The Complexities of Caching: A Review of the Cognitive Mechanisms Underlying Foraging Behaviour in New Zealand Robins

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Recent research has suggested that New Zealand robins (Petroica longipes) possess proto-arithmetic abilities and the ability to numerically track the contents of cache sites through an observational spatial memory system. Novel findings shed light on an area of animal cognition not well studied in avian species apart from corvids. These cognitive mechanisms function to enhance foraging success through optimizing the formation and pilferage of cache sites. The differentiation of caching and pilfering strategies between males and females is hypothesized to result from high intersexual competition. These sex-based differences in foraging are suggested to have arisen from the typical dominance structure in the species and the ongoing seasonal changes in pair dynamics. Reciprocal pilferage and high intersexual competition are proposed as potential phylogenetic influences in the development of the robin’s sophisticated numeracy and memory.

Recent research has aimed to examine numerical ability in non-human animals and identify the selection pressures that may drive the evolution of sophisticated numeracy and related cognitive mechanisms (Brannon & Terrace, 2002). Food-hoarding species are often used to study sophisticated cognitive abilities in non-human animals. Their foraging strategy optimizes food consumption in environments where resource availability may not always be reliable (Vanderwall, 1990). Food-hoarding species hide large quantities of food in various cache sites, consuming it later as needed. As identified by Burns and Steer (2006), food-hoarding species store food in two ways: internally through consumption, or externally through caching. Each storage option has unique costs and benefits. Although caching can be a beneficial way to save food for later, hoarded food can spoil, be forgotten, or be stolen by competitors (Burns & Steer, 2006). According to the ‘selfish-hoarding hypothesis’, food-hoarding is only adaptive if the original cacher has a retrieval advantage over cache thieves (Smulders, 1998). Evidence for this hypothesis is mixed, and some studies reveal that due to excessive cache pilferage, the original cacher often does not recover the majority of their own caches (Vanderwall & Jenkins, 2003). It is suggested that reciprocal cache pilferage may explain this discrepancy, in that food-hoarders also steal food and may thus tolerate high levels of theft from their own caches. The New Zealand North Island robin (Petroica longipes) is a prime example of a food-hoarding bird that actively participates in reciprocal cache pilferage. This territorial songbird is sexually monogamous, and mates will often pilfer from each other’s cache sites (Ardern, Ewen, Armstrong & Lambert, 1997). This bird is endemic to an isolated island and lacks pronounced anti-predatory behaviours.

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(Maloney & McLean, 1995). In turn, they readily participate in food-hoarding experiments and behavioural observations can be made at a close range. Due to high intersexual competition, foraging strategies vary between males and females and can fluctuate between seasons. The function of these foraging strategies can best be understood by examining the cognitive mechanisms possessed by these robins and how they may differ between males and females. The present review pertains to a principal study examining the mathematical competence of New Zealand robins, which will be presented and appraised (Garland & Lowe, 2014). Furthermore, the proposed cognitive mechanisms underlying foraging behaviour in New Zealand robins will be discussed, as well as hypotheses regarding the selection factors influencing the development of these abilities.

Introduction to Principal Study: Addition and Subtraction in Wild New Zealand Robins

In the primary study assessed, New Zealand North Island robins were examined to see if they possessed proto-arithmetic ability (Garland & Low, 2014). Proto-arithmetic ability is referred to as simple, non-symbolic arithmetic computation, such as addition and subtraction with small numbers. New Zealand robins were tested using a Violation of Expertancy (VoE) paradigm in two separate experiments. The apparatus was specifically designed for VoE testing, and the dual-level container permitted experimenters to test if the participants reacted to an unexpected result. Subjects were shown a certain number of worms being added or subtracted to the bottom compartment of the container. A leather flap covered the opening, and the top compartment was slid in to cover the bottom level. The top compartment was baited beforehand and was either congruent or incongruent with what was originally placed in the bottom compartment. After the top compartment was slid in, the subjects were permitted to inspect and forage from the apparatus. Search duration and pecking frequency were recorded and used as indicators for knowledge of incongruence with the number or type of worms the birds viewed originally.

In experiment one, numerical competence was assessed. Subjects were presented with trials that were either numerically congruent or incongruent with the observed number of mealworms (Tenebrio molitor larvae) baited. In experiment two, categorical competence was assessed. Subjects were presented with trials that were either categorically congruent or incongruent to what should have been expected. In experiment two both mealworms and waxworms (Galleria mellonella larvae) were used. The number of worms did not change in these incongruent trials, rather only the type of worms differed from what should have been expected. Further, neutral trials were conducted in both experiments. Neutral trials were used to gain a basal level of exploration behaviour in the absence of available food. In the neutral trials, the VoE apparatus was placed
on the ground with no bait and the behavioral measures were recorded.

New Zealand robins searched longer and pecked more in instances when they were presented with an unexpected outcome rather than an expected one, whether mathematically or materially. However, the only significant difference with neutral exposures was the number of pecks, in which significantly fewer occurred after congruent trials than neutral exposures. Significant differences between incongruent and congruent trials appear to indicate proto-arithmetic ability in these robins. It may only be their search intensity (pecking) rather than search duration that reliably indicates this ability. The authors suggest that searching more intensely rather than searching for longer is part of an optimal foraging strategy.

Ecological Drivers of Numerical Ability

New Zealand North Island robins are territorial songbirds and live in mated pairs year-round (Higgins & Peter, 2002). They will cache readily as an external mechanism for short-term fluctuations in resource supply (Armstrong, Garland, & Burns, 2012). Mates will often pilfer from each other’s cache sites and robins are less likely to store prey if their partner is present. Robins are observed to re-cache previously hoarded food pilfered from their mate, which may act as a cache theft prevention strategy (Andersson & Krebs, 1978). In their natural environment, robins often encounter situations where prey can go missing unexpectedly. As a food-hoarding species, they must pay attention to both the likelihood of prey going missing as a result of being pilfered by a mate, as well as the mobility of their prey. Garland and Low (2014) suggest that increasing search intensity through pecking frequency may be a part of an optimal foraging strategy. Increasing pecking rather than search duration would allow robins to find prey that may have moved slightly from a cache site, and at the same time, avoid the loss of time foraging for new prey or defending remaining caches.

Although ecological factors may play a role in the robin’s foraging strategy, the evolutionary origins of numerical ability are not entirely clear. In order for numerical ability to be selected for in a species, it must provide a considerable benefit. If knowledge of cache pilferage by one’s own mate through numerical ability has no consequence for the likelihood of mating or survival, there are no logical selection pressures for the development of this trait. Numerical ability could function in foraging as a by-product of its use in another context or may have persisted from an ancestor; although, neither of these options seem likely (Miller & Lambert, 2006). Further discussion will assess the role of evolution in the development of numerical ability and other cognitive mechanisms with the assumption that they provide a considerable benefit to the species. The principal aim is to identify the selection pressures that may have assisted in the development and maintenance of the trait.
Optimizing Pilferage Attempts Through Numerical Cognition

Numerical ability may be selected for in foraging contexts if it functions to increase the likelihood of survival. In the winter months, days become shorter and there is reduced food supply, which necessitates efficient food hoarding and accurate cache retrieval (Hunt, Low, & Burns, 2008). New Zealand robins are able to cache efficiently and employ differential strategies based on dominance rank, sex, and season (Burns & Steer, 2006; Van Horik & Burns, 2007; Steer & Burns, 2008). Accurate quantity discrimination between cache sites of a conspecific may be important in making pilfering decisions. Although mates cooperate in raising their young during the breeding season, males monopolize food sources year-round and display highly aggressive behaviour towards females in foraging contexts. Furthermore, females will only access food sources and pilfer from male-made caches when males are absent in the hopes of avoiding an aggressive encounter. Optimizing one’s pilferage strategy to obtain the highest possible reward would make stealing more viable if there is a risk of aggressive repercussions from the owner of the cache.

Robins preferentially select for the larger of two quantities in observational discrimination tasks (Garland, Low, & Burns, 2012; Hunt et al., 2008). This suggests that they may possess observational spatial memory, which refers to the ability to store information about a specific location through observation (Scheid & Bugnyar, 2008). If robins are able to track the number of prey their mate has stored in different locations, they could maximize pilferage success by targeting cache sites with the largest number of prey (Armstrong et al., 2012). There are only short temporal periods when there is an opportunity to pilfer from a mate’s caches. By prioritizing the pilferage of sites with large quantities of prey, the robin would maximize its energetic rewards. Because pilferers face aggression from the original cacher if discovered, the capacity to remember the number of items and locations of cache sites would be advantageous. Possessing observational spatial memory is advantageous for delayed food pilfering and allows for subordinates, often females, to compete for food without having to directly confront a dominant conspecific (Burns & Steer, 2006; Scheid & Bugnyar, 2008). Maintaining a mental representation of cache sites for longer periods of time may be more important for females, who can only pilfer when their mate leaves a site unattended. The robin’s observational spatial memory can decay over time, and accuracy in quantity discrimination decreases as more cache sites are coded in memory and as time passes (Armstrong et al., 2012). Cache recovery by the original hoarder usually occurs on the same day, and always within three days, whereas pilfering often occurs within 30 minutes of caches being created (Powlesland, 1980; Van Horik & Burns, 2007). Robins are less likely to cache if their mate is nearby (Burns & Steer, 2006) which further suggests that observational memory plays a vital role in successful pilferage.
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attempts. Storing prey in the absence of a mate may act as a cache theft prevention strategy, and function to optimize one’s own food hoarding. Numerical ability allows for robins to optimize their pilferage strategy to maximize success, and in combination with a sophisticated observational spatial memory, this ability functions to delay pilferage to avoid the potential risk of an aggressive encounter.

Sexual Differences in Foraging Strategies

As winter turns to spring, conflict turns to co-operation within pairs of New Zealand robins. Seasonal changes in male aggression are suggested to function as a prelude to the upcoming breeding season (Burns & Van Horik, 2007). As previously stated, dominant males monopolize food supplies year-long, and females will only forage in the absence of their mate to avoid aggressive encounters (Armstrong et al., 2012). These sex differences in their ability to obtain and defend food resources further translate into differential caching and pilferage strategies.

Caching Strategies

Caching strategies differ widely between male and female robins, both in spatial distribution and frequency of caching in the presence of their mate. These strategies both function to reduce cache pilferage. Males are observed to aggregate caches, whereas females scatter caches more widely in space (Van Horik & Burns, 2007). Cache spacing patterns are often interpreted as behavioural adaptations to reduce cache theft (Sherry, Avery, & Stevens, 1982; Clarkson, Eden, Sutherland, & Houston, 1986). Males store food items close together, which reduces their travel time to food sources and facilitates cache defence from pilferers. By contrast, females may take on a scatter strategy to increase the area necessary for pilferers to search for their caches (Dally, Clayton, & Emery, 2006). Males are observed to cache more than females, and both sexes are more likely to cache when they are alone than in the presence of their mate. Although there is an interaction between sex and social observation, there is a more considerable decrease in caching rates when females are accompanied by their mate than males (Burns & Steer, 2006). Males almost always displace females in aggressive contests, making females less successful in direct cache defence efforts. In turn, their cache sites are more susceptible to pilferage. The more dramatic reduction in female food-hoarding behaviour in the presence of their mate may be an adaptive response to reduce male pilferage of cache sites.

In a study conducted by Burns (2008), robins were observed both in pairs and alone to examine the likelihood they would immediately consume or cache prey. Solitary males and females as well as paired males were more likely to consume prey until they were satiated. When satiated, they were increasingly likely to cache subsequent prey items. By comparison, paired females did not show this same pattern. In the presence of their mate, the likelihood of caching remained constant regardless of the amount of prey already consumed (satiation
level). This result suggests that internal energy storage may be consistently more advantageous for paired females than external storage in cache sites, where they will likely lose the food in an aggressive encounter. Although no study has been directly conducted with New Zealand robins, willow tits (*Poecile montanus*) show a change in subordinate caching strategies to be less scattered and to be more frequently made, resulting from the removal of a dominant conspecific (Lahti et al., 1998). Differential social dominance between the sexes of robins seems to play a large role in cache formation behaviours, both in spatial distribution and caching frequency in a social context.

**Pilfering Strategies**

With respect to pilferage strategy, there are predominant sex differences and inter-seasonal differences. As previously mentioned, male aggression gradually turns to cooperation in late winter as the breeding season approaches. During fall and early winter, pairs rarely forage together, suggesting that females avoid highly aggressive males during this time. During the winter-spring transitional period, males and females gradually spend more time foraging together and females pilfer more frequently from male-made caches. Robins often re-cache both their own cache sites and pilfered prey, but females will re-cache at higher rates in comparison to males in respect to pilfered prey (Burns & Van Horik, 2007). Although re-caching is typically a cache theft prevention strategy, the differential rates of re-caching between males and females suggest that re-caching behaviour may go beyond a simple pilferage strategy (Vanderwall & Jenkins, 2003).

Burns and Van Horik (2007) propose two alternate hypotheses for the sex difference in the rate of re-caching of pilfered food: sexual dimorphism in observational spatial memory and indirect mate provisioning. The researchers suggest that female robins may simply possess a better observational memory, and are thus able to identify and raid caches more efficiently. Observational spatial memory may be a more important trait for females, as they rely on delayed pilferage to forage effectively from a mate’s cache sites. High intersexual competition may have driven this trait to be sexually dimorphic given the typical dominance structure between pairs. Research directly testing sexual dimorphism in observational memory ability in robins should be conducted to validate this hypothesis. The alternate hypothesis presented suggests that the discrepancy between sexes may be indicative of an indirect mate provisioning mechanism. Males may permit excessive female pilferage to facilitate cooperation in mating and rearing of offspring in the upcoming breeding season. Robins will mate monogamously ranging from a single season to many subsequent seasons, but factors that facilitate maintenance of these bonds over multiple seasons have not been specifically researched. Future research should assess if the level of mate provisioning entering the breeding season has an influence on the likelihood of mating in subsequent seasons. If males direct their own pilferage behaviour during this winter-spring transition to
maintain cooperation, they would have to keep track of the number of worms pilfered by their mate in comparison to the number they have pilfered. Research should examine if excessive male pilferage in comparison to female pilferage influences the likelihood of mating in subsequent seasons. If tracking pilferage rates are important in indirect mate provisioning, numerical ability would be important for robins to judge a mate’s “quality” given the number of worms pilfered from their cache sites. Although no research has been specifically conducted examining sexual differences in pillerage rate and likelihood of mating in the next season, it could provide an alternate explanation to the development of numerical ability through sexual selection.

Considering the spatial distribution of caches made by males, a third possibility is that raiding multiple caches may be easier for females due to male cache aggregation strategies. Male cache spacing strategies facilitate cache defense, but when the male is absent, his cache sites may be more vulnerable to pillerage. Male-made caches are closer together in space, which provides females an opportunity to pilfer from multiple caches in the small period of time that the male is not present. Female-made caches are scattered in space, which may be more difficult for a male to piller from multiple caches in a single pillering bout. Research testing each of these three hypotheses must be conducted across seasons to determine possible explanations behind this sexual difference in cache pillering. Although males are physically dominant and aggressive year-round, females have a seasonally variable foraging strategy that reduces intersexual competition during the non-breeding season and maximizes energy intake through pillerage in the late winter and spring (Menzies & Burns, 2010).

Comparative Analysis of Similar Cognitive Abilities in Other Animal Models

Observational spatial memory is not common in avian species, and before the recent work portrayed this ability in the New Zealand robin, it was thought to only exist in corvids (Corvidae; Seed, Emery, & Clayton, 2009). Corvids are also a food-hoarding species that use observational spatial memory to piller from conspecifics and use highly flexible mechanisms to cache strategically based on the presence of a competitor (Clayton, Dally, & Emery, 2007). Similar cognitive abilities found in the New Zealand robin reflect parallel evolution of observational spatial memory in another avian species. Corvid cognitive abilities highly resemble that of the New Zealand robin, which leads researchers to question the selection factors that have been hypothesized as mechanisms behind the evolution of observational spatial memory in other species.

It has been proposed that sociality and high cache dependence are major influences in the evolution of a sophisticated observational spatial memory system (Bednekoff & Balda, 1996a; Scheid & Bugnyar, 2008). Pinyon jays (Gymnorhinus cyanocephalus) are a highly
social species that depend on cache sites for food during winter. Additionally, pinion jays accurately locate and pilfer cache sites through the sole observation of a conspecific (Bednekoff & Balda, 1996b). The comparison of observational spatial memory possessed by avian species has been conducted to investigate the role of sociality and dependence on cached food in the development of the cognitive ability. The highly social Mexican jay (Aphelocoma ultramarina) consistently outperforms the more solitary Clark’s nutcracker (Nucifraga columbiana) in observational spatial memory tasks, suggesting the role of sociality in the development of this ability (Bednekoff & Balda, 1996a). In contrast, other research has indicated high cache dependence to be as influential as sociality for the development of a sophisticated observational spatial memory system (Scheid & Bugnyar, 2008).

New Zealand robins do not rely entirely on caches and are not highly social animals (Menzies & Burns, 2010). Despite the lack of apparently important traits in the evolution of observational spatial memory, robins show a similar memory capacity to that of corvids. New Zealand robins present a model to study alternate selection factors in the development of similar sophisticated cognitive abilities (Armstrong et al., 2012).

**Conclusions**

Cognitive abilities assist the foraging efforts for the New Zealand robin. In the principal study assessed, intense searching was indicative of their sophisticated arithmetic ability (Garland & Low, 2014). Increasing search intensity rather than search duration may function as an optimal foraging strategy, in which displaced worms can be retrieved without risking lost time that could otherwise be directed to protecting other cache sites, foraging for new prey, or pilfering from other caches. Along with proto-arithmetic ability, New Zealand robins possess the ability to discriminate between quantities as well as possess an advanced observational spatial memory system (Hunt et al., 2008; Armstrong et al., 2012). These cognitive abilities function to optimize pilferage attempts from a mate’s caches, both through cache site choice and delayed pilfering. High intersexual competition has influenced the differentiation of caching and pilfering strategies between males and females. Dominance ranks and seasonal change are the core components suggested to produce these sex-based differential strategies in foraging. The cognitive abilities of the New Zealand robin provide strong evidence that counters the hypothesized factors that were previously considered necessary for the development of observational spatial memory (Bednekoff & Balda, 1996a; Scheid & Bugnyar, 2008). The complex cognitive mechanisms underlying the New Zealand robin’s foraging behaviour provide insight into other possible evolutionary pathways in which high intersexual competition and reciprocal pilferage may be influential factors behind the development of sophisticated numeracy and memory.
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