Larger groups are more successful in innovative problem solving in house sparrows

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Group living offers well-known benefits to animals, such as better predator avoidance and increased foraging success. An important additional, but so far neglected, advantage is that groups may cope more effectively with unfamiliar situations through faster innovations of new solutions by some group members. We tested this hypothesis experimentally by presenting a new foraging task of opening a familiar feeder in an unfamiliar way to house sparrows in small and large groups (2 versus 6 birds). Group size had strong effects on problem solving: sparrows performed 4 times more and 11 times faster openings in large than in small groups, and all members of large groups profited by getting food sooner (7 times on average). Independently from group size, urban groups were more successful than rural groups. The disproportionately higher success in large groups was not a mere consequence of higher number of attempts, but was also related to a higher effectiveness of problem solving (3 times higher proportion of successful birds). The analyses of the birds' behavior suggest that the latter was not explained by either reduced investment in antipredator vigilance or reduced neophobia in large groups. Instead, larger groups may contain more diverse individuals with different skills and experiences, which may increase the chance of solving the task by some group members. Increased success in problem solving may promote group living in animals and may help them to adapt quickly to new situations in rapidly-changing environments.

effectiveness | foraging | group size | innovation | urbanization

The costs and benefits of group living in animals have long been the focus of behavioral ecological research. Although individuals in groups may incur costs by increased competition and other social interactions, these costs may be offset by various advantages of group formation (1). For example, individuals in groups may learn from group mates when, where, what, and how to forage (2), have higher hunting success (3), and exploit the food discoveries of others (4). In addition, the per-capita risk of predation may decrease with group size, e.g., by earlier predator detection or dilution effects, and individuals may convert the time and energy spared by reduced vigilance into foraging efforts (1, 5).

Animals that live in complex or variable environments often encounter novel situations, e.g., their food may be unfamiliar or they may need to adopt new techniques to acquire it, as in the classic example of birds opening milk bottles (6). The ability to solve such problems, e.g., by innovating novel behaviors or using existing behavior in a novel way, may thus be an important determinant of adaptability, especially in generalist species (7–9) or populations colonizing new habitats (10, 11). When facing novel tasks, group members might be at an advantage compared with solitary individuals: they may cooperate to solve the problem (12, 13), or in uncooperative situations they may use the solutions invented by members of their group. In the latter case, solution to novel problems may be found more often or more quickly in larger groups than in smaller ones (or by solitary individuals) simply because more individuals can perform more attempts. Additionally, members of larger groups may be more effective in problem solving, e.g., because their performance may be enhanced by reduced predation risk or neophobia (14,

15), and/or because large groups are likely to contain a diverse sample of individuals with different skills and experiences, and diversity in such traits is likely to increase the chance of success (16, 17). When a solution is found by some group members, the others may profit from it by "copying" it (e.g., through social learning) or sharing in the discoveries (e.g., through scrounging or dividing the acquired food) (9).

The effects of group size on problem solving have been studied mostly in humans, and experimental tests are surprisingly scarce. Recent experiments, usually involving abstract logical tasks, consistently showed that groups performed better than individuals (even than the best individual), and the increase in group size from 2 to 3 or above further improved performance (18). In animals, it has also been demonstrated that groups may perform better than individuals (or, more rarely, that success increases with group size) in situations with some elements of novelty, e.g., in accepting novel food or finding hidden food (15, 19–25). To our knowledge, however, the effect of group size has not been experimentally studied in any task that required the invention of novel approaches or behavioral techniques, which are typical for many animal innovations (9) and may be important in adapting to novel environments (10).

In this study we investigated how the success of groups and individuals relates to group size in a problem-solving task designed to mimic innovative foraging in the field. As test subjects we used house sparrows (*Passer domesticus*) that are highly gregarious birds living in flocks of variable size from a few up to several hundreds. They occupy a wide range of human-altered habitats and opportunistically exploit a variety of resources (26). Among birds, house sparrows have a relatively large brain and a fairly high rate of foraging innovations (10), so problem solving seems both prevalent and relevant in the species.

First, we manipulated the number of wild-caught sparrows in captive groups and observed their success in a task in which familiar food was available from a familiar feeder but could only be acquired in a novel way, by opening the lids of seed-filled wells (27–29). Second, to infer the mechanisms that may lead to differential success in differently-sized groups, we (i) analyzed in detail the behavior of birds during problem-solving tests, and (ii) performed a separate neophobia test to explore any difference between the groups in their propensity to approach novel objects that may also influence problem solving (8, 27). Finally, because both problem solving (30–32) and the effect of sociality on problem solving (15, 33) may depend on the individual's sex and its interaction with group mates' sex, we also manipulated the sex ratio of the groups and investigated all combination of sexes (i.e., males only, females only, or both).

Results

Problem-Solving Success. The total number of wells opened within each group ranged between 0 and 5; only 2 small groups did not

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Table 1. Effects of group size and origin of birds (habitat) on problem solving in house sparrow groups

Dependent variable	Group size			Habitat		
	$F_{1,13}$	P	η^2 (CI)	$F_{1,13}$	P	η^2 (CI)
Group's total no. of opened wells	49.74	<0.001	0.81 (0.46–0.89)	8.96	0.012	0.43 (0.03–0.66)
Group's latency to open the first well	20.88	0.001	0.64 (0.20–0.79)	3.77	0.078	0.24 (0–0.53)
Individuals' latency to first feeding	27.16	0.003	0.69 (0.28–0.82)	4.04	0.070	0.25 (0–0.54)

Results from the final statistical models are shown. Data are reported for the entire 90-min tests of 7 small and 7 large groups. Effect size estimates (η^2) are given as the proportion of variance explained by group size or habitat, along with their 95% confidence intervals (CI).

open any well at all. Of the 52 birds, 20 were successful at solving the task: 16 birds opened 1 well, 3 birds opened 2 wells, and 1 bird opened 3 wells. All birds got food from the wells during the 90-min test, excepting 6 birds in 4 small groups. Birds that did not open any well themselves fed either together with the opener or after the opener left the well (or was chased away).

Large groups were significantly more successful in all aspects of problem solving (Table 1): they opened ≈4 times more wells in total (small groups: 0.71 ± 0.18 wells; large groups: 3.14 ± 0.40 wells; Fig. 1*A*) and opened the first well ≈11 times sooner (small groups: 3,846 ± 836 s; large groups: 343 ± 79 s; Fig. 1*B*) than

small groups. Furthermore, birds in large groups obtained their first food item ≈7 times sooner on average than birds in small groups (small groups: 4,117 ± 536 s; large groups: 593 ± 63 s; Fig. 1*C*). These effects were particularly strong: group size explained 64–81% of the variance in problem-solving success, and even the lowest limit of estimated effects was ≥20% (Table 1).

Independent of group size, urban birds opened more wells than rural ones and tended to be quicker on both opening the first well and getting to the first feeding (Table 1 and Fig. 1). Final models did not include any other main effect or interaction (all $P > 0.108$).

Behavior During Problem Solving. During the first 30 min of the test, the difference in the number of opened wells between small and large groups was even more pronounced (≈9-fold; Table 2) than for the total duration of the test. In this period, almost all group members (92% of birds) made attempts to open at least 1 well, and the proportion of tryers (i.e., the number of birds that attempted to problem solve divided by group size) was similar in small and large groups (Table 2). The total number of problem-solving attempts was significantly higher (≈3.7 times) in larger groups (Table 2). However, before the opening of the first well in the group, small and large groups did not differ in the number of attempts to problem solve (Table 2). Furthermore, small and large groups did not differ in per-capita opening attempts either during the entire 30 min or before the first well opening (Table 2).

In contrast, both the proportion of openers (i.e., the number of birds that opened at least 1 well divided by group size) and the proportion of tryers that became successful openers were higher in large than in small groups (Table 2). As a consequence, the total number of opened wells remained significantly higher in large groups when we controlled for the total number of problem solving attempts (attempt number: $F_{1,13} = 14.62$, $P = 0.003$; group size: $F_{1,13} = 12.20$, $P = 0.005$).

Both the individuals of large groups and large groups as a whole spent more time on the feeder in total and stayed on the feeder for longer bouts than small groups (Table 2). However, when we controlled for the latency to open the first well in the group, large and small groups did not differ in any measure of time spent on the feeder (all $P > 0.144$) except for group total (opening latency: $F_{1,13} = 12.41$, $P = 0.005$; group size: $F_{1,13} = 6.94$, $P = 0.023$). Furthermore, before the opening of the first well in the group, birds in large groups tended to spend shorter bouts on the feeder than birds in small groups (Table 2). The latency to first visit to the feeder did not differ between small and large groups or between individuals in small and large groups (Table 2). Scanning rate did not vary with group size either during the entire 30 min or before the first well opening (Table 2), or when we controlled for the latency to open the first well in the group (opening latency: $F_{1,13} = 0.07$, $P = 0.797$; group size: $F_{1,13} = 2.79$, $P = 0.121$).

Other than group size, no effect or interaction was significant in these analyses, except that urban groups tended to contain
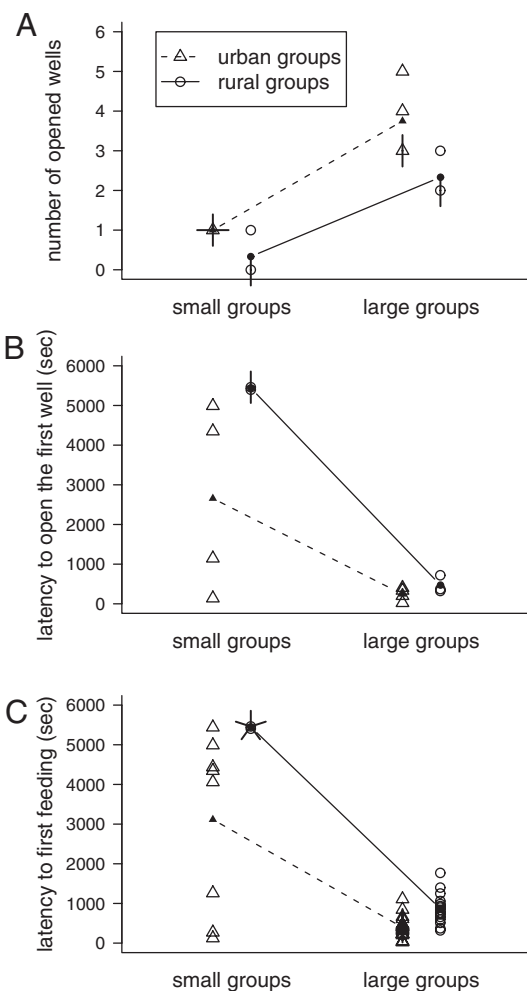

Fig. 1. Problem solving in small (2 birds) and large (6 birds) groups of house sparrows from different habitats. (*A*) Total number of wells opened in the group. (*B*) Latency to open the first well in the group. (*C*) Latency of the birds to first feeding from the opened wells. *A* and *B* show each group as a datum, and *C* shows data for individuals (petals indicate overlapping data points; means are marked by filled symbols).

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Table 2. Attempts and success of small (2 birds) and large (6 birds) house sparrow groups during the first 30 min of the problem-solving test

Dependent variable	Small groups	Large groups	$F_{1,13}$	P
Total no. of wells opened in the group	0.29 ± 0.18	2.71 ± 0.42	27.97	<0.001
No. of birds trying to open the wells	1.86 ± 0.14	5.00 ± 0.38	60.50	<0.001
Proportion of birds trying to open the wells	0.93 ± 0.07	0.92 ± 0.04	0.02	0.879
Total no. of attempts to problem solve	10.57 ± 3.57	38.86 ± 8.7	9.05	0.011
Total no. of attempts to problem solve before the first opening	9.86 ± 3.36	15.86 ± 5.66	0.83	0.380
Per-capita no. of attempts	5.29 ± 1.79	7.05 ± 1.59	0.57	0.466
Per-capita no. of attempts before the first opening	4.93 ± 1.68	2.81 ± 1.07	1.13	0.309
No. of birds opening the wells	0.29 ± 0.18	2.29 ± 0.18	58.8	<0.001
Proportion of birds opening the wells	0.14 ± 0.09	0.43 ± 0.04	7.96	0.015
Proportion of tryers succeeding to open	0.14 ± 0.09	0.48 ± 0.05	9.70	0.009
Per-capita no. of wells opened	0.14 ± 0.09	0.51 ± 0.09	8.33	0.014
Group's total time spent on feeder, s	279.6 ± 77.1	1003.4 ± 138.3	20.92	0.001
Group's feeder bout length, s	31.7 ± 7.6	142.4 ± 37.8	8.29	0.014
Individual's total time spent on feeder, s	168.1 ± 54.4	431.6 ± 63.0	9.86	0.009
Individual's feeder bout length, s	23.4 ± 5.5	59.7 ± 5.9	13.91	0.003
Individual's feeder bout length before the first opening, s	22.3 ± 4.9	11.3 ± 2.4	4.79	0.049
Group's latency to first visit the feeder, s	98 (48–1,490)	93 (0–366)	26.5	0.848
Individual's latency to first visit the feeder, s	131 (48–1,658)	116 (0–869)	21.0	0.710
Individual's scanning rate, no. of scans/s	0.33 ± 0.03	0.28 ± 0.02	2.86	0.117
Individual's scanning rate before the first opening	0.32 ± 0.02	0.30 ± 0.02	0.21	0.652

Data are reported from the analyses of video recordings of 7 small and 7 large groups. Statistics are shown for the effect of group size in the final models. For latencies to visit the feeder, median (minimum–maximum) values and results of Mann–Whitney tests are given because normality and homoscedasticity were not held in these cases.

more openers than rural groups (group size: $F_{1,13} = 77.0$, $P < 0.001$; habitat: $F_{1,13} = 4.71$, $P = 0.053$).

Neophobia. The novel object was effective in triggering neophobic response, because sparrows increased their latency to visit the feeder by ≈15 min on average (control test: 478 ± 65 s; neophobia test: 1,351 ± 84 s; paired t test: $t_{51} = -9.68$, $P < 0.001$). However, we found no difference in first latency to approach the novel object between small and large groups ($F_{1,13} = 0.46$, $P = 0.510$) or between individuals in small and large groups ($F_{1,50} = 0.01$, $P = 0.926$). No other effect or interaction was significant (all $P > 0.361$). The groups' neophobia was unrelated to their problem-solving success (total number of wells opened: $F_{1,13} = 0.08$, $P = 0.777$; latency to open the first well: $F_{1,13} = 0.56$, $P = 0.468$; individuals' latency to first feeding: $F_{1,13} = 0.53$, $P = 0.470$), and the individuals' neophobia was not related to their latency to open their first well ($F_{1,51} = 0.54$, $P = 0.467$) and did not differ between openers and nonopeners ($F_{1,51} = 0.02$, $P = 0.876$).

Discussion

We found that the novel foraging problem presented to house sparrows was solved more effectively in larger than smaller groups, in terms of both the number of successful feeder openings and the time needed to the first opening. In recent work with human groups, Laughlin et al. (18) found that groups consisting of 3–5 individuals achieved significantly higher success in solving an abstract logical task than the best individuals alone and groups of 2 individuals. Similarly, here we showed that sparrows in groups of 6 were disproportionately more successful than 2 birds in a simple task of using a new food-extracting method. This finding suggests that the effect of group size on problem-solving success may also be relevant for animals with more limited cognitive abilities than those of humans and for various situations and types of problems.

A further important result of our study was that all birds profited from being in a larger group by getting their first food much sooner than birds in small groups. Because the opportunity to exploit others' efforts is a frequent benefit of group living (1, 4), and novel solutions can also be learned by group members (9, 33, 34), such benefits obtained through the success of innovative group mates is likely to be a significant factor promoting group living. Webster and Lefebvre (27) found that the success of 5 bird species in a similar problem-solving test was strongly related to their innovation frequencies in the wild, which implies that our finding is likely to be relevant for natural situations (see ref. 28 for further validation). Because the ability to innovate, e.g., to invent new foraging methods, increases the animals' adaptability to novel environments (10), our results suggest that group living may help animals to quickly adapt to unfamiliar situations, which is especially important in species living in diverse or rapidly-changing environments.

An interesting aspect of our results is that large groups were disproportionately more successful in the problem-solving task than small groups. If all birds are trying to get food independently of each other, thrice as many birds should mean thrice as many attempts and, assuming random success, thrice as many problem-solving events. According to this expectation, large groups spent proportionally more time on the feeder and made proportionally more attempts to problem solve than small groups. Although this may partially explain the higher success of large groups, it cannot account for their >10-fold faster problem solving and their opening of >9 times as many wells as in small groups during the first 30 min. The latter results suggest that the effectiveness of all individuals was increased in the large groups and/or there were a greater number of effective individuals in large groups.

Foraging in larger groups may enhance the effectiveness of individuals in several ways. First, the presence of group mates may increase the individuals' motivation through social facilitation, e.g., because they experience lower levels of fear and/or higher levels of competition (14). This may encourage birds to visit the feeder sooner (35) and spend more time exploring (15), increasing the chance of solving the task. Although large groups of sparrows indeed made longer feeder bouts and more attempts to problem solve, these differences were possibly the conse-

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quence rather than the cause of their earlier well opening, because we found no difference in the former behaviors before the first opening. Furthermore, neither the per-capita rate of attempts nor the latency to first visit the feeder differed between small and large groups. Thus, social facilitation was unlikely to contribute significantly to the faster problem solving in large groups. Nevertheless, after the opening of the first well the presence of foraging opportunities and/or feeding group mates may have stimulated other birds to attend the feeder and try opening other wells, thereby facilitating further problem solving in the group. Well-opening behavior might have also spread within groups via social learning (34), especially because sparrows often scrounge at food clumps (36–38) that may inhibit individual learning (39).

Second, individual effectiveness may have increased because better antipredatory protection in larger groups, e.g., by the dilution of predation risk, may enable birds to spend more time on feeding and less on vigilance (1, 5). However, this idea is again inconsistent with our findings that neither visit latency nor feeder time before the first well opening varied with group size. Moreover, sparrows in large groups did not scan for predators less frequently than birds in small groups (even before opening the feeder, when food handling could not influence vigilance). This latter result is similar to that of Barnard (40), who found that when house sparrows were feeding in a cattle shed with minimal predation risk vigilance was a minor component of their time budgets and was not explained by group size. Although our aviaries were exposed to occasional approaches by sparrowhawks (*Accipiter nisus*) and feral cats, the actual risk of predation might have been perceived as low by the captive sparrows. Therefore, the poorer problem solving of small groups is unlikely to be attributed to predation risk, although such an effect might be of greater importance in natural, free-living flocks.

Third, large groups may be more effective in problem solving because of reduced neophobia. Being in a large group may lower the fear of novelty and thereby enhance individual performance (14, 25), or larger groups may be more likely to contain bolder individuals whose explorative efforts may encourage more neophobic group mates (15, 35). However, we found no difference in object neophobia between small and large groups, and problem-solving success was also unrelated to neophobia. Nevertheless, the results of the neophobia test add to recent findings that neither the effect of group mates on neophobic responses nor the relationship between problem solving and neophobia is straightforward. For example, the neophobia of ravens (*Corvus corax*) is either increased or reduced by the presence of companions, depending on sex, affiliations, and "personalities" (15, 41). In foraging tasks, problem-solving success was related to neophobia in pigeons (*Columba livia*; ref. 28) but not in starlings (*Sturnus vulgaris*; ref. 34).

Finally, a possible explanation for large groups being both faster and more productive in problem solving is that they may be more likely to contain skilled individuals who are successful in solving the task, e.g., because of their previous experiences or better abilities necessary for problem solving. The tendency to solve novel tasks varies among individuals e.g., in relation to age (32) and learning skills (28, 34), and some studies suggest that "innovativeness" may be an aspect of animal personalities (30, 31, 42). Increased success of groups containing behaviorally diverse individuals has been shown by recent theoretical (16) and empirical work (17). We suggest that, in the light of our results, the diversity of large groups is a likely explanation for 6 house sparrows being about 10 times as successful as 2. Each large group contained 2 or 3 openers who were quick at solving the novel task, making food available for the whole group within 1–12 min. In contrast, each small group contained only 1

successful bird at best, only 2 of which could solve the task in the first 30 min of the test (after 2 and 19 min, respectively).

In addition to the effects of group size, our results showed a tendency for urban birds to be better at problem solving than rural birds, suggesting that sparrows from more urbanized habitats might be more experienced and/or more talented in solving novel tasks. This finding is in accordance with the common notion that behavioral flexibility and adopting novel behaviors may be especially adaptive in urban habitats (10, 43), although this assumption has not yet been tested within any species to our knowledge. In an interspecific aspect, Sasvári (44) showed that more urbanized species learn faster, whereas Kark et al. (45) found no association between the degree of urbanization and innovativeness. Clearly this topic needs more attention. Last, we did not find any effect of the birds' sex or the groups' sex ratio on their problem-solving success, which again adds to the general picture that whether and how sex affects problem solving varies widely across taxa (28, 30–32).

Taken together, our study demonstrates that house sparrows may benefit from being in larger groups when faced with a challenge of an unfamiliar task. A likely reason for the disproportionately faster and more problem solvings by larger groups is their greater chance to contain more skilled individuals, whose quick innovations might then further enhance the group's success via social facilitation and/or social learning. Our results suggest that, for species such as sparrows that live in habitats being continuously changed by humans, two heads are definitely better than one.

Materials and Methods

Study Subjects. We captured 56 house sparrows with mist nets between February 23 and March 21, 2007 in the suburbs of Veszprém (*n* = 32 urban birds) and in 2 nearby villages (Nemesvámos and Kádárta; *n* = 24 rural birds) in Hungary. Upon capture we ringed each bird with 1 numbered metal ring and 3 color rings. Until the observations, birds were held in 2 outdoor aviaries [≈3 (wide) × 4 (long) × 3 (high) m] that contained roosting trees and small boxes for resting. Urban and rural birds were kept in separate aviaries. Food (millet, wheat, and sunflower seeds) and water was available ad libitum, and multivitamin droplets were regularly added to the water. We provided food in 3 bowls (diameter 30 cm) placed on the ground. After the observations we released each bird at the site of capture. The capturing and keeping of the birds and the procedures used in this study were in accordance with Hungarian laws and were approved by Balaton Upland National Park (permission 9135-2/2004).

Experimental Protocol. Experiments were conducted between April 20 and June 22, 2007 in weekly periods with testing 2 groups each week (by A.L.). On day 1 in each period, 2 groups (see *Group Design*) were captured from the maintenance aviaries and introduced into 2 test aviaries. The test aviaries had similar size and setup as the maintenance aviaries, except that food was provided on a Plexiglas feeder (see *Test Apparatus*) placed on a 1 × 1-m wired-top platform lying on the ground. The platform collected spillage and prevented birds from accessing it. After a 4-day acclimatization period, birds were observed in a control test on day 5, a neophobia test on day 6, and a problem-solving test on day 7. After the last test, birds were released and 2 other groups were taken into the test aviaries. Thus, each bird was included only in 1 experimental group.

Food was provided ad libitum during days 1–4. All food was removed from the feeders in the test aviaries for the nights before the tests (i.e., on evenings of days 4–6, ≈2 h before sunset), then the behavior of birds was recorded after the provision of food the next morning (≈2 h after sunrise). Each morning on days 5–7 the experimenter observed the groups from a hide placed next to the aviary through a 1-way window. The behavior of the birds on the feeder in both groups was recorded by digital video cameras during the whole experiment (90 min for each group). The experimenter switched observations between the 2 groups every 30 min, thereby each group was observed for 2 30-min periods, with a 30-min gap in between. During the gap the video camera kept recording but the experimenter was observing the other group.

Group Design. Birds were allocated into 14 test groups: 7 small groups, each consisting of 2 birds, and 7 large groups, each consisting of 6 birds. However, because 4 birds (2 urban and 2 rural) died in the aviaries before the tests, 2

large groups contained 5 birds and 1 contained 4 birds. Note that this rate of mortality (7%) is lower than in the wild and typical for captive sparrows (26, 38). We composed 5 (3 small, 2 large) male-only groups, 4 (2 small, 2 large) female-only groups, and 5 (2 small, 3 large) groups with even sex ratio. Birds captured from different habitats were allocated into separate groups, thus we had 8 (4 small, 4 large) groups of urban birds and 6 (3 small, 3 large) groups of rural birds. In all other respects, the allocation of birds into test groups was random. We tested 1 small and 1 large group each week, with the testing order of groups from different habitats and different sex ratios randomized for both small and large groups, and we also randomly allocated the groups among the 2 test aviaries.

Test Apparatus and Procedures. The test feeder was a $50 \times 50 \times 5$-cm clear Plexiglas box filled with visible seeds (of the same mixture used in the maintenance aviaries) that could be obtained through 16 (4×4) equidistant wells (diameter 3.5 cm) drilled into the Plexiglas top of the feeder (27). During acclimatization and in the control and neophobia tests (days 1–6), the wells were open and food was readily available. Birds accepted and used the feeder from the first day of the experiments.

In the control test, food was provided in the morning, and the experimenter recorded each bird's latency to approach the feeder as time elapsed from the beginning of the observation until the bird first landed on the feeder. In the neophobia test, a novel object was placed on the middle of the feeder immediately before the start of the experiments (i.e., when food was provided) and was present throughout the entire test period. The object was a paper barrel (13.5 cm high, 7 cm diameter) wrapped in bright golden gift paper, with a blue and a yellow straw attached to it by a red and a blue rubber band (see e.g., ref. 27 for similar design). The experimenter recorded each bird's latency to approach the feeder as in the control test.

During the problem-solving test, each well was covered by a lid (made from a rigid transparent film, similar in appearance to Plexiglas) with a small black rubber knob glued on it. These lids were present on the surface of the feeder throughout the experiment, fixed either in the open (days 1–6) or the closed (day 7) position by small pieces of removable sticky tack. Thus, although birds were familiar with the lids by the time of the problem-solving task, they had no previous experience with closed wells and had no opportunity to learn how the lids could be opened. During the problem-solving test, birds tried to open the closed wells either by vigorous pecks that detached the lid and tossed it away or pulling the lid away from the closed position. The experimenter recorded each bird's latency to its first landing on the feeder, opening well, and first feeding (i.e., pecking seeds from an opened well).

Data Processing and Statistical Analyses. The video recordings were used to check the latencies observed by the experimenter. To quantify the problem-solving success of the groups, we counted (*i*) the total number of wells opened in the group, (*ii*) the latency to open the first well in the group, and (*iii*) the individuals' latency to first feeding. To quantify neophobia, we subtracted each individual's latency in the control test from its latency in the neophobia test (11). Neophobia of the group was then defined as the neophobia of the

first individual that visited the feeder. Latencies of 5,460 sec (i.e., 91 min) were assigned to birds that did not perform the respective behavior (i.e., well opening, feeding, or approaching the feeder) during the 90 min of the tests.

The first 30-min recording of each group's problem-solving test was analyzed in more detail. Because most well openings (21 of 27) occurred during the first 30 min, and the number of wells opened in total correlated strongly with the number of wells opened during the first 30 min (Spearman rank-correlation: $r_s = 0.93$, $P < 0.001$, $n = 14$), the first 30-min well represents the birds' behavior in the problem-solving test. Analyses of the video recordings were conducted as follows (by V.B.). We defined feeder bouts as periods when 1 or more birds were staying on the feeder. For each individual and for each group, the length of feeder bouts were measured as the time elapsed from the individual or the first bird in the group, respectively, landing on the feeder until the individual or the last bird in the group, respectively, left the feeder. Then we calculated the total time spent on the feeder and the average length of feeder bouts for each individual and each group. In each feeder bout of each individual, we counted both the number of scans and the number of attempts to problem solve. Scans were defined following Coolen and Giraldeau (46) as head-up-while-stationary and head-up-while-eating positions that are related to antipredator vigilance (see also ref. 47). For each individual, scanning rate was calculated as the total number of scans divided by the total time spent on the feeder. Attempts to problem solve (i.e., to open the wells) were defined as peckings or probings directed at the lids (when the bird definitely contacted the lid with its bill); repeated pecks at a single lid were counted only once in each bout (27). We calculated the total number of problem-solving attempts for each group and each individual.

We analyzed (*i*) the total number of wells opened in the group, (*ii*) the latency to open the first well in the group in linear models (LMs), and (*iii*) the individuals' latency to first feeding in linear mixed models (LMMs) with group identity entered as random factor. All initial full models included group size, sex ratio, and habitat as fixed factors, the date of tests as covariate, and the interactions of group size $\times$ sex ratio and group size $\times$ habitat. The sex of the individual was also included as fixed factor in the LMM. We reduced the models stepwise by eliminating the least significant effect in each step, retaining only significant ($P < 0.05$) or marginally nonsignificant ($P < 0.08$) effects in the final models. Data from the first 30 min of problem-solving tests were analyzed similarly, i.e., groups' variables (total time spent on feeder, average length of feeder bouts, latency to first visit the feeder, total number of attempts to problem solve) by LMs and individuals' variables (time spent on feeder, average length of feeder bouts, latency to first visit the feeder, number of attempts to problem solve, scanning rate) by LMMs.

All analyses were run in the R statistical computing environment (ref. 48 and www.R-project.org). We report means $\pm$ SE and 2-tailed P values with 95% confidence level throughout.

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