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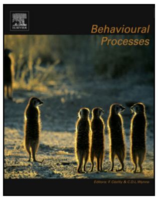

Male–male contests for mates, sexual size dimorphism, and sex ratio in a natural population of a solitary parasitoid

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ABSTRACT

Understanding how different behavioural and life history traits interact is fundamental to developing ethological theory. Here we study the interaction of male–male competition for mates and sexual size dimorphism in a solitary wasp, with implications for sex allocation. In Hymenoptera, females are normally larger than males suggesting that males do not benefit as much as females from larger size. However, in our focal species, a solitary *Eurytoma* wasp, males compete for mates by pairwise contests at female emergence sites, suggesting that male size may strongly affect fitness. In contests observed in the field, larger males were more likely to win fights, and males fighting at female emergence sites were much larger than average males. Males showed higher variance in body size than females, such that all the smallest individuals were males, a majority of medium-to-large individuals were female, but the majority of largest individuals were male. Our data suggest that sexual size dimorphism in this species has been affected by intra-sexual selection for male size, which may have implications for sex allocation.

The development of ethological and life history theory relies on an understanding of the interaction between different traits of organisms, which allows appropriate assumptions, such as trade-offs, to be incorporated (Roff, 1992; Stearns, 1992; Charnov, 1993). The relative body size of males and females (sexual size dimorphism, SSD) is a trait that varies markedly across species and that interacts with several other behavioural and life history traits (Andersson, 1994; Fairbairn et al., 2007). Most especially, the degree of SSD should evolve according to the relative fitness of males and females of different body sizes (Shine, 1989; Isaac, 2005). Strong sexual selection, particularly intra-sexual selection through male–male combat, can strengthen the size–fitness relationship for males, and therefore select for large size in males (Lindenfors et al., 2007). Sex allocation (the relative investment in male and female offspring) also depends on the relative fitness of males and females of different body sizes (Hardy, 2002; West, 2009). Sex allocation can thus also be affected by intra-sexual selection on male size, and thus potentially determine patterns of SSD. In this paper we investigate interactions between male–male combat and SSD in a solitary parasitoid wasp that may have implications for sex allocation in parasitoids.

In most groups of animals, SSD is female-biased (Andersson, 1994; Fairbairn et al., 2007), with females larger than males. A widely accepted explanation of female-biased SSD is "the fecundity advantage hypothesis" (e.g. Han and Fu, 2013), which states that large size increases female fitness disproportionately due to the benefits of greater egg size, egg load, or energy reserves required by females for reproduction. In contrast, in birds and mammals, male-biased SSD predominates, which is generally explained by the increased intensity of sexual selection for male size, particularly intra-sexual selection through male–male combat (Andersson, 1994; Isaac, 2005; Lindenfors et al., 2007). Thus, sexual selection on male size is capable of overriding the fecundity advantage of size for females, and reversing the type of SSD displayed.

Parasitoid wasps are a group of insects that develop by feeding on the still-living body of another host arthropod, eventually killing it (Godfray, 1994). In such wasps, as in most other insects (Teder and Tammaru, 2005), SSD is generally female biased (Hurlbutt, 1987), and experimental evidence supports the fecundity advantage hypothesis (Jones, 1982; van den Assen et al., 1989; Heinz, 1991). Whilst female parasitoid fitness is often strongly dependent on body size because of the need to develop costly eggs, disperse, and survive to find consecutive hosts (e.g. Visser, 1994; West et al., 1996), male mating success is often relatively unaffected by body size (e.g. King, 1988; Seidl and King, 1993; Cloutier et al., 2000; Lacoume et al., 2006; Moynihan and Shuker, 2011).

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Many parasitoid wasps are solitary, meaning that only a single individual develops on each host (Godfray, 1994). In such species, especially in those whose host does not grow after parasitization (idiobionts) (King, 1989; West and Sheldon, 2002), adult females allocate female offspring disproportionately to large hosts and male offspring to small hosts (Charnov et al., 1981; Lewis et al., 2010), a phenomenon known as conditional sex allocation (CSA). In such species, SSD (normally female-biased) is a consequence of the way adult females allocate offspring to different sized hosts. However, CSA is not restricted to parasitoids, but is found in a wide range of organisms (West, 2009), including many ungulate mammals (Sheldon and West, 2004), in which CSA is biased towards males in favourable conditions (e.g. Sheldon and West, 2004), reflecting strong intra-sexual selection on male size in those species.

Although intra-sexual selection on male size is probably generally weak in parasitic Hymenoptera, there are exceptions (Hurlbutt, 1987). For example, lethal male-male combat occurs in the gregarious parasitoid genus *Melittobia*, and larger males are more likely to win fights (Reece et al., 2007). Lethal male–male combat over mates also occurs in fig wasps (Hamilton, 1979), and body size can be an important determinant of contest outcome (e.g. Moore et al., 2008). In some parasitoids, taking account of the advantage that large size confers in combats can make the estimated relationship between size and fitness much steeper (Petersen and Hardy, 1996). Therefore, in parasitoid species where intra-sexual selection on males is strong through contests over mates, it is possible that the relationship between male size and fitness becomes very steep, and this could lead to unusual patterns of sex allocation and sexual size dimorphism, as has apparently occurred in mammals. Teder (2005) suggests that inter-sexual selection has had this effect in some species of Ichneumoninae wasp, making it plausible that the same could be achieved through intra-sexual selection.

In this paper we report observations on a solitary species of *Eurytoma* wasp (Hymenoptera: Eurytomidae) parasitizing a braconid gall wasp developing in the seeds of a leguminous shrub. Male *Eurytoma* seek out females prior to female emergence from seed pods, and contests occur between rival males on the surface of the pod, prior to mating. Here we report field observations on the effect of male size on contest outcome. We also report the degree of sexual size dimorphism from field rearings. We predict that male size will strongly affect contest outcome, such that larger males tend to win fights. We also predict that this will lead to an unusual pattern of male-biased SSD, rather than the female-bias normally found in Hymenoptera. This might, in turn, have interesting implications for the way this species allocates sex.

1. Methods

1.1. Study species

Eurytoma sp. (Fig. 1) is an idiobiont ectoparasitoid solitary wasp which parasitizes the larvae and pupae of *Allorhogas dyspistus* Marsh (Hymenoptera: Braconidae) (Macêdo and Monteiro, 1989), which feeds as a galler on immature seeds of the shrub *Pithecellobium tortum* Mart. (Leguminosae) (Macêdo et al., 1998).

1.2. Field rearing

Fruits of *P. tortum* (Fig. 1) were harvested from the field for rearing from Barra de Maricá Restinga (sand dunes), Maricá County, Rio de Janeiro State, Brazil (22°57′ S, 42°50′ W), and brought to the lab (23 ± 3 °C) from June to August 1995. Fruits (11–34 per plant per sample, depending on the availability of immature fruits) were taken on seven occasions, covering 14 individual shrubs, summing 556 fruits and 8596 seeds. Twelve of the 14 plants were sampled at least twice through the fruiting season, and two just once. The sampling dates were: June 8th (Sample 1 – five plants), 13th (Sample 2 – five plants) and 22nd (Sample 3–four plants), July 5th (Sample 4 – eight plants), 13th (Sample 5 – three plants) and 21st (Sample 6 – one plant) and August 3rd (Sample 7 – two plants). These sampling dates span the length of the main fruiting season and the number of plants sampled was approximately half of the individuals which had available fruits in the right stage of maturity in the sample area. All fruits were checked for exit holes to make sure that no insect had emerged before collection. All collected fruits were at the same green stage of maturity (ready for insect emergence). Groups of about five fruits from the same plant were placed in plastic boxes, 10 cm × 10 cm × 7 cm, covered with a piece of cloth and checked daily for insect emergence. All emerged insects were removed from the boxes and immediately preserved in 70% ethanol.

1.3. Body size of reared adults

Out of the 4021 *Eurytoma* sp. adults reared, 180 males and 180 females obtained from three plants (60 from each plant) were selected at random and measured under magnifying lenses with the aid of a graduated ocular. Characters recorded included gaster length and width, thorax width, head width, foreleg femur length, body length and forewing length.

1.4. Mating and combat observations

Field observations were made of mating behaviour, totalling about 40 h of direct observation ad libitum from 9:00 h to 16:00 h on 10 dates in June, July and August (the sample dates above or the days immediately before or after that), mainly on four plants which were easier to access. *Eurytoma* adults can be easily sexed without visual aid because males have smaller gasters (see Section 2). Mating was observed on 35 occasions and, on 26 of these occasions, combats were observed prior to mating between pairs of males on the surface of the seed pods in the field. For nine of these pairs we successfully collected the winner and the loser, on the pod surface of three different plants on two dates: 22nd July (five fights) and 3rd August (four fights). These males were taken to the laboratory and their size measured as described above. Collecting both combatting males is challenging because losers disperse by flight immediately after fights, and winners after mating. Although we collected the fighting males in nine combats, only 16 individuals were involved in these fights because two of them fought in two different contests over one female each. One of them won the two fights and the other was winner in one and loser in the other. In analyses where individuals were classified as winners or losers (see Section 2), the former individual was, obviously, classified as a winner, but the latter was considered a loser because this made our analyses more conservative, given its body size.

1.5. Sex ratio

Spatial and temporal variation in the sex ratio (proportion males) at adult emergence can potentially strongly affect male fitness (Godfray, 1994). Thus, the sex ratio of emerging adults was measured for each plant separately for each collection date. To test if males tended to emerge before females from each sample, emerging insects were grouped into two intervals of about 1–2 weeks each. To test whether small males emerge prior to large males, the first 20 males to emerge, between the first and the third days in