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Evolution, Volume 53, Issue 5 (Oct., 1999), 1599-1604.

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APPENDIX 2

Here we prove that g_{12} is an increasing function of m .

Proposition 1: Let

$$\mathbf{R} = \begin{pmatrix} r_1 & r_2 \\ r_3 & r_4 \end{pmatrix}, \quad \mathbf{S} = \begin{pmatrix} s_1 & s_2 \\ s_3 & s_4 \end{pmatrix}, \quad \text{and} \quad \mathbf{T} = \begin{pmatrix} t_1 & t_2 \\ t_3 & t_4 \end{pmatrix} = \mathbf{RS},$$

where \mathbf{R} is a positive definite matrix. Then the off-diagonal element t_2 of \mathbf{T} is an increasing function of s_2 .

Proof: We have that $t_2 = r_1 s_2 + r_2 s_4$ and $r_1 > 0$.

Note: Obviously the above result holds also when $\mathbf{T} = \mathbf{SR}$.

Proposition 2: If

$$\mathbf{R} = \begin{pmatrix} r_1 & r \\ r & r_2 \end{pmatrix}$$

is a positive definite symmetric matrix and

$$\mathbf{T} = \mathbf{R}^{1/2} = \begin{pmatrix} t_1 & t \\ t & t_2 \end{pmatrix},$$

the off-diagonal element t of \mathbf{T} is an increasing function of r .

Proof: The equality $\mathbf{TT} = \mathbf{R}$ produces the following system:

$$t_1^2 + t^2 = r_1, \quad (\text{A5a})$$

$$t(t_1 + t_2) = r, \quad (\text{A5b})$$

$$t_2^2 + t^2 = r_2. \quad (\text{A5c})$$

Differentiating the three equations with respect to r , we obtain:

$$\frac{dt_1}{dr} = -\frac{t}{t_1} \frac{dt}{dr}, \quad (\text{A6a})$$

$$\frac{dt}{dr}(t_1 + t_2) + t \left(\frac{dt_1}{dr} + \frac{dt_2}{dr} \right) = 1, \quad (\text{A6b})$$

$$\frac{dt_2}{dr} = -\frac{t}{t_2} \frac{dt}{dr}. \quad (\text{A6c})$$

From the equation (A6b), after substitution with the derivatives of t_1 and t_2 ,

$$\frac{dt}{dr} = \frac{t_1 t_2}{(t_1 + t_2)(t_1 t_2 - t^2)} > 0, \quad (\text{A7})$$

because \mathbf{T} is a positive definite matrix ($t_1 > 0$, $t_2 > 0$, $t_1 t_2 - t^2 > 0$).

Applying the two propositions to the matrix \mathbf{G}_{LE} , obtained from \mathbf{M} after superpositions of multiplication with positive matrices and squaring, we get the desired conclusion that g_{12} is an increasing function of m .

Evolution, 53(5), 1999, pp. 1599–1604

ADAPTIVE SEX ALLOCATION IN A SIMULTANEOUS HERMAPHRODITE

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Abstract.—When applied to hermaphrodite organisms, the local mate competition hypothesis predicts an increase of the ratio of sperm to ova produced as the number of mates increases. Here we test this prediction using a hermaphroditic platyhelminth parasite (trematode), *Echinostoma caproni*. This worm inhabits the small intestine of vertebrates, inevitably inducing the formation of highly subdivided populations, a condition known to promote local mate competition. Moreover this echinostome exhibits an unrestricted mating pattern involving both selfing and outcrossing as well as multiple fertilizations. We quantified the investment in reproductive organs by estimations of testes, cirrus sac, ovary, and egg size and fecundity when echinostomes were isolated alone, in pairs, or in groups of 20 worms. Adult body size was also recorded as a covariate. When mating group size increases (singles, pairs, or groups) we observed a significant increase in resource allocation to male function in addition to a significant decrease in ovary size. Smaller ovaries do not seem to affect egg size, but do result in a reduction in fecundity. Finally, our results are in accordance with the expected theoretical relationship between male allocation and the number of potential mates given local mate competition.

Key words.—*Echinostoma*, local mate competition, parasite, phenotypic plasticity, sex allocation, simultaneous hermaphrodite.

Received July 28, 1998. Accepted May 6, 1999.

The process of resource allocation is an important factor in the evolution of life histories and especially in the evolution of reproductive strategies (Maynard Smith 1978; Char-

nov 1982; Roff 1992; Stearns 1992). Although the principle of resource allocation has now been recognized from more than a century (Darwin 1859), recent work by Charnov (1982), Lloyd (1988), Roff (1992), and Stearns (1992) has contributed to its theoretical and empirical development. This principle simply states that when available resources are limited, the allocation to one function will automatically reduce the resources available to other functions. Numerous questions regarding optimal resource allocation can be raised.

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What is the optimal investment in maintenance and fecundity? Should many small offspring or few large offspring be produced? In the case of sex allocation, the questions addressed are: How many male versus female offspring should a gonochoric individual produce? Is it more advantageous to invest in only one sexual function, male or female (gonochorism), or in both functions (hermaphroditism; Charnov et al. 1976)? What is the optimal male versus female allocation in simultaneous hermaphrodites?

The problem of investment in male and female function in simultaneous hermaphrodites is analogous to the optimal sex-ratio problem faced by gonochoric species. The answer to these questions can be derived from the local mate competition (LMC) model, which was originally developed to seek the equilibrium sex ratio in gonochoric species (Hamilton 1967) and adapted by Charnov (1980, 1982), Fischer (1981), Lloyd (1984), and Lively (1990) to study sex allocation in simultaneous hermaphrodites. The optimal sex allocation depends on the relationship between energetic investment and reproductive success and on the level of competition between nonrelated male gametes. In gonochoric species (e.g., wasps), as the number of foundresses contributing to a local mating population increases, the male-male competition increases and the sex-ratio should shift from a female bias toward a 50:50 sex ratio (Werren 1983; Herre 1985). Similarly, in hermaphrodites when the mating group size is small, male allocation should be low and most resources should be invested in female function. Optimally, male allocation should increase with the number of sperm competitors until it reaches 50% (Maynard Smith 1978; Charnov 1982; Fischer 1984).

Here we report on an experimental study of LMC in a digenetic trematode. The trematode *Echinostoma caproni* (Platyhelminth) is a simultaneous hermaphrodite that, in the adult stage, parasitizes the intestine of vertebrates and exhibits an unrestricted mating pattern involving both selfing and outcrossing (Trouvé et al. 1996). Elsewhere we have demonstrated that a single worm may be inseminated by several different partners, which indicates that sperm competition may be prevalent (Trouvé et al. 1996). Thus, *E. caproni* offers the opportunity to experimentally study the trade-off between male and female investment for different environmental situations. In this study, we investigated the influence of mating group size on sex allocation in this species. In accordance with LMC model, we predicted that an increase in mating group size should result in an increase in male allocation. We manipulated the size of the mating group by experimentally infecting mice with one, two, or 20 worms and then compared the male and female reproductive investment between all three treatments.

MATERIALS AND METHODS

Study Organism

Echinostomes are simultaneous hermaphroditic flukes (Trematoda: Platyhelminth) that parasitize the intestine of mammals or birds. The life cycle of *E. caproni* includes three successive hosts (Fig. 1): a first intermediate host (snail) in which miracidia transform into cercariae by asexual reproduction; a second intermediate host (snail or amphibian) in

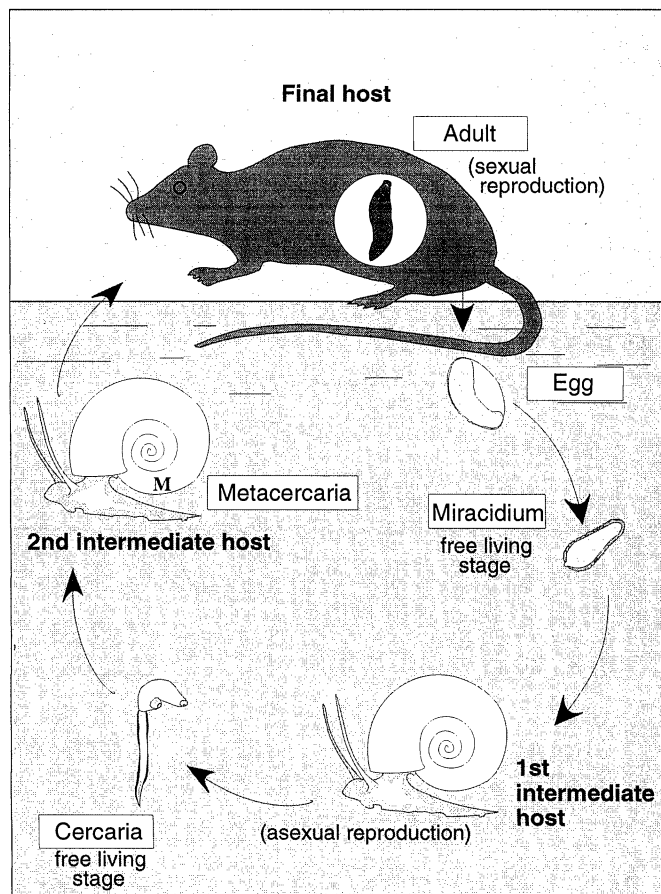


FIG. 1. Life cycle of *Echinostoma caproni*. Metacercariae in the pericardial cavity of the second intermediate host snail is denoted by M.

which cercariae transform into infectious metacercariae, and a final host (vertebrate) in which metacercariae develop into sexually mature adults. In our laboratory *E. caproni* is cycled through *Biomphalaria arabica* snails, which act as first and second intermediate hosts, and mice (Swiss OF1 stock), which serve as the final host.

Experimental Infections

Ten *E. caproni* metacercariae, obtained from snails naturally infected and collected in Mali (Bamako) in May 1996, were fed to each of eight mice. The metacercariae, which are cysts, excyst into adult worms in the mouse intestine. The adults produce eggs that pass with the mouse feces and hatch in water into miracidia. The miracidia were separately brought into contact with one snail. Successful infections result in the asexual production of larvae (cercariae), which attack the second intermediate host. When releasing the asexually produced cercariae, each of these first intermediate host snails was put in contact with one second intermediate host snail. This protocol allowed us to obtain 22 second intermediate host snails each infected by only one clone of metacercariae.

Thirty-three, 20, and 10 mice were infected with one (group A), two (group B), or 20 (group C) metacercariae, respec-

TABLE 1. Experimental design of mice infections to obtain the three treatments.

Treatment	No. of mice infected	No. of parasites per mouse	Clone number used for infections	No. of mice infected by these clones
A	33	1	1	3
			2	3
			3	3
			4	3
			5	3
			6	3
			7	3
			8	3
			9	3
			10	3
			11	3
B	20	2	1, 2	3
			1, 3	3
			3, 4	3
			5, 6	3
			5, 8	3
			7, 9	3
			10, 11	2
C	10	20	1, 2, 3	3
			2, 4, 5	3
			6, 7, 8	2
			9, 10, 11	2
				2

tively. The use of unequal sample sizes (for mice) is explained by the sample design: we harvested multiple worms from mice of treatments B and C, such that in the end the total number of parasites was about the same among treatments. The infection design, presented below and in Table 1, was done in such a way that the clonal metacercariae obtained from several intermediate host snails were assigned to each group to minimize the environmental and genetic differences. Because our purpose was to test the effect of local competition between unrelated male gametes, we infected mice of group A with one clone and mice of groups B and C with multiple clones. For B treatments, one metacercaria originating from each of two different clones was used to infect the 20 different mice (Table 1). For C treatments, six or seven metacercariae from three different clones were used to infect the 10 different mice. Twenty-four days postinfection the mice were sacrificed and their intestines opened. All worms of groups A and B were collected, and five worms from group C were selected at random from each mouse. In total, sexual allocation was determined in 123 parasites (33 for group A, 40 for group B, 50 for group C) using the procedure explained below. The uterus of each adult was torn gently to collect some eggs. Then the adults were flattened between two microscope slides, fixed with bouin, and stained with borasic carmine, which allows different tissues to be distinguished (Gabe 1968).

Measurement of Resource Allocation

The amount of resources allocated to male function was estimated by the area of both testes and the cirrus sac. This sac contains a seminal vesicle, ejaculatory duct, cirrus, and prostate glands. When characters are involved in the same function, it is common that a single gene has a pleiotropic

effect on all of these characters. The development of the male sexual organs may be pleiotropically connected, and thus they cannot be considered as independent datapoints. Therefore, we conservatively pooled the sizes of these male sexual organs (cirrus sac and testes) to perform the analyses on a global male investment.

The resources invested in the female function was estimated by the area of the ovary. In addition on days 21 and 23 postinfection, we counted the number of eggs present in the feces of the infected mice according to the procedure explained in Trouvé et al. (1998). The mean of these values gives us an estimation of the number of eggs produced in one day. For groups B and C, the daily fecundity per worm was estimated as the ratio of the number of eggs divided by the number of parasites recovered in mice during dissection. The volume of 10 randomly chosen eggs, collected from the uterus of each adult, was estimated using the formula of an ellipsoid ($[\text{length}][\text{width}]^2\pi/6$).

Body area was measured for all echinostomes, which allowed us to control for adult size. All the area (length \times width) and volume measurements were made with the aid of an ocular micrometer.

Statistical Procedures

The effect of mating group size on the different variables (adult size, investment in male and female function) was tested on ln-transformed data for which there is homoscedasticity and normality. The analysis of adult size was performed using a nested ANOVA; the analyses of the other characters (male allocation and ovary size) were performed with a nested ANCOVA (covariate: adult size), using SPSS 6.1 for Macintosh. Groups (A, B, and C) were treated as fixed main effect; mice were treated as nested factor within groups. For fecundity, because there is a single value per mouse whatever the group, we used an ANCOVA (covariate: adult size). The analyses were followed by a posthoc Scheffe's test, using SPSS 6.1 for Macintosh. Because our data for the egg volume were not normally distributed, they were analyzed using the nonparametric Kruskal-Wallis test (Sokal and Rohlf 1995) using StatView 4.0.

RESULTS

All the area measurements are the averages from two measurement series done at a one-week interval. The repeatability of measurements was very high and statistically significant (adult size: $r = 0.93$, $P < 0.001$; cirrus sac: $r = 0.99$, $P < 0.001$; anterior testis: $r = 0.99$, $P < 0.001$; posterior testis: $r = 0.99$, $P < 0.001$; ovary: $r = 0.99$, $P < 0.001$), suggesting that the measurements were sufficiently precise to allow analyses.

A nested ANOVA revealed that group A worms (Table 2) were significantly larger than group B worms ($F = 33.62$; $df = 2, 60$; $P < 0.001$; post hoc test: $P < 0.01$) and that group B worms were significantly larger than group C worms (post hoc test: $P < 0.05$).

Male allocation (sum of the cirrus sac and both testes areas) increased significantly with mating group size (Fig. 2; nested ANCOVA: $F = 527.16$; $df = 2, 59$; $P < 0.001$; post hoc test: for all comparisons $P < 0.001$). The same pattern was

TABLE 2. Means (standard deviations) of different characters for each mating-group size.

Character	Group A one worm/host	Group B two worms/host	Group C 20 worms/host
Adult size (mm ²)	12.08 (1.87)	10.82 (1.4)	10.11 (1.53)
		*	*
Male function (mm ²) ¹	0.30 (0.07)	0.78 (0.17)	0.93 (0.21)
		**	**
Ovary (mm ²)	0.17 (0.03)	0.15 (0.03)	0.13 (0.02)
		**	**
Fecundity ²	3896.97 (839.11)	3003.62 (674)	1911.21 (592.71)
		**	**
Egg volume (× 10 ³ μm ³)	235.36 (29.53)	254.8 (49.58)	244.88 (28.96)
		NS	NS
		NS	NS

¹ Sum of cirrus sac and both testes size.

² Mean number of eggs released by worm each day.

* Significant differences.

** Significant differences when body size is controlled.

NS: Nonsignificant differences.

found when the two testes and the cirrus sac were analyzed separately. In addition we observed a significant decrease in ovary size (Fig. 2) as mating group size increased (nested ANCOVA: $F = 11.2$; $df = 2, 59$; $P < 0.001$; post hoc test: for all comparisons $P < 0.05$).

Finally, we tested whether the reduction in ovary size affected fecundity and egg volume. The number of eggs pro-

duced per worm decreased significantly with increased group size (ANCOVA: $F = 24.34$; $df = 2, 59$; $P < 0.001$; post hoc test: for all comparisons $P < 0.001$). Egg volume did not covary with adult size (Spearman rank correlation $P = 0.07$), therefore absolute egg volume could be compared. The Kruskal-Wallis test indicated that egg volume was negatively related to group size, but the result was only marginally significant ($P = 0.07$).

DISCUSSION

Sex Allocation

Our results show that the total investment in male function (cirrus sac and both testes) increased more than threefold, and that ovary size was reduced by nearly 1.5 times when the size of the infrapopulation increased from one to 20 (Table 2). This trade-off between male and female investment clearly suggests that *E. caproni* is able to regulate its sex allocation facultatively, in accordance with LMC model applied to hermaphrodites. However, our data also indicate that female allocation increases with increasing body size. Thus, an alternative explanation for the pattern we observed could be that decreasing environmental stress associated with decreasing number of worms per host leads to increases in both adult size and female investment (size advantage hypothesis). However, male investment in group C worms (small worms) is more than three times higher than in group A worms (large worms). Therefore, to obtain our results, a size advantage hypothesis would imply a massive investment in male function when the worm is small and then, with the growth of the worm, a lysis of a part of male tissues in concert with a development of female organs. However, growth and development of *E. caproni* were studied in detail; both ovary and testes size increase with adult size, meaning that there is no lysis of male tissues when adult size increases (Huffman and Fried 1990; Yao et al. 1991). Another alternative hypothesis could be that our results simply reflect protandric develop-

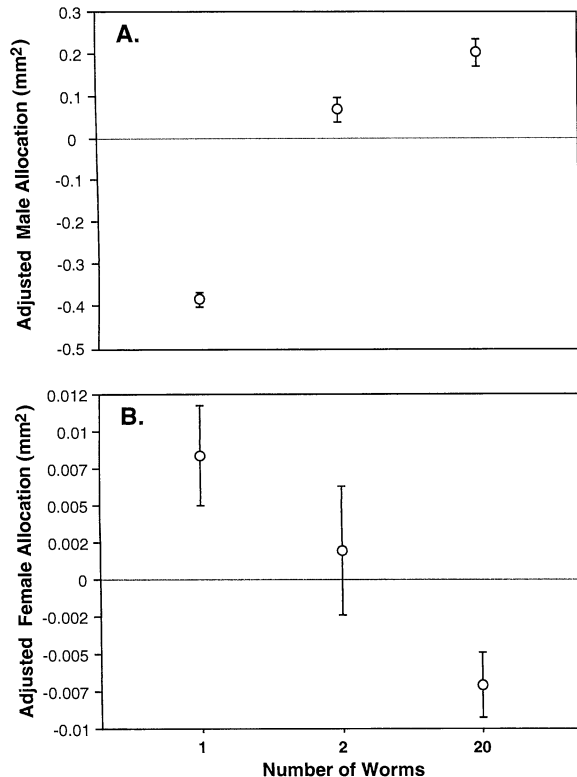


FIG. 2. (A) Cell plot performed on residuals of regression of male allocation (cirrus sac and both testes) on adult size. (B) Cell plot performed on residuals of regression of female allocation (ovary) on adult size. Circles represent means and bars represent 1 SE.

ment. However, if differences in sex investment among our treatments derive from an ontogenetic process, then only a high investment in male organs followed, later in life, by a lysis of a part of same organs would explain our data. The same studies on this parasite allow us to reject this hypothesis: These authors (Huffman and Fried 1990; Yao et al. 1991) never showed protandry in *E. caproni*. Therefore, LMC is the most likely factor influencing the outcome of sex investment observed in the experimental populations studied.

Although we included all major parts of the male reproductive system in our allocation measurement, this was not true for the female system. Yolk glands may represent a large part of the allocation, but it is impossible to measure them because they are diffused throughout the somatic tissue. This may explain why the decline in female allocation is not as marked as the increase in male allocation. However, we were more concerned with the change in male versus female investment with group size, rather than quantitative measures of sex allocation; we do not know the cost of male and female function per unit of tissue.

Recently, Lively (1990) developed an LMC model for the special case of parasitic worms or other organisms producing clonal families that coexist at the time of sexual reproduction in the final host. The main difference of Lively's model is that it considers the number of clonal families per host (rather than the number of mates), which means that there might be several individuals originating from the same clone. The model predicts that as the number of clonal families within a local mating population increases, the investment in male function should increase until it reaches 50%. In this case, the strength of the competition is a function of the number of clonal families available for interclonal outcrossing (group A:zero, group B:one, group C:two) rather than the number of potential mates (group A:zero, group B:one, group C:19). The fact that we do not know the cost of a unit of male and female organs makes it impossible to calculate percentages of investment in male and female function and thus to adjust our data to the model. However, our results seem to support Lively's model: As the number of clonal families decreases, selection for decreased male allocation is due to the increased probability of outcrossing among worms of the same clone. In conclusion, our results are consistent with the key idea in both Charnov's and Lively's hypotheses that simultaneous hermaphrodites should alter the sexual allocation to male and female organs in response to local competition between non-related male gametes.

Assessment of the Number of Competitors

The fact that worms are able to adaptively adjust their allocation strategy suggests that they can estimate the number of competitors. This may be a result of chemical processes (excretory-secretory products). The excretory-secretory products of trematodes trigger various biological processes, including sexual stimulation or pairing behavior (Eveland et al. 1983; for review, see Fried 1986). The existence of such products has been shown for echinostomes and their role in inter-individual attraction has been demonstrated (Fried and Haseeb 1990; Trouvé and Coustau 1998). Because these products largely diffuse in the host intestine, their amount probably

reflects the density and thus the potential number of competitors.

Quality and Quantity of Female Allocation?

Fecundity decreased significantly with increasing group size. This points out that a reduction in ovary size primarily affects the number of eggs produced. Egg size showed marginally significant differences with the low-powered non-parametric method used. However, the marginally significant *P*-value results from slightly higher egg size in the intermediate treatment and therefore cannot compensate for the important decrease in fecundity observed across treatments. Therefore, this does not affect our interpretation that small ovaries do not seem to affect egg size but result in a reduction in fecundity. Optimal egg size is probably determined by numerous physiological constraints, such as embryonic development, infection pathway to the first intermediate host, and resource expenditure. Egg size might therefore be expected to remain relatively unaffected by mating group size.

Phenotypic Plasticity

Phenotypic plasticity occurs when a single genotype produces phenotypic variation in different environments (Roff 1992; Stearns 1992) and must be considered to be a trait itself (for review, see Via et al. 1995). Indeed, when the environmental conditions of a species change spatially and temporally, there is little chance that a unique phenotype will confer a high fitness in all situations. Flexible adjustment of the phenotype to the environment can therefore enhance reproductive success under a wider array of environmental conditions (Solignac et al. 1995; Via et al. 1995).

Charnov and Bull (1977) explained that selection should favor simultaneous hermaphrodites able to control the investment in male and female function in response to environmental conditions (because simultaneous hermaphroditism is commonly associated with immobility in the adult stage). The environmental sex determination depending on the mating group, which the echinostomes have, is probably a consequence of the variability in densities in natural populations. Indeed, parasites exploit particular habitats (the hosts) that are separated spatially as well as temporally (i.e., hosts die). Because of these constraints: (1) echinostomes colonize new habitats at each generation and cannot move to a new host to find a mate if alone; and (2) adults cannot predict the environmental conditions in which offspring enter and develop. These two constraints may have favored the evolution of phenotypic plasticity in sex allocation. However, data on the variability of *E. caproni* intensities in the natural final hosts are not yet available, and thus further field work is needed to test this assumption.

The changes in sex allocation observed here are analogous to the ones observed in gonochoric species with a facultative sex ratio, such as wasps (Werren 1983, 1987; Herre 1985, 1987), ants (Sundstrom 1994) and birds (Komdeur et al. 1997). All of these studies highlight the importance of the environment in shaping sex allocation adjustment and raise the question of the major role of adaptive behavioral plasticity in the evolution of species subject to heterogeneous environments.

ACKNOWLEDGMENTS

We are grateful to M.-T. Almeras, B. Dejean, and P. Pasquereau for excellent technical assistance. We thank T. de Meeüs and F. Thomas for assistance with statistical analysis and P. Fontanillas, J. Greeff, P. Jarne, N. Michiels, and M. Reuter for stimulating discussions on this paper. We wish also to acknowledge two anonymous reviewers for helpful comments. We address special thanks to A. Dabo for collecting the animals in Mali. This work was supported by the CNRS (Sciences de la Vie) and by the Ministère de l'Enseignement Supérieur et de la Recherche through a grant to ST. This manuscript was written while ST was working under a grant from the Robert Schuman Foundation.

LITERATURE CITED

- Charnov, E. L. 1980. Sex allocation and local mate competition in barnacles. *Mar. Biol. Letters* 1:269–272.
- . 1982. The theory of sex allocation. Princeton Univ. Press, Princeton, NJ.
- Charnov, E. L., and J. Bull. 1977. When is sex environmentally determined? *Nature* 266:828–830.
- Charnov, E. L., J. Maynard Smith, and J. Bull. 1976. Why be an hermaphrodite? *Nature* 236:125–126.
- Darwin, C. 1859. On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life. John Murray, London.
- Eveland, L. K., B. Fried, and L. M. Cohen. 1983. *Schistosoma mansoni*: adult worm chemoattraction with barriers of specific molecular weight exclusions. *Exp. Parasitol.* 56:255–258.
- Fischer, E. A. 1981. Sexual allocation in a simultaneously hermaphroditic coral reef fish. *Am. Nat.* 117:64–82.
- . 1984. Local mate competition and sex allocation in simultaneous hermaphrodites. *Am. Nat.* 124:590–596.
- Fried, B. 1986. Chemical communication in hermaphroditic digenetic trematodes. *J. Chem. Ecol.* 12:1659–1677.
- Fried, B., and M. A. Haseeb. 1990. Intra- and interspecific chemoattraction in *Echinostoma caproni* and *E. trivolvis* adults *in vitro*. *J. Helminthol. Soc. Wash.* 57:72–73.
- Gabe, M. 1968. Techniques histologiques. Masson et Cie, Paris.
- Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.
- Herre, E. A. 1985. Sex ratio adjustment in fig wasps. *Science* 228:896–898.
- . 1987. Optimality, plasticity and selective regime in fig wasp sex ratios. *Nature* 329:627–629.
- Huffman, J. E., and B. Fried. 1990. *Echinostoma* and echinostomiasis. *Adv. Parasitol.* 29:215–269.
- Komdeur, J., S. Daan, J. Tinbergen, and C. Mateman. 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* 385:522–525.
- Lively, C. M. 1990. Male allocation and the cost of biparental sex in a parasitic worm. *Lect. Math. Life Sci.* 22:93–107.
- Lloyd, D. G. 1984. Gender allocations in outcrossing cosexual plants. Pp. 277–300 in R. Dirzo and J. Sarukhan, eds. *Perspectives in plant population ecology*. Sinauer, Sunderland, MA.
- . 1988. A general principle for the allocation of limited resources. *Evol. Ecol.* 2:175–187.
- Maynard Smith, J. 1978. The evolution of sex. Cambridge Univ. Press, Cambridge, UK.
- Roff, D. 1992. The evolution of life histories, theory and analysis. Chapman and Hall, New York.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. 3d ed. Freeman, New York.
- Solignac, M., G. Periquet, D. Anxolabéhère, and C. Petit. 1995. Génétique et évolution. Tome I. La variation, les gènes dans les populations. Hermann, Paris.
- Stearns, S. C. 1992. The evolution of life histories. Oxford Univ. Press, Oxford, UK.
- Sundstrom, L. 1994. Sex ratio bias, relatedness asymmetry and queen mating frequency in ants. *Nature* 367:266–268.
- Trouvé, S., and C. Coustau. 1998. Differences in excretory-secretory products from adult echinostomes of related species. *J. Parasitol.* 84:1062–1065.
- Trouvé, S., F. Renaud, P. Durand, and J. Jourdan. 1996. Selfing and outcrossing in a parasitic hermaphrodite helminth (Trematoda, Echinostomatidae). *Heredity* 77:1–8.
- . 1998. Experimental evidence of hybrid breakdown between genetically distinct populations of *Echinostoma caproni*. *Parasitology* 117:133–135.
- Via, S., R. Gomulkiewicz, G. De Jong, S. M. Scheiner, C. D. Schlichting, and P. H. Van Tienderen. 1995. Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.* 10:212–217.
- Werren, J. H. 1983. Sex ratio evolution under local mate competition in a parasitic wasp. *Evolution* 37:116–124.
- . 1987. Labile sex ratios in wasps and bees: life histories influence the ratio of male and female offspring. *Bioscience* 37:498–506.
- Yao, G., J. E. Huffman, and B. Fried. 1991. The effects of crowding on adults of *Echinostoma caproni* in experimentally infected golden hamsters. *J. Helminthol.* 65:248–254.

Corresponding Editor: C. Lively