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Solving problems increases provisioning efficiency, enhancing reproductive success in male great tits

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The ecological and selective processes acting on cognitive traits have received recent attention because of the potentially key role of cognition in rapid behavioural adjustments in response to environmental variation. Innovation, a cognitive process involved in the development of new behaviour, has been linked to fitness in several species but the proximate mechanisms explaining such links are still unknown. We investigated whether problem-solving performance, a proxy of innovation ability, predicts provisioning performance (provisioning rate, prey number, size and type) and used path analyses to explore whether problem-solving was related to reproductive success (number of nestlings, nestling survival) through provisioning performance in 107 female and 92 male great tits (*Parus major*). Solvers delivered prey at a higher rate and brought a higher estimated prey biomass to their nestlings than non-solvers. Path analyses confirmed this link in both sexes, and showed that, in turn, higher provisioning rate underlay higher reproductive success but only in males. Our study highlights the role of problem-solving performance in provisioning performance as a potential underlying mechanism linking innovation to reproductive success, and that this mechanism could be sex dependent. These results support the hypothesis of the adaptive value of problem-solving ability in the context of foraging ecology.

1. Introduction

Due to currently rapid environmental changes, wild animals frequently face unexpected situations that can rapidly be solved by adjusting behaviours [1,2], before longer-term adaptive evolution can take place [3]. Cognitive abilities, defined as the mechanisms through which animals perceive, learn and process information from the environment and subsequently act on it [4], are fundamental for individuals to grasp information and make optimal behavioural decisions allowing them to buffer against changing environments [5,6]. Comparative studies have shown that species with relatively bigger brains and/or specific brain areas, used as a proxy for enhanced cognition [7], are more habitat generalist [8] and tolerant to unpredictable climatic variability [9]. In addition, these species achieve population stabilization more easily and reach higher survival [5,10] as well as higher invasion/settlement

success in variable and/or new environments, including urban areas [11–13]. Although these findings support the hypothesis that enhanced cognition can facilitate individual behavioural responses enabling to cope with challenging conditions, empirical evidence for this process at the individual level remains limited and equivocal [14–17].

Innovation is a behavioural process by which an individual invents a new behaviour or modifies an existing behaviour to address a new situation [18]. By definition, innovation can thus play an important role in fast behavioural adjustments for innovative species. Indirect evidence in line with this comes from correlative studies that compared innovative performances in contrasted conditions where innovative individuals were expected to perform better than non-innovative ones, especially in challenging conditions such as urban areas [19] or harsh meteorological conditions [20]. Yet, studies investigating the link between innovative performance and proxies of fitness at the individual level provided contrasted results: some found a positive link between problem-solving and survival or reproductive success [14,21–24], while others found a negative link or no link at all [14,25]. These discrepancies can be partly explained by the difficulty in assessing cognitive performance in wild non-human animals, but also by the frequent lack of identification of the underlying mechanisms. Indeed, innovation results from both cognitive but also non-cognitive factors acting together in shaping this ability, and this may blur conclusions regarding the fitness consequences of cognitive performance.

Innovation has been proposed to enhance individual fitness by allowing new strategies to (i) better avoid already known or new predators or parasites and/or (ii) more easily find and secure and/or better exploit known or new resources [18]. In the context of foraging, a widely assumed hypothesis posits that individuals capable of integrating new foraging techniques in response to new conditions [6] may have a higher food intake, helping them in particular to meet more appropriately their offspring needs, and in turn enhancing reproductive success and/or survival [24,26,27]. The ability to innovate and integrate new foraging techniques may also correlate with higher general cognitive performance and, therefore, be positively related to other cognitive processes linked to breeding success, such as song learning in songbird species [28]. Yet, the direction or causality of such links remains to be unravelled.

In this study, we investigated whether higher provisioning performance could be the underlying mechanism explaining higher reproductive success for more innovative parents in a wild great tit *Parus major* population [21,26]. First, we explored whether individuals' innovation, measured by problem-solving performance, and provisioning abilities are linked. To do so, we monitored breeding pairs and video-recorded nestling provisioning behaviour within nest boxes, allowing us to measure provisioning both quantitatively (i.e. number and size of prey, estimated prey biomass and feeding rate for each parent) and qualitatively (i.e. type of prey). We subsequently measured parents' problem-solving performance using a device attached to the nest box during nestling rearing, that was previously successfully used in this population [21,26,29]. Second, we used path analyses to test whether problem-solving performance was positively related to reproductive success via higher provisioning performance (scenario 1), or whether the link between problem-solving performance and reproductive success was independent from provisioning (scenarios 2 and 3).

2. Material and methods

(a) Study site and population monitoring

The study was conducted in spring 2015 in a wild population of great tits monitored on the island of Gotland, Sweden (57°10' N, 18°20' E). Each year, 300 to 400 great tit pairs breed in one of the approximately 1800 artificial nest boxes distributed in our 15 to 18 study forest patches, facilitating the monitoring of breeding attempts. This species shows an outstanding record of behavioural innovations in the wild, demonstrating their high cognitive potential. Nest boxes were visited regularly from mid-April to mid-June to collect breeding data (i.e. clutch size, hatching date, number of fledglings). Nestling provisioning was measured at day 6 after hatching and problem-solving at days 7 and 8 (see details below). From day 10 after hatching, adults were trapped and ringed (if previously unringed) or identified (if previously ringed), sexed and aged (yearling versus older) [30]. Adults were therefore trapped after their provisioning and problem-solving behaviour had been measured in the field, which enabled us to avoid any impact of capture and/or handling on behavioural tests [31].

(b) Food provisioning parameters

When nestlings were 5 days old, we installed a miniaturized IR video recorder (CCD Bird Box Camera with IR night vision and wide-angle lens) under the lid of the nest box to let the birds habituate to the presence of the device. We ensured that the recorder inside the nest box pointed to the entrance hole to record images of the parents' head when entering the box. On the next day, we recorded food provisioning behaviour of both parents for 90 min between 06.00 and 11.00 using a digital recorder outside the nest box, connected to the video recorder inside.

Recordings were analysed using the software program MotionMeerkat [32] to detect movements around the entrance hole and extract the single frames when feeding occurred (figure 1). Using these frames, a single observer recorded for each visit: (i) time in and out, (ii) the sex of the parent, based on feather coloration (e.g. whether the black cap was shiny (males) or not (females)), the width of the black tie when observable, etc.), behavioural traits (e.g. female cleaning the nest, brooding the chicks, etc.), and the position of the metal ring when available [33–35], (iii) prey type, distinguishing three categories: caterpillar larvae, spiders and other [36,37], and (iv) the number and size of prey(s), measured on a scale of 1 to 4, with 1 for a prey shorter than the length of the beak, 2 for a prey of about the length of the beak, 3 for a prey approximately twice as long as the length of the beak and 4 for a prey approximately three times the length of the beak (figure 1) [38]. We restricted our observations to three

categories of prey because, for this population (and others), caterpillars and spiders are the most important prey types and other prey groups appear in very low frequencies (distributions can be found in electronic supplementary material, S1) [36,37]. For each parent, we then extracted the following descriptors of provisioning behaviour:

- feeding rate per hour, calculated as the total number of feeding visits made by the individual between the time it was first seen on the video recording until the end of the recording, converted into an hourly rate (e.g. [35,36]);
- mean number of prey brought per visit;
- mean size of prey brought per visit;
- estimated prey biomass delivered to the nestlings per hour, computed as the mean number of prey per visit $\times$ mean size of prey $\times$ feeding rate;
- percentage of caterpillar larvae (respectively spiders), computed as the number of caterpillar larvae (respectively spiders) over the total number of prey delivered to the nestlings per hour.

We excluded from the analyses recordings where doubts about the parents' sex remained after careful checking ($n = 3$ nests out of 117, thus 2.6% of nests).

(c) Problem-solving test and data extraction

On the day following the recording of provisioning behaviour, we started measuring parents' performance on a problem-solving task presented at the nest [21,29] (see also a [video](#) of the task from a previous study). The task featured a door placed temporarily over the nest box entrance hole. The door was closed by default, preventing entrance, and parents could only enter the nest box to feed nestlings by pulling a string hanging under the door, which led to opening it, using their leg and simultaneously sliding their body under the door. The door then closed after each parent's passage but the birds could easily push it from inside the nest box to exit (more details in [29]). This task simulates a natural obstacle that birds could remove by pulling on it with their legs predominantly, as opposed to the more classical use of their beak. The task was considered solved when the bird opened the door by pulling the string and entered the nest box to feed the nestlings. We have shown previously that problem-solving performance measured using this task is primarily explained by associative learning: solvers, but not non-solvers, increase their accuracy (i.e. make fewer errors) after the first cue to the solution, and solvers also improve their accuracy with successive attempts [29]. Moreover, although inter-individual variation in problem-solving performance is often partly attributed to non-cognitive traits such as neophobia or motivation, we found no such confounding effects in our previous studies (no effect of neophobia and solvers spent less time on the task than non-solvers [26,29]). In particular, we experimentally showed that parents raising larger broods were not more motivated to participate or solve this task [26].

The problem-solving test lasted 1 h between 07.00 and 16.00. Tests were launched only if the nestlings were satiated (i.e. not begging intensely at the beginning of the test) so that they would endure not being fed for 1 h should both parents be non-solvers. If the nestlings were begging intensely, we cancelled the test and tried again later. A second test was conducted the day after, allowing us to lengthen the total test duration (2 h in total) to let the parents enough time to explore the task and learn how to open the door, while limiting the time per day during which the nestlings potentially remained unfed. Pairs to be tested were selected randomly, ensuring that they were at least 200 m apart from any other previously tested pair to avoid potential social learning between pairs. Indeed, breeding great tit pairs are highly territorial during the breeding season, defending all-purpose territories of approximately 130 m in diameter [39]. Thus, testing pairs in nest boxes located sufficiently far apart should prevent social learning between pairs. Moreover, the probability to solve the task does not increase with the timing in the season [40], excluding the hypothesis that social learning occurs between pairs. Tests were recorded using a video recorder hidden under a camouflage net, placed in the vegetation approximately 6 to 10 m from the nest box, facing the entrance of the nest box.

Video recordings were analysed by observers blind to the hypotheses tested. Using the two 1 h tests merged as a single test, we measured problem-solving performance as whether or not the birds succeeded in pulling the string and entering the nest box at least up to their shoulders within the 2 h testing period (problem-solving status: 1 = solver, 0 = non-solver). Our previous studies using this task showed that, on average, 43% of the great tits tested are able to solve the task [29], that this ability is linked to several measures of reproductive success [21,26] and to sexually selected plumage signals in this species [26], demonstrating the biological relevance of this binary measure. Neophobia, i.e. the fear of novelty, is often assumed to affect problem-solving performance and blur its relationships with other traits. However, we have previously shown on a large sample (>800 great tits) that neophobia (measured as the time elapsed between the first contact with the nest box and the first contact with the task) did not affect problem-solving performance in our population [29]. Hence, we did not control for neophobia here.

(d) Statistical analyses

We first investigated whether measures of provisioning behaviour (response variables) were linked to problem-solving status (explanatory variable) using linear mixed models (LMMs). Besides problem-solving status, models also included as fixed factors a series of variables known to potentially affect provisioning behaviour: (i) the date of the provisioning recording (and its square value to take into account a potential quadratic effect of the timing of the season), (ii) brood size on the day of the test, (iii) age and sex of the individual tested, as well as all two-way interactions with problem-solving performance to test whether the relationships between problem-solving and provisioning performance could be context-dependent (e.g. only appeared at the end of the season when food becomes less abundant; only observed in large broods; only observed in young

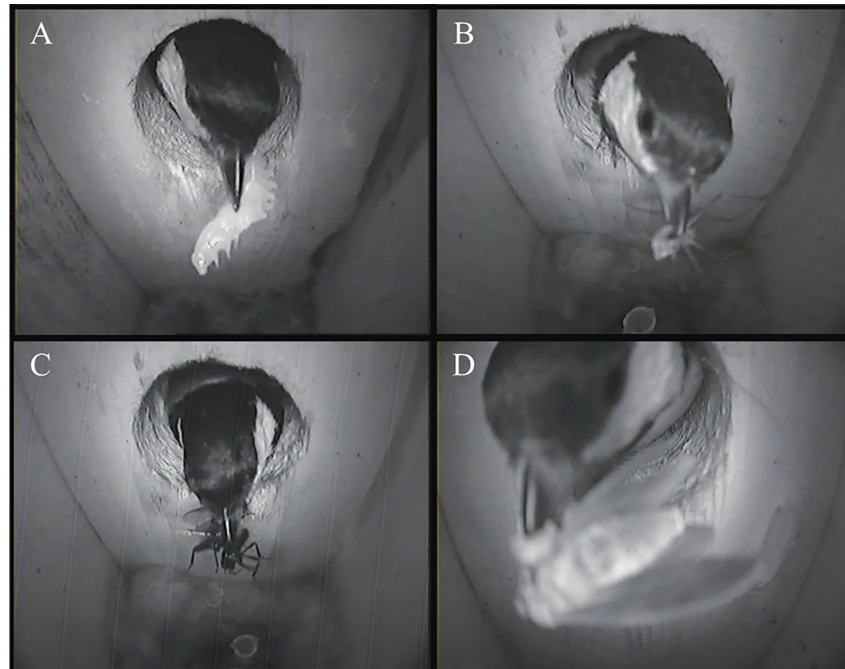


Figure 1. Examples of frames extracted from provisioning recordings in great tits. Prey were divided into three categories: caterpillar larvae (A), spiders (B), and other types of prey (C,D). Prey sizes were scored on this example as size 2 (about the length of beak length: B,C), size 3 (approx. twice as long as beak length: A) and size 4 (>approx. three times as long as beak length: D). Those examples of frames were extracted from entire sequence of movements from the moment a bird enters the nest box until it leaves.

and inexperienced birds; only observed for one sex). The time of the provisioning recording was initially included in the models but then removed as it did not influence any of the provisioning variables (results not detailed here). We added nest box identity and forest patch as random factors to account for the non-independence of pair members and for spatial variation in provisioning behaviour respectively. We ran six separate models for the six provisioning variables measured. In addition, we repeated the analyses restricting the data to the first solver only when both pair members were solvers ($n = 19$), to ensure that potential social learning within pairs did not bias our results (results detailed in electronic supplementary material, S2).

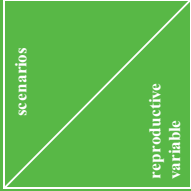
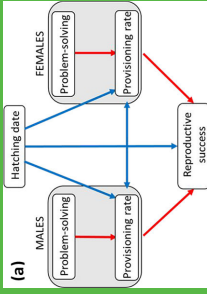
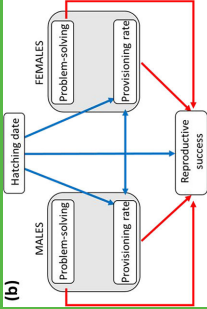
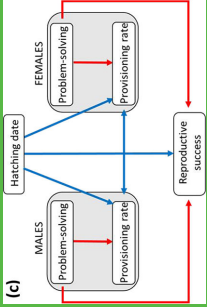
Second, we used path analyses to investigate whether the link between problem-solving performance and reproductive success goes through provisioning performance or through another mechanism, which could be a direct effect or via a different, unidentified variable [41]. Confirmatory path analyses use hypothetical causal relationships (i.e. structural equation models or SEMs) in which predictor and response variables are linked with different directional paths to test for directional links between variables of interest [42]. These relationships (or pathways) can be direct (i.e. a relationship non-mediated by any other variable in the model) or indirect (i.e. a relationship mediated via another variable in the model) and are translated into several linear equations to be individually tested. We designed three hypothetical path diagrams (table 1) to test whether:

- problem-solving performance is linked to reproductive success through provisioning;
- problem-solving performance is linked to reproductive success either directly or through another unknown variable, in the absence of link between problem-solving performance and provisioning;
- problem-solving performance is linked to reproductive success either directly or through another unknown variable, despite a link between problem-solving performance and provisioning.

We performed path analyses using feeding rate as the measure of provisioning performance because it showed the strongest link with problem-solving status among the six provisioning measures (see §3). In great tits, males and females can differ in their investment in the breeding attempt, including the provisioning effort [43,44]. We thus modelled sex-specific pathways to be able to estimate specific effects for each sex, while keeping the directional structure similar for both sexes in each of the three tested scenarios because we had no *a priori* reason to suspect different causal relationships between males and females. In addition, the timing of breeding in the season is known to affect provisioning behaviour and reproductive success [36], thus we added, in our pathway structure, links between hatching date and these variables to account for such effects. Finally, because provisioning by male and female within a pair might not be independent, we included a correlation between the male and the female provisioning variables in the model [44]. We repeated these analyses using two different proxies of reproductive success: (i) the number of fledged nestlings and (ii) nestling survival until fledging (i.e. the probability that each egg laid yielded a fledged nestling). We choose these variables because final fledging success has been shown to be the measure of reproductive success most strongly associated with problem-solving performance in this population [21,26]. We thus created six diagrams in total, one for each of the three hypothetical paths combined with each of the two measures of reproductive success. We used LMMs for analyses of feeding rate and generalized linear mixed models (GLMMs) for analyses of the number of fledged nestlings (with a Poisson distribution) and of nestling survival (with a binomial distribution). We then repeated the analyses using estimated prey biomass as the measure of provisioning performance as it was also linked to problem-solving status; results were qualitatively unchanged (detailed in electronic supplementary material, S3).

Table 1. Output of the confirmatory path analyses exploring the directional relationships between problem-solving status, provisioning rate and reproductive success in wild great tits. Boxes represent measured variables. One-headed arrows represent directional relationships among variables. Double-headed arrows represent simple hypothesized correlations. Blue arrows are tested in all scenarios, and red arrows vary between the hypotheses tested. Summary of Fisher's C , degrees of freedom (d.f.), p -value, number of free parameters (k) and AIC for the six path analyses corresponding to three different scenarios and two measures of reproductive success. The three scenarios tested are: (a) problem-solving performance is related to reproductive success via provisioning behaviour, (b) problem-solving performance is related to reproductive success either directly or through another unknown variable despite a link between problem-solving performance and provisioning behaviour, and (c) problem-solving performance is related to reproductive success either directly or through another unknown variable despite a link between problem-solving performance and provisioning behaviour. The best AIC scores (values lower than other scores by more than 2) are shown in bold. Statistics estimated for both models of scenario (b) are the same; this is expected given the causal structure of model (b) and the use of a d-sep method: in model (b) the fitness variable is directly linked to all other variables in the model and thus does not appear in the basis set of conditional independence used to calculate the Fisher's C . Consequently, the Fisher's C and associated statistics are independent from the fitness measure in this model.

scenarios	(a)					(b)					(c)				
	Fisher's C	d.f.	p	k	AIC	Fisher's C	d.f.	p	k	AIC	Fisher's C	d.f.	p	k	AIC
number of fledglings	3.95	8	0.86	17	20.95	16.52	8	0.03	17	33.52	18.21	12	0.11	15	33.21
nestling survival until fledging	10.25	8	0.25	17	27.25	16.52	8	0.03	17	33.52	18.37	12	0.10	15	33.37



All statistical analyses were conducted using R v.4.2.1 [45] and RStudio v.2022.07.2 [46]. Values for continuous factors were scaled to improve the interpretability of model estimates. Mean prey number, estimated prey biomass and percentage of spiders among prey were square root transformed as these variables were left-skewed. Residuals were visually checked to ensure that model assumptions were met. All tests were two-tailed. Non-significant effects were backward eliminated from the initial models and put back one by one to extract estimates (except for interactions). In the first part of the analyses (link between problem-solving performance and provisioning behaviour), sample size can vary between models because of missing data. In the second part of the analyses, we ran standard confirmatory path analysis using the d-sep method that allows the use of binomial dependent variables, mixed models and unbalanced dataset across variables [47]. For each of the two proxies of reproductive success, we compared the three SEMs to identify which one(s) fitted our data best using *p*-value (i.e. a non-significant *p*-value means that the observed and predicted patterns are not statistically different and the model fits the data) and Akaike's information criterion (i.e. a lower AIC score indicated a better fit to the data). To test for the robustness of our results, we repeated the path analyses using the R package *piecewiseSEM* [48]: this method is frequently used for path analyses, but has some limitations with regards to the response variable distribution and requires similar sample size for all variables; it thus excludes any observation presenting missing values. Reducing the dataset to observations with no missing values ($n = 82$ observations out of 112) nevertheless yielded qualitatively similar results (electronic supplementary material, S4).

3. Results

We obtained data for 199 individuals (107 females, 92 males) out of the 112 pairs of great tits recorded for both provisioning and problem-solving performance. A total of 90 birds solved the task (65 females, 25 males) while 109 failed to find the solution (42 females, 67 males) (i.e. solving success: 45.2% overall; females: 60.7%; males: 27.2%). Feeding rate varied from 1 to 49 visits per hour, with a mean ($\pm$ SE) of 15.4 ± 0.7 visits per hour. On average, birds brought 1.06 ± 0.01 prey per visit, with a mean prey size of 2.38 ± 0.03 . Estimated prey biomass ranged from 2.0 to 221.0 units, with a mean of 50.5 ± 2.4 units. Caterpillar larvae and spiders represented respectively $63.5 \pm 23.4\%$ and $6.4 \pm 9.2\%$ of the prey brought to nestlings.

(a) Effects of problem-solving performance on provisioning behaviour

Feeding rate was higher for solvers compared with non-solvers, even though this difference was modulated by brood size on the day of the problem-solving test (significant interaction problem-solving performance $\times$ brood size, table 2). *Post hoc* comparisons between solvers and non-solvers showed that among non-solvers, feeding rate increased with brood size (estimate = 2.99, SE = 0.84, $t = 3.57$, $p < 0.001$), whereas among solvers, feeding rate was independent from brood size (estimate = -1.34, SE = 1.02, $t = -1.32$, $p = 0.19$) (figure 2A,B). In addition, feeding rate was higher in males than females, increased with the date of the recording, and was higher for yearlings compared with older adults (table 2). Results remained unchanged when removing from the analysis the second solver of pairs where both parents were solvers (electronic supplementary material, S2). We then tested whether birds who provisioned at higher rates were more likely to solve the task because they spent more time at the nest box (i.e. thus had a longer exposure time to the task) and if this could have influenced the results. To do so, we repeated the analysis adding the latency to solve the task (i.e. time spent interacting with the task before the first solving, or during the whole test for non-solvers) as a fixed explanatory effect. The results were unchanged as the time spent interacting with the task was not related to feeding rate (estimate = 0.75, CI = -0.53 to 2.04, $p = 0.249$).

Estimated prey biomass brought by the parents to the nestlings was higher for solvers compared with non-solvers (table 2, figure 2C). In addition, it was higher in males than females, and increased with brood size and with the date of the recording (table 2).

Problem-solving status influenced neither mean prey size and mean prey number per visit, nor the percentage of caterpillar larvae or spiders among prey (table 2). Mean prey size per visit tended to differ between solvers and non-solvers depending on brood size (interaction between problem-solving status and brood size, table 2), but *post hoc* analyses revealed no significant difference between groups (all $p > 0.1$). Mean prey size was higher for older great tits than yearlings (table 2). Mean prey number per visit increased with brood size and was higher for older great tits than yearlings (table 2). Finally, the percentage of caterpillar larvae and spiders among prey varied only with the quadratic date of recording: the percentage of caterpillars was higher in the middle of the period while the percentage of spiders showed a reversed pattern (table 2).

(b) Relationships between problem-solving status, provisioning and reproductive success

Path analyses showed that for both reproductive success measures (i.e. number of fledged nestlings and nestling survival until fledging), scenario (a) fitted best the data compared with other scenarios (i.e. lower AIC values for scenario (a); table 1). Results remained unchanged when using estimated prey biomass instead of feeding rate for number of fledged nestlings, but for nestling survival until fledging, the link with problem-solving was direct and not through estimated prey biomass (scenario (c)) (electronic supplementary material, S3).

Thus, path analyses globally confirmed that problem-solving status is correlated to provisioning rate (only a tendency for males): as found with LMMs, solvers showed higher provisioning rate than non-solvers (figure 3). Moreover, provisioning rate was positively related to reproductive success in males (only a tendency for the number of fledged nestlings; figure 3), but not in females. In addition, the date of the feeding recording was positively related to both provisioning rate in females (but not in males) and reproductive success, and a positive correlation between both partners' provisioning rate was confirmed (figure 3).

Table 2. Outputs of mixed models testing the differences of provisioning behaviour parameters depending on problem-solving status in wild great tits. Effects of other individual and breeding factors are accounted for (see text). The effect of sex is expressed as males compared with females, and the effect of age as yearlings compared with older adults. Non-significant effects were backward eliminated from the initial models: blanks (—) refer to non-significant interactions removed from the final models and non-significant single effects were reintroduced one by one into the final model to report values. Significant fixed effects are shown in bold.

predictors	feeding rate per hour				mean size of preys per visit				mean number of preys per visit				estimated prey biomass per hour				% of larvae among preys				% of spiders among preys			
	est.	95% CI	p		est.	95% CI	p		est.	CI	p		est.	95% CI	p		est.	95% CI	p		est.	95% CI	p	
(intercept)	10.04	7.07 to 13.01	<0.001		2.45	2.35 to 2.55	<0.001		1.04	1.03 to 1.05	<0.001		6.87	6.32 to 7.41	<0.001		0.69	0.64 to 0.73	<0.001		0.13	0.09 to 0.18	<0.001	
date of feeding	1.98	0.59 to 3.38	0.006		0.02	−0.06 to 0.10	0.581		−0.00	−0.01 to 0.01	0.907		0.37	0.02 to 0.72	0.038		0.07	0.03 to 0.10	<0.001		−0.02	−0.05 to 0.01	0.165	
recording																								
brood size	2.99	1.30 to 4.67	0.001		−0.01	−0.10 to 0.08	0.752		0.01	0.00 to 0.02	0.006		0.45	0.11 to 0.79	0.010		0.01	−0.03 to 0.04	0.642		−0.02	−0.05 to 0.01	0.168	
sex (male)	4.71	2.25 to 7.17	<0.001		0.08	−0.03 to 0.19	0.164		0.00	−0.01 to 0.02	0.787		1.22	0.66 to 1.78	<0.001		−0.02	−0.07 to 0.04	0.526		0.04	−0.01 to 0.09	0.141	
age (yearling)	2.74	0.14 to 5.34	0.039		−0.15	−0.28 to −0.02	0.021		−0.02	−0.04 to −0.01	0.005		0.50	−0.19 to 1.19	0.154		−0.00	−0.07 to 0.07	0.982		0.04	−0.02 to 0.10	0.187	
problem-solving	4.39	1.75 to 7.03	0.001		0.01	−0.11 to 0.13	0.860		0.00	−0.01 to 0.02	0.657		1.29	0.64 to 1.94	<0.001		0.0	−0.04 to 0.08	0.571		0.03	−0.03 to 0.09	0.294	
status (PS)																								
(non-solver)																								
date of feeding	—	—	—		—	—	—		—	—	—		—	—	—		—	—	—		—	—	—	
recording × PS																								
brood size × PS	−4.01	−6.38 to −1.64	0.001		<i>0.17</i>	<i>−0.00 to 0.23</i>	<i>0.054</i>		—	—	—		—	—	—		—	—	—		—	—	—	
sex × PS	—	—	—		—	—	—		—	—	—		—	—	—		—	—	—		—	—	—	
age × PS	—	—	—		—	—	—		—	—	—		—	—	—		—	—	—		—	—	—	
date of feeding	—	—	—		—	—	—		—	—	—		—	—	—		−0.05	−0.09 to −0.02	0.003		0.04	0.01 to 0.07	0.008	
recording ²																								
random effects																								
σ^2		56.04				0.11				0.00				3.29				0.04				0.03		
τ_{00} nestbox		7.24				0.08				0.00				1.24				0.01				0.00		
τ_{00} area		8.09				0.00				0.00				0.23				0.00				0.00		
ICC		0.21				0.44				0.02				0.31				0.20				0.11		
N_{Area}		18				18				18				18				18				17		
N_{nestbox}		108				108				108				114				113				109		
observations		182				182				182				199				196				175		
mag R^2 (cond R^2)		0.17/0.35				0.05/0.47				0.09/NA				0.14/0.41				0.14/0.31				0.06/0.16		

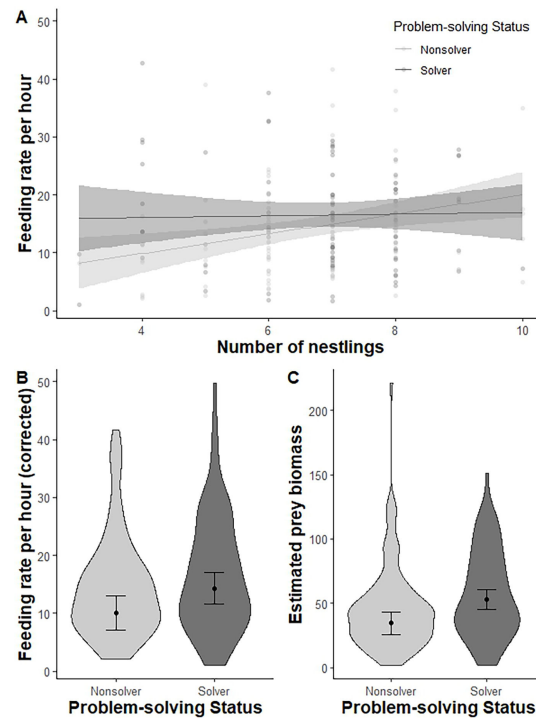


Figure 2. Differences between great tit solvers and non-solvers in provisioning behaviour parameters: (A) parental feeding rate per hour depending on the number of nestlings in the nest (predicted regression lines and 95% confident intervals; dots: raw data), (B) feeding rate per hour (after controlling for the number of nestlings in the nest), and (C) estimated prey biomass brought by parents to their nestlings (violin plots of the distribution of raw data together with predicted means and 95% confidence intervals).

Results remained qualitatively similar when excluding data with missing values (i.e. using R package *piecewiseSEM*; electronic supplementary material, S4).

4. Discussion

Identifying the mechanisms linking cognitive performances to fitness is crucial for understanding how selective pressures can shape the evolution of cognitive abilities in the wild. In this study, we examined the links between problem-solving performance, provisioning behaviour and reproductive success in a wild great tit population. Problem-solving as measured in this study was previously demonstrated to rely on inter-individual variation in associative learning, and thus to mirror inter-individual variation in cognitive performances [29]. Our results showed that solvers provisioned their nestlings at a higher rate, and consequently delivered higher prey biomass, than non-solvers. Path analyses also revealed that problem-solving performance was related to reproductive success via provisioning behaviour, but only in males. These results point to a role of cognitive performances in securing and/or exploiting high quality habitat yielding reproductive success, but call for investigating sex-related differences in this mechanism linking cognitive performance and reproductive success.

(a) Problem-solving performance positively relates to feeding rate

Our results showed that solving great tits outperformed non-solvers in terms of feeding rate (figure 2A,B). Among non-solvers, feeding rate increased with brood size, a result found in many previous studies in this species (e.g. [49,50]). This is usually explained by the balance between the costs and benefits of nestling provisioning: higher provisioning yields higher fledging success and fledgling body condition, thus higher future offspring survival, but also higher reproductive effort for parents. Yet, solvers showed a constant high feeding rate independent of brood size, corresponding to the maximal feeding rate of non-solvers (for broods of 8 or more nestlings; see figure 2A), suggesting that the reproductive effort associated with high provisioning is lower in solvers than non-solvers. This is in line with results from another great tit population, where working day length was shorter for solvers who also tended to use a smaller foraging range size than non-solvers [14], supporting the hypothesis that solvers are more efficient at exploiting their environment to find food, possibly yielding a lower cost of reproduction, than non-solvers. However, the latter study found no difference in provisioning variables between solvers and non-solvers even though solvers produced more fledglings too [14]. Problem-solving ability was also suggested to facilitate the exploitation of food resources in grey lemurs (*Microcebus murinus*), where solving efficiency was positively linked to the magnitude of change in adult body condition after the harsh dry season [27]. Solvers might be able to better process multiple and complex information from the environment, enabling them to make optimal decisions when foraging. Assessing how cognitive abilities allow individuals to process information on resources in general in natural environments (including the nature and use of information sources) is essential to better understand the costs and benefits of cognitive abilities (e.g. [51–55]).

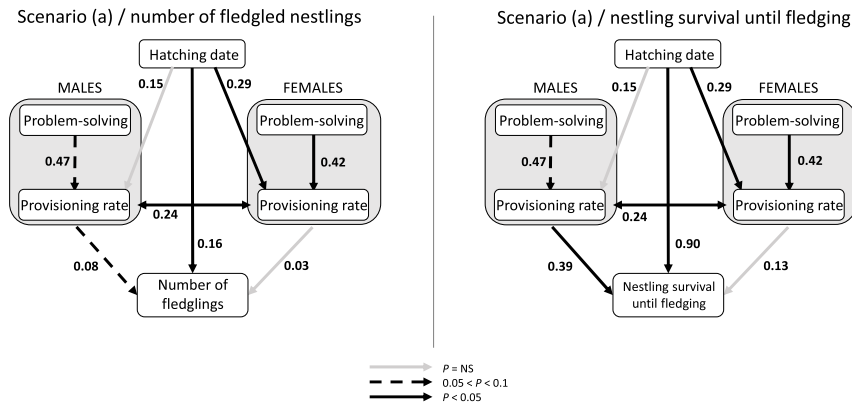


Figure 3. Structural equation models (SEMs) exploring directional relations between problem-solving status, provisioning rate and reproductive success in wild great tits. Boxes represent measured variables. Black arrows represent directional relationships among variables, with solid lines for significant relationships ($p < 0.05$), dashed lines for $0.05 < p < 0.10$, and grey lines for non-significant relationships ($p > 0.10$). Values on the arrows show the standardized path coefficients (i.e. the strength and direction of the effect).

Feeding rate also varied with sex, age and date in the season. Here, males provisioned nestlings more often than females, whereas no difference between sexes is usually reported in this species with biparental care [43,56]. However, we recorded feeding rates when nestlings were 6 days old and early in the morning when spring temperatures can be quite cold in northern Europe. Females were therefore still spending time brooding young that did not fully thermoregulate yet, with males providing a larger fraction of the food to the nestlings in the meantime [57], as reflected in our recordings that showed females frequently staying in the nest for up to several minutes after feeding nestlings, which was not observed in males. Importantly, this sex-biased feeding rate was conservative with respect to the higher feeding rate of solvers found here, because males showed a higher feeding rate but lower probability to solve the task. Feeding rate was also higher for yearlings compared to older parents, as found in another great tit population [56]. Since our results showed no difference between yearlings and older great tits in estimated prey biomass, a higher feeding rate by yearlings might possibly simply be a compensation of their lower prey number and size per visit. Older great tits might use previous experience to hunt on or select bigger or more nutritive prey [34], or they might choose to invest more in their current reproduction (terminal investment, for older age classes [58]). Alternatively, it is possible that yearling and older great tits varied in their preferred provisioning tactics according to environmental or individual factors: for instance, yearlings might prefer shorter but more frequent foraging trips to avoid competition on the boundaries of their territory [59]. Finally, feeding rate increased with date, most likely reflecting increasing prey availability over the recording window [36]. These factors did not, however, interact with problem-solving performance, suggesting no change in the provisioning cost and benefit balance of cognitive performance with sex, age or timing in the season.

(b) Problem-solving performance and other measures of provisioning behaviour

The increased speed in finding and bringing back prey was not traded against prey quality or quantity, since prey size and number per visit as well as the proportion of caterpillars and spiders were similar between solvers and non-solvers. As a result of higher feeding rate but similar prey size and number of prey per visit, estimated prey biomass, calculated by combining these provisioning metrics, was higher for solvers compared with non-solvers, even though we could not measure the exact prey biomass. Overall, these results indicate that solvers were not faster because they were less selective when choosing prey compared to non-solvers, although estimating prey size and availability on each territory would be necessary to conclude about variation in prey selection. The great tit is mostly a single-prey loader [36], as reflected by a mean prey number per visit close to 1 here, thus solvers may have preferred to ensure frequent feeding instead of selectively choosing larger or higher quality prey. In captive great tits, Serrano-Davies *et al.* [60] found no effect of problem-solving performance on food preference. Interestingly, the difference in estimated prey biomass between solvers and non-solvers was not modulated by brood size anymore, suggesting that overall, the costs of provisioning nestlings with high prey biomass are lower in solvers compared with non-solvers.

These results do not preclude differences in prey size, number or diversity depending on problem-solving ability in different conditions. Because the results observed in 2015 might diverge in another year if breeding conditions fluctuate, repeating this study over several breeding seasons would help to better understand how problem-solving is linked to provisioning and reproductive success with regards to environmental conditions. In addition, we measured provisioning at the very start of the provisioning peak during rearing, i.e. when nestlings were still relatively young (6 days old), and at this age, the variability of prey brought by parents may be constrained. Indeed, nestling size and physiological needs during the first week of life determine the size of prey they are able to swallow and the type of prey they need for their development [39,61]. Exploring variation in prey size and type, for instance using metabarcoding to measure prey diversity, along the developmental phase and according to spatial variation in prey availability, would be a promising perspective.

(c) Problem-solving performance is linked to reproductive success via provisioning behaviour in males

Path analyses confirmed that problem-solving performance was related not only to feeding rate in both sexes, but also to two proxies of reproductive success through feeding rate in males. These results not only confirm the findings from previous studies showing a link between problem-solving performance and reproductive success in our great tit population in different years [21,26] and in other populations [14,62], but also highlight a potential mechanism explaining this link. In males, the positive relationship observed between problem-solving performance and reproductive success via feeding rate can be explained by at least three mechanisms. First, solver males could have smaller foraging territories [14], decreasing the travel time away from the nest and increasing their ability to faster address nestlings' food demand but also nest defence [63], thereby ensuring a higher reproductive success [64,65]. A smaller territory is often associated with lower competitive ability, and the latter has been correlated with problem-solving ability [66]: less competitive males might indeed benefit from being more innovative to find food as a compensation. Independently from competitive ability, a small territory could also indicate that solver males are able to find enough food resources without the need for a large territory. Second, solver males could be better competitors during settlement, thus select and secure higher quality territories regardless of territory size: this would enable them to provision young more often and thus reach higher final reproductive success [24]. Finally, solver males might choose to reduce the nestling physiological costs associated with high begging behaviour [67] by provisioning their young more often, whatever the size or quality of their territory, which would lead again to higher reproductive success.

In our study, the path linking problem-solving and reproductive success through provisioning performance was only significant for males. This between-sex difference may simply be explained by the constraints on female provisioning rate, as discussed previously (the cold morning temperatures driving females into brooding instead of provisioning). Consequently, the female provisioning rate measured in our study may not have reflected their full foraging efficiency, limiting our ability to detect an association between female provisioning performance and reproductive success (i.e. a power issue; figure 3 shows that the relationships are similar for the two sexes, although less strong for females). However, it is also possible that selection may act differently on male and female parental care behaviour depending on cognitive performances. Interestingly, the same result was found in wild house sparrows (*Passer domesticus*), where fast solver parents showed higher provisioning rates compared to slow solvers, but only the solving ability of fathers was positively related to offspring survival [24]. In another species, the New Zealand robin (*Petroica longipes*), males with higher spatial learning performance delivered a larger proportion of large prey to the nestlings, fledged more chicks per clutch and tended to produce more offspring over the whole breeding season compared to males with poor spatial learning performance, while there was no difference between females [68]. In females, mate selection and/or early parental care (e.g. egg production, brooding) are important drivers of reproductive success and the corresponding variation in these factors, not accounted for here, could blur the relation between problem-solving performance and reproductive success through provisioning behaviour. Despite their power, path analyses remain correlative, and an experimental confirmation of the mechanism suggested here is needed. The origin of the difference observed here between sexes in the mechanisms underlying the link between problem-solving performance and reproductive success remains to be elucidated in future studies.

5. Conclusions

Our study supports the role of problem-solving performance in provisioning efficiency and indicates that this relation could underlie the link between problem-solving performance and fitness in the wild. It also highlights the possibility that cognition may play a different role in fitness in males and females. Since searching for food can be a complex and costly task with strong fitness consequences, multiple other cognitive abilities, in addition to innovation and associative learning, are likely to shape foraging efficiency, including inhibition (when relying on behavioural flexibility to access food), spatial learning [69] or memory (when choosing or remembering foraging places) [68]. Although our study and others (e.g. [14,23,25]) show that inter-individual variation in problem-solving performance can be related to variation in fitness, much remains to be done to demonstrate the evolutionary potential of problem-solving abilities in nature including assessing their heritability [70–72].

Ethics. Birds were caught, handled and ringed under a licence from the Stockholm Museum Ringing Centre (licence number 644:M03); breeding monitoring and behavioural tests were conducted under a licence from the Swedish Committee for Experiments on Animals for all experiments on the site (licence number C 108/7).

Data accessibility. The datasets and R codes are available in the Figshare repository [73]. A video of the problem-solving task is also available in this repository [74]. Electronic supplementary material is available online [75].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. L.C.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; J.G.A.M.: formal analysis, writing—review and editing; E.M.: data curation, formal analysis, writing—review and editing; P.B.: data curation, formal analysis, supervision, writing—review and editing; B.D.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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