brief communications

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Sexual selection

Condition-related mate choice in sticklebacks

Exactly how the high genetic variance of traits involved in sexual selection through female mate choice is maintained is a much debated issue[1–3]. Theoretical models attempt to explain the high genetic variance of sexual traits, among others, by the evolution of condition dependence[1,4], in which expression of the trait depends on physical condition. If it is costly to be choosy, then these models should also apply to female mate preference and predict that female condition affects the choice of mate. Here we allow female laboratory-bred three-spined sticklebacks, *Gasterosteus aculeatus*, to choose between computer animations of courting males[5], and find that the choice of mate correlates well with female physical condition.

Heritability estimates of mate preference have accumulated in recent years: the average heritability ($\pm$ s.d.) of mate preference in 15 species was 0.41 ($\pm$0.21) (ref. 3), which is high for a behavioural trait[6]. Condition dependence might explain the high heritability of costly mate preferences, as it does the high genetic variance in sexual traits[1,4]. Costs may include physiological as well as choice costs. Condition dependence of sexual traits is well known[7], and there is some evidence for condition-dependent mate choice[3,8]. We have studied the covariance of condition and mate preference in a fish species that is well-known for intensive sexual selection[2].

Sticklebacks were bred from wild-caught parents, and were raised and maintained
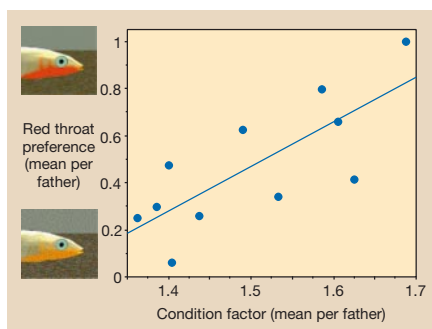
Figure 1 Relation between mean rearing condition (based on mean male winter condition per group) and mean red preference of ripe females from 11 different fathers. Females from one father were full siblings, except in three cases in which they had two different mothers, where the mean condition per father was weighted for the number of females tested per mother. Condition is calculated as $100 \times$ body mass (g)/body length[3] (in cm) (ref. 9) and represents non-reproductive winter condition, estimated from data of 6 (range 2–9) randomly chosen males per full-sib group after one day of starvation. Mate preferences of 2 (range 1–5) ripe females per full-sib group were tested by using computer animations[5]. Females were given 2 min to choose between two 'virtual' males differing only in red throat coloration. We used standard colour chips to match the redness of the virtual males to those on standardized photographic slides of courting males. We selected bright red and bright orange males from the tails of the distribution of red intensity in the field based on densitometer-analysis[10]. Bright red and bright orange males differ mainly in hue (hue/saturation/brightness values of virtual males were 17^0/100%/93% and 31^0/97%/97%, respectively, as determined using Adobe Photoshop Version 4.0.1 software), probably because of differences in carotenoid composition[11]. Male position was alternated between tests. Choice behaviour was video-recorded from above to avoid observer bias. Preferences were calculated as the time directed towards one male divided by the time directed to both males (0.5 indicates no preference; 1, absolute preference for the red male; 0, absolute preference for the orange male). Only females that spawned within 24h of the test with a live male were used.

under standardized laboratory conditions in full-sibling groups of similar size. Paternal effects on offspring traits were excluded by removing clutches from the fathers' nests one hour after fertilization. After reaching adult body size, fish were transferred from simulated summer to winter conditions, under which gonadal development and the development of male breeding coloration are suppressed.

Six months later, the condition factor[9] of a random sample of males per full-sib group was assessed. Average male winter condition per group was taken as an index of group rearing condition because some females showed signs of egg production under the prolonged winter conditions. Male physical condition is not confounded by possible between-group variance in ovarian development. Females were randomly sampled from the full-sib groups about six months later and placed individually in 10-litre tanks under simulated summer conditions, where they became reproductive.

When females became ripe they were tested for their preference for red males by

placing them in a one-litre cuvette in front of a computer monitor on which two virtual males that differed only in red breeding coloration (bright red or bright orange) were courting simultaneously[5]. In this preference test, males differ in only one trait, and there are no costs of choice.

Despite standardized rearing conditions, progeny from different fathers differed significantly in condition during rearing (ANOVA, $F(10,67) = 7.65$, $P < 0.001$) and in preference for red coloration (ANOVA, $F(10,13) = 3.52$, $P < 0.02$). Overall, there was no significant preference for the bright red male over the bright orange one (*t*-test, $t = 0.37$, df $= 10$, $P > 0.71$), but average red preference and rearing condition per father correlated positively ($r = 0.77$, $N = 11$, $P < 0.01$; Fig. 1). Females from groups with a high average condition factor before reproduction therefore preferred the red male, whereas those of lower rearing condition showed a preference for the orange male.

Combined with condition dependence of sexual traits, the covariance of mate preferences with condition may have consequences for the evolution of both preferences and preferred sexual traits. Experiments must show whether mate preferences have condition-dependent expression. When mate preferences appear to be condition dependent, and assuming there is high genetic variance in condition[4], pleiotropic effects of genes that influence condition would be expected to lead to high genetic correlations between sexual trait and mate preference. Alternatively, the covariance of mate preference with condition may be brought about by genetic covariance of sexual male traits with both female preference[10] and male condition. The consequences of these alternatives should be explored using theoretical models of sexual selection.

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