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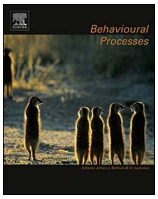

The ontogeny of food-caching behaviour in New Zealand robins (*Petroica longipes*)

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ABSTRACT

Hoarding or caching behaviour is a widely-used paradigm for examining a range of cognitive processes in birds, such as social cognition and spatial memory. However, much is still unknown about how caching develops in young birds, especially in the wild. Studying the ontogeny of caching in the wild will help researchers to identify the mechanisms that shape this advantageous foraging strategy. We examined the ontogeny of food caching behaviour in a wild New Zealand passerine, the North Island robin (*Petroica longipes*). For 12-weeks following fledging, we observed 34 juveniles to examine the development of caching and cache retrieval. Additionally, we compared the caching behaviour of juveniles at 12 weeks post-fledging to 35 adult robins to determine whether juveniles had developed adult-like caching behaviour by this age. Juveniles began caching mealworms shortly after achieving foraging independency. Multivariate analyses revealed that caching rate increased and handling time decreased with increasing age. Juveniles spontaneously began retrieving caches as soon as they had begun to cache and their retrieval rates then remained constant throughout their ensuing development. Likewise, the number of sites used by juveniles did not change with age. Juvenile sex, caregiver sex and the duration of post-fledging parental care did not influence the development of caching, cache retrieval, the number of cache sites used and the time juveniles spent handling mealworms. At 12 weeks post-fledging, juveniles demonstrated levels of caching, cache retrieval and cache site usage that were comparable to adults. However, juvenile prey handling time was still longer than adults. The spontaneous emergence of cache retrieval and the consistency in the number of cache sites used throughout development suggests that these aspects of caching in North Island robins are likely to be innate, but that age and experience have an important role in the development of adult caching behaviours.

1. Introduction

When food becomes temporarily abundant, many animals will respond by storing food in their environment (i.e. caching) thereby preserving the resource for future consumption (Vander Wall, 1990). As such, caching species possess a complex suite of physical skills for creating caches (e.g. preparation, transportation, etc. of food; Bossema, 1979; Kallander, 2007; Vander Wall and Balda et al., 1981), and cognitive skills for remembering the location of caches for subsequent retrieval (e.g. spatial memory; Balda and Kamil, 1992; Jacobs and Liman, 1991). Caching has become an important behavioural paradigm for studying cognition, motivation and foraging decisions (e.g. Clayton et al., 2007; Gerber et al., 2004; Hopewell et al., 2008; Korpimaki, 1987; Vander Wall, 2000)

However, despite the prevalence with which caching is used as an experimental paradigm by comparative cognition and behavioural researchers, few ontogenetic studies of caching behaviour have been made (Vander Wall, 1990). The earliest study was conducted with wild crested tits (*Lophophanes cristatus*) and willow tits (*Poecile montanus*) (Haftorn, 1992). Field observations in 1950 and 1987–90, reported that the food caching behaviour in these species arose approximately two weeks after young left the nest (Haftorn, 1992). At its onset, caching acts were “incomplete”, i.e. juveniles pretended to deposit items at sites and/or immediately retrieved and consumed caches. However, within a week juveniles were observed completing food storing acts by leaving food at cache sites following placement (Haftorn, 1992). Haftorn (1992) concluded that caching was largely innate within tits and that experience, rather than observational learning, was key to the development of this behaviour.

Similar results were also reported for wild pinyon jays (*Gymnorhinus cyanocephalus*; Stotz and Balda (1995)). Object caching (i.e. caching of inedible items such as rotten pinyon pine seeds and pine bark) was first observed in juveniles at 3 weeks post-fledging and was prevalent until 12 weeks post-fledging, when it was replaced by food caching. The

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onset of food caching behaviour coincided with the development of foraging skills, as adults were rarely observed feeding young past 16 weeks post-fledging (Stotz and Balda, 1995). Stotz and Balda (1995) concluded that the observed shifts from caching objects to food suggested that experience, i.e. learning to distinguish between edible and inedible items, was influential in the acquisition of caching behaviour in pinyon jays.

The studies of crested and willow tits (Haftorn, 1992) and pinyon jays (Stotz and Balda, 1995) are the only examples where the emergence of caching behaviour has been documented in the wild. All subsequent research has shifted toward laboratory-based research, tracking the development cognitive traits related to caching. For instance, ontogenetic studies of caching with magpies (*Pica pica*) and ravens (*Corvus corax*) in laboratories have focused on linking the development of skills for storing food with the acquisition of object permanence, i.e. the capacity to understand that an object can still exist while temporarily out of view (Bugnyar et al., 2007; Piaget, 1937; Pollok et al., 2000). Such studies have been invaluable to improving our knowledge of avian cognitive abilities, but the ontogeny of caching behaviour itself remains poorly documented. Additionally, previous ontogenetic studies of caching behaviour have been restricted to just a few groups of birds (e.g. *Paridae* and *Corvidae* spp.) and carried out in laboratory environments (Bugnyar et al., 2007; Clayton, 1992, 1994; Pollok et al., 2000; Salwiczek et al., 2009). Thus, there are significant gaps in our understanding of how other avian families develop and utilise this complex behaviour, as well as how this behaviour emerges in natural settings.

New Zealand robins (*Petroica* spp.) are one of a few species in the southern hemisphere that are known to cache food (Vander Wall, 1990). Like many birds endemic to isolated islands, these small insectivorous passerines lack pronounced anti-predator behaviours and will fearlessly approach humans (*sensu* Carlquist, 1970; Maloney and McLean, 1995). Thus, both species (North Island robin, *Petroica longipes*; South Island robin, *P. australis*) are easily observed performing behaviours that are often difficult to study in other wild passerines, i.e. mating, incubation and caching (Boulton et al., 2010; Burns, 2009; Powlesland et al., 2000).

The diet of NI robins includes some of the world's largest terrestrial invertebrates such as giant earthworms (*Lumbricidae*) and flightless grasshoppers called weta (*Orthoptera*: *Anostostomatidae*). These prey are typically too large to consume whole or in one sitting; therefore, large invertebrates are typically dismembered and pieces not immediately consumed are cached in branch-trunk axils, cavities in branches, broken tree trunks or tree fern crowns (Alexander et al., 2005; Powlesland, 1980). Adult caching behaviour has been well studied in wild New Zealand robins, but as yet there have been no studies of the development of caching in young robins (Alexander et al., 2005; Barnett and Emura, 2014; Burns, 2009; Burns and Steer, 2006; Burns and Van Horik, 2007; Van Horik and Burns, 2007). New Zealand robins therefore offer a valuable opportunity to examine the development of caching in a wild passerine species that does not belong to the Corvidae and Paridae families.

The aim of this study was to examine the development of food caching in wild North Island (NI) robins. We carried out weekly feeding observations with 34 juveniles over a period of 12 weeks post-fledging and examined the development of caching (i.e. external storage of food in the environment) and three related behaviours: cache retrieval, site use and time spent handling items prior to caching. Previous ontogenetic studies in corvids and parids have reported a significant effect of age on the onset and expression of caching (e.g. Bugnyar et al., 2007; Clayton, 1992; Haftorn, 1992). We therefore predicted that age would influence all four caching-related behaviours in robins. Moreover, marked sexual differences in caching behaviour have been observed for adult robins; males cache more mealworms and make fewer cache sites compared to females (Alexander et al., 2005; Van Horik and Burns, 2007). As such, we anticipated that similar sexual differences would also be observed in juvenile caching behaviour. We also examined whether exposure to these differing parent caching strategies during the prolonged post-fledging care period (Armstrong et al., 2000) influenced the development of caching behaviours in young robins. Cache pilfering is well documented amongst robins and previous studies have noted that female robins pilfer more male-made caches than vice versa (Alexander et al., 2005; Burns and Van Horik, 2007; Van Horik and Burns, 2007). We predicted that juveniles with a longer duration of care may separate their caches across a greater number of sites to reduce the risk of cache theft by caregivers.

2. Methods

2.1. Study site and species

We studied juvenile NI robins during the 2015–2016 breeding season at Zealandia Wildlife Sanctuary, Wellington (41°18′S, 174°44′E). The sanctuary consists of 225 ha of regenerating native forest where introduced mammal predators have been removed and are prevented from returning by a specially built mammalian exclusion fence. The robin population at Zealandia was established via translocations in 2001 and 2002 from nearby Kapiti Island (40°50′S, 174°56′E). The species has since been breeding successfully, with an estimated density in 2008 between 2.3 and 3.4 individuals/ha (i.e. approximately 500–765 birds) (McGavin, 2009). NI robins are highly territorial and this density places the territory size for pairs in this population at the smaller end of the range reported for New Zealand robins (i.e. 1–5 ha) (Powlesland, 1980, 1983). A subset of the robin population have been individually banded and are monitored during the breeding season as part of a long-term study on robin cognition and fitness (Shaw, 2017; Shaw et al., 2015, 2017).

NI robins begin nesting in September, with final clutches typically laid by January. Following nest departure at 17–21 days old, young remain in natal territories and are cared for by parents for 4.5–7 weeks (Armstrong et al., 2000). Young are largely immobile upon leaving the nest; being poor fliers, fledglings tend to remain perched high in the canopy and are fed at these perches by parent(s) (Powlesland, 1983). By two to three weeks post-fledging, young are able to fly proficiently and forage independently on the ground. All juveniles were individually marked with a unique combination of 3 colour-bands and one metal band 11–14 days after hatching, or shortly after fledging if nests were inaccessible. Additionally, we removed three pin feathers (i.e. developing feathers) during banding for sex determination analyses. Sex determination was carried out by EcoGene (Landcare Research New Zealand Limited, Auckland, http://www.ecogene.co.nz/) following the PCR method described by Griffiths et al. (1998).

2.2. Field methods

Field observations were undertaken during the austral summer of 2015–2016 to study fledgling caching development under natural conditions. We monitored 34 fledglings from 23 broods on a weekly basis over a 12-week period, commencing at fledging. Our observation protocols were similar to those developed for monitoring robin behaviour (Powlesland, 1997). Parental care is typically divided between parents following nest departure, thus individual fledglings are often exclusively cared for by just one of their parents during this period (Armstrong et al., 2000; Higgins and Peter, 2002).

Observations consisted of two consecutive 20 min periods and where possible, we filmed sessions using an iPad Air 2 (Apple Inc.). Subjects were located by tapping a lid against a container within their territory (Powlesland, 1997). During the first 20 min period, we offered fledglings up to 10 mealworms (*Tenebrio molitor* larvae). Fledglings less than three weeks post-fledging had limited mobility and were unfamiliar with mealworms; we therefore offered mealworms to their caregivers, which fed the items to young. We offered mealworms one by