Sneakers, Satellites, and Helpers: Parasitic and Cooperative Behavior in Fish Reproduction

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I. Introduction

Organisms compete for various resources in the course of sexual reproduction. First, there is intrasexual competition for obtaining mates. Then, there is the need to exclude reproductive competitors who might displace or affect the individual's own gametes (e.g., sperm competition, egg dumping). There is competition for sites that are used to raise progeny and/or that will optimally support them, and it may be highly advantageous to monopolize the resources that are essential for offspring survival and development.

In this chapter I review our current knowledge of the ways in which fish compete at these different levels. I further describe how competition for resources may lead to cooperative behavior, even between the competitors themselves. Finally, I draw attention to the model character of fish social systems and suggest crucial directions for future research.

II. Reproductive Competition

I begin with a description of different levels of reproductive competition among males. Group spawning appears to be a mating pattern with little competition between males, but this impression may result from our ignorance of the subtleties involved in this mating pattern and in its reproductive consequences. The competitive character of male behavior that serves the purpose of gaining access to females is much more obvious when it is coupled with some sort of resource or mate monopolization. The attempt to monopolize resources or females to obtain fertilizations (i.e., the "bourgeois" tactic) may not always be the best choice for a male. He may be

better off choosing alternative tactics when he is not in the position to compete successfully, for example, because of a weak resource holding potential (*sensu* Parker, 1974), or when there are "cheaper" ways to obtain fertilizations, that is, when the cost/benefit ratio of the alternative tactic will fall below that of the bourgeois tactic (see Rubenstein, 1980; Dunbar, 1982; Arak, 1984; Magurran, 1986; for general discussions).

Basically, the monopolization of mates may be overcome in two alternative ways. Males may either obtain partners from others who have already invested in their acquisition, or they may directly try to obtain parasitic fertilizations, that is, release sperm when a female spawns with another male. The first route is chosen by males taking over a nest, mating site, or breeding hole from its owner who already invested in behaviors like nest building, preparation of a spawning surface, site advertisement, or defense (*nest takeover*). A specific version of this tactic is to take charge of the nest for only a limited spawning period and then leave the broodcare to the previous nest owner (*piracy*). Males may also try to steal females within other males' territories or intercept females who are on their way to a spawning site that is monopolized by another male (*female theft* and *interception*).

The second alternative route to obtain fertilizations differs from the first one in that parasitic males do not attempt to get exclusive access to a female, that is, monopolize her for some period of time, but rather shed sperm while a bourgeois competitor spawns (*sperm competition*). This "simultaneous parasitic fertilization" tactic is very widespread in fish and I will give an overview of its taxonomic distribution (see Table I). I summarize the information on the different types of males participating in kleptogamic fertilizations, from bourgeois territory neighbors to males behaviorally and morphologically specialized for this type of mating (e.g., female mimics). In live-bearers, fertilization stealing often involves coercive copulations that may also be at the expense of males investing in courtship to attract females.

I compare bourgeois and parasitic males with regard to their relative abundances, costs (e.g., behavioral, morphological, and gonadal effort), reproductive success, and origin, that is, to what extent their tactics are genetically or phenotypically determined. I then discuss how females behave toward bourgeois and parasitic males, and review female reproductive competition and parasitic behavior (e.g., egg dumping).

A. Group Spawning

Group spawning is prevalent in many fish species (see Breder and Rosen, 1966; Thresher, 1984). In many surgeonfish (Acanthuridae), for example,

thousands of individuals aggregate for spawning (e.g., Robertson *et al.,* 1979; Robertson, 1983; Colin and Clavijo, 1988). Often, there is both pair and group spawning among members of the same species (e.g., in Salmonidae, Cameron, 1940; Mullidae, Colin and Clavijo, 1978, 1988; Sparidae, Smith, 1986; Labridae, Randall and Randall, 1963; Reinboth, 1973; Moyer and Shepard, 1975; Warner *et al.,* 1975; Meyer, 1977; Warner and Robertson, 1978; Pottle *et al.,* 1981; Wernerus and Tessari, 1991; Scaridae, Randall and Randall, 1963; Choat and Robertson, 1975; Robertson and Warner, 1978).

In spite of the fact that male competition for fertilizations or sperm competition is intense in these "explosive breeding assemblages" (*sensu* Emlen and Oring, 1977), no specific behavioral mechanisms have been reported that may give individuals performing them higher fertilization probabilities. However, even where it looks as if gametes are released by many fish simultaneously and without regular pattern, there may well be organized pair spawning (e.g., Brawn, 1961). This leaves ample scope for intrasexual male parasitism (see the following), but there are as yet no data on this in group spawners.

B. COMPETITION FOR ACCESS TO FEMALES

Pair spawning will be discussed in the following sections. It involves at least a short-term monopolization of a mate. The effort of males may be in defense of a place, shelter, or nest, in modification of the substrate (e.g., by digging, cleaning, nest building), in courtship, and in broodcare. There are various ways in which the exclusion shown to them can be overcome by competitors to parasitize this effort and/or the success of territorial males.

1. Temporary and Permanent Nest Takeover for Spawning

Males may save effort by temporarily taking over nests, holes, or other structures that have been obtained and/or prepared by territorial males for the purpose of spawning and/or rearing offspring. In the cyprinid *Margariscus margarita* "adolescent," nonterritorial males may spawn within the territories of adult male conspecifics (Langlois, 1929). Similar observations were made in desert pupfish (Kodric-Brown, 1977) and in the wrasses *Bodianus diplotaenia, Halichoeres maculipinna* (Robertson and Hoffman, 1977), and *Symphodus ocellatus;* in the latter species there was spawning by both "satellites" and "sneakers" (Taborsky *et al.,* 1987). In arctic graylings (*Thymallus arcticus:* Salmonidae), subdominant males spawn within territories when their owners are distracted by other activities (Beauchamp, 1990).

Nest takeovers have been described in creek chub (*Semotilus atromaculatus:* Cyprinidae), in which nonnesting males try to occupy nests of other males temporarily in order to attract females to clasp them for spawning. Males stay and "watch" at the margin of nests and take over when the nesting male is engaged in agonistic interactions away from the nest (Ross, 1977). Toward the end of the season, when few females mate, many of the nests are taken over by males that are smaller than the previous owners. Brightly colored, territorial *Pseudocrenilabrus philander* males (Cichlidae) take over nests of opportunistically courting, semiterritorial males by expelling them from their spawning pits, and spawn with the females that had been attracted by these semiterritorial males (Chan, 1987). In bluegill sunfish (*Lepomis macrochirus:* Centrarchidae), larger males often displace smaller nest owners after vigorous, often prolonged fighting (Dominey, 1981).

Longer-lasting or even permanent nest takeovers also occur in the Mediterranean wrasse *S. ocellatus* (Labridae). Territorial males of this species build complex nests of algae. Fiedler (1964) observed nest takeovers in this species and in *S. mediterraneus*. In a population of the former species off Corsica, more than a quarter of the nests studied were taken over by males in nuptial coloration that had built their own nests before (Taborsky *et al.,* 1987). Two-thirds of these takeover males only fed on the eggs contained in the acquired nests, but the other third courted there and most of these also spawned successfully. When compared to building a nest by oneself, a nest takeover reduced the interval between the completion of one nest and the first spawning in the next by 3.7 days on average, which is more than a third of the average length of a whole nest cycle. Usually, takeover males had been immediate neighbors of the individuals that were ousted. In 3 out of 24 cases the previous owner regained his nest at a later stage (Taborsky *et al.,* 1987).

In the river bullhead (*Cottus gobio:* Cottidae; Bisazza and Marconato, 1988) and in the freshwater goby *Padogobius martensi* (Gobiidae; Bisazza, *et al.,* 1989a) and *Pomatoschistus minutus* (Magnhagen and Kvarnemo, 1983), large males displace smaller spawning or guarding males to spawn themselves in the acquired nest sites. Hastings (1988) demonstrated experimentally the importance of relative male size in the competition for already occupied spawning shelters in angel blennies (*Coralliocetus angelica:* Chaenopsidae). Large male greenbreast darters (*Etheostoma jordani:* Percidae) may displace smaller males which guard a female on the spawning ground by lying on top of her (Orr and Ramsey, 1990). At least in the river bullhead such displacements may be a beneficial tactic, as females prefer to spawn with males that already guard eggs (Marconato and Bisazza, 1986; Bisazza and Marconato, 1988; see Section III,C,3).

2. Piracy

Nonnesting males of the Mediterranean wrasse *Symphodus tinca* (Labridae) may spawn within the nests of territory owners when the latter have "spawning breaks" (i.e., rest between series of spawnings), which occupy a large proportion of the spawning period (Lejeune, 1985). Occasionally, very large males may take over a nest from an owner and spawn there for up to two and a half days, much as in the cases described earlier for the closely related *S. ocellatus* and the bluegill sunfish. In *S. tinca,* however, the original nest owners remain at these nests and continue to guard them after the "pirates" have left (van den Berghe, 1988). Pirates seem to have less success than nest owners. Combining the information given by van den Berghe (1988) with his unpublished data (personal communication), pirates seem to average only one-tenth of the spawnings of nesting males. Contrary to this, van den Berghe (1988) believed that they obtained similar spawning rates to nest owners, but this was based on an erroneous comparison of spawning rates measured over different time periods, and without allowing for the fact that in 67% of the observed cases of piracy the pirated nests were abandoned by their owners before the pirates' eggs could hatch. Despite this, at least some of the nest owners' *own* eggs could have hatched in these cases because they had been laid at an earlier stage in the nesting cycle.

Why then do the largest males in a population adopt a greatly inferior spawning tactic? First, pirates may build their own nests at a different stage of the breeding season (van den Berghe, 1988). Second, in comparing tactics we must examine the possible alternatives for an individual at any given time. Pirates may compensate for their low spawning rate by saving the time and risk associated with guarding and nest building, as well as by feeding in the takeover nest while in charge of it (see van den Berghe, 1988).

In 2 out of 88 observed nests of territorial *S. ocellatus,* an expelled nest owner regained his former nest at a later stage to continue broodcare and guarding (Taborsky *et al.,* 1987). Probably, this takeover reversal resulted from an aggressive expulsion of the intruder (i.e., not from his spontaneous abandonment of the nest) and hence this temporary, parasitic nest occupancy should not be viewed as a behavioral "tactic" (i.e., "piracy"). In the tesselated darter (*Etheostoma olmstedi:* Percidae), Constantz (1985) observed that "fathers" may cruise and search for ripe females and for other nests once they have spawned in their own shelter. They may, "upon encountering consort pairs, attempt to displace courting males" (p. 176). It is not stated, however, if a displaced previous owner will ever regain and guard his shelter afterwards.

3. "Interception" and "Female Theft"

In the American angelfish *Holacanthus passer* (Pomacanthidae), smaller males occasionally interfere with courting males and may spawn with a female in the territories of the latter. This happens primarily when two to three females visit the territory of a large male simultaneously. This female theft is only very rarely successful (Moyer *et al.*, 1983). It has also been observed in wrasses (Labridae: *Thalassoma bifasciatum*, Reinboth, 1973; *Clepticus parrae*, Warner and Robertson, 1978; *Cirrhilabrus temminckii*, Bell, 1983). Peripheral males interrupted spawning harem owners in the hawkfish *Cirrhitichthys falco* (Cirrhitidae) and spawned occasionally with harem females (Donaldson, 1987).

Courting males of the cyprinid *Zacco temmincki* may be attacked at or in a spawning redd by a male competitor. This leads most often to the courting males' loss of the females they were going to spawn with (Katano, 1990). Similarly, females of the pupfish *Cyprinidon variegatus* (Raney *et al.*, 1953), *C. macularis* (Barlow, 1961), and *C. pecosensis* (Kodric-Brown, 1977) and of the Mediterranean wrasse *Symphodus tinca* (van den Berghe, 1988) may be intercepted when they are ready to spawn at or around territories. They may subsequently follow the intercepting males and spawn with them outside a territory. In *S. tinca* this interception by nonnesting males yields apparently very little success, however, as the untended eggs produced by this spawning mode have minute chances of survival (Lejeune, 1985; Wernerus, 1989).

Interception of females on their way to a territory has also been observed by groups of "initial phase males" (i.e., small males that do not have the specific color pattern of territory owners) of the tropical wrasse *Thalassoma bifasciatum* (Warner *et al.*, 1975; Warner and Robertson, 1978) and the parrotfish *Sparisoma radians* (Robertson and Warner, 1978). This may lead to group spawning. Small parasitic or large neighboring territorial fish were observed to intercept females that are ready to spawn in the wrasse *Symphodus melanocercus* (Lejeune, 1985), in parrotfishes (Scaridae, Robertson and Warner, 1978), in *Chaetodon capistratus* (Chaetodontidae, Neudecker and Lobel, 1982), and in tesselated darters (*E. olmstedi*, Percidae, Constantz, 1985). In an experimental situation, large *Padogobius martensi* (Gobiidae) nest-males courted females that were spawning in the nests of smaller males and sometimes got the females to follow them into their own nests, where they continued to spawn with the interlopers (Bisazza *et al.*, 1989a). In the field, two *P. martensi* males "in aggressive livery" were occasionally found together in a nest with a spawning female or freshly spawned eggs (Marconato *et al.*, 1989).

Sexually mature "bachelor" males of *Canthigaster valentini* (Tetrao-

dontidae), a harem species, live either alone in home ranges on the periphery of social groups or as non-site-attached wanderers. They have no access to females of the harem to which they belong, but they may spawn in another male's territory when its owner courts another female at the far end of the territory. Less than 3% of spawnings observed by Gladstone (1987b) involved such bachelor males. When territorial males were removed, bachelor males took over their territories (Gladstone, 1987a).
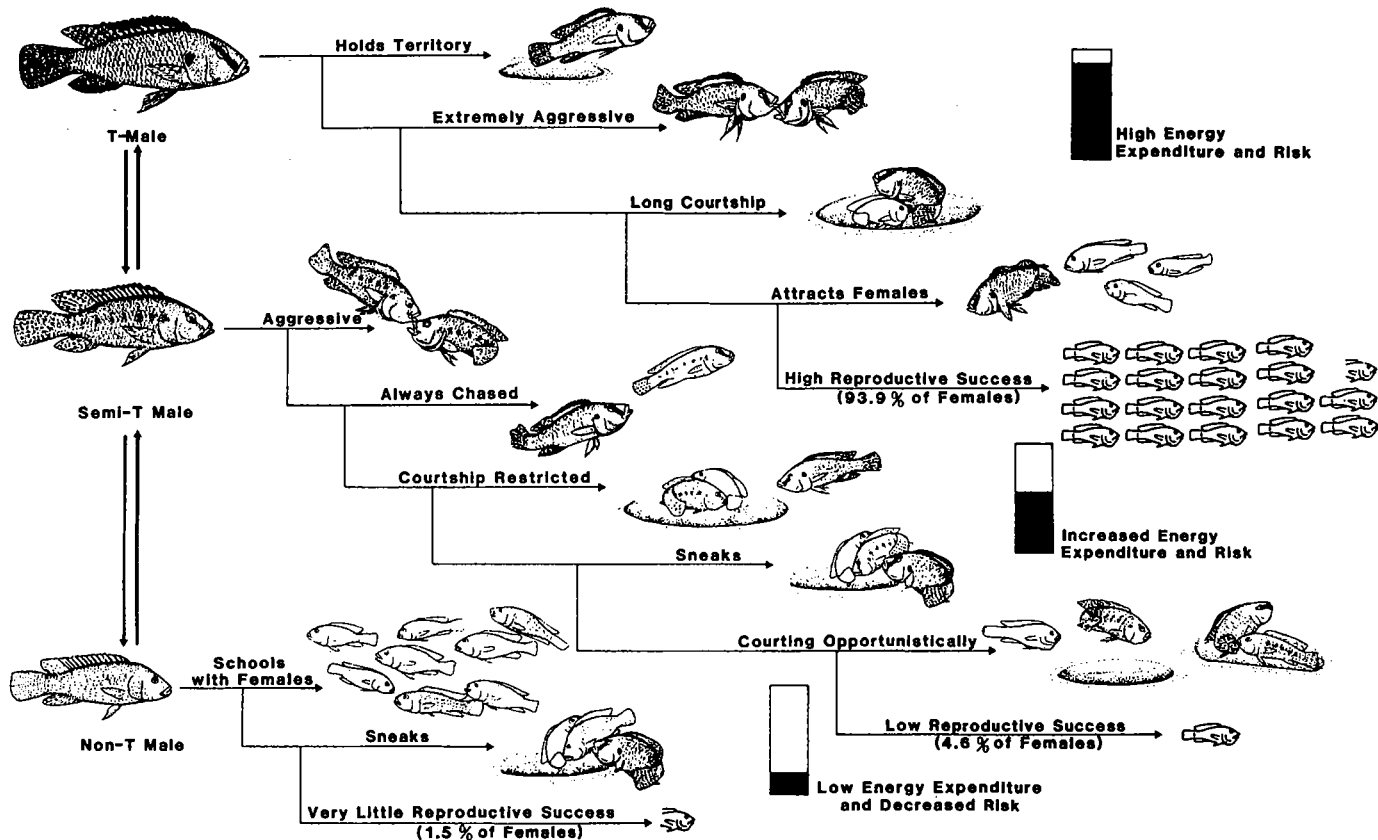
Within the territory of a male, nonterritorial male honey gouramis (*Colisa chuna*) may clasp a female after she has spawned with the territory owner, and quiver, apparently releasing sperm. It is uncertain if the females release eggs on these occasions, but the sperm of these intruders may at least fertilize eggs that had been spawned before (Janzow, 1982).

C. Sperm Competition

So far I have discussed the competition of males for the opportunity to spawn. This involves the parasitism of the effort of other males by obtaining access to females that had been attracted to them or to structures provided by them. I now turn to a type of competition that involves the participation of more than one male in a spawning. I focus on cases that are asymmetric with regard to effort, that is, cases in which the reproductive effort of one male is exploited by others. In such cases of simultaneous spawning of a female with more than one male, sperm competition *adds* to the costs borne by the parasitized male that result from the surreptitious use of his reproductive effort (e.g., courtship, defense, broodcare; see the previous section). Figure 1 shows an example of a species with both types of male reproductive parasitism, resulting from competition for access to females *and* from sperm competition.

1. Fertilization Stealing by Territorial Neighbors

In several fish species, males may leave their territories temporarily and try to steal fertilizations when neighboring males spawn. This was observed in various sticklebacks (Gasterosteidae; three-spined sticklebacks, *Gasterosteus aculeatus,* van den Assem, 1967; Li and Owings, 1978a,b; Sargent and Gebler, 1980; four-spined sticklebacks, *Apeltes quadracus,* Rowland, 1979; Wootton, 1984, p. 142, mentions three more stickleback species). The cuckolding males change from their bright color pattern, which reveals their sex and territorial status, to a drab, femalelike coloration before they sneak into the territory of a neighbor. There they may either prevent females from entering the nest to spawn by lying across it or in its entrance, or they may follow the female through the nest and fertilize the freshly laid eggs before the resident male can do so. In these

T-Male

Holds Territory

Extremely Aggressive

Long Courtship

High Energy Expenditure and Risk

Semi-T Male

Aggressive

Attracts Females

Always Chased

High Reproductive Success (93.9 % of Females)

Courtship Restricted

Increased Energy Expenditure and Risk

Sneaks

Non-T Male

Schools with Females

Courting Opportunistically

Sneaks

Low Reproductive Success (4.6 % of Females)

Very Little Reproductive Success (1.5 % of Females)

Low Energy Expenditure and Decreased Risk

cases, the nest owner might only obtain such fertilizations as are achieved by the sperm he had released earlier, for example, in previous spawnings.

Nest intrusions and fertilization stealing by neighbors also occur in suckers (Catostomidae; *Moxostoma duquesnei,* Bowman, 1970), sunfish (Centrarchidae; *Lepomis macrochirus,* Avila, 1976; Gross, 1982; *L. megalotis,* Keenleyside, 1972; Bietz, 1980, 1981; Dupuis and Keenleyside, 1988; Jennings and Philipp, 1992), cichlids (Cichlidae; *Sarotherodon grahami,* Albrecht, 1968; *Haplochromis (Astatotilapia) burtoni,* Fernald and Hirata, 1977; *Pseudocrenilabrus philander,* Chan, 1987), damselfish (Pomacentridae; *Abudefduf saxatilis, Chromis multilineata,* Albrecht, 1969; *Chromis cyanea,* De Boer, 1981), parrot fish (Scaridae; *Sparisoma radians,* Robertson and Warner, 1978), three species of surgeonfish (Acanthuridae; *Ctenochaetus striatus, Zebrasoma scopas,* and *Z. veliferum;* Robertson, 1983), and in *Tripterygion tripteronotus* (Tripterygidae; Wirtz, 1978). Jennings and Philipp (1992) showed that cuckoldry by neighbors in longear sunfish reduces the reproductive success of colonial males to a level below that of solitary males. Small and less attractive males even seem to specialize in stealing fertilizations in neighbor's nests.

2. Fertilization Stealing in Simultaneous Hermaphrodites

A parasitic, simultaneous release of sperm is also widespread in simultaneous hermaphrodites (e.g., Fischer, 1986). In *Serranus fasciatus,* hermaphroditic members of a large male's harem may try to steal fertilizations when this male is spawning with another harem member, despite the fact that these individuals usually take the *female* role when spawning with the owner of the harem (Petersen, 1987). In *S. Tortugarum* apart from the behavioral adaptations of this intraharem reproductive parasitism in this bass, this is probably the reason why a large proportion of the gonad mass of hermaphrodites is assigned to the production of sperm (*ca.* 25%; Fischer, 1986).

3. Alternative Mating Tactics of Different Types of Males

Commonly, competitively inferior male fish parasitize territorial, often brightly colored or morphologically distinct male conspecifics. Various

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Fig. 1. Schematic representation of male reproductive options in the African cichlid *Pseudocrenilabrus philander*. There are three reproductive tactics in this species and the frequency of these options depends on male size and competitive pressure. Individual males may switch between tactics. The costs and benefits as indicated in this graph only illustrate the order of magnitude and should not be interpreted literally, because of problems with quantitative measurements (e.g., all eggs spawned when parasitic intrusions occurred were attributed to the success of sneakers). Reproduced from Chan (1987).

terms have been used to describe this behavior, and these are often descriptive expressions of how these males try to participate in spawning (e.g., "sneaking" for stickleback males secretively approaching a nest to fertilize eggs that have just been spawned there, van den Assem, 1967; or "streaking" for wrasse males that rush into a male's territory to join its owner and his mate just as they are shedding gametes into the water, Warner et al., 1975). The terms used for the males performing such parasitic behavior are even more diverse. They have been called "sneakers" (e.g., van den Assem, 1967; Taborsky et al., 1987; Hutchings and Myers, 1988), "sneaky males" (Rowland, 1979), "streakers" (e.g., Warner et al., 1975; Maekawa and Onozato, 1986), "scroungers" (Barnard, 1984), "cuckolders" (e.g., Gross, 1984), "machos furtivos" (furtive males; Santos, 1985), "outsider der Befruchtung" (outsiders of fertilization; Soljan, 1930b, 1931), "pseudofemales" (e.g., Morris, 1952), "transvestite males" (e.g., Dipper, 1981), "stunted males" (e.g., Shute, et al., 1982), "hiders" (Hutchings and Myers, 1988), "accessory males" (e.g., Winn, 1958a; McCart, 1969; Hillden, 1981), "Beimännchen" (by-males; Fiedler, 1964), "supernumerary males" (e.g., Ribbink, 1975), "small outlier males" (Keenleyside and Dupuis, 1988), "interference spawning males" (Colin and Bell, 1991), "Type II males" (e.g., Bass, 1992), or "satellites" (e.g., Dipper, 1981; Lejeune, 1985; Katano, 1992).

I focus my discussion on the functional aspects of this phenomenon. The most important distinction between reproductive tactics in this respect is on the basis of effort. As with any parasitic relationship there are individuals investing in some structure, either morphological, physiological, or behavioral, and others exploiting this investment to obtains access to a limited resource (e.g., Barnard, 1984). I use the term "bourgeois" for a male of the former (i.e., investing) type, in line with the nomenclature of the game theoretic treatment of this problem (e.g., Maynard Smith, 1982). A bourgeois individual behaves in a certain way as the owner of a resource (e.g., a female that is ready to spawn), but it may also behave very differently to usurp such a resource if it is "owned" by another individual (e.g., another male that has successfully put effort into its procurement). I generally call the alternative tactic "parasitic." Parasitic spawning is defined as "simultaneous" when the parasite tries to steal fertilizations by participating in the spawning of a pair. Other functional and synonymous terms for male reproductive parasitism that I may use are "kleptogamy" (Barnard, 1984) or "kleptogyny" (Turner, 1986a).

I have found published accounts of simultaneous parasitic spawning (SPS) for 123 species belonging to 24 different fish families, ranging from salmon to midshipman. These are listed in Table I. This list, though fairly comprehensive, is certainly not complete. There is little literature

TABLE I
MALE SIMULTANEOUS REPRODUCTIVE PARASITISM

Species[a]	References
Salmonidae	
Salmo salar	Orton *et al.* (1938); Jones and King (1950b, 1952a,b); Jones (1959); Myers, Hutchings (1987); Hutchings and Myers (1988); Jordan and Youngson (1992)
S. henshawi	Smith (1941)
S. trutta	Jones and Ball (1954)
Salmo gairdneri	Hartman (1969)
Oncorhynchus nerka	Hanson and Smith (1967); McCart (1969); Chebanov *et al.* (1983); Foote and Larkin (1988); Foote, 1990
O. keta	Schroder and Duker (1979); Schroder (1981, 1982)
O. kisutch	Gross (1985)
O. gorbuscha	Wicket (1959); Heard (1972); Chebanov (1980)[b]; Keenleyside and Dupuis (1988); Noltie (1989)
Salvelinus fontinalis	Smith (1941)
S. alpinus	Jonsson and Hindar (1982); Sigurjonsdottir and Gunnarsson (1989)
S. malma miyabei	Maekawa (1983); Maekawa and Hino (1986, 1990); Maekawa and Onozato (1986)
Thymallus arcticus	Kratt and Smith (1980)
Cyprinidae	
Notropis cornutus	Reighard (1943)[b]
Semotilus corporalis	Ross and Reed (1978); Ross (1983)
Zacco temmincki	Katano (1983, 1990, 1992)
Rhodeus amarus	Heschl (1989)
Catostomidae	
Catostomus commersonii	Reighard (1920)
Hypentelium nigricans	Reighard (1920)
Moxostoma erythrurum	Reighard (1920)[b]; Kwak and Skelly, (1992)
M. duquesnei	Bowman (1970)
M. valenciennesi	Jenkins and Jenkins (1980)[b]
Mochokidae	
Synodontis Multipunctatus	Schrader (1993)
Gasterosteidae	
Pungitius pungitius	Morris (1952)
Gasterosteus aculeatus	Morris (1952); van den Assem (1967); Li and Owings (1978a); Sargent and Gebler (1980[d]; Sargent (1982); Wootton (1984); Goldschmidt and Bakker (1990); Goldschmidt *et al.* (1992); Rico *et al.* (1992)
G. inconstans	Wootton (1984)
G. wheatlandi	Wootton (1984)
Apeltes quadracus	Rowland (1979)

TABLE I *(Continued)*

Species[a]	References
Macrorhamphosidae	
Macrorhamphosus scolopax	Oliveira *et al.* (1993)
Cyprinodontidae	
Cyprinodon variegatus	Raney *et al.* (1953)
C. macularius	Barlow (1961); Matsui, unpublished, in Kodric-Brown (1981)
C. pecosensis	Kodric-Brown (1977, 1981, 1986)
C. nevadensis	Soltz (1974)
Aphanius fasciatus	Marconato (1982)
Poeciliidae[g]	
Poeciliopsis occidentalis	Constantz (1975)
Poecilia sphenops	Parzefall (1979)
P. reticulata	Baerends *et al.* (1955); Liley (1966); Farr (1980a,b); Endler (1983, 1987); Luyten and Liley (1985); Farr *et al.,* (1986); Kodric-Brown (1992); Reynolds *et al.* (1993)
P. latipinna	Woodhead and Armstrong (1985); Travis and Woodward (1989)
Xiphophorus nigrensis	Zimmerer (1982); Zimmerer and Kallmann (1989); Ryan and Causey (1989)
Gambusia affinis	Hughes (1985)
G. holbrooki	Bisazza *et al.* (1989b)
Serranidae	
Serranus scriba	Reinboth (1962), P. Lejeune (personal communication)[c]
Hypoplectrus nigricans	Fischer (1980)
S. tortugarum	Fischer (1984, 1986)
S. baldwini	Petersen and Fischer (1986)
S. fasciatus	Petersen (1987, 1990)
Centrarchidae	
Lepomis gibbosus	Miller (1963); Gross (1979)
L. microlophus	Gerald (1970)[c]
L. macrochirus	Gerald (1970)[c]; Gross (1979, 1982); Gross and Charnov (1980); Dominey (1980, 1981)
L. megalotis	L. m. peltastes: Keenleyside (1972); Bietz (1980); Dupuis and Keenleyside (1988); L. m. megalotis; Jennings and Philipp (1992a,b)
Percidae	
Etheostoma caeruleum	Reeves (1907); Winn (1958a)
E. spectabile	Winn (1958b)
E. nigrum	Winn (1958a)
E. exile	Winn (1958a)
E. olmstedi	Constantz (1979)

TABLE I (*Continued*)

Species[a]	References
E. perlongum	Shute *et al.* (1982)[b]
E. jordani	Orr and Ramsey (1990)
Hadropterus maculatus	Petrovicz (1938)
Percina caprodes	Winn (1958a)
Sparidae	
Chrysophrys auratus	Smith (1986)
Cheimerius nufar	Garratt (1991)[d]
Chaetodontidae	
Chaetodon nippon	Susuki *et al.* (1980)
C. multicinctus	Lobel (1989)
Cichlidae	
Sarotherodon niloticus	Heinrich (1967)
S. alcalicus	Albrecht (1968)
S. grahami	Albrecht (1968)[d]
Pseudocrenilabrus philander	Ribbink (1975); Chan (1987); Chan and Ribbink (1990)
P. multicolor	W. Mrowka (personal communication)[c]
Acarichtys heckelii	Cichocki (1976)[e]
Haplochromis burtoni	Fernald and Hirata (1977)[d]
Cyrtocara eucinostomus	McKaye (1983)
Lamprologus brichardi[f]	Taborsky (1984a, 1985a)
L. callipterus	Sato (1988, 1991)
Oreochromis mossambicus	Baerends and Baerands van Roon (1950); Turner (1986b)
Pseudosimochromis curvifrons	Kuwamura (1987)
Simochromis diagramma	T. Sato (unpublished), in Kuwamura (1987)
Nannacara sp.	Römer (1993)
Pelvicachromis pulcher	Martin and Taborsky (1993)
Polycentridae	
Polycentrus schomburgkii	Barlow (1967)
Pomacentridae	
Abudefduf saxatilis	Albrecht (1969)
Chromis multilineata	Albrecht (1969)
C. cyanea	De Boer (1981)
C. atrilobata	P. Wirtz (personal communication)
C. dispilus	M. J. Kingsford (personal communication)[c]
Labridae	
Symphodus ocellatus	Soljan (1930a,b); Fiedler (1964); Taborsky (1984b, 1985b); Lejeune (1985); Warner and Lejeune (1985); Michel *et al.* (1987); Taborsky *et al.* (1987); Wernerus *et al.* (1987); van den Berghe *et al.* (1989); Wernerus (1989)

TABLE I (*Continued*)

Species[a]	References
S. roissali	Soljan (1931); Fiedler (1964); Helas *et al.* (1982a); Lejeune (1985); Warner and Lejeune (1985); Michel *et al.* (1987)
S. tinca	Fiedler (1964); Helas *et al.* (1982b); Lejeune (1985); Warner and Lejeune (1985); Michel *et al.* (1987); van den Berghe *et al.* (1989); Wernerus (1989)
S. mediterraneus	Fiedler (1964); Lejeune (1985)
S. melops	Dipper and Pullin (1979)[b]; Dipper (1981)[b]
S. cinereus	Michel and Voss (1982); Lejeune (1985); Michel *et al.* (1987)
S. melanocercus	Lejeune (1985); Warner and Lejeune (1985); Wernerus *et al.* (1987); Wernerus (1989)
S. rostratus	Lejeune (1985); Michel *et al.* (1987)
Thalassoma lunare	Robertson and Choat (1974)
T. bifasciatum	Warner *et al.* (1975); Warner and Robertson (1978); Warner and Hoffman (1980a,b)
T. cupido	Meyer (1977)
T. lucasanum	Warner and Hoffman (1980a); Warner (1982)
T. pavo	Michel *et al.* (1987); Wernerus (1989)
T. quinquevittatum	Colin and Bell (1991)
Tautoga onitis	Olla *et al.* (1977)
Halichoeres bivittatus	Warner and Robertson (1978)
H. maculipinna	Warner and Robertson (1978); Thresher (1979)
Tautogolaburs adspersus	Pottle and Green (1979a,b); Pottle *et al.* (1981)
Ctenolabrus rupestris	Hilldén (1981, 1984a,b)
Pseudolabrus celidotus	Jones (1981)
Coris julis	Lejeune (1982, 1985, 1987); Michel *et al.* (1987)
Centrolabrus exoletus	Michel *et al.* (1987)
Anampses twistii	Colin and Bell (1991)
Gomphosus varius	Colin and Bell (1991)
Scaridae	
Scarus croicensis	Warner and Downs (1977); Robertson and Warner (1978)
S. vetula	Clavijo (1983)
S. globius	Colin and Bell (1991)
S. psittacus	Colin and Bell (1991)
S. schlegeli	Colin and Bell (1991)
S. sordidus	Colin and Bell (1991)
Sparisoma radians	Robertson and Warner (1978)
Calotomus spinidens	Robertson *et al.* (1982)
Leptoscarus vaigiensis	Robertson *et al.* (1982)[b]
Acanthuridae	
Ctenochaetus striatus	Robertson (1983)
Zebrasoma scopas	Robertson (1983)[d]
Z. veliferum	Robertson (1983)[d]

TABLE I (*Continued*)

Species[a]	References
Gobiidae	
Coryphopterus nicholsi	Cole (1982)[b]
Pomatoschistus spp.	Miller (1984)[b]
P. microps	Magnhagen (1992)
Blenniidae	
Parablennius sanguinolentus	Santos (1985); Santos and Almada (1988)
Tripterygiidae	
Tripterygion tripteronotus	Wirtz (1978); Mohr (1986); de Jonge and Videler (1989)
T. delaisi	Wirtz (1978); De Jonge and Videler (1989)
T. melanurus	Mohr (1986)
Axoclinus carminalis	Thresher (1984)
Belontiidae	
Colisa chuna	Janzow (1982)
Ostraciidae	
Lactoria diaphana	Moyer (1984)
Batrachoididae	
Porichthys notatus	Brantley and Bass (1991); Bass (1992)

[a] Species for which *simultaneous* parasitic spawning (i.e., "sneaking," "streaking," "kleptogamy". . ., see text) has been documented. This table was compiled in collaboration with P. Wirtz, whose generous permission to use his files added nearly 15% of species included in this list.

[b] Reproductive parasitism not directly observed, but very likely.

[c] Unpublished information, communicated through Peter Wirtz (Univ. Madeira, P-9000 Funchal).

[d] Only territorial (i.e., bourgeois) males were observed to parasitize fertilizations.

[e] Cited in Gross (1984).

[f] I do not follow the taxonomic nomenclature suggested by Colombe and Allgayer (1985) for Tanganyika cichlids.

[g] In livebearers, reproductive parasitism is not simultaneous.

specifically dealing with parasitic spawning: most accounts were obtained from papers dealing with quite different aspects of fish biology. Without doubt, many examples have escaped my attention. The list should suffice, however, to demonstrate that kleptogamy is an extremely widespread phenomenon; it might even be viewed as "the rule rather than the exception." This compilation of existing evidence may hopefully encourage observers of this phenomenon to publish their evidence so that a future update of this part of the review could be much more representative.

It is obvious from Table I that some fish families are represented by a great number of species (e.g., wrasses: 21 species; cichlids: 14 species;

salmonids: 12 species), whereas others are either absent or only sparsely represented. The most important reason for this pattern is simply a difference in our knowledge about reproductive behavior of these different taxonomic groups. However, this is certainly not the only reason for variation between families. Damselfish, for example, are a well-studied group, but I found accounts of parasitic spawning in only five species of this group. It is nevertheless too early to draw conclusions from the taxonomic distribution of parasitic spawning shown in Table I. Our knowledge of reproductive behavior is too sporadic at present, especially with regard to parasitic spawning, which is a behavior that has often evolved to be extremely quick and cryptic.

I proceed in this chapter by (i) introducing the phenomenon of simultaneous parasitic spawning with some examples from the most-studied fish family in this respect, the Salmonidae; (ii) demonstrating specific adaptations that are linked with alternative mating tactics; (iii) comparing bourgeois and parasitic mating strategies; (iv) discussing the success of parasitic mating practices; (v) reviewing the present knowledge on the life histories of parasitic males; and (vi) emphasizing the role of females. Table II contains a list of examples on which my discussion of alternative mating tactics is based, in abbreviated and comprehensive form.

4. Alternative Mating Tactics in Salmon and Char: Some Case Studies

Kleptogamy is best understood in salmonids, partly because they have been intensively studied owing to their commercial importance (see Jones, 1959; Keenleyside, 1979; Hutchings and Myers, 1988). Reproductive competition in the genera *Salmo, Oncorhynchus,* and *Salvelinus* may lead to group spawning, with several males spawning with a single female and a dominance hierarchy that is strongly size dependent. Alternatively, large males defend the nesting territories of females and smaller surplus males dart in to steal fertilizations when the pair is spawning (e.g., Jones, 1959; Noltie, 1989; Sigurjonsdottir and Gunnarsson, 1989). In anadromous populations, these smaller males may either be anadromous as well and within the age range of dominant males, but in poorer condition (Noltie, 1989), or they may have spent a much shorter period in the ocean than other males (i.e., "jacks"; e.g., Hanson and Smith, 1967; Gross, 1984), or even be stream resident, much younger and smaller than the migratory territorial males (i.e., *parr;* e.g., Maekawa, 1983; Maekawa and Hino, 1986).

In *Oncorhynchus,* several types of accessory males may be present in one population. The smallest, nonmigratory males may then wait in close proximity to the spawning pair for a chance to participate in fertilization (see Keenleyside, 1979; Keenleyside and Dupuis, 1988). Alternatively,

TABLE II
SUMMARY OF SPECIFIC FEATURES CHARACTERIZING MALE PARASITIC
REPRODUCTION IN THE LISTED SPECIES

Family	Species	References
Female mimicry		
Salmonidae	*Oncorhynchus gorbuscha*	Keenleyside and Dupuis (1988); Noltie (1989)
Gasterosteidae	*Pungitius pungitius*	Morris (1952)
	Gasterosteus aculeatus	van den Assem (1967)
Cyprinodontidae	*Cyprinodon pecosensis*	Kodric-Brown (1986)
Centrarchidae	*Lepomis macrochirus*	Dominey (1980)
Percidae	*Etheostoma caeruleum*	Reeves (1907)
	E. olmstedi	Constantz (1979)
	E. perlongum	Shute *et al.* (1982)
Cichlidae	*Cyrtocara eucinostomus*	McKaye (1983)
	Pseudocrenilabrus philander	Chan (1987)
	Lamprologus callipterus	Sato (1988, 1991)
Polycentridae	*Polycentrus schomburgkii*	Barlow (1967)
Labridae	*Thalassoma lunare*	Robertson and Choat (1974)
	T. bisfasciatum	Warner and Robertson (1978)
	T. lucasanum	Warner (1982)
	T. pavo	Michel *et al.* (1987); Wernerus (1989)
	Symphodus ocellatus	Soljan (1930b); Fiedler (1964); Taborsky (1984b); Lejeune (1985); Michel *et al.* (1987); but see Taborsky *et al.* (1987)
	S. melops	Dipper and Pullin (1979); Dipper (1981)[a]
	S. cinereus and *S. tinca*	Lejeune (1985)[b]
	S. mediterraneus, S. roissali, and *Coris julis*	Lejeune (1985); Michel *et al.* (1987)
	Halichoeres maculipinna	Thresher (1979)
	Pseudolabrus celidotus	Jones (1981)
Scaridae	Several species	Choat and Robertson (1975)[a]
	Scarus croicensis	Robertson and Warner (1978)
	S. vetula	Clavijo (1983)
Tripterygidae	*Tripterygion tripteronotus*	Wirtz (1978)
Majority of males parasitic		
Cyprinidae	*Semotilus corporalis*	Ross (1983)
Poeciliidae	*Gambusia holbrooki*	Bisazza *et al.* (1989b)
Centrarchidae	*Lepomis macrochirus*	Gross (1982)
Labridae	*Thalassoma lucasanum*	Warner and Hoffman (1980a)

TABLE II (*Continued*)

Family	Species	References
	Symphodus ocellatus	Warner and Lejeune (1985); Taborsky *et al.* (1987)
	S. roissali and *S. tinca*	Warner and Lejeune (1985)
Relatively little reproductive effort of bourgeois males to be parasitized upon		
Catostomidae	*Catostomus commersonii, Moxostoma duquesnei,* and *aureolum*	Reighard (1920)
	M. valenciennesi	Jenkins and Jenkins (1980)
Mochokidae	*Syndontis multipunctatus*	Schrader (1993)
Percidae	*Etheostoma caeruleum*	Reeves (1907); Winn (1958a,b)
	E. exile	Winn (1958a)
	E. spectabile	Winn (1958b)
	Hadropterus maculatus	Petravicz (1938)
	Percina caprodes	Winn (1958a)
Cichlidae	*Pseudocrenilabrus philander*	Ribbink (1975); Chan (1987)
	Pseudosimmochromis curvifrons	Kuwamura (1987)
Labridae	*Thalassoma* spp.	Warner and Robertson (1978); Warner and Hoffman (1980b); Warner (1982)
Parasitic males may also eat eggs		
Salmonidae	*Salvelinus malma miyabei*	Maekawa and Hino (1990)
Gasterosteidae	*Pungitius pungitius*	Morris (1952)
Cichlidae	*Pseudocrenilabrus philander*	Ribbink (1971); but see Chan (1987)
	Cyrtocara eucinostomus	McKaye (1983)
	Lamprologus brichardi	Taborsky (1984a, 1985a)
Gobiidae	*Coryphopterus nicholsi*	Cole (1982)
Testes relatively larger in parasitic than in bourgeois males		
Centrarchidae	*Lepomis macrochirus*	Dominey (1980); Gross and Charnov (1980); Gross (1982)
	Lepomis megalotis	Jennings and Philipp (1992a)
Labridae	*Thalassoma lunare*	Robertson and Choat (1974)
	Halichoeres bivittatus, H. maculipinna, and *H. pictus*	Warner and Robertson (1978)
	Symphodus roissali	Warner and Lejeune (1985)
	S. ocellatus	Warner and Lejeune (1985); own data (see fig. 3)
Scaridae	Several species	Choat and Robertson (1975)[c]
	Scarus croicensis	Robertson and Warner (1978)

TABLE II (*Continued*)

Family	Species	References
	Sparisoma radians	Robertson and Warner (1978)
Gobiidae	*Coryphopterus nicholsi*	Cole (1982)[d]
Blenniidae	*Parablennius sanguinolentus*	Santos and Almada (1988)
Tripterygidae	*Tripterygion tripteronotus*	Finck (1985); Mohr (1986); de Jonge and Videler (1989)
	T. delaisi	Finck (1985); Mohr (1986)
Batrachoididae	*Porichthys notatus*	Bass and Andersen (1991); Bass (1992)
Species with information on rates of male reproductive parasitism		
Cyprinodontidae	*Cyprinodon nevadansis*	Soltz (1974)
Poeciliidae	*Poecilia occidentalis*	Constantz (1975)
	P. reticulata	Endler (1987)
	Xiphophorus nigrensis	Zimmerer and Kallmann (1989)
Centrarchidae	*Lepomis macrochirus*	Gross (1982)
Percidae	*Etheostoma caeruleum*	Reeves (1907)
Cichlidae	*Pseudocrenilabrus philander*	Chan (1987)
	Pelvicachromis pulcher	Martin and Taborsky (1993)
Labridae	*Thalassoma bifasciatum*	Warner *et al.* (1975)
	T. pavo	Wernerus (1989)
	Coris julis	Lejeune (1985, 1987)
	Symphodus ocellatus, S. tinca, and *S. melanocercus*	Lejeune (1985); Warner and Lejeune (1985); Wernerus (1989)
	S. roissali	Lejeune (1985); Warner and Lejeune (1985)
	S. cinereus	Lejeune (1985)
Success dependent on proximity at spawning		
Salmonidae	*Oncorhynchus keta*	Schroder and Duker (1979); Schroder (1981)
Cyprinidae	*Semotilus corporalis*	Ross and Reed (1978)
Catostomidae	*Catostomus commersonii* and *Moxostoma aureolum*	Reighard (1920)
Success of male reproductive parasitism proved		
Salmonidae	*Oncorhynchus keta*	Schroder and Duker (1979); Schroder (1981, 1982)
	O. nerka	Chebanov *et al.* (1983)
	Salvelinus malma	Maekawa and Onozato (1986)
	Salmo salar	Hutchings and Myers (1988); Jordan and Youngson (1992)

<div style="text-align: center;">TABLE II (Continued)</div>

Family	Species	References
Gasterosteidae	*Gasterosteus aculeatus*	Rico *et al.* (1992)
Poeciliidae	*Xiphophorus nigrensis*	Zimmerer and Kallmann (1989); Ryan *et al.* (1990, 1992)
Centrarchidae	*Lepomis macrochirus*	Gross and Dueck (1989)
Cichlidae	*Lamprologus brichardi*	M. Taborsky (unpublished data) (see text)
	Pelvicachromis pulcher	Martin and Taborsky (1993)
Interspecific male reproductive parasitism		
Cichlidae	*Lamprologus brichardi* and *Juliodochromis ornatus*	M. Taborsky (unpublished data)
Labridae	*Pseudolabrus fucicola* and *P. celidotus*	Ayling (1980)
	Cirrhilabrus temminckii and *C. cyanopleura*	Moyer (1981); Bell (1983)
Genetic predisposition of reproductive tactic		
Salmonidae	*Oncorhynchus kisutch*	Iwamoto *et al.* (1983)
Poeciliidae	*Poeciliopsis occidentalis*	Constantz (1975)
	Xiphophorus nigrensis	Zimmerer and Kallmann (1989); Ryan *et al.* (1990, 1992)
Centrarchidae	*Lepomis macrochirus*	Dominey (1980); Gross (1982) (see text)
Cichlidae	*Pelvicachromis pulcher*	Martin and Taborsky (1993)
Conditional realization of reproductive tactic		
Salmonidae	*Oncorhynchus gorbuscha*	Noltie (1989)
	O. nerka	Foote (1990)
	Salvelinus alpinus	Sigurjonsdottir and Gunnarson (1989)
	Thymallus arcticus	Beauchamp (1990)
Catostomidae	*Catostomus commersonii* and *Moxostoma aureolum*	Reighard (1920)
Gasterosteidae	*Pungitius pungitius*	Morris (1952)
Cyprinodontidae	*Cyprinodon pecosensis*	Kodric-Brown (1981, 1986)
	C. macularius	Matsui (unpublished), cited in Kodric-Brown (1981)
Poeciliidae	*Poeciliopsis occidentalis*	Constantz (1975)
	Poecilia latipinna	Farr *et al.* (1986)
	Xiphophorus nigrensis	Zimmerer and Kallmann (1989)
Cichlidae	*Lamprologus brichardi*	Taborsky (1984a, 1985a)
	Pseudocrenilabrus philander	Chan (1987)
Polycentridae	*Polycentrus schomburgkii*	Barlow (1967)

<div style="text-align: right;">(continued)</div>

TABLE II (*Continued*)

Family	Species	References
Labridae	*Thalassoma lucasanum*	Warner and Hoffman (1980a); Warner (1982)
	T. bifasciatum	Warner (1982)
	Symphodus melanocercus	Wernerus (1989)
Gobiidae	*Coryphopterus nicholsi*	Cole (1982)
Tripterygidae	*Tripterygion tripteronotus*	Wirtz (1978); Mohr (1986); de Jonge and Videler (1989)

Female choice of bourgeois males

Family	Species	References
Salmonidae	*Salmo salar*	Jones (1959)
Poeciliidae	*Gambusia affinis*	Hughes (1985)[e]
	Xiphophorus nigrensis	Zimmerer and Kallmann (1989); Ryan et al. (1990)
Serranidae	*Serranus fasciatus*	Petersen (1987)
Percidae	*Etheostoma caeruleum*	Reeves (1907)
Cichlidae	*Pseudocrenilabrus philander*	Chan (1987)
	Pelvicachromis pulcher	E. Martin (personal communication)
Pomacentridae	*Chromis cyanea*	De Boer (1981)
Labridae	*Thalassoma bifasciatum*	Warner et al. (1975); Warner and Hoffman (1980b)
	Symphodus ocellatus	van den Berghe et al. (1989); Wernerus (1989); own data (see text)
	S. tinca	van den Berghe et al. (1989); Wernerus (1989)
Tripterygidae	*Tripterygion tripteronotus*	Wirtz (1978)

Interspecific egg dumping

Family	Species	References
Lepisosteidae with Centrarchidae	*Lepisosteus osseus* at *Micropterus dolomieui*	Goff (1984)
Cyprinidae	*Nocomis cornutus, N. rubellus,* and *Campostoma anomalum* at *N. micropogon*	Reighard (1943)
	Notropis lutipinnis and *N.* spp. at *N. leptocephalus*	Wallin (1989, 1992)
Cyprinidae with Serranidae	*Pungtungia herzi* at *Siniperca kawamebari*	Baba et al. (1990)
Cyprinidae with Centrarchidae	*Notemigonus crysoleucas* at *Lepomis punctatus*	Carr (1946)
	Notemigonus crysoleucas at *Micropterus salmoides*	Kramer and Smith (1960)
	Notropis umbratilis at *Lepomis cyanellus*	Hunter and Hasler (1965)[f]

TABLE II (*Continued*)

Family	Species	References
	Notropis ardens at *Lepomis megalotis*	Steele (1978)[g]; Steele and Pearson (1981)
Catostomidae with Centrarchidae	*Erimyzon sucetta* at *M. salmoides*	Carr (1942)
Mochokidae with Cichlidae	*Synodontis multipunctatus* at cichlid mouthbrooders	Sato (1986); Schrader (1993)

[a] Fertilization stealing not directly observed, but very likely.

[b] Only few small males may resemble the female color pattern.

[c] Kleptogamy not mentioned.

[d] Small and probably parasitic males are also weakly territorial.

[e] That is, choice of *large* males.

[f] Authors give information on 22 examples of interspecific nest utilization in cyprinids.

[g] Author gives information on 17 examples of interspecific nest utilization in cyprinids.

they may wait downstream of a pair in a linear dominance hierarchy and dart into the nest during oviposition to release sperm (Hutchings and Myers, 1988). Gross (1984) described how in coho salmon (*O. kisutch*) these smallest males would hide at some distance from a territorial male, but would still reach similar distances to females when releasing sperm as do large, "fighting" males. Medium-sized, anadromous salmon males may defend places near a nest (Gross, 1984), whereas those that are nearly as large as dominant males wait adjacent to the spawning pair and acquire matings through fighting (Hutchings and Myers, 1988).

We may ponder over the reproductive success of parasitic males. As early as 1836, Shaw demonstrated that sperm of male salmon parr (i.e., young, stream resident males) is capable of fertilizing eggs (see also Kazakov, 1981). Since then it has been repeatedly demonstrated that eggs fertilized by them produce viable offspring (Jones and King, 1950a; Thorpe and Morgan, 1980). Jones and King (1952a,b) sterilized large males and observed that parasitically spawning male parr shed sperm. More recently, the proportion of young sired by large and parasitic males, respectively, has been studied with the help of electrophoretic analyses of genetically polymorphic enzyme systems. In *Oncorhynchus keta*, single subordinate males were found to fertilize approximately one-quarter of the eggs deposited by a female when spawning in competition with a large male (weight ratio 0.75 : 1). Two subordinate males fertilized 47% of the eggs deposited into a single nest (Schroder, 1981). In one experiment with three male and one female *O. nerka*, Chebanov *et al.* (1983) demonstrated that the two subordinate, parasitic males together sired 10% of the offspring. In

Salvelinus malma miyabei, Maekawa and Onozato (1986) maintained that nearly 17% of the eggs were fertilized by a subordinate male when experimentally placed with a spawning pair. However, when only cases with "apparent sperm release" (see Table III of Maekawa and Onozato, 1986) are considered and the median is calculated instead of the arithmetic mean, which seems more appropriate, only 7% of the eggs were on average fertilized by the small, kleptogamic males. Hutchings and Myers (1988) measured the proportion of eggs fertilized by varying numbers of *Salmo salar* parr that competed with dominant, anadromous males. Single male parr fertilized only about 5% of the eggs in a nest, but when 20 parr were simultaneously shedding sperm with one anadromous male, nearly a quarter of the eggs deposited by a female were fertilized by these subordinate males.

The progeny of stream resident male Atlantic salmon parr develop faster than those of sea-run males that have themselves matured at a later stage (Thorpe and Morgan, 1978, 1980). The age of first spawning is heritable in this salmon (Thorpe *et al.,* 1983; see also Schaffer and Elson, 1975), which may result in a predisposition of the reproductive tactics of males. Glebe *et al.* (1978) inferred from their (unpublished) data that there are both genetic *and* environmental components to the expression of precocious sexual maturity in this species. Bailey *et al.* (1980) found evidence for important maternal (i.e., nongenetic) and environmental effects of developmental characters. Lundqvist and Fridberg (1982) also demonstrated a strong environmental influence on the ontogeny of *Salmo salar,* and hence on the expression of male reproductive behavior. Faster-growing males become precocious in this species (Dalley *et al.,* 1983; see also Alm, 1959; Schiefer, 1971).

In *Oncorhynchus kisutch,* there is a genetic component to the probability that a male will mature at 3 years of age and develop a "hooknose," which is a weapon in intrasexual conflicts, as opposed to maturing at 2 years and remaining small (Iwamoto *et al.,* 1983). The two different reproductive tactics exhibited by these "jack" and "hooknose" males were suggested to be about equally successful and are maintained by disruptive selection, as medium-sized males do not obtain good spawning positions neither when fighting nor when trying to steal fertilizations (Gross, 1984, 1985). Disruptive selection may also operate in *Oncorhynchus nerka,* in which Foote and Larkin (1988) observed that anadromous and stream resident forms mated assortatively and preferentially with members of the same form. Only if nonanadromous males could not find matching females did they try to steal fertilizations by approaching pairs of anadromous fish. In *Oncorhynchus gorbuscha* and *Salvelinus alpinus,* on the contrary, it is rather conditional whether a male guards or tries to

TABLE III
SUMMARY OF REPRODUCTIVE SYSTEMS THAT ARE CHARACTERIZED BY
ASSOCIATIONS, COOPERATIVE BEHAVIOR, OR ALLOPARENTAL CARE

Family	Species	References
Satellites stay near defended sites, not explicitly tolerated		
Salmonidae	*Oncorhynchus nerka*	McCart (1970) cited in Keenleyside (1979, p. 104)
Cyprinidae	*Semotilus corporalis* (*small males*)	Ross and Reed (1978); Ross (1983)
	Zacco temmincke	Katano (1992)
Centrarchidae	*Lepomis macrochirus* (female mimics)	Dominey (1981); Gross (1982)
Cichlidae	*Sarotherodon alcalicus*	Albrecht (1968)
Satellites tolerated by dominant males		
Cyprinidae	*Semotilus corporalis*	Ross and Reed (1978); Ross (1983)
	Notropis leptocephalus	Wallin (1989)
Mochokidae	*Synodontis multipunctatus*	Schrader (1993)[a]
Cyprinodontidae	*Cyprinodon macularis*	Barlow (1961)
	C. pecosensis	Kodric-Brown (1977, 1981, 1986)
Cichlidae	*Apistogramma borelli*	Burchard (1965)[a]
	Tropheus irsacae	Kuwamura (1986)[b]
	Eretmodus cyanostictus	Kuwamura (1986)[b]
	Lamprologus furcifer	Yanagisawa (1987)
	L. callipterus (female mimics)	Sato (1988)
	Telmatochromis temporalis	Mboko (1989)
	Pelvicachromis pulcher	Martin and Taborsky (1993)[a]
Embiotocidae	*Micrometrus minimus*	Warner and Harlan (1982)
Pomacentridae	*Amphiprion akallopisos*	Fricke (1979)
Labridae	*Symphodus ocellatus*	Soljan (1930a); Fiedler (1964); Taborsky (1984b, 1985b); Warner and Lejeune (1985); Taborsky *et al.* (1987)
	S. roissali	Soljan (1931); Fielder (1964); Lejeune (1985)
	S. tinca	Lejeune (1985)
	Halichoeres maculipinna	Thresher (1979)
	Coris julis	Lejeune (1985)
Blenniidae	*Parablennius sanguinolentus*	Santos (1985); Santos and Almada (1988)
Tetraodontidae	*Canthigaster rostrata*	Sikkel (1990)
Ostraciidae	*Lactoria fornasini*	Moyer (1979)
Joint defense of spawning territory		
Cichlidae	*Sarotherodon alcalicus*	Albrecht (1968)

TABLE III (*Continued*)

Family	Species	References
	Pelvicachromis pulcher	Martin and Taborsky (1993)[a]
Pomacentridae	*Amphiprion akallopisos*	Fricke (1979)
Labridae	*Symphodus ocellatus*	Fiedler (1964); Taborsky (1984b, 1985b); Warner and Lejeune (1985); Taborsky *et al.* (1987)
	S. roissali	Lejeune (1985)
	S. tinca	Lejeune (1985)
	Halichoeres maculipinna	Thresher (1979)
Blenniidae	*Parablennius sanguinolentus*	Santos (1985, 1986); Santos and Almada (1988)
Joint nest building		
Cyprinidae	*Nocomis micropogon*	Reighard (1943)
	Notropis leptocephalus	Wallin (1989)
Joint courtship		
Catostomidae	*Moxostoma carinatum*	Hackney *et al.* (1967)
Percidae	*Etheostoma blennioides*	Fahy (1954)
Joint spawning		
Salmonidae	*Salvelinus namaycush*	Royce (1951)
Cyprinidae	*Notropis lutipinnis*	Wallin (1989)
Catostomidae	*Catostomus commersonii*	Reighard (1920)
	Hypentelium nigricans	Raney and Lachner (1946)
	Moxostoma aureolum	Reighard (1920)
	M. duquesnei	Bowman (1970)
	M. carinatum	Hackney *et al.* (1967); Hackney (1993, cited in Jenkins (1970, p. 245)
	M. macrolepidotum	Jenkins (1970)
	M. erythrurum	Jenkins (1970); Kwak and Skelly (1992)
	M. valenciennesi	Jenkins (1970); Jenkins and Jenkins (1980)
	Erimyzon oblongus	Page and Johnston (1990)
Joint broodcare (intra- and interspecific)		
Cyprinidae	*Hybopsis biguttata* with *Notropis cornutus*	Hankinson (1920)[c]
Cichlidae	*Cichlasoma citrinellum*	McKaye and McKaye (1977)
	Etroplus surantensis	Ward and Wyman (1975, 1977)
	Leptotilapia inuine	P. V. Loiselle (unpublished)[a], cited in McKaye and McKaye (1977)
	Tilapia rendalli	Ribbink *et al.* (1981)
Bagridae with Cichlidae	*Bagrus meridionalis* with *Copadichromis*	McKaye (1985); McKaye *et al.* (1992)

TABLE III (*Continued*)

Family	Species	References
	pleurostigmoides, *Ctenopharynx pictus,* and *Rhamphochromis* sp.	
Cottidae	*Hemilepidotus hemilepidotus*	DeMartini and Patten (1979)
Alloparental care: (a) intraspecific adoptions		
Cichlidae	*Apistogramma trifasciatum*	Burchard (1965)[a]
	A. borellii	Lorenzen (1989); Dieke (1993)
	Tilapia rendalli (?)	Burchard (1967)
	T. mariae	Burchard (1967); Sjölander (1972)
	Chromidotilapia guentheri	Sjölander (1972)
	Pelvicachromis pulcher	Sjölander (1972); E. Martin (personal communication)[a]
	Herotilapia multispinosa	Baylis (1974)[a]
	Cichlasoma citrinellum	McKaye and McKaye (1977)
	C. longimanus	McKaye and McKaye (1977)
	C. nicaraguense	McKaye and McKaye (1977)
	C. nigrofasciatum	Wisenden and Keenleyside (1992)
	Neetroplus nematopus	McKaye and McKaye (1977)
	Etroplus maculatus	G. W. Barlow (unpublished),[a] cited in McKaye and McKaye (1977)
	Perissodus microlepis	Yanagisawa and Nshombo (1983); Yanagisawa (1985a)
	Xenotilapia flavipinnis	Yanagisawa (1985b, 1986)
Pomacentridae	*Acanthochromis polyacanthus*	Thresher (1985)
Alloparental care: (b) mixed-species broods		
Bagridae with Cichlidae	*Bagrus meridionalis* cares for *Copadichromis pleurostigmoides, Ctenopharynx pictus,* and *Rhamphochromis* sp.	McKaye and Oliver (1980); McKaye (1985)
Cichlidae	*Tilapia rendalli (?)* and *T. mariae*	Burchard (1967)
	T. mariae and *T. zillii*	Sjölander (1972)
	Cichlasoma citrinellum cares for *Neetroplus nematopus*	McKaye and McKaye (1977)
	C. longimanus cares for *C. citrinellum*	McKaye and McKaye (1977)

(continued)

TABLE III (*Continued*)

Family	Species	References
	C. nicaraguense cares for *C. longimanus*	McKaye and McKaye (1977)
	N. nematopus cares for *C. citrinellum*	McKaye and McKaye (1977)
	12 *Haplochromis* spp. and *Serranochromis robustus* care for fry of 15 diff. species	Ribbink (1977); Ribbink *et al.* (1980)
	Lamprologus elongatus cares for *Perissodus microlepis*	Yanagisawa and Nshombo (1983)
Cichlidae with Mochokidae	10 mouthbrooding spp. care for *Synodontis multipunctatus*	Brichard (1979); Sato (1986); Schrader (1993)
Alloparental care: (c) pure heterospecific broods		
Esocidae with Centrarchidae	*Esox niger* cares for *Lepomis gibbosus*	Shoemaker (1947)
Cichlidae	*Cichlasoma nicaraguense* cares for *C. dovii*	McKaye (1977)
Alloparental care: (d) nest takeovers		
Cyprinidae	*Pimephales promelas*	Unger and Sargent (1988)[a]
Percidae	*Etheostoma olmstedi*	Constanz (1979, 1985)
Pomacentridae	*Amphiprion clarkii*	Yanagisawa and Ochi (1986)
Labridae	*Symphodus ocellatus*	Taborsky *et al.* (1987)
Gobiidae	*Padogobius martensi*	Bisazza *et al.* (1989a)
Hexagrammidae	*Ophiodon elongatus*	Jewell (1968)
Cottidae	*Hemilepidotus hemilepidotus*	DeMartini and Patten (1979)
	Cottus gobio	Bisazza and Marconato (1988)[a]
Harpagiferidae	*Harpagifer bispinis*	Daniels (1978, 1979)
Alloparental care: (e) egg stealing		
Gasterosteidae	*Gasterosteus aculeatus*	van den Assem (1967); Wootton (1971); Li and Owings (1978b)[a]; Sargent and Gebler (1980)[a]
Cichlidae	*Pseudocrenilabrus multicolor*	Mrowka (1987b)[a]
Alloparental care: (f) broodcare helpers		
Cichlidae	*Lamprologus brichardi*	Kalas (1976)[a]; Taborsky and Limberger (1981); Taborsky (1984a, 1985a); Hert (1985)[a]; Taborsky *et al.* 1986[a]; von Siemens (1990)[a]

TABLE III (*Continued*)

Family	Species	References
	L. pulcher	Taborsky and Limberger (1981)[a]
	L. savoryi[d]	Taborsky and Limberger (1981); Kondo (1986); Abe (1987)
	Julidochromis ornatus	Kalas (1976)[a]; Taborsky and Limberger (1981)[a]
	J. regani	Taborsky and Limberger (1981)[a]
	J. marlieri	Taborsky and Limberger (1981); Yamagishi (1988)
Belontiidae	*Betta brownorum[d]*	Witte and Schmidt (1992)[a]
	B. persephone[d]	Witte and Schmidt (1992)[a]

[a] Aquarium observations only.

[b] Sex of conspecifics that are tolerated within territories is unclear.

[c] Division of labor: *H. biguttata* builds nest and *N. cornutus* guards it.

[d] As yet only cooperative defense of breeding territory observed.

steal fertilizations (Noltie, 1989; Sigurjonsdottir and Gunnarson, 1989). Essential conditions include relative male size and conditions, and male density.

5. Female Mimicry

Kleptogamic males often resemble females in their appearance. These males have been called "pseudofemales" (e.g., Morris, 1952), "female mimics" (e.g., Dominey, 1980), or "transvestite males" (Dipper, 1981). As early as 1907, Reeves observed that bright, territorial male darters sometimes mistake small, drab males for females. Subsequently, mimetic resemblance of kleptogamic males to females has been observed in more than 30 species belonging to 10 different fish families (see Table II).

These mimetic males may resemble females morphologically (including color; e.g., Kodric-Brown, 1986), behaviorally (e.g., Constantz, 1979), or both (e.g., Warner and Robertson, 1978). They may be the same age as territory owners (e.g., Morris, 1952; Dominey, 1980; and in Trivers, 1985; but see Gross, 1982) or younger (e.g., Wirtz, 1978; Mohr, 1986), and they may be "initial phase" individuals (see earlier) that may later change into "terminal colour phase" in sex-changing wrasses (e.g., Jones, 1981; Warner, 1982). They may roam about in small schools or loose aggregations with females (e.g., Robertson and Choat, 1974), or stay in the vicinity of nests (e.g., Keenleyside and Dupuis, 1988) or even within bright males'

territories as unrecognized reproductive parasites (e.g., Thresher, 1979). The feature they all have in common is that they "scrounge by deception" (Barnard, 1984).

In most reported cases of female mimicry it is unclear, however, whether bourgeois males really mistake parasitic males or females. In the ocellated wrasse, *Symphodus ocellatus,* the resemblance between parasitic males and females has been stressed repeatedly (see Table II for references). But detailed behavioral observations revealed that nest owners usually treat females and parasitic males very differently, with regard to both, behavioral qualities and quantities (Taborsky *et al.,* 1987).

6. *Alternative Tactics When Fertilization Is Internal*

In species with internal fertilization, kleptogamy is sequential instead of simultaneous and not so much a matter of escaping recognition by a dominant, bourgeois male. Rather, small- or medium-sized males mate more or less *forcefully* instead of courting females, as the largest males of a population do (e.g., Liley, 1966; Farr, 1980a; Hughes, 1985; Heinrich and Schröder, 1986; Ryan and Causey, 1989). In *Gambusia affinis* and *G. holbrooki,* the vast majority of copulations may even result from males forcibly inseminating females (Bisazza *et al.,* 1989b), and the majority of females of a South Carolina population of mosquito fish had been multiply inseminated (Chesser *et al.,* 1984). Table I contains more examples of poeciliid fish with alternative tactics, that is, courting *and* forced copulations (see also Constantz, 1984, for a discussion of sperm competition in poeciliids).

7. *A Comparison between "Bourgeois" and Parasitic Males*

a. Numbers. Often brightly colored, aggressive individuals constitute the vast majority of reproductively active males (e.g., Albrecht, 1969). In other systems, however, males specialized in parasitic spawning may make up a much larger proportion of reproductive individuals than the more conspicuous males that monopolize some resources (e.g., Ross, 1983). In a population of bluegill sunfish, for example, 85% of the males parasitized the effort of the 15% of males defending territories and providing parental care (Gross, 1982). With regard to *number,* parasitic males could then be viewed as the *primary* reproductive form in these species, even though the occurrence of kleptogamy relies on the existence of some individuals whose effort can be parasitized upon.

b. Costs. Male effort may be behavioral, morphological, and/or physiological. Behaviorally, there is a wide range of possibilities for expenditure on mate recruitment and paternal care. Bourgeois males may defend a territory, spawning place, or "nest," invest in courtship, build or dig to

prepare a spawning site, and care for eggs, larvae, and young. These activities may increase the risk of predation because of conspicuous behavior and/or reduced vigilance. On the other hand, there is only little effort by bourgeois males that can be exploited by kleptogamic males in the mochokid catfish *Synodontis multipunctatus* (Schrader, 1993), in some Percidae (e.g., Winn, 1958a,b), cichlids (e.g., Kuwamura, 1987), and wrasses (e.g., Warner and Hoffman, 1980b). In Catostomidae, for example, often pairs of males spawn with a single female (see the following), but there may be additional males trying to get as close to the female as possible and interfere with the spawning trio (Reighard, 1920), thereby presumably "attempting to sneak fertilizations" (Page and Johnston, 1990). The superior position of the two males adjoining the female on either side of her at spawning may be only a matter of the sequence of making contact with a ripe female, and not represent an expensive investment.

Male effort may also be morphological, for example, involving a change of color or specific body structure. When males of Mediterranean wrasses become reproductively territorial they show a bright color pattern (Fiedler, 1964; Michel *et al.*, 1987). Such morphological changes are probably associated with physiological costs (see Frischknecht, 1993), and the increased conspicuousness will probably increase the risks of predation, as exemplified in three-spined sticklebacks (Semler, 1971; Moodie, 1972) and guppies (e.g., Endler, 1980). A bright nuptial coloration of bourgeois males is also known from other wrasses (e.g., Robertson and Hoffman, 1977; Warner and Robertson, 1978; Colin and Bell, 1991), and from other fish taxa, like shiners and sunfish (Steele, 1978), darters (Petravicz, 1938), cichlids (Voss, 1980), damselfish (Thresher and Moyer, 1983), parrotfish (Colin and Bell, 1991), Hexagrammidae (DeMartini, 1985), and Triperygidae (Wirtz, 1978). Dichromatism in marine fish was reviewed by Thresher (1984). Other temporal features developing toward spawning include morphological structures like the kypes and humps in salmon (e.g., Gross, 1985; Keenleyside and Dupuis, 1988), bright nuptial humps in blennies (e.g., on the head of male Mediterranean *Salaria pavo*, Fishelson, 1963, and my own observations), and breeding tubercles, for example, in suckers ("pearl organs", Reighard, 1920) and cyprinids (Wedekind, 1992). Internal morphological and physiological changes of reproductive males that occur in connection with sound production have been found in the plainfin midshipman (*Porichthys notatus*; e.g., Bass, 1992).

The physiological costs incurred by bourgeois males may be expressed, for example, simply by a difference in growth from other conspecifics. In the Mediterranean wrasse *Symphodus ocellatus*, for example, a proportion of males refrain from reproduction in a given season (Taborsky *et al.*,

1987) and thereby grow during that period while all reproductive males, territorial or parasitic, stagnate in size (Fig. 2). These nonreproductives are very probably the territorial males in subsequent seasons (M. Taborsky, unpublished evidence). In the closely related *S. tinca,* van den Berghe (1992) showed that nesting males had four times greater costs than nonnesting males during a reproductive season, as measured by weight changes.
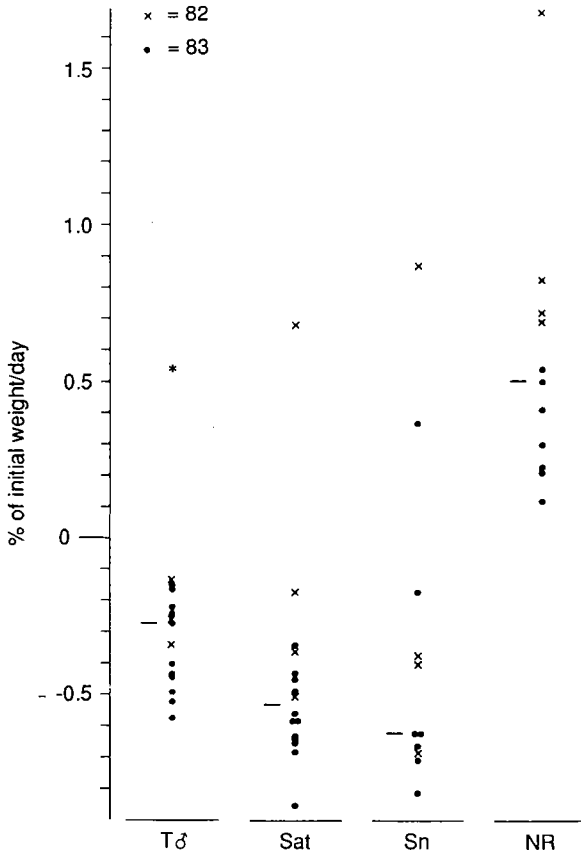

FIG. 2. The change of weights of different types of males during two separate spawning seasons (1982 and 1983) in the Mediterranean wrasse *Symphodus ocellatus* (location: STARESO, Calvi, Corsica). T-male, territorial (bourgeois) male; Sat, satellite; Sn, sneaker (both parasitizing the reproductive effort of T-males by simultaneously spawning with them); NR, nonreproductive males, which do not show any reproductive activities in a specific year (*i.e.,* season). Each dot or cross represents one individual. Medians are marked with a horizontal dash.

In longear sunfish, kleptogamic males have higher gonad/body weight ratios and slower somatic growth rates than bourgeois males.

The costs of generating all these behavioral or morphological structures may be parasitized upon by kleptogamic males, which usurp the effort of bourgeois males and their attractiveness for females and fertilize (or sometimes eat; see Table II) a proportion of the eggs spawned by these conspecifics. Parasites may, however, have considerable costs themselves, as exemplified in *S. ocellatus*. In this species, as a result of their reproductive activities, parasitic males have a similar reduction in growth as that of bourgeois, territorial males (see Fig. 2).

The reproductive costs of parasitic males are even more prominent when it comes to gonadal investment. They cannot, obviously, usurp the gonadal effort of conspecific males. Rather, they should put their own effort primarily into the production of sperm, and hence also into large and prolific testes. A higher gonad/body weight ratio is therefore expected in parasitic than in bourgeois males. This is exactly what is found in *S. ocellatus* (Fig. 3) and in other labroid fish with both types of males, bourgeois and kleptogamic (e.g., Robertson and Choat, 1974; Choat and Robertson 1975; Warner and Downs, 1977; Robertson and Warner, 1978; Warner and Robertson, 1978; Warner and Lejeune, 1985; see also Table II). It has also been demonstrated in the North American bluegill sunfish, in which "female mimics" have a gonad/body weight ratio more than twice that of territorial males (Dominey, 1980), and the smaller "sneakers" even exceed the parental male ratio by fourfold (Gross, 1982). See Table II for examples from other fish families.

The behavioral costs of kleptogamic as compared to bourgeois males are probably low. The only effort they share with the latter is the behavior immediately leading to fertilizations. Apart from that, they need to obtain a good position to interfere in spawning and they may need to interact aggressively with other parasitic males and submissively with bourgeois males. There are very few data with which to compare these costs with the costs of monopolizing males. Time expenditure has been shown to be higher in territorial than in sneaker males in *S. ocellatus,* which means that the latter spend more than twice the time feeding than do the territory owners (Taborsky *et al.,* 1987). Energetically, however, there does not seem to be that much difference between sneakers and territorial males, (see earlier; Fig. 2).

I do not know of any published data that allow a quantitative comparison of the predation risk of bourgeois and kleptogamic male fish. However, the risk of being killed by larger conspecifics may be considerable for small males aiming to share in reproduction. Of 49 yearling male chinook salmon (*Oncorhynchus tshawytscha*) found dead on a spawning ground,
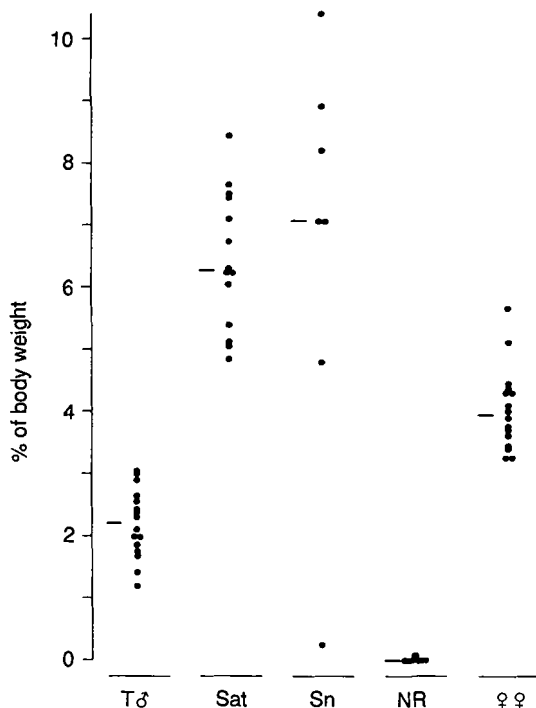
FIG. 3. Relative gonad mass of male and female *Symphodus ocellatus* during the reproductive season of 1983. Location, symbols, and abbreviations as in Fig. 1.

21 had been killed by adult conspecifics, probably by males (Gebhards, 1960).

c. *Success*. Success rates of males may be measured at different levels. The simplest way is to determine the proportions of spawnings that are parasitized. This has been done for 13 species belonging to five different families (Table II, live bearers excluded). For a proper comparison, the number of fertilization attempts should be measured for both types of males on an individual basis. In the cichlid *Pseudocrenilabrus philander*, Chan (1987) found that nearly 10% of spawnings involved attempted fertilizations by parasitic males, and he suggested that the fertilization success of these males was only 6.35% of that of territory owners. He did not take account of the competition of sperm of territorial and parasitic males but assigned all eggs laid while a parasite was present and trying to fertilize them to this male.

Most information on rates of fertilization attempts by bourgeois and

parasitic males exists in wrasses. In *Coris julis,* about 30% of terminal phase male spawnings were interfered with by initial phase parasites (average number of simultaneously spawning parasites was 1.8; Lejeune, 1987). On an individual basis, terminal phase, territorial males spawned nearly 8 times more often than parasites did. Lejeune (1985) observed rates of attempted fertilizations by territorial and kleptogamic males in six Mediterranean species. I calculated from his figures that, in *Symphodus cinereus* and *S. melanocercus,* on an individual basis territorial males spawned about 10 times more often than parasitic males tried to steal fertilizations. Surprisingly, Warner and Lejeune (1985), who observed the same population of *S. melanocercus* at the same location and time, recorded only one parasitic fertilization attempt out of 269 observed spawnings. In *S. roissali,* Lejeune's (1985) measure gave a ratio of 1 fertilization attempt per parasite to 10 attempts per territory owner when all males were considered, that is, regardless of whether they were reproductively active during the observation period or not. When only sexually active males around the nest are considered, however, the fertilization attempts of parasitic and territorial males occurred at a ratio of 1 : 3. In *S. ocellatus* this ratio was about 1 : 6, whereas in *S. tinca* the ratio depended on the size of kleptogamic males. Small parasitic males made three times fewer fertilization attempts than territory owners, whereas medium-sized parasitic males made on average nearly three times more. These fertilization attempts of medium-sized or small males in the nests of territory owners were either interferences with nest owners' spawnings or separate spawnings.

To estimate male success when more than one male is involved in spawning, each fertilization attempt of a male has been divided by the total number of males that have participated in a specific spawning (termed "pair spawning equivalents" by Warner *et al.,* 1975). If one territorial and two parasitic males are involved, for example, each of them is assigned one-third fertilization. This is perhaps not a very good estimate of fertilization success because of differences between the males with regard to position, timing, and the amount (and perhaps quality) of released sperm, but it is probably still closer to the truth than if simultaneous, multiple fertilization attempts were disregarded or assigned to one participant only. Unfortunately, there is no reliability analysis available to check such estimates with the true proportions of fertilized eggs.

If this method is applied to the species discussed in the foregoing, there is some discrepancy with data based on the pure rates of fertilization attempts, but also between data sets from different studies on the same species. In *S. roissali,* one can estimate from the data of Warner and Lejeune (1985) that parasitic males had about 19% of the fertilization success of territory owners; in *S. ocellatus* this estimate would be about

12%. Wernerus (1989), however, measured 25.2 fertilizations per hour (i.e., "pair spawning equivalents") in nest owners and 9.7 in parasites, that is, an estimated fertilization rate in the latter of 38.5% when compared to nest owners. In another data set he reports 41.3 estimated fertilizations per hour for territorial males and 5.7 for parasites, that is, a fertilization rate of 13.8% when compared to territorial nest owners. Van den Berghe *et al.* (1989) also provide two sets of data on pair spawning equivalents of territorial and parasitic males, one of which cannot be further analyzed from published evidence as the time interval for which the territorial male success rate was given is unclear. The other data set gives an estimate of 35.9% success of parasitic males compared to that of territorial males. In *S. tinca* the situation is also somewhat unclear. Warner and Lejeune (1985) documented only a single interference of a parasitic male in 109 observed spawnings. In sharp contrast to this, van den Berghe *et al.* (1989) and Wernerus (1989) both found that in the same population 74% of spawnings involved "peripheral males" (i.e., purely parasitic males and satellites), and their data suggest a fertilization rate of 1.5 per hour for territorial males and 5.4 per hour for reproductive parasites. This discrepancy from the observations of Warner and Lejeune (1985) may be partly due to the fact that van den Berghe *et al.* (1989) and Wernerus (1989) did not separate simultaneous parasitic spawnings from occasions when peripheral males spawned with a female in the nest of a territory owner without participation of the latter.

To summarize these data on Mediterranean wrasses, reproductive parasites always achieved "pair spawning equivalents" that were within the range of about 10 to 40% of those of territorial males. Only in *S. tinca* do nonterritorial males seem to have higher fertilization rates than nest owners. This is, however, only partly due to simultaneous parasitic spawning. Why do males of this species show nesting behavior in the first place? Lejeune's (1985) data suggested that eggs spawned outside nests have only minute survival chances. Because a large part of the attempted fertilizations, especially of medium-sized, nonnesting males, occur outside nests (81%, Warner and Lejeune, 1985), the large nest males may still fare as well or even better than medium-sized and small males, despite their considerably fewer "pair spawning equivalents."

A better estimate of the reproductive success of bourgeois and parasitic males would be possible if position effects of simultaneously spawning males could be accounted for. Position seems to be important in suckers (Bowman, 1970) and fallfish (Ross and Reed, 1978), in which the territories or nests of dominant males serve as spawning sites. In communal spawning acts, parasitic males that stay in a waiting position are always peripheral to the more dominant territory owners. But also in species with very rapid

spawning acts, the distances between eggs at spawning and the positions of bourgeois and parasitic males trying to fertilize them may greatly differ from each other, as may the timing of sperm release (e.g., in *S. ocellatus,* my own observations).

Schroder (1981) demonstrated by paternity analyses that in *Oncorhynchus keta,* male mating success was directly related to female proximity during spawning. Single parasites fertilized on average a quarter of the eggs deposited by a female when spawning in competition with a large, dominant male (see Section II,C,4). On the basis of these data, Gross (1985) estimated reproductive success of kleptogamic and bourgeois (i.e., dominant) males in *Oncorhynchus kisutch.* He showed that the best option for gaining proximity to spawning females differs between males of different sizes. Small males did best by simultaneous parasitic spawning ("sneaking"), and large ones by fighting for position.

Surprisingly few data exist simply showing that parasitic males do sire offspring. A first hint may be obtained by artificial fertilization experiments with sperm of parasitic males (e.g., Jones and King, 1950a). Van den Assem (1967) showed that eggs had been fertilized and developed normally in the nests of three-spined sticklebacks even when only a parasitic male had passed through after the spawning female, and not the nest owner.

The reproductive success of parasitic fertilizations can only be proved unequivocally, however, by comparing genetic patterns between offspring and their potential parents. Paternity analyses have been done by analyzing genetically polymorphic protein markers with electrophoretic techniques in four species of salmonids (see Table II). Hutchings and Myers (1988) concluded from an interspecific comparison of these results that the weight ratio of dominant and parasitic males is probably important for the proportion of eggs fertilized by them. The smaller male fertilized between 0 and 46% of the eggs when only one parasite competed with a bourgeois male during spawning. The weight ratios between them varied from 2 to 75%. Testis mass would probably be an even better correlate of relative fertilization success of simultaneously spawning males, but this has not been analyzed yet. A size-related difference in male reproductive tactics allowed estimation of relative male success in *Xiphophorus nigrensis* (Zimmerer and Kallmann, 1989; Ryan *et al.,* 1990). The technique of genetic fingerprinting was used in a study on three-spined sticklebacks. Rico *et al.* (1992) showed that in one nest 5 out of 10 fry were not sired by the nest owner, in another nest it was 1 fry out of 10. In total, 3.5% of 170 examined fry resulted probably from parasitic fertilizations (cf. also Gross and Dueck, 1989, for a study of bluegill sunfish).

Genetic markers may also be more obviously expressed, as in the form of color patterns. In the West African cichlid *Pelvicachromis pulcher*

there are two male color morphs. These color patterns are expressed relatively early in ontogeny. Martin and Taborsky (1993) found that male offspring sired by the males of one morph always belonged to that morph, whereas males of the other morph produced male offspring of both types. By combining a harem owner of one type with satellites of the other they found that the relative reproductive success of the most dominant satellite male was on average nearly 30% of that of the territory owner, whereas the figures for beta and gamma satellites were about 15 and 5%, respectively. Overall, the seasonal net reproductive success of harem owners was on average seven times higher than that of their satellites, mainly because the latter were completely excluded from spawning with the alpha female of the harem.

Simultaneous parasitic spawning may also occur between members of different species (e.g., Bell, 1983). When viable offspring are produced on these occasions, species-specific features can serve as genetic markers. In a laboratory study of Lake Tanganyika cichlids, I combined specimens of *Lamprologus brichardi* and *Julidochromis ornatus* in one tank. When a pair of *J. ornatus* spawned, males of the other species fertilized a proportion of the eggs, thereby proving that they can successfully sire offspring by simultaneous parasitic spawning (see Fig. 4; the F1 generation was fertile).

d. Origin. In principle, there are two possible origins for parasitic male spawning. At these two extremes, the expression of this reproductive tactic may be purely phenotypic, or it may result from an unmodifiable genetic disposition (see Austad, 1984).
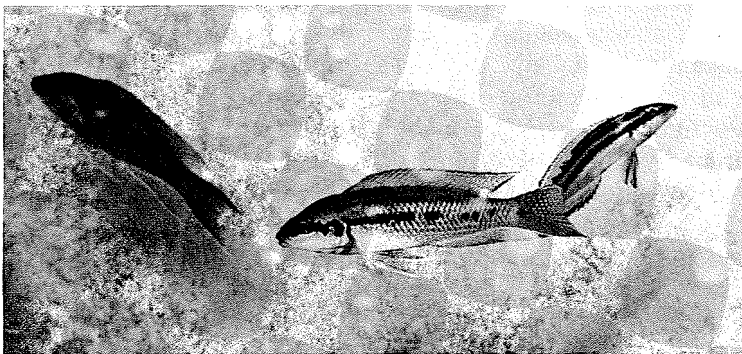

FIG. 4. A hybrid (middle) resulting from the simultaneous parasitic spawning of a *Lamprologus brichardi* (left) male with a pair of *Julidochromis ornatus* (right). This is a proof of successful reproductive parasitism.

There is evidence for a genetic predisposition, albeit perhaps not unmodifiable, toward alternative reproductive strategies in salmonids. In an artificial breeding experiment with coho salmon (*Oncorhynchus kisutch*), Iwamoto *et al.* (1983) found that eggs fertilized by male parasites produced a significantly higher proportion of parasitic male offspring than did those sired by large, "hooknose" males. Gross (1985) suggested, from the spatial distribution of males during spawning, that disruptive selection would stabilize the existence of small and large reproductive males by favoring their respective reproductive tactics, if performed by the "right-sized" males. Large males obtain proximity to females at spawning mainly by fighting for position, whereas small males accomplish this by simultaneous parasitic spawning ("sneaking"). Males of intermediate sizes are at a disadvantage. However, there is another, potentially important reason for the prevalence of large and small males. Spawning in coho salmon is seasonal, and small and large males are recruited from different age cohorts. The small "jack" males stay only one "season" (5–8 months) at sea, and the large hooknose males stay for two "seasons" (17–20 months). This fact alone could explain the bimodal size distribution of reproductive male salmon as schematically depicted by Gross (1984). In other words, there is no age cohort from which to draw intermediate males. The different reproductive behaviors of these males may then be viewed as an adaptation to (i.e., a *consequence* of) the size-dependent opportunities to get close to a spawning female. Gross (1985) estimated a similar lifetime reproductive success for the two male types by using a combination of differential ocean survivorship, reproductively active time at the breeding grounds, and mating success as derived from the different male/female distances during spawning.

A different way of viewing the origin of reproductive parasitism is by looking at whether a male tactic is fixed for life or conditional on circumstances (Dominey, 1984). These two possibilities exist independently of the degree of genetic influence on the form and expression of reproductive behavior. When males remain small and parasitic for life this may primarily result from a genetic disposition, or from an environmental feature that may, for example, set the stage in their early ontogeny. On the other hand, males changing from parasitic to bourgeois reproduction may act purely in a conditional manner or be under a strong genetic influence with regard to the expression of their reproductive tactic. Most likely this behavior will derive from some interaction of genetic and environmental influences. It may be assumed, however, that in species in which males change their tactic the genetic influence is not as strong as it might be in species with fixed, lifelong male reproductive tactics.

Male reproduction in the gila topminnow *Poeciliopsis occidentalis* may

serve to illustrate the two different levels of analysis. Large males of this species often take a conspicuous, black color pattern and become territorial, court females, and show longer bouts of gonopodial thrusting. Small males retain their cryptic color pattern and try to fertilize females without courtship and within the territories of dominant males (Constantz, 1975). If large males are experimentally removed, small males may instantaneously change color and start to defend territories and court females. This demonstrates clearly that their reproductive behavior is conditional. The probability of showing one or the other tactic, however, is strongly size dependent, and these fish cease to grow upon reaching sexual maturity. Size is known to have a strong, genetic component in the *Poeciliidae* (see Ryan *et al.*, 1990). Therefore, the behavior of males is not genetically fixed but dependent on conditions (i.e., relative male size and the existence of competitors), but there is probably a pronounced genetic influence on these conditions. A similar system has been demonstrated in *Xiphophorus nigrensis* (Zimmerer and Kallmann, 1989; Ryan *et al.*, 1990, 1992).

In bluegill sunfish (*Lepomis macrochirus*), Dominey (1980) found that small parasitic males, which he termed "female mimics," and large nesting males were both 6 years of age on average, suggesting that the two behaviors were pure strategies fixed for life. Gross and Charnov (1980) and Gross (1982), however, found that the corresponding kleptogamous males, which they termed "satellites," were on average only 4 years of age in another North American population, whereas most parental males were more than twice as old. This discrepancy may have been caused by either a difference in populations or in methodology (Dominey used the rings in otoliths for an age estimate, Gross used those in scales). Regardless of these different results, Gross (1982) also suggested that the small, parasitic males in his population, which started to reproduce as "sneakers" at an estimated age as low as 1 or 2 years, were not transitional stages toward the bourgeois tactic later in life, but members of a different lifetime reproductive strategy. This suggestion was based on the analysis of scale growth patterns of parasitic and bourgeois males (see also Jennings and Philipp, 1992a, for a similar suggestion in long ear sunfish).

A critical test of this suggestion would be a comparison between the growth patterns of large (bourgeois) and small (kleptogamic) males during their early years of life, that is, when males of the latter type should have reproduced already while those of the former had presumably refrained from reproduction. On the basis of Gross's data (1982, Table 6) I compared the growth increments of males belonging to the 7- to 10-year class (i.e., all being potential or real bourgeois males) with those of 3- to 5-year-old parasitic males (as judged by Gross from their gonadal states), during

years 2, 3, and 4 of their lives. The year in which they were finally caught was excluded from this analysis as the date of capture would have influenced the measurable growth increment in that year. There were 24 possible comparisons between age cohorts, of which 17 revealed significant growth differences (t-tests; the p chosen was 0.001 because of multiple analyses). This strongly supports Gross's conclusion that the males of this species follow reproductive strategies that are fixed for life, at least from the moment when the males have become sexually mature.

It remains unclear whether genes or ontogeny, or both, decide the reproductive fate of a male. Gross and Charnov (1980) and Gross (1982) concluded from intrusion frequencies and the proportions of parasitic males in seven populations at Lake Opinicon that the sum of all parasites fertilized as many eggs as all parental males did (all eggs spawned during "successful" intrusions were ascribed to the parasites, however!). This was regarded as evidence that the tactics had evolved as mixed evolutionarily stable strategies (Gross, 1982, 1984, 1991).

A similar system exists in the Mediterranean wrasse *Symphodus ocellatus*. There are two types of parasites, which were called "sneakers" and "satellites" by Warner and Lejeune (1985) and Taborsky *et al.* (1987), and larger, parental males whose reproductive effort is parasitized upon. There are also males of a fourth type that do not participate in reproduction in a given season and probably become nest-building, bourgeois males in future years (Taborsky *et al.,* 1987). Soljan (1930b) assumed from the growth pattern of scales that the point when these males are born in the season determines whether they will later be "outsiders of fertilization" or nestbuilders. The early-born males, which have extended growth already before the first winter, reproduce early next season (i.e., when they are about 1 year of age) by simultaneous parasitic spawning. They remain parasites for life (i.e., also for their second reproductive season). The males that are born late in the season grow little before the first winter but grow for a long period of time after this first winter and before they start to reproduce. In their second year they are all nestbuilders. Combined with our long-term field information, it seems likely that these bourgeois males are nonreproductive when 1 year old, but start to reproduce right away as bourgeois males in their second year. If Soljan's interpretation of scale growth patterns was right, "birthdate" decides in the males of this species which reproductive strategy they follow for life.

In the West African cichlid *Pelvicachromis pulcher,* there are two male color morphs. "Yellow males" always breed as pair males (i.e., bourgeois) and "red males" may either become pair or harem males (i.e., bourgeois) or reproduce as satellites, which are tolerated as male helpers within the territories of harem owners. This means that only males of the latter

morph become reproductive parasites. The color morphs are fixed for life and their expression is subject to a strong, genetic predisposition (Martin and Taborsky, 1993).

All of these cases illustrate that a male reproductive strategy may be fixed for life, regardless of the extent to which its causes are genetic or environmental. In the majority of known cases, however, the reproductive role of males is conditional, that is, males may take up bourgeois or kelptogamic tactics depending on the circumstances (see Table II for a list of 20 examples from 10 fish families). These circumstances may be either relative size (e.g., *Poecilia latipinna*, Farr *et al.*, 1986; *Salvelinus alpinus*, Sigurjonsdottir and Gunnarson, 1989; *Oncorhynchus nerka*, Foote, 1990; *Tripterygion tripteronotus*, de Jonge and Videler, 1989), male condition (e.g., *Oncorhynchus gorbuscha*, Noltie, 1989), the intensity of intrasexual competition (e.g., *Cyprinodon pecosensis* and *C. macularius*, Kodric-Brown, 1981, 1986; *Symphodus melanocercus*, as demonstrated by removal experiments, Wernerus, 1989), prior residence (e.g., *Oncorhynhus nerka*, Foote, 1990), or the ontogenetic stage of a male (e.g., *Tripterygion tripteronotus*, Wirtz, 1978; Mohr, 1986; *Thalassoma lucasanum* and *T. bifasciatum*, Warner and Hoffman, 1980a; Warner, 1982; *Lamprologus brichardi*, Taborsky, 1985a). In some species males may switch back and forth between bourgeois and parasitic tactics (e.g., *Pseudocrenilabrus philander*, Chan, 1987; see Fig. 5; *Polycentrus schomburgkii*, Barlow, 1967). Often, the choice of tactic and/or its success appears to be frequency dependent (see Gadgil, 1972; Maynard Smith, 1982), although conclusive evidence is missing.

8. Female Choice of Males with Different Reproductive Tactics

In many species females seem to prefer bourgeois males. Atlantic salmon females try to chase away parasitic males (Jones, 1959). Female *Xiphophorus nigrensis* prefer large courting males (Zimmerer and Kallmann, 1989; Ryan *et al.*, 1990). *Thalassoma bifasciatum* females prefer large males in specific territories and are increasingly reluctant to spawn when potential male parasites are nearby (Warner *et al.*, 1975; Warner and Hoffman, 1980b). In *Pseudocrenilabrus philander* (Chan, 1987), *Chromis cyanea* (De Boer, 1981), and *Symphodus ocellatus* and *S. tinca* (Taborsky *et al.*, 1987; van den Berghe *et al.*, 1989; Wernerus, 1989), females often leave the nest when parasitic intrusions occur, even though in *S. ocellatus* they prefer to spawn in nests where satellites are present (but, evidently, with the bourgeois nest owners; Taborsky, 1985b, 1987). Spawning *Tripterygion tripteronotus* females attack parasitic males (Wirtz, 1978).

In *S. ocellatus,* bourgeois nest males and kleptogamic sneakers and satellites all approach and interact with females that are ready to spawn
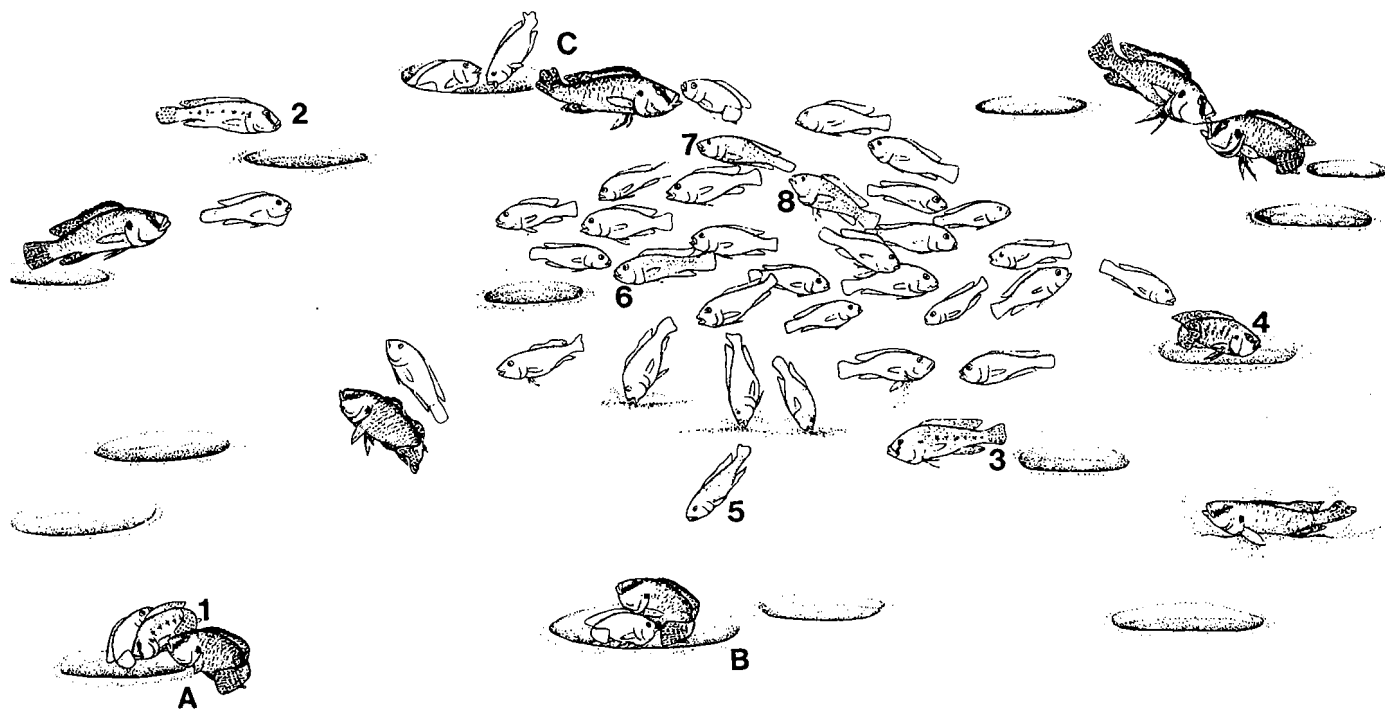
FIG. 5. Schematic description of mating activities in a laboratory lek of *Pseudocrenilabrus philander*. Peripherally placed fishes with dark markings are territorial (bourgeois) males. A group of females (pale fishes) is in the central region. Fishes **1** and **4** are semiterritorial (mostly parasitic) males, whereas **5** to **8** are nonterritorial (purely parasitic spawners). In nest **A,** a semiterritorial male is just caught in parasitic spawning at a territorial male's nest. At nest **B,** parasitic male **5** is about to intrude and join the spawning pair for parasitic sperm release. The spawning in nest **C** is interrupted by the intrusion of an egg-stealing female while the territory owner attempts to ward off other potential intruders. The semiterritorial male **4** has adopted bright colors and courts a female while the nearby territory owners (above) are engaged in fighting. Reproduced from Chan (1987).

and approach a nest. This behavior looks as if females are being herded to the nest by these males (Fig. 6). We followed 30 females in spawning phase for an average period of 25 min each to check their reactions to male approaches. The frequencies with which females were approached did not differ between the male types. However, female reaction did. An approach by a territory owner increased the likelihood that she would enter a nest, which often led to spawning, whereas an approach by a parasitic sneaker or satellite had exactly the opposite effect; females were then more likely to leave (Fig. 7; Taborsky, 1987). This is remarkable as the behavior exhibited by these males looks exactly the same. Yet in the case of nest owners it has the effect of herding females, whereas in the case of the other males it results in female expulsion. The latter was also described qualitatively by Wernerus (1989).

Van den Berghe *et al.* (1989) and Wernerus (1989) removed some of the parasitic sneakers from the vicinity of nests and found a five- to eightfold increase of female spawning rates in these nests. Equivalent removals at *S. tinca* nests gave similar results. Van den Berghe *et al.* (1989) suggested that *Symphodus* females chose mates based on age, defensive ability, or size as an indicator of their genetic quality. Involvement in matings by peripheral males did not show obvious costs to females in assumed fertilization rates, egg mortalities, or the quality of subsequent parental care.

D. PARASITIC BEHAVIOR OF FEMALES

Prezygotic investment is generally higher in females than in males, which limits the potential reproductive rate in the former (Clutton-Brock and Vincent, 1991). Therefore, males compete for access to female

FIG. 6. "Contact following," a behavior that male *Symphodus ocellatus* (black) perform toward conspecific females (white) in the vicinity of a nest (stippled circle). The figure shows a sequence of positions of one contact following event that was derived from film frames of footage taken in the field. The male is behind and above the female when showing this behavior and may touch her at times, as if he would herd her into the nest. After Taborsky *et al.* (1987).
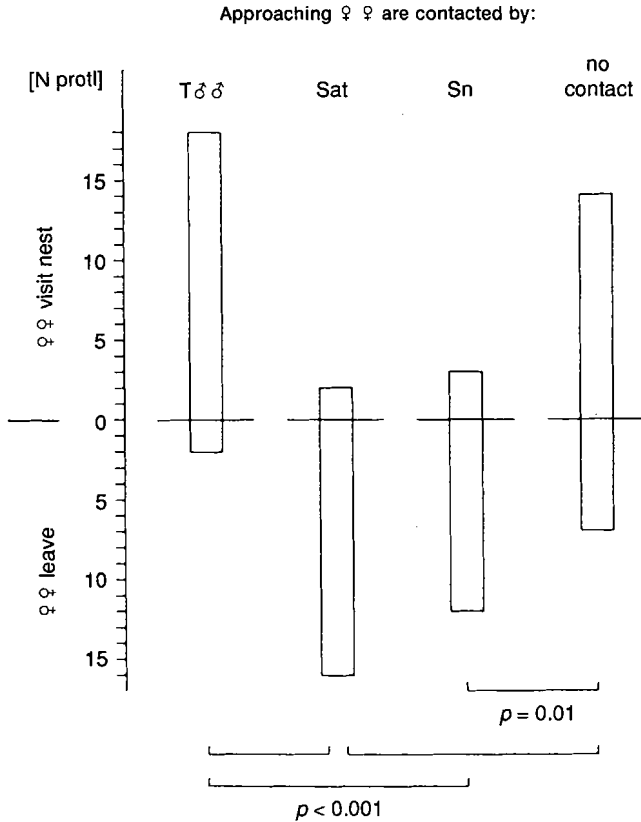
Approaching ♀ ♀ are contacted by:

FIG. 7. Reactions of female *Symphodus ocellatus* who approached a nest of a territorial male to being contacted by conspecific males (see Fig. 6) of different types. Abbreviations as in Fig. 2. Each unit is derived from a 25-min behavioral protocol made in the field (location: see Fig. 2) of an individual female that was ready to spawn. The bars mark the number of recordings in which the focal females reacted to these approaches more often by visiting the male's nest (above zero) or by leaving the area (below zero). The right bar shows how often females completed their nest approaches as compared to leaving the area without visiting the nest, when they were *not* approached by a male; this is intended to serve as a control. Each female was only recorded once.

gametes and not vice versa (e.g., Trivers, 1985). This means that males can parasitize each other's effort to obtain access to these gametes (see the previous sections) whereas females cannot, because even if there is competition for access to mates among females, this does not involve *investment* that could be parasitized by others. Females may, however,

parasitize *post*-zygotic effort of conspecifics when there is female brood-care. The latter is generally rare among fish, although it is common in a few families (e.g., Breder and Rosen, 1966; Baylis, 1981).

Intraspecific brood parasitism is hard to detect (Andersson, 1984; Mac-Whirter, 1989). Therefore, only recently has evidence begun to accumulate on this phenomenon, for example, in birds (e.g., Moller, 1987; Pinxten *et al.,* 1991; Weigmann and Lamprecht, 1991). In fish, an intraspecific mixing of broods that might be viewed as parasitic has been observed in cichlid maternal mouthbrooders (e.g., Ribbink *et al.,* 1980; Yanagisawa, 1985a, 1986). It seems, however, that this is not a specific *female* adaptation to save parental effort. There is no evidence for female egg dumping in these cases. Rather, free-swimming fry are taken into the mouth of a parent and spat into a school of fry guarded by other conspecifics ("farming out"; Yanagisawa, 1985a,b, 1986). This was observed in *Xenotilapia flavipinnis* when both presumed parents were guarding fry, and in *Perrissodus microlepis* only when one partner had been experimentally removed. Remarkably, the only two cases in which the sex was known of the pair member successfully farming out parts of its brood involved females (Yanagisawa, 1985a).

Female egg dumping in fish has been documented, however, on an *inter*specific scale. It appears to be common in cyprinids. The nests of *Nocomis micropogon,* for example, are used as spawning sites by three other species (see Table II). This interspecific egg dumping occurred during nearly all observation periods and at all nests with spawning activity observed by Reighard (1943). Parasitic "associates" were obviously attracted by building activities of the host species, and up to 200 fish were simultaneously present at an active nest. Abandoned nests were taken over and guarded by members of these egg-dumping species. This "insurance" for a successful completion of broodcare (i.e., defense of eggs) might be an ultimate advantage for the host species. The potential *costs* for hosts include competition for oxygen among the eggs in a nest, possible cannibalism occurring during the turmoil at spawning, and the chances of hybridization (eggs of the host might be fertilized by sperm of another instead of their own species).

There are other cyprinids using nests of cyprinid hosts for spawning (see Wallin, 1989). Yellowfin shiners (*Notropis lutipinnis*) failed to reproduce in the absence of bluehead chub (*Nocomis leptocephalus*) nests, into which they usually dump their eggs. Conspecific eggs constituted on average only 3% of all eggs found in bluehead chub nests (Wallin, 1992). Cyprinids use also nests of sunfish for spawning [see Hunter and Hasler (1965) and Steele (1978) for references to egg-dumping *Cyprinidae*]. Sunfish host species inlcude *Lepomis punctatus* (Carr, 1946), *L. cyanellus*

(Hunter and Hasler, 1965), *L. megalotis* (Steele, 1978), and *Micropterus salmoides* (Kramer and Smith, 1960). The latter species may also defend eggs and young of the sucker *Erimyzon sucetta* (Carr, 1942). In that case, the host fry survived better in nests containing fry of the other species ($p < 0.02$, Fisher Exact Probability Test, calculated from data of Carr, 1942; see also McKaye, 1981). Similarly, *M. salmoides* was found to care for eggs and fry of the garpike *Lepisosteus osseus*, and nests containing young of both species were more successful than those containing the host species only (Goff, 1984). In contrast to this, egg dumping of the cyprinid *Pungtungia herzi* at the freshwater perch *Siniperca kawamebari* reduced the reproductive success of the host species by 35%. The reason was that another cyprinid, *Zacco temmincki,* exploited the confusion caused by the spawning *P. herzi* and robbed its eggs (Baba *et al.,* 1990).

A predisposition for egg dumping in cyprinids is probably the habit of pelagically spawning demersal eggs, that is, the eggs spawned in the water column sink passively into the nest below (McKaye, 1981). A mochokid catfish from Lake Tanganyika, *Synodontis multipunctatus,* was found to parasitize mouthbrooding cichlids (Brichard, 1979; Finley, 1984; Colditz, 1986; Sato, 1986), and the good correlation between the sizes of host and parasite fry suggested that they are of equal age, that is, that the transfer of offspring from parasite to host occurred at spawning (Sato, 1987). This was confirmed by aquarium observations (Staats, 1988; Schrader, 1993). Members of ten different cichlid species were found to brood catfish eggs or young, and Sato (1986) found eight broods that consisted *only* of parasite offspring. The reason for this is probably intrabuccal predation, as aquarium observations revealed that catfish fry consume host fry.

In the case of the catfish/cichlid interaction it appears to be clear that the costs of interspecific care for the host by far outweigh any potential benefits. This is not as clear in the spawning associations of cyprinids. The host species may either suffer from competition of their eggs and fry with those of their associates (see the foregoing), or they might somehow benefit from them, for example, by the predator dilution effect, or neither benefit nor suffer. Phrased differently, the relationship may be parasitic, mutualistic, or commensalic. Apart from the two cases in which *Micropterus salmoides* cared for *Erimyzon sucetta* and for *Lepisosteus osseus,* both of which seem to be mutualistic, and the indirect damage of egg dumping *Pungtungia herzi* to their host *Siniperca kawamebari,* the effect of these interspecific associations on the fitness of the host species has not yet been studied.

A mixing of broods may also occur when offspring leaving their parent move to a neighboring, guarded school of fry on their own (Ribbink *et al.,* 1980), or through kidnapping (McKaye and McKaye, 1977; McKaye,

1981), or expulsion of parental guards by other, stronger neighbors (Lewis, 1980). This also leads often to an interspecific mixing of broods (e.g., McKaye, 1977, 1981; McKaye and McKaye, 1977; Ribbink, 1977; Ribbink *et al.,* 1980), which is apparently not *parasitic* behavior in the form of a parent trying to save parental effort by passing its young to the care of a stepparent. It will therefore be treated in a separate section together with other examples of interspecific brood mixing.

III. Associations between Reproductive Competitors and Cooperation

Cooperation might be seen as the opposite of competition. In my view it is instead another form of selfish behavior where individuals attempt to improve access to resources (Taborsky, 1987; see also Harcourt, 1987). Therefore, we should not expect a clear-cut difference between "purely competitive" (i.e., parasitic) and cooperative (i.e., mutualistic) behavior. I trust this will become clear in this section, which aims at summarizing our current knowledge on cooperative behavior in fish reproduction (see Table III, p. 24). I should stress that I am not concerned with nonreproductive forms of cooperation in this review (e.g., Milinski, 1987; Milinski *et al.,* 1990; see Pitcher, 1992, for a review).

I start with a discussion of cases in which males known as "satellite males" associate with bourgeois reproductive competitors. These males are always competitively inferior, but in many cases they are tolerated at or near the bourgeois males' defended area. In some cases there is joint defense, nest building or courtship by the different males. There is nonaggressive, joint spawning that in certain species occurs without exception (*Catostomidae*).

Within the context of *raising* offspring, conflict is often less pronounced than in the competition for *producing* them. This may result from the lower benefits of parasitic behavior the later it is performed in the succession of efforts bearing upon attempts to reproduce. Also, interactions often concern related individuals within the context of broodcare, which also lowers the payoff of parasitic behavior. Cooperative behavior therefore seems more prominent in broodcare systems. For example, parents of different broods may either jointly defend their offspring or one may care for the young of the other. In extreme cases individuals of one species may care for the brood of another even without having young of their own. Such alloparental care may also result from nest takeovers, when the second fish continues to care for the brood of the first. The most advanced forms of intraspecific cooperation are found in systems that are characterized

by higher than average degrees of relatedness. Young of previous broods remain with their parents and help to raise subsequent offspring (broodcare helpers).

In the discussion of cooperative associations I focus on the possible costs and benefits to the participants whenever there are data available. We shall see, however, that there is often ample room for speculation given the lack of data.

I use the term **satellite** simply to refer to a *spatial* relationship of an inferior to a bourgeois male. It does not hint at the role of this male or the type of interactions with the dominant owner of a territory or resource. Time is not included in this definition, but the association should last for some minimum proportion of the reproductive period of these males, to separate this type of association from purely kleptogamic events; for example, when a male parasite enters the territory just to shed sperm when a female is spawning he will *not* be termed satellite. The term **helper** is used operationally for an individual participating in some effort and does not necessarily presume a benefit for the receiver of this help (e.g., parent or brood; see Taborsky, 1984a). **Cooperation** is used in a broad sense and includes behaviors performed by two or more individuals that *appear* to serve a common purpose. Their behavior does not need to be coordinated.

A. SATELLITE MALES

1. Males That Are Not Explicitly Tolerated at a Defended Site

Males may associate with a defended site of a bourgeois male but remain outside or at the margin of the latter's territory. In *Oncorhynchus nerka* (*Salmonidae*), one to eight satellite males stay in the vicinity of a large male's nest. Each of them defends its own position. When the dominant nest owner disappears, the biggest satellite takes his position. The satellites parasitize the nest owner's reproductive effort by kleptogamy (McCart, 1970). Small males of the African cichlid *Sarotherodon alcalicus* defend small pits (i.e., shallow depressions) at the edge of large pits owned by large conspecific males (Albrecht, 1968). There they spawn with very small females. In fallfish minnows (*Semotilus corporalis*), bluegill sunfish (*Lepomis macrochirus*), and the Mediterranean ocellated wrasse (*S. ocellatus*) there are two types of alternative reproductive behaviors. The *small* reproductive parasites in fallfish minnows (Ross and Reed, 1978; Ross, 1983) and ocellated wrasses (i.e., the males termed "sneakers", Taborsky *et al.,* 1987) stay at a nest for some period of time without being tolerated by the nest owner, similarly to the satellite males in dark chub (*Zacco*

temmincki, Katano, 1992). They participate parasitically in spawnings in the nest. In bluegill sunfish, female mimics are only partly expelled. It has been suggested that they are either not recognized as males (i.e., the mimicry is effective) or expulsion may be too expensive for the nesting males (Dominey, 1981). In the hawkfish *Cirrhitichthys falco,* "sneaker" males lived on the periphery of a harem, but it is unclear whether they were tolerated by its owner (Donaldson, 1987).

Satellites also exist in other, nonreproductive stiuations. In the blue-headed wrasse *(Thalassoma bifasciatum),* for example, subordinate males often stay very close to a bright male's stationary place or shelter. They are frequently chased by the latter, but often manage to remain in their vicinity and probably benefit from using the shelters of these bourgeois males (Reinboth, 1973).

2. Males That Are Tolerated by Bourgeois Males

With regards to functional explanations, cases in which satellite males are accepted to some extent at bourgeois male's territories are more interesting than those described in the previous section. Small, parasitic males may be ignored by territory owners, as in the dwarf surfperch *Micrometrus minimus* (Warner and Harlan, 1982), or they may dwell above or at the boundary of defended sites, as found in the pupfish *Cyprinodon pecosensis* (Kodric-Brown, 1977, 1981, 1986). In the latter species these brightly colored satellite males are frequently attacked and pursued but still manage to stay at the edge of a territory. They mate primarily with small females, whereas larger females spawn preferentially with territory owners.

Often, satellites are tolerated amid territories. In the cichlids *Tropheus irsacae* and *Eretmodus cyanostictus,* the sexes of these tolerated individuals are unknown (Kuwamura, 1986); in *Lamprologus callipterus,* these individuals are males with female color patterns (female mimics; Sato, 1988). The same is true for the wrasse *Coris julis,* in which these satellites are sometimes even courted by the owners of the territories (Lejeune, 1985). Satellite males of the blenny *Parablennius sanguinolentus* stay permanently within the territories of large, bourgeois males (Santos, 1985; Santos and Almada, 1988). They court females and share in territory defense (see the following), and steal fertilizations. All of this also applies to the cichlid *Pelvicachromis pulcher.* If there is more than one satellite per territory in this species, there is a strongly size-related dominance hierarchy between them (Martin and Taborsky, 1993). Subordinate males of the anemone fish *Amphiprion akallopisos* are tolerated by a breeding pair at their host anemone. Fricke (1979) suggested from behavioral observations and histological analyses of gonads that these males are psycholog-

ically castrated, perhaps through high levels of stress (see also Reyer *et al.*, 1986), and hence are not capable of stealing fertilizations. In harem species, several small males may stay within the territories of harem owners (*Halichoeres maculipinna*, Thresher, 1979; *Canthigaster rostrata*, Sikkel, 1990; *Lactoria fornasini*, Moyer, 1979). The reproductive role of these satellites is unclear. In *L. fornasini*, harem owners often attack their satellites, which respond with appeasement behavior (Moyer, 1979).

Small males of the pupfish *Cyprinodon macularis* defend subterritories within the territories of large males (Barlow, 1961). They are frequently pursued by the latter but return quickly to their defended places. In *Apistogramma borellii*, males of female size pair up with females within the territories of large males and also defend subterritories (Burchard, 1965).

In the cyprinids *Semotilus corporalis* and *Notropis leptocephalus*, nest-males tolerate other males close to their nests (Ross and Reed, 1978; Ross, 1983; Wallin, 1989). This is similar to the Mediterranean wrasses *Symphodus ocellatus* (Soljan, 1930a; Taborsky, 1984b, 1985b; Warner and Lejeune, 1985; Taborsky *et al.*, 1987), *S. roissali* (Soljan, 1931; Fiedler, 1964; Lejeune, 1985), and *S. tinca* (Lejeune, 1985). There is a hierarchy between satellites if there are several at a nest (*S. ocellatus,* Taborsky *et al.*, 1987; *S. tinca,* Lejeune, 1985). *S. ocellatus* satellites behave submissively toward territory owners and they are explicitly tolerated by them. This was demonstrated by a comparison of the behavior of nest owners between encounters with satellites and with other parasitic males (called sneakers; Taborsky *et al.*, 1987). Once a satellite is accepted by a territorial male he will usually stay at his nest until the end of the spawning activity. Lejeune (1985) documented a similar constancy of residence by satellites in the closely related *S. roissali.*

In most of the cases described here, satellite males parasitize the effort of bourgeois males by stealing fertilizations. Why are they tolerated? Why is there a range in degrees of tolerance?

Expulsion may be simply not possible, as suggested to be the case in *Lamprologus furcifer* (Yanagisawa, 1987). Or attempting to keep these parasites at a distance may be more costly than accepting the loss of a proportion of fertilizations to them (Kodric-Brown, 1977). Ross (1983) suggested that in fallfish tolerance of satellites might be better for nest owners than chasing them, as the latter behavior would interrupt spawning activity. A special benefit from the tolerance of satellite males by territory owners may be found in *Amphiprion akallopisos*. In this protandric, sex-changing species, young males may serve as replacement partners when a pair member disappears (Fricke, 1979), that is, tolerance is an insurance strategy to keep potential partners available.

A fourth possible benefit for territory owners of the presence of satellites

is that they might increase the attractiveness of a spawning site to females (Kodric-Brown, 1977; Ross and Reed, 1978). Data from an experimental field study of the ocellated wrasse (*Symphodus ocellatus*) suggested that territory owners would greatly benefit from the presence of satellites, because females preferred to spawn in nests at which satellites were present (Taborsky, 1985b, 1987). They used satellite males as a cue to assess the probability that their eggs will be tended until hatching (M. Taborsky and P. Wirtz, unpublished data). An attractive function of accessory males was also hypothesized for bluegill sunfish (*Lepomis macrochirus;* Dominey, 1981). However, alternative explanations to these favored by the various researchers cannot be ruled out completely in any of the foregoing examples. Cost/benefit analyses aiming to obtain conclusive evidence on the payoffs of satellites, and especially of bourgeois males, are still a challenge for the future.

Bourgeois males may also benefit from the behavioral effort of satellite males, for example, from territory defense, nest building, courtship, or broodcare activities. These possibilities will be treated in the next section.

B. COOPERATIVE REPRODUCTIVE BEHAVIOR

1. *Joint Defense*[1]

Small pupfish (*Cyprinodon macularis*) satellites tolerated in territories of large males defend their ranges, and hence the common territory as well, against intruding conspecifics (Barlow, 1961). In a functional sense this is similar to the situation in the cichlid *Sarotherodon alcalicus,* in which the small males surrounding the pits of large reproductive males expel large, roaming males and attack neighboring territory owners (Albrecht, 1968).

Harem owners of the West African cichlid *Pelvicachromis pulcher* often host between one and three satellites permanently in their year-round, all-purpose territories. These satellite males defend the common harem range, both intra- and interspecifically, and they put more effort into this defense behavior than the harem owners themselves do (Martin and Taborsky, 1993). Harems of the wrasse *Halichoeres maculipinna* may also contain several satellite males that join in territory defense against neighbors and subordinate male competitors (Thresher, 1979). Subdominant male anemone fish (*Amphiprion akallopisos*) defend the pair's terri-

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[1] "Joint" is used here to classify behavior shared by two or more individuals. It does not assume any coordination between the participants.

tory in which they reside against strange conspecifics, predators, and predators of the host anemone (Fricke, 1979).

Satellite males of the Mediterranean wrasses *Symphodus ocellatus* (Fiedler, 1964; Taborsky, 1984b, 1985b; Warner and Lejeune, 1985; Taborsky *et al.*, 1987), *S. roissali* (Lejeune, 1985), and *S. tinca* (Lejeune, 1985) attack conspecific male parasites that try to steal fertilizations when the nest owner is spawning. In the ocellated wrasse (*S. ocellatus*), satellites exhibit even higher defense frequencies against these reproductive competitors than territory owners (Taborsky *et al.*, 1987). In none of these species do satellites attack neighboring territory owners. Such defense against larger, bourgeois neighbors is shown by satellites of the blenny *Parablennius sanguinolentus*. When frequencies of this behavior are combined with attack rates on smaller competitors, satellites of this species also surpass territory owners with regard to intrasexual defense frequencies (Santos, 1986).

On the ultimate level, the defense effort of satellite males may be purely selfish, that is, only satellites themselves benefit from excluding reproductive competitors because they participate parasitically in spawnings of the territory owner. The latter would in that case tolerate their satellites for other reasons, but not because of a net benefit derived from the satellites' defense effort. Alternatively, the fact that satellites invest in territory defense may functionally result from a reciprocal relationship with the bourgeois male, that is, satellites are tolerated and their fertilization stealing is accepted to an extent by the dominant male, *because* they ward off a host of other, purely parasitic reproductive competitors. This could be termed **paying for staying** (see Taborsky, 1984a, 1985a). A series of removal experiments performed in the field showed that in *Symphodus ocellatus*, when satellites were present at a nest bourgeois nest owners neither saved defense effort nor experienced reduced rates of parasitized spawnings. Therefore, these accessory males acted in a purely selfish manner (M. Taborsky and P. Wirtz, unpublished data).

2. *Joint Nest Building, Courtship, and Spawning*

Cyprinid males may cooperate in nest building. Accessory males of *Nocomis leptocephalus,* which are usually smaller than dominant nest builders, occasionally share in nest building. Their nest building appears to have on average very little effect, however (Reighard, 1943). In the bluehead chub (*Notropis leptocephalus*), several males may contribute to nest construction. These nest-building associations may last for considerable periods of time. Wallin (1989) observed two large, individually recognizable males who jointly constructed five different nests in succession. I do not know of any studies that test whether these associations are mutualistic or parasitic.

Males of the northern greenside darter, *Etheostoma blennioides,* were reported to court females jointly. Fahy (1954) observed in a tank that two males courted a female partly alternating and partly synchronized before the larger one of them spawned with her. In the field, groups of males were found to court a female, one at a time, without any aggressive behavior between these males. Males of the sucker *Moxostoma carinatum* jointly court a female at a site prepared by one of the two participants. The other male duplicates the nuptial dance of the nest builder before both of them spawn with the female in unison (see the following; Hackney *et al.,* 1967; Hackney, unpublished, from Jenkins, 1970, p. 245; see also Page and Johnston, 1990).

In several temperate freshwater fishes two or more males may spawn jointly, without obvious aggression between them. Often, these males do not differ in their roles, that is, there is no distinction possible between a bourgeois and a satellite (or parasitic) tactic. For example, two or more males of the lake trout, *Salvelinus namaycush,* court and spawn with a female simultaneously. There may be up to seven males and three females spawning in unison (Royce, 1951). Six males or more may cluster around a female while spawning in the yellowfin shiner (*Notropis lutipinnis;* Wallin, 1989). Some species of suckers (Catostomidae) spawn either facultatively or usually in trios, involving two males and a single female (Jenkins and Jenkins, 1980; Page and Johnston, 1990). There may be accessory males participating in these spawnings.

In a large number of suckers, perhaps in the majority of species, spawning occurs *only* in trios (see Table III for a listing of species and references; especially Reighard, 1920; Jenkins and Jenkins, 1980; Page and Johnston, 1990). Occasionally, they are joined by additional males that may cause an interruption of the spawning act (Reighard, 1920). The two male spawning partners adjoin the female on either side and press against her flanks. This formation is stabilized by breeding tubercles or "pearl organs" (Reighard, 1920) that roughen the body surface of males. Spawning is usually simultaneous by all three members of a trio and has been suggested to be more "efficient" than in pairs of one male and one female only (Kwak and Skelly, 1992). The river redhorse (*Moxostoma carinatum*) differs from other species because in this sucker a male constructs a redd (i.e., spawning site) and displays there in front of a female. He is then joined and followed in motion by a second male (Hackney *et al.,* 1967; Hackney, unpublished, from Jenkins, 1970 p. 245). The female takes position between the two males for spawning.

The ultimate reason for trio spawning in suckers has so far not been studied. Obviously, there is sperm competition for fertilization of the eggs between the simultaneously spawning males. There are three conventional arguments to explain the mutual tolerance of competing males in this

situation. The participants may (i) be closely related to each other (kinship advantage), (ii) take turns with mutually aiding each other (reciprocal altruism), or (iii) behave cooperatively because one partner forces the other to do so (manipulation). All explanations have in common that the benefit over cost ratio of a male participating in joint spawning exceeds that of a male trying to monopolize a female.

There is no evidence that any of these hypotheses explains the observed behavior satisfactorily. It is unlikely that partners in male duos are closer related to each other than the population average, because suckers do not appear to remain localized between their own egg and reproductive stages. There is some migratory behavior before spawning, and young and adult stages often do not share the same parts of a river (Jenkins, 1970). It is very improbable that brothers, for example, would stay together for years from their hatching until spawning and during all of these migratory movements.

A scenario in which reciprocity was responsible for the observed behavior would require that the same two partners meet repeatedly on successive spawning occasions. This cannot be totally excluded given our present state of knowledge, but observations of some species suggest that males associate with different partners for successive spawning events (Reighard, 1920). The third explanation, manipulation, is unlikely because no agonistic behavior has been observed in most of the reported cases.

(iv) Another possibility to explain this case of apparent cooperation would be if males were forced to spawn jointly because the simultaneous pressure of two individuals is necessary on the flanks of a female for her to release eggs, or simply to induce spawning. Kwak and Skelly (1992) regarded trio spawning as ''more efficient'' than pair spawning. This shifts the question from male to female biology. An advantage from increased genetic variability and/or fertilization certainty could perhaps cause the evolution of a habit that allows females to spawn only with at least two male partners at a time.

(v) A fifth hypothesis would imply that joint spawning in suckers is rather a case of parasitism than of cooperation. The first male, which has just obtained a female and presses on to her flank, may simply be incapable of preventing a second male from doing the same on her opposite side. If this holds, more aggression might then be expected to occur generally between reproductive males at the spawning area.

(vi) The last possibility I would like to discuss includes a simultaneous benefit for both male participants. If a female would release, say, 100 eggs when spawning with one male only, but two males could literally press 1000 eggs out of her oviduct when spawning with her simultaneously, each male would increase its fertilization success fivefold by cooperating

with a competitor (assuming, for ease of argument, fertilizations are on average equally shared between the two male partners). As with the other hypotheses presented to explain trio spawning of suckers, there is no evidence yet that this joint manipulation of females by males occurs.

The evolutionary background of joint spawning in suckers is one of the most puzzling riddles in the reproductive behavior of fishes. It might have implications for our understanding of cooperative processes in animal behavior in general. Future studies, preferably performed on *facultative* trio spawners, should reveal the ultimate and proximate causes of this social phenomenon.

3. Joint Broodcare

Cooperative behavior in fish reproduction is not limited to conspecific associations that have the purpose of obtaining mates or fertilizations. It also occurs between parents tending eggs or young (see Keenleyside, 1991). In this section I discuss cases of communal care, in which different parents jointly raise and protect their respective offspring.

Intraspecific communal care has been documented for cichlids. The green chromide (*Etroplus suratensis*) may occasionally exhibit joint care of large schools of young (Ward and Wyman, 1975). Three out of 28 parent/offspring units (11%) observed in the field contained more than two adults, ranging from four to six (Ward and Wyman, 1977). Presumably, these were the parents of mixed schools of their offspring, although evidence is missing. The young "glanced and micronipped" mucus from these adults, which is a typical form of provisioning by parents in this genus (Ward and Barlow, 1967). McKaye and McKaye (1977) observed three pairs of the Midas cichlid (*Cichlasoma citrinellum*) jointly defending a large school of young, which split into three parts when threatened. A large school of young *Tilapia rendalli* that consisted of two size classes was observed to be guarded by two pairs of adults (Ribbink *et al.,* 1981). In sculpins communal egg guarding, involving mostly one primary female and up to four secondary males, was observed in *Hemilepidotus hemilepidotus* (DeMartini and Patten, 1979). It has been suggested that the secondary guardian males have probably not spawned in the guarded nest, but may use the clutch as a "courtship dummy" to attract ripe females (see Section III,C,3).

More than 50% of the broods guarded by the Lake Malawi catfish *Bagrus meridionalis* contained cichlid young (see Table III for the list of species). In more than half of these cases there were cichlid adults guarding these mixed broods of young as well. McKaye (1985) never observed young of the two *Crytocara* species involved outside mixed cichlid/catfish groups. As with the intraspecific situation in *Etroplus suratensis* (see

preceding), cichlid young fed from the body surface of the guarding catfish, but were forced by the latter to the periphery of the school (McKaye *et al.*, 1992). In cyprinids, Hankinson (1920) observed cooperative broodcare of *Hybopsis biguttata* with *Notropis cornutus*. They showed some division of labor, with the former species building the nest and the latter guarding it.

Joint broodcare by more than one parental unit appears to be relatively rare. This is perhaps not surprising when viewed in the light of cost/benefit ratios of the participating adults. Guarding young involves costs, with regard to both predation risk and time (i.e., subsequent reproduction is postponed). If the offspring are additionally defended by other parental adults, the benefits of leaving the care completely to these alloparents will probably often outweigh the costs of increased predation on the young after desertion. Cost/benefit ratios may be asymmetric between the two parties involved, as was suggested by McKaye's observations (1985). When adult catfish and cichlids jointly care for a mixed school of young, the cichlid parents may desert without great costs, because the catfish are easily capable of defending the offspring alone. When the catfish parents were experimentally removed, however, the entire school of young was eaten by predators in seven out of nine experiments (i.e., *all* trials with young < 6 cm), within a period of 15 min (McKaye, 1985). This asymmetry may be the reason why nearly half of the mixed broods of cichlids and catfish only had catfish guards, that is, the cichlid parents may have deserted in these cases.

This case study nicely illustrates the likely reason why the occurrence of joint broodcare appears to be relatively rare when compared to the widespread phenomenon of brood mixing. It pays to abandon one's offspring if another individual provides care anyway. The same argument has been used to explain uniparental care, in the context of task sharing between male and female parents (see Maynard Smith, 1977). The care of mixed broods by one set of parents will be discussed in the subsequent sections.

C. ALLOPARENTAL CARE

1. Intraspecific Adoptions

In many cichlid species, groups of young that are guarded by parental adults may belong to different size/age classes. In substrate brooding, permanently territorial species, this may be a consequence of prolonged filial philopatry, which may result in helper systems (see the following). In the majority of cases, however, it is more likely that this intraspecific

mixing of broods results from adoptions of strange young. Adoptions can be easily induced experimentally, in both the aquarium and field (e.g., Greenberg, 1963; Sjölander, 1972; Noakes and Barlow, 1973; McKaye and McKaye, 1977; Carlisle, 1985; Wisenden and Keenleyside, 1992), with conspecifics and with young of other species (e.g., Noble and Curtis, 1939; Collins and Braddock, 1962; Myrberg, 1964; Mrowka, 1987a). They also occur on their own, that is, without experimental manipulation (e.g., Burchard, 1965; Baylis, 1974; McKaye and McKaye, 1977; Mrowka, 1987b).

The chances of witnessing adoptions in an undisturbed situation are very low. Therefore, the occurrence of adoptions is usually deduced from the fact that broods contain different size classes, or because broods *increase* in size (McKaye and McKaye, 1977). Table III lists species in which intraspecific adoptions have been directly observed or can be safely assumed to occur from these indirect cues.

There are several possible reasons for the occurrence of adoptions. Unfortunately, no cost/benefit analyses have been performed yet to study the ultimate (i.e., evolutionary) reasons. We may expect different mechanisms of offspring transfer between broodcaring adults, depending on whether it is advantageous to donors or stepparents, or to both. Information on who initiates the transfer of offspring may provide some hint as to who will ultimately benefit from it (although nonadaptive "mistakes" and "accidents" are potential alternatives).

Kidnapping has been observed in the Midas cichlid, *Cichlasoma citrinellum* (McKaye and McKaye, 1977), in the orange chromide, *Etroplus maculatus* (G. W. Barlow, unpublished observations, cited in McKaye and McKaye (1977), in *Apistogramma borellii* (Dieke, 1993), and in *Pseudocrenilabrus multicolor* (Mrowka, 1987). The latter is a maternal mouthbrooder, and kidnapping refers here to an interference of strange females at spawning and take up of eggs by these interlopers. The stealing of eggs or young may have a positive dilution effect on the kidnapper's own young when predation on offspring occurs (McKaye and McKaye, 1977). Wisenden and Keenleyside (1992) suggested that this potential antipredation function of brood adoptions may be the reason why in many species only young of equal or smaller sizes than their own offspring are accepted, as predator efficiency is negatively correlated with prey size.

Farming out of broods is a term used for a behavior by which parents actively transfer young to strange broodcaring adults (with reference to "egg dumping," this behavior might be called **young dumping**). This was observed in the Tanganyika cichlid *Perissodus microlepis* (Yanagisawa, 1985a). It only happened when one parent was left with the brood, either because its partner has been experimentally removed or had disappeared

for unknown reasons. Yanagisawa argued that the reduced chances of raising a brood alone would make farming out very profitable for single parents. This may also hold for convict cichlids. When the males of brood-caring pairs of *Cichlasoma nigrofasciatum* were experimentally removed by Wisenden and Keenleyside (1992), the transfer probability of the brood to other pairs with young increased. In the African mouthbrooder *Xenotilapia flavipinnis*, farming out was observed when both parents were still in charge of the brood (Yanagisawa, 1985b, 1986). Generally, as the transfer of young is initiated by donors, it is likely that they are gaining more from this behavior than the stepparents do, in exact contrast to the previously discussed phenomenon of kidnapping. As a consequence, donors should be expected to transfer their offspring to parents caring for young that are still *smaller* than their own, for the same reasons as Wisenden and Keenleyside (1992) hypothesized that kidnappers should preferably steal offspring that are smaller than their own.

There are two other possibilities for how young of different parents may coalesce. When brood-tending adults meet, their young may join the wrong school (**family conflux**). This is especially likely to happen in species lacking stable territories. It may result in reciprocal adoption, in the displacement of parents (Wisenden and Keenleyside, 1992), or in the collection of all young with the most aggressive parents (Baylis, 1974). Alternatively, young may independently join a guarded brood, after separation from their own parents (**independent offspring inclusion**). Large offspring of the damselfish *Acanthochromis polyacanthus* are expelled at some stage by their parents. They may then join a neighboring school of young that is still guarded by adults (Thresher, 1985). The latter appear incapable of separating the two groups of young and expelling the interlopers.

Both family conflux and independent offspring inclusion may be beneficial, costly, or neutral to stepparents. It is not possible to assess the likely payoff from the form of this behavior alone; measurements of offspring survival are required to unravel this phenomenon.

2.   *Mixed-Species Broods and Care for Pure Heterospecific Broods*

Frequently, when there are mixed broods containing young of different species, these are guarded by one or two adults of only one of the species involved (see Table III for a list of species). For example, *all* broods guarded by adult Midas cichlids (*Cichlasoma citrinellum*) that were older than 5 weeks of age contained young of *Neetroplus nematopus* in addition to their own offspring (McKaye and McKaye, 1977). Some guarded broods of *N. nematopus* also contained Midas cichlid young. Ribbink (1977) observed that mouthbrooding adults of three predatory Lake Malawi cichlids contained young of *Haplochromis chrysonotus*. A closer look revealed

that members of 12 *Haplochromis* species and of *Serranochromis robustus* regularly cared for young of 15 different species, in addition to their own young (Ribbink *et al.*, 1980). The authors concluded from their observations that in Lake Malawi "all species which show well developed parental behavior may have foreign fry mix[ed] with their broods on occasion." Guarded broods of the predatory, substrate-brooding Tanganyika cichlid *Lamprologus elongatus* may contain young *Perissodus microlepis*. Yanagisawa and Nshombo (1983) suggested that these heterospecific young join the host broods on their own. In a later study it was shown that the young of this species are occasionally "farmed out" by their parents (see foregoing), which may be another cause for this interspecific brood mixing.

There are intriguing associations between catfish and cichlids in the great East African lakes. Schools of young guarded by the bagrid catfish *Bagrus meridionalis* often contain young cichlids (McKaye and Oliver, 1980; see preceding), and in nearly half of these cases the mixed broods were guarded by adult catfishes only. The proximate cause for brood mixing was probably active release of cichlid offspring into bagrid broods by their mothers (McKaye, 1985; McKaye *et al.*, 1992), The geometry of these mixed schools is influenced by the aggressive behavior of the catfish parents against cichlid young at the center of the school. Attack frequencies of predators on catfish young were seven times greater in pure broods than in those that were mixed with cichlid offspring (McKaye *et al.*, 1992). Mouthbrooding adults of ten cichlid species were found to tend young mochokid catfish in their mouths, together with their own offspring (Brichard, 1979; Sato, 1986; Schrader, 1993). This is due to egg dumping by female catfishes when the cichlids spawned (see foregoing).

Costs and benefits of interspecific brood mixing are probably similar to those involved with intraspecific adoptions. Donors of young will probably benefit from the relief of broodcare. It remains to be studied whether this advantage outweighs the potential costs of reduced survival of young when they are tended by stepparents. Often, they will even gain *increased* survival probabilities by this transfer to guarding adults of another species, as was suggested by the cichlid/catfish association in Lake Malawi (McKaye, 1985). Cichlid young which are guarded by catfish may even benefit nutritionally because they feed from the body surface of their foster parents (McKaye *et al.*, 1992). Hosts may gain from the inclusion of foreign fry, as demonstrated by the increased offspring survival of the sunfish *Micropterus salmoides* when broods contained young *Erimyzon sucetta* (see Section II,D), and of *Micropterus dolomieui* when the brood was mixed with *Lepidosteus osseus* (Goff, 1984). Catfish young received seven times fewer attacks when cichlid young were present (McKaye *et al.*, 1992). The effect of foreign young on the survival of hosts could also

be neutral, or disadvantageous as demonstrated by the inclusion of catfish fry in the mouths of broodcaring cichlids. Sato (1986) found eight mouth-brooding cichlid individuals that tended *only* catfish young. This was probably due to catfish fry predating cichlid fry within the mouths of the latters' mothers (see Section II,D).

Care of pure heterospecific broods was also demonstrated for chain pickerel (*Esox niger*). Shoemaker (1947) found this species to defend eggs and young of pumpkinseed sunfish (*Lepomis gibbosus*). He assumed that this apparent interspecific altruism would benefit the performing pickerels because they would thereby get access to the predators of the beneficiaries' young (i.e., golden shiners, *Notemigonus crysoleucas*), upon which they prey. In a Nicaraguan crater lake adult *Cichlasoma nicaraguense* males were observed to share in the brood defense of *C. dovii* parents (McKaye, 1977). Four broods guarded by these heterospecific alloparents suffered less mortality than six control broods guarded only by conspecific adults. McKaye (1977, 1979; see also Coyne and Sohn, 1978) suggested an evolutionary scenario to explain this apparent altruism in which the alloparents would take advantage of a population increase of the beneficiaries because the latter prey on the former's main competitors. This would need to involve group selection, however, as individuals refraining from behaving altruistically would gain (from the alloparental care of other altruists) without paying the costs of alloparental care. The population ecological conditions under which this group selection scenario could work as proposed are very restricted (see Barton and Clark, 1990), and it remains to be shown that these conditions prevail in the case described.

3. Nest Takeovers and Egg Stealing[2]

In at least eight fish families, nest takeovers occur in combination with subsequent care of the eggs that were already contained in these nests (i.e., probably fertilized by the previous owners; see Table III for a list of species). In some species this was observed in the natural, undisturbed situation (*Etheostoma olmstedi*, Constantz, 1979, 1985; *Amphiprion clarkii*, Yanagisawa and Ochi, 1986; *Symphodus ocellatus*, Taborsky *et al.*, 1987), or it was inferred from indirect evidence (*Padogobius martensi*, Bisazza *et al.*, 1989a; *Cottus gobio*, Bisazza and Marconato, 1988). It could be induced by experimental removal of nest owners in *Amphiprion clarkii* (Yanagisawa and Ochi, 1986), in *Ophiodon elongatus* (Jewell, 1968), in *Hemilepidotus hemilepidotus* (DeMartini and Patten, 1973), and in *Harpagifer bispinis* (Daniels, 1978, 1979). In the last species, clutches

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[2] The term "nest" is used here in its widest sense for any structure or shelter that serves for spawning and broodcare.

were originally cared for by females, but after the latter had been removed their place was taken invariably by males who continued to guard and care for the eggs, although with much less effort.

Usually, large males displace small nest owners and take over their nests (*Pimephales promelas,* Unger and Sargent, 1988; *S. ocellatus,* Taborsky *et al.,* 1987; *Padogobius martensi,* Bisazza *et al.,* 1989a; *Cottus gobio,* Bisazza and Marconato, 1988). In *E. olmstedi,* however, dominant males frequently abandon the breeding holes in which they had spawned and search for new ones. Subdominant males may then take over their nests and care for the eggs, which includes cleaning and guarding (Constantz, 1979). The eggs get so hard within a day that they cannot be consumed by the new nest owners (Constantz, 1985). The abandonment of clutches by dominant males in order to leave them to the care of smaller conspecifics is reminiscent of the "piracy" tactic observed by the largest males in *S. tinca* (see Section II,B,2).

Why would males compete to take over the nests of others and care for the eggs fertilized by strange conspecifics? Basically, there are two possible benefits to this behavior, **predation dilution** and **mate acquisition.** A necessary prerequisite for both hypotheses is that males taking over a nest will subsequently spawn there. This is generally the case with the examples mentioned (see also Section II,B,1), with the exception of the Antartic plunder fish *Harpagifer bispinis.* The predation dilution hypothesis would predict that the survival probability of eggs fertilized by takeover males will increase from spreading the predation risk to a larger mass of eggs. To my knowledge, this has not yet been demonstrated by empirical data. The second hypothesis proposes that the presence of eggs, or the performance of broodcare behavior, would help to obtain females. In *A. clarkii,* for example, males taking over an anemone with a female pair up with this new mate and can subsequently spawn with her (Yanagisawa and Ochi, 1986), potentially until the end of her reproductive life. In this case, caring for the acquired brood instead of eating it may be a way of "paying for staying." This would hold if females were more likely to reject males that were not willing to care for their clutches (*Amphiprion* females are larger than males and dominant), which remains to be shown. Among species with nest takeovers and alloparental broodcare, an attraction effect of the presence of eggs in a nest was demonstrated in the tessellated darter (*E. olmstedi*), in the river bullhead (*Cottus gobio*), and in fathead minnows (*Pimephales promelas*). In the darter, females seem to prefer nests with several eggs to those with none when deciding where to spawn, but they apparently avoid nests containing large masses of eggs (Constantz, 1985). The latter fact may be the reason why dominant males abandon their breeding shelter after some time to search for new ones

with more bare surface to which eggs can be attached. The likelihood of leaving should additionally depend on the probability of subsequent takeover of the abandoned nest by an inferior male who will continue the broodcare. Female river bullheads chose males depending on the latter's sizes and/or egg presence in their nests (Marconato and Bisazza, 1986; Bisazza and Marconato, 1988). Female fathead minnows preferred to spawn with males who had eggs in their nests, when eggs were randomly assigned to nesting males (Unger and Sargent, 1988). This explains the strong male preference for nest sites with eggs in this species. In an experiment, males preferred to take over nest sites with eggs that were already guarded by another male even when unguarded empty nests were available. However, they provided less care for adopted clutches than for their own ones (Sargent, 1989).

Female preference for males that already guard eggs was also demonstrated in other species (e.g., Sikkel, 1988, 1989, and references therein), for example, in three-spined sticklebacks (Ridley and Rechten, 1981). Males of this species also show alloparental care, but instead of taking over a nest they steal eggs from neighbors and deposit them in their own nests (van den Assem, 1967; Wootton, 1971; Li and Owings, 1978b; Sargent and Gebler, 1980). The ultimate reason why females prefer males with eggs may be predation dilution, an increased broodcare motivation of males with large numbers of eggs, or a signal function of male quality (either in the sense of broodcare capabilities or in the sense of self-reinforcing feedback mechanisms acting on female preferences via indirect selection and genetic correlation; see Kirkpatrick, 1982, 1987; Bradbury and Gibson, 1983; Lande, 1987). These hypotheses are not mutually exclusive. Positive correlations of paternal effort and offspring survival with egg number have been repeatedly demonstrated in fishes (e.g., Pressley, 1981; Coleman et al., 1985; Sargent, 1988). It appears to be especially important for females to provide males with enough eggs to make their broodcare profitable. If the egg number remains below a critical size, clutches are frequently cannibalized by the nest owners and/or the nests are abandoned (e.g., also in three-spined sticklebacks, van den Assem, 1967; I compiled a list of 21 fish species belonging to 9 families in which small clutches or few eggs are abandoned; M. Taborsky, unpublished). Depending on certain brood size and time cost variables, this may be a decision for optimizing male reproductive success (Taborsky, 1985c; see also ten Cate and Taborsky, 1992, for an example with birds).

In conclusion, egg raiding in sticklebacks may be a courtship strategy to attract females, as hypothesized by Rohwer (1978) and suggested by experimental results (Ridley and Rechten, 1981). Experiments of Jamieson and Colgan (1989) challenged this conclusion, however, suggesting that

the presence of eggs would rather work via a "priming effect" on the courtship behavior of males. If this is its only functional significance, egg raiding would be nothing more than self-deception. Another study found, however, that the female preference for nests with eggs is at least partly a consequence of the eggs themselves (Goldschmidt *et al.*, 1993).

Nonadaptive hypotheses for egg stealing and subsequent alloparental care have also been proposed to explain such behavior in mouthbrooding *Pseudocrenilabrus multicolor* females. Mrowka (1987b) suggested that mistaken identity or motivational constraints could be responsible, but he also considered predation dilution and partial cannibalism (of the stolen eggs) as possible adaptive explanations.

4. Broodcare Helpers

Some cichlids endemic to Lake Tanganyika show levels of cooperative behavior not previously suspected in fishes (Harcourt, 1988; Taborsky and Taborsky, 1993). In three *Lamprologus* and three *Julidochromis* species, families have been found that consist of the members of a pair and young of various ages that all share the same territory and the duties of defense, maintenance, and broodcare (Taborsky and Limberger, 1981; see Table III). All species are monomorphic substrate brooders inhabiting the rocky sublittoral zone of the lake. In *Lamprologus brichardi,* an average of 7 to 8 young (7.5 $\pm$ 1.42; $\bar{x} \pm 2$ SE; $N = 60$ families) of up to four different size classes and a pair share a common shelter site in which eggs and larvae are tended (Fig. 8a). There are male and female helpers, and the largest helpers of most families are sexually mature. They leave their territories to become aggregation members before they are big enough to take over a breeding territory on their own, that is, there is a gap in body size between the largest helpers and the smallest breeders (Taborsky and Limberger, 1981). Aquarium experiments revealed that this transition from family to aggregation is caused by the expulsion of helpers by pair members, and not by an independent decision of the helpers (see the following). In the field, the sex ratio of mature helpers was skewed toward females (2 : 1, female : male), whereas the sex ratio of aggregation members of the same size range was exactly reverse (1 : 2, female : male; Taborsky, 1984a).

There is not as much information from the field on the other species with helpers. We collected field data on two other species (see Taborsky and Limberger, 1981), near Magara (Burundi), and I briefly describe their social structure and behavior. *Julidochromis marlieri* is a monogamous species breeding in narrow clefts, and we monitored the composition of 14 families. They consisted of a pair and usually of smaller members of up to four different size classes (Fig. 8b). The larger of these extrapair family members share in intra- and interspecific territory defense, and
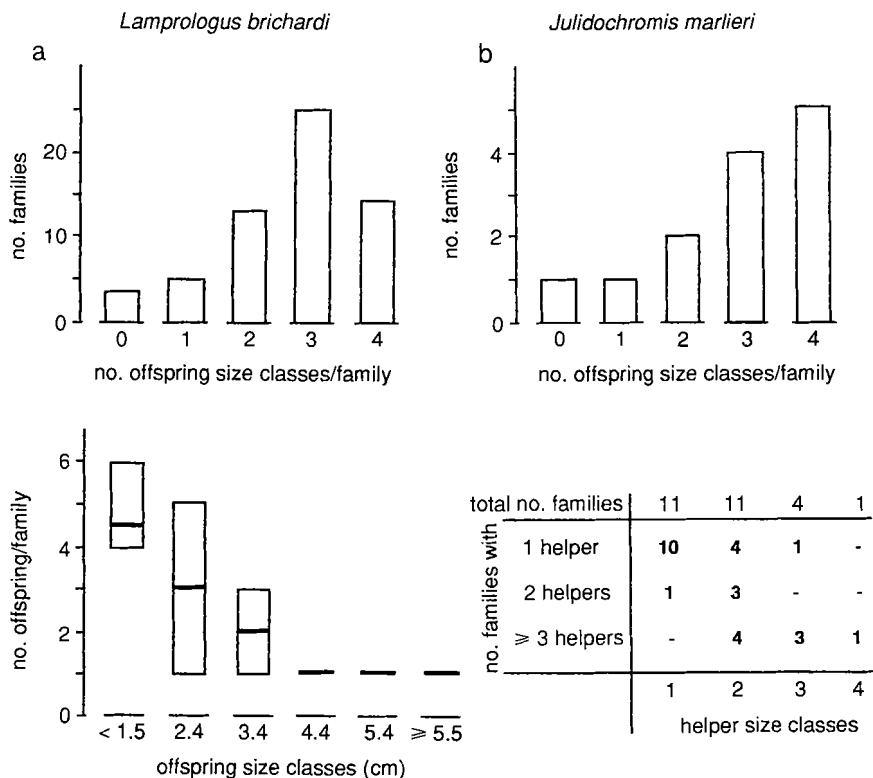
FIG. 8. (a) Top graph: number of families of the cooperatively breeding cichlid *Lamprologus brichardi* in which either no young or offspring of up to four different size classes were simultaneously present in the field (these probably originated from an equivalent number of successive broods of the relevant territory owners; total sample size was 60 families). Bottom graph: average numbers of young simultaneously present in *L. brichardi* families in the field, separated for size. Only families having offspring of the relevant size classes were included in each bar. (b) Top graph: same information as in 8 (a), but for the cooperatively breeding cichlid *Julidochromis marlieri* (field data: total sample size was 13 families out of 14, in which offspring size classes were clearly distinct). Bottom graph: numbers of *J. marlieri* families in which either one, two, or three and more helpers were simultaneously present, separated for different relative size classes of helpers, 1 being the largest and 4 the smallest size class.

we know from aquarium observations that they take part in territory maintenance and direct broodcare as well, just as the helpers of *L. brichardi* do. There was usually only one helper of the largest size class per family (one exception had two, see Fig. 8b), which measured between about 4.5 and 6.5 cm and could be approximately 1 year of age, as estimated

from growth rates measured in the aquarium. It was often hard to estimate the actual offspring number of a family, especially of the smaller size classes, as small young remained hidden in their domestic cleft (the distance that young *J. marlieri* move from their shelter correlates positively with their size, as it does in *L. brichardi*). The average number of offspring, regardless of size, of the nine families that could be counted satisfactorily was 12.6 ± 8.2 ($x \pm 2$ SE). Yamagishi (1988) observed large helpers in five out of seven families. They were responsible for approximately one quarter of all interspecific territory defense of the associated families.

Lamprologus savoryi is another species with helpers. In the field, we observed dense harems in which females defended very small subterritories, which were often shared by smaller fish of one, two, or rarely three different size classes. These family members joined in intra- and interspecific territory defense. They were particularly aggressive toward members of other subterritories. It is not yet known whether they also join in direct broodcare (e.g., egg cleaning, fanning, mouthing of larvae). A similar group structure was also reported for another population of this species by Kondo (1986) and Abe (1987).

Helping in the other three Tanganyika cichlids listed in Table III has only been observed in the laboratory, where the behavior and social structure of *L. pulcher* resemble those of *L. brichardi* in every detail. The helping behavior of extrapair family members of *J. ornatus* and *J. regani* is very similar to that of *J. marlieri*. From the comparison of the results of field and laboratory observations in the two species for which this was possible (*L. brichardi* and *J. marlieri*) it seems very likely that the three species for which helping has as yet only been observed in the aquarium will behave similarly in the wild. Two Bornean fighting fish species, *Betta brownorum* and *B. persephone,* have been recently observed to have helpers. Older offspring tend to stay in parental territories and take part in defense against small interspecific intruders (Witte and Schmidt, 1992, aquarium observations only).

There is a differential sharing of tasks between members of *L. brichardi* families (Taborsky *et al.,* 1986). When different competitors and predators were experimentally introduced into family territories, males attacked large, heterospecifics more than their partners did. Both pair members exhibited more aggressive behavior against large intruders than helpers did, whereas the latter specialized in territory maintenance and direct broodcare. When small fishes entered the territory, the helpers showed more aggression against heterospecific intruders than female breeders did, and more displays against conspecific intruders than male breeders did. Among helpers, the large ones spent more time attacking intruders, while small ones performed more territory maintenance and broodcare. This

specializing in different tasks was dependent not only on the type and size of intruders, but also on the stage of the breeding cycle. In the natural situation, results were similar to those of laboratory experiments with regard to the devotion of helpers to interspecific defense, and that of breeders to attacking conspecifics. Also, large helpers showed more territory defense than small ones did, and even more than the male territory owners (Taborsky and Limberger, 1981). See Limberger (1983) for additional data on task sharing in this species between members of a pair or harem.

For an understanding of the evolutionary background of these helper systems we first need to know the relationship of helpers to pair members and to the eggs/fry produced in their territory. In *L. brichardi,* field and aquarium observations revealed that helpers are earlier offspring that grew up in the territories that they defend. They do not move between territories, but the average relatedness between them and the eggs and fry they tend (i.e., their beneficiaries) declines with their age as a result of the natural replacement of breeders (Taborsky and Limberger, 1980). Helpers stay when one or both parents are replaced by strangers (e.g., because of mortality) and continue to share in the cleaning and fanning of eggs and larvae, removing sand from the breeding hole, removing snails (i.e., egg predators), and defending the territory and breeding hole against conspecific and interspecific competitors and predators. The degree of relatedness (*r*) between the *oldest* helpers and eggs they care for was calculated to be approximately 0.25 (Taborsky and Limberger, 1981).

The costs and benefits to helpers and pair members were studied by a combination of field observations and laboratory experiments (Taborsky, 1984a). As a measure of helpers' costs, their growth rates were compared with those of family-independent aggregation members. The possible benefits that were tested ranged from those accruing to both helpers and breeders (mutualism) to those favoring helpers at the expense of breeders (parasitism). They included the advantage of rearing close kin, getting experience in broodcare, increasing the chances of territory takeover, increased survival probabilities in a protected territory, and parasitism of the breeders' reproduction and cannibalism of eggs and larvae.

Helpers grow more slowly than aggregation members of comparable sizes. They are heavier, however, than the latter, which suggests that they accumulate reserves while being protected in a safe territory so that they can pass the subsequent aggregation phase very quickly. The latter is probably a risky period (see the following), and the demonstrated size/weight relationship implies that it is a growth phase that primarily serves to attain sufficient size for the successful conquest of a breeding site. A comparison of growth between helpers differing in their hierarchical status

and same size territorial controls that were breeding themselves suggested that the delayed growth of helpers is due not only to their behavioral effort but also to their subordinate position within families (Taborsky, 1984a).

Helpers did not affect egg or larvae survival in lab experiments, regardless of the presence of predators and competitors, nor did they influence the length of time intervals between subsequent clutches or the growth of pair members whom they assisted. Still, the effort females saved when having between one and three broodcare helpers increased their reproductive success because they were able to produce larger clutches (Taborsky, 1984a). This may select for a genetic disposition toward helping because of the relatedness between helpers and beneficiaries (see foregoing). Field observations revealed that pair members with helpers spent less time in their territories and more in nearby aggregations, in which they feed, than pair members lacking large helpers (Taborsky, 1984a). This may additionally raise the effect of helpers on parental fecundity and hence promote the evolution of helping behavior via natural selection.

The importance of gaining broodcare experience was tested by a comparison of helpers and inexperienced controls during their own first broods. Experiments revealed that former helpers and naive controls did not differ in broodcare patterns, nor in clutch sizes, breeding intervals, growth rates, or relative and absolute breeding success. This holds for males and females alike (Taborsky, 1984a). Territory inheritance is another potential benefit to helpers that turned out to have no significance for the cost/benefit ratios of helpers. This was demonstrated in part by a series of field experiments in which we removed one or both pair members of the 10 families containing the largest helpers out of our total sample of 60 families, to see whether these sexually mature helpers might take over the vacant position. This never happened, and instead it was always taken by a bigger aggregation member. In most of these cases the helpers stayed with the new breeders (Taborsky, 1984a).

In the natural habitat of *L. brichardi* all suitable shelter sites are occupied by fish of various species. Helping could simply be viewed as paying the price for being allowed to stay in a territory defended by larger and more able hosts, and having permanent access to a shelter site. Field observations revealed that the predation pressure on helpers and aggregation members drops sharply when they reach a size of 4–4.5 cm, because their main predator, *L. elongatus,* is not able to cope with prey above that size. Laboratory experiments showed that the survival probabilities of helpers that are below that size are indeed greatly increased by living in a safe territory and by parental attacks on the predators, even though nonhelper controls had access to shelter sites in this setup that they would

not have in the natural situation (Taborsky, 1984a). This explains the size distribution of family and aggregation members as found in the field (Taborsky and Limberger, 1981, Fig. 3), with a sudden change of the majority of fishes from family to aggregation status when 4–4.5 cm long.

Helpers may also benefit from parasitizing the reproductive effort of the pair they stay with. They may eat eggs and larvae instead of tending them, or share in reproduction by simultaneous parasitic spawning (male helpers) and egg dumping (female helpers). Both types of parasitism are shown by large *L. brichardi* helpers (Taborsky, 1985a). Various experimental analyses suggested, however, that egg cannibalism and reproductive parasitism are probably only of secondary importance for the net balance of helpers and pair members, especially when helpers are below ca. 3.5 cm long and immature. The potential costs incurred to pair members by their helpers are very important, though, with regard to the time and mode of detachment of helpers from their families. When given the chance either to stay in a family as helper or to leave for an aggregation or even for their own breeding territory, a chance helpers would rarely, if ever, get in the natural situation, there was an unequivocal preference for staying (result of two experimental series, see Taborsky, 1985a). Separation from home territories was instead caused by the expulsion of helpers by breeders. This was confined to large helpers, that is, potential reproductive parasties, and to periods of little or no competitive pressure, that is, when the need for helpers was low. Helpers were reaccepted by pair members when the competitive pressure on the territory was experimentally increased by the introduction of conspecifics or heterospecifics, in 11 out of 13 experiments. It was only their own former helpers who were tolerated again and not strange fishes of the same size (Taborsky, 1985a). This points to the capability of breeders to recognize their helpers individually, which was experimentally proven by Hert 1985).

Large helpers must decide whether to continue behaving cooperatively or try to cheat the breeders they stay with by cannibalism of their offspring and/or parasitic participation in reproduction. If caught cheating or during periods of increased cheating probability, that is, at spawning and during egg and larvae stages, parental aggression toward helpers and the latter's chances to be expelled increase (see Taborsky, 1985a, Table I and p. 61, first paragraph). The payoff from these alternatives mainly depends on the potential costs of being expelled. As the predation risk suddenly drops after reaching a size of 4 cm (see earlier), the probability that helpers cheat should be expected to increase greatly at that point. This is exactly what happens. I developed a graphical model to find the optimal solution for helpers caught in the dilemma of having to choose whether they should continue cooperation or start cheating (Fig. 9). It shows that with regard
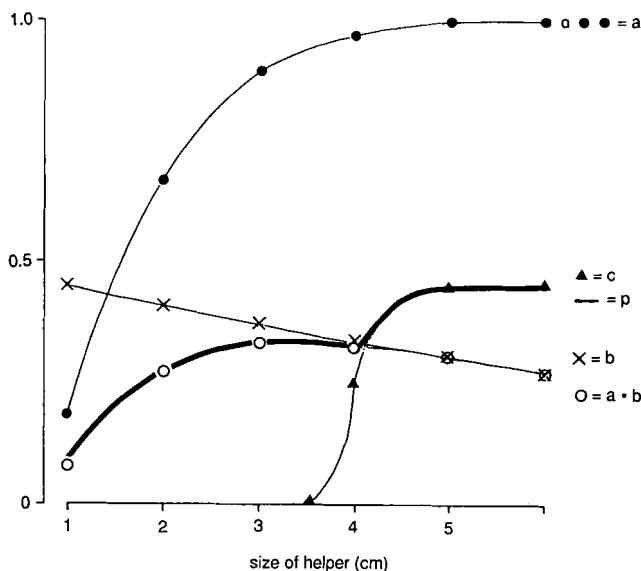
FIG. 9. The hypothetical payoff that *Lamprologus brichardi* helpers receive by helping compared to that for parasitizing the breeders' reproduction. Abscissa: helpers' sizes. Ordinate: relative benefit, except for variable **a,** for which the ordinate is the relative broodcare ability of helpers (1 = perfect ability). **b** = benefit derived from the effects of helping (= increased fecundity of breeders times expected degree of relatedness between helpers and the breeders' offspring). The function is assumed to be directly proportional to *r,* which declines with helpers' age (see Taborsky and Limberger, 1981). **a** times **b** = benefit from helping mutiplied by actual ability to help at that size. **c** = benefit from reproductive parasitism, limited by attainment of maturity, which is size or age dependent, and by the costs derived from the production of gonads and germ cells. The latter prevent the curve from reaching 0.5. **p** = potential maximum payoff of helpers at their optimum, that is, through helping or cheating, whichever is better. Reproduced from Taborsky (1985a).

to immediate fitness consequences helpers should start cheating right after the predation risk has dropped. This suggests that sexual maturity should be reached at this size, which was confirmed by dissection and a check on the gonads of 20 helpers in the field. Thirteen out of 14 helpers ≥4 cm long could be sexed unequivocally: the gonads of one individual (4.4 cm long) were not yet clearly developed. Only 2 out of 6 helpers between 3 and 4 cm long had well-developed gonads already (both were males). The onset of maturity in helpers may hence be phenotypically controlled by the behavior of breeders (i.e., through dominance and punishment by expulsion when helpers try to parasitize their reproduction; see Taborsky, 1985a).

A strong phenotypic control of the behavior of *L. brichardi* helpers by that of breeders was also demonstrated by von Siemens (1990). Results of a series of experiments showed that the submissive status of helpers is the most important factor in causing helpers to clean eggs instead of eating them. When allowed to become dominant, helpers switched to cannibalistic behavior. They could be converted to become egg cleaners again, when combined with dominant conspecifics. The behavior of the dominant fishes directed toward eggs also influenced the probability of egg cannibalism of helpers. Egg cleaning by the dominant individuals increased the likelihood that helpers cleaned eggs as well, and cannibalism by dominant individuals caused helpers also to feed on eggs (von Siemens, 1990). Further experiments revealed that the influence of an egg-cleaning, dominant individual that acted as a "model" was size dependent; large potential helpers ($\bar{x}$ = 4.4 cm) cannibalized eggs regardless of the model's behavior (Ladich and Taborsky, 1991). This also points to the potential costs that breeders may suffer from *large* helpers.

The relationship between helpers and breeders in *L. brichardi* is strongly dependent on age and size of the helpers. Small helpers are highly related to the breeders that they assist. Their tolerance in the territory by breeders and their helping behavior is probably due to **kin selection.** Helpers support close kin and parental tolerance of helpers in their territories may be viewed as prolonged broodcare, which adds to the benefit of receiving help. When helpers have grown up the breeder/helper relationship is characterized by a high degree of **reciprocity.** The breeders tolerate their helpers at the risk of reproductive parasitism and accept the cost of space competition (see Taborsky, 1985a, p. 62), if the helpers pay by sharing in the breeders' duties. The helpers will invest in the breeders' offspring at the cost of reduced growth in order to be protected by the breeders' territoriality and by access to a shelter site. The less important that these potential benefits become for helpers, because they have grown beyond the size range of prey that their major predators can handle, the more important the helpers' costs will become in comparison, which should increase their propensity to cheat. This will in turn raise the costs for breeders to tolerate helpers, which finally leads to the expulsion of helpers, especially when their help is dispensable, that is, in low-competition situations.

Three findings strongly support the conclusion that helpers are **paying for staying.** (i) Young stay and help indiscriminately when one or both breeders are replaced (Taborsky and Limberger, 1981), despite their presumed capacity to recognize individuals (Hert, 1985). (ii) Helpers stay in the territory as long as they can, even when their alternative options are experimentally improved far beyond those found in the natural situation;

this emphasizes the essential importance of a safe territory. (iii) Helpers above a certain size are tolerated by breeders only when they are really needed (Taborsky, 1985a).

IV. GENERAL CHAPTER DISCUSSION

This chapter deals with the different forms of competition that characterize fish reproduction and is limited to the intrasexual level, that is, competition and cooperation between pair members are not considered. The main topics discussed are competition for (i) access to mates (Sections II,B, III,A, III,B,1, III,B,2, III,C,3), (ii) the production of zygotes (Sections II,C, III,A, III,B,1, III,B,2), and (iii) the effort that is put into raising offspring (Sections II,D, III,B,3, III,C). Competition may lead to the parasitic exploitation of investment by individuals employing alternative tactics or, at the other end of the scale, to the seemingly altruistic behavior of individuals supporting others without obvious direct reproductive benefit to themselves. However, these examples could be viewed as extremes of a continuum of social interactions found within the context of reproductive competition. Most of the interactions discussed occur between males, which is partly due to the differences between the sexes in prezygotic investment and reproductive rate (see Section II,D). Yet this may be a biased impression that is caused by conventions in research philosophy, and more could perhaps be gained by looking into female strategies (see, e.g., van den Berghe *et al.,* 1989; Warner, 1990; Ahnesjö *et al.,* 1993).

On the level of competition for mates, there are various ways in which males may improve their chances of being selected by females. These include behavioral and morphological features (e.g., courtship, size, color), which are all subject to intersexual selection through the action of female choice. Another way to improve access to mates is by defense, that is, the exclusion of competitors either directly from mates or from spawning sites. Both types of effort may be exploited by male competitors, who temporarily or permanently take over nests, or intercept and steal females that spawn with another male. These social parasites may either belong to the same type of male as the parasitized individuals, for example, territorial neighbors that intrude to recruit females, or they may be competitively inferior males that exploit opportunities without engaging in aggressive interaction with their victims. Competing males may also combine their effort and jointly defend a spawning territory, or jointly court or build nests. These associations may partly regulate the competition among participants and improve their position against other competitors.

Male intrasexual competition for the production of zygotes (i.e., **sperm**

competition; e.g., Smith, 1984; Parker, 1990b; Birkhead and Møller, 1991) is extremely widespread in fishes (see Table I). This may be partly because fertilization in fishes is usually external, which gives males ample opportunities to attempt to fertilize eggs *simultaneously* with other competitors. The timing of fertilization is exactly predictable for these males (i.e., immediately after egg release), which is in contrast to most systems with internal fertilization. It might be argued that the possibility of flooding the spawning site with sperm *before* a female spawns there could bias the chances of fertilization toward nest owners. This would curtail to some extent the argument that the potentially similar opportunities for bourgeois and parasitic males are a prime mechanism in promoting male reproductive parasitism in fishes. However, the chances are limited that fertilization success can be manipulated by such anticipated sperm release, because of (i) the dilution and dispersal of sperm in water, (ii) the short functional life span of sperm (see Childers, 1967), and (iii) the superior access to eggs of sperm released *at* spawning.

In addition to the predictability of egg release, external fertilization makes it difficult for male fishes to monopolize access to fertilizable eggs. The wide distribution in fishes of simultaneous sperm release by more than one male at spawning is probably a consequence of both factors, perspicuous timing of fertilization *and* the restricted potential to monopolize access to unfertilized eggs (this latter feature limits the ability of the satellite threshold model to explain fish alternative mating systems; Waltz, 1982).

There may be similar costs and similar fertilization probabilities for all participants of simultaneous spawning events, as suggested by group spawning patterns. Fertilization could follow a "fair raffle," with the success of a given male approximating the proportion of his sperm in the total pool of sperm available (Parker, 1990a). The processes of competition and fertilization involved in these group spawning systems, however, are poorly understood. Most often, there are males investing in some way or another to obtain preferential access to fertilizable eggs. This may be accomplished by morphological structures (e.g., humps, color) and behavior (e.g., courtship) influencing female choice (see earlier), or the provision and defense of spawning or breeding sites. Often, this effort is exploited by other bourgeois males who take the occasion to steal fertilizations in a neighbor's territory. Of even greater interest is the fact that often competitors that are specialized in alternative mating patterns parasitize bourgeois males. Again, this specialization may be morphological (e.g., size, color) or behavioral (e.g., sneaking toward a spawning site or streaking toward a spawning female) and often serves to camouflage the parasitic individual from the bourgeois male (see the long list of species with female

mimics in Table II). There are cases with only a minor proportion of kleptogamic males and others in which the majority of males are parasitic. This raises the question of frequency dependence in this interaction of producing and scrounging strategies (see Ayala and Campbell, 1974; Barnard and Sibly, 1981; Barnard, 1984; Ryan *et al.*, 1992). How are they maintained within a population?

In bluegill sunfishes (*Lepomis macrochirus*), the proportion of males who take the parasitic pathway early in life (i.e., when 2 years of age) corresponds roughly to the estimated proportion of eggs fertilized by all parasitic males of the population (Gross, 1982). This would suggest that lifetime reproductive payoff for both types of males, bourgeois and parasitic, is at an equilibrium (Gross and Charnov, 1980; see also Gross, 1991) and represents an evolutionarily stable mixture of strategies (Maynard Smith, 1982; but see Ryan *et al.*, 1992). Dominey (1980) found a different pattern of age-related reproductive tactics in another population, however, and the actual fertilization success of the respective males has not been measured in this species (see, however, Gross and Dueck, 1989). Gross (1982) attributed the fertilization of *all* eggs spawned to these parasites that intruded at spawning. This probably resulted in a substantial overestimate of the success of parasitic individuals (see Section II,C,7,c), which would weaken the former argument. Aside from the need for a more reliable measure of male success rates (see Shuster, 1989), a demonstration of equal morph fitnesses does not necessarily imply that frequency-dependent mating success is the mechanism by which the equilibrium of fitnesses is established. Additional evidence is needed on the fitness effects of *changes* in morph frequency (Ryan *et al.*, 1990), and it will be most rewarding to unravel the nature of the developmental switch, genetic or otherwise, in such systems (see Maynard Smith, 1982) to find the conditions controlling them.

A similar scenario was derived from data on coho salmon (*Oncorhynchus kisutch*). Small parasitic and large bourgeois males were suggested to have equal lifetime reproductive successes, and negatively frequency-dependent disruptive selection was assumed to be responsible for the stability of these alternative strategies (Gross, 1984, 1985). Here, the information used to estimate relative fertilization success of males was distance from females during spawning. This was combined with information on mortality during the ocean phase and on the time period that males stay on the breeding grounds to render relative lifetime fitness estimates. Obviously, there are a number of critical assumptions involved with this approach, and the conclusions drawn may be premature (see also Section II,C,7,d for an alternative explanation of the existence of two distinctly different size classes of reproductive males). A study on

Atlantic salmon (*Salmo salar*) suggested that there might be multiple evolutionarily stable equilibria between the proportions of males maturing at different ages, which is closely related to different male reproductive strategies (Myers, 1986). Here also, good information on fertilization success of different male types is lacking, therefore it remains unclear whether the bourgeois and parasitic tactics are at an equilibrium. These studies on sunfishes and salmon illustrate, however, what kind of data would be needed to solve the question of why more than one reproductive tactic so often exists in male fishes.

There is an alternative way to explain the occurrence of parasitic males within this evolutionary framework. Depending on genetic quality and developmental history, there is often a tremendous variation of male features related to resource holding potential (e.g., body size, Taborsky *et al.*, 1987). This may preclude the smaller individuals from competing successfully for resources with better equipped conspecifics. They have to make the best of a bad job (e.g., Dawkins, 1980; Arak, 1984; Waltz and Wolf, 1984; Koprowski, 1993), which may still lead to evolutionarily stable strategies *within* each phenotype (Parker, 1982).

At present, information on most species is insufficient to test whether the occurrence of alternative mating strategies is a matter of equal payoffs for all participants, or whether certain participants are limited to suboptimal solutions (Ryan *et al.*, 1992). I would suggest, however, that systems that include lifelong, fixed strategies represent mixed evolutionarily stable states, whereas when the male tactic depends on circumstances (e.g., ontogenetic stages), it is more likely that some tactic is the result of males making the best of a bad job. The first case (fixed strategies) is likely to apply only to a small number of species, whereas in the majority of examples studied so far the reproductive tactics chosen by males seem to depend greatly on conditions (see Table II, and Section II,C,7,d; for more extensive discussions see Rubenstein, 1980; Arak, 1984; Caro and Bateson, 1986).

As has been shown for other groups of animals (e.g., Arak, 1983), female fishes apparently prefer to mate with bourgeois males. This may exert additional pressure on parasitic males to conceal their presence and potential to attempt fertilizations, for example, by hiding, sneaking, or female mimicry. In the Mediterranean ocellated wrasse, however, females appear to be attracted to nests by the presence of satellite males, despite the fact that they avoid spawning with them (see Section II,C,8). Satellite males were also assumed to influence female preference in pupfish, in bluegill sunfish, and in fallfish minnows (Kodric-Brown, 1977; Dominey, 1981; Ross, 1983). This appears to be a specific variation of "female copying" (see Bradbury and Gibson, 1983; Dugatkin, 1992). In the wrasse,

females may gain information about the likelihood that the nest will be cared for until hatching. In many other species, females can assess this probability from the presence and number of eggs, but in the thick algae mats provided by bourgeois males of the ocellated wrasse this seems nearly impossible. Satellite males are a reliable cue for the presence of eggs, as they only associate with a nest when females have spawned there already. This interaction between bourgeois male success and satellite behavior illustrates how an initially parasitic system may be stabilized by a substantial degree of reciprocity (i.e., the development toward tolerance of a satellite, see Section III,A,2) via the action of female choice.

At first glance this strict preference of female fishes for spawning only with a bourgeois male may be surprising, in the light of recent evidence that females of other groups of animals often choose to mate with several mates in succession (e.g., Birkhead and Møller, 1991). Potential advantages of multiple inseminations are an increase in the genetic diversity of offspring and a higher fertilization probability. However, a characteristic feature of the spawning patterns of many fish species is that females do not release all their eggs at a time, but rather apportion them between different nests. This allows for the fertilization of their eggs by a number of different bourgeois males, resulting in greater genetic variability of their offspring. At the same time they may choose among these bourgeois males for specific characters related to heritable genetic quality and/or parental abilities. Also, it may benefit females to provide broodcaring males with a high certainty of paternity to provoke their full parental commitment (Knowlton and Greenwell, 1984), which would select against spawning with parasitic males. However, in some species the need to increase fertilization probabilities may override the foregoing factors. For example, species spawning in swift streams may be subject to this problem. The stunning spawning patterns of suckers (e.g., unconditional trio spawning) may have evolved to increase female reproductive success by improving fertilization probabilities.

Another male strategy in the competition for the production of zygotes is to raise sperm production. This investment cannot be parasitized upon by other males. Gonadal investment may result in larger testis size and/or in higher rates of sperm production. To my knowledge, only the first of these two possibilities has been treated to date in any detail (see Fig. 3). Usually, parasitic males produce larger gonads than bourgeois males, when testis mass is related to body mass (see Table II). In the plainfin midshipman (*Porichthys notatus*), for example, the gonad/body weight ratio of parasitic males exceeds that of bourgeois males by a factor of 9 (Bass and Andersen, 1991). These examples illustrate the importance of sperm competition and can be viewed as resulting from an evolutionary

arms race between reproductive competitors. Such competition may also lead to differences between species, that is, the gonads of bourgeois males of species with parasitic spawning are larger than those of males belonging to species without alternative spawning mechanisms (e.g., Mohr, 1986). The huge gonadal investment especially of parasitic males may greatly influence their cost/benefit ratios and should be considered in future studies on the relative payoffs of alternative male reproductive patterns.

Frequently, **satellite males** are tolerated to some extent by bourgeois male conspecifics. These cases appear to be halfway on the scale between purely parasitic intrasexual competition and cooperative associations. There are various transitions between systems in which satellite males lurk at the edge of a territory and those in which they are accepted right in its center, in or at nests. These satellites are virtually always competitors for fertilization, therefore it needs to be explained why they are tolerated. Their expulsion may be either physically not possible for the bourgeois male, or too expensive in comparison to the advantage derived from this effort, or there may be some reciprocal benefit from their presence and/ or behavior. This benefit may be related to their mere presence, for example, in anemonefish as an insurance to have a replacement partner if the animal's own mate disappears, or in the ocellated wrasse to attract females (see Section III,A,2 for a discussion of these possibilities). Or there may be cooperative behavior between bourgeois and satellite males. This does not necessarily mean that males benefit from each others' behavioral effort, as was revealed by field experiments in the ocellated wrasse (Section III,B,1). Joint spawning in suckers might result from mutual benefits of male competitors and is an intriguing behavior with regard to the transition between conflict and cooperation (see the discussion in Section III,B,2).

It is beneficial for parents to adopt behaviors that reduce the costs of broodcare (again, I do not consider *intra*-pair conflict here). This may cause behavioral strategies that differ from those that result from the competition for mates or fertilizations, partly because the broodcare situation mainly involves interactions between relatives, that is, parasitic behavior is not as profitable (see discussion of this argument in Section III). Additionally, broodcare in fishes is often "sharable" (Wittenberger, 1979) or "nondepreciable" (Clutton-Brock, 1991), as it merely amounts to propagule protection; for example, the inclusion of strange offspring into a brood does not necessarily cause extra costs to parents. We have seen, however, that there is still a fair amount of conflict inherent even in the most seemingly altruistic associations between conspecifics, especially as there may be reproductive competition between the participants on top of joint benefits from cooperative behavior (Section III,C).

Adoptions of eggs or young, for example, may be beneficial to donors

and stepparents (mutualism), or to one party only (commensalism), some-times at the expense of the other (parasitism; see the discussion in Sections III,C,1 to III,C,3). They may occur between members of different species, which makes them more obvious, or between conspecifics, which has long been unnoticed in natural situations and is most likely still greatly underestimated because of detection problems (see Andersson, 1984). The benefits involved with alloparental care are clear for the recipients (*if* there are any), that is, a liberation from broodcare duties and hence an increase in the residual reproductive value of these fish. The potential benefits to alloparents are more varied, ranging from predation dilution of their own offspring to mate attraction (see also Rohwer, 1986, for a discussion of a mate-attracting function of adoptions in birds). The benefits to cichlid broodcare **helpers** are closely linked to patterns of relatedness within groups (families) and may greatly change with age. The cost/benefit analysis of an African cichlid with broodcare helpers showed that preda-tion pressure is the key factor in causing the system to switch from kinship-based cooperation to a reciprocal association in which helpers are paying for being allowed to stay in the territory and being protected by its owners (Section III,C,4). This example may illustrate a general difference between fish alloparental care systems and those of other taxa, for example, insects, birds, or mammals. In fish broodcare, protection from predation is proba-bly the factor of greatest importance, whereas in the other groups the provision of food appears to be at least as fundamental (Clutton-Brock, 1991; see also Heinsohn, 1991).

Why are there so many different reproductive tactics in fishes? Fishes are unique in their physiological and morphological plasticity. Most spe-cies show indeterminate growth, that is, there is great variation in size among reproductive competitors. Fishes are faced with the decision to reproduce or grow; they could invest in current reproduction or delay it and invest in growth for future reproductive benefits. Because of lifelong growth this problem is often not confined to a brief period in early ontogeny but is a repeated or permanent dilemma. In addition, sex determination is flexible, ranging from gonochorism to sequential or simultaneous her-maphroditism. And because fertilization is external it is often impossible for males to monopolize access to females or even a single fertilization. All of this predestines fishes to a high level of flexibility in their reproductive behavior and may explain the wealth of alternative reproductive behaviors in this group as compared to the other (in this respect) most heavily studied groups, that is, birds and mammals, and perhpas even insects.

The amazing behavioral flexibility involved in fish reproduction is per-haps best illustrated by species with **three or more** male reproductive strategies. These examples belong to a variety of different fish families,

that is, pupfishes (*Cyprinodon pecosensis,* Kodric-Brown, 1977, 1981, 1986), sunfishes (*Lepomis macrochirus,* Dominey, 1981; Gross, 1982), cichlids (*Pseudocrenilabrus pilander,* Chan, 1987; Chan and Ribbink, 1990; *Lamprologus callipterus,* Sato, 1988; *Pelvicachromis pulcher,* Martin and Taborsky, 1993), wrasses (*Symphodus roissali,* Soljan, 1931; Fiedler, 1964; Lejeune, 1985; *S. tinca,* Lejeune, 1985; Warner and Lejeune, 1985; Wernerus, 1989; *S. ocellatus,* Taborsky *et al.,* 1987), and blennies (*Parablennius sanguinolentus,* Santos, 1985, 1986; Santos and Almada, 1988). The wide taxonomic distribution of highly variable male reproductive behavior might point to the importance of ecological factors and/or of very general biological features of fishes (see earlier). Phylogeny appears to be of great importance, too, as it sets the stage for many characteristics of reproductive competition. The great potential for broodcare in cichlids, for example, leads to many different social phenomena that are closely related to the investment in offspring. A proper comparative analysis of alternative mating patterns in fishes would provide valuable insight into the importance of phylogenetic as opposed to ecological factors in leading to different reproductive strategies (see Harvey and Pagel, 1991).

Fishes are an exquisite group in which to study ultimate and proximate causes of social behavior as a result of their behavioral variability. Other characteristics make this group additionally suitable for studies on sociality (Taborsky, 1987), for example, there are enormous practical advantages. Many species, including those with social structures matching the most complex organizations known among nonhuman vertebrates, are of small size and have small home ranges. They are easy to handle and experiment with, both in the field and in the laboratory. Because of very moderate spatial requirements they can be observed and manipulated under seminatural conditions while showing their full behavioral repertoire and acting in a way that is indistinguishable from the natural situation in many respects (see Taborsky, 1984a, for a discussion). Many have a fast brood succession and short generation times. The fertilization process is usually very obvious, which allows for crucial behavioral observations on male and female roles and on alternative mating tactics. I would suggest that if comparable effort had been put into studies on the social systems of fish as has, for example, been devoted to birds, we would currently have a more complete understanding of functions and mechanisms of complex sexual and social behavior.

Much of our information on reproductive behavior of fishes is still superficial. There is need for more detailed studies of specific model systems that are characterized by great complexity and plasticity of behavioral tactics. In order to understand the evolutionary background of these

systems, we need to address questions concerning, for example, the occurrence and prevention of reciprocity and defection in cooperative systems, and how this might be stabilized by natural selection, and the lifetime reproductive success of individuals performing alternative reproductive strategies could be measured to reveal the evolutionary background of these systems (see, e.g., Shuster and Wade, 1991). Future research should certainly concentrate on the "most interesting" fish families with regard to social behavior, as judged from our present knowledge; but new, exploratory studies on less understood groups should also be encouraged as this may well lead to the discovery of novel reproductive strategies and provide a better perspective on the systems with which we are already familiar.

V. SUMMARY

This chapter reviews our current knowledge of competition in fish reproduction (excluding conflict between members of a pair). The species within this taxonomic group exhibit an impressive range of reproductive tactics. The types of competitive interactions observed range from overt conflict and sexual parasitism at one extreme to cooperation and mutualism at the other.

Most of the examples of competition cited occur between males. Males can exploit the effort of other males to attempt to gain exclusive access to females. This occurs through parasitic behavior such as **nest takeover, piracy, interception,** or **female theft.** Another form of competition for the production of zygotes involves the more or less *simultaneous* release of sperm of different males at spawning (**sperm competition**). This occurs between neighboring bourgeois males (i.e., males that have invested in structures to improve their access to mates, such as territories, nest sites, body coloration, or other morphological structures), but also between bourgeois and parasitic males. The latter may also show morphological, physiological, and behavioral specializations. **Simultaneous parasitic spawning** (SPS) has been described for 123 fish species belonging to 24 families. Frequently, males that are specialized in parasitic spawning resemble females in size, color, and behavior (**female mimics**). Their testis/body mass ratios are frequently higher than those of bourgeois males, and it has been demonstrated that their fertilization success may depend on relative proximity at spawning. In some species, the majority of males specialize in parasitic reproductive tactics. In some species a genetic predisposition was found for the reproductive tactics of males, whereas in many others these tactics are conditionally expressed. Females apparently

prefer to spawn with bourgeois males in most cases, but they may use the presence of subordinate males as a cue for broodcare quality.

Competition may lead to **associations.** Often, subordinate **satellite males** associate with bourgeois males for some time during the reproductive period. Tolerance of these satellites might be a matter of either defense economy or advantages to bourgeois males derived from satellite presence and/or behavior. Such associations have been observed during the defense of spawning territories, courtship, or nest building. There may even be joint spawning that does not involve any aggressive behavior between participants, as is the case in unconditional trio spawning in some suckers. In a functional sense, this appears to differ greatly from "simultaneous *parasitic* spawning."

Within the context of **broodcare,** competition may result in the "donation" of offspring to the care of others (e.g., **egg dumping, young dumping**) or the usurpation of others' offspring (e.g., **kidnapping**). Joint broodcare and **alloparental care** may result from various forms of brood mixing (e.g., **family conflux, independent offspring inclusion**) that occur on both intra- and interspecific levels, and from **nest takeovers** or **egg stealing.** The costs and benefits to donors and stepparents vary greatly, ranging from parasitic through commensal, to mutualistic conditions. Possible benefits to stepparents include a **predation dilution** effect favoring their own offspring, and increased **mate attraction.** Females often choose to spawn with males who already have eggs to care for, because this apparently serves as a cue for an increased survival probability of their own eggs in these nests. A special form of cooperative behavior is exemplified by **broodcare helpers,** which may share in all parental duties and in territory defense and maintenance. Their costs from this behavior include reduced growth, and their benefits result from raising close kin, from being protected by breeders in a safe territory, and from chances to parasitize the reproductive effort of the territory owners. The association of breeders and helpers in an African cichlid changes from a cooperative system among close kin to a reciprocal situation in which helpers are **paying for staying,** that is, they may parasitize the breeders' reproductive effort and are only tolerated by breeders when their help is needed. This demonstrates that the nature of an interaction can vary with conditions between forms of mutualism and parasitism.

Possible reasons for the great variability of reproductive strategies of fishes are discussed. I argue that morphological and physiological characteristics, such as indeterminate growth, external fertilization, and the versatile mechanisms of sex determination, create the potential for this wealth of solutions to reproductive success. Different strategies have been found to result from behavioral plasticity or, at least partly, from genetic

variability. Several reproductive strategies may exist even within single species. It is argued that this variability, combined with practical advantages, renders fishes a model group for studies of the ultimate and proximate causes of social behavior.

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