

Sexual Size and Shape Dimorphism in Three Species of Parasitoid Wasps with Burrowing Females: *Spalangia endius*, *Spalangia nigroaenea*, and *Spalangia nigra* (Hymenoptera: Pteromalidae)

B. H. King,^{1,3} Edwin R. Burgess, IV,¹ and Kaila L. Colyott^{1,2}

¹Department of Biological Sciences, Northern Illinois University, DeKalb, IL 60115, ²Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, and ³Corresponding author, e-mail: bking@niu.edu

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Abstract

The parasitoid wasps *Spalangia endius* Walker, *Spalangia nigroaenea* Curtis, and *Spalangia nigra* Latreille (Hymenoptera: Pteromalidae) develop on filth fly pupae. Females burrow through decaying organic matter and parasitize hosts; whereas, at least in *S. endius*, males tend to stay above ground searching for mates. Both sexes lack obvious digging morphology such as enlarged forelegs and are not known to exhibit physical aggression. Size data were obtained from specimens from Illinois field-collected hosts for all three species and from a Florida laboratory colony for *S. endius*. The degree of sexual size dimorphism varied with body part and species, but the direction of bias was consistent between the field and laboratory specimens of *S. endius*. Females had wider abdomens in *S. nigroaenea* and *S. nigra* (not measured in *S. endius*). In all three species, females had longer heads than males, both in absolute size and relative to width. The latter is referred to as narrowness. Forewings were significantly narrower in females compared with in males for both *S. endius* and *S. nigroaenea*. Thorax narrowness was either greater in males (*S. endius*) or was not significantly different between the sexes (*S. nigroaenea* and *S. nigra*). Patterns of sexual size dimorphism seem consistent with females' need to store eggs and burrow. For all three species, there was overlap between males and females in all body parts measured. Thus, these size measurements will be unreliable to differentiate the sexes. Size ratios also overlapped.

Key words: body size, parasitoid wasp, Pteromalidae, sexual size dimorphism, shape

Sexual size dimorphism is body size differences between males and females within a species (Stillwell et al. 2010). Female-biased sexual size dimorphism is a common pattern among insects and invertebrates generally (Vollrath 1998, Teder and Tammaru 2005, Irie and Morimoto 2008, Stillwell et al. 2010). This pattern is evident in many parasitoid wasp species. In a literature review of 361 species in 21 families, overall body length was the most common measure of size, and female-biased sexual size dimorphism in length was observed in a majority of species and families (Hurlbutt 1987). For most species, only minimum and maximum length was available.

The traditional explanation of female-biased sexual size dimorphism in parasitoids is that body size has a greater effect on female egg production than on male mating success (Charnov 1982). Males may benefit from emerging as adults before females do, because it allows males to intercept emerging females (e.g., Moynihan and Shuker 2011). Emerging before females necessitates that males develop for a shorter time period, which may lead

to female-biased size dimorphism (Roff 2000). Other fitness effects of parasitoid size may also be important in influencing sexual size dimorphism, e.g., larger females may win contests over hosts and be able to disperse farther in search of hosts, which will be important in species that are time-limited rather than egg-limited (Petersen and Hardy 1996, Ellers et al. 1998). On the other hand, larger males may achieve greater mating success through female preference and male–male competition (Reece et al. 2007, Blaul and Ruther 2012, Avila et al. 2017).

The direction and magnitude of sexual size dimorphism is known to vary with body part in some insects (Fairbairn 2005, Teder 2005, Da Rocha et al. 2007), yet quantitative analyses of sexual size dimorphism for several aspects of body size are generally lacking in parasitoid wasps (but see Petrović et al. 2014). The present study examines sexual size and shape dimorphism in three *Spalangia* species, *S. endius* Walker, *S. nigroaenea* Curtis, and *S. nigra* Latreille (Hymenoptera: Pteromalidae), looking at multiple body parts.

Congeners may be similar because of ancestry or because of adaptation to similar niches (Harvey et al. 2013, Symonds and Elgar 2013). However, where congeners coexist, dissimilarities in body dimensions may arise from niche specialization and selection to avoid interspecific competition and interspecific matings (Macedo et al. 2013).

The hosts of *S. endius*, *S. nigroaenea*, and *S. nigra* are the pupal stage of certain filth fly species, which are found at variable depths in decaying organic matter or manure (Rueda and Axtell 1985a). These *Spalangia* lack the enlarged forelimbs typically seen in diggers, but females move through spaces (Lindquist 1936) to reach buried hosts (Rueda and Axtell 1985a, Geden 2002). Female *S. endius* and *S. nigroaenea* parasitize hosts as deep as 10 cm (Rueda and Axtell 1985a); *S. nigra* has not been tested at that depth. In contrast to females, male *S. endius* tend to stay above ground, presumably to intercept emerging females (King 2002).

Once a female locates a host, she may drill through its puparium with her ovipositor. In *S. endius*, drilling takes roughly 17 min and considerable force (Broski and King 2015). Usually, only one offspring develops per host. In all three species, females tend to be longer than males (Rueda and Axtell 1985b).

Males begin emerging from their hosts a day or two before females (*S. nigroaenea* and *S. nigra*: Lindquist 1936; *S. endius*: Napoleon and King 1999; King 2000, 2006; de Araujo et al. 2012). Then males stay several days with their natal group of parasitized hosts (*S. endius*: King 2006). Males wing fan as they chase females in *S. endius* and *S. cameroni*, but mating behavior has not been described for *S. nigroaenea* and *S. nigra*. Larger size in one sex is often associated with physical aggression in that sex. However, at least in *S. endius*, neither males nor females fight (Napoleon and King 1999, King 2010).

For *S. endius*, *S. nigroaenea*, and *S. nigra*, we present data on field-collected specimens from Illinois. To see how consistent sex-based size differences are, for *S. endius*, we also examined a laboratory strain originating from Florida, and we compare narrowness of head width to that reported for *S. endius* by Gibson (2009). Data from field specimens are valuable because sexual size dimorphism may vary with host size or quality (Mackauer 1996, Da Rocha et al. 2007), which will not be consistent under field conditions (King 1990, 1991). Specimens from field-collected hosts are expected to reflect the size of wasps that will exist in nature, provided that hosts are collected at random with respect to host size and quality.

Because females burrow for hosts, we predicted that, for all three species, female bodies would be narrower, narrowness being defined as the ratio of length to width. Whether there would be differences in the relative length of legs, wings, and antennae was difficult to predict, except that female *S. endius* were predicted to have relatively longer hind legs than males, because a female brushes those legs across the dorsal surface of her abdomen after copulation, eventually dislodging the male (King and Fischer 2005). Whether *S. nigroaenea* and *S. nigra* also do so is unclear (Richardson 1913). Size and shape (e.g., ratios) information not only allows connections to be made between morphology and behavior but may also help differentiate the sexes (Baur and Leuenberger 2011). Thus, overlap was also examined.

Materials and methods

Field-Collected Illinois *Spalangia* Species

The field wasps emerged from house fly, *Musca domestica* L., and stable fly, *Stomoxys calcitrans* (L.), pupae that were collected from

a dairy farm in Harvard, IL (Olbrich and King 2003). The fly pupae were collected from the second week in June to the first week in September of 2000. During this time and for 9 mo prior, no pesticides were applied. Fly pupae were collected weekly from one or two sites within each of three habitats (calf hutches, drainage areas, and edges like fence lines). At each site, substrate was collected with a trowel within a 20-cm radius of where fly pupae were seen and up to 10-cm deep. Intact house fly and stable fly pupae were picked out and isolated in test tubes, with collection continuing for about 1 h or until about 80 pupae were obtained. Emerged parasitoids were identified (Rueda and Axtell 1985b, Gibson 2000). Vouchers are at the Illinois Natural History Survey Center for Biodiversity, catalog numbers 12,272 through 12,309 in the Insect Collection.

For *S. endius*, a total of 58 adult wasps were measured, for *S. nigroaenea* a total of 40, and for *S. nigra* a total of 35. Body parts from dead, air-dried wasps were attached to double-sided sticky cellophane tape on a microscope slide, and photographed with a calibration slide through a microscope using SPOT Microscope Imaging Software (SPOT Imaging, Sterling Heights, MI). Measurements were then made using Image Pro Plus (Media Cybernetics, Inc., Rockville MD).

Lengths and widths were recorded at the longest and widest part of the head, thorax, and a forewing (Fig. 1). On the posterior of the thorax and on the anterior of the abdomen, there were a pair of protrusions, and length was extended to an imaginary line across the tips of those parts. For an antenna, a middle leg, and a hind leg, the length down the center was measured. For the antenna, legs, and wing, whether we measured the left or the right was haphazard. Analysis of wing measurements of *S. endius* from a laboratory experiment showed no side-bias; the population mean of the left minus the right wing measurement was normally distributed with a mean of zero for both male and female forewing width and length (Napoleon and King 1999). Consideration of *S. endius*'s behavior and qualitative assessment of their leg dimensions also suggested no difference between the left and right sides. Abdomen dimensions were measured for *S. nigroaenea* and *S. nigra*, but unfortunately not for *S. endius*. Abdomen dimensions are of interest because they are the site of egg storage. However, upon drying, some abdomen segments may telescope inward and some abdominal sclerites may move outward. Abdomen dimensions were not collected from specimens with such noticeable distortions, except for male abdomens, which almost always telescope inward at the posterior tip. Because the telescoping impacts length, abdomen length was not compared between males and females. Abdomen measurements may still be useful for comparison with other dried specimens, e.g., museum specimens.

Laboratory-Reared Florida *S. endius*

The laboratory wasps were a Florida strain of *S. endius* that was maintained on a natural host, *M. domestica* (Napoleon and King 1999). Vouchers are at the Illinois Natural History Survey Center for Biodiversity, catalog numbers 'Insect Collection 6035 through 6054'. The wasps were from a previously published experiment (Napoleon and King 1999). Each wasp had developed on a small host or a large host, because the mothers of these wasps had been allowed to freely choose which of 10 hosts of each size to parasitize. Then, one male and one female offspring had been randomly chosen from each mother. There had been no correlation in head area between brothers and sisters, suggesting that each wasp was an independent sample in terms of body size. Each body part ($n = 26\text{--}28$ of each sex) was placed on double-sided sticky tape on a slide, projected onto a

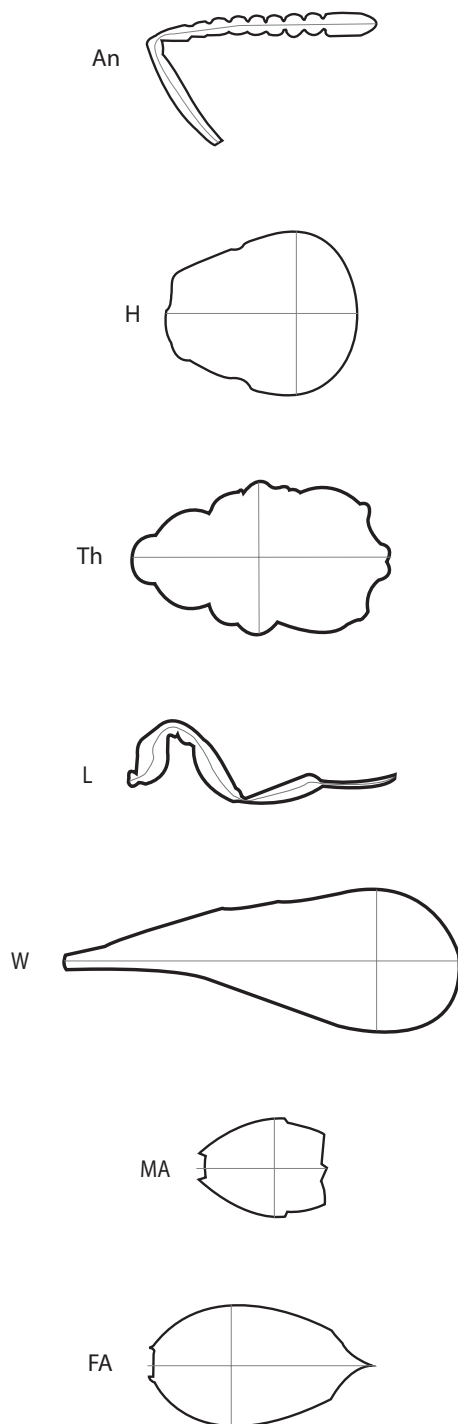


Fig. 1. Measurements (thin gray lines) for antenna (An), head (H), thorax (Th), leg (L), wing (W), male abdomen (MA), and female abdomen (FA). Anterior end on the left for all parts.

digitizing tablet with a microprojector and measured using Sigma Scan (Systat Software, Inc., San Jose, CA). Width and length of the head, thorax and forewing were measured at the widest and longest parts, respectively. Forewing length and width were the mean of the left and right wing when both were available.

Statistical Analyses

Statistical analyses were with SPSS Version 21 (SPSS 2012). Pairwise comparisons of each body part between sexes was by a

Mann–Whitney *U* test, because the assumption of normality was not consistently met as assessed by visual inspection and by *z*-tests of skewness and kurtosis. To test whether female bodies were narrower than males, we compared males versus females in terms of the length-to-width ratio for the head, the thorax, and the forewing. We analyzed and present direct measurements and ratios, because they are widely usable and interpretable, as evidenced by the high frequency with which the relative size of different body parts are used in species identification keys (Baur and Leuenberger 2011). Sample sizes were insufficient for meaningful multivariate analysis (Baur and Leuenberger 2011). Thus, we are not testing whether males and females differ overall in size or shape, as a multivariate analysis would determine, but rather our hypotheses are whether males and females differ in each of various individual body parts and ratios.

Results and Discussion

Females: Wide Abdomens, Relatively Narrow Head and Forewings

The degree of sexual size dimorphism depended on a combination of species and body part (summarized in Table 1; means \pm SE and ranges in Supp Tables 1, 4, and 7 [online only]). Abdomen width and head length were two of the measures that exhibited the greatest sexual size dimorphism, with females being larger.

Consistent with the importance of egg storage and the force needed to drill into hosts, females had significantly wider abdomens than males did in the two species in which abdomens were measured, *S. nigroaenea* and *S. nigra* (Table 1; Supp Tables 4 and 7 [online only]). In *S. endius*, more than twice as many offspring are produced by the largest females as by the smallest females (King and Napoleon 2006). In contrast to females, in *S. endius*, male mating success is not greater with greater body size, nor is longevity and development time for either sex.

Consistent with females burrowing in search of hosts, in all three species, females had narrower heads than males (Table 2; Supp Tables 2, 5, and 8 [online only]). In terms of absolute size, head width of males was greater or about the same as that of females (Table 1; Supp Tables 1, 4, and 7 [online only]). Forewings were relatively narrower for females than for males, significantly so for *S. endius* and *S. nigroaenea* (Table 2; Supp Tables 2, 5, and 8 [online only]). Sexual dimorphism in thorax narrowness differed among all three species. The thorax was narrower for females than for males in *S. nigra*, was narrower for males in *S. endius*, and was not significantly different between the sexes in *S. nigroaenea*. Future studies might test the effect of narrowness on the ability to find and parasitize buried hosts. This could be done by examining natural variation or perhaps by constraining parasitoid pupae in narrow containers prior to sclerotization.

That males tend to stay above ground and females tend to burrow may result in visual cues being more important for males than for females. Consistent with this, male *Spalangia* had less narrow (i.e., wider) heads than females did (Table 2; Supp Tables 2, 5, and 8 [online only]). Wider heads can accommodate larger eyes. What is known about *Spalangia* chemical biology does not lead to such clear expectations for sexual dimorphism. Chemical cues are used by both sexes, e.g., for location of mates and hosts (Myint and Walter 1990, Nichols et al. 2010, Mowles et al. 2013).

In the present study, contrary to our prediction for *S. endius*, females did not have relatively longer hind legs than males (Table 3; Supp Table 3 [online only]); and this was also true in the other two *Spalangia* species (Table 3; Supp Tables 6 and 9 [online only]). We hypothesize that instead of extra length, what allows females to

Table 1. Direction of sexual size dimorphism by body part by species

Body measurement	<i>S. endius</i> field	<i>S. endius</i> lab	<i>S. nigroaenea</i>	<i>S. nigra</i>
Antenna length	NS	-	M	NS
Head length	F	F	F	F
Head width	NS	F	M	NS
Thorax length	F	F	NS	F
Thorax width	F	F	NS	F
Middle leg length	F	-	M	F
Hind leg length	F	-	M	F
Forewing length	F	F	NS	NS
Forewing width	NS	NS	M	NS
Abdomen width	-	-	F	F

F: female-biased, M: male-biased, NS: $P > 0.05$ for sex difference.

Table 2. Direction of sexual dimorphism in narrowness (ratio of length to width) of head, thorax, and forewing by body part by species

Narrowness of	<i>S. endius</i> field	<i>S. endius</i> lab	<i>S. nigroaenea</i>	<i>S. nigra</i>
Head	F	F	F	F
Thorax	M	M	NS	F
Forewing	F	F	F	F

F: female-biased, M: male-biased, NS: $P > 0.05$ for sex difference.

Table 3. Direction of sexual dimorphism in relative length of head, thorax, and wing length to forewing length by body part by species

Relative length of	<i>S. endius</i> field	<i>S. endius</i> lab	<i>S. nigroaenea</i>	<i>S. nigra</i>
Antenna	NS	—	M	M
Middle leg	NS	—	M	NS
Hind leg	NS	—	NS	NS

F: female-biased, M: male-biased, NS: $P > 0.05$ for sex difference.

use their hind legs for brushing off males is extreme flexibility of their hind leg joints. Furthermore, both sexes use their hind legs for grooming.

Overlap in Size and Shape Between the Sexes

Between males and females, for all three species in the present study, there was overlap in every body part that we measured (Supp Tables 1, 4, and 7 [online only]) and for every size ratio that we calculated (Supp Tables 2, 3, 5, 6, 8, and 9 [online only]). There is also overlap in body length (Rueda and Axtell 1985b; Gibson 2009). Head area also overlaps between the sexes, at least in *S. endius* (King and Napoleon 2006).

Field Versus Laboratory Specimens: Similar Patterns of Sexual Dimorphism

For *S. endius*, patterns of sexual dimorphism were similar for the field specimens from Illinois and the laboratory specimens from the Florida strain (Tables 1–2; Supp Tables 1–3 [online only]). This was true even though the field specimens included individuals that emerged from both house flies and stable flies, whereas all laboratory specimens emerged from house flies. That field and laboratory results were so similar may at first seem surprising, because of potential differences in host size and quality in the laboratory versus field. Host size is positively correlated with parasitoid size in the majority of species of parasitoid wasps (King 1989). However, the similarity in sexual dimorphism between field and laboratory specimens of *S. endius* is less surprising once one realizes that the relationship between parasitoid size and host size, although positive, is not very

strong in the Florida strain of *S. endius* for both males and females. There is no significant relationship in an India strain (Napoleon and King 1999) and in a Southwell strain (Donaldson and Walter 1984). Furthermore, sexual dimorphism in head area is independent of host volume, at least in laboratory *S. endius* from a Florida strain and from an India strain (Napoleon and King 1999).

Consistency in patterns of sexual dimorphism in species from different sources may be a general feature of *Spalangia*. In addition to the consistency for *S. endius* between the Illinois field specimens and the Florida laboratory specimens, for all three *Spalangia* species in the present study, values of head length relative to width (Supp Tables 2, 5, and 8 [online only]) were consistent with values in Gibson (2009), who studied a variety of New World specimens.

Sex Differences Varied Among the Species

In *S. endius*, females were larger than males and significantly so for most body parts (Table 1, Supp Table 1 [online only]). The female-biased size dimorphism was particularly striking for head length and thorax width. The body measurements with little to no sexual size dimorphism were head width and forewing width. Head width was significantly greater in females than in males for the laboratory specimens from the Florida strain, but not for the field specimens from Illinois; however, the magnitude of the difference in means was the same and small in both sets of specimens, 0.01 mm (Supp Table 1 [online only]).

In *S. nigra*, females were larger than males for most measures, and in more measures than *S. nigroaenea*, although not in as many measures as for *S. endius* (Table 1; Supp Tables 1, 4, and 7 [online

only]). Female *S. nigra* were larger than males in head length and in size of the thorax, legs, and abdomen. As in *S. endius*, the sex difference in head length was particularly striking. The *S. nigra* body measurements with no significant sexual size dimorphism were head width, antennae length, and wing size, although males had longer antennae relative to wing length compared to females (Table 3; Supp Table 9 [online only]). *S. nigra* females were narrower than males not only in the head and forewing like the other two species but also in the thorax (Table 2; Supp Table 8 [online only]).

In *S. nigroaenea*, which sex was larger varied among body parts much more so than for the other two species (Table 1; Supp Tables 4 vs 1, 7 [online only]). *S. nigroaenea* females were significantly larger than males in head length and abdomen size; but males were larger than females in head width, antennae length, leg length, and wing width. Male antennae and middle legs were longer than those of females, not only in absolute size (Table 1; Supp Table 4 [online only]) but also relative to wing length (Table 3; Supp Table 6 [online only]).

Behavioral data, e.g., courtship, dispersal, and any aggressive behavior, remain to be collected for *S. nigroaenea* and *S. nigra*. Such data may help make sense of patterns of sexual dimorphism in these species and may show why some aspects of sexual dimorphism differ among the three species. Perhaps the male-biased ratio of antennae length to wing length in *S. nigroaenea* and *S. nigra* and the male-biased middle leg length to wing length in *S. nigroaenea* and neither of those male-biases in *S. endius* are related to the importance of the antennae and middle legs in mating. The male biases in relative length of antennae and middle legs were not a result of female-biased wing length; males did not have shorter wings than females.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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References Cited

- de Araujo, D. F., R. F. Kruger, and P. B. Ribeiro. 2012. Phenology of *Spalangia endius* Walker (Hymenoptera: Pteromalidae) in pupae of *Musca domestica* Linnaeus (Diptera, Muscidae) under laboratory conditions. *Rev. Brasil. Entomol.* 56: 504–507.
- Avila, G. A., T. M. Withers, and G. I. Holwell. 2017. Courtship and mating behaviour in the parasitoid wasp *Cotesia urabae* (Hymenoptera: Braconidae): mate location and the influence of competition and body size on male mating success. *Bull. Entomol. Res.* 107: 439–447.
- Baur, H., and C. Leuenberger. 2011. Analysis of ratios in multivariate morphometry. *Syst. Biol.* 60: 813–825.
- Blaul, B., and J. Ruther. 2012. Body size influences male pheromone signals but not the outcome of mating contests in *Nasonia vitripennis*. *Anim. Behav.* 84: 1557–1563.
- Broski, S. A., and B. H. King. 2015. Drilling-in and chewing-out of hosts by the parasitoid wasp *Spalangia endius* (Hymenoptera: Pteromalidae) when parasitizing *Musca domestica* (Diptera: Muscidae). *Environ. Entomol.* 44: 1116–1124.
- Charnov, E. L. 1982. *The theory of sex allocation*, Princeton University Press, Princeton, NJ.
- Da Rocha, L., R. Kolberg, M. D. Mendonca, and L. R. Redaelli. 2007. Body size variation in *Gryon gallardoii* related to age and size of the host. *Biocontrol* 52: 161–173.
- Donaldson, J. S., and G. H. Walter. 1984. Sex ratios of *Spalangia endius* (Hymenoptera: Pteromalidae), in relation to current theory. *Ecol. Entomol.* 9: 395–402.
- Ellers, J., J. J. M. van Alphen, and J. G. Sevenster. 1998. A field study of size-fitness relationships in the parasitoid *Asobara tabida*. *J. Anim. Ecol.* 67: 318–324.
- Fairbairn, D. J. 2005. Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider *Aquarius remigis*. *Am. Nat.* 166(Suppl 4): S69–S84.
- Geden, C. J. 2002. Effect of habitat depth on host location by five species of parasitoids (Hymenoptera: Pteromalidae, Chalcididae) of house flies (Diptera: Muscidae) in three types of substrates. *Environ. Entomol.* 31: 411–417.
- Gibson, G. 2000. Illustrated key to the native and introduced chalcidoid parasitoids of filth flies in America north of Mexico (Hymenoptera: Chalcidoidea). October 2000. <http://canacoll.org/Hymenoptera/Staff/Gibson/PDFs/chalkey.pdf> (accessed 11 February 2018).
- Gibson, G. A. P. 2009. Revision of new world Spalanginae (Hymenoptera: Pteromalidae). *Zootaxa* 2259: 1–159.
- Harvey, J. A., B. Visser, C. Le Lann, J. de Boer, J. Ellers, and R. Gols. 2013. Convergence and divergence in direct and indirect life-history traits of closely related parasitoids (Braconidae: Microgastrinae). *Evol. Biol.* 41: 134–144.
- Hurlbutt, B. L. 1987. Sexual size dimorphism in parasitoid wasps. *Biol. J. Linn. Soc.* 30: 63–89.
- Irie, T., and N. Morimoto. 2008. Phenotypic plasticity and sexual dimorphism in size at post-juvenile metamorphosis: common-garden rearing of an intertidal gastropod with determinate growth. *Biol. Bull.* 215: 126–134.
- King, B. H. 1989. Host-size-dependent sex ratios among parasitoid wasps: does host growth matter? *Oecologia*. 78: 420–426.
- King, B. H. 1990. Interspecific differences in host (Diptera: Muscidae) size and species usage among parasitoid wasps (Hymenoptera: Pteromalidae) in a poultry house. *Environ. Entomol.* 19: 1519–1522.
- 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.
- King, B. H. 2000. Sex ratio and oviposition responses to host age and the fitness consequences to mother and offspring in the parasitoid wasp *Spalangia endius*. *Behav. Ecol. Sociobiol.* 48: 316–320.
- King, B. H. 2002. Sex ratio response to conspecifics in a parasitoid wasp: test of a prediction of local mate competition theory and alternative hypotheses. *Behav. Ecol. Sociobiol.* 52: 17–24.
- King, B. H. 2006. Mate location and the onset of sexual responsiveness in the parasitoid wasp *Spalangia endius* (Hymenoptera: Pteromalidae). *Environ. Entomol.* 35: 1390–1395.
- King, B. H. 2010. Which sex controls the duration of postcopulatory courtship and to what effect in the parasitoid wasp *Spalangia endius*? *Behavior* 147: 993–1007.
- King, B. H., and C. R. Fischer. 2005. Males mate guard in absentia through extended effects of postcopulatory courtship in the parasitoid wasp *Spalangia endius* (Hymenoptera: Pteromalidae). *J. Insect Physiol.* 51: 1340–1345.
- King, B. H., and M. E. Napoleon. 2006. Using effects of parasitoid size on fitness to test a host quality model assumption with the parasitoid wasp *Spalangia endius*. *Can. J. Zool.* 84: 1–5.
- Lindquist, A. W. 1936. Parasites of horn fly and other flies breeding in dung. *J. Econ. Entomol.* 29: 1154–1158.
- Macedo, M. V., R. F. Monteiro, M. P. Silveira, and P. J. Mayhew. 2013. Male-male contests for mates, sexual size dimorphism, and sex ratio in a natural population of a solitary parasitoid. *Behav. Processes.* 100: 1–8.
- Mackauer, M. 1996. Sexual size dimorphism in solitary parasitoid wasps: influence of host quality. *Oikos* 76: 265–272.
- Mowles, S. L., B. H. King, R. S. T. Linforth, and I. C. W. Hardy. 2013. A female-emitted pheromone component is associated with reduced male courtship in the parasitoid wasp *Spalangia endius*. *PLoS One* 8: e82010.

- Moynihan, A. M., and D. M. Shuker. 2011. Sexual selection on male development time in the parasitoid wasp *Nasonia vitripennis*. *J. Evol. Biol.* 24: 2002–2013.
- Myint, W. W., and G. H. Walter. 1990. Behaviour of *Spalangia cameroni* males and sex ratio theory. *Oikos* 59: 163–174.
- 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.
- Nichols, W. J., Jr, A. A. Cossé, R. J. Bartelt, and B. H. King. 2010. Methyl 6-methylsalicylate: a female-produced pheromone component of the parasitoid wasp *Spalangia endius*. *J. Chem. Ecol.* 36: 1140–1147.
- Olbrich, D. L., and B. H. King. 2003. Host and habitat use by parasitoids (Hymenoptera: Pteromalidae) of house fly and stable fly (Diptera: Muscidae) pupae. *Great Lakes Entomol.* 36: 179–190.
- Petersen, G., and I. C. W. Hardy. 1996. The importance of being larger: parasitoid intruder-owner contests and their implications for clutch size. *Anim. Behav.* 51: 1363–1373.
- Petrović, A., Ž. Tomanović, N. G. Kavallieratos, A. M. Bogdanović, P. Starč, and A. Ivanović. 2014. Sexual dimorphism in the parasitoid wasps *Aphidius balcanicus*, *Aphidius rosae*, and *Aphidius urticae* (Hymenoptera: Braconidae: Aphidiinae). *Ann. Entomol. Soc. Am.* 107: 1027–1032.
- Reece, S. E., T. M. Innocent, and S. A. West. 2007. Lethal male–male combat in the parasitoid *Melittobia acasta*: are size and competitive environment important? *Anim. Behav.* 74: 1163–1169.
- Richardson, C. H. 1913. Studies on the habits and development of a hymenopterous parasite, *Spalangia muscidarum* Richardson. *J. Morphol.* 24: 513–557.
- Roff, D. A. 2000. Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. *J. Evol. Biol.* 13: 434–445.
- Rueda, L. M., and R. C. Axtell. 1985a. Effect of depth of house fly pupae in poultry manure on parasitism by six species of Pteromalidae (Hymenoptera). *J. Entomol. Sci.* 20: 444–449.
- Rueda, L. M., and R. C. Axtell. 1985b. Guide to common species of pupal parasites (Hymenoptera: Pteromalidae) of the house fly and other muscoid flies associated with poultry and livestock manure. North Carolina Agricultural Research Service, North Carolina State University. Technical Bulletin 278 (88 pp).
- SPSS. 2012. IBM SPSS statistics for windows, version 21.0. Released 2012. IBM Corp, Armonk, NY.
- Stillwell, R. C., W. U. Blanckenhorn, T. Teder, G. Davidowitz, and C. W. Fox. 2010. Sex differences in phenotypic plasticity affect variation in sexual size dimorphism in insects: from physiology to evolution. *Annu. Rev. Entomol.* 55: 227–245.
- Symonds, M. R., and M. A. Elgar. 2013. The evolution of body size, antennal size and host use in parasitoid wasps (Hymenoptera: Chalcidoidea): a phylogenetic comparative analysis. *PLoS One.* 8: e78297.
- Teder, T. 2005. Male-biased size dimorphism in ichneumonine wasps (Hymenoptera: Ichneumonidae) - the role of sexual selection for large male size. *Ecol. Entomol.* 30: 342–349.
- Teder, T., and T. Tammaru. 2005. Sexual size dimorphism within species increases with body size in insects. *Oikos* 108: 321–334.
- Vollrath, F. 1998. Dwarf males. *Trends Ecol. Evol.* 13: 159–163.