Ethology / Éthologie

Rapid assessment of female preference for male size predicts subsequent choice of spawning partner in a socially monogamous cichlid fish

L'évaluation rapide de la préférence des femelles pour la taille des mâles permet de prédire le choix d'un partenaire de ponte chez un poisson cichlidé socialement monogame

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ABSTRACT

Although size-assortative mating in convict cichlids, *Amatitliana nigrofasciata*, is supposed to result from mutual mating preference for larger individuals, female choice in relation to male size remains ambiguous. We revisited the evidence for directional preference for larger males in female convict cichlids using a classical two-way choice apparatus in which each female could decide to spend time in front of a small male or a large one. We found evidence for female preference for large males, as assessed from association preference during a 4-hour period following encounter. Furthermore, females decided to spawn in front of the initially preferred male more often than expected by chance. Our results thus confirm the existence of a directional preference for large males in female convict cichlids, and indicate that association preference measured over a short period of time can provide a quick and reliable proxy for reproductive preference in this species.

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RÉSUMÉ

Bien que l'appariement pour la taille chez le cichlidé zébré, *Amatitliana nigrofasciata*, soit supposé découler d'une préférence mutuelle pour les plus grands individus, le choix des femelles relatives à la taille des mâles est encore ambiguë. Nous avons revisité les arguments en faveur d'une préférence directionnelle pour les plus grands mâles chez les femelles cichlidé zébré au moyen d'un dispositif de choix binaire classique dans lequel chaque femelle pouvait décider de passer du temps à proximité d'un petit ou d'un grand mâle. Nos résultats attestent d'une préférence pour les grands mâles mesurée à partir de la préférence affiliative pendant les quatre premières heures suivant la rencontre. En outre, les femelles ont finalement pondu en face de leur mâle préféré plus souvent qu'attendu par hasard. Nos résultats confirment donc l'existence d'une préférence directionnelle pour les grands mâles chez les femelles cichlidé zébré et indique que la mesure de la préférence associative sur une courte période d'observation peut être un indice rapide et fiable du choix de partenaire chez cette espèce.

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1. Introduction

Positive size-assortative mating occurs when individuals in a pair are more similar in size than what would be expected under the assumption of random mating [1]. This is a common pattern of mating in both invertebrate and vertebrate species [2–5], and particularly in monogamous ones [6–10]. However, the behavioural mechanisms involved in size assortative mating are difficult to infer from the mere observation of a correlation in size between reproductive partners, as contrasted mating preferences can lead the same pattern of mating [1]. On the one hand, both males and females may show a directional preference for large mates, such that the largest males and females pair first, then individuals of middle size, thus leaving the smallest individuals no other choice than mating between themselves. On the other hand, positive size-assortative mating can also result from both males and females having a homotypic preference, i.e. preferring to mate with individuals of similar size to themselves.

Positive size-assortative mating has been regularly reported in cichlid fishes [10–13], and particularly in convict cichlids, Amatitliana nigrofasciata [11,14,15]. This species provides an ideal biological model to investigate the relation between mate choice and size-assortative mating. Convict cichlids are socially monogamous, although cases of bigamy have been reported [14], and evidence exists for choosiness in both sexes [16]. However, the precise influence of male and female mating preferences on positive size-assortative pairing in convict cichlids remains ambiguous. Previous evidence clearly suggests that male convict cichlids show a preference for large, gravid females [17–19]. By contrast, female preference in relation to male size in convict cichlids is unclear. Whereas some experimental studies have reported a directional preference for larger males [18,20,21], other have concluded to the absence of a significant preference for large males [22] or to the existence of a homotypic preference, with female preferring males of similar size to themselves [23]. However, differences in methodology could explain the observed discrepancies between studies. For instance, female preference was estimated using a two-way choice apparatus in some studies [20–22], whereas in others, a three-way choice apparatus was used [23]. More to the point, Keenleyside et al. [24] found contrasting results on female preference for large males when using either a two-way or a three-way choice apparatus. In addition, differences also exist between studies in the measure of female preference. In several studies, female preference was estimated from the relative time spent close to males of different sizes. However, the time frame over which female preference was measured varies extensively between studies, ranging from few minutes [21] to a few days [22,23]. Although time spent near a male has been found to be a good index of female preference in some fish species [25–28], it is still unclear whether association preferences can be generally regarded as a reliable proxy for reproductive preference [29–32]. Indeed, association preference could result from non sexual preference [33]. Here, as part of a larger research program on female choice in convict cichlids, we reconsider the evidence for the existence of a directional preference for large males in female convict cichlids when placed in a two-way choice apparatus, and further explore the possibility that female preference can be reliably assessed from association preference over a short period of time, as suggested by the results of Santangelo [22].

2. Materials and methods

2.1. Biological material

Individuals used in our experiments came from local pet stores. Evidence exists that the behaviour of convict cichlids obtained from local pet suppliers does not differ from that of fish collected in the wild [34]. Although all individuals were sexually mature, their previous breeding experience was unknown. In order to ensure sexual receptivity, all individuals were kept for at least one month in same-sex tanks before starting the experiments. Fish were maintained on a 12–12-hour light–dark cycle at $25 \pm 1\,°C$ and fed ad lib twice a day with tetramin cichlid flakes.

2.2. Choice arena

Following Noonan's [20] two-way choice design for dichotomous mate choice tests, 90 L aquariums were partitioned into three sections with two leakproof clear plastic partitions. The two end compartments 1 and 3 each contained one male, while the central compartment contained the female. The central compartment was delineated into three areas (the left area, the central or neutral area, and the right area) using opaque plastic partitions. These two opaque partitions were placed in such a manner that the female could freely swim in the central area without being able to see both males at the same time. In addition, the partitions prevented visual interactions between males, thus removing any effect of male–male competition [35]. Each side of the aquarium was covered by an opaque piece of cardboard to prevent adverse effects from artificial lightning. During video-recordings, the opaque piece of cardboard on the front face of the aquarium was removed, allowing the simultaneous observation of left, neutral and right areas while the room was maintained in the dark. Light was provided by daylight neon lamp tube (Sylvania Aquastar 30 W, 10,000 K).

Acclimatization time lasted for 19 hours. During this time, opaque plastic partitions were placed at each end of the central compartment, to visually isolate it from compartments 1 and 3. All individuals (41 females and 82 males) were used only once in the experiments. During the preference test, each female was presented with a pair of males consisting of a large male and a small one (Table 1), with at least 1 cm difference in size [16]. Positions of the large male and the small one were randomized to avoid any bias associated with systematic female preference for one side of the aquarium. Contrary to Santangelo [22], females were not able to physically interact with males. We chose this option to minimize the risk that male aggressive

Table 1

Standard length (cm) and weight (g) of the 41 females and 82 males.

		Female	Smaller male	Larger male
Length	Mean ± standard deviation	6.5 ± 1.0	7.8 ± 1.1	10.2 ± 1.0
	Range	5.0–8.1	5.2–9.0	8.5–12.0
Weight	Mean ± standard deviation	7.1 ± 4.0	10.0 ± 4.0	23.7 ± 7.0
	Range	2.8–23.1	3–16.5	10.2–44.7

behaviour influenced female mate choice or spawning behaviour as observed, for instance, in the threespine stickleback, *Gasterosteus aculeatus* [36,37], or the blenny *Salaria pavo* [26].

The activity of the female and that of the two males was continuously recorded for 4 hours with a numeric camera (JVC everio GZMG21). Videos were then analysed using Media Player Classic (http://sourceforge.net/projects/guliverkli), and behavioural sequences were recorded. For each triad of one female and two males, the following parameters were recorded. Time spent by the female in each part of the aquarium was used to provide an index of female preference for each of the two males, while the number of switches from one side to the other was taken as an index of female exploratory activity. Relying on the time recording technique [38], the behaviour of each male in presence of the female was analysed for 1 minute at 10-minute intervals for the whole duration of the video recording in order to estimate the proportion of time spent in interaction with the female (i.e. synchronized swimming through the clear plastic partition).

Twenty-two of the females were then provided with a choice between two spawning sites made of a plastic box (16 × 10 cm) filled with sand and placed in the left and right areas. Females were monitored twice daily until spawning occurred, at which time spawning boxes were removed from the aquarium and eggs were counted.

All the individuals were measured (standard length, from the tip of the mouth to the caudal peduncle) with a precision of 1 mm, and weighed (using a Pesola digital scale MS 500) with a precision of 0.1 g, at the end of each test.

2.3. Statistical analysis

Data were inspected for homoscedasticity using Brown–Forsythe test, and for normality using Shapiro-Wilk test, prior to the use of parametric tests (linear regression or *t* test). Proportions were normalized using square root-arcsine transformation [39]. When conditions for a *t* test were not met, we used a Wilcoxon rank-sum test [40]. We reported either Cohen's *d* or odds ratio and their 95% confidence interval [41] as measures of effect size [42,43]. As an index of female preference for the large male, we used the proportion of time the female spent in front of the large male divided by the total time she spent in front of any of the two males [44]. A female was recorded as consistent if she chose the same male both during the 4-hour observation period and when spawning. All the tests were performed using R 2.11 software [45].

3. Results

3.1. Early spatial proximity

During the first 4-hour of observation, the 41 females spent on average 62.1% (95% CI = 57.4 to 66.8%) of their time on the side of the larger male. This proportion significantly differed from 50% (*t* test *t* = 4.81, df = 40, $P < 10^{-4}$). There was no effect of female body size (*F* = 1.33, df = 1.39, *P* = 0.28), absolute male size difference (*F* = 0.33, df = 1.39, *P* = 0.57), relative male size difference (*F* = 2.03, df = 1.39, *P* = 0.16) or female exploratory activity (*F* = 0.66, df = 1.39, *P* = 0.42) on this proportion. None of the interactions between covariates was significant. There was no mean difference in activity between larger and smaller males (paired *t* test: *t* = 0.30, df = 35, *P* = 0.77).

3.2. Spawning

All the 22 females spawned within 2 weeks (median time before spawning: 5 days, range = 3 to 13 days). On average, the females laid 167 ± 106 eggs (range = 32 to 423 eggs). Female body size had a marginal influence on clutch size (*F* = 3.6, df = 1.20, *P* = 0.07), whereas neither preferred malebody size (*F* = 2.94, df = 1.20, *P* = 0.11), or the proportion of time spent on the preferred male's side during the 4-hour observation (*F* = 0.63, df = 1.20, *P* = 0.44) had a significant effect. Females preferentially spawned in front of the larger male (Table 2, exact binomial test *B*[16,22], *P* = 0.026). The decision to spawn in front of the large or the small male was not influenced by female size (Cohen's *d* = 0.47 with 95% CI = −0.6 to 1.8, *t* test *t* = 0.87, df = 7.5, *P* = 0.41), and had no effect on clutch size (Cohen's *d* = 0.18 with 95% CI = −0.77 to 1.42, *t* test *t* = −0.93, df = 6.2, *P* = 0.39). However, females that spawned in front of the larger male did so significantly more rapidly (5.1 ± 2.4 days) than those that chose the smaller male (7.8 ± 3.4 days) (Cohen's *d* = 1.1 with 95% CI = 0.6 to 3.1, Wilcoxon test *P* = 0.021).

3.3. Consistency between early spatial proximity and spawning

We could not reject the null hypothesis that females generally spawn close to the male they preferred during the initial 4-hour-observation (Table 2; odds ratio [OR] = 5 with 95% CI = 0.55 to 236). Given that the number of inconsistent females was rather small (six females), a binomial test was used [40]: a total of 16 females among 22 made a consistent choice, which was significantly more than expected by chance (exact binomial test *B*[16,22] with a individual probability of choosing the same male in the two tests of 1/2, *P* = 0.026). There was no evidence for

Table 2
Number of females as a function of their association preference for a given male (defined from the side where a female spent more than 50% of their time) and their sexual preference (defined by the side where a female spawn).

	Spawning preference for the larger male	Spawning preference for the smaller male	Total
Association preferences for the larger male	15	5	20
Association preferences for the smaller male	1	1	2
Total	16	6	22

inconsistent females being less choosy during the preference test (Cohen's $d = -0.16$ with 95% CI = -1.25 to 0.80, t test $t = -0.31$, df = 9.5, $P = 0.76$). In addition, consistent and inconsistent female did not differ in body size (Cohen's $d = 0.45$ with 95% CI = -0.64 to 1.73, t test $t = 0.81$, df = 7.5, $P = 0.44$) or in brood size (Cohen's $d = 0.18$ with 95% CI = -0.78 to 1.4, t test $t = 0.35$, df = 8.6, $P = 0.73$). Consistent females spawn, however, more rapidly (4.8 ± 1.6 days) than inconsistent ones (8.5 ± 4.0 days) (Cohen's $d = 1.6$ with 95% CI = 0.36 to 3.81, Wilcoxon test, W = 18.5, $P = 0.026$).

4. Discussion

Our results clearly confirm that female convict cichlids show a preference for large males, when placed in a classical two-way choice apparatus, both in terms of time spent near the male and choice of spawning partner. The observed proportion of females spawning near the large male in the present study (16 out of 22) is in good accordance with that observed by Noonan [20] (16 out of 20) and Santangello [22] (21 out of 31). Using a similar experimental design, Santangelo ([22], p. 145) reported that "females did not select the larger male significantly more often (21 chose the large male, 10 chose the small male; one-tailed binomial test: $n = 31$, $P = 0.05$)". Gagliardi-Seeley et al. [21] suggested that the discrepancy between the study by Noonan [20] and that of Santangelo [22] was possibly due to the fact that the difference in size between males was larger in the former study. However, our calculation of the very same test used Santangleo [22] provides weak but statistically significant support for female preference for large males ($P = 0.035$).

Our results indicate that neither the absolute nor the relative difference in size between males had an influence the proportion of time females spent near the large male. Gagliardi-Seeley et al. [21] reported that females were unable to express a preference for the larger of two males when they did not see them together. Although our females were unable to see both males at the same time, they clearly expressed a preference for large males. However, the two studies cannot be directly compared as females were able to physically interact with males in the study by Gagliardi-Seeley et al. [21] but not in the present one.

More importantly from a methodological point of view, the preference exhibited by a female over a 4-hour period after encountering the two males was a reliable predictor of her choice of a spawning partner. Our results, thus, confirm that time spent near a male does predict female mate choice, as previously reported for the Malawian *Pseudotropheus* cichlid [25,26]. Overall, in 73% percent of cases, the preference initially shown by the female during the first 4 hours was indicative of her future mate choice. Interestingly, inconsistent females took more time to spawn than consistent ones. This suggests that inconsistent females might have been in a different physiological state than consistent ones at the start of the experiment. Previous evidence [46] indeed suggests that female association preference can depend on her reproductive state in cichlid fishes. However, five out of six inconsistent females decided to spawn in front of the small males after having spent more time near the large one during the first 4 hours of cohabitation. One possibility, then, is that the initial choice of females was later modified in reaction to the response of large males to females [47,48]. In particular, large males might have been more aggressive towards females if they did not spawn rapidly, or court them less than smaller males.

In summary, our results confirm the choice of large males as spawning partners by female convict cichlids when tested in two-way apparatus, and further indicate that this choice is mirrored in their significant attraction to large males over a short term period following their encounter with two males varying in size. Therefore, the assessment of female mating preference over a short-time period is a reliable method that could be used in the future to acquire more consistent data on female choice in convict cichlids, including repeatability and rationality.

Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

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