## SEXUAL SELECTION

# Problem-solving males become more attractive to female budgerigars

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Darwin proposed that mate choice might contribute to the evolution of cognitive abilities. An open question is whether observing the cognitive skills of an individual makes it more attractive as a mate. In this study, we demonstrated that initially less-preferred budgerigar males became preferred after females observed that these males, but not the initially preferred ones, were able to solve extractive foraging problems. This preference shift did not occur in control experiments in which females observed males with free access to food or in which females observed female demonstrators solving these extractive foraging problems. Our results suggest that direct observation of problem-solving skills increases male attractiveness and that this could contribute to the evolution of the cognitive abilities underlying such skills.

One intriguing hypothesis for the evolution of cognitive abilities in both humans (*1*, *2*) and nonhuman animals (*3*) is that sexual selection may have contributed to their evolution. Mating with a "smart" partner can give rise to immediate benefits, such as obtaining a partner with enhanced food extraction abilities (*4*) or one that is better at coping with varying environmental conditions (*5*). In some species (*6*, *7*), variation in cognitive abilities is correlated with reproductive success. A preference for smart mates can therefore contribute to selection on cognitive abilities.

Preferences for mates with better cognitive abilities have been inferred from experiments in which mate choice was based on secondary sexual traits correlated with bigger brains or better cognitive skills (*8–10*), as well as from positive correlations between mate attractiveness and cognitive ability when testing these variables separately (*11–13*). However, the most direct support for this "mate choice for cognitive traits" hypothesis would be to demonstrate that mate preferences are affected by observing differences in cognitive abilities. We tested this hypothesis by examining whether female budgerigars alter their preference for males after observing these males' ability to open two types of problem-solving devices (referred to as "problem boxes") to get access to food.

Problem-solving tasks are frequently used to examine innovation and cognitive performance. Multiple processes and mechanisms may underlie such problem-solving, including noncognitive ones, such as motivation or neophobia (*14–16*). Nevertheless, an individual that can open different problem boxes, especially multistep ones involving sequential learning, demonstrates that it has acquired a complex skill. This ability may also suggest skills involving physical cognition or some degree of causal understanding (*14*, *15*).

Opening problem boxes to get access to food represents a complex food extraction task. Budgerigars are native to dry and arid areas in Australia. Although food availability may be relatively stable in parts of this range, in others it can be low, unpredictable, and variable from year to year (*17*). Detailed studies of the food extraction skills that budgerigars need in these conditions are lacking, but finding and extracting food can be challenging, and thus having cognitive skills for accessing food is likely adaptive. Moreover, because female budgerigars incubate, brood, and feed their young after hatching, while male mates provide food for the females (*18*, *19*), finding a partner with the skills to solve foraging problems is advantageous. Budgerigars also imitate demonstrators in an operant task to obtain food (*20*, *21*), and problem-solving in budgerigars correlates with detour reaching and exploration (*22*). Thus, we hypothesize that females attend to and prefer males that show cognitive skills in extracting food.

In our first experiment (experiment 1), females were exposed to two males: (i) a visibly skilled male problem solver that was able to open two different problem boxes and (ii) a male unable to do so (Fig. 1). We examined how this exposure affected female preferences for these males. To control for the effect of observing an eating male, which might affect female preferences (*4*, *23*), females in a control group were exposed to both an eating and a noneating male. In a second experiment (experiment 2), we examined whether the increased preference shown for problem-solving individuals reflected an increased social, rather than sexual, preference for problem-solving individuals. Experiment 2 was identical to experiment 1, except that females were exposed to two females, rather than two males, and their preference for both types of females was assessed.

Thirty-four males (17 pairs) and 17 females took part in experiment 1. They were divided into a problem-solving group (18 males and 9 females) and a control group (16 males and 8 females). Females in both groups were first given a series of tests (preference test 1) in which each female was tested with one pair of males in a two-choice cage (fig. S1 and movie S1). The male near which the female spent most of her time was identified as the preferred male and the other one the less-preferred male. Females in both the problem-solving group and the control group spent more time near the preferred male (problem-solving: $t = -2.395$, df = 31.99, $P = 0.023$; control: $t = -2.226$, df = 28, $P = 0.034$) (Fig. 2A). The time allocated to preferred and less-preferred males was similar for both groups (preferred males: $t = -1.290$, df = 30, $P = 0.207$; less-preferred males: $t = 0.148$, df = 30, $P = 0.883$). There were no significant morphological differences between preferred and less-preferred males (table S1).

After preference test 1, less-preferred males of the problem-solving group were trained to solve two foraging problems to get access to food—opening a petri dish and opening a three-step box. The preferred males in this group did not receive such training. During a subsequent observing phase, females were allowed to observe the problem-solving task performance of their familiar pair of males (movie S2). All nine less-preferred males, but none of the preferred males, successfully opened the petri dish and the three-step box in front of the females. After observing the successful problem-solving of the less-preferred males and the failure of the preferred males, the females were again allowed to choose among these males (preference test 2). The females significantly increased their time spent near the less-preferred males while decreasing their time spent near the preferred males compared to preference test 1 (Fig. 2A and fig. S2). The time allocated to the less-preferred males was significantly higher than that allocated to the preferred males during preference test 2 ($t = 3.129$, df = 31.99, $P = 0.004$). In addition, the time spent near the preferred male minus the time spent near the less-preferred male was significantly different between preference tests 1 and 2, showing that female preferences changed after the observing phase ($t = -3.167$, df = 15.99, $P = 0.006$).

In the observing phase for the control group, females saw the less-preferred male having free access to food in a regular food container and the preferred male having no food (movie S2). During preference test 2 (as in preference test 1), females again spent significantly more time near the preferred males than near the less-preferred males ($t = -2.642$, df = 28, $P = 0.013$) (Fig. 2A and fig. S3). The difference in time allocation to both males did not change between preference tests 1 and 2 ($t = 0.346$, df = 7.00, $P = 0.740$). Thus, a shift in preference between tests, resulting in a significant preference for less-preferred males, occurred only in the problem-solving group. Females in the problem-solving group also spent proportionally more time near the less-preferred males than did the females in the control group during preference test 2 (time near the less-preferred males divided by time near both males: $t = 2.417$, df = 14.02, $P = 0.030$).

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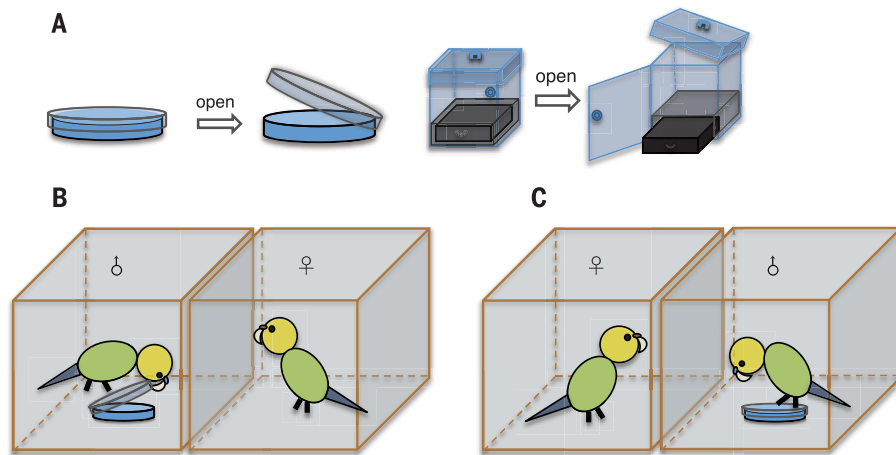*Corresponding author. Email: sunyh@ioz.ac.cn

**Fig. 1. Design of the observing phase.** (**A**) Problem-solving devices: the petri dish and the three-step box. (**B**) A focal female observing a trained male opening the petri dish. (**C**) A focal female observing an untrained male trying unsuccessfully to open the dish.
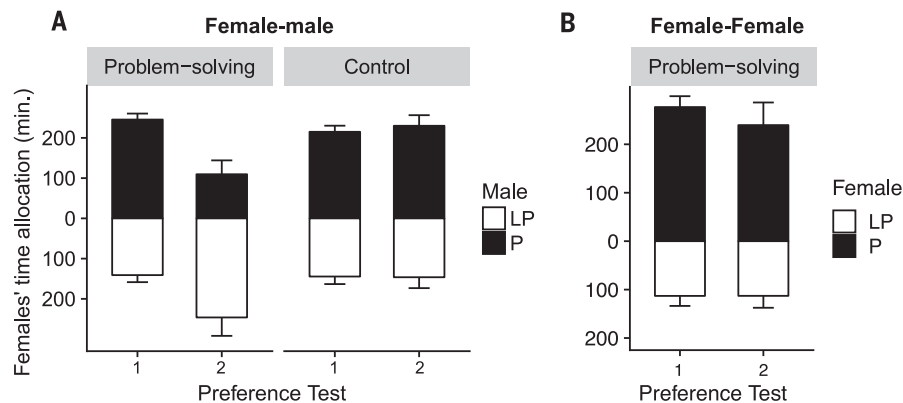


**Fig. 2. Time spent by focal females near preferred and less-preferred individuals (mean ± SEM).** The time spent near (**A**) males (experiment 1) and (**B**) females (experiment 2). Observation of less-preferred male demonstrators opening problem boxes resulted in a significant shift in preference toward these males. No significant preference shift was found in the control group or the female-female group. P, preferred; LP, less-preferred.

In experiment 2, eight focal females were given preference tests with two females (8 pairs of matched females) and observed female demonstrators. The focal females spent significantly more time with one female of their matched pairs in both preference test 1 ($t = -3.928$, df = 21, $P < 0.001$) and preference test 2 ($t = -3.037$, df = 21, $P = 0.006$) (Fig. 2B and fig. S4). The differences between the time allocation to the preferred and less-preferred females were similar for preference tests 1 and 2 ($t = -0.556$, df = 6.98, $P = 0.596$). Morphological characteristics were not significantly different between the preferred and less-preferred females (table S2). The preference for skilled individuals in experiment 1 is thus specifically linked to male demonstrators, suggesting that it has a clear sexual component.

The hypothesis that the evolution of cognitive abilities can be affected by a preference for smart partners has so far mainly been discussed for humans (2, 24, 25). Our results show that direct observation of behavior indicating the presence of cognitive skills in potential mates can affect mate preference in a nonhuman animal. Observing males that are more effective foragers may in itself increase attractiveness of such males (4, 23), but our control experiment showed no change in the preference for males that had been observed eating without having to open problem boxes. Also, observing female instead of male demonstrators did not affect preferences. Thus, observing potential mates opening the boxes to get access to food seems to be the crucial factor for changing female preferences.

Earlier studies have shown that mate choice is based on traits that might be correlated with cognitive skills (8, 26) or larger brains (9, 27). Our study demonstrates that direct observation of cognitive skills can affect mate preference and, thus, that cognitive abilities may be selected by mate choice directly. This finding supports hypotheses, starting with that of Darwin (1), that sexual selection may affect the evolution of cognitive traits across animal species. Further studies are required to examine how general our findings

are and which species are likely to undergo such selection. Species that imitate cognitive skills from conspecifics, such as budgerigars (20, 21) and humans, might be those that benefit the most from discriminating mates on the basis of observing their skills.

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