



Resource Defence or Exploded Lek? – A Question of Perspective

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Received: August 13, 2010

Initial acceptance: August 17, 2010

Final acceptance: August 17, 2010

(J. Kotiaho)

doi: 10.1111/j.1439-0310.2010.01831.x

Abstract

It becomes increasingly obvious that animal mating systems cannot be classified into distinct categories, but transitions between mating system classes are continuous. Positioning a certain mating system at this continuum is often not straightforward, however. Depending on which characteristic is considered, a mating system may end up at very different positions on this gradient. Here, we explore the potential conflict between mating system classifications that may arise when they are based on different criteria by investigating the mating system of the cichlid fish *Simochromis pleurospilus* in which males defend small patches of homogeneously distributed food resources (turf algae) vigorously against food competitors, but they allow specific females to use them. We hypothesized that male defence may generate high-quality feeding patches serving to attract females, and hence male territoriality constitutes a form of courtship. Our field data show that males selectively allow approximately one-third of the visiting females to feed on their territory and that females preferentially feed in male territories and usually sample several territories successively. As males protect food patches against other algae grazers and guard females from harassment by food competitors, females gain nutritional benefits from visiting male territories. Hence, males appear to generate essential resources for females, which is the key feature of resource-defence mating systems, although the distributions of resources and of males and females are characteristics of an exploded lek.

Introduction

Mating systems involving male territorial defence are usually characterized based on categorical characteristics (Emlen & Oring 1977), for instance the number of mates per male or per female, the presence of resources within territories, the spatial distribution of neighbouring territories, whether male territories include female territories and how many, or the purpose of female visits at territories (see Shuster & Wade 2003). In leks, the purpose of female visits seems to be clear, as a *lek* is defined as 'aggregated male display that females attend primarily for the purpose of fertilization' (Höglund & Alatalo 1995). In *exploded leks*, male territories within

such aggregations are fairly large, and sometimes may contain resources used by females (Emlen & Oring 1977). *Resource-based leks* differ from exploded leks in that they contain resources that are critical for females and males display close to or at these critical resources (Jiguet 2002). Finally, in *resource-defence mating systems*, males control the access to critical resources that females require for reproduction (Emlen & Oring 1977). Although these categories seem well defined, it is not always straightforward to classify a certain mating system of interest as they often include characteristics of different categories. When males set up territories in which females may feed or even breed, a mating system would still be classified as an exploded lek, if the resources present

are not essential for females and the females do not base their mate choice on the quality of these resources but rather on male quality (e.g. in Little Bustards, *Tetrax tetrax*; Jiguet 2002). The same system would have been classified as resource-defence mating system, if females were observed to preferentially feed at male territories.

Thus, even if the conventional mating system classification based on categorical characteristics implies that mating systems represent discrete entities, they may often be better described by their position along a continuum of each of the characteristics. In this study, we investigate different characteristics of the mating system of *Simochromis pleurospilus*, a cichlid fish of the Tropheini tribe from Lake Tanganyika, East Africa, to explore the potential conflict between mating system classifications that may arise when they are based on different criteria. Cichlids of this tribe exhibit a remarkable diversity of mating systems ranging from classical leks (*Pseudosimochromis curvifrons*; Kuwamura 1987) to a temporal, resource-based monogamy, where females establish a pre-mating bond for approximately 2 wk to get access to a male's feeding territory (*Tropheus moori*; Yanagisawa & Nishida 1991). Another member of this tribe, *S. pleurospilus*, uses turf algae as its sole food source, and these algae follow a uniform distribution, similar to grassland and heath, where lekking species are often found (e.g. Deutsch 1994; Höglund & Alatalo 1995). Male territories have been observed to be small and spatially clustered. Thus, superficially the distribution of resources and male territories resembles an exploded lek. Given the uniform algae distribution, it appears unlikely that *S. pleurospilus* male territories represent particularly attractive foraging grounds for females. Nevertheless, females are often observed to feed at these territories. This suggests that possibly territory defence *per se* might improve the resource quality and/or the feeding opportunities for females. In this case, males may defend territories primarily to attract females.

If male defence can generate patches of essential resources that otherwise would not be available, a comparison of the spatial distribution of resources relative to the distribution of males and females may not suffice to distinguish exploded leks from resource-defence mating systems. If resources such as turf algae were *a priori* homogeneously distributed, which would normally exclude the monopolization of essential resources by territory holders, direct observations of female resource use may nevertheless reveal the existence of high-quality feeding sites. Here, we investigate whether in

S. pleurospilus male territorial defence creates an essential resource for females and whether it attracts females to a certain location, thereby generating opportunities for males to court them. Specifically, we investigate (1) the spatial distribution of male territories, (2) whether the prime purpose of male territory defence is to attract and to court females and (3) whether there is evidence that only receptive females are allowed to feed. Moreover, we test (4) whether females are attracted to male territories and (5) whether they obtain nutritional benefits from feeding in male territories. Based on our results, we conclude that the mating system of *S. pleurospilus* cannot be assigned unambiguously to a single mating system category. While the distribution of resources and male territories reminds of exploded leks, the creation of high-quality feeding sites through male defence and their preferential use of these sites by feeding females are clearly features of resource-defence mating system.

Materials and Methods

Study Species

Simochromis pleurospilus is a maternally mouth-brooding cichlid of the Tropheini tribe. It inhabits the rocky lakeshores between 0.5 and 12 m depth, where it feeds on epilithic turf algae. Juvenile food availability determines adult behaviour (Kotrschal & Taborsky 2010), and the productivity of algae declines greatly with depth, differing by two orders of magnitude already within the first 2 depth meters (Taborsky 1999). This decline goes along with a decline of biomass of algae-grazing cichlids (B. Taborsky, unpub. data). *S. pleurospilus* reproduces all year round.

Simochromis pleurospilus are sexually dimorphic with males being larger and expressing an iridescent green colour and red spots lacking in both females and juveniles. Mature females and juveniles can be distinguished by size. Adult males defend small, adjoining territories of 2–4 m² vigorously against con- and heterospecific food competitors. The area of a male territory is clearly defined by the locations where attacks and displacements of all other algae grazers take place. Juveniles and females are non-territorial and use large home ranges. Females spawn within male territories (B. Taborsky, laboratory obs.). After spawning, females leave the male territory immediately and care for the clutch on their own (Taborsky 2006a,b).

Study Site

We collected our data at the southern tip of Lake Tanganyika at the western shore of Nkumbula Island, Zambia (8°45'16.40"S, 31°5'28.81"E) by SCUBA diving. The study area included 100 m of shoreline down to a water depth of 12 m. In the first depth meter of the littoral zone, the lake bottom is covered by rounded stones of approximately 20 cm in diameter turning into smaller pebbles below 1 m depth. Below 3 m, there are sandy patches mixed with stones of 5–30 cm. All stones are covered by a layer of turf algae and from 3 m downwards additionally with a thin layer of fine sediment.

Distribution of Males and Females

We recorded the size structure of the population by conducting transects of 100 m length in parallel to the shore, every 0.5 depth metre between water depths of 0.5 and 12 m. We repeated these transects at the same location three times for each hour of the natural daylight period (7.00–16.00) on three different days, adding up to a total of 720 (3 × 10 × 24) 100-m transects. During each transect, we swam approximately 1 m above the transect line and noted the estimated size (to the nearest 1.0 cm) of each male, female and juvenile *S. pleurospilus* occurring within 2 m to the left and to the right of the transect line. The slope of the lake bottom at our study site is very shallow, so that the parallel transect lines at the different depths were several metres away from each other and no overlap between transect areas occurred.

Focal Female Observations

We chose the focal females for our behavioural observations such that they represented the natural

distribution of females' sizes across their natural water depth range. With help of the distribution data described previously, we compiled 60 combinations of times of day, depths and female size classes for our behavioural recordings, so that they were spread equally over the day and represented the natural female size and depth distribution. Of the 60 focal females that were observed, in 46 cases, we obtained a complete 20-min recording. In the remaining 14 cases, females were lost prematurely during the recording, and these data were discarded for all but one analyses. We observed only non-incubating, adult females (i.e. females of adult size: ≥6 cm) that did neither hold a clutch in their buccal cavity nor guarded a clutch, which can easily be seen from a distance of several metres.

During 20-min focal observations, we continuously recorded several behaviours of the focal females. We noted the number of feeding bites and whether a female exhibited courtship or whether it was courted (i.e. the male circles around the female, adopting an upright position and quivers with its entire body in front of the female) and whether it responded by body quivering. A female may alternately be courted by a male, leave a territory to feed alone, and then start courtship at another territory with another male (see Fig. 1). Furthermore, we recorded threat behaviour, where a focal fish stops feeding and spreads its fins towards another individual resulting in a change of the opponents' swimming direction. We also noted when females were displacing other fish or were displaced. During displacements, the focal fish moves 1–2 body lengths towards another fish when being the initiator or away from it when being the recipient of an aggressive interaction. Finally, when the focal fish moved more than two body lengths when being the initiator or recipient of an aggressive interaction, we classified this as chasing or being chased, respectively.

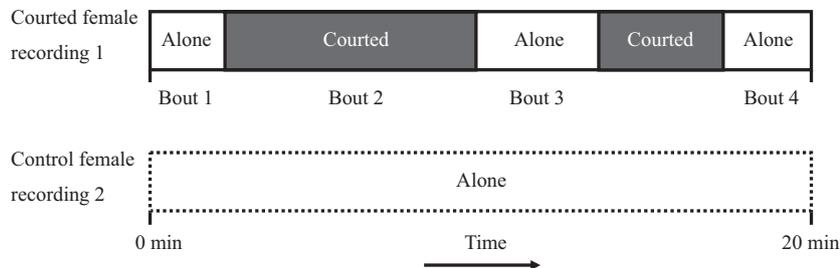


Fig. 1: Examples of the temporal patterns of observations. A box represents one 20-min recording. Recording 1 (solid frame): female that was courted at least once per recording, white: feeding on her own, before and after leaving a male territory; black: feeding while being courted at a male territory. Recording 2 (dashed frame): female that was not courted during a recording but was of similar size at similar depth at the same daytime on another day (matched recording).

Along with the time of observation and the average depth during 20 min, we noted the status of initiator and receiver of each social interaction (conspecific male, female, juvenile or heterospecific). Additionally, we noted the position of any males relative to the focal female and, as a measure of feeding efficiency per covered distance, we noted whenever a female had moved an estimated distance of 50 cm ('50-cm swim'). We did 46 complete 20-min recordings, in 19 of which courtship occurred. In 16 of these 19 recordings, a territorial male had initiated the courtship, and in the other three cases, the female had initiated courtship but was immediately displaced by the male. The 16 recordings where the males started courting were used to compare the behaviour of females feeding within or outside a male's territory.

We chose not to mark our animals individually as for our study species no individual marking technique exists that would keep visible during the entire 3 mo of this study, and repeated catching would have been too stressful for the fish. Nevertheless, it is highly unlikely that repeated recordings were performed on the same females for the following reasons: There were at least 85 females present at the study area (as determined by a live-capture survey during a single morning at the end of the study season; it is likely that a certain proportion of females escaped the survey). The recordings were equally spread over an observation period of 3 mo, which means that most females will have spawned once during this period and were therefore unavailable for our observations for a brooding period of at least one-third of the study, which generated a certain turnover of females available for our observations. The starting locations of our female recordings were equally distributed over the entire study area, and the observation of interactions therefore took place at different territories (between 2 and 7 m depth).

Data Analysis

We performed several analyses to test whether females accrue nutritional benefits from feeding in male territories. We tested whether females were exposed to less aggression (being displaced or being chased by other fish) when feeding in a male's territory. To assess the overall influence of a male's presence on a female's ability to feed without being disturbed, we compared the rates of aggressive acts received in 20-min recordings with or without courtship taking place (16 vs. 27 recordings; see Fig. 1: recording 1 vs. recording 2). However, the likelihood

of being disturbed while feeding might be confounded by behavioural characteristics of the focal female itself or by the level of food availability to algae-grazing competitors, which varies with time of day because of the diurnal rhythm of algal photosynthesis and with water depth (see Taborsky 1999). To control for these possibilities, we compared the number of feeding bites taken by individual females successively without being interrupted when either within or outside a male territory (1) for individual females (intra-individual comparison of 16 recordings between phases with and without courtship; see Fig. 1: recording 1, black vs. white bars) and (2) between different females feeding at the same time of day and water depth by matching the 16 recordings, during which courtship occurred repeatedly, with another 16 recordings taken within the next 3 d, during which no courtship occurred (inter-individual comparison, see Fig. 1: black bars of recording 1 vs. recording 2). To assess whether females had a higher net energy gain of feeding in territories, we tested whether individual females fed more per travelled distance within or outside the male territories (number of feeding bites taken per '50-cm swim'; intra-individual comparison within 16 recordings where courtship occurred; see Fig. 1: recording 1, black vs. white bars). Finally, to test whether differential female food intake inside and outside male territories is solely because of disturbance by other fish, we compared female bite rates between the 16 recordings with the occurrence of courtship and another 16 recordings without courtship that were matched for the amount of aggression received, water depth and female size (inter-individual comparison, see Fig. 1: recording 1 vs. recording 2).

We used a generalized linear model (GzLM) to estimate the effect of depth on the rate of aggressive acts females were exposed to. We included as a categorical variable whether or not females were allowed to feed at a territory during a recording. For this analysis, we used all observations with observation times >10 min and present the data as rates of aggressive acts received per minute for each observed female (as aggressive interactions with other algae feeders occur at a high rate for this behaviour, 10 min is suffice to obtain a representative estimate). To account for diminishing variance with increasing depth, we adjusted the scaling parameter using the maximum likelihood method (Norusis 2007). We used non-parametric statistics whenever the data distributions violated the assumptions of parametric testing. All analyses were performed with SPSS 17.0; SPSS Inc., Chicago, IL, USA.

Results

Distribution of Males and Females

In our study area, *S. pleurospilus* occurred between 1 and 12 m depth, and the mean densities of the sexes were similar (males: mean: 1.44 males/100 m, range 0.09–4.29; females: mean: 1.78 females/100 m, range 0.32–4.0; $N = 30$ surveys). Males defended territories only between 1 and 8 m depth, and their densities peaked at a single depth of 2 m (mean: 4.43 males/100 m, $N = 30$ surveys). In contrast, females were bimodally distributed (Fig. 2). The upper peak coincided with the peak of the male distribution at 2 m (mean: 3.0 females/100 m), and there was a second peak at 7 m (mean: 4.0 females/100 m).

The above figures on male densities also demonstrate that within a given depth, males defend only a small fraction of the available habitat. Even if we assume that all territories are of maximal size (4 m^2), and the entire area of the territories was included within the area covered by a transect count (400 m^2 ; cf. 'Methods'), male territories at the peak density depth of 2 m would cover only 4.43% of the available habitat ($100 \times 4.43 \times 4 \text{ m}^2 / 400 \text{ m}^2$) and much less in all other depths.

Courtship Function of Male Territories

If the prime purpose of male territories is to attract females for courtship, only reproductively active males should defend a territory, and all courtship

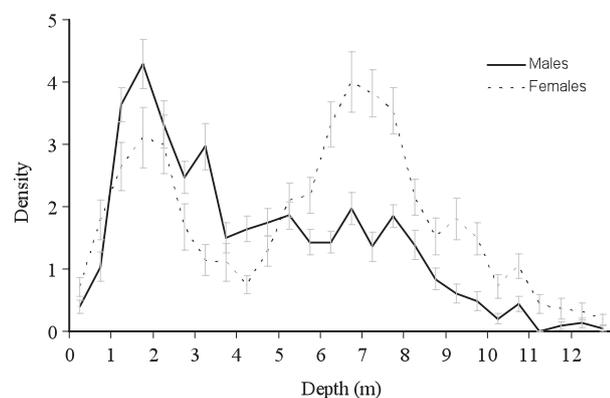


Fig. 2: Distribution of male and female *Simochromis pleurospilus* across different depths (mean number of individuals \pm SE). Solid line: males; dashed line: females. The low abundance of *S. pleurospilus* (and other algae feeders; A. Kotrschal, pers. obs.) between 3.5 and 5.5 m depth reflects a peculiarity of our study site: the substrate in these depths consists of coarse sand and is hence unsuitable for turf algae growth.

should take place on these territories. None of 83 adult focal females in 28 h of observation (20-min recordings; this study) and 154 females in 13 h of observation (5-min recordings; B. Taborsky, unpubl. data) defended a territory. Also juveniles are non-territorial; they form mixed flocks with other algae-feeding cichlids (A. Kotrschal & B. Taborsky, unpubl. data). All observed courtship displays during the 20-min recordings took place at male territories. We never observed any courtship behaviour by territorial males outside their territories or by non-territorial males (41 h of observation).

Selective Tolerance of Females

It was not possible to assess the state in the breeding cycle of our focal females. However, if males tolerate only receptive females on their territories, we expect that males evict a substantial proportion of the visiting females. Of 133 females observed approaching a male territory, females were immediately chased away in 77 cases (58%). In 56 cases (42%), males initiated courtship and continued to court the female at short intervals. While at a male territory, females fed continuously only interrupted by courtship responses (body quiver) to male displays. When the female did not show body quivering during the first three male displays, she was evicted by the male. Seven times a female visited two male territories and three times a female visited three male territories within 20 min. Within a 20-min recording, females approaching male territories were either always accepted (8 recordings, 35%), always evicted (7 recordings, 30%) or both responses occurred at different territories (8 recordings, 35%).

Are Females Attracted to Male Territories?

If male territories provide essential feeding resources to females, *S. pleurospilus* females should actively sample male territories, and they should be attracted to territories in the first place. If male territories vary in resource quality because of different male defence abilities, females should reject some of the territories, i.e. they should leave without being evicted by the owner. Male territories covered only roughly 2% of the area *S. pleurospilus* use for feeding, but in 32 (69%) of our recordings, females attempted to feed at a territory at least once, despite relatively low chances of being tolerated by a territory holder (only 42% of these attempts). In 23% of the cases, in which females were tolerated, they left the territories, while the territory owner was still courting them.

Nutritional Benefits for Females at Territories

Aggression received

During recordings with courtship, females were exposed to lower rates of aggression from food competitors (mainly by *T. moorii*) than during recordings without courtship (aggression received per min: Mann–Whitney *U*-test; $Z = -2.07$, $p = 0.038$, $N = 61$; Fig. 3a). Moreover, females feeding within territories fed in longer undisturbed bouts than the same females when feeding outside the male territories during the same 20-min recording (paired *t*-test: $t = 3.24$, $p = 0.006$, $N = 16$; Fig. 3b central bar) or than different females of the same size feeding outside territories at the same daytime and depth (paired *t*-test; $t = 2.88$, $p = 0.011$, $N = 16$; Fig. 3b right bar).

Feeding efficiency

Whether a female was inside or outside males' territories affected their feeding rates: to reach the same

number of feeding bites, females outside males' territories had to swim longer distances during the same recording (Wilcoxon matched-pairs signed-ranks test: $Z = -2.64$, $p = 0.008$, $N = 16$, Fig. 4a). Also, when comparing recordings from different females within and outside territories (individuals matched for the number of aggressive actions received, water depth and body size), females feeding inside male territories had higher feeding rates than females outside territories (paired *t*-test: $t = 2.88$, $p = 0.011$, $N = 17$; Fig. 4b).

Feeding in shallow vs. deeper water

The algae-grazing cichlids of Lake Tanganyika face a trade-off between feeding in shallow vs. deep water. In shallow water, algae productivity is high, but there is also a high density of food competitors present (Taborsky 1999) resulting in strong food competition and high rates of disturbance during feeding. In deeper water, both the productivity and

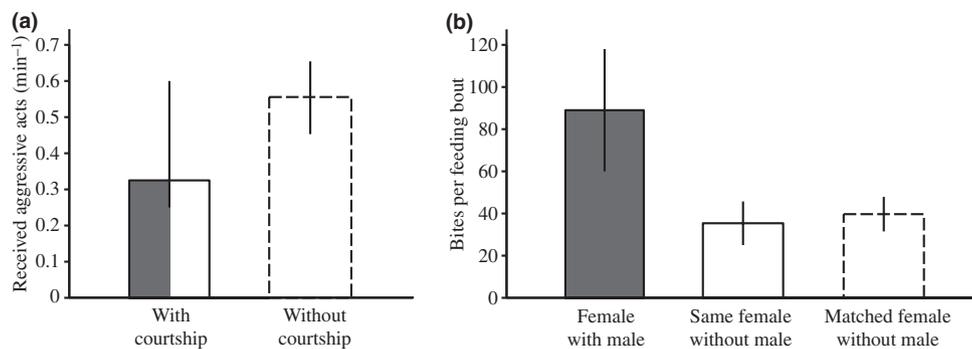


Fig. 3: Protection from aggression. (a) Aggression received per minute during recordings with and without courtship events (medians \pm 95% CI). (b) Mean number of feeding bites taken by females in succession without being disturbed by an aggressive interaction (mean \pm SE); left: female at male territory together with a courting male; centre: same female outside a male territory; right: a different, same-sized female that was recorded at the same daytime and depth outside of male territories and without being courted.

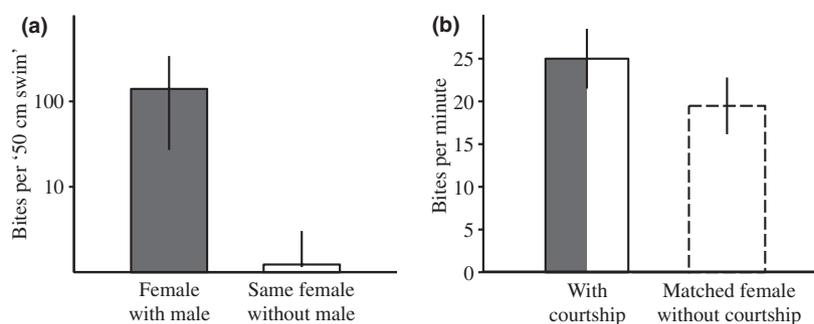


Fig. 4: Feeding efficiency. (a) Intra-individual comparison of bites per travelled distance ('50 cm swim') between females feeding with and without a male (medians \pm 95% CI). (b) Inter-individual comparison of feeding rates between females feeding with a male and matched females feeding without a male (means \pm SE); non-courted females matched for number of received aggression, size, daytime and depth).

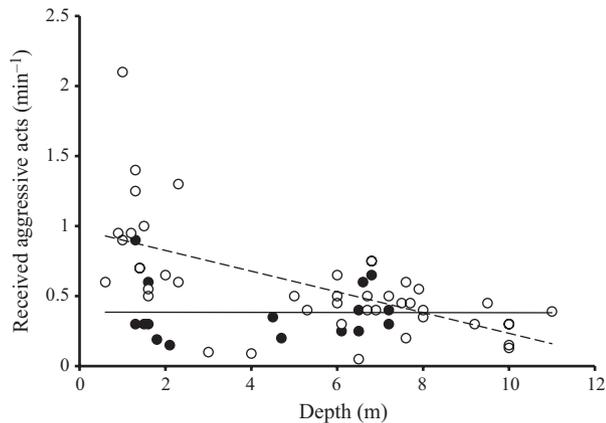


Fig. 5: Rates of aggression experienced by females across water depths. Open circles: females feeding alone, filled circles: females feeding within a male territory at least once during a recording. Model fit: black line; aggression received (with males) = $18.584 (\pm 6.623) - (1.41 (\pm 1.304)) \times \text{depth} (\pm \text{SE})$; hatched line; aggression received (without males) = $-8.1 (\pm 3.119) - (0.068 (\pm 0.625)) \times \text{depth} (\pm \text{SE})$.

the competitor densities are low. If males defend females from aggression by food competitors, females feeding within male territories should not face this trade-off. Indeed, overall, females received more aggression the shallower they fed, but females feeding outside male territories received more aggression in shallow water than females feeding inside male territories (Fig. 5), as shown by a significant interactions term of our analysis (GzLM, depth: Wald $\chi^2 = 4.75$, $p = 0.029$; female feeding with or without a male: Wald $\chi^2 = 8.95$, $p = 0.003$; depth \times feeding with/without male: Wald $\chi^2 = 3.91$, $p = 0.048$; $N = 60$).

Discussion

Our results suggest that male territory defence may serve primarily a courtship function, as it attracts females to the vicinity of males. Moreover, only adult males of this species defend territories, all courtship takes place at territories and males evict all intra- and inter-specific food competitors except approximately a third of the visiting females. Females use male territories preferentially for feeding, and our results suggest that they gain nutritional benefits from feeding at male territories. At male territories, females fed at higher rates than in a similar habitat outside territories suggesting higher food availability, and they were exposed to lower levels of aggression by food competitions.

The value of algae as food resource depends on algae productivity and nutritional composition,

which are mainly determined by sunlight exposure and should therefore be very similar within the same water depth. Why should females be attracted to male territories, if the turf algae that make up the sole food source of these fish are homogeneously distributed over the rock surfaces of the littoral zone? Within a given depth, territorial *S. pleurospilus* males occupy only a small fraction of the algae-covered substrate. The distribution of male territories relative to the resources is clearly a feature of exploded leks where females primarily can gain genetic benefits from visiting male territories (Bradbury et al. 1981; Höglund & Alatalo 1995). Our finding that females obtain direct benefits by feeding inside male territories is a key feature of resource-based mating systems. However, there is an important difference in classical resource-defence mating systems: In *S. pleurospilus*, males do not defend existing resources critical for females but rather create a high-quality feeding patch by their territorial behaviour. To our knowledge, this is the first case of courtship-related food provisioning observed in a fish. Active food transfer from males to females during courtship or copulation in the form of nuptial gifts (arachnids and insects; e.g. Steele 1986; Vahed 1998) or courtship feeding (birds; e.g. Lack 1940; Green & Krebs 1995; Helfenstein et al. 2003) is well documented. Conclusive evidence that males actively improve the resource quality by territory defence to attract females towards a certain location is as yet lacking, however. Males of the solitary bee *Anthidium manicatum* defend patches of nectar-producing flowers against other nectar-feeding insects except against conspecific females (Wirtz et al. 1988; Wirtz 1992), and male defence appears to raise the nectar content of flowers within territories (Wirtz 1992). Also, males of the hummingbird *Eulampis jugularis* (Wolf 1975) may increase the food availability within their territories by territorial defence against food competitors. In these species, however, it is not known whether females prefer to feed at male territories and hence males might use the defended resource to attract females. Male bees do not court the incoming females but mount them indiscriminately and try to copulate (Wirtz 1992). In the hummingbird, females seem to trade copulations against feeding opportunities prior to the breeding season, which appears to serve a pair bonding function (Wolf 1975). Interestingly, in the harem cichlid *Neolamprologus tetracanthus*, almost the opposite behaviour has been suggested to occur than in *S. pleurospilus*, but with similar effects on males and females. In this species,

males appear to refrain from feeding at female sub-territories to maintain these areas in good foraging condition and thereby to prevent females to disperse away from a male's territory (Matsumoto & Kohda 2007).

Several results support the idea that the territorial defence of *S. pleurospilus* males creates an essential resource for females (high-quality feeding patch) and that the resources attract the females to the males' territories, thereby generating opportunities for male courtship.

Courtship Function of Male Territories

As only adult-sized males defended territories, all observed courtship displays took place at these territories, and we never observed courtship outside a male territory or with non-territorial males, and we can safely conclude that male territories serve a reproductive function. As we did not observe spawning directly during our observation periods, we cannot exclude that spawning occurs outside of territories. However, given that territorial males do not leave the defended areas and that females deliberately visit male territories, this possibility seems unlikely. Hence, as in other territorial fish, a territory seems mandatory for the access to females (Itzkowitz 1977; Kohda 2006). Males defended their territories against food competitors in a similar intensity than do fish species that defend territories for own food acquisition (Kohda 2006).

There are two possible reproductive functions of male territories. It might be necessary to defend a safe area around a spawning site to protect the clutch from potential egg predators during spawning. In this case, males should defend their territories against all other cichlids, as all of them are potential egg predators (A. Kotrschal, pers. obs.). This is unlikely, however, because males only attacked other algae grazers. Alternatively, male territories may serve to attract females. Male territories are clustered in 1–2 m depth. This depth range offers almost ideal conditions for algae feeders (Taborsky 1999). The algae productivity is still relatively high (it decreases exponentially with depth), while the avian predation risk (highest near the surface; Steinmetz et al. 2003) and predation risk by carnivore fish (increasing with depth; Power et al. 1987) are relatively low. This results in peak densities of algae-eating food competitors in this depth range (Taborsky 1999). Hence, by keeping their territories free of food competitors, the males can offer females optimal conditions for feeding.

Selective Tolerance of Females

As we could not check the physiological state of females within their reproductive cycle, we can only speculate that females evicted by males from their territories are not ready to spawn, while females that are tolerated and courted by males are receptive. There are several mechanisms by which males might be able to distinguish receptive from non-receptive females. Males immediately evicted those females that did not respond to courtship display, by showing courtship behaviour themselves. During courtship, females usually exhibit a peculiar body quiver, which has been shown to be an energetically costly behaviour in other Lake Tanganyika cichlids (Grantner & Taborsky 1998). Hence, body quivering may honestly signal female receptivity and may be robust against potential cheater females. Furthermore, males might be able to detect female reproductive state by visual, behavioural or olfactory cues. Remarkably, the females responding to courting males were always allowed to stay at least until after a certain behavioural sequence had occurred: during courtship, males 'sniff' at the basis of females' anal fin (genital papilla) and thrust females side- and upwards, which is followed by a vortex of male and female circling each others. This sequence was terminated by either female expulsion or further courtship (A. Kotrschal, pers. obs.). Males might thus assess a females' receptivity via olfactory cues, similar to many other vertebrates (Agosta 1992) including many fish (Sørensen & Stases 1999).

Are Females Attracted to Male Territories?

Females visited male territories more often than expected by their abundance, but females tolerated by a male at its territory often left the territory deliberately and continued feeding at neighbouring territories. This suggests that females actively sampled male territories. We do not know, however, whether female mate choice is eventually influenced by the quality of feeding sites males offer. Notably, females were distributed bimodally across depths. Possibly, the peak at around 2 m represents receptive females inspecting and grazing male territories, whereas the peak at 7 m depth might represent non-receptive females. At this depth, algae productivity is still sufficiently high to sustain a certain density of algae eaters, but because of a lower density of food competitors, the frequency of aggressive interactions is much lower than in shallower depths (Kohda & Yanagisawa 1992; this study).

Nutritional Benefits for Females at Territories

When females were allowed to feed in male territories, they were less strongly exposed to con- and heterospecific aggression, they fed in longer undisturbed bouts, they fed at a higher rate and they had to move less far to obtain a certain number of feeding bites. These findings indicate that male territories constitute high-quality feeding patches for females. *S. pleurospilus* females are among the smallest algae feeders in Lake Tanganyika. As they do not defend territories, larger food competitors constantly displace the feeding females. Because primary productivity but also algae feeder densities decrease with depth, females face a trade-off between high-quality food and competition intensity. Thus, male protection appears to release females from this trade-off allowing them to feed in habitats with high food quality and low levels of competition.

Conclusions

Our results suggest that *S. pleurospilus* males defend territories to attract females by providing them with high-quality feeding opportunities. To confirm this conclusion, experiments disentangling food quality from male quality should be performed along with a proof that male territorial behaviour results in improved food availability. An interesting and unexpected implication of the modification of resources through male defence is that mating systems classified as leks based on male clustering and a uniform resource distribution may possess as well important features of resource-defence mating patterns and can therefore not be assigned unambiguously to one category of mating systems. In general, when resources are homogeneously distributed and hence cannot be monopolized, it may be a common strategy of males to improve the food quality of certain patches by defence, thereby creating a high-quality feeding site for females. Suggestive evidence from humming birds and solitary bees indicates that this behavioural mechanism may occur in very different taxonomic groups.

Acknowledgements

We thank Martin Jiskra for help with the collection of field data, and Michael Taborsky, Dik Heg, Markus Fischer and an anonymous referee for valuable comments on the manuscript, Roger Schürch, Fardo Witsenburg, Oliver Otti and the Fisheries Department Mpulungu of the Ministry of Agriculture and

Cooperatives, Zambia for logistic and scientific support in Zambia, and Evi Zwygart and Janne Schöning for logistic support in Europe. This study was funded by the Swiss National Science Foundation (grant 3100A0-111796 to B.T) and the Austrian Science Fund (FWF; grant P18647-B16 to B.T.).

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