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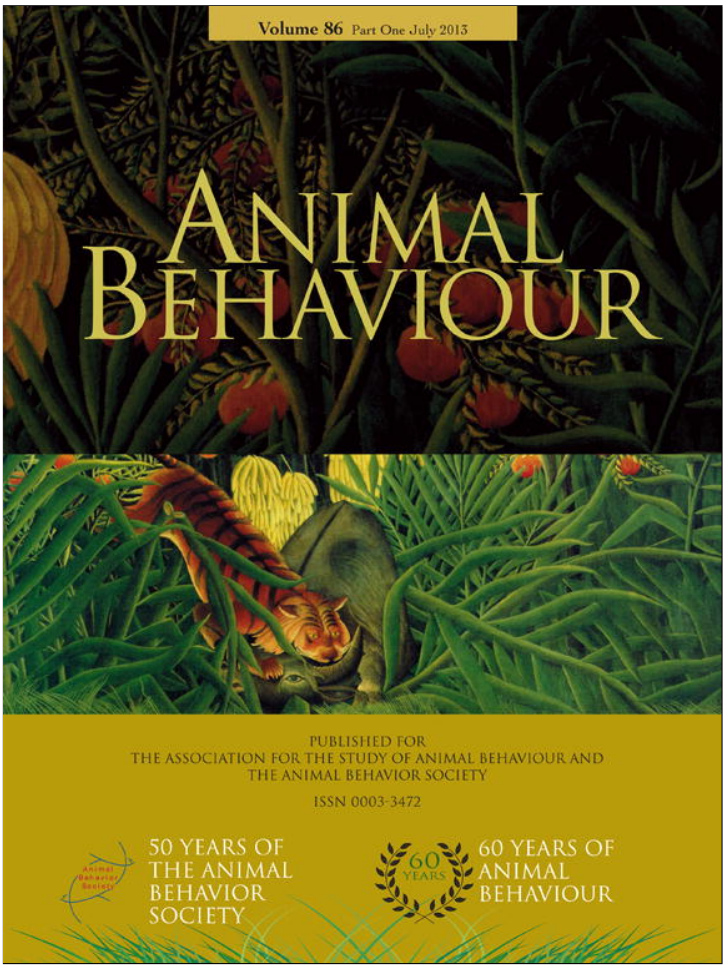

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Animal Behaviour 86 (2013) 75–83

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Local enhancement via eavesdropping on courtship displays in male guppies, *Poecilia reticulata*

M. M. Webster*, K. N. Laland

School of Biology, University of St Andrews, St Andrews, U.K.

ARTICLE INFO

Article history:
Received 3 January 2013
Initial acceptance 14 February 2013
Final acceptance 8 April 2013
Available online 14 June 2013
MS. number: 13-00018

Keywords:
communication network
guppy
mate choice copying
Poecilia reticulata
producer–scrounger
public information
social information
social transmission

Courtship interactions often take place within the setting of a communication network, with signals sent from senders to target receivers also being detectable to third-party eavesdroppers. Potentially, eavesdropping males may be able to use signals produced by courting males to locate females indirectly. Furthermore, where male courtship vigour varies according to the quality of females (e.g. fecundity, receptivity or number), eavesdroppers observing multiple courting males may be able to use differences in courtship vigour to gauge indirectly the relative quality of the females. We tested these predictions in an experiment in which observer male guppies were presented with a binary choice between two demonstrator males courting differently sized groups of females, which were hidden from the observer. We found that the demonstrator males courted larger groups of females at a higher rate, and that observer males tested in the presence of the demonstrators spent more time and performed more courtship displays in the location of the demonstrator courting the larger group of females. Observers tested after the demonstrator males had been removed, however, showed no preference for either of the demonstrated locations and for the most part performed no courtship displays at all. Our results provide evidence for male–male local enhancement, but not delayed local enhancement, via demonstrator male courtship behaviour. Such behaviour may be adaptive, allowing eavesdropping observer males to locate females indirectly. We discuss how this system could be employed to explore social transmission of information further.
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For many species, courtship displays are rarely performed in seclusion, occurring instead within the wider context of a communication network. A communication network is an assemblage of individuals that comprises not only the performer of the display and its intended targets but also a whole range of other parties, for whom the display might not be intended, but who can benefit from detecting and responding to it (McGregor 2005). These may include conspecifics competing with the performer (Grafe 2005; Milner et al. 2010; Clark et al. 2012), potential receivers, some of whom may be receptive to the performer (Nordell & Valone 1998; Witte & Nöbel 2011), and others who may be unreceptive, and who may even use the signal to avoid unwanted attention (Brooks 1999). In a rather different context, predators (Igaune et al. 2008) and parasitoids (Gray et al. 2007) can also use conspicuous displays to locate their prey or hosts.

As such, individuals performing courtship displays may pay significant costs, which must be balanced against the benefits of courting, namely attracting mates and reproducing with them. Use of socially transmitted information may have evolved in part because it can reduce the costs associated with sampling the environment directly. Social information use is seen in a variety of different contexts, including mate finding and courtship interactions (Zentall & Galef 1988; Heyes & Galef 1996; Giraldeau & Caraco 2000; Giraldeau et al. 2002; Danchin et al. 2004; Kendal et al. 2005; Hoppitt & Laland 2008). One way in which individuals may reduce the costs of courting then is to exploit the efforts of others, by eavesdropping upon their courtship behaviour in order to locate prospective mates. Males seeking mates are therefore predicted to respond not only to cues emanating from females, but also from the conspicuous courtship behaviour of rival males who have already discovered females, by approaching them and beginning to court themselves, even if the females that they are courting are not directly detectable to the observing eavesdropper. Such behaviour, local enhancement and socially facilitated courtship, has already been documented in species that court within communication networks (Grafe 2005; Milner et al. 2010; Clark et al. 2012). Local enhancement is a social process by which the presence, behaviour or products of one individual cause another to visit the area that it occupies (Thorpe 1956; Hoppitt & Laland 2008). Social facilitation, also sometimes referred to as contagion, describes the unconditioned process whereby the performance of

* Correspondence: M. M. Webster, School of Biology, Bute Building E47, University of St Andrews, St Andrews, Fife KY16 4TS, U.K.
E-mail address: mike.m.webster@gmail.com (M. M. Webster).

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http://dx.doi.org/10.1016/j.anbehav.2013.04.014

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a given behaviour by one individual increases the likelihood of the same behaviour being performed by another, observing individual (Thorpe 1963; Zajonc 1965; Visalberghi & Addessi 2000; Hoppitt & Laland 2008).

Beyond this lies the prediction that where male courtship vigour varies with female quality or number (Ojanguren & Magurran 2004), then selection should favour the ability in eavesdropping males to discriminate between the courtship behaviour of males courting different females in separate locations, in order to locate larger groups or higher quality females. Indirect resource assessment based upon socially transmitted information has already been identified in other contexts, such as foraging patch selection (Valone 1989; Laland et al. 2011), and in principle similar behaviour should be expected for mate-searching behaviour among animals that court within communication networks.

We tested this idea in a laboratory experiment, using the guppy, a sexually dimorphic poeciliid fish with elaborate courtship interactions and internal fertilization, which is a well-established model species in the field of evolutionary ecology in general, and courtship and reproductive behaviour in particular. Guppies have been widely used to explore courtship interactions within the context of communication networks (reviewed in Earley & Dugatkin 2005), as well as other forms of social information transmission (reviewed in Webster & Laland 2011). Brightly pigmented males court the drably coloured females by performing a sigmoid display, a stereotyped courtship behaviour in which the male approaches the female and assumes an 'S' shape (as seen from above) and vibrates his body while moving slowly in front of or alongside her (Magurran 2005).

This study had three aims. Our first aim was to determine whether male guppies were attracted to areas where they could see other males courting females that were hidden to the observer male. Such behaviour constitutes local enhancement.

Second, we sought to determine whether male courtship rates varied with the number of females present, and if so whether under binary choice conditions, observer males were attracted to the location of the male that was courting at the greater rate. To our knowledge the relationship between rate of courtship and female number or density has not been previously explored in guppies. Other species of fish are known to be able to assess relative differences in resource distribution (such as food) between locations, solely by using cues derived via observing conspecific foraging behaviour (e.g. Webster & Laland 2008; Laland et al. 2011). In this study we asked whether male guppies observing the courtship behaviour of other males would exhibit similar preferences for richer 'patches', that is patches that held more females. Moreover, we investigated whether the observer males themselves would begin to court in the presence of courting males, even though the females were not directly detectable, as has been observed in other (nonfish) species that court within communication networks (Milner et al. 2010; Clark et al. 2012).

The third aim of our study was to determine whether male guppies were subject to local enhancement both in real time, while the courting males were still present, and after a delay following the removal of the courting males. The latter condition, where the observer male is tested in the absence of courtship cues, tests for a form of local enhancement known as delayed local enhancement (Coolen et al. 2003). The distinction between real time and delayed local enhancement is an ecologically meaningful one. In the case of foraging sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*), for example, some species make foraging decisions based upon delayed local enhancement while others are incapable of doing so, where it is thought to form the basis of a species-specific adaptation for social learning (Coolen et al. 2003; Laland et al. 2011). Identifying a similar learning mechanism in eavesdropping male guppies could therefore open the way for further research into the kinds of learning strategies, evolved behavioural rules, that dictate the frequency and patterns of eavesdropping behaviour (Laland 2004; Galef 2009; Rendell et al. 2011).

We tested the following specific predictions: (1) that the courtship rate of the demonstrator males courting the larger of two groups of females (one versus no females or three versus one females) would be higher than the rate of males courting the smaller group; (2) that, under binary choice conditions, the observer male would spend more time, and perform more displays, in the vicinity of the male courting the larger group of females than the male courting the smaller group; and (3) that the observer male would learn and exploit this information, exhibiting such preferences even after the removal of the courting males, providing evidence for delayed local enhancement.

METHODS

Study Animals

We used wild-type guppies taken from a population of several thousand maintained in a pond inside a greenhouse at the University of Leicester Botanical Gardens, U.K. These guppies were the descendants of wild fish from Trinidad. Unfortunately, the drainage from which they originated is unknown. Several hundred were taken to our laboratory at St Andrews University, U.K., in November 2006, where they were held in mixed-sex groups of around 75 adult fish per 120-litre aquarium. Each aquarium contained gravel and rocks for cover, an internal filter, an air stone and a heater. The fish were held at 26 °C on a 10:14 h light: dark regime and fed standard flake food twice daily. New-born fry were removed daily to separate rearing tanks. The experiments described below were conducted in December 2008.

Experimental Arena

The aim of this experiment was to determine whether focal males ('observers') were attracted to locations where they could see, or had previously seen, other males ('demonstrators') courting females that were undetectable to the observer. Trials were conducted in a binary choice arena (Fig. 1a, b). This consisted of an opaque tank measuring 45 × 45 cm and 15 cm tall. A 1 cm deep layer of gravel was provided across the base of the tank, and the water depth was 6 cm. The experimental arena was designed so that the observer male could see the demonstrator males, but not the females, from which it was visually and chemically isolated. The demonstrator males received visual and chemical cues from the females, but could not physically interact with them. The main chamber of the experimental arena was shaded, while the sections holding the demonstrator males and females were illuminated from above using white LED desk lamps. This allowed the observer male to observe the demonstrator males, but prevented the demonstrator males from seeing or interacting with the observer male in the main chamber. One-way glass proved to be ineffective in pilot studies because it resulted in a reflection of the observer male, with which it interacted.

Two watertight stimulus chambers were provided at one end of the tank. These measured 20 × 6 cm and 6 cm tall. Each was divided in two with a colourless, transparent perforated barrier, each half measuring 10 × 6 cm and 6 cm tall. One half held the demonstrator male, the other held the female(s). The front of the half holding the demonstrator male was transparent and colourless, except for a 1 cm wide opaque strip next to the half of the chamber holding the female(s). The remaining walls were opaque. We used two white LED desk lamps to provide lighting in the

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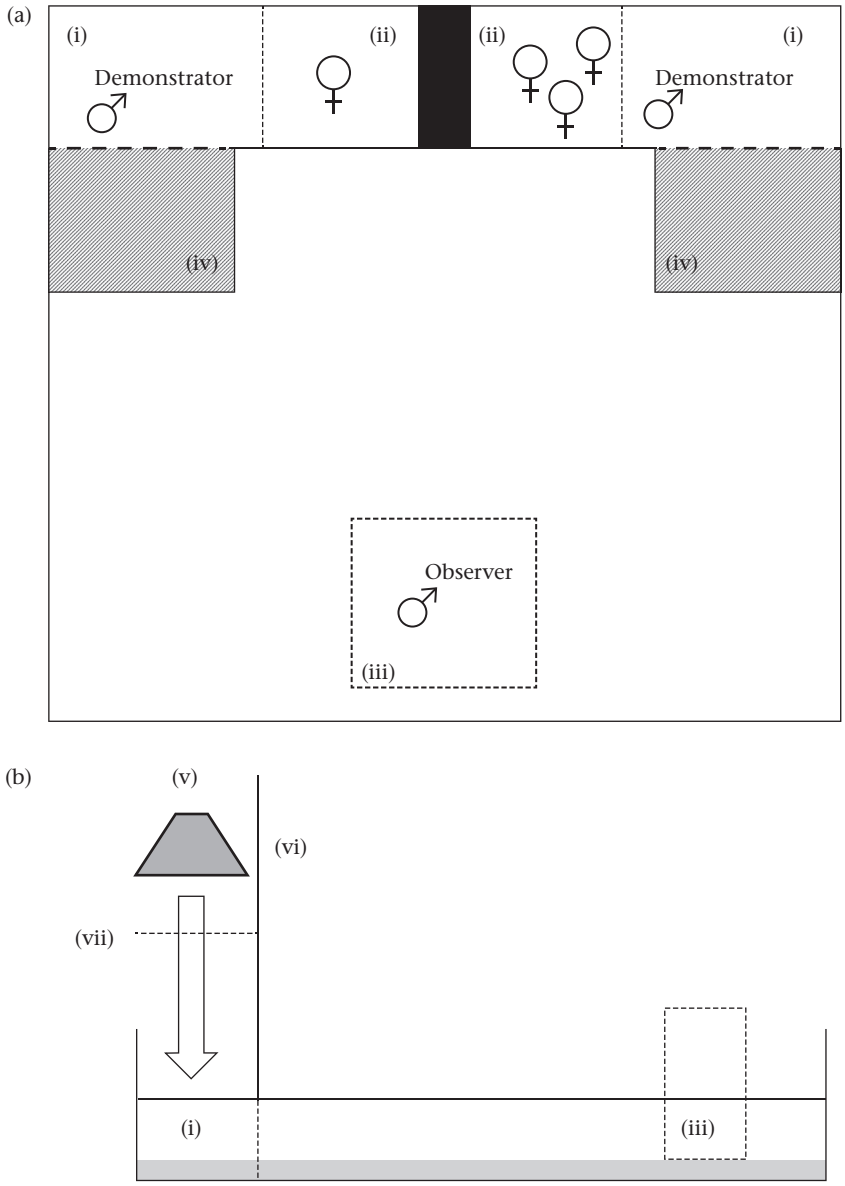

Figure 1. (a) Plan view of the binary choice test arena (not to scale). The chambers holding the demonstrator males (i) were visible to the observer male, while the chambers holding the females (ii), were visible to the adjoining demonstrator males only. A removable holding chamber (iii) housed the observer male during the demonstration phase. Two preference zones (iv) were used to determine association preferences during the choice phase. (b) Profile view of the binary choice test arena (not to scale). LED desk lamps (v) were used to illuminate the demonstrator holding chambers. An opaque black plastic screen (vi) was used to prevent the lamps from illuminating the main arena, housing the observer. Diffusion filters (vii) were used to disperse the light from the lamps evenly across the demonstrator holding units. Solid lines indicate opaque, nonpermeable surfaces. Large-dashed lines indicate colourless, transparent nonpermeable surfaces, allowing the transmission of visual but not chemical cues. Small-dashed lines indicate colourless, transparent, permeable surfaces allowing for both visual and chemical cues to pass between compartments. The fine grey solid line indicates the water level. See main text for details of the experimental procedure.

demonstrator holding units. These were placed 40 cm above the two demonstrator chambers. White diffusion filter paper (Lee Filters, Andover, U.K.) was placed 10 cm beneath the lamps to diffuse the light and to ensure a more even distribution of light within the demonstrator holding units. To prevent light illuminating the area of the arena housing the observer, a 60 cm tall black plastic screen running the width of the arena was placed so that it sat immediately above the fronts of the demonstrator units (Fig. 1b). There was no exchange of water between the stimulus chambers and the main tank, ensuring that the observer had no access to chemical cues from either the demonstrator males or the females. At the other end of the tank was a holding chamber measuring 10 × 10 cm and 12 cm tall. This was constructed from colourless, transparent perforated plastic, and held the observer during the demonstration phase of the trial. The holding chamber was positioned centrally against the wall of the tank, 29 cm from the stimulus chambers. In front of the male side of each stimulus chamber we delineated a preference zone measuring 6 × 6 cm, corresponding to three fish body lengths, to give a conservative measure of observer association preferences. The preference zone boundaries were marked with 1 cm tall, 3 mm wide black plastic strips set in the gravel and level with its surface.

Experimental Procedure

We gave observer males the opportunity to observe two demonstrator males each courting a different-sized group of females. Our experimental design encouraged demonstrators to

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perform sigmoid displays but prevented them from copulating, or from circumventing female choice by performing forced copulations (Matthews & Magurran 2000). Thus the observer could not detect the females directly, but could infer the location of the females indirectly, by monitoring the behaviour of the demonstrator males. In one treatment observers were allowed to join the demonstrators in real time, as they were courting, while in the second they were tested after the demonstrators had been removed. The latter treatment tested whether the observers could learn the location of areas where they had previously seen conspecifics courting.

The demonstrator males (15–20 mm long) and females (25–30 mm long) were added to the tank and allowed to acclimatize for 10 min. At this point the stimulus chambers were not illuminated. Demonstrator males and observers were matched for size (to within 2 mm within trials), marking pattern and coloration as closely as possible, since these traits are known to be important in female mate choice (e.g. Karino & Urano 2008) and may therefore also have a bearing upon male–male interactions in a mate competition context. We used females that had given birth within the last 72 h to standardize receptivity to males across treatments. Females were drawn from a limited pool of fish, although none were used twice on the same day. We used a limited pool of females to ensure that the largest could be used, reasoning that these were more likely to elicit more courtship attempts from the demonstrators (Ojanguren & Magurran 2004). They were size matched between chambers within trials. No demonstrator male was used more than once. The position of the chamber with the larger group of females was determined using a random systematic approach; within each treatment, the larger group of females was presented on the left or right an equal number of times but the order of these presentations was randomized.

Following the acclimation period a single observer was added to the holding chamber. It was allowed to settle for 5 min, after which the lights were turned on over the stimulus chambers, revealing the demonstrator fish. For a further 5 min the observer was allowed to observe the demonstrator fish (the demonstration phase). Following this, the lights were switched off for 1 min and the demonstrator males were either carefully removed or retained, depending upon the treatment (described below). Switching the lights off ensured that the observer could not see the removal of the demonstrators, which could potentially act as a stressor. Following this the lights were turned back on and after a further 1 min the observer was released, by gently removing the holding chamber. This began the choice phase, which lasted a further 5 min, during which we recorded the proportion of time spent inside each preference zone, and the number of courtship displays performed in each. Sigmoid displays (described above) were seen to last for 2–3 s in this experiment. Mean durations of 3–4 s were reported in the field for guppies from four separate natural populations (Luyten & Liley 1985), suggesting that the behaviour of our fish was representative of that seen under natural conditions. Following each trial the observer males were measured (standard length) to the nearest 0.1 mm using digital callipers. We saw no differences in the body lengths of the males in the different conditions, described below (means ± SE: local enhancement: 1:0 female ratio: 17.3 ± 0.20 mm; 3:1 female ratio: 17.6 ± 0.34 mm; delayed local enhancement: 1:0 female ratio: 17.3 ± 0.21 mm; 3:1 female ratio: 17.7 ± 0.28 mm; one-way ANOVA: $F_{3,44} = 0.68$, $P = 0.53$).

We varied both the number of females presented to the demonstrator males (one versus none and one versus three) and the timing of exposure to the demonstrator males, comparing local enhancement and delayed local enhancement, in a two-by-two factorial design with 12 replicates per group. In the first timing condition the observer was released while the demonstrators were still present and interacting with the females, allowing them to receive demonstrator courtship cues during both the demonstration and the choice phases of the trial. In the second timing condition the demonstrators were removed immediately following the demonstration phase, such that the observer male received no further social information during the choice phase. No observer was used more than once.

From the demonstrators we recorded the number of sigmoid courtship displays performed during the demonstration phase, and during the choice phase in the local enhancement trials, where the demonstrators were retained throughout the choice phase. From the observers we recorded the first preference zone that they entered, the amount of time spent in each of the two preference zones in front of the stimulus chambers during the choice phase, as well as the number of sigmoid displays that they made in them. Data were analysed as described below. Two-tailed tests were used throughout.

Statistical Analysis

Demonstrator display rates

In the 1:0 female ratio treatments, the demonstrators that were not exposed to females tended not to perform courtship displays. Accordingly, the data sets for these demonstrators were dominated by zero values and could not be normalized through transformation. For the 1:0 female ratio treatments we therefore did not perform any statistical analyses. In the 3:1 female ratio treatments the data were normally distributed, and so the within-treatment demonstrator courtship rates were compared using *t* tests for both the local enhancement and the delayed local enhancement treatments. In the delayed local enhancement treatments we compared the display rates of the demonstrators in the observation phase and the test phase separately.

Observer responses: first preference zone entered

We compared the first preference zone entered by the observers in the four groups using a binomial regression analysis. Treatment (local enhancement or delayed local enhancement), the ratio of females presented to the demonstrators (1:0 or 3:1) and the location of the male courting the larger group of females (left or right) were included as fixed factors. The body length of the observer (mm) was included as a covariate. Across all treatments, five males failed to enter either goal zone, and these were excluded from this analysis. Of the five excluded trials, one was from the local enhancement 3:1 treatment and two each were from the delayed local enhancement 1:0 and 3:1 treatment groups.

Observer responses: time allocation

We compared the difference in amount of time that the observers spent in the two association zones using a general linear model. We calculated the time difference as the amount of time spent in the association zone of the demonstrator male courting the larger group of females minus the time spent in the association zone of the demonstrator male courting the smaller group. We included treatment (local enhancement or delayed local enhancement), female ratio (1:0 or 3:1) and the location of the male courting the larger group of females (left or right) as fixed factors. The body length of the observer (mm) was included as a covariate. Finally, we made observer patch choice comparisons within treatments using *t* tests.

Observer responses: courtship displays

We compared the number of courtship displays that the observers made in the association zones of the males courting the larger and smaller groups of females. In the delayed local

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enhancement treatments the observers performed very few courtship displays, zero in most trials. We therefore treated the data as binary. We subtracted the number of courtship displays that the observers made in the association zones of the males courting the smaller group of females from that performed in the association zones of the males courting the larger groups. These data were then recoded as 1 if the value was positive (i.e. if more displays in the zone of the demonstrator courting more females were recorded) or 0 if the value was zero or negative. These binary data were compared using a binary logistic regression analysis, with treatment (local enhancement or delayed local enhancement), female ratio (1:0 or 3:1) and the location of the male courting the larger group of females (left or right) as fixed factors. The body length of the observer (mm) was included as a covariate. Finally, we compared the within-treatment observer courtship rates using *t* tests. This was only performed for the local enhancement treatment, since virtually no courtship displays were documented in the delayed local enhancement treatments.

Ethical Note

The guppies were transported from Leicester to St Andrews by car, in bags containing oxygenated water placed within insulated boxes containing heat pads to maintain a temperature of 25 ± 1 °C. In designing this experiment we consulted the University of St Andrews' Home Office Liaison Officer. The procedures detailed above were noninvasive and did not require U.K. Home Office licensing or further institutional ethical approval. We observed no mortality, illness or aberrant behaviour immediately after testing in any of the fish that took part in these experiments. Following the completion of the experiments this guppy stock was passed on to the University of Glasgow, U.K., for use in another research programme.

RESULTS

Demonstrator Display Rates

Demonstrator males observing larger groups of females performed more displays than those observing no females, or smaller groups of females, during the demonstration phase of the experiment (Fig. 2). Unsurprisingly, in the 1:0 female ratio trials, demonstrators that were not exposed to any females tended not to produce courtship displays. They consequently performed fewer displays than those paired with a single female in all 12 trials in the demonstration phases of both the local enhancement and delayed local enhancement treatments, and in 11 of 12 trials in the choice phase of the delayed local enhancement treatment. No statistical analyses were performed for these comparisons; however, courtship data (mean displays/min) are presented in Fig. 2. In the 3:1 female ratio trials, *t* tests revealed that males exposed to the larger groups of females performed more courtship displays in both the demonstration and choice phases of the trial in the local enhancement treatments ($t_{11} = 4.48$, $P = 0.001$ and $t_{11} = 4.81$, $P = 0.001$) and also during the demonstration phase of the delayed local enhancement treatment ($t_{11} = 6.85$, $P < 0.001$).

Observer Responses: First Preference Zone Entered

A binomial regression revealed that observers in local enhancement treatments were more likely to enter the goal zone of the male courting the larger group of females first, compared to those in the delayed local enhancement treatments (Wald $\chi^2_{1,39} = 4.88$, $P = 0.03$; Fig. 3). We saw no effect of the ratio of females presented to the demonstrators (Wald $\chi^2_{1,39} = 0.04$, $P = 0.85$), observer body size (Wald $\chi^2_{1,39} = 0.89$, $P = 0.35$) or the location of the high- and low-courting demonstrators (Wald $\chi^2_{1,39} = 0.98$, $P = 0.32$).

Observer Responses: Time Allocation

A general linear model revealed that observers spent more time in the preference zone close to the stimulus chamber that held the demonstrator male courting the larger group of females when the demonstrators were still present (local enhancement) compared to when they were absent (delayed local enhancement) in the choice phase of the experiment ($F_{1,43} = 9.95$, $P = 0.006$; Fig. 4). The ratio of females being courted by the demonstrators ($F_{1,43} = 0.19$, $P = 0.66$), the location of the two demonstrator chambers ($F_{1,43} = 0.23$,

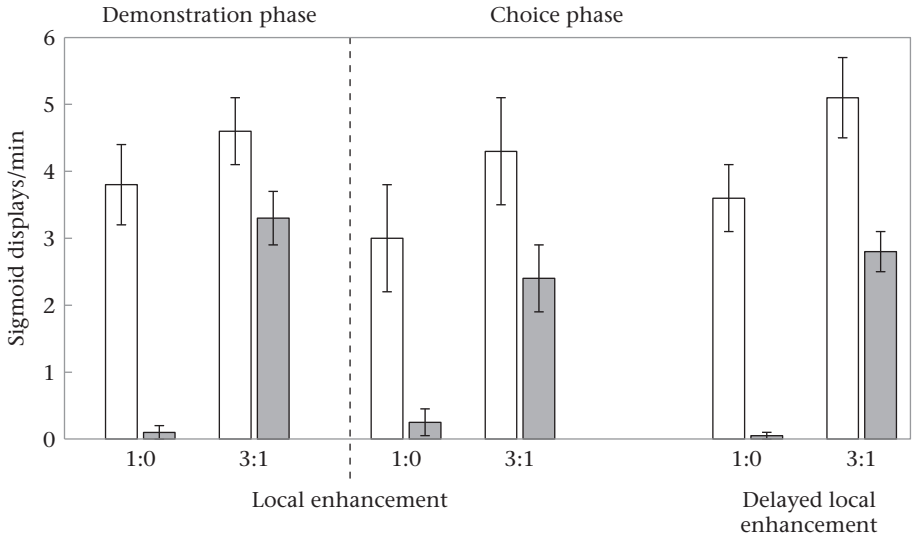

Figure 2. The number of courtship displays/min performed by the demonstrator males housed next to the larger (□) and smaller (■) groups of females. In the local enhancement treatment the demonstrator males were present during both the demonstration phase and the choice phase. Display rate data are presented separately for these two phases. In the delayed local enhancement treatment the demonstrator males were present only during the demonstration phase of the experiment. Means are given ± 95% confidence intervals.

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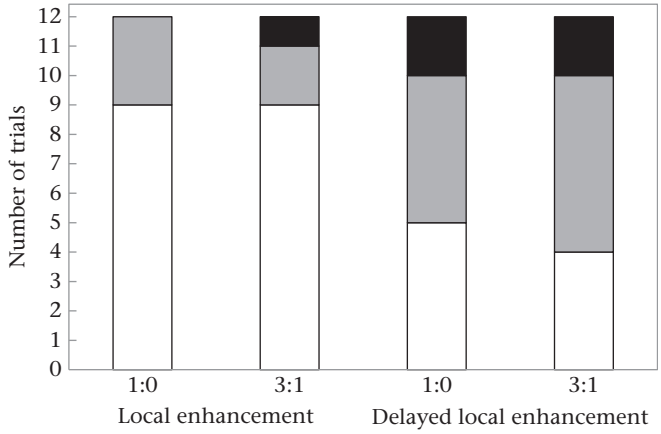

Figure 3. The number of trials in which the observer first entered the goal zone of the demonstrator courting the larger (□) and smaller (■) groups of females, or in which they failed to enter either goal zone (■).

$P = 0.63$) and the body length of the observer male ($F_{1,43} = 2.17$, $P = 0.15$) had no effect on time allocation differences.

The observer fish spent more time in close proximity to the stimulus chamber holding the male courting the larger group of females than to the stimulus chamber containing the other demonstrator male in the trials in which they chose while the demonstrator males were still present, but not while they were absent (t tests: local enhancement: 1:0 female ratio: $t_{11} = 3.09$, $P = 0.010$; local enhancement: 3:1 female ratio: $t_{11} = 3.92$, $P = 0.002$; delayed local enhancement: 1:0 female ratio: $t_{11} = -0.57$, $P = 0.57$; delayed local enhancement: 3:1 female ratio: $t_{11} = 0.12$, $P = 0.90$).

Observer Responses: Courtship Displays

Binary logistical regression revealed that observers were more likely to perform more displays in the preference zone of the demonstrators displaying to the larger than the smaller group of females in the local enhancement treatments than they were in the delayed local enhancement treatments (Wald $\chi^2_{1,44} = 10.65$, $P = 0.001$; Fig. 5). The ratio of females being courted by the demonstrators (Wald $\chi^2_{1,44} = 0.42$, $P = 0.51$), the location of the two demonstrator chambers (Wald $\chi^2_{1,44} = 2.09$, $P = 0.15$) and the body length of the observer male (Wald $\chi^2_{1,44} = 0.17$, $P = 0.73$) had no effect on time allocation differences.

In the local enhancement treatments, the observer fish performed more courtship displays in the preference zone next to the stimulus chamber holding the male courting the larger group of females than it did in the other preference zone (t tests: 1:0 female ratio: $t_{11} = 4.00$, $P = 0.002$; local enhancement: 3:1 female ratio: $t_{11} = 2.60$, $P = 0.025$). In the delayed local enhancement trials virtually no courtship displays were observed, and statistical analyses were therefore not performed. (Count data for display rates in each preference zone for all treatments, including the delayed local enhancement treatments are presented in Fig. 5.)

DISCUSSION

Our results provide evidence for local enhancement, but not for delayed local enhancement, mediated by male courtship behaviour in male guppies. The rate of sigmoid courtship displays of the demonstrators increased with the number of females present, and we suggest that this cue was also picked up by the observer males, suggesting eavesdropping. In the local enhancement trials, in which the demonstrators were present during the observer's

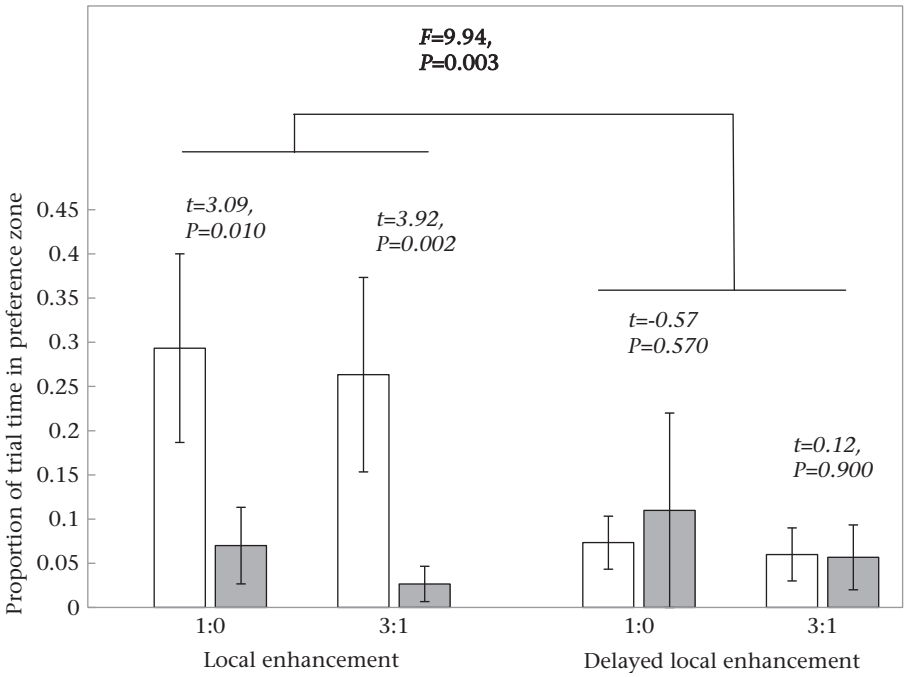

Figure 4. The proportion of time spent by the observer males in the preference zones closest to demonstrator males housed next to the larger (□) and smaller (■) groups of females. In the local enhancement treatment the demonstrator males were present during both the demonstration phase and the choice phase. In the delayed local enhancement treatment the demonstrator males were present only during the demonstration phase of the experiment. Means are given ± 95% confidence intervals. The test statistics in italics show the results of paired-sample t tests comparing the time the observer male spent in the preference zones corresponding to the locations of the demonstrator males courting larger and smaller female groups within each treatment. The test statistics in bold show results from a general linear model comparing the overall difference in time allocation (between time spent in the preference zone corresponding to the location of the demonstrator males courting the larger versus the smaller female group) between the local enhancement and delayed local enhancement treatments. See main text for details of the experimental procedure and statistical analysis.

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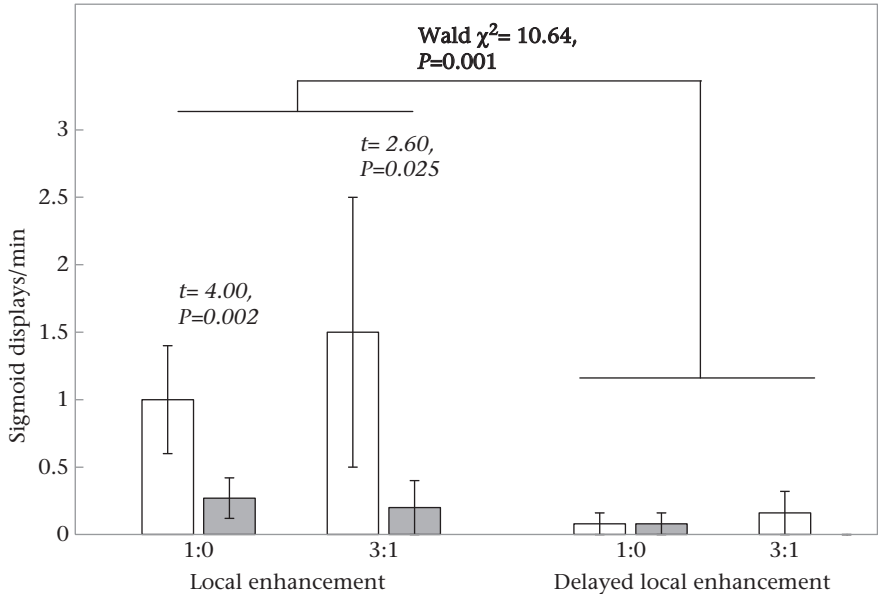

Figure 5. The number of courtship displays/min performed by observer males in the preference zones closest to demonstrator males housed next to the larger (□) and smaller (■) groups of females. In the local enhancement treatment the demonstrator males were present during both the demonstration phase and the choice phase. In the delayed local enhancement treatment the demonstrator males were present only during the demonstration phase of the experiment. Means are given ± 95% confidence intervals. The test statistics in italics show the results of paired-sample *t* tests comparing the courtship rate of the observer male in the preference zones corresponding to the locations of the demonstrator males courting larger and smaller female groups within each treatment. Analyses were not performed for the delayed local enhancement treatments, owing to the low frequency of displays by the observers. The test statistics in bold show results from a binary logistic regression comparing the overall difference in courtship rate (between courtship rate in the preference zone corresponding to the location of the demonstrator males courting the larger versus the smaller female group) between the local enhancement and delayed local enhancement treatments. See main text for details of the experimental procedure and statistical analysis.

choice test, the observers spent more time in close proximity to the demonstrator males courting the larger group of females, and performed more courtship displays in the immediate area of those demonstrators, compared to males courting the smaller group. In the delayed local enhancement trials, however, where the demonstrators were removed before the observer male was released, we saw no observer preferences for the areas formerly occupied by the higher-rate courting demonstrator, in terms of either time allocation or display rate. This latter finding suggests that in guppies, males are either unable to learn about the distribution of courting conspecifics, or that if they are, this information does not play a role in determining their space use patterns.

Joining males that are already courting may be adaptive, even if the female is not yet visible. If courtship behaviour performed by males is a likely indicator of the presence of females, then eavesdropping observers have the opportunity to gather valuable information about the location of a fitness-enhancing resource, females, cheaply without having to pay the costs of searching for them directly. For example, in several species of chorusing frogs, males increase their call rate significantly as females approach, while silent satellite males monitoring this interaction can respond by moving towards the calling male and beginning to call themselves which may enable them to intercept the approaching female (Grafe 2005). Males may eavesdrop on female signals too. Within pairs of European robins, *Erithacus rubecula*, females use a specific call to beg for food from their partners during the breeding season. The call is loudest and performed most frequently during the female's most fertile period, and potentially provides eavesdropping males with information about her location and reproductive state. Accordingly, Tobias & Seddon (2002) found that playbacks of female calls attracted males from neighbouring territories, and that higher call rates and those originating from territory edges (rather than centres) were most effective. They suggested that neighbouring males eavesdrop on female begging calls allowing them to achieve extrapair copulations.

One of the more noteworthy findings of our study was that demonstrator courtship rate increased with female number, and that the observer male was attracted to the demonstrator courting at the greater rate. This suggests a mechanism through which observers may be able to locate larger groups of females (or higher quality females (Ojanguren & Magurran 2004), although we did not test this here) indirectly via socially transmitted cues from demonstrator males, and is analogous to public information use reported in a foraging context in other species of fish (Laland et al. 2011) and some birds (Templeton & Giraldeau 2002).

Why should observer males begin courting if the females are not directly detectable? In guppies, as with many species, courtship occurs within communication networks consisting of signalling males, females, the intended receivers, and also rival males, which can detect and eavesdrop upon courting. Within such networks, mate competition can be intense. Males that delay courting until they are able to detect females directly may miss mating opportunities, losing out to the 'founder' male that is already signalling, or to other eavesdroppers that begin courting sooner. There may therefore be significant selection pressure favouring both eavesdropping and courting in response to other, nearby courting males under such conditions, and similar behaviour is seen in other species that court within communication networks. For example, in fiddler crabs, *Uca mjoebergi*, males court receptive females by conspicuously waving their enlarged claw. Eavesdropping males respond to this by courting themselves, even when they cannot directly detect the receptive female (Milner et al. 2010). Similarly, in wolf spiders, *Schizocosa ocreata*, observer males exposed to videos of demonstrator males performing courtship behaviour not only begin to court themselves, but also match the courtship rate of the demonstrator (Clark et al. 2012). While we cannot rule out the possibility that the courtship displays exhibited by the observer male guppies in our study have an alternative function, such as signalling dominance, we are aware of no evidence in the literature that any such alternative

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function is found in this species. In contrast, given the extensive evidence for both social facilitation and local enhancement in nature (Hoppitt & Laland 2008), including in guppies (Brown & Laland 2003), it seems plausible that joining and courting near already courting males might be favoured by selection because it allows the joiner to locate females indirectly via the courtship behaviour of other males.

Third-party females may also eavesdrop on courtship interactions between males and other females, and in doing so avoid areas in which unwanted male attention might be received. Brooks (1999), investigating mate choice copying in female guppies, saw that they avoided the areas in which they had seen males courting other females. Receiving courtship can be costly to females, in terms of increased predation risk (Pocklington & Dill 1995) and reduced foraging rate (Magurran & Seghers 1994), and because it can lead to forced copulations that undermine female mate choice (Matthews & Magurran 2000).

Relying solely upon social information is not in itself an adaptive strategy (Rendell et al. 2010). Information can quickly become outdated in changeable environments, while copying errors can accumulate as information is successively transmitted, precipitating cascades of inaccurate information and leading to maladaptive behaviour (Giraldeau et al. 2002). In our study, courtship-joining behaviour on the part of the eavesdropper seemingly required real-time reinforcement in the form of continuous observation of courting by the demonstrators; in the delayed local enhancement treatment we saw no preference for the former location of the more vigorously displaying demonstrator. At a mechanistic level, this may reflect the lack of a cognitive mechanism for learning and recalling this kind of information, or it may be that the intensity or duration of the stimulus was too short for learning to occur. With respect to function, learning in this context may not be adaptive if females move around too rapidly to render learning about their former locations useful. Alternatively, a failure to learn may reflect an adaptation to prevent males from performing costly courtship behaviours in areas that have since been vacated; courting male guppies are persistent (Magurran 2005) and may be likely to leave an area only if the females have moved on, or if a threat has been detected.

Because blind copying is maladaptive, selection is instead predicted to favour the evolution of social-learning strategies (Laland 2004; Galef 2009; Rendell et al. 2011), which determine when and from whom individuals should be expected to use socially acquired information. Eavesdropping upon courtship interactions could form a useful study system for investigating social-learning strategies experimentally. The guppy model system is strongly suited to this purpose. Research into guppy courtship interactions is well established from a communication networks perspective (Earley & Dugatkin 2005), while the ecology of the guppy populations of the various drainages in their native Trinidad is well studied and documented (Magurran 2005), in terms of predation pressure, productivity and other factors predicted to bear upon the evolution of social-learning strategies, potentially facilitating comparative research. Advances in network-based diffusion analysis (Franz & Nunn 2009; Hoppitt et al. 2010), in combination with developments in social-learning strategy theory, are providing better ways to quantify how information is taken up and transmitted through populations under natural conditions. While network-based diffusion analyses have typically been used to address questions related to social-foraging problems to date (e.g. Aplin et al. 2012; Atton et al. 2012; Hoppitt et al. 2012; Webster et al. 2013), there is potential to employ these analyses in the study of eavesdropping and mate choice copying, and the conditions that promote these behaviours, in communication networks.

Acknowledgments

This work was funded by grants from NERC and the ERC (NE/D010365/1 and EVOCULTURE 232823) to K.N.L. We thank the Editor and three anonymous referees for their helpful comments.

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