Behav Ecol Sociobiol (2008) 62:945–951
DOI 10.1007/s00265-007-0519-7

ORIGINAL PAPER

Dynamic female preference for multiple signals in *Rhinogobius brunneus*

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Received: 24 February 2007 / Revised: 25 September 2007 / Accepted: 4 November 2007

Abstract Many species base their choice of mates on multiple signals which provide them with different kinds of information. Choosers may assess the signals together to evaluate the overall quality of potential mates, but individuals often pay attention to different signals in different contexts. In *Rhinogobius brunneus*, a fish displaying exclusive male parental care, females generally prefer males showing larger first dorsal fins (FDF) and more active courtship displays as mates. Females choosing a mate usually initially assess the FDF and later utilize courtship for the final decision. In our experiments, females with different hunger states used different signals when selecting mates. Females in both hunger states preferred males with larger FDF in the first stage. In the second stage, well-fed females showed highly repeatable choice, whereas poorly fed females responded only to variation in the courtship activity of males. The males preferred by poorly fed females exhibited significantly higher offspring survival than non-preferred males. Under conditions of food shortage, males allocate more energy to future reproduction at the expense of the present brood, and females may prioritize signals predictive of offspring survivorship over signals reflecting other aspects in male quality to minimize the losses in direct benefits. We conclude that *R. brunneus* females may employ information from both signals but dynamically adjust their prioritization of each signal to current conditions to ensure the choice that is currently most adaptive.

Keywords *Rhinogobius brunneus* · Multiple traits · Context-dependent benefits · Female choice · Paternal care

Introduction

In a variety of species, males perform sexual displays composed of multiple signals that females use in the assessment of potential mates (Candolin 2003). Several models have proposed mechanisms by which female preference for multiple signals can arise (Møller and Pomiankowski 1993; Johnstone 1996; Candolin 2003; van Doorn and Weissing 2004): different cues can provide different kinds of information, or cues may be mutually reinforcing.

There has recently been a great deal of interest in how females use different kinds of information to assess mate quality (Candolin 2003). Females may assess signals together to form an impression of the overall quality of potential mates (e.g., Lindström and Lundström 2000; McGraw and Hill 2000; Møller et al. 2000; Candolin and Reynolds 2001; Scheuber et al. 2004). However, different females often prioritize different male signals and, thus, focus on different aspects of mate quality (reviewed in Jennions and Petrie 1997; Sheldon 2000; Candolin 2003). How females assess male signals depends on aspects of the

Communicated by K. Lindström

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females' internal or external condition, such as physiological condition (e.g., Soler et al. 1998; Hunt et al. 2005), age (e.g., Coleman et al. 2004), or genetic compatibility with potential mates (reviewed in Neff and Pitcher 2005). A few studies also show that females may prioritize signals differently in different social contexts and physical environments (e.g., Kodric-Brown 1993; Endler and Houde 1995; Backwell and Passmore 1996; Marchetti 1998).

These plastic female preferences with regard to sexual signals may be due to context-dependent differences in benefits derived from each choice (Qvarnström 2001). A sexually selected trait that provides direct or indirect benefits to females in one condition may be relatively unimportant for females in another condition. Therefore, it is crucial to address whether the different choices made in different contexts result in optimal outcomes for choosers. In this paper, we report on experiments with *Rhinogobius brunneus* (Gobiidae) which are small fishes characterized by exclusive male parental care. The male first dorsal fin (FDF) is markedly larger and more conspicuous than that of females, and females generally prefer to mate with males having larger FDFs (Suk and Choe 2002a). During the breeding season, gravid females move between males' territories, while territory-holding males often keep their FDFs erected. Females seem to receive cues about FDF at this stage (Suk and Choe 2002a). Once a female selects and approaches a male's nest, the male folds his FDF and performs the courtship display, which involves swimming a short distance towards the female and then leading her back towards the entrance of his nest. Females decide whether to spawn at this stage. The intensity of the male courtship display also affects female mate choice (Takahashi and Kohda 2004; Suk and Choe 2002a). The female preference for males showing more active courtship displays results in selection of males having sufficient energy reserves for male parental care and, therefore, a higher probability of hatching success (Takahashi and Kohda 2004). However, the size of FDF is not related to the intensity of courtship display (Suk and Choe 2002a).

We conducted experiments designed to allow *R. brunneus* females to make stage-specific decisions in the initial and final stages of mate choice. The two male signals considered, FDF and courtship intensity, are expected to reflect different aspects of mate quality. The experiments were designed to determine how females weigh each aspect of male quality in the mate-choice process. Test males and females were subjected to either good or poor food conditions. Paternal care entails costs to the males in terms of energy, which may affect their future reproductive success (Rohwer 1978; Gross and Sargent 1985; Sargent 1992). Since the cost of care is especially high for males with limited energy reserves (Rohwer 1978; Clutton-Brock 1991; DeMartini 1987; Petersen and Marchetti 1989; Lindström and Sargent 1997), males experiencing severe food shortage should be expected to reduce parental investment in their current offspring (Kvarnemo et al. 1998). Our aim in this study was to experimentally determine the effects of variation in food availability on female choice behaviour. Specifically, we considered two questions: (1) does feeding treatment affect female preferences regarding the two male signals in each stage of the mate-choice decision, and if so, (2) how does this context-dependent variation in mate choice affect female reproductive success?

Materials and methods

Subjects

R. brunneus is a species complex represented by eight types that have been described as distinct species (Suk and Choe 2002a). *R. brunneus* of the OR (orange colour; Kawanabe and Mizuno 1989) type was used in this study. Males and females were collected from the Gapyeong Stream in Korea using push-nets in early February in 2000 and 2001, and experiments were conducted from mid-April to early May in the collection year. We separated individuals by sex into nine large holding tanks (five 180-l tanks for females and four 250-l tanks for males). All laboratory setups had natural dark/light cycles, and water temperature was maintained at approximately that of the collection site (12.7±2.67°C). At the end of the experiment, all fish were released at the site of capture.

Hunger manipulation

Fish were subjected to one of two different feeding regimes over a period of 57–65 days. Well-fed individuals were fed frozen chironomid larvae (0.009–0.026 g per individual) twice daily, while poorly fed individuals were fed only once every 2 days.

Female choice

The apparatus ($L \times D \times H$, 80×60×45 with natural bottom substrate; Fig. 1) consists of a female choice arena containing a single test female, and two male chambers, each containing a single male. Each male was supplied with a ceramic tile measuring 14×14 cm as a nest substrate. The males were given 2 days to acclimate to their surroundings and build their nests. The male chambers and the female choice arena were divided by a transparent partition, but males were visually isolated from each other with an opaque partition.

Choice tests consisted of two stages. In the first stage, a clear box (12×35×45 cm) was placed near the rear end of

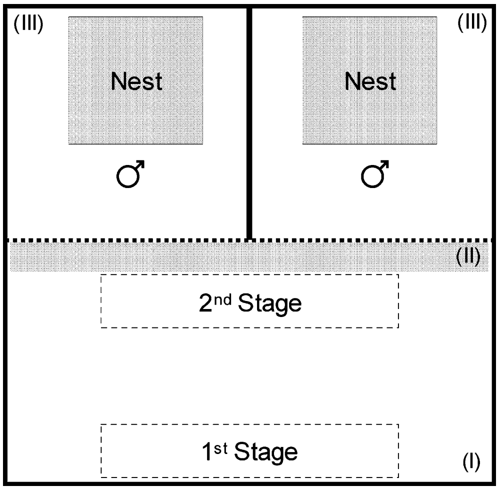

Fig. 1 Design of experimental aquaria used in dichotomous female choice test; (*I*) female choice arena, (*II*) preference zone, and (*III*) male chamber

the female choice arena (Fig. 1), and an opaque partition was situated between the box and male chambers. A gravid female was introduced into the box. Approximately 1 h later, the opaque partition was removed, allowing her to view both males for 30 min from a distance of more than 25 cm, a distance at which males do not court. The box was then lifted, freeing the female to move. A male was considered to be 'preferred' if the female moved into the preference zone and attempted to enter his chamber first. The preference zone was defined as the area located within 10 cm of the males' partition (Fig. 1). Female preference was determined only when the female did not idle in the choice arena and the male(s) did not court. If the female idled or the male(s) courted, the replicate was discarded, and all the fish were replaced.

After completion of the first stage of the experiment, we conducted a second experiment with the same individuals by placing the box at a distance of 5 cm from the preference zones and gently reintroducing the female into the box (the second stage; Fig. 1), again placing an opaque partition between the box and male chambers. Approximately 1 h later, the opaque partition was removed, but this time, we allowed females to view males for 10 min prior to selecting a male. At this distance, males usually actively court. During the viewing period, we measured the frequency at which each male approached the female and swam back to the nest as an index of the intensity of courtship activity. We accepted the trial as successful if both males courted actively when the female viewed males from the box.

The female choice experiment involved four combinations of conditions (hunger state by sex): (1) $♀^W♂^W$ (N=26): well-fed females (standard length, mean±SD=64.52±2.98 mm) and well-fed males (69.88±3.07 mm); (2) $♀^W♂^P$ (N=17): well-fed females (64.23±2.47 mm) and poorly fed males (68.67±1.12 mm); (3) $♀^P♂^W$ (N=19): poorly fed females (63.27±2.42 mm) and well-fed males (70.79±1.48 mm); and (4) $♀^P♂^P$ (N=29): poorly fed females (62.83±3.03 mm) and poorly fed males (71.65±2.20 mm). Each individual was used in only one complete choice test. For each test, the male pair was matched for body length (with difference less than 2 mm) and coloration. FDF size was measured as the distance from the basal margin to the tip of the FDF (Suk and Choe 2002a), and the difference of FDF size in each pair was >3 mm (the size of FDF; males, mean±SD=16.21±3.37 mm; females, 8.82±0.84 mm; see Suk and Choe 2002a).

Immediately after the completion of both stages of the trial, a condition index was calculated as weight/length^3 as an estimate of each individual's energetic state. All of the test males were then bred with well-fed females. Same-sized females were randomly selected from the well-fed aquaria to control for variation in female egg numbers. After spawning, the female was removed, and the nest was briefly taken away. We estimated the number of eggs in each nest as the product of the egg clutch area and the average density count (see Suk and Choe 2002b for details). We calculated hatching success (the proportion of eggs hatching) by comparing the number of eggs just after spawning (4 days later) with the number just before hatching. We also allowed the test females to spawn in the nests of males randomly selected from the well-fed aquaria and examined hatching success in the same way to determine whether our feeding treatment affected female fecundity and offspring survival.

Statistical analyses

All statistical tests were two-tailed, with significance set at α=0.05. All statistical analyses were performed using JMP 4.0.2 (SAS Institute, Cary, NC, USA).

Results

Female choice tests

In the first stage, females chose males with longer FDF in 62 of 91 trials (68%; χ^2=6.58, df=1, p=0.01), and displayed a significant preference for males with longer FDF in three of four experimental conditions (Fig. 2). However, female choice was random with respect to FDF size in the trials involving well-fed females and poorly fed males (Fig. 2). Females did not show a significant preference for the longer FDF in the second stage (Yates' correction for continuity: χ^2=14.50, df=1, p<0.001), where they were allowed to interact visually with courting males overall (48%, χ^2=0.05, df=1, p=0.82), or in any experimental conditions (Fig. 2); rather, males with higher

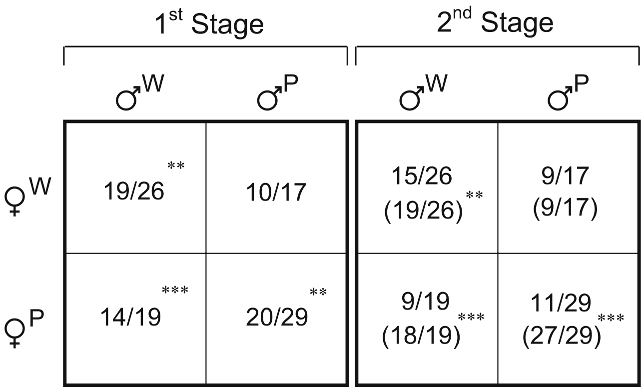

Fig. 2 Proportion of females choosing males with longer FDF in four mate-choice combinations in the first and second stages of dichotomous female choice tests. Proportion of females choosing males with higher courtship activity in the second stage are *in brackets*. Significance was tested under the expectation of random choice (χ^2 test; *single asterisk* $p<0.05$, *double asterisk* $p<0.01$, *triple asterisk* $p<0.001$)

courtship activity were preferred overall (77%; $\chi^2=14.50$, $df=1$, $p<0.001$) and in three of the four experimental conditions (Fig. 2).

Female hunger state clearly affects their mate-choice pattern. In the second stage of the experiment, 90% ($\chi^2=31.34$, $df=1$, $p<0.001$) of the poorly fed females chose males showing higher courtship activity, as compared with only 63% ($\chi^2=3.27$, $df=1$, $p=0.07$) of well-fed females (Fisher's exact test: $p=0.006$). Well-fed females showed a repeatable preference, with 74% of females choosing the same male in the second stage as in the first (♀^{W}♂^{W}, 20 of 26; ♀^{W}♂^{P}, 12 of 17; binomial test, $p=0.003$, 0.04, respectively), suggesting that the initial preference for males with larger FDF affects the final decision. In contrast, the final decision of poorly fed females apparently depended only on the intensity of courtship regardless of their initial preference for males with larger FDF; no consistency was found in poorly fed females between the initial and final choice (♀^{P}♂^{W}, 9 of 19; ♀^{P}♂^{P}, 14 of 29; binomial test, $p=0.26$, 0.14, respectively). The repeatability of mate choice is significantly different between well-fed and poorly fed females (Fisher's exact test, $p=0.01$).

Our feeding treatment affected condition indices in both males [one-way analysis of variance (ANOVA), $F_{1,180}=25.39$, $p<0.001$] and females ($F_{1,89}=28.84$, $p<0.001$) used in the mate-choice tests. The intensity of courtship activity was significantly lower in poorly fed males (courtship index, mean±SE; 15.93±0.83) than that of well-fed males (22.84±0.84; $F_{1,180}=34.34$, $p<0.001$).

Offspring survival

There was no significant difference in the number of eggs produced by females paired with well- and poorly fed males (mean±SE; ♂^{W}, 899±24; ♂^{P}, 950±24, $F_{1,132}=2.22$, $p=0.14$), but hatching success was higher in nests guarded by well-fed males than in those guarded by poorly fed males (Table 1). The hatching success of males chosen by females in the first stage of the trial did not significantly differ from that of males not chosen. However, males preferred by females in the second stage of the trial exhibited significantly higher hatching success than did nonpreferred males (Table 1). The significant interaction between female hunger state and female choice in the second stage (Table 1) suggests that the overall difference in hatching success between preferred and nonpreferred males in the second stage is produced by a strong preference by poorly fed females for males with substantial energy reserves. Well-fed females did not prefer males with greater hatching success, but a significant difference was found in the hatching success of males preferred and not preferred by poorly fed females (Fig. 3). When hatching success was tested, with male hunger state and the size of FDF as fixed factors and the intensity of courtship as covariate (ANCOVA), we found significance in feeding treatment ($F_{1,130} = 51.15$, $p < 0.001$) and courtship intensity ($F_{1,130} = 8.71$, $p = 0.004$) but not in FDF size ($F_{1,130} = 0.74$, $p = 0.39$).

Females used in the experiments were also allowed to spawn in the nest of random males selected from well-fed aquaria. No significant difference was found in the number (♀^{W}, 879±45; ♀^{P}, 782±43; $F_{1,89}=2.42$; $p=0.12$) and hatching success (♀^{W}, 58±4%; ♀^{P}, 55±3; $F_{1,89}=0.25$, $p=0.62$) of eggs spawned by well- and poorly fed females.

Discussion

Female *R. brunneus* base their choice of mates on two different cues, the size of the FDF and the intensity of male courtship displays. We found that the female mate-choice process involves sequential and stage-specific assessments of male signals. Females sample potential mates using the size of FDF in the initial stage of mate choice, while the intensity of the courtship display affects female choice in the final stage. In addition, mate-assessment behaviour by females apparently interacts with female condition in a dynamic way. During the first stage of mate choice, females, irrespective of their hunger state, prefer males with larger FDF. However, while well-fed females in our experiments usually chose the same males in both stages of the trial, suggesting that FDF size affected the preferences of well-fed females during both stages of mate choice, poorly fed females relied only on male courtship activity for mate decision in the second stage of the trial. We conducted additional experiments to determine offspring survival to examine the potential consequences of different mate choices for females. The males preferred by poorly fed females in the second stage of the trial exhibited

Table 1 Analysis using a four-way ANOVA of mean hatching success (±SE) as a function of male and female hunger state and female choice in the first and the second stage

Factors	State	Hatching success (%)	*F*	*p*
Male hunger state	Well-fed	62.81±1.92	*89.62*	*<0.001*
	Poorly fed	36.81±1.91		
Female hunger state	Well-fed	50.28±1.95	0.12	0.73
	Poorly fed	49.33±1.88		
Female choice in the first stage	Preferred	52.01±1.96	2.33	0.13
	Nonpreferred	47.61±1.97		
Female choice in the second stage	Preferred	52.97±1.88	*5.39*	*0.02*
	Nonpreferred	46.64±1.94		

There was a significant interaction between female hunger state × female choice in the second stage ($F=8.41$, $p=0.004$), but no other significant interactions were detected ($p>0.05$).
Significant values are in italics.

significantly higher hatching success than did the nonpreferred males. This result suggests that poorly fed females primarily prefer males displaying reliable signals of high parental competence during the later stages of mate choice.

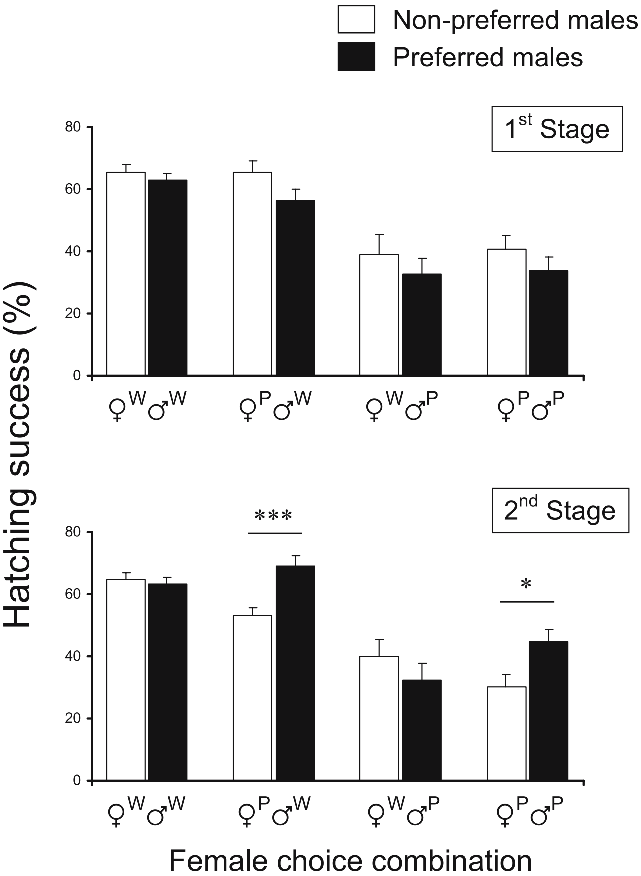

Fig. 3 Mean hatching success (%) ±SE of eggs guarded by preferred and nonpreferred males across four mate-choice combinations in the first stage and the second stage (*t*-test; *single asterisk* $p<0.05$, *triple asterisk* $p<0.001$)

Both of the examined traits may be relevant in signaling aspects of mate quality that have the potential to affect female reproductive success, but the two traits differ in their reliability as indicators of the immediate fitness benefits that females may gain by selecting high-quality mates. Courtship provides females with reliable cues of future parental effort by males. In a laboratory study of *Rhinogobius* sp. DA (a member of *R. brunneus* species complex), Takahashi and Kohda (2004) found that performance of courtship requires the expenditure of high levels of energy, especially in fast-running water. From this result, they concluded that male courtship is an honest indicator of parental quality in relation to body condition. The population used for this study inhabits an upstream region with fast currents. Therefore, only males with adequate energy reserves may be able to produce courtship displays. In other teleosts with paternal care, courtship displays have consistently been implicated as important cues for females of paternal competence (e.g., Knapp and Kovach 1991; Östlund and Ahnesjö 1998; Wong 2004; c.f. Svensson et al. 2004). Our experimental design does not shed light on the benefits that females may derive from selecting males having larger FDF. In previous studies, FDF size was not associated with any behavioural trait or with the physical condition of males (Suk and Choe 2001; 2002a). It may signal information about intrinsic (genetic) quality that is not affected by stochastic environmental factors and physiological condition (Suk and Choe 2002a) or may simply have become attractive to females through a runaway process.

Why should females use different mate-choice cues depending on their own hunger state? Under low food conditions, males may prioritize investment in their future reproductive success or their own survival, potentially at the expense of the present brood (Kvarnemo et al. 1998). If high egg mortality is likely, females should primarily select mates that display reliable signals of their ability to make a greater paternal effort so as to maximize offspring survival in the short term. As suggested by Qvarnström (2001), females may utilize their own condition at the time of mate choice as a cue to predict the quality of the natal environment that the offspring will experience. Our results support this. Females in poorer physiological condition may also produce smaller broods or weaker offspring. In this situation, the best tactic available to females to maximize reproductive success is to select the male showing the greatest potential for parental investment (e.g., Soler et al. 1998). However, in our study, female condition did not affect female fecundity, and offspring of poorly fed females did not experience reduced hatching success relative to offspring of well-fed females. Therefore, we found no support for this interpretation.

Feeding condition clearly influenced male parental behaviour in the present study, but it is not clear how male hunger state affected male parental care. One possibility is that poorly fed males ate their own eggs more often than did well-fed males. We witnessed egg-eating behaviour by 11 of 12 poorly fed males (92%) and 6 of 14 well-fed males (43%), although we were not able to observe all of the study males. Many studies have found that rates of filial cannibalism increase as parental energy reserves decrease (DeMartini 1987; Marconato et al. 1993; Kraak 1996; Okuda and Yanagisawa 1996; Kvarnemo et al. 1998). However, only a few studies have experimentally demonstrated the effect of food availability on filial cannibalism (e.g., Hoelzer 1992; Kvarnemo et al. 1998). Alternatively, we cannot exclude the possibility that poorly fed males spend less energy fanning their eggs. Townsend and Wotton (1985) detected a positive correlation between food availability and the duration of fanning shown by female convict cichlids (*Archocentrus nigrofasciatus*), and Stanley (1983) reported the same relationship in male three-spined sticklebacks (*Gasterosteus aculeatus*). In *R. brunneus*, fanning may be the most energetically demanding part of parental care, and decreased fanning can result in significantly increased egg mortality (Suk and Choe 2002b). Unfortunately, we did not collect data on male fanning behaviour in this study.

In fish with paternal care, the most obvious tactic that females may employ to minimize egg mortality is to spawn eggs in nests that already contain eggs (Unger and Sargent 1988; Gronell 1989; Kraak and Groothius 1994; Forsgren et al. 1996); males are expected to increase their share of care as the size of their broods increases, and per capita egg loss (from filial cannibalism) may be reduced by the presence of other eggs (Manica 2002). Common goby (*Pomatoschistus microps*) females prefer to mate with males already caring for eggs in their nests in normal conditions, but this preference was reversed in low level of dissolved oxygen, demonstrating that this preference varies with the abiotic environmental conditions (Reynolds and Jones 1999). Under oxygen stress, additional broods may often require more fanning than males can provide, which subsequently results in lower egg survival. Accordingly, females avoided males that were likely to be unable to meet the demands of care for additional broods under unfavorable conditions.

The observed dynamic nature of female preferences for male signals raises questions about the effects of context-dependent mate choice on the strength of sexual selection that operates on male FDF size. Females under food shortage may be more likely to mate with a wider range of males with respect to the size of FDF, which will reduce the effects of male FDF size on variance in male mating success and weaken selection on FDF size. Feeding condition alone is unlikely to influence the strength and the direction of the female preference itself for longer FDF in this population but does apparently affect the actual pattern of mate choice. Accordingly, it is possible that geographic variation in energy-resource availability may produce variation in the strength of sexual selection for some male traits across space.

Taken together, our results are of general interest to the study of how females utilize information from multiple male displays in different contexts. Many previous studies have examined how females process and prioritize different traits during mate selection. However, there have been few empirical studies demonstrating how females use the information contained in multiple male signals to optimize their fitness across a range of conditions. Our results demonstrate that the relative importance placed on reliable signals of male parental investment by *R. brunneus* females varied significantly with food availability. Females may integrate information from multiple male signals in selecting mates but dynamically adjust the prioritization of each signal according to their present circumstances to select the option that is currently most adaptive.

Acknowledgements We are grateful to BD. Neff, TE. Pitcher, D. Repka, Susan Lappan, and anonymous referees for offering valuable comments on previous versions of the manuscript. Research was supported by BK 21 Research Fund from the Korean Ministry of Education and Human Resources Development (scholarship to H. Y. S. and grant to J. C. C.) and Ewha Womans University (grant to J. C. C.). This research conformed to the 'Guidelines for the Use of Animals in Research' of Seoul National University, where experiments were conducted, and the legal requirements of Republic of Korea.

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