

An experimental evaluation of food hoarding by North Island robins (*Petroica australis longipes*)

LAUREL ALEXANDER, CATHERINE DUTHIE, JOSHUA FYFE, ZOË HAWS, SIMON HUNT, ISABEL MONTOYA, CARLOS OCHOA, ARUN SIVA, LLOYD STRINGER, JAYDEN VAN HORIK, K.C. BURNS*
School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand.
kevin.burns@vuw.ac.nz

Abstract We experimentally evaluated the food hoarding behaviour of North Island robins (*Petroica australis longipes*) at Karori Wildlife Sanctuary, Wellington. Mealworms were offered to free-ranging pairs of male and female robins to evaluate whether their food hoarding behaviour was similar to previous observations of South Island robins. We also tested theoretical predictions derived in the Northern Hemisphere, which argue that competitively subordinate birds should hoard more food than dominant birds. Results showed that the food hoarding behaviour of North Island robins was similar to South Island robins, except that North Island robins repeatedly used the same cache sites, which is rare in South Island robins. Data did not support the prediction that competitively subordinate birds hoard more food than dominant birds. Males acquired most of the mealworms offered to birds during trials, and won nearly all aggressive interactions observed between sexes. Therefore, males appeared to be competitively dominant to females in winter. However, males stored over five times as many mealworms as females, which is opposite to theoretical predictions. We interpret the reluctance of females to cache food as a strategy to avoid food loss to competitively dominant males.

Alexander, L.; Duthie, C.; Fyfe, J.; Haws, Z.; Hunt, S.; Montoya, I.; Ochoa, C.; Siva, A.; Stringer, L.; Van Horik, J.; Burns, K.C. 2005. An experimental evaluation of food hoarding by North Island robins (*Petroica australis longipes*). *Notornis* 52(3): 138-142.

Keywords: Food hoarding; competition; experiment; North Island robin; *Petroica australis*

INTRODUCTION

Recent studies of food hoarding behaviour in birds have generated important insights into avian cognition (Krebs *et al.* 1996; Emery & Clayton 2001; Milius 2004), social dynamics (Heinrich & Pepper 1998; Pravosudov *et al.* 1999; Vanderwall & Jenkins 2003) and foraging behaviour (Pravosudov & Grubb 1998; Brodin 2001; Smith *et al.* 2002). Although some southern hemisphere birds hoard food (e.g. bowerbirds (Ptilinorhynchidae); Pruett-Jones & Pruett-Jones 1985), nearly all previous work has come from the northern hemisphere. Our knowledge of food hoarding in New Zealand birds is restricted to a single study on South Island robins (*Petroica a. australis*) (Powlesland 1980).

Theoretical work predicts that competitively subordinate birds should hoard more food than dominant birds to offset losses resulting from cache pilfering (Brodin *et al.* 2001). Empirical tests of this prediction have been conducted mostly on tits (Paridae) and jays (Corvidae) in aviaries, and their results are mixed (see Lundborg & Brodin 2003 for a recent review). Additional tests on species with

different life history traits may help elucidate the factors responsible for the conflicting results of the aviary tests.

Like many bird species endemic to isolated islands, New Zealand's robins lack pronounced anti-predatory behaviours (see Carlquist 1965). They are fearless of humans and wild birds will consume food offered to them by hand (Armstrong *et al.* 2000). Although this attribute enhances their vulnerability to predation by introduced mammals, it might also generate a unique opportunity to test food-hoarding theory.

In winter 2003, we conducted a field experiment on free-ranging North Island robins (*Petroica australis longipes*) to evaluate their food-hoarding behaviour. We offered mealworms (*Tenebrio molitor*) larvae to pairs of robins on their winter territories to evaluate whether: 1. their food-hoarding behaviour was similar to that of South Island robins; 2. females were competitively subordinate to males; and 3. females hoard more food than males.

METHODS

The experiment was conducted in the Karori Wildlife Sanctuary (KWS: 41° 18' S, 174° 44' E), a 2.5 km² catchment of regenerating forest within Wellington city. The area experiences a mild, temperate climate, with annual rainfall averaging

1270 mm and cloud cover obscuring the sun 54% of daylight hours (Karori Wildlife Sanctuary 1997). Evergreen trees and tree ferns dominate the forest canopy, while shrubs and vines inhabit the forest understory (Dawson 1988). The population of North Island robins in KWS was transferred there from Kapiti Island: 40 birds were released in 2001 and 36 birds in 2002 (Small 2004). At the commencement of our study, approximately 15 breeding pairs had established within the sanctuary. All birds were colour banded, facilitating the identification of birds that were repeatedly encountered.

Mealworms were fed to pairs of robins on their winter territories during July and August 2003. Each trial began by locating a pair of robins, which unvaryingly consisted of one male and one female. When both birds were within 2 m of the three or more observers a single mealworm was positioned on flat ground that could be easily seen from both birds' vantage points. Mealworms were categorized as "acquired" if a robin removed it from where it was placed by the experimenter. "Acquired" mealworms were then classified as "consumed" if swallowed, or "cached" if transported to another location and abandoned. After the first mealworm was placed on the ground, additional mealworms were placed in the same location at 20-sec intervals until a total of 10 mealworms were cached by either sex. We recorded the fate of all acquired mealworms and the identity of birds that acquired them.

Males and females frequently engaged in aggressive physical interactions, most often in the immediate vicinity of where mealworms were offered, which resulted in one individual being displaced or supplanted (i.e., competitive displacements). We recorded the identity of each bird displaced during each aggressive interaction.

We conducted 42 trials on nine pairs of robins; some pairs were sampled up to nine times, others only once (Table 1). Differences in sampling intensity resulted from differences in our ability to locate particular pairs. To maintain independence among replicates, we averaged the results for all trials conducted on multiply-sampled birds prior to statistical analyses. Seven mealworms were not acquired (i.e., ignored) by robins. These mealworms were treated as structural zeros and removed from statistical analyses.

Two statistical tests were conducted to evaluate differences in competitive ability between sexes. Differences in the proportion of prey acquired by each sex and differences in the number of competitive displacements won by each sex were compared using two-tailed, paired *t*-tests ($n = 9$). Two additional analyses were conducted to test whether subordinate birds cached more food than dominant birds. First, the proportion of prey cached, calculated as the number of mealworms

cached by each bird divided by the total number of worms acquired by that bird during each trial, was compared between sexes with a two-tailed, paired *t*-test ($n = 9$). Second, to ensure that differences in the number of prey acquired by each sex did not confound results, caching rates of sequentially acquired mealworms was compared between sexes. For each of the first five mealworms acquired by each bird, the proportion cached was compared between sexes with repeated measures ANOVA. The proportion of worms cached was used as the dependent variable, the sequence of prey acquired was used a repeated measure and sex was considered a fixed factor. All statistical analyses were conducted in SPSS (LEAD Technologies, Inc. 2002).

RESULTS

Birds consumed approximately 60% of the mealworms offered during trials and the remainder were cached. Most caches were made above the ground (mean = $3.1 \pm sd 1.4$ m) in branch-trunk axils, tree fern skirts or in depressions in branches. Birds often made repeated trips to the same cache site, and most cache sites contained more than two mealworms at the close of trials (mean = 2.6 ± 0.4). Mealworms were either crushed in the bird's bill or slammed against the ground prior to caching, presumably to immobilize the prey. However, some were still moving at the time they were cached. Mealworms were always cached intact. No attempt was made to conceal caches and no evidence for the use of saliva to secure prey to the substrate was found. On several occasions birds were observed removing previously cached mealworms from their cache sites and relocating them to new sites. Re-caching behaviour typically occurred when a bird's mate approached the cache site. Kleptoparasitism, or the consumption of mealworms cached by another bird, was also observed.

Males dominated females. Males acquired approximately three times as many mealworms as females (Fig. 1a; $t = 32.2$, $p < 0.001$). Males also won nearly all competitive displacements observed between individuals in each pair (Fig. 1b; $t = 6.02$, $p < 0.001$). During trials, males usually approached the prey first, while females watched from a distance. Males then proceeded to physically monopolize the food source, with females gaining access to mealworms only when males were elsewhere caching previously acquired prey. Infrequently, females approached the prey first. Under these circumstances, males typically displaced them from the food source.

No support was found for the prediction that competitively subordinate birds hoard more food than competitively dominant birds (Table 1). In fact, results were opposite to predictions. Males cached

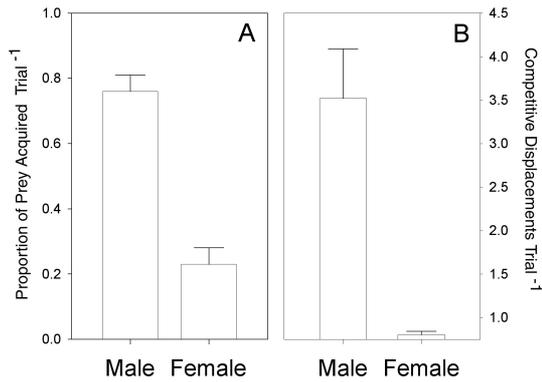


Figure 1 Competitive relationships between male and female New Zealand robins on their winter territories: A - the proportion of prey acquired by each sex during experimental trials; B - the average number of competitive displacements won by each sex. Data illustrated are means ($\pm se$) of nine male-female pairs

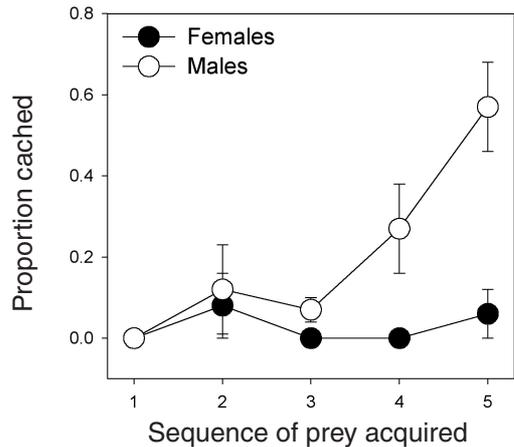


Figure 2 The mean ($\pm se$) proportion of sequentially acquired prey cached by male and female New Zealand robins, based on trials conducted on nine male-female pairs. The sequence of prey acquired refers to the order in which prey were handled; 1 refers to the first mealworm handled, 2 refers to the second mealworm handled, and so on.

Table 1 Results of a field experiment investigating the food hoarding behaviour of New Zealand robins. Nine pairs of North Island robins (*Pair*) were sampled between 1-9 times (*N*). Each pair consisted of one male and one female (*Sex*), and all birds were individually identified from leg bands. The average number of competitive displacements per trial ($\pm se$, *Displacements*), the average percentage of prey acquired per trial ($\pm se$, % *Acquired*) and the average percentage of acquired prey that were cached ($\pm se$, % *Cached*) by each bird are also shown. Averages are based on the number of trials conducted on each pair.

Pair	N	Sex	Displacements	% Acquired	% Cached
I	9	F ₁	0	13 \pm 4	19 \pm 15
		M ₁	3.33 \pm 2.00	85 \pm 7	62 \pm 7
II	7	F ₂	0	15 \pm 10	0
		M ₂	3.83 \pm 1.57	85 \pm 10	64 \pm 5
III	7	F ₃	0	26 \pm 5	0
		M ₃	3.86 \pm 1.61	75 \pm 4	66 \pm 2
IV	7	F ₄	0.17 \pm 0.24	10 \pm 4	0
		M ₄	2.67 \pm 1.40	89 \pm 5	50 \pm 9
V	6	F ₅	0	17 \pm 14	15 \pm 14
		M ₅	4.33 \pm 1.78	83 \pm 14	59 \pm 9
VI	3	F ₁	0.33 \pm 0.33	2 \pm 2	0
		M ₆	2.67 \pm 0.33	88 \pm 7	65 \pm 4
VII	1	F ₆	0	38	30
		M ₇	6	62	56
VIII	1	F ₇	0	0	-
		M ₈	5	100	69
IX	1	F ₁	0	42	25
		M ₉	0	58	64

over five times as many mealworms as females ($t = 9.52$, $p < 0.001$). Results were not confounded by differences in the number of prey acquired by each sex. Results from repeated measures ANOVA showed that the proportion of prey cached differed between sexes ($F_{1,40} = 10.3$, $p = 0.006$) and the sequence of prey acquired ($F_{3,40} = 10.3$, $p = 0.001$). An interaction between sex and handling sequences was also observed ($F_{3,40} = 10.3$, $p = 0.007$). This result indicated that both sexes consumed initially handled mealworms, while males cached greater proportions of subsequently acquired prey (Fig. 2).

One bird (female 1) was observed with three different males (male 1, 6 & 9, see Table 1). Therefore, not all replicates (i.e. pairs) were statistically independent. To correct for pseudoreplication, results were reanalyzed after removing repeated pairings. Separate tests were then conducted with all pairings involving female 1. These comparisons of prey acquisition rates, competitive displacement rates and caching frequencies, were similar to initial analyses ($p < 0.014$ for all).

DISCUSSION

The food-hoarding behaviour of North Island robins was generally consistent with Powlesland's (1980) observations of South Island robins. Both subspecies cached food in similar locales, namely branch axils and depressions in low-lying branches, and at approximately the same heights in the forest canopy (North Island, 3.1 ± 1.4 m; South Island, 2.9 ± 1.5 m). Both subspecies injured prey prior

to caching, but were often ineffective in causing mortality. Their apparent inability to kill prey may have been accidental. However, it could also have been intentional, as live prey is likely to persist in caches for longer periods before spoiling. Cache retrieval, kleptoparasitism, and re-caching behaviours were also observed in both subspecies.

Some aspects of the food hoarding behaviour of North Island robins differed from that of South Island robins. First, South Island robins dismembered large prey prior to caching, while North Island robins never broke mealworms into pieces and always cached mealworm prey whole. However, mealworms are much smaller than weta and giant earthworms, and the relatively small size of mealworms may account for the apparent reluctance of North Island robins to dismember prey prior to caching. On two occasions we observed robins catching and caching weta and giant earthworms: both were dismembered and treated in a similar manner to that described by Powlesland (1980). Second, North Island robins frequently cached several mealworms in cache sites whereas South Island robins rarely used the same cache site more than once and typically used different sites to cache separate food items. Why North and South Island robins differed in this respect is unclear, and the processes responsible for variation in "scatter" vs. "larder" hoarding strategies (*sensu* Vander Wall 1990) might be an interesting avenue of future research.

Clear differences in competitive dominance were observed. Males won more aggressive encounters and acquired more mealworms than females. These results are consistent with other previous work that has documented males as dominant to females in winter (see Higgins & Peter 2002). Clear differences in caching rates were also observed. After controlling for differences in the number of prey acquired, males cached nearly five times as many mealworms as females. Given that males were competitively dominant, our results are opposite to theoretical predictions (see Brodin *et al.* 2001), and add to conflicting evidence for the effects of competitive dominance on food hoarding behaviour.

Several previous studies have also documented that dominant birds hoard more food than subordinates. In field observations of willow tits (*Parus montanus*) and Siberian tits (*Parus cinctus*), Pravosudov (1985) found that dominant birds stored more than subordinates. Similarly, Lahti *et al.* (1998) observed that dominant willow tits cached more than subordinates. Subordinate willow tits also increased caching rates after dominant birds were experimentally removed, providing a more direct link between social dominance and caching rates. On the other hand, Lahti & Rytönen (1996), Pravosudov & Lucas (2000) and Lundborg &

Brodin (2003) found that food hoarding behaviour was not consistently associated with competitive dominance. Oppositely, Lucas & Zielinski (1998) found that subordinate Carolina chickadees (*Poecile carolinensis*) stored more food than dominant birds, which supports theoretical predictions.

McNamara *et al.* (1990) illustrated that birds can store food in two ways, either as fat (internally) or as caches (externally), and that each storage mechanism has unique costs and benefits (see also Pravosudov & Grubb 1998). Internal food storage is advantageous because once consumed, food cannot be lost to competitors (Vander Wall & Jenkins 2003, Thayer & Vander Wall 2005). However, it is disadvantageous because fatter, heavier birds are more susceptible to predators (Macleod *et al.* 2005). Trade-offs between internal and external food storage may explain differences in caching rates between male and female robins. Females may cache less frequently to avoid pilfering by competitively dominant males, while males may cache more frequently to reduce their risk of predation. However, confirmation of this interpretation awaits future research on the effects of body mass on predation risk and comparisons of cache pilferage between sexes.

Overall results from this study revealed that North and South Island robins have similar food hoarding behaviours. However, these behaviours were inconsistent with the prediction that subordinate birds cache more than dominant birds. Differences in caching rates between sexes were quite pronounced, and the clarity of our results is likely enhanced by the bold and inquisitive nature of New Zealand robins and our ability to view these wild birds in very close proximity. Future food hoarding experiments on New Zealand robins may generate further insight into avian cognition, social dynamics and foraging behaviour.

ACKNOWLEDGEMENTS

We gratefully acknowledge Victoria University of Wellington for financial support and the Karori Wildlife Sanctuary for permission to conduct the study and for access to banding records. Delia Small provided valuable logistical assistance and Ralph Powlesland provided comments to an earlier draft of the manuscript.

REFERENCES

- Armstrong, D.P.; Ewen, J.G.; Dimond, W.J.; Lovegrove, T.G.; Bergström, A.; Walter, B. 2000. Breeding biology of North Island robins (*Petroica australis longipes*) on Tiritiri Matangi Island, Hauraki Gulf, New Zealand. *Notornis* 47: 106-118.
- Brodin, A. 2001. Mass-dependent predation and metabolic expenditure in wintering birds: is there a trade-off between different forms of predation?. *Animal Behaviour* 62: 993-999.

- Brodin, A.; Lundborg, K.; Clark C.W. 2001. The effect of dominance on food hoarding: a game theoretical model. *American Naturalist* 157: 66-75.
- Carlquist, S. 1965. *Island life*. Natural History Press, New York.
- Dawson, J. 1988 *Forest vines to snow tussocks. The story of New Zealand plants*. Victoria University Press.
- Emery, N.J.; Clayton, N. S. 2001. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* 414: 443-446.
- Heinrich, B.; Pepper, J.M. 1998. Influence of competitors on caching behaviour in the common raven, *Corvus corax*. *Animal Behaviour* 56: 1083-1090.
- Higgins, P.J.; Peter, J.M. (eds.). 2002. *Handbook of Australian, New Zealand, and Antarctic birds. Volume 6: Pardalotes to shrike – thrushes* Oxford University Press, Melbourne.
- Karori Wildlife Sanctuary. 1997. *Karori wildlife sanctuary. Draft management plan*. Karori Wildlife Sanctuary Trust Inc., Wellington.
- Krebs, J.R.; Clayton, N.S.; Healy, S.D.; Cristol, D.A.; Patel, S.N.; Jolliffe, A.R. 1996. The ecology of the avian brain: food-storing memory and the hippocampus. *Ibis* 138: 34-46.
- Lahti, K.; Rytönen, S. 1996. Presence of conspecifics, time of day and age affect willow tit food hoarding. *Animal Behaviour* 52:631-636.
- Lahti, K.; Koivula, K.; Rytönen, S.; Mustonen, T.; Welling, P.; Pravosudov, V. V.; Orell, M. 1998. Social influences on food caching in willow tits: a field experiment. *Behavioral Ecology* 9:122-129.
- LEAD Technologies, Inc. 2002 *SPSS for Windows*. Release 11.5.0.
- Lucas, J. R.; Zielinski, D. L. 1998. Seasonal variation in the effect of cache pilferage on cache and body mass regulation in Carolina chickadees: what are the trade-offs? *Behavioral Ecology* 9: 193-200.
- Lundborg, K.; Brodin, A. 2003. The effect of dominance rank on fat deposition and food hoarding in the Willot tit *Parusus montanus* – an experimental test. *Ibis* 145: 78-82.
- MacNamara, J.M.; Houston, A.I.; Krebs, J.R. 1990. Why hoard? The economics of food storing in tits *Parus* spp. *Behavioral Ecology* 1: 12-23.
- Macleod, R.; Barnett, P.; Clark, J.A.; Cresswell, W. 2005. Body mass changes in blackbirds *Turdus merula*: the starvation-predation risk trade-off. *Journal of Animal Ecology* 74: 292-302.
- Milius, S. 2004. Where'd I put that? *Science News* 165: 103-105.
- Powlesland, R.G. 1980. Food-storing behaviour of the South Island robin. *Mauri Ora* 8: 11-20.
- Pravosudov, V.V. 1985. Search for and storage of food by *Parus cinctus lapponicus* and *P. montanus borealis* (Paridae). *Zool. Zhurnal*. 64: 1036-1043. [In Russian]
- Pravosudov, V.V.; Grubb, T.C. Jr. 1998. Management of fat reserves in tufted titmice (*Parus bicolor*): evidence against a trade-off with food hoards. *Behavioral Ecology and Sociobiology* 42: 57-62.
- Pravosudov, V.V.; Grubb, T.C.; Doherty, P.F.; Bronson, C.L.; Pravosudova, E.V.; Dolby, A.S. 1999. Social dominance and energy reserves in wintering woodland birds. *Condor* 101: 880-884.
- Pravosudov, V.V.; Lucas, J.R. 2000. The effect of social dominance of fattening and food-caching behaviour in Carolina chickadees, *Poecile carolinensis*. *Animal Behaviour* 60: 483-493.
- Pruett-Jones, M.A.; Pruet-Jones, S.G. 1985. Food caching in the tropical frugivore, MacGregor's bowerbird (*Amblyornis macgregoriae*). *Auk* 102: 334-341.
- Small, D.P. 2004. Survival, breeding success & habitat selection of North Island robins (*Petroica australis*) translocated to the Karori Wildlife Sanctuary. Unpublished thesis, Victoria University of Wellington, Wellington.
- Smith, R.D.; Ruxton, G.D.; Cresswell, W. 2002. Do kleptoparasites reduce their own foraging effort in order to detect kleptoparasite opportunities? An empirical test of a key assumption of kleptoparasite models. *Oikos* 97: 205-212.
- Thayer, T.C.; Vander Wall, S.B. 2005. Interactions between Steller's jays and yellow pine chipmunks over scatter-hoarded sugar pine seeds. *Journal of Animal Ecology* 74: 365-374.
- Vander Wall, S. B. 1990. *Food hoarding in animals*. University of Chicago Press.
- Vander Wall, S.B.; Jenkins, S.H. 2003. Reciprocal pilferage and the evolution of food-hoarding behaviour. *Behavioral Ecology* 14: 656-667.