Memory performance influences male reproductive success in the wild

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SUMMARY

Despite decades of comparative research, how selection shapes the evolution of cognitive traits remains poorly understood [1–3]. Several lines of evidence suggest that natural selection acts on spatial memory in food-caching species [3–6]. However, a link between reproductive fitness and spatial memory ability has yet to be demonstrated in any caching species [1,3,7]. Here we show that memory performance influences reproductive success differentially for males and females in a caching songbird, the New Zealand robin (*Petroica longipes*). Males' memory performance in a spatial task during winter influenced their subsequent breeding success; individuals with more accurate performance produced more fledglings and independent offspring per nesting attempt. Males with superior memory performance also provided an increased proportion of large prey items to chicks in the nest and spent less time flying while foraging and provisioning. No such effects were found for females. Previous research reveals that trade-offs may constrain selection and act to maintain variation in cognitive traits [8,9]. The gender dimorphism in the reproductive benefits of robin memory performance suggests an additional role for divergent selection between the sexes in constraining runaway selection on male memory ability [10], ultimately maintaining variation in this cognitive trait.

KEYWORDS

spatial memory; food caching; cognitive evolution; reproductive success; evolutionary ecology

RESULTS AND DISCUSSION

Individual variation in cognitive performance is well documented across the animal kingdom [11], yet the ecological and evolutionary significance of cognitive variation is poorly understood [2,3]. Understanding the evolutionary ecology of cognitive traits requires examining whether and how selection acts on cognitive traits in the wild [1]. Pioneering studies of the fitness consequences of cognition have primarily examined the link between reproductive success and problem solving performance [8,12–14] or the 'general' cognitive performance captured by cognitive test batteries [15–17] (but see [18]). However, making clear predictions about how these broad measures of cognitive performance (which will presumably underpin a suite of behaviours) should influence fitness remains challenging [17,19]. To further our understanding of cognitive evolution, we must therefore target specific cognitive traits [19] underpinning behaviours directly linked to survival and reproduction in the wild [2,3].

Food caching is a well-established study system for investigating the evolution of spatial memory [20], making caching species excellent candidates for studying the evolutionary ecology of a specific cognitive trait [1,3]. There is intraspecific evidence that spatial memory and its neural correlates can undergo fine scale selection in response to environmental variation. For example, food storing chickadees (*Poecile* sp.) from harsher, more unpredictable, high altitude environments possess neurological adaptations and more accurate memory for cache locations compared to conspecifics from lower altitudes [5,7,21–23]. To date, however, the fitness consequences of intraspecific variation in spatial memory have not been examined in any caching species [1,3,7].

In the current study we investigate how memory performance in a spatial task influences reproductive success in a caching songbird, New Zealand's North Island robin (*Petroica longipes*; hereafter referred to by their Māori name, toutouwai). The toutouwai is a socially and genetically monogamous [24] forest dwelling species. Toutouwai regularly consume some of the largest invertebrates on earth [25] and will cache year round, with a peak in intensity in winter, particularly for males [26]. These bold and curious birds are highly territorial; traits that make wild, free living individuals amenable to cognitive testing across a range of domains [27–29], as well as easily monitored during the breeding season [30]. During the austral winter (June 2016) we measured individuals' (N_{male} = 36, N_{female} = 27) performance in an associative-learning task where a spatial cue signalled the presence of a reward [31]. We hid a mealworm inside one of eight compartments in a circular apparatus (Figure 1 A). Each toutouwai was tested once in the experiment: we gave the apparatus to a bird several times in a single day, always at the same location within their territory, with the reward concealed in the same compartment, such that it was in a consistent location relative to territory landmarks across all trials (Figure 1A). Toutouwai cache their invertebrate prey over short time intervals [25,32], we therefore used an ecologically relevant delay interval of one hour between trials in our spatial memory experiment (the experiment consisted of an initial probe and consolidation trial, followed by four separate test trials, ending with a control trial).

Spatially based associative-learning tasks can provide a measure of spatial memory performance [31]; individuals who remember the correct location and quickly form an association between the spatial cues and reward will open the fewest lids during test trials. Toutouwai learned the specific location of the food reward, as they opened fewer compartment lids to retrieve it over the course of the trials (Figure 1B; GLMM trial coefficient estimate, CE = -0.064, 95% confidence interval, CI = -0.103 to -0.026; also see Table S1). There was moderate individual consistency in memory

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performance over time, as there was repeatability in the number of lids that an individual opened across their test trials (when statistically controlling for the influence of trial sequence [33], $R_{adjusted}$ ± SE = 0.199 ± 0.062, P = 0.0001, 95% CI = 0.046 to 0.295). This moderate repeatability estimate for toutouwai memory performance is consistent with repeatability estimates for cognitive performance in a range of non-human species [34]. To examine the link between reproductive success and spatial memory we quantified individual memory performance as the total number of lids opened during the four test trials (following the methods of [35,36]). We investigated whether this memory performance measure was influenced by possible confounds; there was no effect of age, body condition or sex on individual memory performance (GLM: body condition CE = 1.345, 95% CI = -0.671 to 3.397; Cohort CE = 0.032, 95% CI = -0.016 to 0.082; Sex CE = -0.041, 95% CI = -0.240 to 0.161).

To examine whether memory performance influenced an individual's subsequent reproductive success we monitored all test subjects that remained in the study area during the following breeding season (September 2016 – March 2017; N_{males} = 31, $N_{females}$ = 18) and used a multi-model averaging approach [37], controlling for life history traits. Table 1 provides the factors that were included in these models; we ran all possible models based on combinations of these predictors and calculated estimates for model parameters by averaging across models (as none of the top candidate models were clearly the best fit, i.e. AICw ≥ 0.9, see Table S2) [37,38]. Individual memory performance did not affect the reproductive success of either sex in the earlier stages of nesting (i.e. season start date, the number of clutches laid and hatching success; see Table S3). However, spatial memory performance influenced male, but not female reproductive success during the later stages of each breeding attempt (Figures 2A-D; Table S3). Compared to males with poor spatial task performance, males with superior memory performance fledged more chicks per clutch (N_{nests} = 54; mean $\beta \pm$ SE = -0.075 ± 0.035, 95% CI = -0.146 to -0.003; Figure 2A) and produced more independent offspring per clutch (i.e. independently foraging and beginning to disperse [39]; N_{nests} = 54; mean $\beta \pm$ SE = -0.071 ± 0.032, 95% CI = -0.135 to -0.006; Figure 2C), but only tended to produce more independent offspring over the whole season (N_{males} = 31; mean $\beta \pm$ SE = -0.052 ± 0.30, 95% CI = -0.113 to 0.010). While our analyses controlled for several potential determinants of toutouwai reproductive success (see Table 1), without experimental manipulation we cannot completely exclude the possiblity that memory performance covaried with unexamined ecological or life history factors [8]. Nonetheless, this evidence that memory performance in a spatial context is associated with reproductive success in the wild supports the prediction that spatial memory is likely to be under directional selection in food-caching species [2].

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Cognition is only visible to selection via ecologically relevant behavioural variation [3]. In a toutouwai pair the female builds the nest, incubates eggs and broods chicks, while the male assists in provisioning her until the chicks have hatched, at which point both sexes provision the young [39]. The brood is divided post fledging, with males often caring for more young than females and frequently caring for fledglings for longer periods of time [39]. Thus male provisioning behaviour is likely to make a larger contribution to the overall success of the later stages of each breeding attempt (i.e. from post-hatching through to fledgling independence). We observed a pair's foraging and provisioning behaviour when chicks in the nest were 15-16 days old, fully feathered and no longer reliant on brooding by the female. We estimated the total mass of food delivered to each chick per hour (see methods for details). The total mass fed to chicks increased as parents spent more time foraging (Table S4) and was lower for females with superior memory performance (mean β ± SE = 0.015 ± 0.006, 95% CI = 0.001 to 0.030). By contrast, there was no effect of male memory performance on the total mass of food delivered to chicks (Table S4). However, memory performance influenced a male's provisioning strategy. Males with superior memory performance delivered a larger proportion of large prey to the nest (Figure 3A; mean β ± SE = -0.120 ± 0.041, 95% CI = -0.207 to -0.033) and increasing food delivery size was associated with a lower provisioning rate (i.e. the number of provisioning trips made per minute spent foraging; mean β ± SE = -8.915 ± 3.565, 95% CI = -16.456 to -1.373). In sparrow chicks (*Passer domesticus*) the provisioning rate of only the largest food items, rather than the overall food delivery rate, is associated with increased fledging mass and future recruitment [40]. Thus although male toutouwai memory performance did not influence the overall provisioning rate, if toutouwai chick growth rates are similarly dependent on the provisioning of larger prey items [40], selection may act on male memory via provisioning behaviour during the breeding season, by favouring those males that are better able to provision larger prey to offspring.

We suggest it is likely that our memory task provides a measure of an individual's ability to accurately form associations between food rewards and spatial cues and/or landmarks. In the context of provisioning, this type of recall may allow birds to efficiently locate, process and deliver large prey to chicks on the nest. Some of the large invertebrate species in the toutouwai's diet have a clumped diurnal spatial distribution (e.g. Wellington tree wētā, *Hemideina crassidens* [41]). Moreover, due to their size such prey must be broken into smaller pieces before they can be consumed [42]. This activity is usually carried out in a secluded, ground-level location on the territory, with pieces then carried to the nest in multiple trips [42,43]. In the context of provisioning, accurate memory for spatial or landmark cues may therefore increase

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efficiency of movement between the nest and high value food patches. In the context of caching, toutouwai also dismember large prey in the same manner, before moving pieces to individual cache sites in the canopy [25,42]. Experimental evidence from caching corvid and parid species suggests that accurate cache retrieval is underpinned by associations formed between food caches and spatial cues or landmarks [44–47]. The use of landmarks and spatial cues during cache retrieval has yet to be investigated in toutouwai; however, our behavioural observations do provide some putative evidence that male memory performance influences provisioning efficiency. Males with superior memory performance spent less time flying per hour (Figure 3B; mean β ± SE = -0.102 ± 0.027, 95% CI = -0.159 to -0.045), while this was not the case for females (Table S4). For males, flight time was also negatively associated with the proportion of large prey delivered to the nest (mean β ± SE = -1.692 ± 0.671, 95% CI = -3.131 to -0.253), but not with overall provisioning rate (see Table S4). These links cannot be attributed to a correlation between territory quality and memory performance, as we found no associations between memory performance and foraging rates (Table S4) or breeding territory size (median size = 3640 m^2, range = 1300 – 8340 m^2; correlation for males: R_s = 0.05, N = 32, P = 0.78; correlation for females R_s = -0.28, N = 19, P = 0.24). Instead, these patterns suggest that males with better memory performance are expending less energy to provision offspring, both by delivering larger prey to the nest and by reducing costly movements within their territory. To further investigate how selection may act on memory performance in the context of both provisioning and caching, future research should aim to test the links between toutouwai memory performance, natural prey search and processing efficiency and the spatial cues used by toutouwai during cache retrieval.

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Males and females did not differ in their performance in our spatially based associative-learning task, yet individual variation in cognitive performance influenced provisioning behaviour and reproductive success differentially for each sex in our study population. This difference may arise both because female toutouwai typically contribute less to the overall provisioning of offspring (see above discussion) and because they are less reliant on their own caches of food at all times of the year, particularly when they must compete for food with their more dominant mates [48]. When the sexes have different selective optima for shared phenotypic traits, divergent selection may act to maintain variation within a population [10,49,50]. Our results raise the possibility that male and female toutouwai differ in terms of their selective optimum for memory performance. Ultimately, this difference may constrain runaway selection on male memory ability and contribute to the maintenance of interindividual variation in spatial memory within the toutouwai population [50]. In addition, as there was only a tendency for males with more accurate memory performance to produce more independent young across the whole season, it also remains possible that undetected costs or life history trade-offs constrain selection on male memory ability in this population [8]. Our data represents selective processes shaping cognitive variation within a single season for this relatively long-lived passerine. Nonetheless, it points towards mechanisms that may maintain individual variation in spatial memory in food-caching species.

SUPPLEMENTAL INFORMATION

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Supplemental Information includes 4 tables and the three datasets supporting this study.

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AUTHOR CONTRIBUTIONS

R.C.S., N.S.C. and K.C.B. conceived the study. R.C.S. designed the spatial task methodology, collected cognitive performance and breeding season data, carried out analyses and wrote the manuscript. R.D.M collected behavioural observation and breeding season data. All authors discussed the results and commented on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Figure 1. The experimental set-up (A) and the number of lids opened by toutouwai during the memory test (B). The dashed line in (B) represents the number of lids opened to find the reward if birds search at random, calculated following [51]. By the second test trial (2 h after the probe and consolidation trials) the birds' search efficiency was better than the random expectation and remained so until the end of the experiment (see Table S1). Error bars give the 95% confidence interval, adjusted for within subjects repeated measures.

Figure 2. The association between memory test performance and the number of fledglings and independent young produced per nest. The mean memory performance (measured as the number of lids opened during test trials) associated with each level of nest success is shown for males in blue (A, C) and females in red (B, D). A smaller value (on the right of each x-axis) represents a more accurate performance in the memory test (i.e. fewer lids opened to retrieve mealworms during the experiment). Error bars give the standard error. The number of nests associated with each mean is shown above each point. As very few nests had 3 fledglings/independent young, these nests are grouped together with nests that had 2 fledglings/independent young. See Tables S2 and S3 for full multi-model averaging results for both males and females.

Figure 3. The relationships between male memory performance and provisioning behaviour. Males with superior memory performance fed their chick(s) a larger proportion of food that was equivalent to or larger than a mealworm in size (i.e. ~1.5 cm in length and 0.1 g in weight; A). The amount of time males spent flying per hour also decreased for males with superior spatial memory performance (B). See Table S4 for full multi-model average results for the behavioural observations of both males and females.

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Table S1. Comparison of actual search efficiency with the random search expectation. Related to Figure 1.

Table S2. The top models for each measure of reproductive success. Related to Figure 2.

Table S3. Multi-model average for the models of reproductive success. Related to Figure 2.

Table S4. The multi-model average for the models of foraging and provisioning behaviour. Related to Figure 3.

Table 1. The factors included in models of our measures of reproductive success in the 2016 – 2017 breeding season. Bird ID was specified as a random factor in all GLMMs where the response was at the level of the nest (these models were also weighted by clutch size). Models were run separately for males and females, as the sample size was insufficient to analyse at the level of pairs.

Response	Variables included in the full model
Start date for the season* *Quasipoisson GLM*	parent cohort, paired last season, memory performance
Total clutches produced in season *Poisson GLM*	parent cohort, start date, parent survived entire season (Y/N), nest predation in season ('1' if at least one nest predation, '0' for no confirmed nest predation), memory performance
Chicks hatched per nest *Poisson GLMM*	parent cohort, start date, parent survived nesting† ('1' if survived until fledgling independence, '0' if not), sequence of the clutch within the season (e.g. 1, 2, 3; hereafter 'clutch number'), memory performance
Total fledglings per nest *Poisson GLMM*	parent cohort, start date, parent survived nesting†, clutch number, memory performance
Independent young per nest *Poisson GLMM*	parent cohort, start date, parent survived nesting†, clutch number, memory performance
Total independent young per season *Poisson GLM*	parent cohort, start date, parent survived entire season, nest predation in season, memory performance

* We only examined individuals that started the season together (i.e. we excluded pairs where the partner had already attempted to breed with another mate).

† Only included in the full models for males, as all females survived all nesting attempts in the 2016/2017 breeding season.

STAR+METHODS

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Rachael Shaw (rachael.shaw@vuw.ac.nz).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The North Island robin (*Petroica longipes*; here we use their Māori name, toutouwai) study population is located within a 25 hectare area at Zealandia Wildlife Sanctuary in Wellington, New Zealand (the site is described in more detail elsewhere [27]). Since 2014 all birds holding territories or hatched within the study site have been banded with a unique combination of three leg band colours for individual identification. We have monitored resident adult birds at our study site since 2014. In the 2016/2017 season the median age of breeding birds was 3 years, with a range of 1-10 years (N_{males} = 40, $N_{females}$ = 32). Toutouwai may successfully nest up to three times per season, with the first clutch typically containing 2 eggs and later clutches 2 – 3 eggs [30,39]. Chicks fledge at around 21 days old and both parents provision offspring from hatching through to independence (defined as juveniles surviving until at least 4.5 weeks post-fledge, which is when young independently forage and may begin dispersing [39]). This research was approved by Victoria University of Wellington's Animal Ethics Committee and carried out under permit from New Zealand's Department of Conservation (Authorisation number: 38497-FAU).

METHOD DETAILS

Memory test

In the winter (6th June 2016 – 29th June 2016) we gave a memory test to 63 (N_{male} = 36, N_{female} = 27) toutouwai. The test apparatus was a grey plastic ring (outer diameter = 40 cm, inner diameter = 30 cm, height = 1.5 cm) with eight wells (width = 1.5. cm, depth = 1 cm) evenly spaced around the circumference. Each well was covered with a white plastic lid that was held in place with a screw and could be swivelled open (Figure 1A). All individuals had previously learned how to open these lids [28]. We chose a test location on a bird's winter territory that was at least 5 m from the nearest neighbour (territory boundaries were identified by observing boundary displays between neighbours). Trials were only conducted when no conspecific intruders were present (including mates, as toutouwai pairs typically maintain separate territories in winter [52]). The apparatus was placed on a cleared, flat area that was ca. 10cm from a single tree (minimum diameter of 6 cm). The tree was used as a landmark to ensure that the orientation and location of the apparatus, as well as the position of the mealworm reward, were consistent across all trials. In every trial the eight well lids were fully closed. The location of the mealworm (relative to the landmark tree) was randomised between birds, but was consistent across all trials for each individual.

We conducted trials between 8:30 and 14:30. We began with a probe trial in which we allowed a bird to open all lids to search for the mealworm. At the start of the probe trial we placed a single mealworm on the forest floor in the centre of the apparatus (to ensure that every bird would begin a trial from the centre). After a bird took this mealworm we gave it 6 min to open all lids. If the bird did not open all lids within 6 min, we opened the remaining closed lids slightly (1 mm) and gave the bird an additional 3 min to open these lids, before removing the apparatus. All birds completed the probe trial. We began a consolidation trial 2 min after the probe trial had ended. At the start of the consolidation trial we threw a small (< 2cm) stick into the centre of the apparatus; toutouwai typically followed the stick and thus began the trial in the centre of the apparatus. We gave birds up to 3 min to find the mealworm. The apparatus was removed once the toutouwai had retrieved the mealworm. Following the consolidation trial, we gave a bird five more trials that day, with trials spaced 1 h apart. Each trial followed the same procedures as the consolidation trial. The final trial (5 h after the consolidation trial) served as a control. In this trial no mealworm was present in the apparatus to control for the possibility that birds relied on non-spatial cues (e.g. olfactory cues, or subtle visual cues indicating the presence of the mealworm) to locate the hidden mealworm. To check motivation and weight, all toutouwai hopped on electronic scales to retrieve a mealworm before the first probe trial and after the final control trial. All birds took both worms.

Breeding season monitoring and foraging observations

We monitored the breeding success of resident pairs at our study site following established protocols [30]. In the 2016/2017 breeding season we monitored 32 of the males and 19 of the females that had participated in the memory test. One pair never nested and so could not be included in analyses. Four male and eight female subjects disappeared prior to the breeding season (and were assumed to have either died or dispersed). Females that remained in the study area during the breeding season did not differ in terms of memory performance compared to those that either died or dispersed prior to breeding (Mann-Whitney U test: $N_{stayed} = 19$; $N_{dispersed} = 8$, $W = 96.5$, $P = 0.29$). We also mapped pairs' territories by using a Garmin® GPSMAP 62c to mark boundaries. Boundaries were found by observing territorial disputes, noting individuals' refusal to approach and take mealworms from the ground, or by the presence of geographic boundaries (large bodies of water or open spaces). We recorded at least eight GPS points on the territory boundary for each pair. ArcMap® was used to create territory polygons from these points and obtain area estimates.

In the 2016/2017 breeding season we conducted behavioural observations for 25 pairs when they were caring for the first clutch of the season with chick(s) that survived to 15 – 16 days post hatching. This observation timing was chosen to ensure that chicks were capable of thermoregulation, so that females were not overly constrained in terms of the time they could spend away from the nest, and that the breeding stage and testing conditions were as comparable as possible across pairs. Within these pairs, 18 males and 14 females had participated in the spatial memory experiment. Observations occurred on days with wind speed <40kph and without heavy rain and were preceded by 15 min habituation time after the observer (R.D.M.) arrived on the territory. Each parent was observed for 1 h; the order (male or female first) was determined by a coin toss. The first observation began by 0830 and the second by 1000. The observer was positioned with a view of the nest and as much of the territory as possible and minimised their movement during the observation. If a bird moved out of visual range it was followed only to the point that the nest still remained in view. All prey acquisition and food sharing events were recorded. Prey size was recorded as smaller, equivalent to, or larger than a mealworm (which are typically ca. 1.5 cm in length and 0.1 g in weight). We used these size categories to estimate the mass of food delivered to each chick during the observation. We estimated that provisioning bouts equivalent in size to a mealworm provided 0.1g of food; sharing bouts that were larger were conservatively estimated to contain 0.15 g of food, and smaller bouts 0.05 g of food. We divided the summed mass of all sharing bouts by the number of chicks in the nest to estimate the total prey mass delivered to each chick per hour. The observer had extensive prior experience monitoring and feeding mealworms to robins but was naïve to individual's memory performance scores. Data were scored in the field using the app ATracker Pro®.

QUANTIFICATION AND STATISTICAL ANALYSIS

All analyses were conducted in R (v. 3.1.1). We first investigated the birds' performance as a group in the spatial memory experiment. We calculated search efficiency as the number of lids an individual opened to find the mealworm (e.g. if a bird found the food under the third lid it opened, its search efficiency was 3 for that trial). To examine whether search efficiency improved over the spatial memory trials (excluding the consolidation and control trials), we ran a generalized linear mixed model (GLMM, using the *lme4* package in R) with a Poisson error structure and log link, including trial number as a fixed factor and individual as a random factor. We also compared the birds' actual search efficiency to a 'sampling without replacement' random search strategy (i.e. once a lid was open, a bird could not re-open it; calculated using equation 8 in [51]). We used a two-tailed, one-sample Wilcoxon sign ranks test to evaluate whether the actual search efficiency was better than the random search expectation in each trial (reported in Table S1). In addition, we examined whether an individual's performance was repeatable across the four test trials (i.e., trials on hours 1-4, excluding the initial probe, consolidation and control trial). We used the package 'rptR' to implement a mixed-effect model approach with a poisson error structure to estimate the repeatability, adjusted for trial order [33]. Finally, we tested whether non-cognitive factors affected birds' spatial memory performance. Following previous studies of avian spatial learning [35,36], performance was the summed search efficiency, measured as lids opened to find the food reward, of the test trials (i.e. trials on hours 1-4). We used a Generalised Linear Model (GLM) with a Quasipoisson error distribution (as a Poisson error structure with a logarithmic link yielded overdispersion) to examine whether performance was affected by body condition (calculated as body mass divided by tarsus length [28]), sex and banding cohort (used as a proxy for age, as not all individuals were of known age). We calculated an individual's average body mass from each reliable scale reading. We used profile likelihood to calculate the 95% confidence intervals (CI) for the fixed factors included in these models.

For the reproductive success measures we examined 'start date', which was defined as the date that incubation began for a pair (the first pair to breed in the study population had a start date of 0, the start date for subsequent pairs was the number of calendar days that had elapsed relative to this baseline, i.e. a pair that began incubation two weeks later had a start date of '14'), the total number of clutches produced in a season, the number of eggs hatched per clutch, the number of chicks fledged per nest, the number of independent young produced per nest and the total independent young produced in a season. We used a multi-model inference approach [37] to assess the relationship between winter memory performance in 2016 and subsequent reproductive success in the 2016/2017 breeding season, while controlling for other life history variables. We modelled the factors influencing our reproductive success measures using GLMs and GLMMs with a Poisson distribution and log link (with the exception of 'start date', which was overdispersed and thus modelled with a Quasipoisson distribution, see Table 1). For each response variable we ran all possible combinations of the predictors outlined in Table 1. For each model in the resulting set we calculated the Akaike information criterion corrected for small samples sizes AICc (for Poisson models), or quasi-AICc (QAICc, for Quasipoisson models), as well as the change in AIC relative to the best model in a set (ΔAICc/ ΔQAICc) and the Akiake weight (AICw), which gives the conditional probability of the model [37,38]. In Table S3 we report these measures. We obtained averages of model parameters by averaging across the full model set (as is recommended best practice [38]). We used profile likelihood to calculate the 95% CI for the averaged predictor variables. The average models for each reproductive measure are reported in Table S4. For all our analyses we examined the sexes separately, as sample sizes were insufficient to analyse at the level of pairs. We also tested the correlation between 2016/2017 breeding territory size (measured in m^2) and memory performance using Spearman rank correlations.

Finally, we examined parental foraging and provisioning behaviour. We used a multi-model inference approach (as described above) to investigate the factors affecting four measures of foraging and provisioning behaviour: foraging rate (items acquired per minute spent foraging), provisioning quantity (estimated mass of food delivered to a chick per hour), the proportion of large items shared (the proportion of sharing bouts in which the items shared were equivalent to or larger than a mealworm) and the amount of time spent flying during the observation. We used linear models (LM) to examine the influence of spatial memory performance and the number of chicks in the nest on the foraging rate (log transformed). We used LMs to examine the influence of foraging duration (min spent foraging in the hour), memory performance, the amount eaten by the parent and the flying duration on provisioning quantity. We examined the proportion of large items shared using a binomial GLM, with the number of mealworm sized or larger items out of the total items shared as the response, and memory performance, the number of chicks in the nest and the provisioning rate (no. of sharing trips made per min spent foraging) as predictors. Finally, we used a LM to examine how memory performance, provisioning rate and the proportion of large items shared influenced flying duration. We ran separate models for the two sexes and used profile likelihood (LM) and bootstrapping (binomial GLM) to calculate 95% CI for the averaged model

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parameters. The model averaging results for these models and their parameters are reported in Table S4.

Data availability. The data that support the findings of this study are included as supplementary datasets 1-3.