

'Prudent habitat choice': a novel mechanism of size-assortative mating

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Abstract

Assortative mating, an ubiquitous form of nonrandom mating, strongly impacts Darwinian fitness and can drive biological diversification. Despite its ecological and evolutionary importance, the behavioural processes underlying assortative mating are often unknown, and in particular, mechanisms not involving mate choice have been largely ignored so far. Here, we propose that assortative mating can arise from 'prudent habitat choice', a general mechanism that acts under natural selection, and that it can occur despite a complete mixing of phenotypes. We show that in the cichlid *Eretmodus cyanostictus* size-assortative mating ensues, because individuals of weaker competitive ability ignore high-quality but strongly competed habitat patches. Previous studies showed that in *E. cyanostictus*, size-based mate preferences are absent. By field and laboratory experiments, here we showed that (i) habitat quality and body size are correlated in this species; (ii) territories with more stone cover are preferred by both sexes in the absence of competition; and (iii) smaller fish prudently occupy vacant territories of worse quality than do larger fish. Prudent habitat choice is likely to be a widespread mechanism of assortative mating, as both preferences for and dominance-based access to high-quality habitats are generic phenomena in animals.

Introduction

Nonrandom mating, which occurs in most natural populations, often has profound consequences for evolutionary dynamics (Gillespie, 2004). Arguably, one of the most important processes leading to nonrandom mating is assortative mating where phenotypically similar individuals mate more often than expected by chance. It is ubiquitous in nature, and assortment traits are often tightly related to Darwinian fitness. Mate assortment has been reported, for instance, with respect to age (e.g. Ferrer & Penteriani, 2003), size (e.g. Shine *et al.*, 2001), reproductive quality (Rintamaki *et al.*, 1998), ornamental traits (Andersson *et al.*, 1998) and the level of heterozygosity (Garcia-Navas *et al.*, 2009).

It is widespread among animals, both in invertebrates (flatworms, Vreys & Michiels, 1997; molluscs, Cruz *et al.*, 2004; annelids, Michiels *et al.*, 2001; arthropods Crespi, 1989) and in vertebrates (fish, Kolm, 2002; Olafsdottir *et al.*, 2006; amphibians, Arak, 1983; reptiles, Olsson, 1993; Shine *et al.*, 2001; birds, Delestrade, 2001; Helfenstein *et al.*, 2004; mammals, Preston *et al.*, 2005; including humans, Bereczkei *et al.*, 2004), and it also occurs in plants (Weis, 2005).

Assortative mating can have profound influences on the genetic structure and demographics of populations (reviewed in Crespi, 1989). It has received particularly strong attention in models of speciation because of its presumed crucial role in causing and/or maintaining reproductive isolation in sympatry (e.g. Kondrashov & Shpak, 1998; Dieckmann & Doebeli, 1999; Schneider & Bürger, 2006; De Cara *et al.* 2008) and in maintaining patchy mating distributions in species hybrid zones (e.g. M'Gonigle & FitzJohn, 2010). In contrast to its ecological and evolutionary consequences, the underlying processes generating assortment have received

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rather little attention (Rowe & Arnqvist, 1996; Snowberg & Bolnick, 2012). Studies explicitly addressing these processes have mostly focused on mating preferences and mate choice. For example, most studies on assortative mating by body size reported a directional preference for a larger body size in one or both sexes, which was coupled with an intrasexual competitive advantage of larger over smaller individuals, allowing large individuals to monopolize partners of the preferred body size (Olsson, 1993; Harari *et al.*, 1999; Baldauf *et al.*, 2009).

So far, accounts of assortative mating *not* involving sexual selection involved mechanisms requiring rather specific conditions such as mechanical constraints (reviewed in Crespi, 1989; Galipaud *et al.*, 2013) or segregation of phenotypes in time (reviewed in Crespi, 1989; Miyashita, 1994), space (Rice, 1984; Rice & Salt, 1990; Johannesson *et al.*, 1995; Flockhart & Wiebe, 2007; Snowberg & Bolnick, 2012) or between different hosts (Bush, 1969; Via, 1999). Here, we propose that assortative mating can result from 'prudent habitat choice', a general mechanism that acts under natural selection and can occur despite a complete mixing of phenotypes. Even if all members of a population share a common preference for high-quality habitats in the absence of competition, partially truncated phenotype distributions can arise when individuals differ in their competitive abilities (Parker & Sutherland, 1986; Milinski *et al.*, 1995). If competition for high-quality sites in heterogeneous environments is intense, the strength of selection on morphological traits may differ between high- and low-quality habitats, and an assortment by morphological type may occur between habitats of different quality (Duckworth, 2006). Assortative mating may ensue from habitat choice, if males and females of a species compete independently for access to preferred habitats and if the correlation between the assorted trait and the habitat trait is sufficiently strong in both sexes (Snowberg & Bolnick, 2012). Here, we provide the first *experimental* evidence for habitat choice as a route to assortative mating in nature.

In general, truncated phenotype distributions of unequal competitors may arise either from direct interference between competitors or, alternatively, from prudent behaviour (Hårdling & Kokko, 2005). Here, we propose 'prudent habitat choice' as a mechanism of assortative mating. It can be understood as a concept analogous to the well-established 'prudent mate choice', where individuals of weaker competitive ability benefit from ignoring potential high-quality, preferred but strongly competed partners, even if in case of successful mating with these partners they would yield a higher fitness (Fawcett & Johnstone, 2003; Hårdling & Kokko, 2005). In case of prudent *mate* choice, variation in competitive ability can either lead to a reduced choosiness of competitively inferior

individuals (Candolin & Salesto, 2009), or inferior individuals may even actively prefer the options rejected by dominant individuals (Bel-Venner *et al.*, 2008). Thus far, the occurrence of prudent *habitat* choice has been suggested only by results of a simulation model based on spacing data of age-assortatively mating Imperial Eagles (*Aquila adalberti*), a species where adult individuals are dominant over juveniles (Ferrer & Penteriani, 2003).

The monogamous cichlid *Eretmodus cyanostictus*, in which body sizes of pair partners are tightly correlated (Morley & Balshine, 2002), lacks size-based mating preferences (Morley, 2000; Taborsky *et al.*, 2009). Thus in this species, an alternative mechanism must give rise to size assortment. Habitat choice has been proposed as a promising candidate mechanism in this species (Taborsky *et al.*, 2009), as adult body sizes (Morley & Balshine, 2002; Taborsky *et al.*, 2009) and the habitat quality (B. Taborsky, personal observation) between neighbouring territories both vary considerably within a population. Here, we show experimentally that 'prudent habitat choice' can cause assortative mating in *E. cyanostictus*. We show that (i) both sexes have a preference for high-quality habitat territories in the absence of interference competition with other conspecifics, but that (ii) smaller fish of both sexes restrict themselves prudently to settle at territories of lower quality, because larger individuals are strictly dominant over smaller ones within each sex (see Taborsky *et al.*, 2009).

To conclusively demonstrate the existence of assortative mating resulting from prudent habitat choice, we must show that (i) body size and territory habitat quality are positively correlated within a population in both sexes; (ii) good habitats are preferred over poor ones in the absence of competition; (iii) despite a preference for good habitats, smaller fish occupy vacant territories of lower habitat quality than larger fish do (Fawcett & Johnstone, 2003; Hårdling & Kokko, 2005); (iv) furthermore, we have to show that territory ownership is dynamic; the latter condition is particularly important in animals, which continue to grow during adulthood such as fish (i.e. 'indeterminate growth'). If body size constrains the maximum habitat quality that can be monopolized, organisms with indeterminate growth will 'outgrow' the habitat quality of their current territory after some time and will be able to settle at better territories. Maintaining an association between body size and territory quality in a population thus requires a rather dynamic territory ownership in species with indeterminate growth. We tested the four listed conditions in the cichlid *E. cyanostictus* by a habitat manipulation experiment in the field, a laboratory experiment testing for female habitat preferences independent of male preferences, a population survey and a large-scale female removal experiment.

Materials and methods

Study species

Eretmodus cyanostictus is a monogamous, biparental mouthbrooder endemic to Lake Tanganyika (Neat & Balshine-Earn, 1999). Females brood the clutch for 7–10 days before transferring them to the male to be brooded for another 12–16 days (Grüter & Taborsky, 2004); parental care shares depend on the energetic state of parents (Steinegger & Taborsky, 2007) and on operational sex ratio (Grüter & Taborsky, 2005). Pairs co-defend all-purpose territories along the rocky shores of the lake against conspecifics and other food and space competitors. Territories increase in size with depth and comprise an area of about 2.0 m² at our study site (Morley, 2000), which is located at depth of 3.0–3.5 m at Kasakalawe Point (8°46.849'S, 31°04.882'E), Zambia, at the southern tip of Lake Tanganyika. At this study site, the available rocky surface is densely occupied by algae-eating cichlids, and among the territorial, rock-dwelling fish, *E. cyanostictus* is by far the most abundant species at this site.

Previous work in *E. cyanostictus* suggests that in this species mate choice is absent, as we did not find indications for mate preferences in general (Taborsky *et al.*, 2009). Moreover, three independent experiments failed to detect size-based mating preference in *E. cyanostictus*: (i) a simultaneous, forced-choice experiment in the laboratory (Morley, 2000), (ii) a sequential choice experiment and (iii) a partner removal experiment, both in the field (Taborsky *et al.*, 2009). In the partner removal experiment, no active mate choice occurred. Instead, experimentally 'widowed' fish of both sexes accepted the first incoming opposite-sex fish as new partner. Fights over territory ownership between two same-sex fish only occurred when they were staged experimentally. In these staged fights, always the larger fish won the resource and became the new territory owner (Taborsky *et al.*, 2009). This indicates that smaller fish are strictly subordinate to larger fish and that they would face a high risk of losing out to larger individuals when competing directly with them for territories.

General field methods

Territorial individuals were identified and permanently recognizable by their unique pattern of light-blue, iridescent spots (Morley & Balshine, 2002; Taborsky *et al.*, 2009). We recognized members belonging to a pair by their mutual sociopositive behaviour, joint feeding and joint defence against conspecifics (Morley & Balshine, 2002; Taborsky *et al.*, 2009). Territory boundaries were mapped by observing the locations of aggressive encounters between territory owners and neighbouring territorial fish (Morley & Balshine, 2002). An experimental territory was marked by placing a numbered

pebble of 5–7 cm in diameter near its centre. To catch a fish, we waited until it stayed motionless under a stone. Then we placed a tent-shaped, fine-meshed net over the stone and coaxed the fish to swim into the net by carefully lifting the stone. All body size measurements were taken under water to minimize handling stress. We placed the fish on a measuring board with a 1-mm grid and read their standard and total lengths to the nearest mm. Unless mentioned otherwise, after measuring all captured fish were released in a natural shelter near the centre of their territory. All field data were collected by SCUBA diving at water depth between 3 and 3.5 m.

At our study site, territories consist of up to two layers of rounded granite stones covering a sandy bottom. *E. cyanostictus* feed almost exclusively on turf algae growing at the surface of these stones, and they use crevices between the stones as shelters. Thus, the habitat quality of a territory increases with its amount of stone cover. Furthermore, stone cover is also the only obvious habitat parameter that greatly varies between territories at our study site within a given water depth. To estimate the habitat quality of a territory, we quantified the amount of total stone cover as follows: we determined the major and minor axes of a territory and measured the stone cover along both axes with help of a graduated measuring rod. We measured the distances (in cm) covered by 0 (= sand), 0.5 (= stone half dug in sand), 1, 1.5 or 2 stone layers. From these data, we calculated the total stone cover index S_T as

$$S_T = \sum d_L L$$

where L is the number of stone layers and d_L are the distances along the two axes covered by the respective number of layers.

For the habitat manipulation experiments, we needed a stone cover index that is independent of territory size, as by our manipulations (removing the owner pair) the territory boundaries of the vacant territory could potentially change, for instance when previous neighbours partly shifted their boundaries into the vacant area. For these experiments, we therefore used a relative stone cover index S_R calculated as

$$S_R = \frac{S_T}{d_{\text{tot}}}$$

where d_{tot} is the summed lengths of the major and minor axes.

Dynamics of territory ownership

To obtain an estimate of the natural dynamics of territory ownership with time, we measured how often one or both territory owners were exchanged in the field. In 2005 and 2006, we monitored 40 and 30 territories, respectively, from the middle of September to end of November to estimate the natural duration of pair

bonds. These territories were directly adjacent to each other at 3 to 3.5 m depth and were located along transects in parallel to the coastline. Every 2–3 weeks we visited the 70 territories and noted the identity of the owners. From these data, we calculated the mean pair tenacity separately for the 2 years. For each day in the monitoring period, we calculated the mean proportion of pairs that broke up or vanished entirely. As we did not check the pairs daily, we split the probability that a pair broke up equally between the days since the last check of a pair. Likewise, if two partners were still together, the pair was considered to have been continuously present since the last check. Mean pair tenacity T was calculated as $T = 1/p$, where p is the mean proportion of pairs breaking up each day.

To obtain a better understanding of how the estimates of territory tenure and pair tenacity relate to the mating system (serial monogamy vs. long-term monogamy), at each check we also noted whether one of pair partners was mouthbrooding. We calculated the mean breeding cycle length $C = d/m$, where d is the mean mouthbrooding duration and m is the mean proportion of mouthbrooding pairs per check. The mean mouthbrooding duration d was set to 22.75 days based on two published accounts obtained in captivity (mean duration in experimental control groups in Grüter & Taborsky, 2004: $21.5d$ and in Steinegger & Taborsky, 2007: $24.0d$), because natural brood care durations are unknown. Although we cannot entirely exclude that the captivity-derived value of d deviates from natural mouthbrooding durations to some extent, we argue that d is likely to be close to the natural value, because parents do not feed their offspring during mouthbrooding in this species and because in the laboratory we breed the fish under temperatures matching natural conditions.

Body size–habitat relationship

To test whether larger fish occupy territories with more stone cover, we once captured the owners of the 30 territories surveyed in 2006 for body length measurements and we measured the habitat quality of these 30 territories by estimating the stone cover (Materials and Methods see above). The sample sizes for the body size–habitat correlations are $N = 30$ for males and $N = 29$ for females, as one female could not be captured.

Habitat manipulation experiment

To test whether ‘good’ habitats with high stone cover are preferred over ‘poor’ ones with little stone cover and whether poor habitats are occupied by smaller fish more likely than are good habitats, we either enhanced or reduced the stone cover of 20 territories. The focal territories for this experiment were chosen haphazardly

along a transect in 3 m depth in parallel to the shoreline and had to meet the following criteria: the distance between any two focal territories had to be at least 10 m to ensure independence of trials. Sufficient medium-sized stones had to be present within a territory allowing us to perform manipulations (above a certain size stones could not be lifted by SCUBA diving). We chose focal territories of intermediate quality to ensure that by our manipulations we could turn them into good or poor territories.

Each selected territory was marked by a numbered stone. We observed the territory and its surroundings for 30 min. We mapped the territory borders and noted the unique spot pattern of its owners and of all conspecific territorial neighbours. Then, we removed the owners of the focal territory and transferred them to large outdoor tanks at the shore, to be released back to the lake once the trials were finished. We measured the initial relative stone cover index S_R of each focal territory. Then, we manipulated the habitat quality by distributing ten medium-sized stones (c. 30–40 cm in diameter) uniformly over the entire territory area ($N = 10$), or by removing ten medium-sized stones ($N = 10$). When decreasing the quality, we additionally flipped around 30–40% of the remaining stone cover, thereby even further reducing food availability. We took care, however, that at least one suitable shelter for a pair remained intact (i.e. a cluster of 1.5–2 layers of medium sizes to large stones). After the manipulations, we determined S_R again. Our manipulations significantly changed the values of S_R in the direction intended by our manipulations ($F_{1,18} = 45.0$, $P < 0.001$, ANOVA; Fig. 1).

In the 2 weeks following the manipulations, we checked daily for the presence of new territorial fish at the experimental territories and noted their spot pattern. If the final ownership of a territory was not determined within the first 2 weeks, we continued to check these territories for up to a maximum of 30 days after the manipulation. In 13 of 20 cases, the first new owners stayed until the end of the experiment; in five cases, the second or third new owners stayed to the end, once no final settlement occurred, and one territory remained empty during the entire experiment. The sample size for body sizes in this experiment is $N = 17$ for males and $N = 18$ for females, as one male could not be captured for size measurement. Once a new pair was detected at a territory, we recorded for 10 min all aggressive interactions between the new male owner and any other fish. We recorded only male behaviour, as males contribute more to the joint defence of a territory (Morley & Balshine, 2002). Of all recorded aggressive interactions, 24% involved heterospecifics, mostly with the cichlid *Variabilichromis moorii*, which defend territories in the same habitat than do *E. cyanostictus*. We never observed heterospecifics to settle at the manipulated territories, however, and the proportions

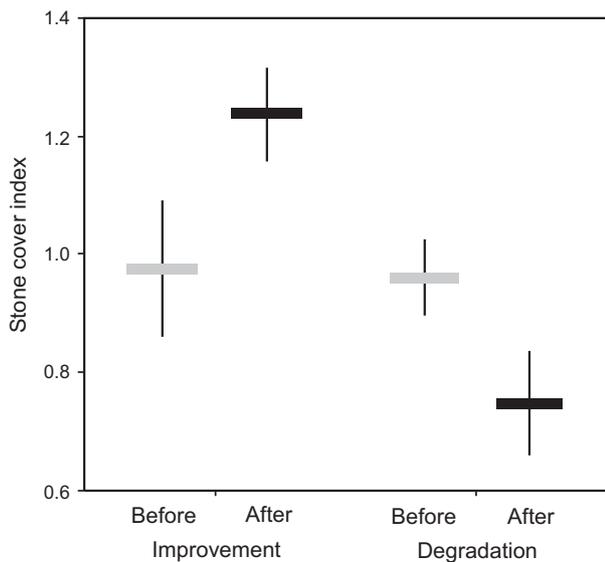


Fig. 1 Index of total stone cover, S_T , before (grey) and after (black) stones were added ('improvement') or removed ('degradation') to the experimental territories in the habitat manipulation experiment (means \pm SE).

of aggressive interactions involving heterospecifics were similar in improved (12.3) and degraded (11.7%) territories. It is thus unlikely that heterospecific aggression had an important influence on habitat choice in *E. cyanostictus*, and we therefore restricted our analyses to intraspecific aggression. After the 10-min behavioural recording, the owner new pair was captured, measured and released again.

Female habitat choice in the laboratory

Assortative mating via prudent habitat choice can only be achieved if both sexes independently prefer the same habitat properties. In *E. cyanostictus*, males are on average 12% larger than their female partners (Tabor-sky *et al.*, 2009), they are generally more aggressive than females (Morley & Balshine, 2002), and they are socially dominant over their female partners. Thus if a pair rather than a single fish occupies an empty territory, which happened in 90% of our 20 experimental territories in the field, we cannot safely exclude that this reflects the habitat choice of the socially dominant male only rather than an independent choice of both partners.

Thus to test whether females prefer to settle in patches containing more stone cover independently of the habitat choice of males, we did a supplementary experiment in the laboratory. Twelve paired adult females were temporarily separated from their pair partners and given the choice between two equal-sized patches in a simultaneous choice task. Females were

allowed to choose between (i) a 'good habitat' consisting of nine stones of 15–20 cm in diameter surrounding a clay flowerpot halve and (ii) a 'poor habitat' containing only two stones and a flower pot halve. We added one flower pot halve per habitat as these are the type of shelters fish are familiar with in our laboratory populations. The two habitats were installed at the left and the right side of a large, central compartment of three 400-L tanks (see Fig. S1). A biological filter was placed at the middle of the back screen of the central compartment, and a single flower pot halve was placed near the middle of the front screen. The filter and the frontal flower pot offered the test fish the opportunity to hide outside the preference zones (see Fig. S1). Adjacent to the right and the left of the central compartment, separated by clear partitions, two small compartments were installed. They contained each a patch of habitat consisting of a flower pot and two stones, which was aligned directly to habitats of the central compartment, thus forming two experimental territories at the two sides of the tank, only dissected by a transparent partition (Fig. S1). To test which habitat females prefer in the absence of conspecifics, and whether their preference is influenced by the presence of males, each female was exposed to three types of displays presented in the small compartments: (i) a large male next to the good habitat and a small male next to the poor habitat, (ii) a large male next to the poor habitat and a small male next to the good habitat and (iii) no males in the tank. All presented males were unfamiliar to the focal females. We balanced the following conditions across trials: the sequence of the three displays, in which tank which display was presented, and the sides of tanks where the good and the poor habitat were installed. All fish were taken from our laboratory stock tanks, and after the experimental trials, they were placed back to their home tanks. All fish were kept at a 13 : 11-h L : D cycle with 10 min of dimmed light in the morning and the evening to mimic the light conditions at Lake Tanganyika. In our laboratory, the light phase starts at 8:00 h and ends at 21:00 h.

A trial, including all three displays, took about 3 days, during which each female spent 22 h (including acclimatization time) in each of the three 400-L tanks. First, the focal female and the males were captured from different stock tanks, and their standard length was determined to the nearest 0.5 mm (mean SL, females: 6.42 cm; large males: 7.44 cm; small males: 6.42 cm; mean difference between simultaneously presented males: 1.20 cm). One hour before a display started, that is, at 14:00 h, a focal female was gently placed in the central flower pot near the front screen and a net basket was placed over the pot to prevent her moving away immediately. If males were involved in a display, they were now placed in their compartments. All trials were monitored by video. After 1 h of acclimatization, we slowly removed the net basket that

confined the female and left the aquaria room immediately. From the videos, we noted a female's location in the tank every 30 min (i.e. at every half and full hour) between 15:00 h to 21:00 h and between 8:00 h to 12:00 h. A female was considered to be within either the good or the poor habitat, if she was within 10 cm of the stones, above the stones or within 10 cm of the clear partition (see 'preference zones', Fig. S1). All locations outside the preference zones (e.g. being at or under the filter, in the central flower pot or staying over the open sand area) were subsumed as 'neutral zone'. During most parts of the light phases, females were actively moving around and regularly switched between zones within a period of 30 min. Therefore, we can safely assume independence of our location data collected every 30 min. Between 21:00 h and 8:00 h, the lights in the room were off, so no location data are available of the dark phase. This experiment was conducted at the Institute of Ecology and Evolution, University of Bern, Switzerland, under licence 21/08 of the Veterinary Office of the Kanton Bern.

Over all trials, females spent on average 63.7% of time in the good habitat, 20.0% of time in the poor habitat and 16.3% in the neutral zone. For analysis, we were only interested whether females prefer one of the experimental habitats over the other, either when alone or in the presence of large or small males. Thus, our null hypothesis expects equal location frequencies in the two experimental habitats. Separately for the three displays, we compared how often females stayed in the good habitat (observed frequencies) vs. the expected frequencies (i.e. 50% of all locations within the good and the poor habitat), using chi-squared tests.

Female removal experiment

To investigate the dynamics involved in territory settlement and, in particular, to test whether interference competition or prudent behaviour is involved territory occupancy, we performed a large-scale female removal experiment. By this manipulation, we aimed to further enhance the intrasexual competition between males. Intrasexual competition should be generally stronger among males than among females. Apart from the higher aggressiveness of males, this is also expected because our study population is male biased (Neat & Balshine-Earn, 1999; Morley & Balshine, 2002). Therefore, males should be more likely to engage in fights over territory ownership and access to mates. By simultaneously removing 30% of the territorial females of a defined 10 × 10 m study plot, we created a strong local male bias to elicit potential aggressive territory takeovers.

We mapped all 53 territories present at the study plot and identified all original owners by their spot patterns. Then, we assigned 18 of the 53 territories to a female

removal treatment. These 18 territories were chosen such that each of them was surrounded by the territories of undisturbed pairs. On a single morning, we captured all 18 pairs of the assigned territories, measured the total and standard lengths of both pair partners, released the males at the centre of their territories and transferred the females to large outdoor tanks at the shore for temporary storage until the end of this experiment. In the afternoon of the day of removal and at the following 11 days, we recorded every 1–2 days who was present at the 53 territories. Further scans of the territories were performed at days 15 and 21 of the experiment. After day 8, territory ownership almost never changed. A switch of territory ownership from 1 day to the next between two pairs or two same-sex fish was classified as direct 'takeover', because in these cases it is possible that the new owner(s) forced the previous owner(s) to leave. Most new fish came from outside the square, and most leaving fish were not seen again at the square.

Ethical note

Twenty pairs (habitat manipulation experiment) and 18 females (female removal experiment) were temporarily removed from their original territories and kept in large, fully shaded outdoor tanks. The fish were fed daily with commercial cichlid flake food. Water quality in the outdoor tanks was maintained by air pumps to provide oxygen and by regular, partial exchanges of tank water by the equivalent amount of clean lake water. As soon as an experiment was completed, the fish were released in the vicinity of their place of capture. In the meantime, the experimentally created vacancies had been occupied by new owner in most cases (see Results). We are confident, however, that the released fish reintegrated quickly in their home population. In pilot trials of a previous field season, we showed that displacement of *E. cyanostictus* from their territory does not impact their survival. During these pilot trials, instead of keeping removed fish in tanks, we had released them a few hundred metres away from their original territory. All of the moved fish returned within 2 days to their home territory, which had been occupied in the meantime by new owners. We were able to follow the fate of most of these displaced fish until their re-settlement, because they stayed near their original territory. We saw that the displaced fish reintegrated quickly in their home population, either by gaining back their original territory or by occupying a free area as their new territory.

All other field manipulations were carried out as non-invasively as possible. Individuals were only captured if we needed their body size measurements, as we used natural markers for individual identification making the capturing of all experimental individuals unnecessary. We did all length measurements underwater at 2–3 m

distance from the home territory of the fish, and afterwards, the fish were released immediately in a safe shelter in the centre of their territory for recovery. We stayed close to the territory for a few minutes after each release to make sure the released fish stayed in the shelter, which they always did.

Prudent habitat choice in *E. cyanostictus*

In the following sections, we will address five questions in order to demonstrate that assortative mating results from prudent habitat choice in *E. cyanostictus*, and we use different lines of evidence from our experiments and survey data to answer them as outlined here. For the first question ‘Do larger fish occupy territories with more stone cover?’ we provide results from the ecological survey on body size and habitat quality in unmanipulated territories. To answer the question ‘Are territories with high stone cover preferred?’ we provide results (i) of the time to settlement in the habitat manipulation experiment and (ii) of female preferences in the female habitat choice laboratory experiment. For the third question ‘Do settlements involve interference competition?’ we analysed the temporal pattern of territory (re-)occupations after one or both owners had been removed both in the habitat manipulation experiment and in the female removal experiment. For the question ‘Does territory stone cover predict the size of settling fish?’ we calculated the correlations between owner size and stone cover at the end of the habitat manipulation experiment both for males and for

females. Finally to answer the question ‘Does territory ownership change with time?’ we provide survey data on how long natural pairs stay together at a given territory, and we report the dynamics of re-settlement, re-pairing and ownership changes ensuing from the female removal experiment.

Results

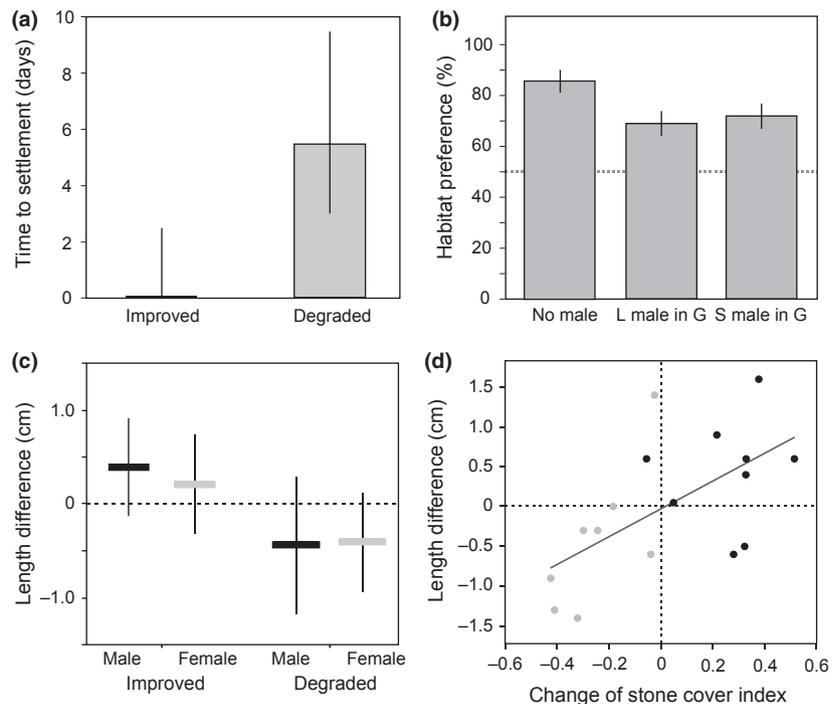
Do larger fish occupy territories with more stone cover?

The total stone cover index S_T of unmanipulated territories was positively correlated with the total lengths of male territory owners ($r = 0.48$, $P = 0.008$, $N = 30$), and it also tended to increase with the length of female owners ($r = 0.36$, $P = 0.057$, $N = 29$). Territory size was not correlated with owner size (male: $r = 0.21$, $P = 0.26$, $N = 30$; female: $r = 0.24$, $P = 0.21$, $N = 29$; Pearson’s correlations).

Are territories with high stone cover preferred?

In the habitat manipulation field experiment, we analysed the time until stable settlement occurred as measure of preference for a given territory. Time to settlement was significantly shorter in improved territories than in degraded territories ($U = 20.5$, $P = 0.022$, $N_1 = 10$, $N_2 = 10$, Mann–Whitney U -test; Fig. 2a). Of these settlers, 61% were previous neighbours of the experimentally removed pair.

Fig. 2 Habitat preferences and body size changes of new vs. original territory owners; (a) time to settlement of improved or degraded territories in the habitat manipulation experiment (medians and quartiles); (b) proportion of locations (means \pm SE) females stayed in the good (rather than in the poor) habitat patch in the laboratory experiment; ‘L’ = large male; ‘S’ = small male; ‘G’ = good habitat; dotted line: random expectation; (c) difference in total length (= compared to previous owners; means \pm SE) after habitats of experimental territories had been improved (left) or degraded (right) in the habitat manipulation experiment; (d) regression of difference between new vs. original male owner’s size on the experimentally induced change of habitat quality; black dots: improved territories; grey dots: degraded territories.



In the simultaneous habitat choice experiment in the laboratory, females preferred better habitats over poorer habitats in all three test situations. Females spent significantly more time in the patch containing more stones (i) when being alone in the tank ($\chi^2 = 52.93$, $P < 0.001$), (ii) when a large male was near the good patch and a small male near the poor patch ($\chi^2 = 34.46$, $P < 0.001$) and (iii) when a small male was near the good patch and a large male near the poor patch ($\chi^2 = 38.99$, $P < 0.001$; χ^2 -tests, all $N = 12$; Fig. 2b).

Do settlements involve interference competition?

Most new settlements at our experimental territories both in the habitat manipulation experiment and in the female removal experiment did not involve direct interference of new and old owners. In the habitat manipulation experiment, in almost 80% of the re-occupied territories, no aggressive usurpations of territories took place. In 13 cases, the first new owners stayed until the end of the experiment, and in two cases, there was a considerable time gap between the first new pair leaving and a second new pair arriving at a territory. In the remaining 20% of cases, we do not know how takeovers took place. The number of aggressive interactions involving new male territory owners in the habitat manipulation experiment decreased with increasing relative stone cover S_R ($R^2 = 0.37$, $P = 0.010$, $N = 15$, linear regression), which contradicts the existence of enhanced competition for better territories. The number of aggressive interactions was not influenced by male size ($R^2 = 0.039$, $P = 0.46$, $N = 15$).

In the female removal experiment, only eight of in total 54 moves to and away from territories (= 15%) were involved in potential direct territory takeovers (i.e. changes took place from 1 day to the next; see Fig. S2). In two further cases, we cannot exclude the possibility of a direct takeover, because we had not checked the respective territories the day before the arrival of new fish.

Does territory stone cover predict the size of settling fish?

At the end of the habitat manipulation experiment, males owning the improved territories were larger than male owners of degraded territories ($F_{1,15} = 4.65$, $P = 0.048$) and the same tendency was found in females ($F_{1,16} = 3.54$, $P = 0.078$, ANOVAS; Fig. 2c). Interestingly, the degree of experimental habitat change significantly predicted the difference in body size between new and old male owners on a continuous scale ($R^2 = 0.37$, $F_{1,15} = 8.98$, $P = 0.009$; Fig. 2d) and there was a strong tendency for the same relationship in females ($R^2 = 0.22$, $F_{1,16} = 4.45$, $P = 0.051$).

Does territory ownership change with time?

During the population surveys in 2005 and 2006, in total 11 partner replacements (three in males and eight in females) were observed and one female and two pairs disappeared without being replaced. Averaged over the two sampling years, pairs remained stable at a given territory for 226.5 days and a breeding cycle took 156.4 days. This suggests that about 50% of pairs will breed together twice (Table 1).

In the female removal experiment, changes in ownership by single fish or by pairs occurred at all 18 manipulated territories and at seven of the 35 unmanipulated territories within the experimental square. New fish settled at a territory 33 times (29 females, one male and three pairs), and 21 times fish left a territory (15 females, four males and two pairs; see Fig. S2 for details on all moves). Fifteen of the 18 experimentally widowed males stayed at their territories and formed a stable pair with a new female. The time until they stably re-mated was independent of male body size ($r_s = 0.032$, $P = 0.91$, $N = 15$, Spearman's rank correlation).

Discussion

Our results suggest that prudent habitat choice, a so-far neglected mechanism of assortative mating, is responsible for size assortment of *E. cyanostictus* pairs. In brief, (i) we found a positive relationship between habitat quality and body size in unmanipulated territories of our study population, and our experiments revealed (ii) that territories with enhanced stone cover and thus an improved habitat quality were generally preferred in the absence of competition, but (iii) that smaller fish prudently chose to settle in worse habitats than larger fish did, most likely because small fish are subordinate to large ones and therefore have a high risk to lose potential contests over territories with larger fish (Taborsky *et al.*, 2009). (iv) Finally, we showed that territory ownership is considerably dynamic, allowing for size-assortative mating based on habitat choice to occur also in a species where the competitive trait (body size) changes throughout lifetime due to indeterminate growth.

Experimental territories with increased stone cover were re-settled faster than those with decreased stone cover. Time until settlement can be regarded as a reliable indicator of habitat preference (Stanley *et al.*,

Table 1 Estimated mean pair tenacity T , mean breeding cycle length C and mean number of cycles a pair stays together (C/T) in two sampling years; third column shows means of the 2 years.

	2005	2006	Mean
T	158.0	295.0	226.5
C	160.7	152.2	156.4
C/T	0.98	1.94	1.46

2012). In most cases of the habitat manipulation experiment, the vacant territories were settled by pairs (only in one case a singleton female moved in and in two cases one of the pair partners was exchanged shortly after settlement). Therefore, we could not establish the habitat preferences of males and females independently. As males are the socially dominant sex in our study species, it is well possible that the choice of where to settle was more strongly determined by male pair partners than by females. The fact that the relationship between habitat and body size was weaker in females than in males both in the population survey and in the habitat manipulation experiment lends further support to this possibility. Therefore, we confirmed that also females alone prefer territories with more stone cover by performing a separate habitat choice experiment with females in the laboratory. This experiment revealed a strong preference of females for patches with high stone cover, irrespective of the presence or absence of larger or smaller males.

As in the habitat manipulation experiment territory vacancies were filled mainly by pre-existing pairs, one might argue that pair formation, possibly involving mate choice, and settling at territories are two separate processes. This is unlikely, however, as in a previous experimental study we failed to find any indication for a mate choice process being involved in pair formation. Instead, (i) after removal of a male or a female from a territory, the remaining partner formed a pair with the first new opposite-sex fish that arrived at the territory (Taborsky *et al.*, 2009); (ii) a simultaneous choice experiment in the laboratory (Morley, 2000) and a sequential choice experiment in the field (Taborsky *et al.*, 2009) failed to show size-based preferences in *E. cyanostictus*; and (iii) the time to stable re-mating of the experimentally widowed males in the current study was independent of male body size, also suggesting a lack of preference for large males. Moreover, in *E. cyanostictus*, there is now evidence from three independent removal experiments showing that males and females do move into and settle at territories alone when vacancies for single fish open up, even if this involves a divorce from a previous partner (Morley & Balshine, 2002; Taborsky *et al.*, 2009; this study).

The majority of settlements in the habitat manipulation experiment (80%) and in the female removal experiment (85%) occurred without direct takeovers by new owners and thus cannot have involved aggressive usurpations, suggesting that settlement occurs largely by prudent behaviour. Moreover, apparently fish did not compete more strongly over better territories, because new owners of high-quality territories were not involved in more aggressive conspecific interactions than owners of low-quality territories. Theoretical modelling showed that prudent choice is likely to evolve if opportunities for successful takeovers exist (Hårdling & Kokko, 2005). This requires the existence of a reliable predictor of the outcome of fights based on phenotypic

traits of the opponents. Obviously, in *E. cyanostictus* body size is such a reliable predictor of dominance, as during experimentally staged fights in the field smaller fish competing over territory ownership with larger fish where strictly inferior to the latter (Taborsky *et al.*, 2009). Consequently, as long as larger fish occur in a population, a small fish claiming a high-quality territory would waste its time and energy, as it would not be able to sustainably defend this territory.

When growth is indeterminate, size-assortative mating based on habitat choice can only persist in a population, if territory ownership is sufficiently dynamic allowing fish that have reached a larger size and thus a higher size-based resource holding potential to move to better territories. In our study population, natural changes of territory ownership of one or both partners occurred on average every 7 months. *E. cyanostictus* surviving to a size where they can hold a territory (i.e. at a total length of about 5.5 cm corresponding to an age of approximately 200 days according to growth trajectories in the laboratory; Segers & Taborsky, 2012) can expect to live on average for about 1–2 more years based on the observed size distribution in the field. Taken together, this means that most fish will change their territory at least once or twice during their lifetime allowing them to ‘upgrade’ the quality of their territory.

By combining the available quantitative information on the relationships between habitat quality, male size and female size in unmanipulated fish, we can show graphically that prudent habitat choice can explain the strength of size assortment found in our study population at least for individuals displaying mean body sizes and mean strength of habitat–size relationships. Figure 3 demonstrates this from the perspective of an average-sized female (Fig. 3a) and an average-sized male (Fig. 3b), respectively. The mean deviation from a linear relationship between body size and habitat quality (S_R) in our study was $\pm 11.2\%$ in males and $\pm 12.1\%$ in females (i.e. % of the total range of habitat quality present in the study area, $S_R = \{0.5..2.0\}$). We defined these mean deviations as the ‘habitat quality tolerance’ of the two sexes (grey shaded regions in Fig. 3). Given a habitat tolerance of $\pm 11.2\%$, the blue shaded area in Fig. 3a shows the size range of males that would opt to settle at a territory inhabited by an average-sized resident female of 6.6 cm (red dot). Correspondingly, given a habitat tolerance of females of $\pm 12.1\%$, Fig. 3b shows the size range of females (red shaded area) that would settle at the territory of an average-sized male (7.5 cm, blue dot). The sizes of almost all of these settling males (size range projected to x -axis by blue arrows, Fig. 3a) and settling females (red arrows, Fig. 3b) would fall within the 95% confidence intervals (CIs) of the male to female size relationship of pair mates (95% CIs shown as horizontal blue and red bars in Fig. 3a,b, respectively). Moreover, habitat choice might explain why in *E. cyanostictus* typically male pair partners are larger than their

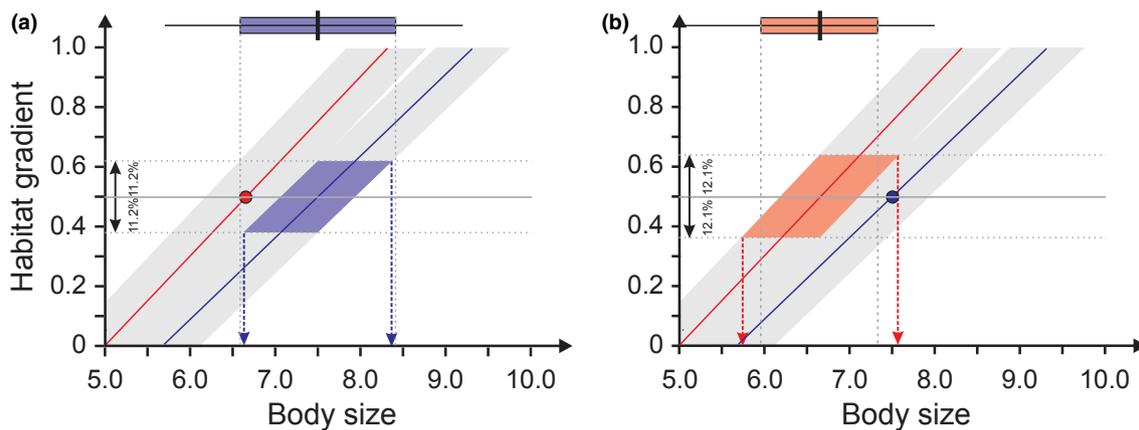


Fig. 3 Scheme to illustrate the size range of partners that (a) an average-sized resident female (red dot) or (b) an average-sized male (blue dot) inhabiting a territory of average quality can expect to mate with if incoming fish exhibit prudent habitat choice (figure based on data of unmanipulated pairs). For simplicity, we assume here that the gradient of habitat qualities varies between 0 (poorest) to 1 (best possible habitat). The blue and red linear trend lines are drawn assuming that the smallest territorial fish of each sex measured at our study site occupy the worst habitat (i.e. females of 5.0 cm TL and males of 5.7 cm TL are located at values 0 of the habitat gradient) and that average-sized territorial females (6.6 cm TL) and males (7.5 cm TL) inhabit average-quality habitats (i.e. habitat quality gradient = 0.5; this value is highlighted as horizontal grey line for reference). The grey shaded areas represent the mean deviations in % of the correlation between male size and habitat quality ($\pm 11.2\%$) and female size and habitat quality ($\pm 12.1\%$) as determined in the field. Now we can draw the size range of males (sizes between the dashed blue arrows, panel a) and of females (sizes between the red arrows, panel b), which would settle at a territory of average quality (habitat gradient = 0.5). Horizontal bar charts at the top of the panels show the mean, the 95% confidence intervals (CIs) and the ranges of (a) male and (b) female size distributions; CIs are taken from the regression of male size on female size (Fig. S3a) and female size on male size (Fig. S3b) from a data set of 77 unmanipulated pairs published in Taborsky *et al.* (2009) and determined at the x -axis value of 6.6 cm TL (= mean female size, blue chart; Fig. S3a) and 7.5 cm TL (= mean male size, red chart, Fig. S3b). Vertical, dashed grey lines project these 95% CIs to the x -axes of a and b.

female mates [cf. female size (red dot) to range of settling males in Fig. 3a and male size (blue dot) to range of settling females in Fig. 3b].

In this study, we provide the first experimental evidence that assortative mating can emerge from prudent habitat choice despite the existence of a common habitat preference for high-quality habitats in the absence of interference competition. Prudent habitat choice as mechanism of nonrandom mating is conceptually different from scenarios where assortative mating arises as by-product of preference for different habitats (e.g. Rice, 1984; Rice & Salt, 1990) or different hosts (Bush, 1969; Via, 1999). In case of such differential preferences, assortment can arise 'automatically' when mating occurs locally at the preferred habitat or host species (Servedio *et al.*, 2011). Experiments showed that this mechanism can readily lead to disruptive selection and premating reproductive isolation (Rice & Salt, 1990). In contrast, prudent habitat choice, where all members of a population share a common preference for high-quality habitats in the absence of competition, should rather be expected to give rise to positive selection on the competitive trait determining resource holding potential (e.g. body size).

Mechanisms of assortative mating arising solely from ecological preferences have not yet received a

broad attention, which may be due both to a strong *a priori* expectation that mate choice will always be involved in assortative mating and to the difficulty to prove the absence of mate choice in natural populations (see Taborsky *et al.*, 2009). We would like to stress, however, that prudent habitat choice is highly likely to be a widespread mechanism of assortative mating in territorial species, because two of its key ingredients are ubiquitous features in animals: (i) the expression of habitat preferences and (ii) the existence of differences in resource holding potential that can be perceived by conspecifics. These ingredients can promote the expression of prudent, conditional habitat choice depending on the available options under competition as it has been previously shown in the context of mating preferences and mate choice (Bel-Venner *et al.*, 2008; Candolin & Salesto, 2009).

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Schematic drawing of one example of a randomized sequence of choices given to a female at three subsequent days in three different tanks: day 1: poor habitat/large male vs. good habitat/small male; day 2: good habitat vs. poor habitat; day 3: poor habitat/small male vs. good habitat/large male.

Figure S2 Detailed results of the female removal experiment in the field; number of males and females that entered or left a territory after the resident female had been removed (manipulated territories, left side of figure) or an unmanipulated territory (right).

Figure S3 Relationships between the sizes of male and female pair members (shown as total length, TL [cm]) in 77 *Eretmodus cyanostictus* pairs captured at Kasakalawe Point (data from Taborsky *et al.* 2009).

Data deposited at Dryad: doi:10.5061/dryad.t03h0

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