Sequential female choice and the previous male effect in sticklebacks

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Summary. Female choice, identified as a major force in sexual selection theory, has recently been demonstrated in a number of species. These tests concentrated on simultaneous choice situations although females have to compare males sequentially in most territorial species, which is the more demanding task. Here it is shown that female three-spined sticklebacks, *Gasterosteus aculeatus* L., rate sequentially presented males according to their brightness. With increasing costs of sampling the females become less choosy. Furthermore, a male's attractiveness has a significant effect on the female's rating of the next male; a given male is rated higher when preceded by a duller male than by a brighter one and vice versa. Female sticklebacks use a stochastic decision rule in sequential mate choice that is attuned to the attractiveness of the present and previously encountered male. This demonstration of a "previous male effect" not only indicates an efficient mechanism for finding the best of a number of males but also extends the applicability of sexual selection theory.

Introduction

The evolution of male sexual ornaments by female choice is both theoretically (e.g., Darwin 1871; Fisher 1930; O'Donald 1980; Lande 1981; Kirkpatrick 1982; Hamilton and Zuk 1982; Bradbury and Andersson 1987) and experimentally (e.g., Andersson 1982; Majerus et al. 1982; Kodric-Brown 1985; Klump and Gerhard 1987; Møller 1988; Milinski and Bakker 1990; Houde and Endler 1990; Zuk et al. 1990) well established, although the empirical evidence is bound to simultaneous choice situations in which a direct comparison facilitates the preference for the more ornamented male. In nature, simultaneous choice is restricted either to situations in which males are displaying in a common area, a lek [e.g., in grouse: Bradbury and Gibson 1983, but Gibson

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(1990) argues that even in leks female grouse have to visit males sequentially], or to cases in which females use acoustical male ornaments [e.g., in birds: Catchpole et al. 1984; in frogs: Ryan and Wilczynski 1988, but Ryan (1985) reports that female túngara frogs approach calling males sequentially] for choosing among spread out males. In most of the remaining cases the female must visit males sequentially and compare the present male with what she has stored in her memory of those met previously (Janetos 1980; Janetos and Cole 1981; Wittenberger 1983; Parker 1983; Real 1990, in press). This appears to be a more difficult task than that of simultaneous choice. It is, however, a prerequisite for the application of models of sexual selection to most territorial species. In several species it has been implicitly shown that females are able to exert sequential choice (e.g., Brown 1981; Moore and Moore 1988) or at least that females visit several males before mating (Kynard 1978; Ryan 1985; Arak 1988; Gronell 1989; Dale et al. 1990).

Several rules have been formulated according to which females might base their mating decision when males are encountered sequentially. Females may mate with the first male encountered that meets some minimum quality criterium: "fixed-threshold rule" (Janetos 1980; Janetos and Cole 1981), or "threshold-criterium rule" (Wittenberger 1983): females should not mate with any male below the criterium but they should mate with any male exceeding it. Or she may compare males sequentially until the most recent male encountered is of lower quality than the previous male encountered and mate with the previous male: "sequential-comparison rule" (Wittenberger 1983). She may compare males sequentially and mate when the quality of the male encountered is greater than the male quality expected from continued search: "one-step decision rule" (Janetos 1980; Janetos and Cole 1981), "sequential search rule" (Real 1990, in press). Or she may sample as many potential mates as possible and then mate with the highest quality male: "best-of-n rule" (Janetos 1980; Janetos and Cole 1981; Real 1990), "pool-comparison rule" (Wittenberger 1983). Mathematical modelling showed

that without costs associated with sampling and searching for mates, the best-of-n rule is the most advantageous strategy (Janetos 1980; Real 1990). When search costs are being included in the models, the best-of-n rule is no longer superior to the sequential search rule (Real 1990). Costs of sampling can be divided into two basic types: direct costs (e.g., risk of predation, expenditures of time and energy) and opportunity costs (e.g., the loss of mating status of previously encountered mates) (Real 1990). Sampling becomes increasingly costly when a female is approaching her latest spawning time. We are not aware of any empirical study that has investigated the mechanism of sequential female choice. The recent analytical models of Real (1990, in press) generated many testable hypotheses and will provoke necessary empirical studies of this neglected area of sexual selection theory.

A male three-spined stickleback fish at about 6 cm in length develops a bright red coloration and claims a territory of up to several square meters at the start of the breeding season. He may collect up to 20 clutches of eggs from different females for each breeding cycle (Wootton 1976). The females have been shown to prefer the more intensely red-colored male in simultaneous choice situations (Milinski and Bakker 1990; McLennan and McPhail 1990). Their preference is based almost exclusively on the intensity of the male's coloration, which reveals his physical condition (Milinski and Bakker 1990). However, under natural conditions the distance between the males and also vegetation forces a female to compare potential mates sequentially if she is able to do so. Therefore the three-spined stickleback seems to be an ideal species to study sequential female choice.

Our experiments were conducted before we became familiar with Real's models and therefore can not be considered as tests of his sequential search models. We aimed to investigate whether female sticklebacks are able to exert sequential mate choice and, if so, what decision rules are used to find the highest quality male. Since our previously published (Milinski and Bakker 1990) experiments also contained a sequential choice situation in that the pairs of males were presented in increasing order of intensity of their red breeding coloration, we reanalyzed the video recordings using the criteria of the present experiment.

Methods

Twenty male three-spined sticklebacks with varying degrees of breeding coloration were caught from a Swiss freshwater population (near Roche/Montreux) and placed individually into tanks. The tanks (17.8 cm × 34.5 cm, 16.5-cm water level, temperature about 15° C) were separated by grey opaque partitions. Each pair of tanks was illuminated 16 h/day by a 60-W reflector bulb (Osram Concentra PAR-EC). Each male was stimulated with a ripe female enclosed in a plexiglass cell (11 cm × 7.5 cm, 16-cm water level) placed close to the front wall of its tank for 5 min twice daily in order to accelerate its nestbuilding behavior (Milinski and Bakker 1990). After several weeks most males had a complete nest built out of filamentous algae in a Petri dish that had been filled with sand and placed close to the backwall; these males courted

vigorously. Out of nine males that could easily be categorized as either bright, medium, or dull according to the intensity of their red breeding coloration, we used five different combinations of three males, one of each color type, for presentation to ripe females.

Females were caught from the same population and stored in female groups under simulated summer conditions. They were used in experiments when they were ready to spawn, as judged from their color, the extension of their bellies, and from the opening of their cloacae.

A plexiglass cell (11 cm × 7.5 cm, 16-cm water level) containing a single gravid female was placed in front of a male's tank, and the female's and male's behavior was video-recorded. The duration of her "head-up" display, which correlates positively with her probability to spawn with that male (McLennan and McPhail 1990), was scored for a 2-min period after 1 min of acclimatization. During the same period, the intensity of the male's courtship was quantified by counting the number of zigzags of the male's courtship display (van Iersel 1953; Sevenster 1961). Five females that did not show the head-up posture in two successive tests were discarded. Half of the remaining 28 females used were presented to the 3 males in the following order: bright, medium, bright, pause of 30 min (which should reduce a potential after-effect of the first 3 tests), dull, medium, dull. The other half saw the males in the reverse order: dull, medium, dull, pause, bright, medium, bright. Each female was used only once.

Videotapes of previously published (Milinski and Bakker 1990) choice tests were reanalyzed. In these simultaneous choice experiments, pairs of males were presented sequentially to ripe females under white and green lighting conditions (details in Milinski and Bakker 1990). The female's total duration of head-up posture during the choice test was scored according to the same criterion as in the present experiments.

Results

Sequential choice among single males

In our present experimental design, each female saw each male twice, and the position of each type of male in the order of presentation was the same averaged over all females. Therefore, we can compare the duration of head-up display each type of male received per presentation to a female with that of the other two. The duration of the females' head-up posture significantly increased with the intensity of the males' brightness (Fig. 1). This
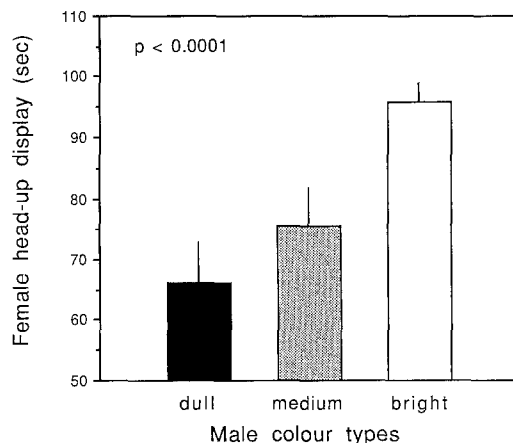

Fig. 1. Average (+1 SE) duration of the female head-up display (seconds) directed at each of three different male color types, i.e. dull, medium, bright, by 28 females. $P < 0.0001$ after one-tailed Page test for ordered alternatives (Siegel and Castellan 1988)
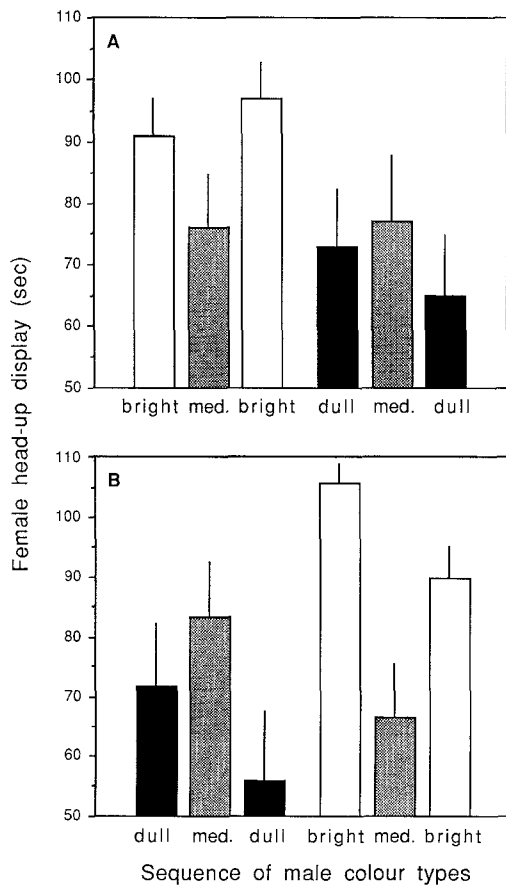
Fig. 2 A, B. Average (+1 *SE*) duration of the female head-up display (s) directed at each of three different male color types, i.e. dull, medium, bright, in the specified sequence *A* by the 14 females starting with a bright male, *B* by the 14 females starting with a dull male
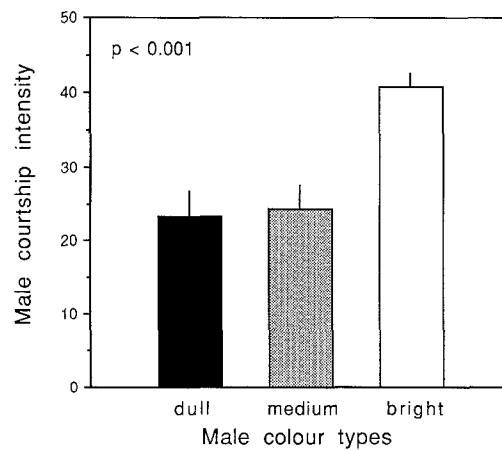

Fig. 3. Average (+1 *SE*) male courtship intensity (number of zig-zags) of each of three different color types, i.e. dull, medium, bright, directed towards ripe females. $P < 0.0001$ after one-tailed Page test for ordered alternatives (Siegel and Castellan 1988)

result demonstrates the females' ability to prefer the brighter male also when they see only one male at a time. Thus female sticklebacks are able to exert sequential mate choice.

The probability to spawn with a given male may not only depend on its rank in the female's internal standards but could also be influenced by the brightness of the previous male (Janetos 1980; Janetos and Cole 1981; Wittenberger 1983; Parker 1983; Real 1990, in press). The female may rate a male higher when the previous male was duller and vice versa. Hence, we would expect that the duration of the head-up posture is longer during the second presentation than during the first one with a given color type when the male met before the second presentation is duller. We would expect that this duration is shorter when the male in between is brighter. Thus we can test for the existence of 6 different inequalities (Fig. 2). For females starting with a bright male (Fig. 2a), we expect for the duration of the head-up posture the following inequalities: bright2 > bright1 (because the male in between is medium), medium2 > medium1 (because medium2 follows dull whereas medium1 follows bright), dull1 > dull2 (because the male in between is medium); for females starting with a dull male (Fig. 2b): dull1 > dull2, medi-

um1 > medium2, bright2 > bright1. Each of these inequalities was tested with a 1-tailed Wilcoxon matched-pairs signed-ranks test with $N = 14$, and the six probabilities were combined with a Fisher combination test (Sokal and Rohlf 1981; the probability of one inequality that was in contrast to our hypothesis was entered as 1-P). A potential habituation effect by which the second presentation of each color type is expected to score lower than the first one is neutralized by this procedure, i.e. three of the inequalities would be in the same direction and the other three would be in opposite direction of a potential habituation effect. The combined probability supports our hypothesis of a previous male effect ($P < 0.01$ after Fisher combination test).

A male's courtship intensity significantly increased with the intensity of its brightness (Fig. 3). Although female sticklebacks did not make use of differences in courtship intensity between simultaneously presented males in their mate choice (Milinski and Bakker 1990), this does not preclude a possible interaction between male and female courtship intensity, thereby either raising or reducing the female's duration of the head-up posture when she is presented with a given male a second time. If male courtship intensity changed from the first to the second presentation and this change directed female sequential choice, then we would expect that the demonstrated previous male effect (see above) is reflected in differences in male courtship intensity of the respective color types between first and second presentations to ripe females (Fig. 4). Testing of the six inequalities generated by the previous male effect hypothesis (see above) for differences in male courtship intensity between the first and the second presentation did not reveal a significant effect ($P > 0.50$ after Fisher combination test).

Sampling costs should increase when a female approaches her latest spawning time, i.e., when she cannot retain her eggs any longer (Wootton 1974a). We would expect that females become less choosy when they approach their latest spawning time. Since such females
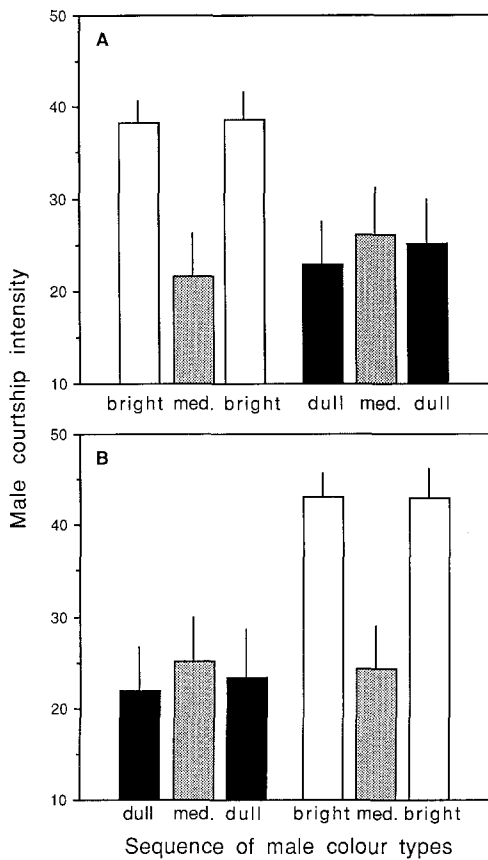
Fig. 4A, B. Average (+1 *SE*) male courtship intensity (number of zigzags) of each of three different color types, i.e. dull, medium, bright, directed in the specified sequence *A* towards the 14 ripe females starting with a bright male, *B* towards the 14 ripe females starting with a dull male
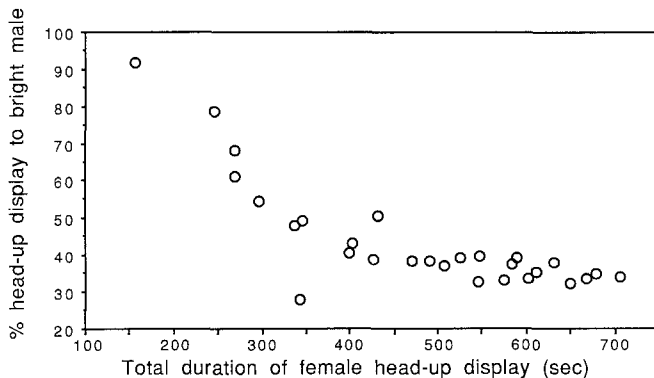

Fig. 5. Percentage of total duration (summed over the six male presentations of each female) of the female head-up display directed at the bright male as a function of the female's total head-up duration ($r^2 = 0.633$, $P < 0.01$, two-tailed, $N = 28$)

display the head-up posture increasingly often (Wootton 1974b), we can test whether females with longer total duration of head-up posture are less selective. There was a negative correlation between total duration of female head-up display and the percentage of head-up directed to the bright male (Fig. 5). Thus, with increasing sampling costs the females became less choosy.
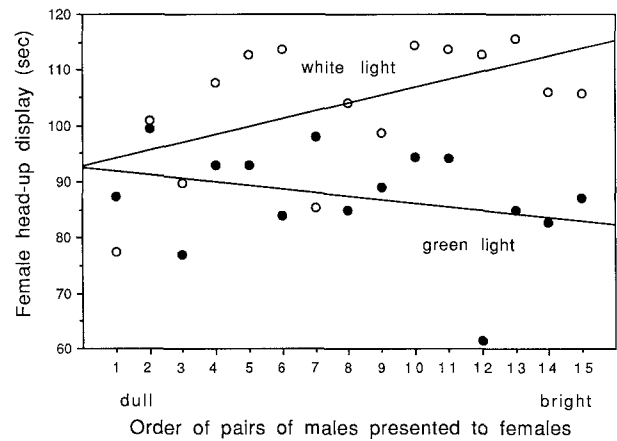

Fig. 6. Average (+1 *SE*) total duration of the female head-up display (seconds) by 3 different females per pair (13 females in total) directed at 15 pairs of males presented in an increasing order of intensity of red breeding coloration under white light (*open circles*; $y = 92.552 + 1.414x$, $r^2 = 0.294$, $F = 5.42$, $df = 1,13$, $P < 0.02$, 1-tailed) and by 3 other females per pair of males (11 females in total) under green light (*filled circles*; $y = 92.314 - 0.623x$, $r^2 = 0.087$, $F = 1.24$, $df = 1,13$, $P > 0.10$, one-tailed), data reanalyzed from Milinski and Bakker (1990)

Sequential choice among pairs of males

When the female's spawning probability is attuned to the intensity of red coloration of the present and previously encountered male, we would expect similar changes of duration of the head-up posture directed towards sequentially encountered pairs of males. We therefore reanalyzed the videotapes of previously published (Milinski and Bakker 1990) choice experiments done under white and green light. The green light condition reduces differences in the intensity of red between males and all males have a similar dull appearance.

In these choice experiments, two males were presented simultaneously, and different pairs of males were presented sequentially to ripe females. The pairs of males were presented in increasing order of intensity of their red breeding coloration, i.e., both males of the second pair were brighter than both males of the first pair, etc. An analysis of the female's total (= to both males of a pair) head-up posture during the simultaneous choice tests under white light showed that the more intense the red coloration of the pairs of males, the longer was the females' head-up posture (Fig. 6). In choice experiments with the same pairs of males under green light, the females' preference for the brighter pairs disappeared (Fig. 6). The average duration of head-up posture was significantly longer under white light than under green light (mean duration of head-up display, 103.87 s, $SE = 3.01$, under white light; and 87.33 s, $SE = 2.44$, under green light; $P < 0.002$, Wilcoxon matched-pairs signed-ranks test, 1-tailed). These results suggest that female sticklebacks are able to compare the overall intensity of red breeding coloration of sequentially presented pairs of males. The female's probability to spawn is attuned to the attractiveness of the pairs of males based on the intensity of the males' red coloration.

The average duration of the head-up posture the fe-

males directed within 2 min towards the pairs of males under green light (87.33 s, $SD=9.43$, $N=15$) was longer than that directed towards single dull males in the present sequential choice experiments under white light (66.25 s, $SD=35.41$, $N=28$, $P<0.05$ after 2-tailed Mann-Whitney U-test). Similarly, the average duration of head-up posture the females directed within 2 min towards the pairs of males under white light (103.87 s, $SD=11.66$, $N=15$) was longer than that directed towards single medium males in the present sequential choice experiments under white light (75.66 s, $SD=32.62$, $N=28$, $P<0.002$ after 2-tailed Mann-Whitney U-test). In both cases fish originated from the same freshwater population. There were, however, some differences between the two studies that might have contributed to this discrepancy. First, in our previous study, females were discarded when they refused to show the head-up posture for longer than 1 min. In the present study, females that failed to show the head-up posture during two successive tests of 2 min were discarded. Second, during choice tests males frequently visited their nests and were then furthest away from the females, although they remained visible (except during creeping through). When she stopped courting during a male's nest visit in the simultaneous choice situation, she had the opportunity to court the neighboring male, and of course she always had a choice of two males. Moreover, the pause between successive presentations of a female to pairs of males was about 7 min, whereas females in the present experiment were moved immediately to the next male. If time is costly, the females in our previous experiment had higher travel costs and therefore should have been, and were indeed, less choosy.

Discussion

We have shown that the preference female sticklebacks have for intense red male breeding coloration demonstrated in simultaneous choice tests (Milinski and Bakker 1990; McLennan and McPhail 1990) is also pronounced when they can see only one male at a time. This result alone does not prove, however, that females have actually compared the different males with each other, but it can result from comparing each male with an internal order of standards.

How does a female decide whether to spawn with the present male or to sample further males? Since the female's duration of head-up posture directed towards a given male, which is our measure of female preference, correlates positively with her probability of spawning with this male (McLennan and McPhail 1990), she would not need to have an additional rule for continuing to sample further males. Thus, her probability of spawning with a bright male would be higher than with a dull one. She would continue to sample further males with a higher probability when she meets a dull male than when she has found a bright one. Such a stochastic decision rule contrasts with assumptions of existing models on sequential female choice (Janetos 1980; Parker 1983; Wittenberger 1983; Real 1990, in press).

If females used the best-of-n rule (Janetos 1980; Wittenberger 1983; Real 1990) in sequential mate choice,

one would not expect that the probability of spawning with a male is attuned to his attractiveness. There would be an increase of the female's display intensity by exactly one step from all the males that are only sampled to the one chosen to spawn with. Other decision rules (Janetos 1980; Wittenberger 1983; Real 1990) predict mating when male quality exceeds some criterion. All males that do not exceed the criterion are rejected in the same way, and all males above the criterion are accepted in the same way. No attuning of female behavior to male quality is expected here either.

If the female would have a fixed internal standard determining the probability of spawning with a male of a given quality, she would often end up with a male of relatively low quality in a population of high quality males. Here a female that is able to adjust her internal standard would do better. Indeed, the females rated a given male higher when it had been preceeded by a duller than by a brighter male. Our demonstration of this previous male effect not only shows that the females have actually compared the different males with each other but also provides a means to update an assumed internal standard.

Increased costs of sampling should shift the internal standard or the threshold male quality of sequential search models (Wittenberger 1983; Real 1990) so that less attractive males are also accepted. We found an indication of such an effect when females were presented with the first male after the pause of about 30 min (see Fig. 1), which may have simulated an increased search cost (see Introduction). The first dull male after the pause (Fig. 2a) received the same amount of female courtship as the starting dull male (Fig. 2b) although the former was preceded by a bright male before the pause. Similarly, the first bright male after the pause (Fig. 2b) received the highest amount of female courtship of all presentations (Fig. 2) although this result is ambiguous with respect to the previous male effect. A more direct test of the influence of sampling costs on female choosiness consisted in comparing females that were closer to their inevitably latest spawning time with those that were further away from this point but ready to spawn. These latter females were choosier than the former ones, thus supporting a prediction of Real's (1990) model.

Do the females have also an absolute preference for brighter males? Half of our females were presented first with a dull male, the other half started with a bright male. If they have an absolute preference (Zuk et al. 1990) or an internal order of standards, they should rate the bright male higher than the dull male, which was indeed the case (significant difference between relative height of first column of Fig. 2a and that of Fig. 2b after one-tailed Mann-Whitney U test, $P<0.01$). This conclusion, however, must be interpreted with caution. Since all our females had been wild-caught as adults between a few days to several weeks before the experiment, they could have retained some memory of the males seen previously.

Our previously published (Milinski and Bakker 1990) choice experiments under white and green light contained a sequential choice situation. Pairs of similarly

colored males were presented to females in increasing order of intensity of their red breeding coloration. Reanalysis of the data showed that under white light the females' head-up display was attuned to the intensity of the males' red breeding coloration. The females' duration of display towards a pair of males increased when they moved to brighter pairs. Under green light the females' head-up display was unrelated to the males' coloration and reached a level characteristic of dull males under white light (Fig. 6), although the number of choices the females were willing to make was the same as under white light (Milinski and Bakker 1990). Thus, our present results are confirmed by the reanalyzed data of our previous experiment.

Our finding of the females' ability for exerting sequential mate choice and of the previous male effect concerns the mechanism of female mate choice, the existence of which is a necessary prerequisite of most models of sexual selection. It broadens the application of these models to species in which females can choose a potential mate only by visiting a number of males sequentially. Since the specific mechanism of female choice has consequences on the conclusions drawn from any model (e.g., Seger 1985; Pomiankowski 1987), both the theoretical impact and the generality of our results needs to be investigated.

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