des femelles est un facteur important pour la compréhension de l'évolution du dimorphisme sexuel de la taille et de la manipulation maternelle du rapport mâles:femelles. Chez la plupart des guêpes parasitoïdes, les mères pondent un pourcentage plus élevé de rejetons femelles dans les hôtes de plus grande taille. Le modèle de la qualité de l'hôte décrit de quelle manière ce phénomène peut être adaptatif. Une présupposition majeure du modèle est que la taille de l'hôte a un effet plus important sur la fitness des rejetons femelles que sur celle des mâles. Cette présupposition a souvent été vérifiée indirectement par l'examen des effets de la taille du parasitoïde sur sa fitness, parce que la taille du parasitoïde augmente généralement en fonction de la taille de l'hôte sur lequel il se développe. Nous examinons la validité de cette méthode indirecte chez la guêpe parasitoïde *Spalangia endius* Walker, 1839 vivant sur *Musca domestica* L., 1758. Si la méthode est valide, les effets de la taille du parasitoïde sur sa fitness devraient être semblables à ceux de la taille de l'hôte sur la fitness qui ont été observées dans une étude antérieure. Les effets concordent en ce que tant la taille du parasitoïde que celle de l'hôte affectent la fitness des femelles, mais pas celle des mâles. Cependant, il y a des différences dans les aspects de la fitness des femelles qui sont affectés. Le fait que la taille des femelles, mais non celle des mâles, ait des effets sur la fitness est en accord avec dimorphisme sexuel de la taille qui favorise les femelles chez *S. endius*.

[Traduit par la Rédaction]

Introduction

The validity of a theoretical model can be tested by examining its predictions and (or) its assumptions. Quite often, for logistical reasons, such tests are indirect; e.g., if the most relevant variable is difficult to measure, a correlated variable may be measured in its place. Here we examine the validity of an indirect test that has been used to examine a critical assumption of the host-quality model. The host-quality model is an adaptive sex-ratio model (Charnov 1979; Charnov et al. 1981). It is a parasitoid version of the general hypothesis that selection will favor mothers with the ability to manipulate sex ratio in response to the amount of resources available to offspring when resource availability differentially affects the sexes (for similar hypothesis applied to vertebrates see Trivers and Willard 1973). Consistent with the host-quality model, most parasitoid wasps produce a greater proportion of daughters from larger hosts (reviewed in King 1993), and the model has become well accepted (e.g., Mousseau and Fox 1998).

Received 7 July 2006. Accepted 3 October 2006. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 15 December 2006.

B.H. King[1] and M.E. Napoleon.[2] Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115, USA.

[1] Corresponding author (e-mail: bking@niu.edu).
[2] Present address: John G. Shedd Aquarium, Chicago, IL 60605, USA.

doi:10.1139/Z06-162

A major assumption of the model is that the host size on which a parasitoid develops increases the fitness of daughters more than that of sons. This assumption has frequently been tested indirectly by examining effects of parasitoid size on fitness (e.g., van den Assem et al. 1989; Heinz 1991; Ueno 1998, 1999; Ji et al. 2004). Indirect tests seem logical because, as the model's authors suggested, the model's assumption could be met if the size of both male and female parasitoids generally increases with the size of the host on which it develops, and increased parasitoid size positively affects female fitness more than male fitness (Charnov et al. 1981). That a parasitoid's size generally increases with the size of the host on which it develops has been demonstrated for almost all species that have been examined (reviewed in King 1993). Indirect tests may sometimes be more practical, e.g., in the field when wasps have already left the hosts at the time that fitness is being measured (e.g., Karsai et al. 2006).

However, the host quality model equations deal only with host-size effects on fitness, not with parasitoid size, and it is the former not the latter that is critical to the model's predictions. Parasitoid-size effects may differ from host-size effects because of the imperfect relationship between host size and parasitoid size (see below), or in a small number of species, the absence of a relationship between parasitoid size and host size (e.g., Seidl and King 1993). Furthermore, host-size effects on fitness may occur through avenues other than parasitoid size (King 1993).

Here we examine the validity of the indirect method of testing the host quality model assumption with the parasitoid wasp *Spalangia endius* Walker, 1839 (Hymenoptera: Pteromalidae), a very small wasp that parasitizes the pupal stage of certain fly species found in and on decaying organic matter or manure (Rueda and Axtell 1985). A female *Spalangia* uses her ovipositor to drill through the outer shell of a host. She then deposits an egg on the host developing within or feeds on fluids exuding from wounds that she makes in the host. The parasitoid larva feeds on the host, with one parasitoid produced per host. Females are monandrous; males are polygynous (King et al. 2005).

In the strain of *S. endius* studied here, mothers tend to preferentially oviposit daughters in larger hosts, consistent with the host-quality model (Napoleon and King 1999). Also, consistent with the host-quality model, both female and male *S. endius* are larger when they develop on larger hosts, and developing on a larger host affects some aspects of female, but not male, fitness (Napoleon and King 1999). These results suggest how sex-ratio manipulation in response to host size may be adaptive in *S. endius*. If testing the model's assumption indirectly is valid, effects of parasitoid size should parallel these effects of host size, that is parasitoid size should affect female, but not male, fitness. Our test was under laboratory conditions. If the indirect test is not valid under the controlled conditions of the laboratory, it seems unlikely to be so under the less-controlled conditions of the field where the relationship between host size and parasitoid size will be much noisier. For example, in *Spalangia cameroni* Perkins, 1910, host width explains about 40% of the variation in parasitoid head width in the laboratory (B.H. King, unpublished data) vs. <5% in the field (King 1991).

Methods

A Florida strain of *S. endius* that was maintained on a natural host, *Musca domestica* L., 1758, was used (Napoleon and King 1999). Vouchers are at the Illinois Natural History Survey Center for Biodiversity, catalog numbers "Insect Collection 6035 through 6054". Parasitoid size was measured by removing heads from dead parasitoids, attaching them to a slide, projecting them onto a digitizing tablet, and then measuring head area using SigmaScan® version 3.90 (Systat Software, Inc. 1988). Head size is positively correlated with other measures of body size in *S. endius* (e.g., total wing area vs. head area: $r = 0.75$ for males and $r = 0.80$ for females; B.H. King, unpublished data). Wasps had no previous contact with other parasitoids (excluding mating) prior to use in an experiment. Experiments are summarized below; for details see Napoleon and King (1999). The care of our animals was in accordance with the principles and guidelines of the Canadian Council on Animal Care.

The effect of parasitoid size on a mother's offspring production was examined by presenting each of 30 mated females with 15 hosts and honey for each of 5 d. Then each female was kept in a vial plugged with cotton that was moistened daily, and day of death was recorded. Lifetime offspring production is positively correlated with production over the first 5 d in *S. cameroni* (King 1988). Total number of adult offspring and days that the mother was alive were each regressed against the mother's head size.

The effect of parasitoid size on a male's mating success was examined by presenting each of 14 males with 7 virgin females for 1 h in a glass vial plugged with cotton. Each female was then given 10 hosts for 24 h. The number of adult daughters produced by these females was determined for each father (only production of daughters requires sperm in haplodiploids such as wasps). The number of daughters was regressed against the father's head size. This initial male mating success experiment was suggestive but not statistically significant (see Results), so the experiment was repeated.

The effect of parasitoid size on longevity in the absence of hosts or other food was examined for 49 females and 25 males. Newly emerged parasitoids of both sexes were kept individually in test tubes plugged with moist cotton and day of death was recorded. Longevity was examined in the absence of food based on the significant effects in earlier studies with a congener (King 1988; King and King 1994).

Whether development duration is correlated with parasitoid size was also examined; e.g., parasitoids that achieve greater adult size may pay a cost in terms of longer development. So that we would know the time of oviposition relatively precisely, hosts were exposed to parasitoids for only 4 h at about 29 °C. Then each potentially parasitized host was isolated in a test tube and allowed to develop at a relatively cool 22 °C to lengthen development (Shibles 1969), accentuating any differences among parasitoids in duration of development. Date of emergence from the host was recorded. Correlation between development duration and parasitoid size was analyzed separately for each sex because of the sex difference in size (see Results).

Results

Large mothers produced more offspring than did small

Fig. 1. Number of offspring produced by *Spalangia endius* mothers with different head areas (mm^2) ($R^2 = 0.27$, $F_{[1,28]} = 10.11$, $P = 0.002$; $y = 245.62x - 25.06$).

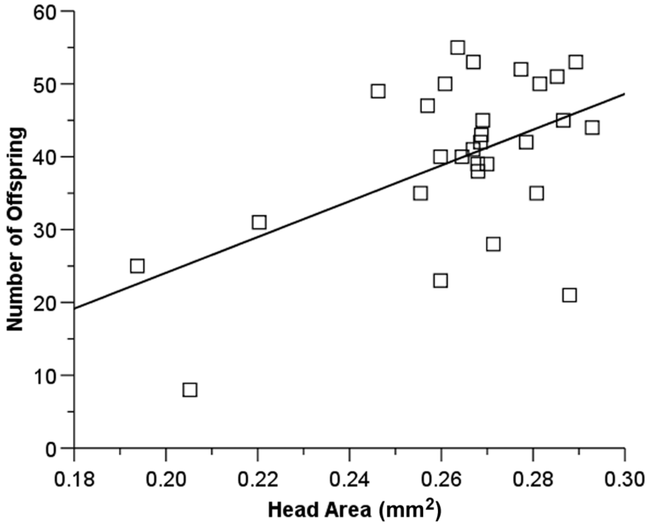
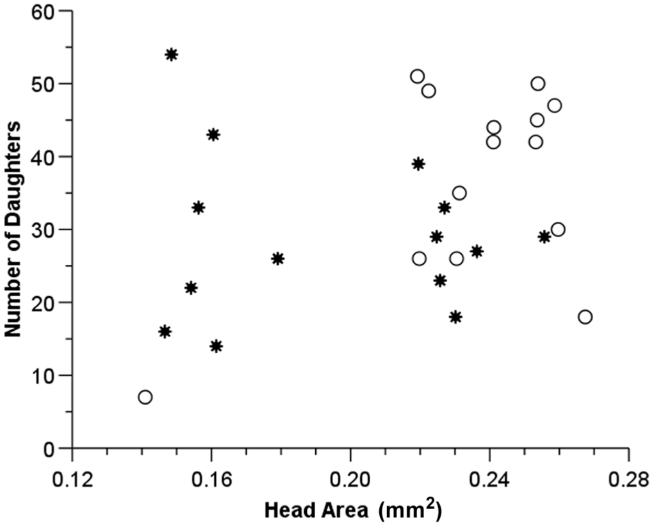


Fig. 2. Mating success as measured by the number of daughters produced by the mates of males with different head areas (mm^2). ○, experiment 1; *, experiment two (across both experiments: $R^2 = 0.093$, $F_{[1,26]} = 2.66$, $P = 0.12$; $y = 94.40x + 12.50$).



mothers (Fig. 1). Mothers produced 40 ± 2 offspring (mean ± SE, range 8–55, $n = 30$) of which 19% ± 1% (mean ± SE) were sons (range 4%–38%, $n = 30$). Longevity of these same mothers did not increase significantly with the mother's size ($R^2 = 0.012$, $F_{[1,28]} = 0.35$, $P = 0.28$). There was a positive relationship between a mother's size and the number of offspring that she produced even when the analysis was restricted to her first day of producing offspring ($R^2 = 0.24$, $F_{[1,27]} = 8.67$, $P = 0.007$).

In the first male mating success experiment, there was a tendency for larger males to have greater mating success as measured by the number of daughters produced by their mates (Fig. 2; $R^2 = 0.24$, $F_{[1,12]} = 3.81$, $P = 0.075$). However, the relationship was not statistically significant, and a single male was disproportionately smaller than the rest and responsible for the tendency towards significance. When the experiment was repeated, using as many small males as large males, the relationship was in the opposite direction and did not even approach significance (Fig. 2; $R^2 = 0.012$, $F_{[1,12]} = 0.14$, $P = 0.71$).

An analysis of covariance showed no significant effect of experiment ($F_{[1,25]} = 0.88$, $P = 0.36$), so data from the two experiments were pooled. However, a regression of the number of daughters on male size still showed no significant relationship (Fig. 2). The percentage of females that were successfully inseminated as indicated by producing any daughters was 70% ± 4% (mean ± SE, range 17%–100%, $n = 28$) and did not differ between the two experiments ($t_{[26]} = 0.86$, $P = 0.40$).

In the absence of hosts and other food, there was no significant relationship between longevity and head area for either females ($R^2 = 0.011$, $F_{[1,47]} = 0.53$, $P = 0.47$) or males ($R^2 = 0.017$, $F_{[1,23]} = 0.40$, $P = 0.53$). Development duration was not significantly correlated with head size among females ($r = -0.038$, $n = 93$, $P = 0.72$) or males ($r = -0.011$, $n = 57$, $P = 0.93$). The heads of females were, on average, of greater area than the heads of males (0.30 ± 0.002 mm^2 (mean ± SE) vs. 0.25 ± 0.002 mm^2; $t_{[148]} = 17.17$, $P < 0.001$). The heads of females were also wider (0.58 ± 0.002 mm vs. 0.57 ± 0.002 mm; $t_{[148]} = 4.33$, $P < 0.001$).

Discussion

The general effects of parasitoid size on female fitness vs. male fitness paralleled the effects of host size. Specifically, both host size (Napoleon and King 1999) and parasitoid size (this study) were not significantly related to male mating success, but were significantly related to female fitness. Thus, for *S. endius*, the host quality model assumption was supported regardless of whether one examined the effect of host size on fitness or the effect of parasitoid size on fitness.

However, having both data sets provided further information. This is because the aspects of female fitness that were affected were not identical. A female's offspring production increased with both parasitoid size and host size, but longevity and development duration were significantly affected only by host size, not by parasitoid size. The two data sets together suggest that the effect that a female's host size has on her subsequent offspring production may be mediated through effects on her size. In contrast, the two data sets suggest that the positive effects of a female's host size on her development duration and longevity (Napoleon and King 1999) do not occur through effects on her size: parasitoid-size effects on longevity and development time were both nonsignificant and in a negative direction.

Most studies of the host quality model assumption provide data on how female fitness vs. male fitness is affected by either host size (Jones 1982; Garcia Saez de Nanclares 1988) or parasitoid size (van den Assem et al. 1989; Heinz 1991; Ueno 1998, 1999; Ji et al. 2004), but not both. The present study illustrates the value of providing both. Likewise, examination of data on two other parasitoid wasps, *Muscidifurax raptor* Girault and Sanders, 1910 and *S. cameroni*, also suggest that the effects of parasitoid size on fitness will not necessarily parallel the effects of host size on fitness (Seidl and King 1993; King and King 1994: based on comparison of Tables 2 and 3 and assuming that offspring production is a more relevant measure of fitness for females than egg number at emergence). In the case of *M. raptor*, this is not surprising given that host size and parasitoid size are unrelated (Seidl and King 1993). In *S. endius* and *S. cameroni*, parasitoid size tends to be positively correlated with host size, although not very strongly and not in every strain (Table 1 in Napoleon and King 1999).

Taken together, the results of these earlier studies and the present one show that the indirect method sometimes, but not always, leads to the same conclusion about the host quality model assumption as the direct method. Thus, the indirect method should be avoided in species without strong correlations between parasitoid size and host size. Whether the indirect method works consistently in species with stronger correlations remains to be seen.

That female but not male size affected fitness in *S. endius* was consistent with the female-biased sexual size dimorphism observed in this species (Napoleon and King 1999). Sexual size dimorphism is female-biased in most parasitoid wasp species (Hurlbutt 1987). However, reported effects of size on relative fitness appear to be quite variable among species and not related to sexual size dimorphism in a consistent pattern (van den Assem et al. 1989; Heinz 1991; Seidl and King 1993; King and King 1994; Ueno 1998, 1999; Ji et al. 2004). In most species, size positively affects female fitness; however, effects on male fitness are more variable among species and have been less studied. Interestingly, the magnitude of the effect of female head size on offspring production in *S. endius* in the present study was similar to the magnitude in an experiment with a significant effect for *S. cameroni* (King and King 1994), about 20–30 more offspring in the first 5 d of production for every 0.1 mm increase in head width.

Effects of parasitoid size on parasitoid fitness are relevant not only to understanding the host-quality model and sexual size dimorphism but also biological control. Some of the fly species that *S. endius* parasitizes are pests (Rueda and Axtell 1985). *Spalangia endius* provides some natural control of these pests and is sold commercially for biological control purposes (Hunter 1997; Johnson 1998). That fitness of female *S. endius* increased with parasitoid size suggests that size may be a useful measure of their quality in mass rearing programs. Size may be an important predictor of their effectiveness in rapidly building up numbers during mass rearing and in pest control upon release in the field.

Acknowledgements

Thanks go to C. Geden for starter *S. endius*, C. Cowan for measuring heads, and R. King for comments on the manuscript and for statistical advice. This research was supported by the Department of Biological Sciences at Northern Illinois University.

References

Charnov, E.L. 1979. The genetical evolution of patterns of sexuality: Darwinian fitness. Am. Nat. **113**: 465–480. doi:10.1086/283407.

Charnov, E.L., Los-den Hartogh, R.L., Jones, W.T., and van den Assem, J. 1981. Sex ratio evolution in a variable environment. Nature (London), **289**: 27–33. doi:10.1038/289027a0. PMID:7453809.

Garcia Saez de Nanclares, C. 1988. Sex ratio and fitness in a parasitic wasp. Ph.D. dissertation, University of London, London.

Heinz, K.M. 1991. Sex-specific reproductive consequences of body size in the solitary ectoparasitoid *Diglyphus begini*. Evolution, **45**: 1511–1515. doi:10.2307/2409897.

Hunter, C.D. 1997. Suppliers of beneficial organisms in North America. California Environmental Protection Agency. Available from http://www.cdpr.ca.gov/docs/ipminov/bscover.htm [accessed 15 June 2006].

Hurlbutt, B.L. 1987. Sexual size dimorphism in parasitoid wasps. Biol. J. Linn. Soc. **30**: 63–89.

Ji, J., Choi, W.I., and Ryoo, M.I. 2004. Fitness and sex allocation of *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae): relative fitness of large females and males in a multi-patch system. Ann. Entomol. Soc. Am. **97**: 825–830. doi:10.1603/0013-8746(2004)097[0825:FASAOA]2.0.CO;2.

Johnson, D. 1998. Vendors of beneficial organisms in North America. Available from http://www.uky.edu/Agriculture/Entomology/entfacts/fldcrops/efl25.htm [accessed 15 June 2006].

Jones, W.T. 1982. Sex ratio and host size in a parasitoid wasp. Behav. Ecol. Sociobiol. **10**: 207–210. doi:10.1007/BF00299686.

Karsai, I., Somogyi, K., and Hardy, I.C.W. 2006. Body size, host choice and sex allocation in a spider hunting pompilid wasp. Biol. J. Linn. Soc. **87**: 285–296. doi:10.1111/j.1095-8312.2006.00576.x.

King, B.H. 1988. Sex-ratio manipulation in response to host size by the parasitoid wasp *Spalangia cameroni*: a laboratory study. Evolution, **42**: 1190–1198. doi:10.2307/2409003.

King, B.H. 1991. A field study of host size effects on sex ratio of the parasitoid wasp *Spalangia cameroni*. Am. Midl. Nat. **125**: 10–17. doi:10.2307/2426364.

King, B.H. 1993. Sex ratio manipulation by parasitoid wasps. *In* Evolution and diversity of sex ratio in insects and mites. *Edited by* D.L. Wrensch and M.A. Ebbert. Chapman and Hall, New York. pp. 418–441.

King, B.H., and King, R.B. 1994. Sex ratio manipulation in response to host size in the parasitoid wasp *Spalangia cameroni* — Is it adaptive? Behav. Ecol. **5**: 448–454.

King, B.H., Saporito, K.B., Ellison, J.H., and Bratzke, R.M. 2005. Unattractiveness of mated females to males in the parasitoid wasp *Spalangia endius*. Behav. Ecol. Sociobiol. **57**: 350–356. doi:10.1007/s00265-004-0863-9.

Mousseau, T.A., and Fox, C.W. 1998. The adaptive significance of maternal effects. Trends Ecol. Evol. **13**: 403–407. doi:10.1016/S0169-5347(98)01472-4.

Napoleon, M.E., and King, B.H. 1999. Offspring sex ratio response to host size in the parasitoid wasp *Spalangia endius*. Behav. Ecol. Sociobiol. **46**: 325–332. doi:10.1007/s002650050626.

Rueda, L.M., and Axtell, R.C. 1985. Guide to common species of pupal parasites (Hymenoptera: Pteromalidae) of the house fly and other muscoid flies associated with poultry and livestock manure. N.C. Agric. Res. Serv. Tech. Bull. No. 278.

Seidl, S.E., and King, B.H. 1993. Sex ratio response to host size in the parasitoid wasp *Muscidifurax raptor*. Evolution, **47**: 1876–1882. doi:10.2307/2410228.

Shibles, D.B. 1969. *Muscidifurax raptor* Girault and Saunders, *Spalangia endius* Walker and related species (Hymenoptera: Pteromalidae) as parasites of house flies in New Jersey. Ph.D. dissertation, Rutgers University, New Brunswick, N.J.

Systat Software, Inc. 1988. SigmaScan®. Version 3.90 [computer program]. Systat Software, Inc., San Jose, Calif.

Trivers, R.L., and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science (Washington, D.C.), **179**: 90–92. PMID:4682135.

Ueno, T. 1998. Adaptiveness of sex ratio control by the pupal parasitoid *Itoplectis naranyae* (Hymenoptera, Ichneumonidae) in response to host size. Evol. Ecol. **12**: 643–654. doi:10.1023/A:1006577314205.

Ueno, T. 1999. Host-size-dependent sex ratio in a parasitoid wasp. Res. Popul. Ecol. (Kyoto), **41**: 47–57.

van den Assem, J., van Iersel, J.J.A., and Los-den Hartogh, R.L. 1989. Is being large more important for female than for male parasitic wasps? Behavior, **108**: 160–195.