



ORIGINAL RESEARCH

Differences in gonadal sex allocation in a simultaneous hermaphrodite commensal flatworm under field conditions

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Introduction

In simultaneous hermaphrodites, both male and female reproductive functions are active at the same time in the same individual, and the amount of resources allocated to each sex can vary considerably depending on the situation (Charnov, 1982; Schärer, 2009). The sex allocation theory in simultaneous hermaphrodites predicts that resource investment in male and female functions is influenced by the mating group size. In small mating groups, copulation and fertilization opportunities are fewer than in large mating groups, and consequently, sperm competition to fertilize eggs is lower. Thus, in small mating groups, allocating extra resources to increase the male function to produce more sperm than needed would be an inefficient use of resources. In such circumstances, hermaphrodites can maximize their fitness by reallocating resources from sperm production (male function) to egg production (female function). In contrast, in large mating groups, the number of sperm donors increases, intensifying sperm competition. In such

Abstract

The theory of sex allocation in simultaneous hermaphrodites predicts that resource investment between male and female reproductive functions varies with the size of the mating group. To test this theory in commensal flatworms that are simultaneous hermaphrodites, in the present study, we evaluated the variations in the sizes of male and female gonads in *Temnocephala iheringi* (Platyhelminthes, Rhabdocoela), a species that inhabits the pallial cavity of the golden apple snail *Pomacea canalicularata* (Mollusca: Gastropoda). We evaluated two snail populations, each naturally exhibiting different infestation intensities of *T. iheringi*, assuming distinct mating group sizes. We found that the total size of the gonads of flatworms from both snail populations was similar, but that the proportion of the male gonad was higher in flatworms from the snail population with higher infestation intensity (larger mating group) than in those from the snail population with lower infestation intensity. Additionally, the proportion of the female gonad was lower in flatworms from the snail population with higher infestation intensity. These findings support the theory of sex allocation and, for the first time, demonstrate differences in gonadal sex allocation in a commensal organism in its natural environment.

circumstances, investing in the male function can secure more fertilizations, thereby maximizing fitness. Thus, in large mating groups, sex allocation would shift toward the male function (Charnov, 1982; Schärer, 2009; Schärer & Pen, 2013; Singh et al., 2020). The earliest sex allocation theoretical models proposed that energy investment in male and female functions, influenced by the mating group size and sperm competition, could be a genetically fixed trait that evolved over many generations (Charnov, 1986). However, more recent studies suggest that sex allocation can also be influenced by the environmental conditions experienced by hermaphrodites, indicating a degree of plasticity in this reproductive trait (e.g., Brauer et al., 2007; Hart et al., 2011; Janicke et al., 2016; Lorenzi et al., 2005; Santi et al., 2018; Schärer & Ladurner, 2003; Schärer & Wedekind, 2001; Schleicherová et al., 2014; Tan et al., 2004).

Temnocephalid flatworms (Platyhelminthes, Rhabditophora) are a group of simultaneous hermaphroditic turbellarians, which live as commensals of other freshwater animals

(Damborenea et al., 2017). These commensals have coevolved with various hosts, including decapod crustaceans, hemipteran and trichopteran insects, snails, and turtles. Most of these temnocephalids exhibit host specificity and are adapted to their lifestyle (Martínez-Aquino et al., 2017). Some commensal species are adapted to living externally on their hosts. Those associated with crustaceans and insects must contend with the molting exoskeleton of hosts. Other commensal species live internally, occupying cavities such as the pallial cavities of mollusks or the branchial chambers of crustaceans (Damborenea & Cannon, 2001). The genus *Temnocephala*, endemic to the Neotropical region, mainly infests decapod crustaceans and gastropod mollusks (Damborenea & Cannon, 2001). Among the species of this genus, *Temnocephala iheringi* is abundant in the Parano-Platense basin, Argentina (Moretto & Durquet, 1977; Seixas et al., 2010). This species is mainly associated with the “golden apple snail” *Pomacea canaliculata* (Gastropoda, Ampullariidae), with adult flatworms living in the snail pallial cavity and laying their eggs on its shell. Juveniles emerge from the eggs and move to the snail pallial cavity, where they grow and reproduce (Damborenea et al., 2017). Although it is difficult to accurately estimate the number of flatworm mates within each snail’s pallial cavity, it would be reasonable to assume that the assemblage of adult flatworms in each host could constitute the primary mating group.

Temnocephala iheringi is a simultaneous hermaphrodite. The male reproductive system has two bilobate testicles on each side of the body, with their efferent ducts opening into a seminal vesicle, and prostatic glands that empty into the prostatic bulb in the proximal region of a sclerosed copulatory stylet. The female reproductive system has one ovary, which produces ectolecithic oocytes, and branched yolk glands, generally located dorsal to the intestine, which produce the yolk for embryo nutrition. Additionally, the female gonad includes ducts and an atrium that stores an egg after fertilization (Damborenea, 1992; Damborenea & Cannon, 2001; Moretto & Durquet, 1977; Seixas et al., 2010). The most notorious components of the gonads are the testicles, ovary, and yolk glands, all of which can be measured in the same units (area). In contrast, the ducts, seminal vesicle, prostatic glands, stylet, and atria are small and challenging to measure accurately. Therefore, given the relatively small size of these reproductive accessories, in this study, we preferred excluding them. Therefore, measuring the sizes of testicles, ovaries, and yolk glands allows the estimation of gonadal sex allocation toward the male or female functions (Brand et al., 2022; Schärer, 2009).

These characteristics make *T. iheringi* a suitable model to assess differences in gonadal sex allocation in response to the mating group size, as suggested by the sex allocation theory (Charnov, 1982; Schärer, 2009). To investigate this, we examined variations in the sizes of male and female gonads in *T. iheringi*, from two *P. canaliculata* populations that naturally exhibit different infestation intensities, thereby assuming distinct mating group sizes. We characterized each snail population and its corresponding flatworm assemblages and estimated the proportion of the sizes of the male and female gonads relative to the total size of the gonads. We hypothesized that, in the snail population with higher infestation intensity of

T. iheringi (larger mating group), the flatworm gonadal sex allocation would shift toward a male reproductive function. The novelty of our study lies in the fact that certain aspects of the sex allocation theory were assessed in a natural environment, in contrast to most previous research on sex allocation, which has been conducted under laboratory conditions (Schärer & Pen, 2013; Singh et al., 2020). Also, this is the first time that the sex allocation theory has been tested in simultaneous hermaphrodite flatworms that live as commensals.

Materials and methods

Pomacea canaliculata specimens, hosts of *T. iheringi*, were collected from two urban ponds located in two parks (Parque Saavedra and Paseo del Bosque) of La Plata city, Buenos Aires province, Argentina, between May 2022 and February 2023. These aquatic environments present stable populations of *P. canaliculata*. Fifty adult snails were taken to the laboratory, where they were measured and then dissected to extract the commensals from the pallial cavity. The temnocephalans extracted were quantified, and the infestation intensity, which reflects the density of the flatworms in each snail and, consequently, the probable size of the mating group, was estimated as the number of *T. iheringi* per snail (Bush et al., 1997).

Between two and nine adult temnocephalans were selected from each snail (depending on the intensity of infestation), fixed in 95% ethanol, and slowly squashed between two slides. They were then dehydrated, stained with hydrochloric carmine, and mounted in synthetic Canada balsam (Langeron, 1942). The mounted specimens were photographed under a microscope and the images analyzed using the image processing software ImageJ (<http://imagej.nih.gov/ij/>). These images were used to measure the length of the body without tentacles and the total size (area) of the gonads of each temnocephalan, distinguishing the surface area of the two testicles (male function), the surface area of the ovary, and the surface area of the yolk glands (female function) (Fig. 1).

To measure the gonadal sex allocation toward a male and female function, we determined the proportion of the male (testicles) or female (ovary + yolk glands) gonad size relative to the total size of the gonads (testicles + ovary + yolk glands) (Brand et al., 2022; Schärer, 2009). The male gonadal sex allocation was determined as the area of the testicles/total area of the gonads $\times 100$, and the female gonadal sex allocation was determined as the area of the ovary + yolk glands/total area of the gonads $\times 100$. The male and female gonadal sex allocation of *T. iheringi* is expressed as a percentage.

To compare the sizes of snails and temnocephalans, infestation intensity, total size (area) of the gonads, and male and female gonadal sex allocation of *T. iheringi* between the two *P. canaliculata* populations studied, we used *t*-Student or Mann–Whitney tests, depending on data homogeneity, which was assessed using Levene’s test.

Results

The snails from both ponds showed similar sizes: 5.1 ± 0.5 cm in length for those from Parque Saavedra

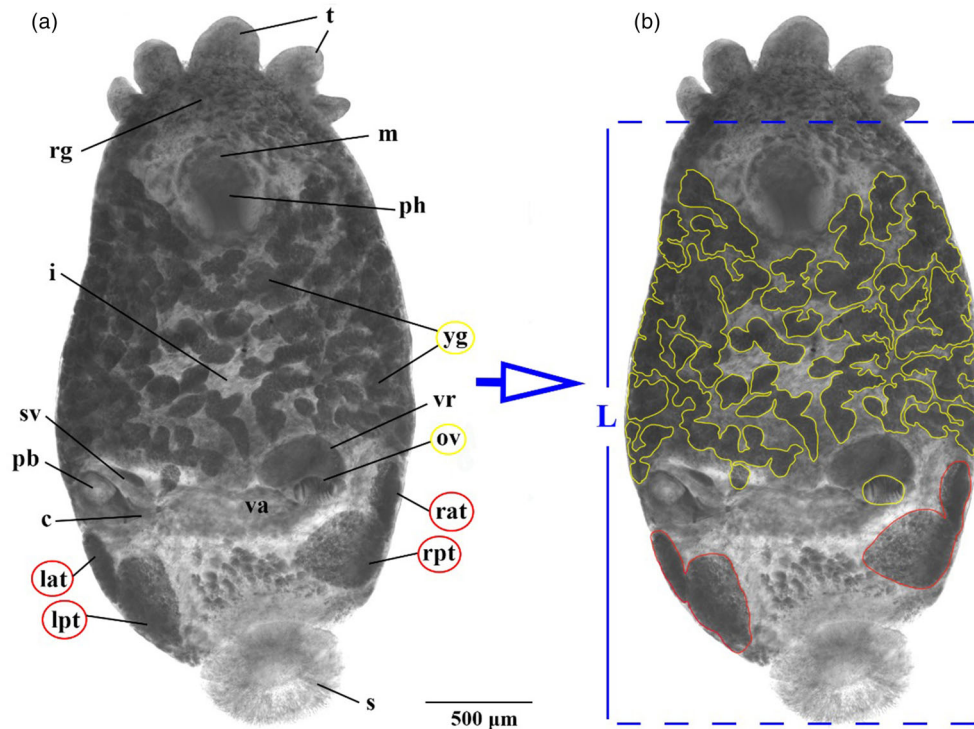


Figure 1 (a) General anatomy of a fixed and stained specimen of *Temnocephala iheringi* showing its main organs: c, cirrus; i, intestine; lat, left anterior testicular lobe; lpt, left posterior testicular lobe; m, mouth; ov, ovary; pb, prostatic bulb; ph, pharynx; rat, right anterior testicular lobe; rg, rhabditogenic glands; rpt, right posterior testicular lobe; s, sucker; sv, seminal vesicle; t, tentacles; va, vagina; vr, vesicula resorbens; yg, yolk glands. (b) The same specimen showing the surfaces of the different parts of the hermaphrodite gonad (yellow: female, red: male) measured. (L) Body length (without tentacles).

($N = 27$) and 5.5 ± 0.8 cm in length for those from Paseo del Bosque ($N = 23$) (Mann–Whitney result: $U = 193$; $P = 0.08$). The temnocephalans from both ponds also showed similar sizes: 3.5 ± 0.9 mm in length for those from Parque Saavedra ($N = 97$) and 3.7 ± 0.9 mm in length for those from Paseo del Bosque ($N = 42$) (t -Student: $t = 1.10$; d.f. = 137; $P = 0.27$). The infestation intensity of *T. iheringi* in snails from Parque Saavedra (49.7 ± 47.3 temnocephalans per snail) was 84% higher than that in Paseo del Bosque (7.9 ± 10.7 temnocephalans per snail) (Fig. 2), indicating that the mating groups in Parque Saavedra were probably larger than those in Paseo del Bosque.

The total size of the gonads (testicles + ovary + yolk glands) of *T. iheringi* in individuals from both snail populations was similar: $2388 \pm 798 \times 10^3 \mu\text{m}^2$ in specimens from Parque Saavedra and $2342 \pm 993 \times 10^3 \mu\text{m}^2$ in those from Paseo del Bosque (Fig. 3). This suggests that the gonadal investment of *T. iheringi* in both snail populations was equivalent and unaffected by the infestation intensity. In both snail populations, the area of the female gonad (ovary + yolk glands) of *T. iheringi* predominated, accounting for 77% of the total area of the gonads (ranging from 71% to 80% in flatworms from Parque Saavedra and from 74% to 85% in those from Paseo del Bosque). In the female gonad, the yolk glands occupied 97% of the surface area, whereas the ovary

accounted for only 3%. The testicles constituted about 23% of the total size of the gonads.

Although the total size of the gonads of *T. iheringi* was similar in both snail populations (Fig. 3), the proportion of the male gonad was 12.5% higher in flatworms from Parque Saavedra than in those from Paseo del Bosque (Fig. 4a), suggesting that the gonadal sex allocation of *T. iheringi* toward the male function was higher in the snail population with high infestation intensity. Also, the proportion of the female gonad in individuals from Parque Saavedra was lower than that in individuals from Paseo del Bosque (Fig. 4b).

Discussion

Gonadal sex allocation to male and female functions in the commensal flatworm *T. iheringi* differed with the infestation intensity, probably as a response to the mating group size, as suggested by the sex allocation theory. As predicted, in Parque Saavedra, where snail hosts exhibited higher infestation intensity, assuming larger mating groups, the gonadal sex allocation of *T. iheringi* was biased toward the male reproductive function. This was supported by a larger proportion of the male gonad in the flatworms from Parque Saavedra compared to that in flatworms from Paseo del Bosque, where the snails had lower infestation intensity (smaller mating group).

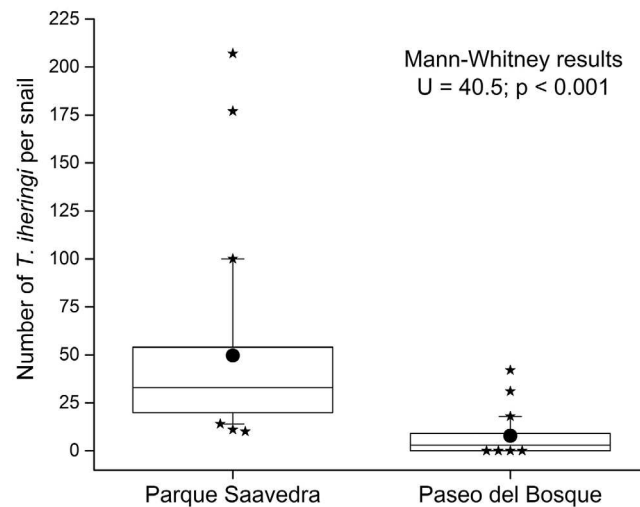


Figure 2 Infestation intensity of *Temnocephala iheringi* in snails from the two ponds studied (Parque Saavedra and Paseo del Bosque). Point = mean, line = median, box = 25%–75%, whiskers = 10–90, stars = outliers.

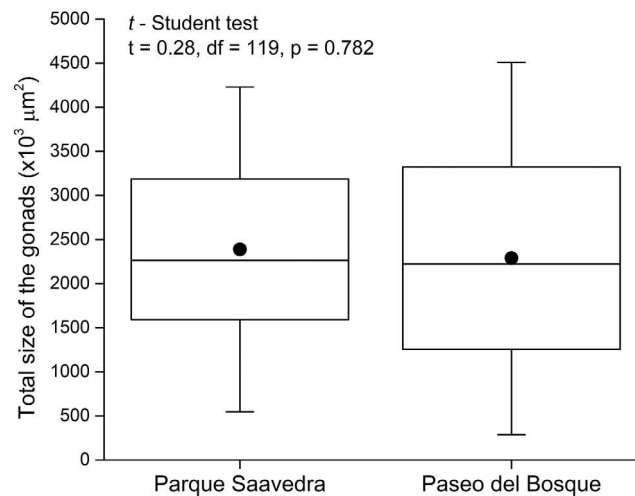


Figure 3 Total area of the gonads (testicles + ovary + yolk glands) in *T. iheringi* from the two ponds studied (Parque Saavedra and Paseo del Bosque). Point = mean, line = median, box = standard deviation, whiskers = min–max.

Since this is the first study on sex allocation in temnocephalids, there is no available information for comparison within this taxon. The existing research primarily focuses on the biological systematics of temnocephalids (e.g., Blair *et al.*, 2023; van Steenkiste *et al.*, 2021), with lesser emphasis on ecological aspects (Damborenea, 1996, 1998; Damborenea *et al.*, 2006; Zivano *et al.*, 2020). In contrast, many studies have assessed sex allocation in other simultaneously hermaphrodite invertebrates such as Platyhelminthes Macrostromorpha (e.g., Schärer, 2009; Singh *et al.*, 2020), Platyhelminthes Neodermata (Schärer & Wedekind, 2001; Trouvé *et al.*, 1999), snails (Koene, 2006), Annelida Polychaeta (Lorenzi *et al.*, 2005), shrimps (Baeza, 2007), and Bryozoans (Hughes *et al.*, 2003).

Studies on sex allocation in simultaneous hermaphrodite flatworms have experimentally manipulated the size of the mating group (Janicke *et al.*, 2016; Schärer & Ladurner, 2003; Schärer & Wedekind, 2001; Singh *et al.*, 2020; Singh & Schärer, 2022; Trouvé *et al.*, 1999). In contrast, in this study, we conducted a novel evaluation of changes in gonadal sex allocation under natural conditions by examining commensal temnocephalids living in the snail *Pomacea canaliculata* at different infestation levels, assuming different mating group sizes. Because we did not control or manipulate the number of individuals in each enclosure (snail pallial cavity), we were not able to accurately estimate the number of mates. However, it is reasonable to assume that the mating rates were higher in flatworms from Parque Saavedra than in those from Paseo del Bosque and that

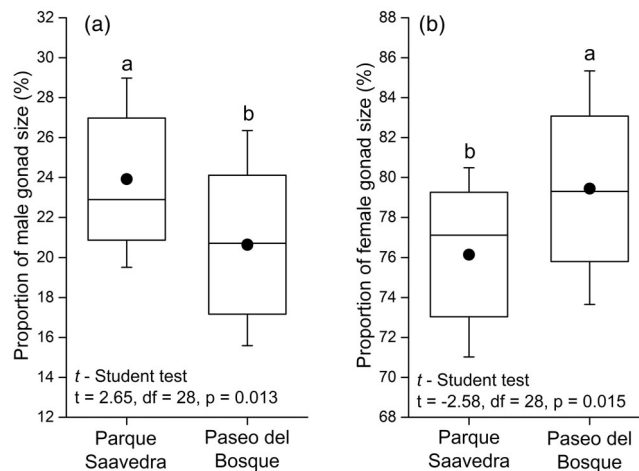


Figure 4 Male (a) and female (b) gonadal sex allocation of *Temnocephala iheringi*. Variation in the proportion of the male gonad size (testicle) and female gonad size (ovary + yolk glands) relative to the total size of the gonads in the flatworms from the two ponds studied (Parque Saavedra and Paseo del Bosque). Different letters indicate significant variation ($P < 0.05$) between the mean values. Point = mean, line = median, box = standard deviation, whiskers = min–max.

this likely led to increased post-copulatory sexual selection (Schärer, 2009).

Environmental conditions and food availability often affect how organisms allocate resources between growth and reproduction, and the trade-offs between these life history traits can modulate reproductive strategies (Lord et al., 2021; Siems & Sikes, 1998). In this study, body size (length) and total gonadal investment (size of the total gonads) of *T. iheringi* were similar in both ponds, suggesting that resource allocation for growth and reproduction was similar in both environments and thus not key factors in the differences observed in gonadal sex allocation. In addition, in contrast to the results observed by Singh et al. (2020) in three *Macrostomum* species, the group size did not affect the body size of *T. iheringi*. Although the overall gonadal investment of *T. iheringi* did not differ between the flatworms from the two snail populations, the gonadal sex allocation toward the male function was greater in flatworms from Parque Saavedra, where the infestation intensity was higher. This finding suggests that the primary factor modulating the gonadal sex allocation of *T. iheringi* is likely the social conditions, aligning with results from studies on other flatworms with different lifestyles. Studies with parasitic flatworms have shown that resource allocation to male function increases as the number of mating partners increases as well (Schärer & Wedekind, 2001; Trouvé et al., 1999). Among free-living Platyhelminthes, *Macrostomum* species have been widely studied and tend to exhibit male-biased gonadal sex allocation as mating group size increases (Janicke et al., 2016; Schärer, 2009; Schärer & Ladurner, 2003; Singh et al., 2020; Singh & Schärer, 2022). However, comparisons across multiple species have revealed interspecific variation in sex allocation, suggesting that reproductive strategies can also vary among closely related species (Brand et al., 2022; Singh & Schärer, 2022). This is the first study on a commensal

flatworm, and, although our findings align with our hypothesis and with other studies on Platyhelminthes – showing that higher infestation intensities lead to an increased gonadal allocation toward the male reproductive function – additional research on other temnocephalids (or more snail populations with different intensities of infestation) is necessary to corroborate this trend for the taxon. In contrast to the male function, in the flatworms from Parque Saavedra, where the infestation intensity was higher, the proportion of the gonads allocated to the female function was lower than that in the flatworms from Paseo del Bosque.

This study contributes to our understanding of how ecological factors, such as intensity of infestation, can influence the reproductive strategies of commensal simultaneous hermaphrodites. In addition, it highlights the role of variation in gonadal sex allocation and provides an intriguing case of how commensal organisms like temnocephalans can adjust their reproductive investment to maximize fitness under varying ecological conditions. The results support the sex allocation theory and expand its application to commensal species in natural ecosystems.

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Author contributions

FB, KDC, and CD conceived the ideas and designed the methodology; HGG and LN collected the data; FB, KDC, and HGG analyzed the data; FB and KDC wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest

All authors declare no competing interests.

Data Availability Statement

The data that support our findings are available at the repository of the Universidad Nacional de La Plata (<https://doi.org/10.35537/10915/181698>; <https://doi.org/10.35537/10915/181697>).

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