

# Larger groups of passerines are more efficient problem solvers in the wild

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Group living commonly helps organisms face challenging environmental conditions. Although a known phenomenon in humans, recent findings suggest that a benefit of group living in animals generally might be increased innovative problem-solving efficiency. This benefit has never been demonstrated in a natural context, however, and the mechanisms underlying improved efficiency are largely unknown. We examined the problem-solving performance of great and blue tits at automated devices and found that efficiency increased with flock size. This relationship held when restricting the analysis to naive individuals, demonstrating that larger groups increased innovation efficiency. In addition to this effect of naive flock size, the presence of at least one experienced bird increased the frequency of solving, and larger flocks were more likely to contain experienced birds. These findings provide empirical evidence for the “pool of competence” hypothesis in nonhuman animals. The probability of success also differed consistently between individuals, a necessary condition for the pool of competence hypothesis. Solvers had a higher probability of success when foraging with a larger number of companions and when using devices located near rather than further from protective tree cover, suggesting a role for reduced predation risk on problem-solving efficiency. In contrast to traditional group living theory, individuals joining larger flocks benefited from a higher seed intake, suggesting that group living facilitated exploitation of a novel food source through improved problem-solving efficiency. Together our results suggest that both ecological and social factors, through reduced predation risk and increased pool of competence, mediate innovation in natural populations.

animal innovation | sociality | risk-sharing | personality | swarm intelligence

From chemical interactions between microbes to cooperative breeding among group-living animals, sociality has evolved through a wide variety of mechanisms that commonly help organisms exploit resources more efficiently (reviewed in refs. 1–3). Although benefits of sociality are often simply linked to shared investment or shared risk, social interactions can also help individuals cope with cognitively challenging problems—for instance, when navigating (4) and problem solving (5). In humans, it is well known that group size and composition influence collective performance on a variety of tasks (reviewed in ref. 6), with groups exhibiting emergent properties that are not always evident among isolated individuals (7, 8). A recent study suggests that group living can also lead to increased innovative problem-solving efficiency in nonhuman animals (ref. 9, but see ref. 10). To date, however, the significance of this finding is unclear because no studies on group problem solving have yet been undertaken in the wild.

Several factors could theoretically lead to improved solving efficiency with increasing group size. Two of these relate to risk sharing: a reduction in object neophobia (11, 12) and shared antipredatory vigilance (13, 14). A third, nonexclusive possibility is that individuals intrinsically differ in their probability of success, and, as a consequence, larger groups are more likely to contain individuals with specific skills, individual tendencies, or past experience, making them competent at solving the current problem (9, 15). We will refer to this possibility as the “pool of

competence” hypothesis. Although some studies now provide evidence that individuals differ consistently in their problem-solving ability (16, 17)—a necessary condition for the pool of competence hypothesis—the idea that larger groups can innovate more efficiently because they are more diverse, and therefore more likely to contain potential solvers, has not yet been tested in nonhuman animals. However, a study on captive flocks of house sparrows could rule out alternative risk-sharing explanations for more efficient novel problem solving in groups of six versus two individuals, with larger flocks obtaining food sooner than smaller flocks (9).

In humans, group problem-solving efficiency seems to level off after an intermediate group size (e.g., ref. 18). Similarly, food intake usually first increases with the size of nonhuman animal groups because of risk sharing, but it then decreases because of competition (1, 19). Large group sizes seen in wild aggregations of nonhuman animals may therefore decrease problem-solving efficiency because of increased interference (e.g., ref. 20) or an increase in the proportion of individuals resorting to scrounging as an alternative tactic, leading to reduced per capita intake when group size increases (19, 21). Consequently, an optimal group size where the net benefits of grouping on problem solving are maximized might be expected if increased efficiency in larger groups results from reduced risk—the importance of which diminishes as group size becomes larger (22, 23). In contrast, a linear increase in problem-solving efficiency with group size would support the pool of competence hypothesis, which predicts that larger groups will contain more individuals that are likely to solve the problem. These predictions remain untested.

In this study, we examined the relationship between natural flock size and foraging problem-solving efficiency in a wild population of small passerine bird species (Paridae) in Wytham Woods, Oxford. All great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) born or breeding in Wytham are equipped with a passive integrated transponder (PIT) tag, allowing the automated detection of large numbers of individuals in the field. Great and blue tits form mixed-species flocks during winter in Wytham (24) and are known to spontaneously innovate at high rates in the wild (25–27); they are therefore ideal species for examining the benefits of flocking on innovative foraging efficiency in natural conditions.

## Results

**Are Larger Groups Better at Problem Solving?** Six problem-solving devices (*Materials and Methods* and *Movie S1*) were deployed for 5–7 d at five locations in the woods. We recorded a total of 4,775 problem-solving attempts by 148 tagged great tits and 49 tagged

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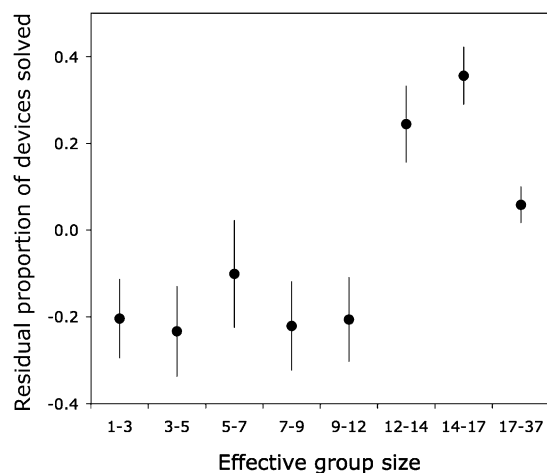
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blue tits. Of these attempts, 313 were successful ( $n = 300$  by 28 great tits, rate of success = 7.9%;  $n = 13$  by 5 blue tits, rate of success = 1.4%). Total group size per trial as measured from the automated devices ranged from 1 to 58 (mean  $\pm$  SEM =  $19.8 \pm 1.7$ ), and effective group size, which included only those individuals that visited a solvable device, ranged from 1 to 37 (mean  $\pm$  SEM =  $11.6 \pm 1.0$ ). We assumed that group size values obtained from the automated devices were representative of natural flock size because total group size during the first trial of a day was positively correlated with an independent bird count (three replicates of 2-min periods) conducted at a regular multiaccess feeder, before baiting the problem-solving devices in the morning (Pearson's product-moment correlation;  $r = 0.45$ ,  $t = 2.4$ ,  $df = 23$ ,  $P = 0.025$ ). The proportion of devices solved per trial increased with the number of birds attempting to solve [Fig. S14; generalized linear mixed model (GLMM), Wald test; effective group size:  $Z = 5.2$ ,  $P < 0.001$ ]. This finding held when controlling for total duration of attempts by all birds (Fig. 1 and Table S1; GLMM, Wald test; effective group size:  $Z = 4.2$ ,  $P < 0.001$ ; group effort:  $Z = -0.6$ ,  $P = 0.518$ ), suggesting that larger groups were more efficient problem solvers than smaller ones.

**Mechanisms for Increased Problem-Solving Efficiency in Larger Groups.** We first examined whether larger groups were less neophobic than smaller groups, resulting in shorter latencies to contact devices after initial baiting in the morning. There was no evidence for this hypothesis: although latency to contact devices during the first trial of a day decreased over consecutive days at a location, latency was not predicted by morning bird count [Table S2; linear mixed model (LMM); group size:  $F_{1,17} = 1.3$ ,  $P = 0.2$ ; days:  $F_{1,17} = 8.8$ ,  $P = 0.009$ ].

We examined the effect of variation in predation risk on problem-solving efficiency by comparing the behavior of birds using safe and exposed devices. Three of the six devices were installed in a row 1 m away from dense vegetation cover, and the other three were installed 4 m away from the same cover. Use of the devices located far from cover should be associated with increased perceived predation risk because great tits seek cover when surprise attacked by their most important predator, the sparrowhawk *Accipiter nisus*, and the risk of being caught by a sparrowhawk is greatest in the open (28, 29). Birds were more efficient when solving devices near rather than far from cover

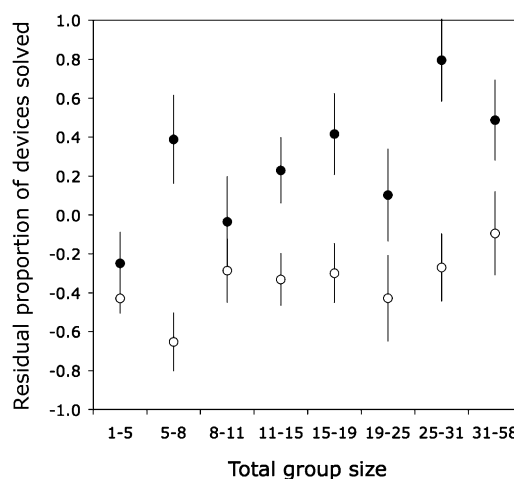


**Fig. 1.** Residual proportion of devices solved (mean  $\pm$  SEM) in relation to effective group sizes. Plotted values are residuals from a binomial GLMM of proportion of solved devices for group effort, with day nested within location as a random effect ( $n = 162$ , split into seven categories of 20 and one category of 22 data points each).

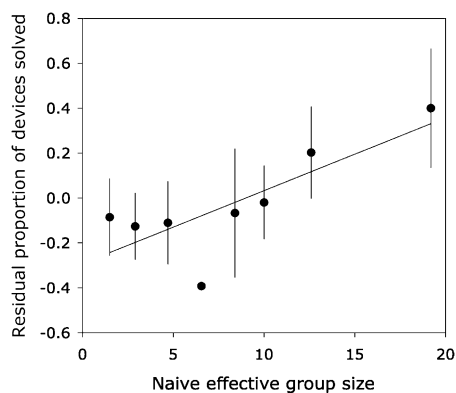
(Fig. 2 and Table S3; GLMM, Wald test; distance from cover:  $Z = -6.0$ ,  $P < 0.001$ ; total group size:  $Z = 6.6$ ,  $P < 0.001$ ; group effort at devices near or far from cover:  $Z = 0.3$ ,  $P = 0.763$ ), suggesting a role for risk of predation on problem-solving efficiency.

The pool of competence hypothesis predicts that larger groups contain a higher diversity of skills, tendencies, or experience, thereby increasing the probability of solving the problem. Some birds had previously been tested for a similar, but simpler, task when kept for 24 h in captivity (17, 30), and larger flocks contained more individuals having solved this problem previously in captivity (LMM;  $F_{1,132} = 244.9$ ,  $P < 0.001$ ) or in the field (LMM;  $F_{1,132} = 37.9$ ,  $P < 0.001$ ). However, the presence of solvers from captivity did not have an impact on the proportion of devices solved in the field (Table S4; GLMM, Wald test; presence of a solver from captivity:  $Z = 0.2$ ,  $P = 0.829$ ; effective group size:  $Z = 3.9$ ,  $P < 0.001$ ; group effort:  $Z = -0.6$ ,  $P = 0.525$ ). In contrast, the presence of at least one individual having solved the current, more complicated problem in the field increased problem-solving efficiency, even when controlling for group size and other factors (Table S5; GLMM, Wald test; presence of an experienced individuals in the field:  $Z = 2.0$ ,  $P < 0.001$ ; effective group size:  $Z = 3.1$ ,  $P = 0.002$ ; group effort:  $Z = 0.2$ ,  $P = 0.828$ ). The presence of experienced individuals improved the solving competence of the group.

Increased problem-solving efficiency in larger groups was also observed when restricting attempts and solving to individuals that had never solved this problem in the field, suggesting that increased efficiency was not solely due to previous experience (Fig. 3 and Table S6; GLMM, Wald test; naive effective group size:  $Z = 2.1$ ,  $P = 0.035$ ; naive group effort:  $Z = 0.6$ ,  $P = 0.544$ ). The shape of the relationship between problem-solving rate and effective group size in naive birds did not exhibit a leveling off at larger group sizes as expected if the relationship was only due to reduced perceived predation risk; instead, it featured a linear increase with group size, as expected if increased efficiency in larger naive groups was due to the presence of more numerous individuals potentially competent at solving the problem (Fig. 3; GLMM, Wald test; quadratic term for naive effective group size:



**Fig. 2.** Residual proportion of devices solved (mean  $\pm$  SEM) in relation to total group sizes in low and high perceived predation-risk positions (low risk was near cover, filled circles; high risk was far from cover, open circles). Plotted values are residuals from a binomial GLMM of proportion of solved devices for group effort, with trial nested within day and location as random effects ( $n = 324$ , split into seven categories of 20 and one category of 22 data points, allocated separately for data points near and far from cover).



**Fig. 3.** Residual proportion of devices solved (mean  $\pm$  SEM) by naive individuals in relation to the total number of naive individuals in the group, with linear fit shown. Plotted values are residuals from a binomial GLMM of proportion of solved devices for naive group effort, with day nested within location as a random effect ( $n = 161$ , split into seven categories of 20 and one category of 21 data points each; 1 trial out of the 162 had no attempt by naive individuals and was therefore excluded from the analysis).

$Z = 1.1$ ,  $P = 0.914$ ; model with naive effective group size and naive group effort).

To further explore the mechanisms underlying solving efficiency, we analyzed the data at the level of attempts, restricting the data to visits by individuals that ever solved the task during the experiment. The probability of solving increased with the number of companions present 5 min before the attempt, the duration of the attempt, and the number of previous attempts made by this individual, whereas it decreased with distance to cover (Table 1). The additive effects of both the number of companions and distance from cover on solving efficiency thereafter probably arose because of perceived variation in predation risk, which presumably influenced the extent to which birds could focus on solving the task. The random “individual” effect was also highly significant, suggesting consistent individual differences in the probability of success among solvers, even after accounting for all of these contextual variables (repeatability = 0.654; likelihood ratio-test:  $X^2 = 215.1$ ,  $df = 1$ ,  $P < 0.001$ ). This result supports the idea that individuals differ consistently in their problem-solving ability, a necessary requirement for the pool of competence hypothesis.

**Table 1.** Test of the reduced predation risk hypothesis at the level of problem-solving attempts

	Estimate $\pm$ SE	Wald Z	P
Group size*	0.241 $\pm$ 0.100	2.396	0.017
Distance to cover <sup>†</sup>	−0.583 $\pm$ 0.178	−3.277	0.001
Effort <sup>‡</sup>	0.066 $\pm$ 0.013	5.205	<0.001
No. of previous attempts <sup>§</sup>	0.028 $\pm$ 0.004	7.815	<0.001
Device state <sup>  </sup>	0.219 $\pm$ 0.173	1.280	0.208

Predictors of success among 33 individual solvers in the field (binomial GLMM;  $n = 1,439$ ). The model included random effects for location and individual.

\*Number of different individuals present at all devices within the 5 min preceding the attempt ( $\log_{10}$ -transformed).

<sup>†</sup>Distance to cover was either 1 or 4 m and indicated the position of the device relative to the nearest protective tree cover.

<sup>‡</sup>Duration of the attempt in seconds.

<sup>§</sup>Number of previous problem-solving attempts at all devices by this individual.

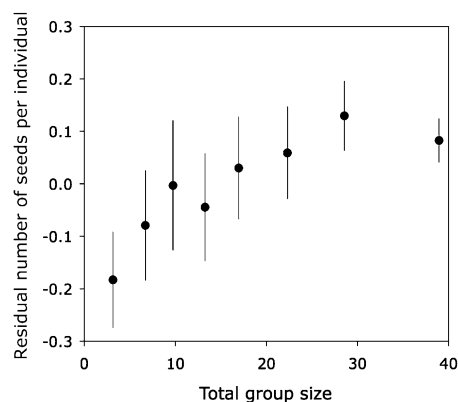
<sup>||</sup>Device state was either one or two, indicating whether there were one or two levers to be pulled out on the device before accessing the seeds.

**Alternative Explanations.** An alternative explanation for the link between problem-solving efficiency and group size is that age, sex, species, body size, or some other variable that can influence problem-solving performance (31) might vary in composition with group size. We examined this possibility and found that only body size changed with group size, with larger flocks containing individuals with smaller wing length (Table S7). The “necessity drives innovation” hypothesis (32) suggests that subdominant, smaller individuals may be more likely to innovate, which could have driven the observed effect. However, wing length did not influence the effect of group size on problem-solving efficiency (GLMM, Wald test; effective group size:  $Z = 4.4$ ,  $P < 0.001$ ; group effort:  $Z = -0.6$ ,  $P = 0.535$ ; mean wing length:  $Z = 2.0$ ,  $P = 0.048$ ). The same was true for the analysis examining the effect of at least one experienced bird on increased problem-solving efficiency (GLMM, Wald test; presence of at least one experienced bird:  $Z = 4.8$ ,  $P < 0.001$ ; effective group size:  $Z = 3.2$ ,  $P = 0.002$ ; group effort:  $Z = 0.2$ ,  $P = 0.823$ ; mean wing length:  $Z = 0.7$ ,  $P = 0.470$ ). Furthermore, none of the group composition variables differed among groups using devices located near versus far from protective tree cover (Table S8). These results increase the likelihood that the above-mentioned effects are indeed due to an increased pool of competence and reduced predation risk at large group sizes.

**Did Larger Groups Obtain More Food Items per Capita?** In our experimental setup, each device was loaded with 30 seeds at the start of each trial, and yet great and blue tits can only handle one food item at a time, allowing for scrounging to occur—a behavior that is almost ubiquitous among group foragers (19). We were therefore able to show that total group size was a significant, positive predictor of the mean number of seeds obtained per individual group member (Fig. S1B), while controlling for total time spent at the devices by all birds, suggesting that individuals in larger groups were more successful at foraging compared with those in smaller groups, irrespective of whether they themselves could solve the problem (Fig. 4 and Table S9; LMM; total group size:  $F_{1,131} = 23.6$ ,  $P < 0.001$ ; total time spent at the devices:  $F_{1,131} = 1.9$ ,  $P = 0.171$ ).

## Discussion

Our experiment revealed more frequent and more efficient problem solving by larger natural, mixed-species flocks of great and blue tits. This increased efficiency was not due to a reduction in neophobia among larger groups, although reduced perceived



**Fig. 4.** Residual number of seeds per individual (mean  $\pm$  SEM) against total group size. Plotted values are residuals from an LMM of the mean number of seeds per capita for group effort, with day nested within location as random effects ( $n = 162$ , split into seven categories of 20 and one category of 22 data points each).



predation risk was a significant determinant of problem-solving efficiency. Larger flocks were more likely to contain at least one experienced individual, leading to increased problem-solving efficiency and seed intake among individuals joining these aggregations. Our results support the hypothesis that larger groups confer benefits to individual flock members by increasing group efficiency at solving innovative foraging problems.

Liker and Bókonyi's (9) study on captive flocks of house sparrows demonstrated that flocks of six individuals could solve a novel problem more efficiently than dyads. Our results also demonstrate increased innovative problem-solving efficiency in larger groups, but they show such an effect in natural conditions, where individuals were free to join and leave a variable range of flock sizes and where predation risk was not reduced by conducting tests in an aviary. The group size effect reported in our system did not seem to be due to increased motivation and/or reduced neophobia at larger flock sizes (11, 12, 33, 34). Latency to contact the devices after the experimenter left the site was not associated with morning bird count but decreased over consecutive days at a location, suggesting an habituation process that was independent of flock size. However, we found evidence for an important ecological effect, both at the group and individual attempt levels: Problem-solving efficiency was lower at devices located further away from protective cover where perceived predation risk is generally higher (28, 29). A difference of even 3 m between feeders is likely to have a critical effect on predation risk because sparrowhawks attack prey at a velocity of up to 25 m·s<sup>-1</sup>, and they target the last individuals to escape (35, 36). In contrast, previous work on Carib grackles (*Quiscalus lugubris*) reported that experimental manipulation of perceived predation risk resulted in increased latencies at contacting a novel task during playback of conspecific alarm calls but did not have an impact on efficiency at solving the problem (37). Variation in ecological conditions is likely to have a strong impact on innovation rates but have received limited empirical attention (38); further studies that use novel foraging problems could help uncover evidence for ecological drivers of innovation in the wild.

Our results also support the idea that larger groups contain more individuals with relevant past experience, as well as other inherent characteristics contributing to solving the current problem (9). We found that larger flocks of tits were more likely to contain one experienced individual whose presence increased problem-solving efficiency, providing evidence for the pool of competence hypothesis. This effect was not observed when the individual had experience with a similar but simpler problem from captivity, suggesting low intraindividual correlation in problem-solving propensity in the captive versus wild context (30); this result underlines the importance of examining collective problem solving in a natural context. Problem-solving efficiency was still positively associated with group size when restricting attempts and solving to individuals without prior success in the field. This relationship showed no apparent decline in efficiency with increasing naive group size, suggesting that a larger pool of competence is a likely explanation for increased problem-solving efficiency in larger flocks of inexperienced birds.

Solvers differed consistently in the probability of success when attempting to solve, suggesting that problem-solving ability varies among individuals—a necessary condition for the pool of competence hypothesis. The advantages of diversity in group decision making have just begun to be investigated, with recent theoretical and empirical studies suggesting that collective diversity can sometimes trump individual ability (7, 15, 39). Individual consistency in problem-solving ability over a range of different tasks could be used to determine the extent to which skills at solving one problem are useful when encountering other novel problems (e.g., ref. 16, but see ref. 40). It is likely that a higher diversity of cognitive abilities, coping styles, or motor tendencies may have helped

groups of tits at solving the novel problem over and above effects from reduced predation risk, given that a quadratic term was not significant in modeling the relationship between solving and group size in naive individuals, which would have been a known characteristic of the group-size effect due to reduced predation risk (1, 22, 23). Larger flocks have also been suggested to equate with greater opportunities for social learning (9), thereby increasing the efficiency of individuals attempting to solve the problem (41, 42). However, previous work on this system did not find evidence for observational learning with the devices used here in the field (30) and is therefore unlikely to explain our results. Variation in group composition caused by changes in group size could potentially explain increased problem-solving efficiency in the wild; however, controlling for a significant predictor of flock size, mean wing length, did not change our conclusions. It is possible that other aspects of group composition change with flock size, and therefore experiments manipulating group size and various aspects of group composition independently would be a logical follow-up in investigating the impact of individual versus group-level processes on innovative output.

In conclusion, our study provides unique evidence for increased innovative efficiency with group size in the wild. Our results also show that ecological conditions and group size simultaneously influence innovative problem solving in a natural population, which has not been described previously. In humans, groups of problem solvers are often subject to "process losses"—that is, they perform below the optimal level of performance expected from the combination of members' abilities and knowledge (6, 43), such that groups of moderate size perform optimally (18). In contrast, flocks of great and blue tits in Wytham exhibited a positive relationship between group size and innovative efficiency, with no apparent decrease in performance in very large flocks. Moreover, individuals joining larger flocks benefited from larger intake rate at the devices, suggesting that group living in wild tits facilitates exploitation of a novel food source through reduced predation risk and a wider pool of competence. This finding contrasts with the general view that competition increases with group size, leading to decreased intake after an optimal group size (1, 19). More generally, these findings imply that social species from invasive or expanding populations—or those from captive-bred release programs—might benefit from forming large groups, which should allow them to exploit more efficiently resources requiring the use of novel foraging techniques. Increased innovative output might be a previously overlooked, general benefit of group living for both humans (44) and nonhuman animals (ref. 9 and this study).

## Materials and Methods

**Study Site and General Protocol.** The study took place in Wytham Woods (51° 46'N, 1°20'W), Oxfordshire, United Kingdom, from 2 February to 15 March 2010. Five locations containing an open area with dense cover nearby were chosen in different parts of Wytham so as to maximize the distances between the locations. To increase the proportion of marked individuals at these locations, we installed a multiaccess feeder filled with black husked sunflower seeds for 5–7 d before the experiment and caught birds using a mist net under ringing licenses from the British Trust for Ornithology (BTO). All unringed individuals were fitted with a unique BTO metal leg-ring, and great tits were also equipped with a plastic ring containing a unique PIT tag (Core RFID). We recorded age, sex, body mass, and wing length—a common measure for body size in passerines (45)—for all birds caught. Great tits were brought into captivity for 24–48 h in the context of another study using a similar foraging problem (17, 30). Two days after releasing great tits at their point of capture, we installed six lever-pulling devices and ran field observations for 5–7 d (no observations under rain or snow) before removing the devices and proceeding to the next location.

**Field Observations.** We used six automated lever-pulling devices (see [Movie S1](#)), each installed on a 1.5-m wooden pole planted in the ground. Each device was made from a transparent perspex tube and two levers supporting two trapdoors, the top one of which carried the food reward. Pulling the two levers sequentially, in any order, released 30 sunflower seeds into a re-

ceptacle where food was available for consumption. The timing of the removal of each lever was automatically recorded by a data logger. A PIT reader located in the perch, 2 cm away from the perspex lever-pulling device, recorded the timing and duration of visits by marked individuals.

We assumed birds visiting the feeder at similar times formed a functional group on the basis that they were likely to be in relative close proximity and therefore within audible range of one another's alarm calls. To test the assumption that our estimate of effective group size at feeders is representative of the overall flock size, we counted the number of birds using a regular multiple-perch feeder filled with sunflower seeds every morning before baiting the devices; we used the mean of three 2-min counts as "morning bird count." This regular feeder was then removed and replaced only at the end of the day before leaving the site. A trial started when the experimenter left the site after baiting each device with 30 sunflower seeds and ended when he or she returned 40 min later or the next morning to bait devices that had been solved, leaving others untouched. The relationship between group size and problem-solving efficiency was not affected by whether trials were run during the day or overnight ( $n = 137$  and  $25$ , respectively; interaction between trial type and group size in a model explaining proportion of devices solved; GLMM, Wald test;  $Z = 0.71$ ,  $P = 0.478$ ); we therefore pooled both types of trials for all analyses. We defined a problem-solving "attempt" as any visit to a closed device (i.e., with one or two levers to go before accessing food) and a "solving event" as any attempt leading to opening of the devices (i.e., to the food reward falling into the receptacle where it was available for consumption). We defined "total group size" as the number of different individuals detected at any solved or unsolved device during a trial, and "effective group size" was the number of different individuals detected at unsolved devices only (i.e., those exhibiting at least one problem-solving attempt, excluding those birds that only ever visited devices that had already been opened). We used effective group size unless otherwise mentioned to exclude birds visiting solved devices only and not contributing to the overall problem-solving effort. For analyses conducted at the level of attempts, we defined group size as the number of different individuals present 5 min before each attempt; we excluded all cases where an attempt occurred <5 min after the start of a trial. When calculating food intake, we assumed that the 30 seeds released in the re-

ceptacle at each solving event were depleted after 20 visits because birds could carry only 1 seed at a time and the mean proportion of PIT-tagged individuals using the devices was 0.704 (30).

**Statistical Analyses.** When examining the relationship between group size and problem-solving efficiency, we ran binomial GLMMs (with Laplace approximation; ref. 46), using as response variable the proportion of the six devices that were solved in a given trial and including group effort as a covariate (i.e., mean-centered total time spent at unsolved devices by all birds). We  $\log_{10}$ -transformed group size values before analysis to improve homoscedasticity of residuals. We included "day" nested within "location" as random intercepts to take into account that we conducted multiple trials per day and that trials conducted at a given location were probably affected by more similar conditions (weather, habitat, etc.) than those conducted at different locations (47). When examining the effect of distance from the devices relative to protective tree cover, we used "trial" as an additional random factor to account for pseudoreplication due to having two data points per trial in the dataset (one for devices 1 m from cover and one for devices 4 m from cover). When examining predictors of success at the level of problem-solving attempts, we used a binomial GLMM including a random intercept for location and individual to account for multiple attempts by each wild solver. When examining the relationship between total group size and mean number of seeds obtained per capita, we used LMMs on  $\log_{10}(y + 1)$ . The consistency of individual differences in behavior was assessed by comparing a model with versus without a random intercept for the individual term using a likelihood ratio test, after mean centering of covariates (48, 49). All analyses were conducted using R software (Version 2.9.1 for Mac; ref. 50).

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