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REDUCED MALE ALLOCATION IN THE PARTHENOGENETIC HERMAPHRODITE *DUGESIA POLYCHROA*

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Abstract.—Parthenogenetic lineages that arise in a hermaphroditic, sexual population will inherit the male function from their sexual progenitors. Natural selection then acts to reduce male allocation of the parthenogens, freeing resources presumably for the female function. Depending on age and the available genetic variation, one therefore expects to find reduced male allocation in naturally occurring parthenogenetic lineages. We investigated the allocation to sperm production in the hermaphroditic flatworm *Dugesia polychroa* in three lakes containing a sexual (S), a (pseudogamous) parthenogenetic (P), and a mixed sexual-parthenogenetic population (M). Parthenogenetic lineages from M were assumed to be relatively young due to recurrent origins from the coexisting sexuals, whereas those from P were assumed to be older on biogeographical grounds. As predicted, we found drastically reduced sperm production in parthenogens compared to sexuals, even in the parthenogenetic lineages from M, which may be younger. M parthenogens did not have more testes, but produced more sperm than individuals from the purely parthenogenetic population (P). However, the latter result could not be reproduced with laboratory-raised animals and therefore may be a consequence of different ecological conditions in the different lakes, for example, differences in mating rates. To study the behavioral component of male allocation, copulation frequencies were recorded for sexuals from M and for parthenogens from P. Compared to the drastic reduction in sperm production, copulation frequency was less reduced in parthenogens. This may be a consequence of allosperm limitation in pseudogamous parthenogenetic populations.

Key words.—Cost of sex, *Dugesia*, hermaphroditism, parthenogenesis, Plathelminthes, polyploidy, sex allocation.

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Many sexual hermaphrodites invest heavily in sperm (e.g., Grassé 1961; Alvarino 1992), probably as a consequence of sperm competition for access to eggs (Charnov 1982; Parker 1990). Sperm competition, however, does not play a role in parthenogenetic populations, where paternal reproductive success does not exist. Since the production of male gametes is costly (Rameau and Gouyon 1991; Partridge and Harvey 1992; Van Voorhies 1992; but see Gems and Riddle 1996), natural selection is expected to eliminate sperm production in parthenogenetic hermaphrodites. Nevertheless, male gametes are produced by many parthenogenetic hermaphrodites (Christensen et al. 1978; Nogler 1984; Ó Foighil and Smith 1995). The low evolutionary potential of clonal organisms (Fisher 1930; Muller 1932; Crow and Kimura 1965; Maynard Smith 1978), and the young age of many parthenogenetic lineages (Suomalainen et al. 1987; Asker and Jerling 1992; Avise et al. 1992) are two nonadaptive explanations for this observation.

There are also at least two adaptive explanations for sperm production by parthenogenetic hermaphrodites. First, they may obtain paternity when mating with coexisting sexuals. However, even under such conditions, parthenogens should shift resources to the female function (Joshi and Moody 1995), because they are 100% related to maternal offspring but only 50% related to paternally sired offspring. Also, if sexual eggs fertilized by a parthenogen sometimes develop into parthenogenetic offspring, new clonal lineages with high fitness may arise (Clausen 1961; Turgeon and Hebert 1994; Menken et al. 1995) again favoring some male allocation.

A second benefit can arise in pseudogamous parthenogenetic species. Here, sperm are necessary to trigger egg de-

velopment through gamete fusion, but are expelled later without contributing genetically. Such a hermaphrodite could use self sperm to trigger their own eggs (Smith 1963; Ó Foighil and Eernisse 1988; Ó Foighil and Thiriot-Quievereux 1991; Asker and Jerling 1992; Mogie 1992). When “self-triggering” is not possible, kin or group selection may favor altruistic sperm donation (Aoki 1982), as it avoids the infertility costs resulting from sperm limitation within the local population. In both cases, however, sperm should only be produced in small quantities, just enough to ensure the (parthenogenetic) development of all eggs, whether an individual’s own eggs or that of the local group.

We studied male allocation in the flatworm *Dugesia polychroa* (Tricladida, Platyhelminthes), from which diploid sexuality as well as several types of polyploid parthenogenesis have been described (Benazzi 1957). Parthenogenesis is pseudogamous (Benazzi 1950; see above). Although polyploid, they produce functional, haploid sperm. This is accomplished by elimination of one or more chromosome sets, resulting in a diploid male germ line that produces sperm meiotically (Benazzi Lentati 1970). The parthenogenetic populations studied here are triploid and the female germ line is hexaploid due to chromosome duplication. Eggs are produced meiotically, bringing chromosome number back to triploidy (Benazzi 1957). Neither sexuals nor parthenogens use self sperm for fertilization (or egg-triggering). Sperm from parthenogens can fertilize the eggs of sexuals, and although the resulting “hybrids” are diploid and sexual, they sometimes give rise to new polyploid parthenogenetic forms among their offspring (Benazzi Lentati 1966). Male allocation in sexual flatworms is usually high (Hyman 1951), and copulations are frequent (Peters et al. 1996). Female reproduction involves the production of cocoons: dark brown, spherical egg cases that mainly contain yolk, in addition to a few, small zygotes.

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Up to six young may hatch from a single cocoon (pers. obs.). In *D. polychroa* both mating and cocoon production take place throughout the reproductive life span of an individual (Peters et al. 1996).

We compared sperm production by sexual and parthenogenetic *D. polychroa* from four localities: One sexual (S), two mixed (M_1 and M_2), and one purely parthenogenetic population (P). Parthenogenetic lineages from M are genetically similar to the coexisting sexuals (Pongratz, Sharbel, Beukeboom, and Michiels, unpubl. data). Since recurrent origin of parthenogens from sexuals is possible in mixed populations (Benazzi Lentati 1966) we therefore assume that parthenogenetic lineages in M are younger than those from P, which are separated from the closest sexual population by a mountain range (the Alps; Beukeboom et al. 1996). We also measured male allocation in individuals raised in the laboratory. To study the behavioral component of male investment, copulatory activity of parthenogens was compared with known results from sexuals. A comparison of female fecundity and fertility of sexuals and parthenogens is the scope of another study.

MATERIALS AND METHODS

Study Populations

We sampled the north Italian lakes Lago di Caldonazzo (M_1 : east shore; M_2 : west shore) and Lago di Toblino (S) and the south German lake Ammersee (P). P contains only parthenogens, S only sexuals, and M a mixture of sexuals and parthenogens. Sampling dates were between March 11 and 21, 1995, for the "March" samples and between April 28 and May 15, 1995 for the "May" samples. From the mixed population M, we have collected ecological data that indicated little, if any, ecological separation between sexuals and parthenogens and a high degree of genetic similarity between sexuals and parthenogens within sampling sites relative to between sampling sites. Matings between sexuals and parthenogens take place in the field (Streng and Michiels, unpubl. data) and the rate at which sexuals produce parthenogens has been estimated to be 1.0–1.5% of all offspring produced by 20 sexual individuals collected from M_2 (R. P. Weinzierl, P. Schmidt, and N. Michiels, unpubl. data).

Field-Collected Animals

Animals were flushed off stones picked from a few meters of the shoreline. Each locality was visited at least twice, once in March and once in May 1995, which coincides with the peak of reproductive activity in *D. polychroa* (Reynoldson et al. 1965). Small animals (< 8 mm²) were considered juvenile and discarded. The remaining individuals possessed normal genitalia, indicating sexual maturity.

Laboratory-Raised Individuals

To reduce the effect of different environmental conditions, we also measured sperm amounts in laboratory-raised animals. We collected eight sexual and two parthenogenetic individuals from M_2 on January 10, 1995. In addition, we collected 29 parthenogens from P on February 10, 1995. From March 20 onward cocoons were collected from each indi-

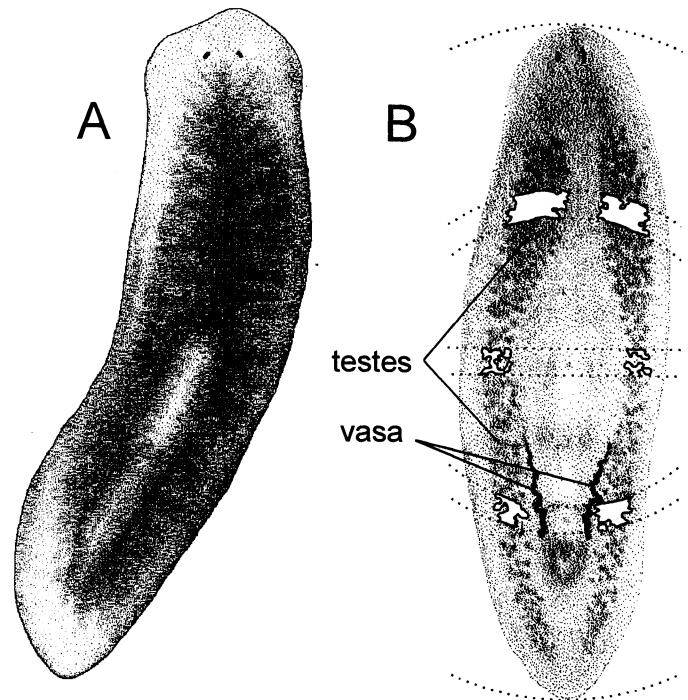


FIG. 1. (A) Live *Dugesia polychroa*. (B) Similar individual after Feulgen treatment, showing the positions of the transects in which testes were measured. First, the worm was magnified to fit the outer oval as indicated. Subsequently, testes circumferences were drawn as shown. Transects were curved to reduce measurement error when worms were slightly bent after fixation.

vidual during four days, and young hatching until April 1 were used for the experiment. Ten hatchlings were selected randomly from large families.

Hatchlings were raised in 200-mL pots with two mesh-covered holes on opposite sides and placed in a bigger container through which filtered water from an aquarium was pumped continuously. Worms were fed twice a week with minced beef liver and frozen *Chironomus* larvae. A 14:10 L:D diurnal cycle was used and water temperature was kept at 18°C. After 10 weeks, 142 surviving young had reached adult size, and the presence of a penis in most of them (94%) indicated that they were sexually mature.

Staining Method

The Feulgen DNA staining technique to visualize sperm was used (Feulgen and Rosenbeck 1924; Romeis 1968). Due to the high concentration of DNA in sperm-filled testes and vasa deferentia (sperm ducts), it is easy to recognize these organs after this treatment (Fig. 1). Preparations were preceded by one week of starvation to clear the gut, followed by a colchicine treatment (0.15%, 6–8 h) for karyotyping (see below). Individuals were subsequently killed with a drop of 1 N HCl (10 s), then fixed with Carnoy's fluid (3:1 ethanol: acetic acid) and stored at –20°C. After rinsing with deionized water, specimens were incubated (25 min) in 5 N HCl at 20°C, and rinsed again for 10 min. They were then stained with Schiff's reagents (3 h, 4°C), followed by a final treatment with 22.5% acetic acid (16 h, 4°C) to clear the worms of unbound dye and bleach out epidermal pigments.

Measurements

Planarians are strongly dorsoventrally flattened and, hence, can be sized reliably by measuring the outline of the dorsal view (planar surface in mm²). Animals were digitized alive while gliding in a petri dish using a video camera mounted on a binocular microscope. The area was determined using an image analysis system (Mocha, Jandel Scientific). Feulgen stained specimens were photographed under standardized conditions and the resulting slides were used for later measurements.

Vasa were drawn using a camera lucida and measured in mm² using the equipment described above. We investigated the relationship between vasa size and body size for each combination of sample and ploidy level and found a significant, positive, linear relationship in some cases, but not in others (usually in parthenogens and when sample size was small). A log-log transformation did not affect these results, probably because both values are measured in the same units (mm²). We conclude that there is an overall trend for vasa size to increase linearly with body size, but that individual variation is high. To be able to compare animals from different sites (which differ in average body size), we corrected vasa size for body size by simply dividing the former by the latter, resulting in the "adjusted vasa size" used in the results section.

Testes consist of small globules that occur in a flat layer under the dorsal epidermis. They are particularly dense in the frontal half of the body, and more dispersed in the caudal half (Fig. 1B). Estimating their amount is difficult, and after a series of unsuccessful attempts to count, draw, or image-analyze them as a whole, we decided to use a relative measure of testes number instead. A reference drawing with three transects was used, one in the anterior, one in the central, and one in the posterior part of the worm (Fig. 1B). A slide of a worm was placed under a binocular microscope and magnified to match the reference drawing under the camera lucida. Subsequently, contours of testis tissue were drawn within the three transects only. This procedure automatically corrects for body size, assuming a simple linear relationship between body area and testes area as discussed for vasa size above. Drawings were measured as described above and the measurements (in pixels) were divided by the largest value obtained over all specimens, resulting in individual values for "adjusted testis size" between zero and one.

Before drawings were made, testis activity was determined. A testis globule was considered active if a dark spot was visible in its center, indicating the presence of sperm in its lumen. Testis activity in an animal was classified into four categories (1: < 25% of testis globules active; 2: 25–50% active; 3: 50–75% active; 4: > 75% active). For animals that were damaged during preparation, certain measurements could not be taken.

Karyology

Sexual and parthenogenetic *D. polychroa* are morphologically identical and can only be distinguished on the basis of their chromosome number. The former are diploid, whereas the latter are triploid. Two tetraploid parthenogens were found, but discarded. To determine karyotypes a piece of

tissue was taken from Feulgen stained worms stored in 22.5% acetic acid, placed on a microscope slide, and squashed under a cover glass using a mechanical press. Slides were examined under phase contrast at a 1000× magnification. No karyotypes were determined for animals from P because this lake had been reported to contain only parthenogenetic triploids (Beukeboom et al. 1996).

Behavioral Observations

For comparison of mating activity in sexuals and parthenogens, 16 pairs from the P population as well as 16 mixed pairs comprised of one sexual partner from M₁ and one parthenogenetic partner from P were observed in February–March 1994. The experiment was performed for 120 h in the "copulation carousel" described by Peters et al. (1996). The number and duration of copulations was recorded for each pair, as well as the number of cocoons laid during the experiment. Animals had been kept in groups of approximately 20 prior to the experiment. Observations are compared to published data on M₁ sexuals obtained in the same way by Peters et al. (1996).

Statistics

Statistical analyses were performed with SPSS for Windows 6.1.2. All *P*-values are two tailed and averages are given with their standard deviation. Box-plots show the median, first, and third quartile and range. Points outside one and a half box-lengths are displayed as outliers. If not stated otherwise, measurements are averages per mother.

RESULTS

Do Parthenogens Have Lower Male Allocation than Sexuals?

Sexuals from different populations showed consistently higher male investment than parthenogens (Fig. 2). A three-way ANOVA of adjusted testes size on M₁ and M₂ individuals revealed no effects of site ($P = 0.53$), but a significant effect of date ($F = 25$; $df = 1$; $P < 0.001$) and mode of reproduction ($F = 55$, $df = 1$, $P < 0.001$) (overall model: $F = 21.6$; $df = 7, 100$; $P < 0.001$). A similar 3-way ANOVA of adjusted vasa size for M₁ and M₂ individuals revealed no effects of site ($P = 0.21$) or date ($P = 0.874$), but again a significant effect of mode of reproduction ($F = 70$, $df = 1$, $P < 0.001$) (overall model: $F = 20.3$; $df = 7, 172$; $P < 0.001$). S sexuals had quite small testes and vasa relative to body size, but because these animals were larger than animals from M (data not shown) absolute sizes of testis and vasa were similar to M sexuals.

Table 1 shows that sexuals had more active testes than parthenogens in M (March: Wilcoxon $Z = -4.1$, $P < 0.001$; May: $Z = -3.2$, $P = 0.001$) but similar testes activity when compared to sexuals from S (March: Wilcoxon $Z = -1.5$, $P = 0.12$; May: $Z = -2.3$, $P = 0.07$). Parthenogens from P had less active testes than those of M (May sample only: Wilcoxon $Z = -3.4$, $P = 0.001$). Low testis activity in parthenogens was, however, not a universal condition because testes were found to be fully active in some parthenogens from both M and P.

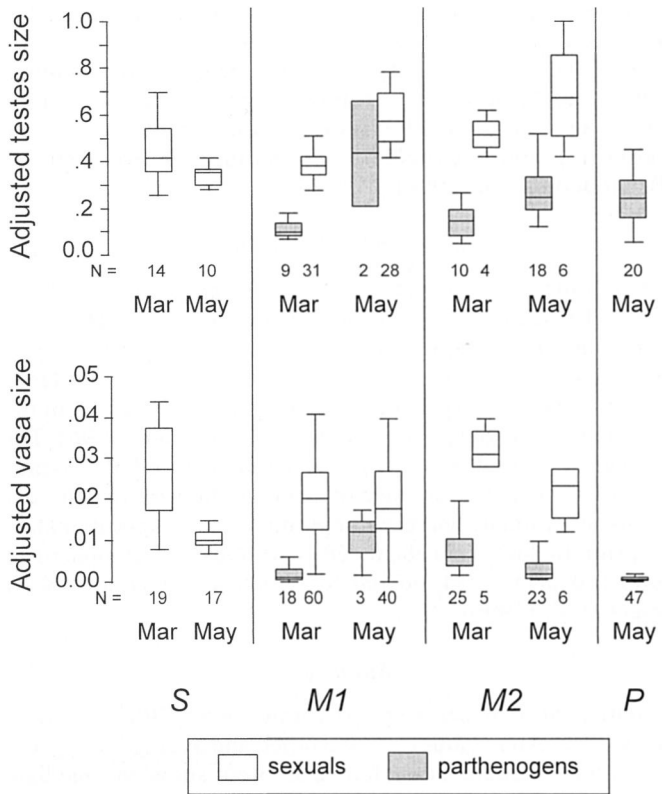


FIG. 2. Top: adjusted testes size in sexual and parthenogenetic *Dugesia polychroa* from four field sites (S, M₁, M₂, and P). Bottom: adjusted vasa size in the same samples.

Do Parthenogens from a Mixed Population Differ from Those in a Pure Population?

Parthenogens from P and M (both sites combined) did not differ in testes size (May sample only) ($t = 1.14$; $df = 38$; $P = 0.26$). P animals had, however, fewer sperm in their vasa than those from M ($t = 5.6$; $df = 70$; $P < 0.001$). It suggests that sperm were produced at a lower rate in P, which is confirmed by the lower testes activity in P parthenogens relative to M parthenogens (Table 1).

Laboratory-Raised Animals

The three groups did not differ in body size (Fig. 3; K-W, $P = 0.59$) and therefore absolute vasa size could be compared. M sexuals had larger vasa than did either parthenogenetic group (K-W $\chi^2 = 16$, $df = 2$, $P < 0.001$; post-hoc test: all groups differ for $\alpha = 0.05$). Despite the small sample size in M parthenogens, they had significantly smaller vasa than P individuals, which is the opposite from what was found in the field samples (Fig. 2). Environmental effects may therefore be important in determining male allocation in the field.

All parthenogenetic families from M and P contained at least one member that had sperm in its vasa. Within P, parthenogenetic families varied significantly in vasa size (K-W $\chi^2 = 44.1$, $df = 29$, $P = 0.036$). All this indicates that families that stopped producing sperm are rare and that male allocation is, to some extent, family-specific.

TABLE 1. Testis activity in sexuals and parthenogens from individuals collected from a purely sexual population S, a mixed population M, and a purely parthenogenetic population P in 1995. Testis activity was subdivided in four categories representing <25%, 25–50%, 50–75%, and >75% of the testes globules active. Medians (range) and sample sizes are given for each sample.

	S		M		P
	March	May	March	May	
Sexual <i>n</i>	4 (2–4) 14	4 (4–4) 10	3 (1–4) 35	4 (1–4) 34	—
Parthenogenetic <i>n</i>	—	—	1 (1–3) 19	2 (1–4) 20	1 (1–4) 20

Is the Mating Behavior of Sexuals and Parthenogens Different?

There were no obvious differences in copulatory behavior between the three groups. Hence the general description of mating behavior in sexuals, given by Peters et al. (1996), is valid for both biotypes. There was no significant difference in the proportion of pairs copulating and the average copulation rate or duration (Table 2). Parthenogens did, however, produce 1.6 times more cocoons than sexuals.

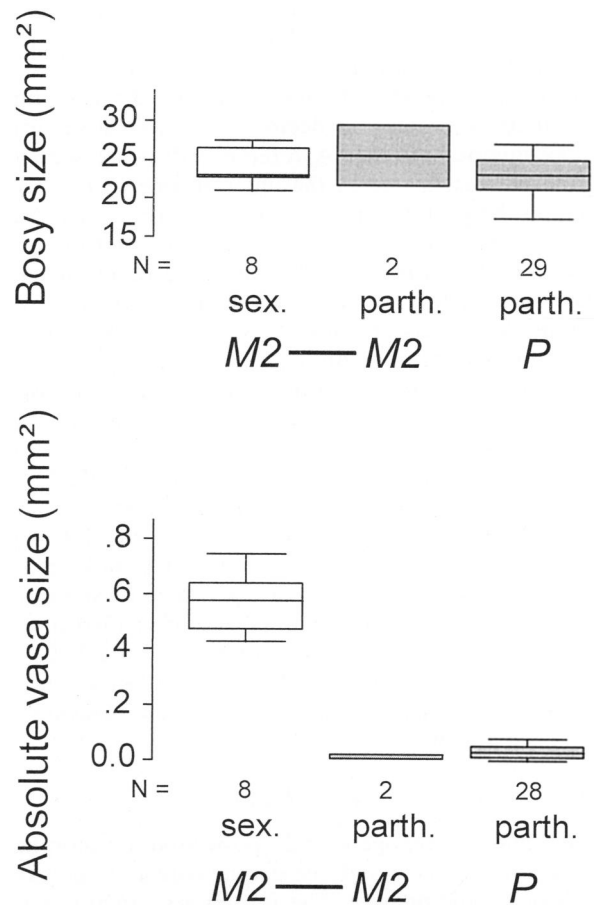


FIG. 3. Body size and (absolute) vasa size in laboratory raised animals from the mixed (M) and the purely parthenogenetic (P) populations. The total number of individual offspring was 142.

TABLE 2. Copulatory behavior and cocoon production in pure and mixed pairs of sexuals and parthenogens. Sexuals came from the mixed population M₁, parthenogens from the purely parthenogenetic population P.

	Sexual pairs ¹	Mixed pairs	Parthenogenetic pairs	P
Copulating : noncopulating pairs	47:8	13:3	14:2	0.91 ²
Avg. number of copulations ³	2.9 ± 1.5	3.7 ± 2.5	2.3 ± 1.1	0.27 ⁴
Avg. copulation duration (min)	64.3 ± 25.9	59.3 ± 20.2	47.9 ± 30.1	0.21 ⁴
Avg. number of cocoons	2.2 ± 1.1	2.8 ± 1.3	3.5 ± 1.7	0.02 ⁴

¹ Data from Peters et al. 1996.

² Exact P (StatXact).

³ Only pairs that copulated at least once.

⁴ K-W test.

DISCUSSION

Male organs of parthenogens were considerably smaller than those of sexual *D. polychroa*. This was true in the natural populations as well as under laboratory conditions. Parthenogens in the mixed population M, which are able to inseminate sexuals, do not have more testes than those of the purely parthenogenetic population P, which cannot have paternal reproductive success. M individuals had, however, more active testes and more sperm stored in their vasa. Since the opposite was found in laboratory-raised animals, environmental conditions may play an important role. One likely possibility is that P animals were not as sexually mature as M animals because spring is a few weeks later in P lakes relative to M lakes. Behavioral observations showed that the copulation frequency of animals from a purely parthenogenetic population was somewhat lower than that of sexuals, but still high for animals that have no opportunity to achieve male reproductive success. The reduction of male allocation in P parthenogens coincided with a 60% increase in cocoon production relative to M sexuals. This confirms results from another study, in which M parthenogens showed a 40% increase in fecundity relative to coexisting sexuals (Weinzierl, Schmidt and Michiels, unpubl. data).

Reduced Sperm Production in Parthenogens: Adaptation or Physiological Defect?

Because most parthenogenetic *D. polychroa* in this study were triploid, a straightforward explanation for reduced sperm production would be that irregularities in meiotic pairing and segregation could interrupt spermatogenesis. Meiotic problems of this kind can lead to male sterility in triploids and are common in parthenogenetic plants (Nogler 1984; Suomalainen et al. 1987; Asker and Jerling 1992).

Even though diploidization of the male line (see introduction) circumvents the problems of meiosis in triploid cells, the process of ploidy reduction itself might have a high error rate. This is unlikely, however, because no deviating chromosome numbers have ever been observed in the spermatogenesis of triploid *D. polychroa* (Benazzi and Benazzi Lentati 1976, 1992). Male meiosis of parthenogenetic *D. polychroa* is reported to be entirely regular, and the resultant sperm are able to fertilize the eggs of sexual conspecifics (Benazzi and Benazzi Lentati 1976). Even the putatively more ancient parthenogens from P are efficient in fertilizing sexual eggs (Weinzierl and Lamatsch, unpubl. data). Even if the reduction were due to aberrant spermatogenesis, we would expect a

lower productivity of individual testis globules, rather than the decrease in the extension of testicular tissue found in this study. Although testes of parthenogens were less active than those of sexuals, testes were fully active in at least some parthenogens, showing that the lower activity in other individuals is not due to constraints inherent to pseudogamous parthenogenesis. To summarize, it seems unlikely that reduced sperm production in triploid *D. polychroa* is caused by aberrant spermatogenesis, supporting the view that reduced sperm production is an adaptive response rather than an accidental by-product of polyploidy. The fact that parthenogens produce significantly more cocoons than sexuals (Table 2) is an additional indication that adaptive changes are possible.

This observation does not necessarily imply that parthenogenetic lineages have evolved lower male allocation by accumulating favorable mutations. Instead, many different parthenogenetic lineages may have arisen from sexuals, which span a wide range of male allocation strategies. Only those new lineages with the lowest male allocation may have survived in the parthenogenetic population. It has been demonstrated that this kind of "frozen variation" can explain adaptive color variation in some parthenogenetic fishes (Vrijenhoek 1984; Lima et al. 1996). However, in *D. polychroa* sperm production by parthenogens is clearly at the lowest end of the range seen in sexuals, particularly when we assume that those rare cases of sexuals with very small male organs result from their poor nutritional state rather than of a genetically fixed strategy. Therefore, gradual evolution by mutation and selection remains the most likely explanation for low male investment of parthenogens.

High Copulation Frequency in Contrast to Low Sperm Production

The observed rate of approximately two copulations per five days for P parthenogens is surprisingly high for animals that have no opportunity to fertilize the eggs of their partners, and that are able to store sperm for triggering development of their own eggs for more than one month (Streng, unpubl. data). The only adaptive explanation for high mating propensity could be that they would need sperm from several copulations for the development of all their eggs. It is known that sperm from a single parthenogenetic partner is not sufficient to achieve maximal egg development (Storhas, unpubl. data). Because the number of sperm is, in any case, disproportionately large compared to the number of eggs, it remains

a puzzle why parthenogens have not evolved means to use sperm more efficiently, and why they resorb most of what they receive (Sluys 1989).

An additional indication of evolutionary inertness is the fact that parthenogens in pure populations still depend on cross-insemination. Independence of sperm, or at least using their own sperm to trigger development, would be an obvious advantage in low density populations where partners are difficult to find, and would not lead to inbreeding depression as in sexuals. Selfing is known from some sexual planarians. It is common in *Cura* spp. (Anderson and Johann 1958; Benazzi 1991) and has been observed in *Polycelis nigra* (Benazzi 1952; Benazzi and Benazzi Lentati 1992). There seem to be no anatomical barriers to its evolution in *D. polychroa*: the penis and the ends of the oviducts are situated close to each other in a common genital atrium. In another parthenogenetic hermaphrodite, the clam *Lasnea*, selfing has evolved as a mechanism to trigger pseudogamous eggs (Ó Foighil and Eernisse 1988; Ó Foighil and Thiriou-Quévereux 1991).

Altruistic Sperm Transfer in Parthenogens?

Purely pseudogamous parthenogenetic populations of *D. polychroa* can only persist if at least some worms are prepared to donate sperm to a partner. But sperm donation is not favored by individual selection because sperm does not contribute genetically to the partner's offspring. Instead, individual selection would favor an egoistic mutant that produces no sperm and reallocates all resources from sperm to egg production. The spread of such mutants could drive a parthenogenetic population to extinction. The situation might, however, be stabilized by the evolution of altruistic behavior: Altruism is cheap, because the energetic cost of a small ejaculate is low compared to the benefit for the receiver who needs allosperm to stimulate the development of its eggs. Furthermore, the subdivided structure of *D. polychroa* populations (unpubl. data) creates favorable conditions for the operation of kin or group selection (Wilson 1983; Nowak and May 1992; Hammerstein and Hoekstra 1995). Kin selection could favor altruistic sperm donation if Hamilton's rule (Hamilton 1964) is met, that is, if the probability of meeting a member of the same clone multiplied by the benefit of receiving an ejaculate exceeds the cost of producing an ejaculate. Even when Hamilton's criterion is not fulfilled, group selection might be strong enough to maintain altruistic sperm donation, because local groups can rapidly go extinct if they contain too many "egotists" (Aoki 1982).

Kin as well as group selection can lead to polymorphic equilibria where "egotists" and "altruists" coexist in stable proportions. Sperm producing and male sterile strains are known to coexist in (sperm-dependent) parthenogenetic populations of the earthworm *Lumbricillus lineatus* (Christensen et al. 1978). Male sterility is also known from pseudogamous plants where male sterile strains "parasitize" pollen producing forms (Smith 1963; Asker and Jerling 1992). However, in our sample of 29 families of parthenogenetic *D. polychroa* from P, no lineage that had stopped producing sperm was found, despite significant differences in male allocation between families.

Conclusion: Consequences for the Coexistence of Sexuals and Parthenogens

Parthenogenetic hermaphrodites have two ways to use their male resources when coexisting with sexual conspecifics. They can either maintain the male function and have male reproductive success by fertilizing sexual eggs, but this can only be selectively advantageous if genes from parthenogens frequently flow back from the sexuals into the parthenogenetic subpopulation. Alternatively, they can reallocate male resources to female reproduction. Parthenogenetic *D. polychroa* have taken the second route. They have strongly reduced male organs, and it appears that resources are reallocated to female reproduction. Theory (Charnov 1982) as well as results from other species (Rameau and Gouyon 1991; Van Voorhies 1992; De Visser et al. 1994) suggest that the associated gain in female reproductive success can be substantial. As a consequence, parthenogens would have a competitive advantage over sexuals, in analogy to the "cost of males" (Maynard Smith 1978) in gonochoristic species.

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