7 Mating Conflicts and Sperm Competition in Simultaneous Hermaphrodites

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> 'In the lowest classes the two sexes are not rarely united in the same individual, and therefore secondary sexual characters cannot be developed. . . . Moreover, it is almost certain that these animals have too imperfect senses and much too low mental powers to feel mutual rivalry, or to appreciate each other's beauty or other attractions.' (Charles Darwin 1871, Part II, p. 321).

I. INTRODUCTION

Although it is now generally accepted that sexual selection applies to all types of gender expression (Arnold 1994a,b; Morgan 1994), hermaphroditic animals are still largely absent from the sexual selection literature (see Andersson 1994). This is not due to a lack of conceptual basis – many theoretical contributions have been made (Ghiselin 1969;

Williams 1975; Heath 1977; Charnov *et al.* 1976; Charnov 1979, 1982; Bell 1982). In this chapter I speculate on the consequences of sexual selection and sperm competition in an hermaphroditic mating system. First, I show that hermaphrodites have the unique property that they can optimize their allocation to the male and female function. Second, I explain how conflicts between mating partners arise in hermaphrodites, and why they are particularly strong during copulation because of different mating interests. This is expected to result in mechanisms such as elaborate *conditional reciprocity* or aggressive *hypodermic impregnation*, both of which will be subject to ongoing adaptation and counter-adaptation. I shall show that sperm competition is expected to be common and that the adaptations resulting from it are sometimes drastic and unique to hermaphrodites.

Unfortunately, quantitative data that relate to the theme of this chapter, such as mating frequency, sperm transfer, sperm usage and fertilization success, are very rare for hermaphrodites. As a result, many of the views presented here are speculative and I have no doubt that some might eventually be proved wrong once appropriate data are available. Yet, I want to be thought-provoking and make clear that the animal taxa that Darwin deliberately ignored deserve a more central place in the evolutionary biological literature.

II. WHAT ARE HERMAPHRODITES?

Hermaphrodites are individuals that possess a functional male and female reproductive system during at least part of their lives. This type of gender expression is ubiquitous among plants (see Chapter 5) and widespread in the animal kingdom (Ghiselin 1969). Table 7.1 shows that 20 out of the 28 phyla listed have at least some hermaphroditic representatives and seven are exclusively hermaphroditic. These are the sponges, the entoprocts, the bryozoans, the free-living and parasitic flatworms, the arrowworms, the gastrotrichs, and the comb jellies. Three further phyla contain major classes or orders that are also almost entirely hermaphroditic: (1) anemones and corals, (2) sea slugs and pulmonate snails (see Chapter 8) and (3) gnathostomulids, leeches and earthworms. Although hermaphroditism is less common in other groups, some of these exceptions are well-studied: the nematode *Caenorhabditis elegans*, for example, is without doubt the best-studied hermaphrodite (Wood 1988). Hermaphroditism is also known as an aberrant condition in mammals (Bunch *et al.* 1991; De Guise *et al.* 1994), including humans (Akin *et al.* 1993; Krob *et al.* 1994; Spurdle *et al.* 1995). It is obvious that not only is this mode of gender expression widespread, but that it must have evolved repeatedly.

A. *Sequential and simultaneous hermaphrodites*

Two major types of hermaphroditism will be distinguished in this chapter. Sex-changing or *sequential hermaphrodites* (e.g. corals, certain fish and polychaetes) are well studied. These start out as one sex and change into the other later in life. In some polychaetes and fish, repeated, alternating changes are possible (Teuchert 1968; Kuwamura *et al.* 1994; Nakashima *et al.* 1995). Inspired by the size-advantage hypothesis proposed by Ghiselin (1969), many studies of sequential hermaphrodites have focused on the question of when to change sex (Warner 1975, 1988; Warner *et al.* 1975; Leigh *et al.* 1976; Policansky 1982; Berglund 1986, 1991; Charnov 1982).

The second type, and focus of this chapter, are *simultaneous hermaphrodites*. These have functional male and female genitalia simultaneously present for most of their lives and reproductive acts usually involve both the male and female function in each individual. Throughout this chapter, I use the term hermaphrodite to refer to simultaneous hermaphrodites. The term gonochorist refers to species where individuals are either male or female. In order to avoid confusion about the source of sperm, autosperm will be used for the self sperm an individual donates to its partner, whereas allosperm is used for the sperm an individual receives from its partner. With the exception of a few important case studies, I will not elaborate on hermaphrodite systems in which gametes are spawned into the (aquatic) environment (see Chapter 6), but concentrate on hermaphroditic groups that copulate or at least transfer a spermatophore. Gastropods are the best studied examples in this respect and are reviewed in a separate chapter (see Chapter 8).

III. WHY ARE HERMAPHRODITES HERMAPHRODITIC?

A. *The resource allocation model*

Hermaphroditism is favoured whenever the overall reproductive success achieved by a hermaphrodite is greater than that of a pure male or a pure female (Charnov *et al.* 1976; Charnov 1982). Although this may appear trivial at first, this leads to the more interesting question of under what sorts of conditions this may be expected. The resource allocation model (Charnov *et al.* 1976) predicts that, whenever offspring produced by one sex function are increasingly expensive as their number increases (diminishing returns), it is more efficient to limit investment in this function and to become hermaphroditic; the remaining resources can then be relocated to the other sex function, within the same individual. A limitation is that the additional costs arising from having two sexual functions

Table 7.1. A limited overview of the presence of hermaphroditism in the animal kingdom, as well as a rough indication of the presence of gamete exchange via spawning or copulation and external versus internal fertilization. Taxa where hermaphroditism is the dominant mode of gender expression are in **bold**. (Int.: internal fertilization; Ext.: external fertilization.)

Phylum	Lower taxon	Popular name	Hermaphroditism	Type of sperm transfer	Fertilization	N species
Porifera		**Sponges**	**Ubiquitous**	Spawning	Int.	5000
Cnidaria	Hydrozoa	Hydras and hydroids	Rare	Spawning	Int.	2700
Cnidaria	Scyphozoa and Cubozoa	Jellyfish	Rare	Spawning	Int.	215
Cnidaria	**Anthozoa**	**Anemones and corals**	**Ubiquitous**	Spawning	Ext. and Int.	6000
Sipunculida		Peanut worms	Rare	Spawning	Ext.	320
Annelida*	Polychaeta		Rare	Spawning	Ext.	8000
Annelida*	**Gnathostomulida**		**Ubiquitous**	Copulation	Int.	80
Annelida*	Pogonophora		Rare	Spawning	Int.	80
Annelida*	Echiura	Spoonworms	Absent	Spawning	Ext.	140
Annelida*	**Oligochaeta**	**Earthworms, freshwater oligochaetes**	**Ubiquitous**	Copulation	Int.	3100
Annelida*	**Hirudinea**	**Leeches**	**Ubiquitous**	Copulation or spermatophore	Int.	500
Onychophora		Velvet worms	Absent	Spermatophore	Int.	70
Arthropoda	Chelicerata	Horseshoe crabs, scorpions, spiders, mites, harvestmen, sea spiders	Absent	Copulation or spermatophore	Int.	72 000
Arthropoda	Crustacea	Crabs, shrimps, crayfish, woodlice, copepods, barnacles	Rare	Copulation	Int.	38 000
Arthropoda	Myriopoda	Centipedes, millipedes	Absent	Spermatophore	Int.	10 500
Arthropoda	Insecta	Insects	Rare	Copulation	Int.	750 000
Tardigrada		Water bears	Rare	Copulation	Int.	600
Entoprocta			**Ubiquitous**	Spawning	Int.	150
Ectoprocta		**Bryozoans**	**Ubiquitous**	Spawning	Int.	5000
Platyhelminthes	**Cestoidea**	**Tapeworms**	**Ubiquitous**	Copulation	Int.	3400
Platyhelminthes	**Trematoda**	**Flukes**	**Ubiquitous**	Copulation	Int.	11 000
Platyhelminthes	**Monogenea**	**Monogenean ectoparasites**	**Ubiquitous**	Copulation	Int.	1100
Platyhelminthes	**Turbellaria***	**Free-living flatworms**	**Ubiquitous**	Copulation	Int.	3000
Nemertini		Ribbon worms	Rare	Spawning	Ext.	900
Rotifera			Absent	Copulation	Int.	1500
Acanthocephala			Absent	Copulation	Int.	1150
Chaetognatha		**Arrowworms**	**Ubiquitous**	Copulation	Ext. and Int.	70
Gastrotricha			**Ubiquitous**	Copulation	Int.	430
Nematoda		Roundworms	Present	Copulation	Int.	12 000
Nematomorpha			Absent	Copulation or spermatophore	Int.	320
Priapulida			Absent	Spawning	Ext. and Int.	16
Kinorhyncha			Absent	Spermatophore	Int.	150
Ctenophora		**Sea walnuts, comb jellies**	**Ubiquitous**	Spawning	Ext.	50
Phoronidae			Present	Spermatophore	Int.	14
Brachiopoda		Lamp shells	Rare	Spawning	Ext.	325
Pterobranchia			Male and Female zoids	Spawning	Int.	21
Echinodermata		Starfish, brittle stars, sea urchins, sea cucumbers, sea lilies	Rare	Spawning	Ext. and Int.	6000
Enteropneusta		Acorn worms	Absent	Spawning	Ext.	70
Urochrodata		**Sea squirts, salps, ...**	**Ubiquitous**	Spawning	Ext.	1250
Cephalochordata		Lancelets	Absent	Spawning	Ext.	25
Vertebrata	Pisces	Fish	Present	Spawning (copulation)	Ext. and Int.	20 500
Vertebrata	Tetrapoda	Amphibians, reptiles, birds, mammals	Absent	Copulation (spawning)	Ext. and Int.	21 500
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* Polyphyletic groups for which the systematics have not been resolved satisfactorily. Molluscs are reviewed separately by Baur (Chapter 8). The taxonomic subdivision was taken from Nielsen (1995), and the other data from Barnes and Ruppert (1994).

Table 7.2. A summary of possible differences between gonochorists (species with separate sexes) and hermaphrodites.

Typical gonochorists (males and females)	**Simultaneous hermaphrodites**
No self-fertilization	Self-fertilization possible
Traits of only one sex expressed per individual	Traits of both genders always expressed
Sexual specialization less constrained	Sexual specialization constrained
Coevolution of males and females	Coevolution of male and female structures within one individual
Cost of paternal offspring lower than that of maternal offspring	Cost of paternal and maternal offspring balanced
Allocation to males and females 1:1: low flexibility to adjust sex allocation to conditions	Allocation to sperm and eggs: opportunistic resource utilization possible
Sexual conflict *before* copulation	Mating conflict *during* copulation
Nuptial gifts possible	Nuptial gifts *not* expected
Reluctance to donate sperm rare in males	Reluctance to donate sperm not uncommon?
Mating not necessarily assortative	When mate choice, then assortative
Females may 'allow' access to sperm stores	Access to sperm stores *not* expected
Manipulation of partner's sex allocation not possible	Manipulation of partner's sex allocation expected?

should not exceed the benefits that can be achieved (Heath 1977; Charnov 1982). Differences between hermaphrodites and gonochorists are summarized in Table 7.2.

B. *Diminishing returns for the male and/or female sex*

Diminishing returns for the male function may arise under conditions where few mating opportunities exist, so that inseminating a few partners may be easy, whereas inseminating many is very costly or simply impossible owing to low mobility or density (Charnov 1979). That optimal male allocation is reduced when the mating group is small, as predicted by the Local Mate Competition model adjusted for hermaphrodites (Charnov 1980, 1982), has been shown for serranid fish (Fischer 1984b; Petersen 1990, 1991), polychaetes (Sella 1990) and barnacles (Raimondi and Martin 1991). Strong mate choice could result in diminishing returns in dense populations.

The female function could show a saturating gain curve when offspring dispersal is limited and results in increased local sib competition, or when the number of young that can be produced per unit time is limited. Brooding, which is common in many hermaphroditic taxa, may exemplify such limitation (Ghiselin 1969; Charnov 1982).

C. *Selfing*

Hermaphrodites can, in principle, self-fertilize their eggs. Selfing is common among plants (Jarne and Charlesworth 1993) and well known from parasitic flatworms (Joyeux and Baer 1961), oligochaetes (Needham 1990), arrowworms (Jägertsen 1940; Reeve and Walter 1972; Alvariño 1990) and pulmonate snails (Jarne *et al.* 1993). Initially, selfing may appear to serve as an 'emergency exit' for reproduction when a partner cannot be found (Ghiselin 1969). However, if inbreeding is not too costly, a mixture of selfing and outbreeding may allow combination of the advantages of increased genetic propagation with those of outcrossing (Jarne and Charlesworth 1993). Extending the resource allocation model to selfers, it can be shown that they should reduce male allocation and produce more ova instead (Charlesworth and Charlesworth 1981; Charnov 1982). An extreme example is the nematode *C. elegans*, where selfing hermaphrodites have minimized autosperm production to such an extent that autosperm depletion is the rule later in life (Barker 1992).

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D. *Does hermaphroditism equal opportunism?*

When a population is outcrossing and panmictic and neither function is limited in its access to common resources, hermaphrodites should spend, on average, equal amounts on the male and female function in accordance with the basic 1:1 sex ratio rule (Fisher 1958; Williams 1975). Under the resource allocation model, however, most situations that result in stable hermaphroditism are characterized by sex allocation that diverges from this ratio (Charnov 1982). Such conditions may arise when one sex function is limited by resources that are unimportant for the other. At first, this suggests that there is strong selection for one particular, optimal sex allocation.

What is somewhat misleading in these models is that, in both cases, the optimal sex allocation is the predicted average for the population. For the individual hermaphrodite, a major advantage is that it can diverge from this ratio. Whenever the two sex functions require different resources (which is probably the rule rather than the exception), and the presence of these resources changes unexpectedly or rapidly in time or space, a hermaphrodite may exploit such fluctuations opportunistically. For example, it can produce more sperm when mating opportunities are plentiful, or produce more eggs when certain food types are abundant. This view implies that they are (to some extent) able to shift resources from one function to the other, depending on which one produces offspring more cheaply at the time; note that this automatically results in the expected equal overall expenditure on paternal and maternal offspring.

not necessarily

It may be expected that opportunistic allocation is particularly important when competition for food is severe, as occurs in populations of planarian flatworms (Reynoldson and Young 1965; Reynoldson and Bellamy 1973) and when the local habitat is characterized by fluctuations in opportunities or limitations with regard to food and mate availability. Owing to low mobility in many hermaphroditic taxa (e.g. flatworms, snails, earthworms, leeches) such fluctuations cannot be averaged out by mobility alone, leaving sex allocation as an intra-individual solution to local perturbations.

In gonochorists, instant sex ratio adjustments are not possible: a pure female has only very limited possibilities to adjust the number of sons or daughters she produces. An important exception, however, are haplodiploid insects in which females can optimize the sex ratio of their clutch according to the mating arena in which their offspring find themselves when hatching (Werren 1980).

In hermaphrodites, the relative cost of paternally and maternally produced offspring must be equal (Williams 1975). When maternal offspring become cheaper to produce than paternal offspring, animals with higher maternal allocation would be favoured. This increase in egg production would, in turn, make paternal offspring cheaper, resulting in a new equilibrium at which paternal and maternal offspring cost the same again. If this prediction holds, classic sexual conflict does not exist in hermaphrodites: a cheap (and therefore) preferred sexual role cannot persist. However, offspring produced by one sex function can remain cheaper than those produced by the other when reproduction by the first is strictly constrained by external factors (e.g. brief mating period per day or brooding space).

Note that, in gonochorists, typical males have the potential to produce offspring at a lower cost than females, resulting in sexual conflict over matings. One could consider males as individuals with 'spare' resources relative to females, which they may invest in courtship or ornaments rather than directly into individual offspring.

IV. SEXUAL SELECTION IN HERMAPHRODITES

A. Evolutionary constraints

Before speculating on what traits may be favoured by sexual selection, it is important to stress four constraints resulting from hermaphroditism (see also Table 7.2). First, in hermaphrodites, selection on male traits

cannot be independent from selection on female traits of the same individual (Morgan 1994). This means that in a hermaphroditic population, it is impossible to find the optimal male and female strategy combined in one individual, but one may find the optimal compromise between both. A second constraint exists on the evolution of genitalia: internally fertilizing hermaphrodites with reciprocal penis insertion must evolve compatible, yet identical genitalia. Simultaneous penis insertion may require special postures or even asymmetrical genital structures with the same skew towards left- or right-handedness, allowing a better 'handshake' between genitalia (e.g. *Polycelis tenuis*, Ball and Reynoldson 1981; gastropods, see Chapter 8). A third limitation involves mate choice. Whenever one trait is favoured by most individuals in the population (i.e. large body size), hermaphrodites are almost automatically expected to mate assortatively. Large individuals will prefer to mate with a large partner, leaving only small partners for small individuals (see also Ridley 1983). This reduces the impact of mate choice since skewed mating rates (known from species in which one successful male can mate with many females of all ranks) are prevented. In fact, assortative mating may actually stabilize selection on the trait involved, since average individuals may find a partner more easily. A fourth limitation follows from the fact that, in hermaphrodites, sexual preferences and traits are expressed simultaneously in each individual. No traits remain 'hidden', as female traits are in pure males and male traits are in pure females. The fact that in gonochorists, sex-related traits can jump one or more generations, allows them to recombine several times without being exposed to selection. Such a source of new variation is absent from hermaphrodites. However, despite these limitations, I shall show why I believe that sexual selection is not only strong in hermaphrodites, but may also favour rather peculiar traits.

B. Sex roles in hermaphrodites?

Assuming that the female function of a hermaphrodite rarely runs short of sperm (but see Chapter 6), and that the benefits of receiving multiple ejaculates are limited, one could expect hermaphrodites to mate mainly in order to inseminate their partner rather than to receive allosperm (Charnov 1979). This view stems from gonochorists, where females usually limit male mating opportunities and, as a result, males will rarely refuse to donate sperm when given an opportunity by a female partner (Bateman 1948). In hermaphrodites, however, mating opportunities are not limited in this way. Here, all conspecifics may want to donate autosperm and, as a result, copulate readily and accept allosperm in order to have an opportunity to inseminate a partner. Hence, a donor may not be limited by the number of mating partners, but by its own capacity to inseminate them. Consequently, it may be the donor who is 'choosy' about who to donate sperm to. This is particularly likely when individuals vary in quality (e.g. fecundity), when copulations are costly and when choice is possible owing to high density (see also Ridley 1983). For the reasons listed above, such sex-role reversal may be more common among hermaphrodites than among gonochorists.

Evidence suggestive of a 'choosy' donor function was found in the planarian flatworm *Dugesia gonocephala*. In this species, size is positively related to fecundity (Vreys and Michiels 1995). Under such conditions, size-assortative mating is expected (see earlier). Partners of this species engage in frequent precopulatory contacts, during which both lie on top of each other and flatten out completely. Genital contact is not possible in this position (Vreys *et al.* 1997a; Fig. 7.1). Experimental investigation indicated that partners use this peculiar behaviour to size each other up and mate only when both are of a similar size, resulting in very pronounced size-assortative mating in the field (Vreys and Michiels 1997).

If sperm donors can be choosy, this may eventually lead to a situation where the receiving function must advertise its receptivity to seduce reluctant sperm donors. Although this may be a logical expectation, it appears very difficult to distinguish whether partners stimulate each other to donate or to receive. The fact that up to one-third of all matings in the planarian *Dugesia polychroa* end without sperm transfer in either direction strongly suggests that matings are not always driven by an intention to inseminate (Fig. 7.2). Particularly interesting are observations of unilateral insemination when reciprocity is the rule. Reise (1995) observed that, after occasional unilateral sperm transfer in the slug *Deroceras rodnae*, sperm donors became aggressive when their partner (who had not donated sperm) tried to escape. Ghirardelli (1968) observed that in the arrowworm *Spadella cephaloptera* unilateral matings are prolonged until reciprocity occurs.

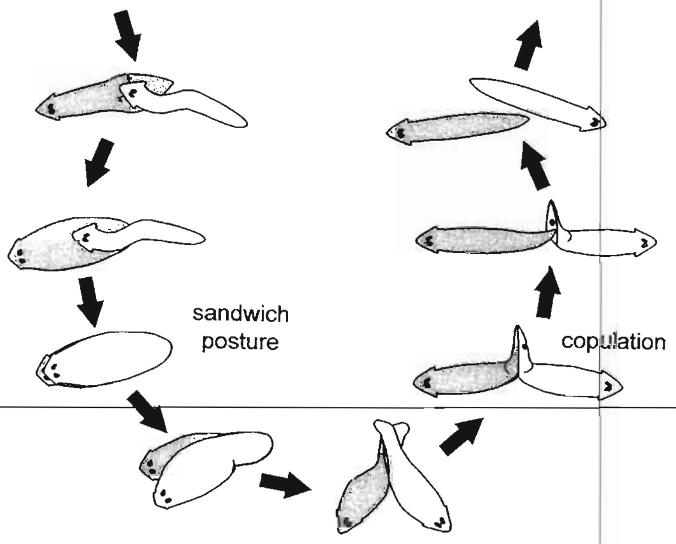

Fig. 7.1. *Mating sequence in the planarian flatworm* Dugesia gonocephala. *In this species, a typical 'sandwich' posture always precedes copulation. During this phase, individuals are assumed to measure each other's size (modified after Vreys* et al. *1997a). This behaviour is not known from any other planarian.*

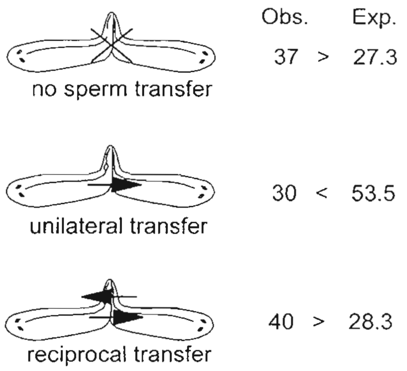

Fig. 7.2. *Summary of sperm transfer in 107 copulating pairs of the planarian* Dugesia polychroa. *One-third of all copulations ended without sperm transfer in either direction. A comparison with a binomial distribution showed that 'no exchange' or 'bilateral exchange' were more common than expected whereas 'unilateral sperm transfer' was less common than expected. This result is indicative of sperm trading (see text) (N. K. Michiels and B. Bakovsky, unpublished data). Obs., observed; Exp., expected.*

V. MATING CONFLICT

Confusion about the role that each partner plays during a copulation does not exist in gonochorists: when a male and a female agree to mate, their sexual role is implied. When two hermaphroditic partners intend to mate, however, they may not know what the interests of the partner are. Because both individuals can have three different interests (donate autosperm, receive allosperm, or both), their combined interests will vary from totally compatible to totally incompatible (Fig. 7.3). Mating interests will be incompatible when both partners want to donate but not receive sperm or vice versa (Fig. 7.3, areas 1 and 4). Only when both want to give and receive are their interests compatible (Fig. 7.3, centre). Compatibility also prevails when one partner wants to receive and the other to donate sperm (Fig. 7.3, areas 2 and 3). However, since it can be

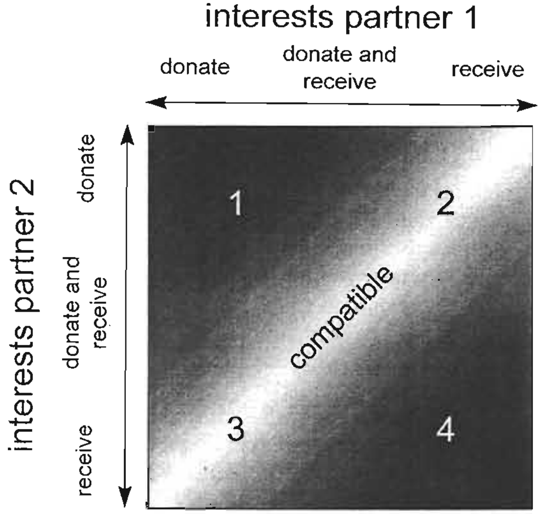

Fig. 7.3. *Interest matrix of all situations (likely or not) that can arise when two hermaphroditic partners with internal fertilization meet with the intention to mate. Each partner can have different interests, indicated as a gradient on the horizontal and vertical axis, ranging from 'donate only' to 'donate and receive' to 'receive only'. Black areas are where interests are incompatible because they are unilateral and identical. White indicates the zone of complete compatibility, either because of a difference in interest (away from the middle) or because both animals want to donate and receive sperm (in the centre). Numbers indicate four possible situations explained in the text: 1, both partners want to donate, but not receive – they trade sperm; 2 and 3, both partners have different, but compatible interests – mating can proceed; 4, both partners want to receive, and trade sperm; 5 (the centre), partners will insist on donating and receiving and trade this if necessary. Note that, for species with separate sexes (gonochorists), the situation is very simple and limited to the upper right or lower left corner of the matrix.*

expected that mating interests will be identical more often than they are different, it is also likely that hermaphrodites have a high likelihood of encountering mating conflicts. One way for hermaphrodites to resolve these is conditional, reciprocal exchange of gametes.

A. Reciprocity of gamete exchange

In the black hamlet *Hypoplectrus nigricans*, a hermaphroditic, coral reef fish, Fischer (1980) observed that two partners alternate the release of a small part of their clutch for fertilization by their partner. He coined the term 'egg trading' for this (Fischer 1984a, 1987) and interpreted the system as one in which individuals prefer to donate sperm in order to fertilize the partner's eggs (Fig. 7.3, area 1), but are allowed to do so only when they release some eggs themselves. This trade goes on for as long as both partners have some eggs left to give. This behaviour has now also been described in another serranid (Petersen 1995). Egg trading has also been observed in the hermaphroditic polychaete *Ophryotrocha diadema* and *Ophryotrocha gracilis*, in which pairs live together for several reproductive cycles (Sella 1985, 1988; Sella *et al.* 1997). Mating events consist of one partner spawning eggs and the other fertilizing them. Roles are alternated several times in a regular pattern, usually with the same partner. Both partners care for all the eggs. The advantage for traders is clear: by being 'monogamous' and sharing brood care, they can minimize sperm production (Sella 1990) and thus maximize the overall number of offspring (Premoli and Sella 1995).

The only known example of alternating sperm exchange in hermaphrodites with internal fertilization is in the opisthobranch sea slug *Navanax inermis*. In this species, penis insertion is unilateral but alternated repeatedly in the course of a copulatory bout, which Leonard and Lukowiak (1984, 1985, 1991) interpreted as sperm trading. They argued that in internal fertilizers the female role is preferred (Fig. 7.3, area 4) because it controls fertilization, in contrast to the male role, which has no guarantee that it will gain fertilizations in its partner. As a result, they expect mating partners to parcel their autosperm and alternate the exchange of small quantities in order to reduce the risk of donating a whole ejaculate without receiving allosperm or fertilizations in the partner. It implies that partners are reluctant to donate sperm and receivers risk running short of allosperm. Although I agree that a reluctance to donate sperm may evolve readily in hermaphrodites (see above), the 'risk' argument used by Leonard and Lukowiak (1984, 1985, 1991) is not a good explanation because the risk that autosperm are discarded by the partner simply adds to the total paternal cost, which ought to be compared with the total maternal costs before deciding which role may be cheaper. Since the number of paternally and maternally produced offspring is always equal in a sexual population, this 'risk' may actually average out as a low, rather than a high cost.

Whatever the primary mating interest of an hermaphroditic individual, it remains a fact that internally fertilizing hermaphrodites almost always show reciprocal insemination. This is true for free-living flatworms (Costello and Costello 1938; Hyman 1951; Apelt 1969; Peters *et al.* 1996; Vreys *et al.* 1997a,b; Figs 7.1 and 7.2), parasitic flatworms (Joyeux and Baer 1961; Williams and McVicar 1968; Kearn 1992; Kearn and Whittington 1992), oligochaetes (Grove 1925; Grove and Cowley 1926; Bahl 1928; Needham 1990), leeches (Brumpt 1900; Hoffman 1956; Wilkialis 1970; Wilkialis and Davies 1980; Kutschera 1989; Fig. 7.4), gastrotrichs (Ruppert 1978), arrowworms (Ghirardelli 1968; Reeve and Walter 1972; Alvariño 1990; Fig. 7.5), snails (Chapter 8). Therefore, I

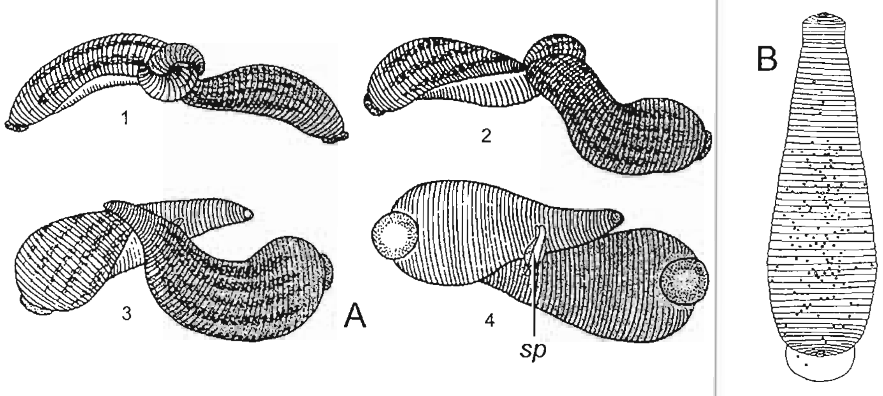

Fig. 7.4. **A.** *Reciprocal spermatophore (sp.) exchange in the leech* Glossiphonia lata *and deposition in the genital region.* **B.** *Summary chart of the distribution of spermatophore implantations observed in* Placobdella parasitica, *a species with random, unilateral spermatophore implantation. Filled dots are dorsal, open circles ventral (modified after Myers 1935).*

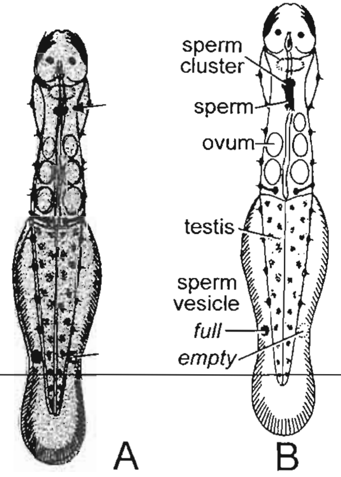

Fig. 7.5. *Sperm exchange in the arrowworm* Spadella cephaloptera. **A.** *Partners align head-to-tail and reciprocally transfer a cluster of sperm from their sperm vesicles to a specific spot under the head of the partner.* **B.** *After copulation, sperm (sp.) stream towards the vaginal opening (modified after Ghirardelli 1968, with permission).*

explore the ultimate causes of reciprocity and look more specifically for conditions under which reciprocity might be conditional, i.e. whether sperm donation depends on sperm receipt. If it does, it may solve conflicts arising from incompatible interests.

I limit the usage of the term 'trading' to systems where partners alternate roles such as egg trading in serranid fish and polychaetes, and sperm trading in *Navanax*. The more general term 'conditional reciprocity' is better suited to include all other copulatory mechanisms where sperm donation depends on sperm receipt, including those with synchronous sperm exchange. Although internal fertilizers with simultaneous, mutual penis insertion or spermatophore exchange are a large group among hermaphrodites, there are only very few studies that address the question of conditional reciprocity in this group (Michiels and Streng 1998; Vreys and Michiels 1998; Chapter 8).

B. *Unconditional reciprocity*

If sperm donation is the main reason why hermaphrodites mate (Charnov 1979) and partners do not refuse sperm donations, reciprocal insemination could simply be a coincidental side-effect of the mutual willingness to donate. This may be a trivial explanation for why reciprocity is so common and may make it difficult to recognize truly conditional reciprocity.

C. *When is conditional reciprocity expected?*

For conditional reciprocity to evolve, one important initial condition must be met: it must be possible to give up a partner at low cost when there are signs that it will not reciprocate. This implies that a new partner can be found easily, which may be true in high-density populations. Once this assumption is fulfilled, three situations should be distinguished.

First, partners may insist on receiving as well as donating (centre of Fig. 7.3). It is clear that donating frequently may be beneficial at high density. But why insist on sperm receipt when matings are common? If ejaculates are not infinitely small, nutrients derived from the ejaculate may be a reason to insist on reciprocity. As I shall show later, sperm digestion is widespread among hermaphrodites. A sperm donor may have no choice other than to accept that the majority of its sperm will be digested: it is part of the paternal costs that the donor may attempt, but fail, to minimize and it should therefore not be seen as a nuptial gift.

Second, both partners may wish to receive, but not donate sperm (Fig. 7.3, area 4). Such hermaphrodites may stimulate each other to donate but may not themselves donate before reciprocity has been assured. This may escalate in elaborate stimulation and assessment bouts before sperm transfer takes place. The donor function can be expected to have a simple 'come-and-get-it' sperm donation mechanism that may not even insert the sperm into the receiving function of the partner, as occurs in some flatworms (Ullyot and Beauchamp 1931) and slugs (see Chapter 8). Many planarian flatworms possess penis-like musculo-glandular organs associated with the genitalia that have been interpreted as sexual stimulators (Hyman 1951; see Fig. 7.9), and that may induce the partner to donate. It is difficult to force a partner to donate sperm. Therefore, escalation to physically damaging strategies appear unlikely.

Finally, both partners may want to donate, but not to receive (Fig. 7.3, area 1) because receiving is costly (e.g. manipulation by the donor or parasite transmission). Such situation may favour the evolution of hit-and-run mechanisms similar to hypodermic injection (see below). In response to these, the receiver may evolve successful avoidance tactics resulting in matings that can be best described as ritualized, reciprocal stabbing, suggestive of conditional reciprocity. This type of mating is common among leeches (Brumpt 1900; Hoffmann 1956; Nagao 1958; Kutschera and Wirtz 1986; Kutschera 1989; Fig. 7.4) and free-living and parasitic flatworms (Hyman 1951; Apelt 1969; Kearn 1992; Kearn and Whittington 1992; Newman and Canon 1994; Michiels and Newmann 1998; Fig. 7.6).

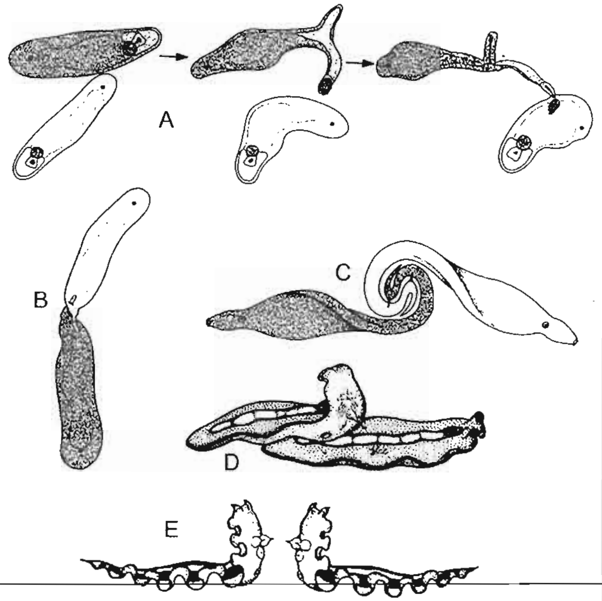

Fig. 7.6. *Several types of hypodermic impregnation in free-living flatworms.* **A.** *'Hit-and-run' injection of sperm in* Pseudophanostoma psammophilum *(modified after Apelt 1969, with permission).* **B.** *Reciprocal injection in* Archaphanostoma agile *(modified after Apelt 1969, with permission).* **C.** *Mutual tail holding and injection in* Monocelis fusca *(modified after Giesa 1966, with permission).* **D, E.** *Unilateral and bilateral stabbing in the polyclad flatworms* Pseudoceros *and* Pseudobiceros, *respectively. Note the double, everted penises in the latter (modified after Newman and Cannon 1994, with permission from the Queensland Museum).*

D. Evidence for conditional reciprocity

Except for the black hamlet fish, the polychaete *Ophryotrocha* and the sea slug *Navanax*, published data that suggest conditional reciprocity are lacking. Possible candidates appear to be oligochaetes. In the species *Pheretima communissima*, for example, the receiver function has three pairs of spermathecae which are reciprocally filled during one copulation using only one pair of penises. In order to achieve this, spermathecae are filled pair by pair, which takes 1.5 h per set, for 4–5 h in total (Avel 1959). It is clear that, since sperm exchange is simultaneous, interruption results in identical amounts of sperm exchanged. It is systems like these that may offer the best opportunities to collect quantitative data on conditional reciprocity in internal fertilizers with mutual penis insertion. In order to demonstrate conditionality in systems where ejaculates are exchanged in one single action rather than as a series of parcels, one would have to demonstrate that copulations with a symmetrical outcome (both or neither donate sperm) occur more often than expected by chance relative to unilateral inseminations. Indications that this may be true were found in the planarian *D. polychroa* (Michiels and Streng 1998) (Fig. 7.2). Alternatively, partners can trade by volume and donate as much sperm as they receive, as shown recently for *D. gonocephalia* (Vreys and Michiels 1998).

Conditional reciprocity is likely to be associated with pre-copula or in copula stimulation or assessment mechanisms whereby interruptions before or during early copulation should be relatively frequent. Of particular interest are cases where animals copulate in such a way that one partner keeps the other physically under control, thus preventing it from leaving before reciprocity is completed. The physical contact between earthworms during copulation is, for example, extreme and probably allows accurate control over what the partner is doing (Grove 1925; Grove and Cowley 1926). Many leeches intertwine during copulation as if to hold each other and it has been observed that this lasts longer when one partner does not reciprocate (Hoffmann 1956). In gastrotrichs, both partners intertwine in a tight 'knot' and first transfer sperm externally to a special sperm transfer organ, then to the partner (Ruppert 1978). The first step of this two-step process may reliably signal to the partner that sperm transfer will take place. In the flatworm *Amphiscolops langerhansi*

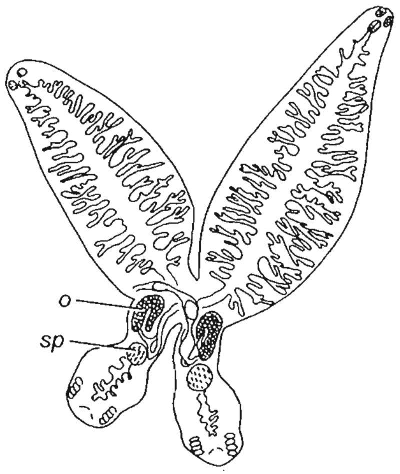

Fig. 7.7. *Extreme monogamy in the parasitic flatworm* Diplozoon paradoxum, *where partners fuse and stay together for life; o, ova; sp, sperm. Yolk glands are not indicated but if their size is similar to that seen in other monogeneans, sperm investment can be considered low (modified after Baer and Euzet 1961, with permission).*

partners use their penis only to hold on to that of their mate in a 'handshake' posture (Hyman 1951). Sperm exchange takes place on the outside of the interlocked penises and copulation takes a total of 40–60 min, which is unusually long. In another flatworm species *Monocelis fusca*, partners lock their tail ends into each other (Giesa 1966; Fig. 7.6C). The most extreme case is that of the fish parasite *Diplozoon paradoxum* (Fig. 7.7). In this species, larvae that have found a host do not mature until they pair up with another larva (Baer and Euzet 1961). Both individuals connect and fuse in the middle. Only then do they become sexually mature and stay together for life (which may be years).

Further detailed studies of copulatory mechanisms and behaviour should reveal how common conditional reciprocity really is. Unfortunately, descriptions of genitalia are rarely made *in copula* and data on reproductive behaviour are usually anecdotal and too vague to be useful in this context. If proven, conditional reciprocity will have important consequences for the evolution of assessment and signalling mechanisms in hermaphrodites. It may actually stabilize hermaphroditism because it sets additional limits to reproduction by one or both sexual functions. Conditional reciprocity may also result in the rejection of gonochoristic partners. In populations of the polychaete *Ophryotrocha diadema*, young individuals are male (protandry) and are rejected as partners by (older) hermaphrodites in favour of other hermaphrodites (Sella 1988).

VI. SPERM COMPETITION IN HERMAPHRODITES

A. A Contradiction?

As explained above, low population density is traditionally seen as one important explanation for the origin of hermaphroditism, suggesting a low importance of sperm competition. However, although many taxa indeed occur at low densities, population densities are so high in many others, that multiple matings are common (Brumpt 1900; Pearse and Wharton 1938; Nagao 1958; Ghirardelli 1968; Apelt 1969; Kutschera 1984; Nagasawa and Marumo 1984; Goto and Yoshida 1985; Kutschera and Wirtz 1986; Kearn 1992; Peters and Michiels 1996a,b; Peters *et al.* 1996; Vreys *et al.* 1997a). In leeches (Wilkialis 1970; Wilkialis and Davies 1980) and snails (see Chapter 8) multiple mating sometimes occurs in aggregations of several individuals during which partners are exchanged. Mating events whereby autosperm are donated to one partner while receiving allosperm from a third individual are known from sea slugs (see Chapter 8) and a monogenean flatworm (MacDonald and Caley 1975). In free-living flatworms one mating partner can also be actively displaced by a third individual (Darlington 1959; own unpublished observation). All this indicates that sperm competition may be as important in hermaphrodites as in any other animal species.

Even if low density were the general rule, it may actually have resulted in four preadaptations to sperm competition: (1) low density promotes promiscuous mating, since partners may be too rare to be selective; (2) long-term sperm storage is needed to assure continued fertility and is known from all hermaphrodites with internal fertilization (Adiyodi and Adiyodi 1983, 1988, 1990); (3) when new mating opportunities do occur, accurate control of the fertilization chances of old and new ejaculates may be favoured; (4) low density may also favour selfing. In order to control the optimal degree of inbreeding and outbreeding, mechanisms similar to selective storage will evolve in order to control the overlap between autosperm and allosperm, which then may also be used to distinguish between allosperm from different partners. An alternative is to have less fit autosperm. This may be disadvantageous in an outcrossing hermaphrodite, but is known from *C. elegans*, in which hermaphrodites use autosperm only to self-fertilize and where (rare) males inseminate hermaphrodites and subsequently outcompete their sperm (Dix *et al.* 1994; LaMunyon and Ward 1994, 1995). I shall now survey some of the possible responses to sperm competition, and consider the consequences for the sperm donating as well as the sperm receiving function (Table 7.3).

Table 7.3 Overview of possible adaptative responses to sperm competition, subdivided in adaptations related to the role of the receiver and that of the donor. Note that both roles are always combined in one hermaphroditic individual.

Donor		Receiver
Advertise own quality		*Selectively use allosperm*
• Genetical or phenotypical	↔	• Store and use allosperm selectively
• Sperm surface signals	↔	• Compatibility mechanisms
Improve chances of autosperm		*Counter-measures*
• Increase number of autosperm per ejaculate	↔	• Digest excess allosperm
• Optimize sperm packaging	↔	• Control allosperm movement
Reduce competition with allosperm stored by partner		*Counter-measures*
• Spermicidal ejaculatory fluid	↔	• Neutralize spermicide
• Evolve access to sperm stores	↔	• Prevent access to sperm stores
Reduce likelihood of future matings of partner		*Counter-measures*
• Induce refractory period	↔	• Recover mechanisms
• Mate guarding	↔	• Ignore
Increase immediate fecundity of partner		*Counter-measures*
• Suppress partner's male function	↔	• Stimulate own male function
• Stimulate partner's female function	↔	• Suppress own female function
Circumvent partner's counter-measures		*Counter-measures*
• Hypodermic impregnation	↔	• Behavioural avoidance
Reluctant to donate sperm (when sex-role reversed)		*Stimulate partner to donate*

(↔ indicates that the inscriptions in both columns are responses and counter responses to each other.)

B. *Postcopulatory sperm selection*

When multiple ejaculates overlap, the receiver function may develop postcopulatory mechanisms for sperm selection. This is particularly important in hermaphrodites since precopulatory mate choice may reflect the preference of the individual as a donor, rather than its preference as a receiver. It may therefore be essential to possess mechanisms that discriminate less favoured from preferred allosperm after a copulation. However, data suggestive of sperm selection in hermaphrodites are very rare. A preliminary survey of female reproductive organs across taxa suggests that a wide variety of mechanisms exist that have the potential of controlling which sperm are used for fertilization. Sperm resorption in the female genital tract is known from free-living flatworms (Cernosvitov 1931, 1932; Fischlschweiger and Clausnitzer 1984; Sluys 1989; Fischlschweiger 1991, 1994), oligochaetes (Grove 1925; Lasserre 1975; Adiyodi 1988) and snails (Chapter 8). In leeches, the behaviour of a spermatophore receiver indicates that it tries to rub it off immediately after receipt (Myers 1935), and particularly when in a poor condition, receivers may actually consume it (Brumpt 1900). Eating allosperm before they had a chance to enter the sperm receptacle has also been observed in arrowworms (John 1933). In leeches, hypodermically injected sperm are intensively phagocytosed in the coelomic sinuses, particularly in the vicinity of the ovaries (Brumpt 1900). A duct through which excess allosperm are transported from the sperm-receiving bursa copulatrix into the gut is characteristic of many free-living flatworms (Bock 1927; Hyman 1951; Ball and Reynoldson 1981). Others have 'nozzles' or 'mouthpieces' in the wall of the bursa that may function as sperm filters. Allosperm apparently have to move through their extremely narrow lumen to leave the bursa and reach the eggs (Costello and Costello 1938; Henley 1974). Selective usage may also be acquired through separate storage, as suggested by the presence of multiple bursae in some flatworms (up to 40 in *Oligochoerus limnophilus*; Henley 1974) and the large number of spermathecae seen in some oligochaetes (Adiyodi 1988; Fig. 7.8). In planarian flatworms, sperm are received in the caudally situated bursa (Fig. 7.9), and subsequently have to migrate from there, via the oviducts, to the sperm receptacles in the head region (Ball and Reynoldson 1981). The sheer length of this trajectory, plus the fact that sperm can be resorbed everywhere along it (Sluys 1989) suggests that the female system may function as a 'race track' for

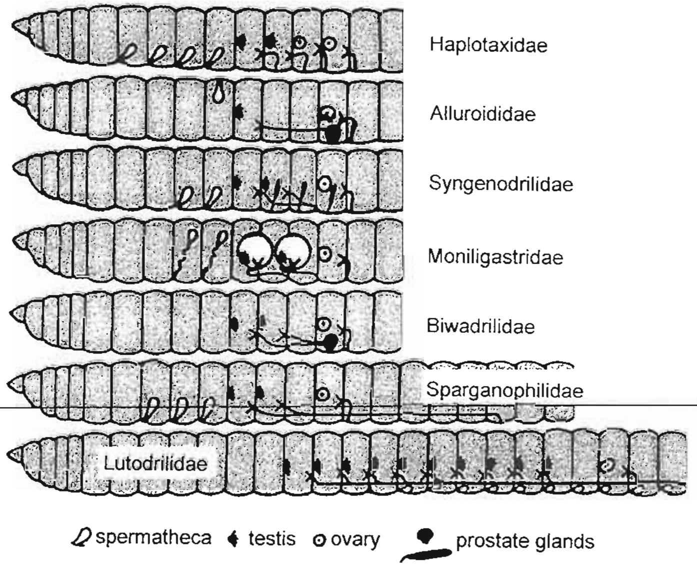

Fig. 7.8. *Diversity in reproductive systems in a few selected families of oligochaetes. Note the occasionally high number of testes and spermathecae (modified after Adiyodi 1988).*

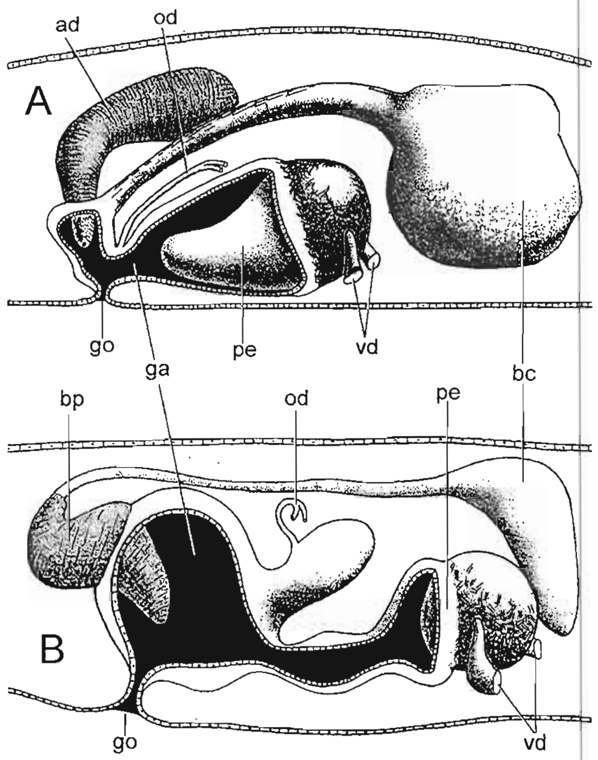

Fig. 7.9. *Two examples of peculiar genital morphologies in planarian flatworms.* **A.** Planaria torva *possesses a musculo-glandular organ or adenodactyl* (ad) *that may function as a sexual stimulator during copulation (Hyman 1951).* **B.** Bdellocephala punctata *(lower) has a penis* (pe) *that is not evertable. Instead, sperm are collected in the partner using the papilla-like extension* (bp) *of the bursal canal, a 'female penis'. Other abbreviations:* bc, *bursa copulatrix;* ga, *common atrium;* go, *gonopore;* od, *oviduct;* vd, *vasa deferentia (modified after Ball and Reynoldson 1981).*

sperm, similar to that in mammals (see Chapter 16) or in flowers (see Chapter 5). Arrowworms have specialized cells that connect the sperm receptacle directly to the cytoplasm of the ripening eggs (Kapp 1991), thus allowing individual sperm to migrate straight into eggs (Reeve and Lester 1974). This morphology suggests a sperm sieving function. The only known example of sperm incompatibility in hermaphrolitic animals comes from ascidians. In *Diplosoma listerianum*, autosperm and allosperm of the same type are blocked at the entrance of the female reproductive system (Bishop 1996; Bishop *et al.* 1996). This system bears a clear resemblance to the pollen–pistil interactions described by Delph (Chapter 5). In

the ascidian *Ciona intestinalis*, eggs are enveloped by follicle cells which can selectively block autosperm (De Santis and Pinto 1991).

Sperm selection by the receiver poses a problem to the donor, who now has to convince its partner to use its sperm to fertilize eggs. Costly nuptial gifts are an unlikely solution since both functions of the hermaphroditic partner will benefit from them. A paternal offspring produced via such gift is therefore likely to be more expensive than using the gift oneself to produce additional maternal offspring. Hence, sperm selection in hermaphrodites must be based on less costly indicators of a donor's quality. Less expensive ornaments that enhance the attractiveness of an individual as a receiver and as a donor may be a cheaper strategy. The prediction of Eberhard (1986, 1993) and Eberhard and Cordero (1995) that genitalia and prostate products may be used in mate choice may very well apply to hermaphrodites. In free-living flatworms genitalia, as well as prostate glands, are complex (Hyman 1951). In the acoel flatworm *Convoluta convoluta*, for example, the penis is everted like a glove with finger-like glandular extensions that anchor the penis within the vagina (Apelt 1969). Because most hermaphroditic animals have poor eyesight, it is very likely that they require tactile or chemical signals that can only be detected over short distances, or while already in contact, or even in copula.

C. *Maximize success of autosperm in receiver*

A classic response to sperm competition is to increase the number of autosperm transferred per mating (see Chapter 1). Using principles from sperm displacement mechanisms in insects, Charnov (1996) investigated how sex allocation should change in response to sperm competition, and developed an ESS model that predicts that allocation to the male function is directly related to the number of sperm the donor can produce maximally, divided by the number of sperm that can be stored by the receiver. Although the simplicity of this result is appealing, data to test both the model and its assumptions may prove hard to obtain.

A rough comparison of anatomical drawings of the relative size of testes plus prostate glands vs. ovaries plus yolk glands (Grassé 1959, 1960, 1961) suggests that male allocation is high in most hermaphrodites (Figs 7.4, 7.8 and 7.10). Such measures may, however, represent an unreliable indicator of sperm competition. It may be necessary to limit comparisons to cases where the degree of sperm competition is the most important difference between a few related species (Petersen 1990). In addition, differential costs to maintain prostate glands, male genitalia and mating behaviour may make differences between species misleading. Finally, many hermaphrodites show a slight temporal separation in sex development. If, for example, young hermaphrodites start out as a male

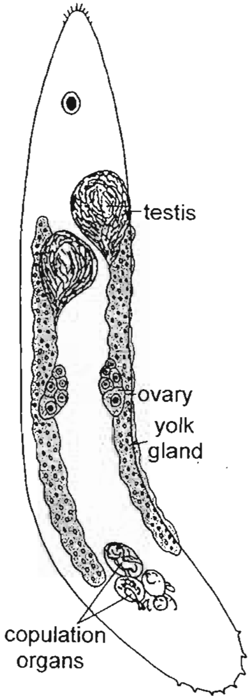

Fig. 7.10. *A free-living flatworm,* Monotoplana diorchis *with multiple copulatory complexes. It is assumed that copulatory complexes are lost during copulation and replaced (modified after Ax 1958, with permission).*

(protandry), this may reduce the apparent male allocation in 'adult' hermaphrodites.

When the receiver can obtain amounts of sperm that considerably exceed the amounts needed for fertilization, it may further extend the previously mentioned ability to digest sperm. Allosperm digestion by the receiver may, in return, result in the evolution of compensating traits in the donor such as chemicals that neutralize digestive enzymes or protective sperm packaging methods, such as a spermatophore. In the planarian *D. polychroa*, the transfer of a sperm clump is preceded and followed by the injection of a heterogeneous, sperm-free seminal fluid which might function as an inhibitor for digestion by the bursa copulatrix (A. Streng pers. comm.). In the related species *D. gonocephala*, however, sperm are transferred in a spermatophore and most of these are able to leave the bursa before the spermatophore is digested (Vreys *et al.* 1997b). Interestingly, the latter species also produces fewer sperm than the former (personal observation). But even when a spermatophore is used, the receiver function may still control the movement and survival of sperm further down the genital tract by employing many of the mechanisms mentioned above.

Prolonged copulation may also increase the fertilization chances of autosperm. This is particularly so when sperm need time to migrate away from a dangerous area. Arrowworms, for example, deposit a sperm cluster on each other's skin, and sperm subsequently move actively to the gonopores (Ghirardelli 1968). John (1933) observed that arrowworm partners held each other for up to 2 h (although sperm donation takes only seconds) and that the receiver ate the allosperm at the outside of its vagina after separation, suggesting that partners may hold each other to minimize the amount eaten. In the leech *Piscicola geometra* copulations last 5–6 h, even though spermatophores are exchanged at the beginning (Brumpt 1900). In this case, copulation may prevent the receiver from removing the spermatophore before it has discharged its content.

D. *Reduce competition with allosperm*

The ability to physically remove sperm directly from the sperm storage organs, as occurs in some insects (see Chapter 10), appears to be absent from hermaphrodites. Although hooked or spined penises are common among parasitic and free-living flatworms (Hyman 1951; Joyeux and Baer 1961; Williams and McVicar 1968), this armament appears to function as an anchor rather than a sperm displacement device. The only data suggestive of a sperm removal mechanism in hermaphrodites is from a study of the oligochaete *Euthyphoeus waltoni*, in which the paired penises carry a set of setae (Bahl 1928). Two of them are used during a single copulation and subsequently replaced. They are 5.5 mm long and can extend at least 1 mm beyond the tip of the penis. As the spermathecal duct is only 0.09 mm long it seems likely that the setae are driven deep into the spermathecae. Whether they are able to displace sperm is, however, not known. The rare occurrence of active sperm displacement among hermaphrodites may be due to the fact that they may not benefit from providing access to their sperm stores. In gonochorists, females can offer males increased paternity in this way in return for benefits such as guarding against other males and access to resources (see Chapter 10). In hermaphrodites, however, there appears to be nothing in terms of access or protection that a partner can offer that the receiver does not have already. Hermaphroditic partners could, in principle, 'trade' certainty of paternity with each other, but in internal fertilizers this possibility seems wide open for cheating.

E. Induction of a refractory period in the sperm receiver?

A donor would benefit if it could prolong the remating interval of the partner. Prostate fluids or other secretions may have an, as yet unknown, function here. Alternatively, deliberate injury of the partner could switch on an 'emergency physiology' and result in lower mobility and relocation of resources from storage to reproduction because of reduced survival perspectives. Hypodermic impregnation, although described in a different context below, may have such a function. Even if the receiver pays high long-term costs for such matings, the donor will be selected to inflict a wound on its partner if it can increase its short-term fertilization success in this way. This could explain the often aggressive way in which many hermaphrodites copulate. Some oligochaetes, for example, possess specialized, grooved chaetae that carry the secretion of specialized glands deep into the partner's body and might even transverse it completely (Needham 1990). It also offers a speculative explanation for dart-shooting and aggressive biting in mating snails (see Chapter 8).

A more direct reduction of the partner's maleness can be achieved by mutilating its male function so that it can no longer donate sperm, thus reducing its mating rate. In the slug *Ariolimax columbianus* (Mead 1943; see Chapter 8), individuals frequently lose their penis during copulation. It becomes stuck in the female genital tract and is bitten off either by the receiver or by its possessor (Leonard 1991). The presence of multiple copulation organs in some free-living flatworms (e.g. Hyman 1951; Fig. 7.10) has been interpreted as a way to replace copulatory complexes lost during copulation (Ax 1958).

Guarding against rival conspecifics is another possible way of forcing a refractory period onto the partner, but seems to be rare or even absent in hermaphrodites. One explanation may be that when a third individual interferes, the original partners may start to compete for the new, possibly better, individual rather than to protect each other. Another explanation may be that inducing a refractory period in the partner is likely also to breach the own optimal mating interval. However, an indication that mutual, 'traded' guarding might take place, comes from the flatworm *D. gonocephala*. When copulating, sperm transfer is completed after precisely 4.5 h, but partners remain in copula for up to 10 h (average 5 h) (Vreys *et al.* 1997b). Because in this species copulations take place mainly at night, a prolongation may reduce the chances that a partner mates again that same night, leaving the day for sperm migration within the female tract.

F. Manipulation of the receiver's sex allocation

Hermaphrodites might not only attempt to prolong the refractory period of their partner, but also unbalance its sex allocation to make it more female and less male. This not only increases the number of eggs it will produce, but may also reduce its mating rate. Although such a manipulation has not yet been documented, selection on the donor to do so must be high. This may be yet another explanation for the importance of prostate products. Hermaphrodites could defend themselves against feminizing products from the partner by a priori biasing allocation to the male function so that, when being feminized by the partner, the resultant sex allocation is still close to optimal for the manipulated individual. This could explain the widespread occurrence of protandry among hermaphrodites. Eventually, feminizing agents may result in hermaphrodites that are masculine as long as they are virgin and must receive an ejaculate in order to feminize. Arrowworms, for example, have to mate in order to produce eggs for the first time (Alvariño 1990). In order to keep feminizing factors separate from their own reproductive system, donors could exploit ejaculate resorption by the receiver (see earlier) and transfer products that become biochemically active when metabolized. Data for snails suggest that young individuals indeed need to metabolize an ejaculate from a partner in order to induce egg development (Kruglov 1980). A major difference with gonochorists is that, when males induce females to produce more eggs, they may only be able to do so by offering her additional resources, which is not in conflict with her interests. In a hermaphrodite, however, a donor is not interested in topping up the resources of its partner (see above), but may attempt to free resources by reallocation within its receiver instead, resulting in a conflict that is unique to hermaphrodites.

G. Circumvention of the partner's defences: hypodermic impregnation

Copulatory mechanisms may eventually become so complicated and costly for the donor function, particularly if the receiving function has managed to keep pace and controls fertilization completely, that it may pay the donor to circumvent completely the receiver's control. Injecting sperm hypodermically rather than into a female sperm-receiving organ is common among hermaphrodites but not in gonochorists. It is ubiquitous in large groups of free-living flatworms (Hyman 1951; Michiels and Newman 1998; Fig. 7.6), and is also known from parasitic flatworms (Joyeux and Baer 1961; Baer and Euzet 1961; Ubelaker 1983; Kearn 1992), polychaetes (Westheide 1979; Olive 1983; Adiyodi 1988) and sea slugs (see Chapter 8). Such species usually have a stylet-shaped penis. Leeches, however, glue a highly specialized spermatophore onto the skin of the partner (Myers 1935; Lasserre 1975; Kutschera 1989; Sawyer 1986; Fig. 7.5). Enzymes first dissolve the skin, after which sperm are injected into the body cavity by a spontaneous contraction of the spermatophore, which continues to inject sperm until long after the donor has gone.

In addition to circumventing the receiver's control, hypodermic impregnation saves time by being one order of magnitude shorter. Unilateral hit-and-run usually takes only seconds (Myers 1935; Apelt 1969; Borkott 1970; Kutschera 1984) whereas reciprocal hypodermic impregnation ranges from a few seconds up to 60 min (Brumpt 1900; Hyman 1951; Harrison 1953; Hoffman 1956; Nagao 1958; Apelt 1969; Kutschera and Wirtz 1986; Kutschera 1989; Kearn 1992; Kearn and Whittington 1992; Michiels and Newman 1998). Although normal copulation can be short in some species (Costello and Costello 1938; Hyman 1951; Darlington 1959; Apelt 1969) it often takes hours (Kato 1940; Yanagita 1964; Wilkialis and Davies 1980; Peters *et al.* 1996; Vreys *et al.* 1997a) or even days (Brumpt 1900). An unusual, unilateral mechanism of hypodermic impregnation has been described for the parasitic flatworm *Diclidophora merlangi* in which the penis applies suction to the epidermis of the partner and dissolves the skin, after which spines hold the wound open while sperm are injected (MacDonald and Caley 1975). This process takes 1 h.

One explanation for the relatively low occurrence of hypodermic impregnation in gonochorists may be that unreceptive females can simply hide or avoid males. Only when they are receptive will they seek a partner. As a result, males will not need forced sperm donation to inseminate them or could even lose attractiveness. In hermaphrodites, however, animals that do not want to receive still have to copulate in order to donate. Under such conditions, it may be advantageous to develop forced sperm transfer.

H. *Sperm competition and sex-role reversal*

Thus far, I have assumed that hermaphrodites mate because they want to donate sperm and that sperm receipt still leaves the option to accept or reject it. However, as explained earlier, sex-role reversal might be common in hermaphrodites. Sperm competition will be less significant as a result, and the receiving function may even become sperm limited and start to develop advertisement tactics to get its eggs fertilized. This may explain why, for example, some planarian flatworms have no evertible penis, but instead have a female intromittant organ that is used to suck up the donor's sperm (e.g. *Bdellocephala*; Ullyott and Beauchamp 1931; Fig. 7.9). An even more extreme case is offered by the suggestion that certain turbellarians obtain allosperm by cannibalizing their partner (Sterrer and Rieger 1974).

VII. CONCLUDING REMARKS

Although constrained in their evolutionary response to sexual selection, it is clear that there is scope for evolutionary arms races in hermaphrodites that may result in adaptations that are at least as diverse as those seen among gonochorists. Comparisons between gonochorists and hermaphrodites also show that the dominance of the former in sexual selection theory might actually hamper our understanding of the latter. Certain aspects of hermaphrodite biology, such as the extreme diversity in sperm morphology, the importance of cannibalism or the many specialized glands and receptors have been ignored, but would further enrich this image. Although I have (artificially) separated sex allocation, reciprocity of sperm transfer and sperm competition, it is obvious that the selection pressures that result from each of these are not independent, but will often result in similar adaptations. This may make it difficult to find out whether, for example, assessment occurs to measure the partners quality as a donor, as a receiver, or as a reciprocating partner. As a result, many of the examples that I have mentioned in one section, may equally serve as 'suggestive evidence' in another. In order to disentangle these phenomena, it is very important to have accurate data on sperm production, transfer, depletion, storage and selection, as well as life history data for the species. Events that diverge from the typical pattern for a given species may be of particular importance (e.g. unilateral transfer in an otherwise reciprocally inseminating species).

It is unfortunate that I have to confirm what Eric Charnov wrote 15 years ago: although the theoretical basis for the understanding of hermaphroditic mating systems is available, far too few examples have been worked out sufficiently to put the theory to the test (Charnov 1982). I hope that my (speculative) attempts to further elaborate existing ideas will prompt new students in behavioural ecology to consider the unexplored aspects of hermaphroditic systems and share my excitement. In the end, I hope it may also lead to enhanced communication between botanists (the professionals in this context) and zoologists.

ACKNOWLEDGEMENTS

This manuscript has benefited from frequent discussions on hermaphrodite mating behaviour with Rolf Weinzierl. I gratefully acknowledge helpful comments from Leo Beukeboom, Angél Martín Algánza, Bruno Baur, Tim Birkhead, Philippe Jarne, Anders Møller, Anne Peters, Tim Sharbel, Andrea Streng, Claus Wedekind, Jack Werren and Julie Zeitlinger. Many of the ideas presented have been positively influenced by the presentations and discussions at a workshop of the European Science

Foundation on the evolution of hermaphrodite mating systems (Jarne and Charlesworth 1996).

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8 Sperm Competition in Molluscs

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I. INTRODUCTION

Molluscs are numerically the second largest phylum in the animal kingdom with more than 120 000 living species, which are divided into eight classes (see Table 8.1). The visual differences between a snail, a clam, and a squid, each an example of a major class of the molluscs, belie the closeness of their relationship. Sexual behaviour is also extremely variable in this phylum. Many species are promiscuous and there are different forms of sperm storage, providing the potential for sperm competition. However, with a few exceptions, evolutionary and behavioural aspects of sperm competition have not been examined in this phylum. Most of the available evidence for sperm competition in molluscs is published in studies with other aims and therefore is indirect.