Review Article

Mating and Parental Care in Lake Tanganyika's Cichlids

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Cichlid fishes of Lake Tanganyika display a variety of mating and parental care behaviors, including polygamous and monogamous mouthbrooding and substrate breeding, cooperative breeding, as well as various alternative reproductive tactics such as sneaking and piracy. Moreover, reproductive behaviors sometimes vary within species both in space and in time. Here, I survey reports on mating and parenting behaviors of Lake Tanganyika cichlid species and address the evolution of mating and parental care patterns and sexual dimorphism. Notes on measures of sexual selection intensity and the difficulties of defining mating systems and estimating selection intensities at species level conclude the essay.

1. Introduction

Mating and parental care patterns are shaped by evolutionary mechanisms, and in turn, reproductive behavior bears on the course of evolution. Both directions of this feedback loop have received attention in theoretical and empirical studies (e.g., [1–3]), but a number of issues around the interplay of sexual selection, ecology, mating, parenting, and phenotypic divergence remains controversial (e.g., [1, 4, 5]). Hypotheses have been tested in taxa ranging from yeast to humans [6, 7], with a strong case made for fishes as models to study sexual selection and parental care by Amundsen [8]. The opportunities offered by fishes are manifold: different ecological backgrounds, a variety of life histories, including sex change and alternations of reproductive tactics as well as fixed behavioral polymorphisms, external and internal fertilization, brood care ranging from none to biparental and even cooperative, and different levels of sexual dimorphism and speciation rates, allow to address consequences of sexual selection as well as factors influencing it. Except for sex change (but see [9]) and internal fertilization, cichlid fishes provide a broad width of study topics at varying phylogenetic levels. In particular, the diversity in morphology, ecology, mating, and parenting behavior of the Lake Tanganyika (LT) cichlids matches their phylogenetic diversity [10], and their potential for comparative phylogenetic studies has been tapped in various contexts [2, 3, 11–18].

The comprehensive synopsis of parental care and mating systems of Lake Tanganyika's cichlids by Kuwamura [19] has become a widely used source of information to researchers in this field. Kuwamura classified the mating systems of LT cichlid species into monogamy, characterized by biparental care or consistent spawning with the same partner, harem polygyny with the male territories including those of several females, male-territory-visiting polygamy, in which females visit the males' territories for spawning but do not form pair bonds, and nonterritorial polygyny, in which males defend spawning sites only during courtship. All cichlids perform brood care, either by mouthbrooding or by guarding eggs and fry (substrate breeding), or, as in several species, by a mixture of both, when mouthbrooding of eggs and small fry is followed by guarding of free-swimming fry. Kuwamura [19, 20] further classified the parental care patterns of LT cichlids into biparental guarding in monogamous substrate breeders, maternal guarding in haremic substrate breeders, mouthbrooding (sometimes followed by guarding) in monogamous species, and maternal mouthbrooding in polygamous species. True to the title of his article [19], Kuwamura developed a model of the evolutionary transitions between parental care patterns in LT cichlids and discussed the forces and opportunities driving these changes. A list of species with parental care, nest site, and mating system type completes his compilation. Since the publication of Kuwamura's article in 1997, further field

and laboratory work and, more recently, genetic parentage analyses have unearthed even more detail about the reproductive behavior of LT cichlids. In particular, attention to alternative reproductive tactics (especially cooperative breeding) has ever been increasing, and a small number of selected species became prominent subjects to address the causes, functions, and mechanisms of different behavioral options. The role of natural selection in the evolution of sexual size dimorphism in shell breeding cichlids has been established by a series of studies. Finally, recent molecular phylogeny-based approaches to the evolution of mating and parental care patterns provided detailed reconstructions of behavioral character transitions, with good support for Kuwamura's original model.

The present paper collects both pre- and post- 1997 data on LT cichlid mating and parenting behavior, then summarizes studies addressing the evolution of mating and parenting patterns in cichlids and of sexual dimorphism in certain LT cichlid species, and concludes with notes on the estimation of sexual selection intensity. Intraspecific variation in reproductive behavior, the employment of various alternative tactics, and finally behaviors, which cannot unambiguously be assigned to one of the defined mating system categories (e.g., the combination of lek and resource-defense mating system characteristics by *Simochromis pleurospilus* [21]), render the classification of species-level mating systems difficult, and no attempt is made here to update Kuwamura's categorization of species by mating or parenting behavior.

2. Substrate Breeding and Mouthbrooding

Substrate breeders (Lamprologini and Boulengerochromini, Table 1) attach their adhesive eggs to different solid surfaces meeting species-specific requirements in orientation, angle, and seclusion. Hatched embryos are often transferred in the female's mouth to rock crevices or pits [22–25]. Larvae of some species remain close to the substrate and spread horizontally while those of others expand their area into the water column [23]. Brood care includes egg cleaning and fanning, as well as defense from predators. The eggs and fry of mouthbrooders are incubated in the buccal cavity of one or both of their parents. Advantages of mouthbrooding include protection from predators and environmental stressors [26], the possibility to breed independently of the availability of suitable surfaces for egg attachment [27], and the possibility to move fry to suitable habitats for release [26], but also incurs considerable costs (see below). Egg and clutch sizes differ between substrate breeders and mouthbrooders. The eggs of the mouthbrooders are typically quite large with diameters up to 7 mm (except for some biparental mouthbrooders [28]), and clutch size is naturally restricted by the capacity of the buccal cavity to <50–80 eggs depending on egg size and brooder body size [28–31]. In contrast, eggs of substrate breeders are smaller with diameters around 2 mm [28], and clutch sizes vary widely between species, ranging from 10–20 eggs in the small shell breeders to hundreds and thousands of eggs in larger species

TABLE 1: Alphabetical list of genera mentioned in the text and their tribal association according to Koblmüller et al., [10]. Lamprologini and Boulengerochromini are substrate breeders, all the other LT cichlids are mouthbrooders.

Genus	Tribe
Altolamprologus	Lamprologini
Asprotilapia[2]	Ectodini
Aulonocranus	Ectodini
Boulengerochromis	Boulengerochromini
Chalinochromis	Lamprologini
Ctenochromis horei[1]	Tropheini
Cyathopharynx	Ectodini
Cyphotilapia	Cyphotilapiini
Cyprichromis	Cyprichromini
Eretmodus	Eretmodini
Gnathochromis pfefferi[1]	Tropheini
Haplotaxodon	Perissodini
Julidochromis	Lamprologini
Lamprologus[3]	Lamprologini
Lepidiolamprologus[3]	Lamprologini
Limnochromis	Limnochromini
Microdontochromis[2]	Ectodini
Neolamprologus[3]	Lamprologini
Ophthalmotilapia	Ectodini
Paracyprichromis	Cyprichromini
Perissodus	Perissodini
Petrochromis	Tropheini
Plecodus	Perissodini
Pseudosimochromis	Tropheini
Reganochromis	Limnochromini
Simochromis	Tropheini
Spathodus	Eretmodini
Tanganicodus	Eretmodini
Telmatochromis	Lamprologini
Triglachromis	Limnochromini
Tropheus	Tropheini
Variabilichromis[3]	Lamprologini
Xenotilapia	Ectodini

[1] The genus names *Ctenochromis* and *Gnathochromis* are shared with species belonging to other tribes [10, 38].
[2] within *Xenotilapia* [38].
[3] Current generic assignments of *Lamprologus*, *Neolamprologus*, *Lepidiolamprologus*, and *Variabilichromis* species may differ from those in earlier publications.

[28, 32, 33]. Time to hatching is positively related to egg size [11] and takes three to five days after fertilization in substrate breeders [23, 32, 34, 35] and three to eight days postfertilization in mouthbrooders [36, 37]. The duration of posthatching brood care is often longer in substrate breeders than in mouthbrooders and varies widely among species of both groups (see below).

In all LT cichlid species, females invest in brood care, either with or without male assistance. Male investment

in reproduction is not entirely restricted to direct care-taking and nest defense; sometimes, males also provide resources such as foraging opportunities to females prior to spawning and thereby supposedly increase female fertility and their own reproductive output. In several species with uniparental maternal brood care, this kind of male investment in reproduction has been observed. In a population of *Neolamprologus tetracanthus*, harem-holding males avoided feeding in the females' territories, probably in order to preserve food resources for females, to provide them with an incentive to stay, and to promote their gonadal maturation [39]. Likewise, no paternal brood care is provided in the mouthbrooding *Tropheus* species, as females mouthbrood their offspring by themselves. Prior to spawning, however, the female *Tropheus* (except for *T. duboisi*) stay in their mates' territories for several days to weeks, where they feed heavily under their mates' protection [40]. Upon spawning, females leave their mates to mouthbrood solitarily. Paired females in a population of *Tropheus* sp. "black" [41, 42] had higher gonadosomatic indices and condition factors than solitary females, which suggests that the resources available in the males' territory are crucial for gonadal recovery and maturation of ovaries [40]. Opportunities for efficient and protected feeding in the courting males' territories are also used by females of the maternal mouthbrooder *Simochromis pleurospilus* [21].

2.1. Mating and Parenting Behavior of Substrate Breeders.

In substrate breeders, brood care is carried out by both parents or by the female alone or with the assistance of helpers, and resource distribution and brood care requirements often determine whether or not individuals—usually males—can have more than one mating partner at a time. Harem breeders with little, if any, paternal brood care include the lamprologines *Lepidiolamprologus profundicola*, *L. lemairii*, *Altolamprologus compressiceps*, *Neolamprologus furcifer*, *N. mondabu*, and *N. modestus* [19, 24, 32, 34, 43, 44]. In contrast, exclusive monogamy and biparental guarding were observed in *Neolamprologus tretocephalus* [24, 43, 44], *Boulengerochromis microlepis* [45], and *Variabilichromis moorii* [35, 46, 47]. Males of several predominantly monogamous lamprologine species (*Lepidiolamprologus elongatus*, *L. attenuatus*, and *Neolamprologus toae* [22, 32, 44, 48]) sometimes breed with two and occasionally more females when adjacent breeding sites are available [24]. Parental roles are often divided between the sexes, with the smaller partner, which is in many species the female, remaining closer to the fry and providing direct brood care and the larger partner defending the peripheral parts of the territory (or the adjacent breeding sites) against intruders [19, 35, 43, 46, 48–50]; but see [47]. In biparental *Telmatochromis temporalis* and *Neolamprologus toae*, removal of the nest-tending males resulted in the loss of the clutches [22, 51], which exemplifies the necessity of biparental care as a constraint to polygyny. Sexual conflict over care became apparent in a study of *Julidochromis ornatus*, where the larger fish of the pair, irrespective of sex, induced their smaller partners to spend more time close to the brood and provide direct brood care, and the difference

in the amount of care between the sexes increased with increasing size differences [50]. Size-dependent division of labor was also observed in other *Julidochromis* species and contrasts with the situation in most other substrate breeders where direct brood care is usually provided by the female (D. Heg, pers. comm.).

The duration of brood care varies between a few weeks to several months. *Lepidiolamprologus profundicola*, *L. lemairii*, *Lamprologus callipterus*, *Telmatochromis vittatus,* and *Altolamprologus compressiceps* do not guard free-swimming young, and brood care extends to no more than 2-3 weeks [25, 52, 53]. Including guarding of free-swimming fry, parental care is performed for 4-5 weeks in *Neolamprologus furcifer* [34], for 8–12 weeks in *Lepidiolamprologus attenuatus*, *L. elongatus* [32], *Neolamprologus modestus*, and *N. toae* [23], for 14 weeks in *Variabilichromis moorii* [35], and for 20 weeks in *Neolamprologus tretocephalus* [32]. In *N. furcifer*, the next brood was often produced before the previous one had left the territory of their mother [34].

Years of genetic parentage studies in fish have demonstrated that the social behavior does not always reflect the true shares in parentage and have led to the distinction between social and genetic mating systems [54]. This applies to cichlids as well: an exceptionally high level of multiple paternity was found in broods of the socially monogamous *Variabilichromis moorii*, where each of ten broods was sired by two to >10 males. In contrast, all offspring in a nest shared the same mother. The nest-tending males of this species apparently suffer substantial cuckoldry and provide care for a large number of unrelated fry [55]. Alloparental brood care is also provided by males of the socially monogamous biparental substrate breeder *Telmatochromis temporalis*. In this species, females spawn in small holes or under stones and nest entrances are too narrow for the large, territorial males to enter. However, small males stayed inside the nests of some pairs and sired offspring in several instances [48]. These small males had high gonadosomatic indices, indicating that they represent a sneaker phenotype adapted to sperm competition with the paired male. Several of the nests with small males contained offspring sired by both territorial and sneaker males. Moreover, a small number of nests without small males contained offspring, which were unrelated to one or even both of the nest-tending individuals, perhaps as a consequence of replacement of the parental fish. Some of the paired males were also observed to visit one or two additional females [48]. In another study, large unpaired males were observed to attack nest owners, court with paired females, and then leave the nests again in the care of the nest owner [56]. This pirating behavior might be a source of unrelated offspring in nests without sneaker males.

2.2. Shell Breeding.

A specialized form of substrate breeding in lamprologine cichlids is shell breeding, whereby the inside of empty gastropod shells is used as a protected nest site [57]. Several substrate breeders facultatively utilize shells in addition to rock crevices and holes (*Lamprologus lemairii*, *L. laparogramma*, *L. signatus*, *Lepidiolamprologus pleuromaculatus*, *Neolamprologus caudopunctatus*, *N. fasciatus*, *N.*

leleupi, *N. multifasciatus*, *N. similis*, *Telmatochromis dhonti*, and *T. vittatus*), while others are specialized, obligatory shell breeders (*Altolamprologus* sp. "shell" of Cameron and Nkamba Bay, *Lamprologus callipterus*, *L. meleagris*, *L. ocellatus*, *L. ornatipinnis*, *L. speciosus*, *Lepidiolamprologus boulengeri*, *L. hecqui*, *L. meeli*, *Neolamprologus brevis*, *N. calliurus*, and *Telmatochromis temporalis* "shell-bed dweller" [58, 59], summarized in [57, 60]). Shell size constrains the body size of the shell-breeding cichlids; in some species, both sexes are sufficiently small to fit into shells (e.g., *L. ocellatus*) while other species display extreme size polymorphism with small females and males too large to enter the shells (most notably *Lamprologus callipterus* [61, 62], see below). Males control one to several females, and harem formation and size may depend on shell availability (e.g., in *L. callipterus* [57, 63] and *T. vittatus* [64]). While beneficial to the male, the recruitment of additional female breeders may conflict with the interests of the resident female [65–67]. In the facultatively polygynous *Lamprologus ocellatus*, males control female access to shells. In aquarium experiments, aggression by a resident female delayed the settlement of additional females, and mutual aggression among females continued in established harems. Peace-keeping interventions by the males occurred in the majority of aggressive situations and were crucial for the maintenance of the harem [66]. Further experiments suggested that the fitness of harem females suffers from offspring mortality due to aggressive interactions between juveniles from different cohorts [67].

Maternal guarding predominates among the shell breeding species; only the facultative shell breeders *N. caudopunctatus* and *N. leleupi* are biparental guarders [19, 20, 57]. At a study site in southern Lake Tanganyika (Wonzye Point), a population of a strict shell breeder, which was initially identified as *Neolamprologus meeli* but later recognized as a new species *Lepidiolamprologus* sp. "meeli-boulengeri" [68], contained ten monogamous pairs and two harems with two and five females, respectively, and both males and females defended against nest predators [69]. Genetic parentage analyses of these monogamous and polygynous breeders and the young in their nests revealed that about one-third of the 19 young of monogamous pairs were not related to either the male or the female, and three additional young were not related to the male; furthermore, the two analyzed young of a polygynous group were not related to the harem holder. Sneaking and stepfathering were suspected to be the origin of unrelated young [69].

Alternative reproductive phenotypes and tactics, including cooperative breeding, have been observed in many more LT cichlid species and are addressed later in further detail.

2.3. Mouthbrooding. LT cichlids other than the Lamprologini and *Boulengerochromis microlepis* are mouthbrooders. Several combinations of mating and mouthbrooding behaviors exist. In some species, mouthbrooding of eggs and small fry is followed by biparental guarding of free-swimming fry, which are retrieved into the parents' mouths when danger is perceived. In most mouthbrooders, however, brood care is performed exclusively by the female, and periodical release

of fry for feeding has been reported in only a few maternal mouthbrooders including *Ctenochromis horei*, *Simochromis pleurospilus,* and *Tropheus* spp. [20, 31, 70, 71].

The costs of mouthbrooding, such as reduced growth, delayed gonadal recovery, and increased intervals between spawning [37, 72–75], are particularly high when the breeding parents feed little or not at all during mouthbrooding [20, 31, 73, 76] and become even higher when parents expend energy and incur predation risks for buccal feeding of their young to subsidize their growth and prolong protective brooding past resorption of the yolk [31, 76]. Mouthbrooders of some species take up food to nourish both their fry and themselves. Brooding *Cyphotilapia frontosa* achieved 25% of the gut fullness index of nonbreeders but did not recover their gonads while they were breeding [74]. Buccal feeding started while young were still in an early developmental stage with large yolk sacs, and gut fullness of young increased over the long mouthbrooding period (54 days [30]) [74]. Continuous foraging during mouthbrooding was also observed in *Tropheus duboisi*. The gut fullness index of mouthbrooding females amounted to 80% of that of nonbreeders, and no difference in condition factors was detected between breeding and nonbreeding females [31, 77]. Likewise, brooding *Microdontochromis* (*Xenotilapia* [38]) *rotundiventralis* parents had only slightly lower food picking rates and the same condition factors as nonbreeding fish, and females even recovered their gonads during the breeding period [28]. Buccal feeding requires some extra room in the buccal cavity. The necessary reduction of clutch size may be compensated by shorter spawning intervals of females if they are able to remain in good condition by feeding themselves along with their fry [31].

The duration of continuous mouthbrooding is shorter in species with a subsequent guarding phase than in those species which mouthbrood their fry till independence. Mouthbrooding and guarding last for 1.5 and 4.5–7 weeks, respectively, in *Haplotaxodon microlepis* [78] and *Perissodus microlepis* [79], for 2 and 0.5–3.5 weeks, respectively, in *Xenotilapia flavipinnis* [80], for 2 weeks each in *Simochromis pleurospilus* [71], and for 2-3 and 0–4 weeks, respectively, in *Ctenochromis horei* [70]. Without subsequent guarding, 3-4 weeks of mouthbrooding are shared between females and males in *Tanganicodus irsacae* [37] and *Eretmodus cyanostictus* [75], and 4-5 week long maternal mouthbrooding is performed in *Tropheus* spp. [31]. Particularly long continuous mouthbrooding for 54 days (i.e., almost 8 weeks) was observed in *Cyphotilapia frontosa* [81].

The duration of mouthbrooding differs not only between species, but also sometimes between individuals. While there was little variance in the duration of mouthbrooding in *Tropheus moorii* ($n = 7$; 33.2 ± 1.1 days) [31], *Ctenochromis horei* females mouth bred for shorter but more variable periods ($n = 8$; 19.1 ± 3.1 days) [70] and were shown experimentally to prolong mouthbrooding when exposed to fry predators [82]. Tuning of reproductive investment may be even more comprehensive. In *Simochromis pleurospilus*, females adjust their reproductive rate and offspring size according to the environmental conditions, which they had encountered as juveniles. Females experimentally raised

in poor conditions produced larger eggs and young and spawned at shorter intervals than females raised on a high-food diet, irrespective of the conditions during adulthood [71, 83]. *Simochromis pleurospilus* juveniles disperse into the shallow habitat, whereas the adults occupy deeper water. Therefore, the conditions experienced during the mother's own juvenile phase are a better predictor of her offspring's juvenile environment than the conditions in her current habitat [71]. The impact of egg size on potential survival benefits of young was pronounced when food was scarce. Young hatched from large eggs maintained a size advantage over young from small eggs, had higher burst swimming speed, and, importantly, spent less time foraging and more time sheltering, which—in a natural setting—should markedly reduce their predation risk. In contrast, young raised with plentiful food supplies behaved similarly regardless of egg size [84].

2.4. Mating Behavior and Paternity in Maternal Mouth-brooders.

In maternal mouthbrooders, the investment in reproduction, in terms of energy and time, is clearly skewed towards the female. Mating generally occurs in the males' territories, which can be arranged in expanded leks, and polygamy is the norm in these species. Indeed, multiple paternity was demonstrated by genetic data in some of the broods of *Ctenochromis horei* with up to five sires per brood [85] and *Simochromis pleurospilus* with one or two sires per brood [86]. Multiple paternity can result from successful alternative male reproductive behavior such as sneaking or from deliberate polyandry when females visit several males for spawning [20]. The latter was observed, for example, in *Paracyprichromis brieni*, in which males establish courtship territories in the water column near rocks [87], in the lekking, crater-building *Cyathopharynx furcifer* [88, 89] and *Ophthalmotilapia ventralis* [90], and in *Ctenochromis horei*, where a female temporarily escaped the mate guarding dominant male [70]. A female *Pseudosimochromis curvifrons* was seen visiting and courting with two males, but no spawning occurred on this occasion [91]. Intrusions by neighboring territory owners and attempts of parasitic spawning may also cause a female to interrupt spawning with her current mate and perhaps later resume spawning with a different male, as observed in, for example, *Gnathochromis pfefferi* [92] and *Ophthalmotilapia ventralis* [93]. In contrast, females of another open-water spawner, *Cyprichromis microlepidotus*, were observed to spawn their entire clutch with one male [87], and several of the genetically analyzed broods of *Ctenochromis horei* (43%) [85] and *Simochromis pleurospilus* (65%) [86] were in fact sired by a single male each. Only one or two broods have so far been analyzed with respect to genetic relatedness in other polygamous maternal mouthbrooders (the Tropheini species *Simochromis diagramma*, *Petrochromis fasciolatus*, *P. orthognathus,* and *Gnathochromis pfefferi*). Except for one of the two investigated broods of *P. fasciolatus*, the Tropheini broods were sired by a single male each [94]. The peculiar mating system of *Tropheus* spp. (excluding *T. duboisi*) with pair bonding prior to spawning and maternal mouthbrooding has already been mentioned above. No evidence of multiple paternity was found in a total of 19 broods of *Tropheus moorii* from southern Lake Tanganyika [94], and although the males siring the broods were not identified, it is likely that they are indeed those with whom the females paired prior to spawning [40].

2.5. Biparental Mouthbrooding.

In monogamous mouth-brooders with biparental care, we find maternal mouthbrooding followed by biparental guarding in *Perissodus microlepis* [79], *Plecodus straeleni* [20]), and *Xenotilapia papilio* [19]. Biparental mouthbrooding, whereby the female broods eggs and early fry before the male takes over all (or part, as in *Microdontochromis rotundiventralis* and *Haplotaxodon microlepis*) of the larger fry, is either followed by biparental guarding as in *Xenotilapia longispinis*, *X. flavipinnis*, *X. spilopterus*, *Asprotilapia* (*Xenotilapia* [38]) *leptura* [19, 80], and *Haplotaxodon microlepis* [78] or occurs without guarding as in *Xenotilapia boulengeri* [80], *Microdontochromis rotundiventralis* [28], *Eretmodus cyanostictus* [37, 95, 96], and *Tanganicodus irsacae* [37]. Pairs of *Eretmodus cyanostictus*, *Xenotilapia flavipinnis*, *X. spilopterus,* and *Asprotilapia leptura* remain together for several breeding cycles [28, 75, 80].

The remaining Perissodini species (in addition to the above-mentioned *P. microlepis*, *P. straeleni* and *H. microlepis*) are also biparental care givers, but it is not known whether it is maternal or biparental mouthbrooding that precedes biparental guarding [19]. In contrast to the biparental *E. cyanostictus* and *T. irsacae*, another Eretmodini species, *Spathodus marlieri*, performs exclusively maternal mouthbrooding [37], and no information exists on *S. erythrodon*. Three Limnochromini species, *Limnochromis auritus*, *Reganochromis calliurus,* and *Triglachromis otostigma*, were described as biparental mouthbrooders with guarding in the popular science literature [41]. Several Ectodini species in addition to the above-mentioned *Xenotilapia*, *Microdontochromis,* and *Asprotilapia* species are also biparental mouthbrooders, while other species of the tribe perform maternal brood care [97, 98].

Advantages of biparental over uniparental care during the guarding phase of monogamous mouthbrooders can readily be conceived with regard to defense against fry predators, whereas the adaptive value of monogamy is less clear in species lacking the guarding phase. One conceivable advantage is the doubling of brooding space resulting from the division of broods between the parents, as in *Microdontochromis rotundiventralis* [28], but different explanations must be found for species in which females shift the entire brood to males. The constraints on mate desertion have been discussed in some of the above-cited studies, and were addressed in more detail in *Eretmodus cyanostictus*. Genetic parentage analyses of broods collected in the field confirmed that the species is both socially and genetically monogamous [99]. Different reasons for monogamy were proposed: costs of desertion arising from remating prospects were identified by Morley and Balshine [95], who concluded from removal experiments in the field that monogamy results from the need to guarantee high-quality mates and territories

in a competitive environment, and by Taylor et al. [99] who argued that the difficulty of finding a new partner, given a male-biased sex ratio and assuming costly locomotion (suggested by the reduction of the swim bladder) along with vigorous mate guarding preclude polygyny (see also [96]). Benefits of biparental mouthbrooding were identified by Grüter and Taborsky [100] after experimentally separating mouthbrooding females from their mates. After a prolonged incubation period, single mothers released smaller and less-developed young than paired controls, and it was concluded that monogamy was favored by the necessity of male care. In another experiment of Grüter and Taborsky [101], experimental manipulation of sex ratios did not significantly alter mate desertion rates, but sexual conflict about brood care became apparent as males took the offspring later when several females were present [101], and females made up for condition-dependent reduction of male care by prolonged incubation [102].

3. Mixed Broods: Farming Out and Fry Dispersal

Broods containing unrelated con- or heterospecific fry have been observed in both substrate breeders and mouth-brooders. In general, possible origins of foreign young include kidnapping, nest takeovers, egg stealing, accidental mixing among neighbors, fry dispersal, communal care, egg dumping, and farming out [103, 104]. With the exception of brood parasitism by the catfish *Synodontis multipunctatus* [105], brood mixing in the Lake Tanganyika cichlids has been attributed to farming out, nest takeover, and fry dispersal between schools. By farming out (also termed "young dumping" [104]), the parents transfer their fry to the nests or brooding sites of other breeders and abandon them to the foster parents' care. Benefits of delegating parental duties are quite obvious. The less intuitive adaptive value of brood adoption to the foster parents derives in some species from predation dilution and heightened success in mate acquisition [103, 104]. For mouthbrooders with their limited buccal brooding space, involuntary brood adoption may be disadvantageous, and targeted foster parents have been observed to drive away young-dumping adults [106, 107] and to be reluctant to accept foreign young [80, 108].

In the biparental mouthbrooder-guarder *Perissodus microlepis*, farming out was induced experimentally by removal of one parent during the guarding phase. Some of the remaining parents attempted—sometimes successfully—to put the brood under the care of another conspecific brooding pair, which was interpreted as adaptive behavior to cope with occasional mate desertion and increase the chances of brood survival [108]. Later, "farming out" of young was also observed under natural conditions [107] and as a tactic adopted by paired males, presumably to evade paternal investment [106]. Young *Perissodus microlepis* were also found in broods of other species (e.g., of *Lepidiolamprologus elongatus* [104]).

Brood mixing and farming out of young, both to conspecific and to heterospecific parents, occur in several species in addition to *Perissodus microlepis*. A number of observations of heterospecific brood mixing have been reported with guest species including several biparental mouthbrooders, *Cyprichromis* species, *L. elongatus,* and *L. attenuatus*, and hosts including *P. microlepis* and the substrate breeders *L. elongatus*, *L. attenuatus*, *L. profundicola*, *Neolamprologus caudopunctatus*, *N. pulcher*, *N. savoryi,* and *N. tetracanthus* [36, 109, 110]. Three out of 23 mouthbred broods of *Haplotaxodon microlepis* contained conspecific young of obviously different sizes, presumably as a consequence of farming out, and larger juveniles mixed with guarded broods of *P. microlepis* [78]. Free-swimming young of the biparental mouthbrooder *Microdontochromis rotundi-ventralis* were found under parental care of *P. microlepis*, *L. elongatus*, and several other substrate breeders [28]. One event of successful farming out of free-swimming fry and several unsuccessful attempts were observed in the biparental mouthbrooder *Xenotilapia flavipinnis*. Additionally, brood mixing was indicated by increasing numbers of young in several territories [80].

The mouthbrooders' habit of taking fry into the mouth facilitates the transport involved in farming out, but brood mixing may also be initiated by the young themselves. For example, large young *X. flavipinnis* invaded a neighboring territory and eventually were accepted by the guarding pair [80]. Likewise, foreign conspecific young in nests of the substrate breeder *Lepidiolamprologus* sp. "meeli-boulengeri" (*Neolamprologus meeli* in the original publication) were large enough to have entered their foster parents' territories on their own, although nest takeover could not be excluded as a source of nonkin young [69]. Similarly, replacement of breeders and immigration of large fry from neighboring nests were suggested as alternative explanations for mixed broods in *Julidochromis ornatus* [111]. Foreign fry were also detected among large mouthbred young of the maternal mouthbrooder *Simochromis pleurospilus* [86]. Mouthbrooding *S. pleurospilus* occasionally release late-stage fry to feed and then collect them back into their mouths, which may be an opportunity for neighboring females to accidentally or deliberately mix fry [20, 71].

4. Cooperative Breeding

Several of the substrate-breeding cichlids of LT breed in groups consisting of dominant breeders and a variable number of subordinate helpers. Heg and Bachar [112] listed 19–21 (counting aquarium observations of two species) cooperatively breeding LT cichlid species from several different lineages in the tribe Lamprologini [60, 113]. Characteristics of helper systems vary among LT cichlids, with differences in group sizes, degrees of helper-breeder relatedness, and levels of direct helper reproduction. Therefore, different hypotheses about benefits and costs of helping, such as kin selection, paying to stay, and helper reproduction as an alternative reproductive tactic, can be addressed and tested in the different species. *Neolamprologus pulcher* has been the prime model species among the LT cichlids to study causes, effects, costs, and benefits of helping and the regulation of

group composition, group size, and division of labor [114–145].

Data on group composition and helping behavior of *Neolamprologus pulcher* have recently been reviewed by Wong and Balshine [119] and are summarized here only briefly. In fact, the first detailed studies of brood-care helping in fish were made in *N. brichardi* (conspecific with *N. pulcher* [146]) in northern LT [114, 147]. Subsequently, a wealth of field data were collected from *N. pulcher* in southern LT. Social groups are arranged in clusters and consist of dominant breeders and up to 20 male and female helpers, with an average group size of 7–9 individuals. Direct brood care, for example, fanning and cleaning of eggs and larvae, is usually provided by dominant females and female helpers [121, 130, 147]. Breeders and helpers of both sexes participate in territory defense and maintenance [147]. Both monogamy and polygyny occur, and although males holding several breeding territories were shown to be larger, less parasite-infected and to invest more in spermatogenesis, there was no difference in number and survival of young between monogamous and polygynous breeders [148]. Breeders are eventually replaced by dominant helpers [149], and the turnover rate is higher for male than for female breeders [150]. Offspring remain at home for a prolonged period of time, but eventually, some helper turnover results from dispersal into other groups, often associated with a rise in the helper dominance hierarchy [149, 151]. Female helpers are more likely than male helpers to inherit the breeding position of their relatives [150, 152], whereas dispersal rates are biased towards large males [153]. Probably as a consequence of both helper and breeder turnover, genetic relatedness of helpers to breeders declines with helper age, and helpers are more closely related to the female than to the male breeder [150]. Although related individuals may achieve breeding positions in the same group, apparently no measures are taken to avoid pairing among relatives [154].

Helpers were shown to reproduce in experimental groups (e.g., [121, 122, 141, 145, 155]). In field groups, genetic data confirmed a low level of female, but no male, helper reproduction [156, 157], but the detection of helper reproduction in the field may be compromised by the possible expulsion of reproducing helpers from the group [156]. Indeed, cage experiments in the field revealed that helper males do sometimes gain parentage (D. Heg, pers. comm.). Reproductive suppression of male helpers may make them inefficient sperm competitors to breeder males [133, 158]. The reproductive success of female helpers may be curbed by suppression of egg laying and the destruction of their clutches, although some reproduction may be tolerated in return for continued brood care [117, 130].

In Dierkes et al.'s study [156] of 12 social groups, maternity of the dominant females was confirmed in all but one group (in which the breeding pair had probably been replaced), whereas paternity of the dominant males varied from 0 to 100%. The fathers of the extra-pair young could not be identified. Paternity levels of harem males were not significantly different from those of monogamous males. Stiver et al. [157] examined five social groups from the same location and found both multiple maternity, in one case due to reproduction by a female subordinate, and multiple paternity, in two cases with offspring sired by dominant males from other groups. Paternity of dominant and subordinate males from neighboring groups was also observed in an experimental setup (D. Heg, pers. comm.).

A similar composition of cooperative breeding groups to that in *N. pulcher* was described in the closely related *Neolamprologus savoryi* [159]. Males were either monogamous or, when larger, polygynous with up to four females, each of which defended a separate subterritory (subgroup). Helper numbers ranged from three to 33, and mean group size was 14 individuals. Sexual size dimorphism between breeders was more pronounced in *N. savoryi* than in *N. pulcher*, entailing potential differences in life history strategies, for example, regarding age at reproduction and helper strategies, between the two species [159]. Genetic analyses of relatedness and parentage in two populations in southern LT (Kasakalawe and Kasenga) revealed a low level of helper reproduction, with higher reproductive success of male than of female helpers [160]. In groups with multiple breeding females, the females breeding within the same patch of stones were more closely related to each other than to breeder females from separated patches, which suggests that subgroups within a patch are founded by close relatives through expansion of the territory. Overall, subgroups and groups consisted mainly of related individuals with only 16–25% immigrants, and both patrilinear and matrilinear territory inheritance were common (33% and 52%, resp.). In contrast to *N. pulcher*, helpers in *N. savoryi* groups are more closely related to the dominant male than to the dominant female, probably as a result of a lower turnover rate of male breeders and a higher level of patrilinear territory inheritance [160].

The tiny, shell breeding *Neolamprologus multifasciatus* lives in groups of several reproductive males, females, and their offspring. Genetic analyses [161] identified these groups as extended families, with close relatedness among breeding males and between adult females and the alpha male. Mating occurred between full sibs and between offspring and parents, and large male helpers shared in reproduction. Exchange between groups is female-biased [65, 162]. Cooperative breeding is also performed in the closely related *N. similis* [112].

In all species of the genus *Julidochromis*, at least some of the breeding pairs are assisted by helpers. In a population of *J. marlieri* at Bemba, northern DR Congo, monogamous pairs predominated while a particularly large female bred with two males, and some of the breeders were assisted by one subordinate helper [49]. Similarly, Taborsky [104] observed helpers in several families of *J. marlieri* at Magara, Burundi. Following up the observed occurrence of polyandry, experiments demonstrated female-biased aggressiveness and dominance in this species [163].

Details of social interactions and genetic parentage have been studied in breeding groups of *J. ornatus* in southern LT [111, 112]. At Kasenga Point, Awata et al. [111] found that the majority of groups consisted of monogamous breeding pairs without helpers, followed by monogamous pairs with

helpers, and a small proportion of groups representing polygynous (with two or three females) or polyandrous (with two or three males) harems with helpers. Typically, only one helper was present in a nest, but haremic nests could include up to six helpers. Male helpers were commoner than female helpers. In nearby Kasakalawe, Heg and Bachar [112] studied 28 groups consisting of breeding pairs and zero to five helpers. Importantly, the formation of several new groups could be documented, whereat breeding pairs established themselves at previously unoccupied sites and were joined by subordinates. In the Kasenga Point population [111], kinship analyses revealed that offspring in both monogamous and polygamous nests were either full sibs, half sibs, or unrelated, and the degree of intrabrood relatedness decreased with increasing size of young, consistent with both replacement of adults and immigration of unrelated young. Most of the helpers were not the offspring of the current breeders. The reproductive success of helpers was about as high as that of breeders, making helping an alternative option to pair breeding for small males [111]. Similar kinship structures and high rates of helper reproduction were detected in two additional populations of *J. ornatus* [164] as well as in *Chalinochromis brichardi* (Kohda et al.'s unpublished data cited in [111]), a close relative of *J. ornatus* [113]. In *J. ornatus*, the presence of sperm competition between male breeders and helpers was strongly indicated by the finding that both helpers and male breeders invest more in testis mass in cooperative breeding situations than do breeding males without helpers. Moreover, the gonadal investments of helpers and breeders of the same nests were positively correlated, and finally, offspring numbers increased with increasing testis mass [164]. Responses to perceived risk of sperm competition were also observed in the cooperative breeder *J. transcriptus*, where males kept in polyandrous groups developed larger testes than males in monogamous groups [165]. In the field, the breeding system of *J. transcriptus* resembles that of *J. ornatus* and *J. marlieri* with predominantly monogamous, biparental brood care and a smaller proportion of cooperative breeding groups. In experiments, the mating system depended on body size, with polygamous mating of large individuals of each sex and monogamous pairing among similar-sized individuals [166]. Female *J. transcriptus* prefer wedge-shaped rock crevices as nest sites, which apparently allow them to control paternity shares of differently sized males in polyandrous breeding groups and to reduce reproductive skew among males in a group: eggs laid on the wider part of the wedge are fertilized by large males, whereas males, which are small enough to enter the nest, escape aggression by large males and fertilize eggs in the inner part of the wedge [167].

5. Sneakers, Satellites, and Other Parasites

External fertilization, indeterminate growth, and high investment in brood care invite the employment of alternative reproductive tactics [168]. Individuals of many LT cichlid species exhibit a variety of phenotypes and behaviors to take their share in reproduction despite reduced investment

in mate attraction and brood care. Helper reproduction in cooperatively breeding groups is one such example. Another example is the farming out of brood to conspecific pairs in order to reduce own brood care effort (note that interspecific brood care does not meet the definition of alternative tactics [169]). Different male phenotypes, associated with different reproductive behaviors, were detected in several substrate-breeding species, whereas reproductive parasitism in mouthbrooders was not found to be associated with pronounced morphological differentiation between bourgeois and parasitic individuals.

An extreme and well-studied example for divergence in male reproductive tactics is represented by the obligatory shell breeder *Lamprologus callipterus* [52, 61, 63], recently reviewed in [168]. Females enter shells completely, attach eggs to the wall of the shell, and perform brood care for about two weeks. The largest males, which are about 12 times heavier than the females [62], adopt the bourgeois tactic of courtship and nest defense, often preceded by active transport of scattered shells into their nests [52] and hold large harems with up to 18 females [57]. Other ways to come by or augment nests are shell stealing and territory takeover, typically associated with female expulsion and infanticide [52, 170]. Nest-holding males feed little or not at all, fuelling their "capital breeding" strategy on previously accumulated reserves, and extend their tenure to an average of 33 days [171]. Prior to becoming territorial, these males opportunistically spawn parasitically in the nest of bourgeois males by releasing sperm into the shell opening, but this behavior was assumed to result in only low reproductive outcomes [172]. In addition to these conditional tactics, there is also a fixed, genetically determined tactic of dwarf males [171], which are only 2.5% the size of nest males and considerably smaller than females. Dwarfs take advantage of temporary absences of the nest-holding males to wriggle past the females into the inner whorl of the shell, where they exploit the safety of their position to fertilize eggs in competition with the nest owners [52, 63, 171, 172]. The gonadosomatic index of dwarf males is much higher than that of nest-holding males [171]. Genetic analyses revealed that the dwarf males' share in paternity is low, which is perhaps compensated by their earlier onset of reproduction [63]. The polymorphism of reproductive pathways is probably maintained by frequency-dependent selection [63, 171]. Body size of dwarf males is determined by the small inner space of the shell left over by the breeding female and covaries with shell size and female body size among populations [173]. Apparently, the pronounced intrasexual size dimorphism among *L. callipterus* males is promoted by disruptive selection for large size in nest-holding males and small size in males adopting the parasitic tactic [173].

A similar variety of male tactics was observed in the hole-breeding *Telmatochromis temporalis*, which features large nest-holding males, small-sized males with large testes spawning inside nests and large pirates temporarily replacing the nest owner [48, 56] (see above). Small males with high gonadosomatic indices were also found in the shell-breeding *Neolamprologus brevis* (M. Aibara, pers. comm. to Katoh et al. [48]).

Four reproductive tactics were observed in a population of the facultative shell breeder *Telmatochromis vittatus* in southern LT, where this species breeds as guest in the large shell beds assembled by *L. callipterus* [174]. In this species, pronounced sexual size dimorphism allows the females to enter rock crevices or shells for spawning and brood care, while males in the upper size range spawn at the nest entrance. Large males defended shells and controlled several females; males even larger than the territorial males acted as pirates, temporarily ousted the nest owners during spawning and performed the posture of sperm ejaculation at the shell entrance; medium-sized males pair-spawned in single shells; small males acted as sneakers by spawning either inside the shell or at the shell entrance during absence of the nest-holding male. Sperm competition among territorial and parasitic males was inferred from the increasing gonadosomatic indices between pair spawners, polygynous nest holders, nest pirates, and sneakers [174], from similar differences in sperm swimming speed [175], and from the plastic increase in sperm longevity of territorial males when faced with the risk of reproductive parasitism [176]. Although the number of sneakers per nest is high, pirates present an even greater threat to nest holders as they procure unrestricted access to fertilization [64]. The home ranges of pirates include several nests, between which they travel repeatedly in order to detect ongoing spawning events. The incidence of piracy is high with 0.3 to 1.8 invasions per hour during the 3-hour period of spawning by the territorial male and is negatively correlated with the distance between nests and with the size of the nest owner [53, 64]. The quality of a nest is, therefore, determined not only by the number of shells it contains, which is positively correlated with the number of females at the nest [64], but also by its position relative to other nests, which predicts the risk of piracy. In fact, keeping the risk of piracy low seems to be a more important criterion for nest choice than nest size [53].

Parasitic reproduction was inferred from genetic parentage data in the biparental substrate-breeding cichlids *Lepidiolamprologus* sp. "meeli-boulengeri" (*Neolamprologus meeli* in the original publication [69]) and *Variabilichromis moorii* [55] (see above), but no alternative reproductive phenotypes and behaviors were observed, and the social status of the extra-pair males remains unknown. Spawning synchrony in *V. moorii* may constrain paired males to their own nests during the period when fertilizable eggs are available, such that extra-pair fertilization may mostly be achieved by unpaired males [55].

Extra-pair spawning and fertilization were also detected in several maternal mouthbrooding species. Some males parasitize on the mate attraction success of territorial, courting, colorful, or otherwise attractive males. *Paracyprichromis brieni* males establish courtship territories in the water column near vertical rock surfaces and lead approaching females to the rock surface for spawning [87]. Attempts of sneaking were observed in this species but not in another open-water spawner (*Cyprichromis microlepidotus*) mating away from the substrate, probably because sneaking males find hiding space and refuge more easily in the rocky

area [87]. Interruptions of pair-spawning by neighboring or other conspecific males were also observed in *Gnathochromis pfefferi* [92], *Ctenochromis horei* [70], and *Pseudosimochromis curvifrons* [91]. In *G. pfefferi*, intruders were repulsed by the mating males, but in *C. horei*, the intruder quivered in parallel with the dominant male while the female nuzzled the dominant male's genital area, and extra-pair fertilization may have occurred. In a different population of *C. horei*, genetic analyses revealed multiple paternity of some broods, which could be due to both sneaking and deliberate polyandry [85].

In *P. curvifrons*, intruders either placed themselves in a spawning position parallel to the resident male or assumed a spawning position while the resident male and female were changing their display positions, which sometimes led to the female nuzzling the intruder's genital area. Intrusions occurred one to several minutes after the last spawning of the pair while the pair still continued reciprocal display and nuzzling, and sneak fertilization may depend on the extent to which eggs have previously been fertilized by the resident male. Intruders were either of the same size as or smaller than the resident males and seemed to be nonterritorial floaters [91].

In two closely related species, *Ophthalmotilapia ventralis* and *Cyathopharynx furcifer* [97], intruding males take advantage of the resident male's temporary distraction from defense. Territorial *O. ventralis* males spit sand onto horizontal rock surfaces to mark their mating territory by a small and rather untidy crater, to which they lead females for spawning. Quite frequently, floater males were observed to sneak into the territory and court the female, when the bourgeois male was temporarily absent chasing off other males. The small body size and good body condition of floaters suggested that floating (and sneaking) represented a transitional stage on the way to territoriality although males might also switch back and forth between the two behaviors [93].

The large mating craters built by males of *Cyathopharynx furcifer* (and an undescribed congener) and the activity associated with their construction apparently provide cues for female mate choice [89, 177]. The female deposits eggs in the crater and picks them up into her mouth after the male has passed over (and probably fertilized) them [88]. In a population in southern LT, the efforts of the crater-holding males were exploited by floaters, which occasionally succeeded to enter the crater, when the owner was occupied fending off other potential intruders, and rapidly performed spawning motions on the same spot where the crater owner had previously done so. Probably the intruding male mixed his sperm with that of the territory owner for the female to subsequently take up into her buccal cavity [178]. Four alternative male behaviors (sneakers, satellites, pirates, and female mimics) in addition to territoriality were described in one population of another crater-building species, *Aulonocranus dewindtii* [179].

Among biparental mouthbrooders, intraspecific brood farming out (see above) remains the only alternative reproductive tactic described so far.

6. Intraspecific Variation in Mating and Breeding Behavior

Interindividual variation in the number of mates, that is, monogamy versus polygamy, was detected in many of the studied populations, both in substrate breeders and in mouthbrooders (mentioned previously). A second component of mating system variability, which has repeatedly been encountered, is introduced by differences between populations, often correlated with differences in nest-site availability or predation pressure. In the substrate-breeding *Neolamprologus tetracanthus*, monogamy with male participation in brood care predominated in northern LT (Nyanza Lac), whereas males in southern LT (Wonzye) held harems with up to 14 females, and brood care was performed by females. Densities of *N. tetracanthus* were similar in the two locations, but nest predation pressure was higher in the northern population, such that biparental brood care may be indispensable in this population. Moreover, the lower density of potential nest sites in the northern location might also contribute to monogamy [180]. A relationship between nest-site (gastropod shell) density and mating system was also hypothesized in connection with disparate levels of polygyny (predominant monogamy versus predominant polygyny) detected in two studies of *Neolamprologus meeli* (now *Lepidiolamprologus* sp. "meeli-boulengeri" [68]) in southern LT [57, 69].

Differences in shell supply and shell sizes between localities may also influence the level of polygyny in *Lamprologus callipterus*, perhaps indirectly through an effect on male size [52, 57, 63]. In one location in southern LT (Wonzye), large shells are abundant and males grow to large sizes in order to be able to transport these shells to their nests; here, males hold large harems (average of 4 and maximum of 18 females). In a site in northern LT (Kalundu), large shells are less abundant, males grow on average somewhat smaller than in Wonzye, and maximum, but not average, harem size is smaller (average of 5.5 and maximum of 14 females). Finally, on the north-east coast (Rumonge), males do not transport shells, which already occur at high density in the habitat, and remain distinctly smaller and hold smaller harems (average of 2.4 and maximum of 7 females) (see also [181]).

Local shell size was proposed to determine not only the nest-holding male sizes but also the occurrence of dwarf males, which would only evolve in the presence of sufficiently large shells and when there was a lot to be gained by early onset of parasitic reproduction [63]. However, the more recent finding that dwarfs adjust their growth to available shell size [173] and observations of dwarfs at all of the three ecologically distinct locations (K. Ota, pers. comm.) reject this hypothesis for *L. callipterus*. It may still apply to another species, *Telmatochromis temporalis*, where a relationship was observed between the nest hole size and the occurrence of dwarf males [48]. In southern LT (Nkumbula (=Mbita) Island), nest burrows were too small for large males to enter, and small males with high gonadosomatic indices entered the nests to spawn inside. In contrast, in a population in northern LT (Bemba), the rocky crevices used for nesting can be entered by the nest males, and sneaker phenotypes were not observed there [48].

Geographic variation in social structure and in the occurrence of alternative reproductive phenotypes was also found in maternal mouthbrooders such as the crater-building *Aulonocranus dewindtii*, where nonterritorial males in one isolated population exhibited various alternative reproductive phenotypes not found in other places [179]. It was suggested that the limited opportunities for crater construction at this particular location imposed pressure on males to employ alternative reproductive tactics. In the likewise crater-building *Cyathopharynx furcifer*, the reported interpopulation differences in the mating and social behavior included the habitat type, on which territories and mating craters were established, the size of males defending mating craters, and the occurrence of parasitic reproduction. Craters were built both on rock and sand in Luhanga in northern LT but only on rock in Wonzye, southern LT. In Luhanga, small males held craters on sand, whereas in Wonzye, small males held territories without craters. Parasitic reproduction occurred only at Wonzye. Differences in predation pressure at the two sites were considered to account for these behavioral differences [178], but another, taxonomic rather than ecological, explanation is possible. A closely related, not yet formally described species (currently known as *C. foae*) occurs sympatrically with *C. furcifer* in southern LT while it is not clear whether both species or only *C. foae* occur in northern LT [33]. It is also not clear whether previous studies distinguished between the two species and putative intraspecific variation could in fact be an interspecific difference between *C. furcifer* and *C. foae*. The same applies to observed differences in female mate choice behavior between *Cyathopharynx* populations in northern and southern LT. Here, a relationship between female preferences and characteristics of the males' mating craters was detected in a southern (Kasakalawe) population of *Cyathopharynx furcifer*, but not in a northern (Bemba) population [88, 89]. Rather, in the latter population, the number of visiting females was related to the length and symmetry of the males' pelvic fins [88].

In *Ctenochromis horei*, dominant males monopolized mating in a northern population (Bemba) [70], whereas genetic parentage reconstructions in a southern population (Kalambo) were not compatible with monopolized reproduction but rather suggested that a large number of males sired offspring [85]. Moreover, there was a difference in the levels of multiple paternity of broods between two seasons, since all broods had two to five sires in March, while all but one October broods had only a single (but different) sire each. The sampling times fell into the rainy season (March) and the dry season, such that a seasonal effect is possible and requires further studies [85].

7. Evolution of Mating Systems and Parental Care Patterns

Models of the evolution of parental care patterns in fish have been summarized, for example, by Mank and Avise [182] and Balshine-Earn and Earn [183]. The stepping stone model assumes stepwise transitions starting from the absence of parental care followed by male-only care arising as a side

effect of territoriality and defense of a spawning site, followed by a switch to biparental care in conditions either when care by both parents is required to assure survival of the brood or when females spawn only once in a season. Finally, changes in the operational sex ratio may increase the remating opportunities for one sex and promote mate desertion and uniparental (usually maternal) brood care. A competing model postulates independent origins of paternal, maternal, and biparental care from the ancestral absence of care. Comparative phylogenetic analyses across actinopterygian families accumulated stronger support for the independent origins than for the stepping stone model [184]. Within Cichlidae, however, maternal care (and paternal care in species of one genus, *Sarotherodon*) apparently evolved from biparental care systems, as predicted by the stepping stone model: the ancestral care type is biparental substrate-breeding, and several transitions occurred towards mouthbrooding and towards female-only care [2, 19, 183, 185, 186]. Additionally, among the Ectodini of LT, reversals from maternal to biparental mouthbrooding occurred in the genera *Xenotilapia* and *Microdontochromis* [97, 98].

The habit of mouthbrooding may have its origin in the oral transport of young by substrate guarders after hatching or repeatedly during the entire care period as, for example, in the LT cichlid *Boulengerochromis microlepis* [25]. Furthermore, biparental mouthbrooding, followed by biparental guarding in some LT cichlids, likely represents an intermediate form along the way from biparental substrate-breeding to uniparental mouthbrooding [19, 183]. Constraints on mate desertion in a biparental mouthbrooder, *Eretmodus cyanostictus*, were examined and discussed in several of the studies addressed above [95, 96, 99–101]. Uniparental, that is, female-only substrate-guarding evolved in biparental guarders as a response to opportunities for resource defense polygyny and harem formation, presented by high nest-site densities and numbers of receptive females [19, 24] and is contingent on the efficacy of uniparental guarding [22]. An additional constraint on both the social mating behavior and the employment of alternative tactics is imposed by lunar synchronization of spawning [55, 187–190], adopted by several substrate-guarding species presumably in order to increase nest-guarding efficiency and the safety of juvenile dispersal in moonlit and dark nights, respectively [24, 35], and by at least one mouthbrooder (*Cyprichromis leptosoma*) with less obvious adaptive value [36]. The observation of synchronized brooding in *Eretmodus cyanostictus*, which could have served to reduce remating opportunities and hence prevent male mate desertion in the biparental brooder [96], could not be confirmed in subsequent studies [75].

By assigning LT cichlids to two levels of sexual selection and tracing the correlated evolution of sexual selection intensity and parental care patterns on a phylogenetic tree, Gonzalez-Voyer et al. [2] concluded that transitions to female-only care were contingent on a previous intensification of sexual selection. As such, the study lends support to a view on the relationship between parental care and sexual selection [4] opposite to the more traditional notion that sex-specific differences in parental care investment underlie the operation and strength of sexual selection [191].

7.1. Mapping Evolutionary Transitions on Phylogenetic Trees: Not All Is Yet Resolved. The great diversity of traits and the generally good resolution of gene trees make LT cichlids profitable and promising subjects for phylogenetic studies of trait evolution, not only with respect to parental care behavior, but also regarding life history and morphological traits [2, 12, 13, 15]. Nonetheless, when counting character transitions on phylogenetic trees of LT cichlids, it must be kept in mind that the placement of some taxa in mitochondrial gene trees may differ from their true relationships, for example, due to ancient incomplete lineage sorting and ancient hybridization among species, and that some nodes are endorsed only by low-statistical support [60, 68, 113, 192–194]. Taxon clades reconstructed from multiple nuclear loci (AFLP), at odds with mitochondrial clades in several instances, are often considered better representatives of species relationships than are mitochondrial gene lineages (e.g., [42, 194–196]), but often suffer from even lower statistical support for branching order than the mitochondrial trees (which can be improved by assembling data from a very large number of loci). A successful example of trait reconstruction on a well-resolved AFLP phylogeny is the study of parental care pattern evolution in the tribe Ectodini [98]. Beyond that, a useful basis for future studies could be established by building multilocus nuclear phylogenies, perhaps utilizing next-generation sequencing techniques rather than AFLP, of all LT cichlid species and tribes, and their allies outside LT. Despite some caveats, though, the general patterns identified so far are most likely bound to hold.

8. Sexual Dimorphism

The general correlation between mating systems and sexual selection intensity is reflected by the degrees of sexual dimorphism in taxa assigned to different mating systems [54], also when comparing the pronounced dimorphism in many of the female-only mouthbrooding LT cichlid species with the generally low levels of dimorphism in the biparental substrate breeders. Based on these apparent relationships, mating patterns and the occurrence of size and color dimorphism have been used to infer the action of sexual selection and approximate its strength [2, 12, 14, 15]. In a few cichlids of LT, however, presence or absence of sexual dimorphism is at least in part due to reasons other than sexual selection.

In the extremely size-dimorphic *Lamprologus callipterus*, the females, which breed in gastropod shells, can be less than 10 percent of the weight and half the length of the nest males, which fertilize clutches by spawning at the shell opening. While female size is constrained by the requirement to fit into shells, nest males must be large enough to be able to carry shells to their nests [52]. Studying a population in southern LT (Wonzye), Schütz and Taborsky [62] concluded from the observation of female preferences for large shells and the absence of sheltering within shells that *L. callipterus* descended from large- or intermediate-sized ancestors. This proposition is consistent with current phylogenetic data [60]. Hence, it was suggested that small female body size was

a derived trait, following from natural selection imposed on females by the dimensions of their breeding substrate [62]. This was endorsed by subsequent field and laboratory studies [197] as well as modeling studies [198] addressing the selective forces acting on male and female body sizes. The absence of female preferences for male or nest size (number of shells) argued against intersexual selection for large male size, and small effects of intrasexual selection due to longer nest tenure of larger males were considered possible. A minimum size proved to be necessary for males to carry shells, whereas female body size was obviously limited by shell size and females adjusted growth to available shell sizes [197]. Likewise, the model suggested an effect of intrasexual selection and shell carrying on male size and a strong constraint on female size by the breeding substrate [198]. Contrasting with the above mate choice behavior, another study revealed female preferences for large males at a location, where shells were less abundant (Kasakalawe) than in the locality of the above study (Wonzye). When shells are scarce, females associated with small males face the risk of nest takeover or shell stealing by larger males and hence, the risk of expulsion and infanticide [170]. Furthermore, another population (Rumonge), which is notable for its small males, was recently reported to deviate from the general habit of using shells for breeding but not for sheltering. The habitat at this location provides no other refuge than shells, and at the same time, males at this location are not required to transport shells due to their natural distribution. Small male size in this population was suggested to be an adaptation to sheltering in shells made possible by the relief from shell transport [181]. In the populations other than Rumonge [181], both male and female body sizes were positively correlated with shell size, and the observed negative size allometry (the average size differences between males and females decreased with increasing average body size across populations) was explained by the female growth adjustment to shell size availability. Additionally, male-male competition for nests and fecundity selection on females were shown to affect body sizes [181]. All in all, the extreme sexual size dimorphism in *L. callipterus* appears to be a consequence of multiple and variable selection regimes, with only an auxiliary role for sexual selection.

In another shell breeder, *Lamprologus ocellatus*, sexual selection on females was shown to work against the rather moderate size dimorphism (4–6-cm versus 3–5-cm body size in males and females, resp.), since both male choice and female competition for breeding opportunities favor larger females [67]. Female body size is of course constrained by shell size, such that natural selection contributes to maintaining the existing dimorphism.

A maternal mouthbrooding species, *Tropheus moorii*, is notable for being sexually monochromatic while at the same time displaying most pronounced geographic color pattern diversity. Here, the diversification of male and female coloration was probably synchronized by the social system. Both sexes defend their feeding territories against competitors and neighbors of the same and opposite sexes. Body coloration is used as a means of communication in social interactions: Sturmbauer and Dallinger [199] distinguish between neutral, aggressive, subordinate and moving coloration (see also [200, 201]). Territoriality of males and females has been suggested to drive the evolution of conspicuous coloration while simultaneously constraining the evolution of sexual dichromatism [40, 199, 200, 202], but studies directly addressing this hypothesis are still needed. At any rate, the action of sexual selection in *Tropheus* cannot be excluded despite the absence of sexual dimorphism. For males, the possession of a sizeable territory is a prerequisite for mating success [40]. The outcome of male-male competition for good-sized territories, therefore, influences male reproduction, resulting in intrasexual selection (while the dual function as mating and feeding territory puts its defense under natural selection as well). Despite the pair-bonding prior to spawning, the operational sex ratio is likely to be male-biased due to the long female time-out periods during mouthbrooding and recovery [31, 203]. Concordant female preferences for certain males and concordant shunning of others were observed in laboratory female-choice experiments [204], such that intersexual selection may occur as well. In the natural setting, the variance in male reproductive success may be substantial, and sexual selection may be acting in *Tropheus* but has not been expressed as sexual dichromatism due to constraints by other forces.

9. Quantifying Sexual Selection

Estimates of sexual selection intensity in LT cichlid species have been derived from their mating systems [14] in combination with sexual dichromatism and size dimorphism [2, 15] for comparative phylogenetic studies. A cross-season comparison of potential sexual selection in a single population, based on genetic paternity data, employed indices representing the opportunity for selection [85]. Further proxies and measures of sexual selection include the operational sex ratio, potential reproductive rates of each sex, selection differentials, and Bateman and selection gradients, each with its own strengths and weaknesses [205]. Bateman's gradients and indices of the opportunity for selection, I, address some of the preconditions for the action of sexual selection, such as covariance between reproductive and mating success and variance in fitness among individuals of a population. While these conditions are prerequisite to sexual selection, positive values of their measures fail to tell whether or not sexual selection is indeed acting in the system [205]. For example, the opportunity for sexual selection is calculated as the variance in relative mating or reproductive success among individuals of a sex. However, any variance among males could also be random, in particular when there are fewer receptive females than males such that some males remain without a mate even though there may be no discrimination on the part of the females. The confusion of random and selection-based variance is acknowledged by the interpretation of I as the upper limit of sexual selection intensity [205–207]. Measures of I will become more meaningful with regard to the operation of sexual selection if they are combined with a demonstration of female choice or if they are calculated across several breeding

seasons as random variances within seasons are likely to cancel out, at least to some degree, across seasons.

Few studies addressed mate choice and variance in reproductive success in LT cichlids. In *Cyathopharynx furcifer*, males differ considerably in their attractiveness to mate-searching females, and both their ornamented fins and their craters are candidate targets for sexual selection [88, 89]. Reproductive variance among males of *Lamprologus callipterus* results from complex interplays between intra- and intersexual as well as natural selection; both body size and nest characters may serve as mate-choice cues under different circumstances [170, 197]. In *Tropheus moorii*, female mate-choice may cause variance in male reproductive success, but the responsible traits have yet to be identified [203, 204, 208–210]. Not always, however, do mate preferences translate into actual mating patterns: size-assortative pairing of the biparental mouthbrooder *Eretmodus cyanostictus* [95] is not driven by preference (which would favor larger individuals) but rather by ecological constraints and intrasexual competition [211].

Another issue is the distinction among intrasexual, intersexual, and natural selection. Components of the variance in reproductive success often include territoriality and fertility, which may be considered to fall into the realm of intrasexual and natural selection, whereas being chosen for mating is clearly a matter of intersexual selection. Here, the researcher must take decisions on which individuals to include in the measurement of variance (All? Only nest holders? Only mated individuals? See [212] for the different implications of these approaches) and on the currency of fitness (Number of mates? Number of offspring? See [207]). While counting offspring rather than mates includes fertility (a component of natural selection), a restriction to mate numbers ignores unobserved alternative tactics and sperm competition, which can be highly relevant to the intensity of sexual selection [90, 213–216]. Collecting genetic data for the analysis of reproductive variance can be a challenge in itself [217]. In highly abundant species, such as *Tropheus*, *Variabilichromis moorii,* and other littoral LT cichlids, the probability of capturing close relatives is small even in large population samples due to the sheer numbers of individuals in a population [55, 203, 218], which makes the identification of nonparenting sires and dams difficult. In less abundant or pelagic species, dispersal may essentially create the same problem. Moreover, the number of nonreproductive individuals is difficult to establish. Some shortcuts are possible: for example, Wade and Shuster [219] showed that in haremic systems, the opportunity for sexual selection on males is proportional to the mean harem size of mated males, which can more easily be determined. For LT cichlids, this would allow to grade sexual selection intensity in polygynous populations with different harem sizes, provided that parasitic reproduction is negligible.

Selection gradients and selection differentials are more directly linked to sexual selection as they address the effect of the phenotype on reproductive success and the effect of sexual selection on phenotype evolution (contingent on heritability), respectively [205]. Obviously, though, it is necessary to identify the crucial trait(s) in order to include

them into the analysis, and these may not be immediately obvious in some species (e.g., [204]).

Certainly, the best (or most feasible) approach to the assessment of sexual selection intensity depends on the aim and the scope of the investigation. Questions associated with the action of sexual selection at the population level are typically quite concise, for example concerning particular phenotypic traits and mate choice, and can be targeted by determining mate preferences, selection gradients, and selection differentials. At species levels, for example concerning correlates of species richness and phylogenetic studies of trait evolution, traits under selection will vary between taxa, and the available options will be limited to assessing the potential for sexual selection in the different taxa from benefits of multiple mating and from variances in reproductive success, to some degree represented by the mating system, or to infer the action of sexual selection from the presence of sexual dimorphism. However, alternative reproductive behaviors affect the distribution of reproductive success and hence sexual selection in different ways depending on the underlying social mating system and the details on status and success of the parasitic spawners [213–215]; moreover, sexual dimorphism may also result from natural selection (see above). Adding geographic and seasonal variations, it may in fact be very difficult to grade sexual selection intensity at the level of species.

10. Conclusions

Over the last decades, a tremendous amount of information on the mating and parental care behavior of LT cichlids has been assembled through extensive field work and, especially more recently, through experiments addressing the proximate and ultimate causes of different behaviors. Additionally, genetic techniques have proven valuable tools to complement observational data and, specifically, to target relatedness, parentage, and reproductive success.

Comprehensive insight into a range of topics associated with reproductive behavior and evolution has been gained by detailed studies of individual LT cichlid species, including cooperative breeding systems in *Neolamprologus pulcher*, *Julidochromis* spp., and *N. savoryi*, alternative male phenotypes and sexual size dimorphism in *Lamprologus callipterus*, sperm competition in *Julidochromis* spp., *L. callipterus,* and *Telmatochromis vittatus*, biparental brood care in *Eretmodus cyanostictus*, brood farming out in *Perissodus microlepis,* and context-dependent maternal investment in *Simochromis pleurospilus.*

Overall, alternative reproductive behaviors and phenotypes are well understood in some species, while for others, the evidence is presently rather anecdotal. Furthermore, in some species, alternative tactics have been described, but their success remains unknown, while in others, genetic parentage analyses indicated brood mixing and multiple mating, but information on the involved individuals is lacking. While each of the two approaches (genetic and behavioral) have provided valuable information, our understanding of mating and parental behavior will further benefit

from an increased integration of behavioral studies and genetic analyses of individual reproductive success, a strategy which has already been practiced in several exemplary studies. Sexual conflict appeared in connection with harem formation and parental investment in at least four species (*L. ocellatus*, *N. multifasciatus*, *J. ornatus*, and *E. cyanostictus*), and may arise in many more species as well as on additional occasions such as the choice of mating and fertilization partners. The role of ecology in shaping behavioral patterns of LT cichlids has long been recognized and certainly merits further experimental work. Mate choice has been addressed in only few species, perhaps because sexual selection has long been considered of secondary importance in the evolution of LT cichlids. Nonetheless, a variety of potential mate-choice cues, including body coloration, body size, territory quality, nest, and mating crater characteristics, invite further studies about male and female decision making.

When the information on mating or parental care behavior originates from single populations and single points in time, as is still the case for many species, geographic and temporal variation may go unnoticed. Already, numerous examples document that intraspecific variation and alternative behaviors vitiate species-level classifications of mating and parental care systems, on the one hand creating a predicament for studies relying on the categorization of a species' behavior into one of few discrete categories and on the adherence to a certain behavioral pattern across short terms as well as evolutionary timescales. On the other hand, it is exactly this variability that provides the opportunities to examine how the interactions of different factors—such as genetic influences, sexual conflict, and all aspects of ecology—culminate in the display of certain behaviors by particular individuals or populations.

Acknowledgments

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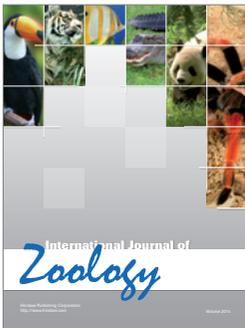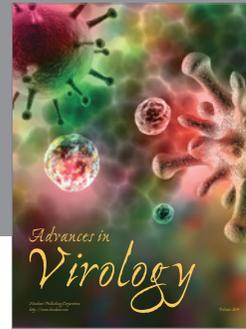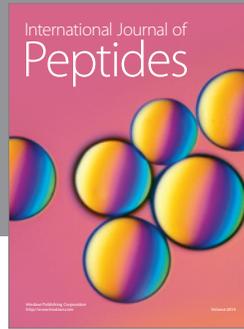[56] S. K. Mboko and M. Kohda, "Piracy mating by large males in a monogamous substrate-breeding cichlid in Lake
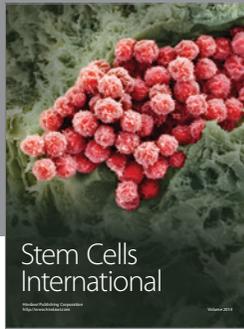
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