

SHORT COMMUNICATION

Temporal shifts in the pair-bond dynamics of New Zealand robins (*Petroica australis*)

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Abstract: Winter is a challenging time for temperate insectivorous songbirds, due to colder temperatures, reduced prey activity and shorter diurnal foraging times. For species that are non-migratory, territorial and monogamous, winter conditions may result in within-pair competition. However, little is known about how monogamous pairs coexist on their winter territories. We investigated temporal patterns in male–female interactions of the New Zealand robin (*Petroica australis*) to better understand mechanisms of coexistence during winter. Previous work has shown that male robins are physically dominant over females and maintain priority access to food year-round. We quantified female behaviour throughout the 2008 non-breeding season to better understand how females coexist with physically dominant males on winter territories. Results showed that pairs rarely forage in close proximity in autumn and winter, suggesting females avoid males at this time of year. Males and females begin to spend more time foraging together as winter turns to spring. During this winter–spring transitional period, females steal large amounts of food hoarded by males. These results indicate that male and female New Zealand robins use different behavioural mechanisms to coexist on their winter territories. While males are dominant physically, females show a seasonally variable strategy where they avoid males in autumn and winter, and then steal male-made caches from early spring until the onset of inter-pair cooperation and the breeding season.

Keywords: cache; competition; sexual conflict; winter behaviour

Introduction

In many bird species, breeding pairs form life-long associations and reside together upon stable territories year-round (Lefebvre et al. 1992; Gorrell et al. 2005). Long-term pair bonds and stable territories are particularly prevalent among insectivorous passerines (Rowan 1966; Morton 1980). The territory size of such birds is hypothesised to result from a balance between the minimum foraging area required to obtain sufficient resources (Greenberg & Gradwohl 1986), competition with neighbouring conspecifics, and the increased energetic costs of defending a larger area (Hixon 1980). This trade-off between foraging requirements and competition will likely result in a territory just large enough to support the resident pair. However, if resource levels decline, competition with neighbouring birds will constrain the capacity of pairs to expand their territories. Under these conditions, behaviours such as spatial segregation, intersexual differences in foraging techniques and diet may help reduce within-pair conflict (Holmes 1986; Sodhi & Paszkowski 1995; Kelly & Wood 1996; Pasinelli 2000).

The New Zealand robin (NZ robin *Petroica australis*) is a monogamous, food hoarding passerine (Higgins & Peter 2002). Pairs usually form long-term associations and reside on permanent territories (Flack 1976; Powlesland 1980; Arden et al. 1997; But see: Armstrong et al. 2000). Although both members of the pair cooperate to raise young in the breeding season, males are competitively dominant to females and aggressively monopolise food sources year-round (Steer & Burns 2008).

In winter, NZ robins potentially face difficulties fulfilling their daily metabolic requirements due to reduced insect activity and shorter day lengths. During this time it is unclear how female NZ robins avoid conflict with their mates while co-occurring within a shared territory. Previous researchers have speculated that during winter female robins avoid close contact with males (Powlesland 1980; Armstrong et al. 2000). However, others have found that females steal large amounts of food from hoards made by males, which may also promote coexistence with physically dominant males (Van Horik & Burns 2007; Steer & Burns 2008). Results from studies of sexual segregation often hinge on the timescales in which observations are made (Breed et al. 2006). Therefore, the monthly interval between

Steer and Burns' (2008) trials may have obscured finer scale variations in robin foraging behaviour.

Here, we document temporal variation in potential coexistence behaviours of female NZ robins through winter into spring. We conducted regular censuses throughout the 2008 non-breeding season to determine whether females avoid foraging with their mate. Whenever pairs were encountered foraging together, we carried out feeding trials to assess temporal trends in the rate of female cache theft. Results are then used to examine how the pair-bond dynamics of NZ robins change between winter and spring.

Materials and methods

The study was carried out within Karori Wildlife Sanctuary (KWS), a 2.5-km² reserve of regenerating forest and wetlands, located near Wellington city (41°18' S, 174°44' E). Introduced mammals have had a profound impact on New Zealand's biota, resulting in severe declines and extinction in many species (Diamond & Veitch 1981; Bell 1990). In 1995, a mammal-proof fence was erected around KWS allowing the subsequent reintroduction of threatened avian, reptile, and amphibian species. NZ robins were first introduced to KWS in 2001 and have successfully established (Small 2004). The most recent survey estimates population densities of 2.6 robins ha⁻¹ (McGavin 2008). A more detailed description of KWS can be found elsewhere (Alexander et al. 2005; Steer & Burns 2008).

Although elsewhere food hoarding is a common strategy to overcome increasing energetic demands during winter, the NZ robin is one of the very small number of food-hoarding birds in the Southern Hemisphere (Vander Wall 1990). Like many animals endemic to isolated islands, robins are 'naïve' (*sensu* Carlquist 1965). They are fearless of humans and will carry out activities such as caching, cache theft, nuptial feeding and mating in close proximity to observers.

Observations were made by walking a circular track that intersected several (c. 15) NZ robin pairs' territories within KWS. The track was walked approximately once every 10 days between 9 May 2008 and 29 October 2008 (mean interval between walks = 9.1 days, SD = 5.1 days), resulting in a total of 21 observational periods. Each NZ robin that was encountered had its leg-band combination

recorded and was observed for 5–10 min to determine its foraging status (alone/together). A bird was recorded as ‘alone’ if no other NZ robin was seen or heard within c. 10 m during the observation period. If another robin was detected within c. 10 m, the pair would be recorded as foraging ‘together’ and both birds would be included in the subsequent feeding trial, following the protocol detailed in Burns & Steer (2006). If a robin was encountered more than once per walk it was ignored to avoid pseudo-replication. For each sampling period, the number of birds that were observed foraging alone was divided by the total number of birds sampled to estimate the proportion of females that were foraging alone. We then used a Spearman’s rank correlation to test for a relationship between foraging status and the ordinal date of each census.

When males and females were observed foraging together, rates of cache theft were obtained in experimental trials as described by Burns and Steer (2006). After the experimenter had engaged the attention of the pair, 3 g of mealworms (*Tenebrio molitor* larvae, approximately 30–40 individuals) were placed on the ground and subsequent behavioural interactions were observed for 30 min. The fate of each worm was classified as consumed, cached, recached or stolen. The identity of the bird handling each worm was recorded in addition to the fate of stolen caches (eaten or reached). During each trial we also noted the occurrence of nuptial feeding, which we defined as when one member of a mated pair fed the other. All observed instances of nuptial feeding involved males feeding females. After two consecutive walks by the authors where 100% of the worms were fed to females, accompanied by the ‘food acquisition display’ (Steer & Burns 2008), it was assumed that robin pairs were fully cooperating in an effort to raise young and that the breeding season had commenced. Feeding trials were conducted only on mated pairs of males and females. If a third bird joined, or if it became clear that the two birds were not a mated pair (e.g. they were a parent and fledgling), then the trial was halted and omitted from consideration.

To assess the seasonal relationship between cache theft and time, a Spearman’s rank correlation (r_s) was again used to test whether the proportion of male-cached worms that were stolen by females during each trial varied with the ordinal date of each census. Similarly, the relationship between nuptial feeding (i.e. the proportion of worms fed to the female by the male robin per trial) and ordinal date was analysed with a Spearman’s rank correlation. Data were analysed using SPSS (2007).

Results

A total of 98 foraging status observations were obtained from 15 banded robins. The proportion of pairs that were observed foraging alone decreased through time ($r_s = -0.851$, $P < 0.001$). Therefore, males and females seemed to avoid one another in late autumn and winter, but spent an increasing amount of time foraging together as the breeding season approached (Fig. 1a). Males frequently cached mealworms that were offered to them during trials, but females frequently retrieved them. The proportion of mealworms cached by males that were stolen by females showed no consistent trends through time ($r_s = -0.202$, $P > 0.300$); the majority of observations of female cache theft behaviour were distributed within a time period occurring after robin pairs ceased foraging separately, but before males began to feed females at the onset of the breeding season (Fig. 1b). Nuptial feeding began in spring (Fig. 1c), when the proportion of male-handled worms that were fed to females increased through time ($r_s = 0.741$, $P < 0.001$). By mid-spring all mealworms that were acquired by males were fed to females.

Discussion

In early winter, when inter-pair competition is hypothesised to be highest for temperate, territorial birds, NZ robin pairs were very rarely found foraging together, confirming speculation by Powlesland (1980) and Armstrong et al. (2000). Conversely, Steer and Burns

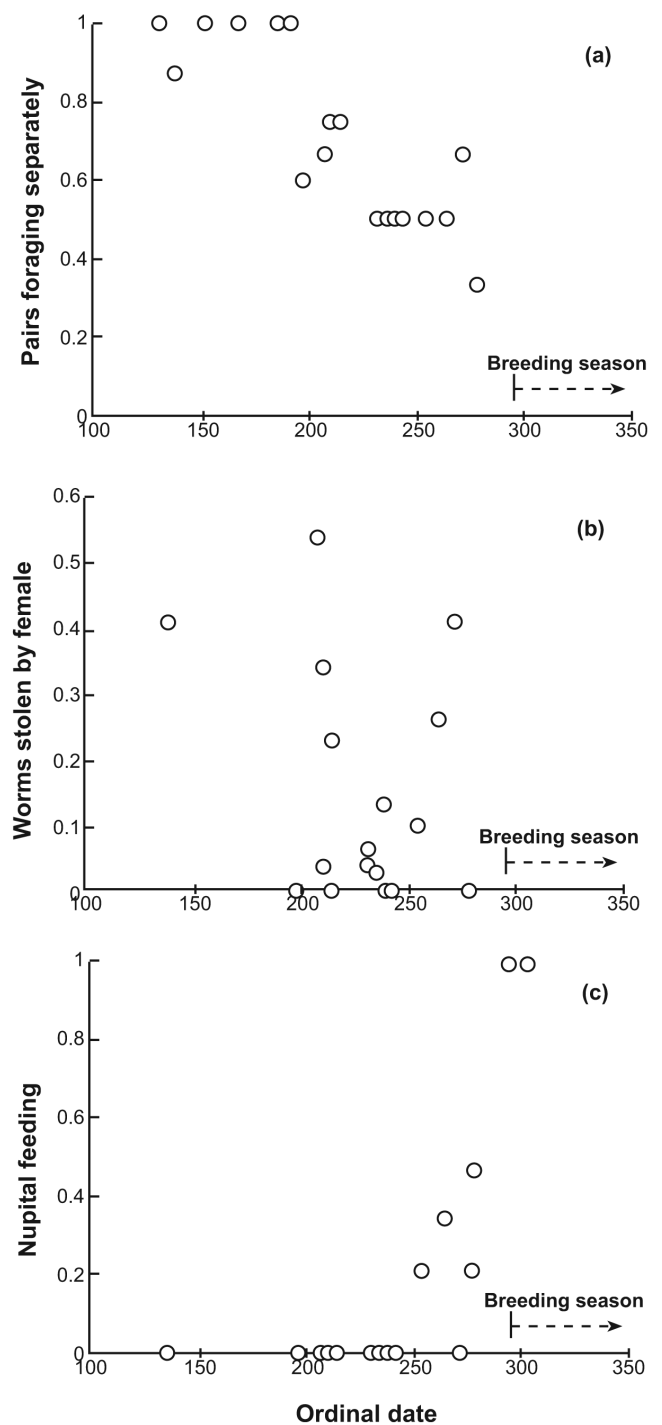


Figure 1. Rates of three behaviours and time: (a) a negative relationship between the proportion of NZ robin pairs observed foraging separately (no. of birds observed alone / total no. of pairs observed each walk) and ordinal date; (b) differences in the proportion of male-cached worms stolen by female NZ robins (no. of worms stolen by females / total no. of male-cached worms per feeding trial) and ordinal date; (c) a positive relationship between the proportion of male-handled worms fed to female (no. of worms fed to female / total no. of worms handled by male, per feeding trial) and ordinal date. Timing of each behaviour within non-breeding season: a, b and c, viewed together.

(2008) remarked that mate-avoidance did not appear to be evident in KWS. However, their trials were conducted over a coarse timescale, in monthly intervals, and they did not test for segregated foraging behaviour. Our finer scale behavioural observations showed that males and females often forage alone in winter, which likely reduces intersexual conflict over food resources. This behaviour begins to subside at the onset of spring, when males and females forage alongside one another more frequently.

Similar seasonal patterns in the foraging behaviour between the sexes have been described in other temperate bird species (Holmes 1986; Sodhi & Paszkowski 1995; Kelly & Wood 1996; Pasinelli 2000). However, segregated foraging has not been described among pairs of territorial birds inhabiting tropical climates (Gradwohl & Greenberg 1984; Gorrell et al. 2005). In New Zealand, spatially segregated foraging patterns in robins likely results from an interaction between a decline in resource availability and the competitive dominance of males (Powlesland 1981; Higgins & Peter 2002; Burns & Steer 2006; Steer & Burns 2008). Alexander et al. (2005) found that almost all aggressive encounters between the sexes were won by males. Therefore, spatially segregated foraging likely originates from females avoiding food pilfering by physically dominant males. An alternative explanation is that the observed spatial separation in winter may be driven by male behaviour, wherein the independent use of space by females results from a lack of male attentiveness. However, our study design did not enable us to determine which member of the robin pair altered its winter foraging behaviour.

Females stole large numbers of worms from male-made caches. Linear trends in the rate of cache theft were not observed within the seasonal period when cache theft was observed. However, the majority of observations of female cache theft behaviour were distributed within a coarser scale time period between when males and females forage separately and when they cooperate during the breeding season. Cache theft by females may be an effective strategy in obtaining food that was originally caught by males, while avoiding direct competition at the food source. Because males frequently pilfer food obtained by females (Alexander et al. 2005; Van Horik & Burns 2007), it may also be an effective way of re-obtaining food that they originally obtained but which was pilfered by males.

Additionally, as the breeding season approaches, an increase in female contact and consequently an increased risk of cache theft may be tolerated by males as a trade-off for indirect benefits of foraging together as a pair. Foraging in close proximity may be a form of mate guarding, to help ensure paternity (Brylawski & Whittingham 2004; Johnsen et al. 2008). Early pair formation has been hypothesised to be beneficial for both males and females. For example, many waterfowl form pairs well in advance of their spring fertile period (Bluhm 1988; Nakamura & Atsumi 2000; Rodway 2007). Burns and Van Horik (2007) speculated that cache theft by females may be tolerated as a form of indirect mate provisioning. Cache theft has not previously been posited as a conflict-avoidance behaviour for pairs who reside on permanent territories. However, in many food-storing animals, males allow females access to their caches during the breeding season. For example, male shrikes (*Lanius excubitor*) store food on their territory that is later consumed by females that nest within their territory, which may therefore be an indirect form of reproductive investment (Yosef & Pinshow 1989, 2005). European nuthatches (*Sitta europaea*) are monogamous, territorial food hoarders and both sexes store food on their winter territories. However, in this instance males and females store seeds in different parts of their territories, which reduces the risk of male–female conflict and results in low rates of cache theft (Hårdling et al. 1995). Our feeding trials in this experiment were designed to resemble conditions experienced by robins in the wild. NZ robins feed upon some of the world's largest invertebrates and robins frequently catch prey that is longer and/or heavier than themselves (Powlesland 1980; Daugherty et al. 1993), such as giant earthworms (Lumbricidae) (Lee 1959), stick insects (Phasmatodea) (Jewell & Brock 2002) and weta (Orthoptera: Anostomatidae) (Gibbs 1998). It is possible that male tolerance of female cache theft may also be partially explained by the superabundance of food presented by such large prey items.

NZ robin females appear to have two behavioural strategies to reduce intersexual conflict on winter territories. In early winter, females seem to avoid competitively dominant males and both sexes are rarely found foraging in close proximity. As the breeding season approaches in spring, females spend more time foraging close to males, and frequently steal male-made caches. Therefore, female NZ robins show a suite of temporally separated behaviours that appear to minimise direct competition with males, which likely reduces conflict between the sexes.

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References

- Alexander L, Duthie C, Fyfe J, Haws Z, Hunt S, Montoya I, Ochoa C, Siva A, Stringer L, Van Horik J, Burns KC 2005. An experimental evaluation of food hoarding by North Island robins (*Petroica australis longipes*). *Notornis* 52: 138–142.
- Arderm SL, Ma W, Ewen JG, Armstrong DP, Lambert DM 1997. Social and sexual monogamy in translocated New Zealand robin populations detected using minisatellite DNA. *Auk* 114: 120–126.
- Armstrong DP, Ewen JG, Dimond WJ, Lovegrove TG, 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.
- Bell BD 1990. Recent avifaunal changes and the history of ornithology in New Zealand. *Acta XX Congressus Internationalis Ornithologici*. Vol. 1. Pp. 193–230.
- Bluhm CK 1988. Temporal patterns of pair formation and reproduction in annual cycles and associated endocrinology in waterfowl. In: Johnston RF ed. *Current Ornithology* 5. New York, Plenum. Pp. 123–185.
- Breed GA, Bowen WD, McMillan JI, Leonard ML 2006. Sexual selection of seasonal foraging habitats in a non-migratory marine mammal. *Proceedings of the Royal Society London B* 273: 2319–2326.
- Brylawski AMZ, Whittingham LA 2004. An experimental study of mate guarding and paternity in house wrens. *Animal Behaviour* 68: 1417–1424.
- Burns KC, Steer J 2006. Dominance rank influences food hoarding in New Zealand Robins *Petroica australis*. *Ibis* 148: 266–272.
- Burns KC, Van Horik J 2007. Sexual differences in food re-caching by New Zealand robins *Petroica australis*. *Journal of Avian Biology* 38: 394–398.
- Carlquist S 1965. *Island life*. New York, Natural History Press.
- Daugherty CH, Gibbs GW, Hitchmough RA 1993. Mega-island or micro-continent? New Zealand and its fauna. *Trends in Ecology and Evolution* 8: 437–442.
- Diamond JM, Veitch CR 1981. Extinctions and introductions in the New Zealand avifauna: cause and effect? *Science* 211 (4481): 499–501.
- Flack JAD 1976. The use of frontal spot and crown feathers in inter- and intraspecific display by the South Island Robin, *Petroica australis australis*. *Notornis* 23: 90–105.
- Gibbs GW 1998. *New Zealand weta*. Auckland, Reed. 71 p.
- Gorrell JV, Ritchison G, Morton ES 2005. Territory size and stability in a sedentary neotropical passerine: is resource partitioning a necessary condition? *Journal of Field Ornithology* 76:

- 395–401.
- Gradwohl JA, Greenberg R 1984. Search behavior of the checker-throated antwren foraging in aerial leaf litter. *Behavioral Ecology and Sociobiology* 15: 281–285.
- Greenberg R, Gradwohl JA 1986. Constant density and stable territoriality in some tropical insectivorous birds. *Oecologia* 69: 618–625.
- Hårdling R, Källander H, Nilsson J-A 1995. Experimental evidence for low intra-pair cache pilfering rates in European nuthatches. *Proceedings of the Royal Society London B* 260: 127–130.
- Higgins PJ, Peter JM eds 2002. *Handbook of Australian, New Zealand and Antarctic birds*. Volume 6: Pardalotes to shrike-thrushes. Victoria, Oxford University Press.
- Hixon MA 1980. Food production and competitor density as the determinants of feeding territory size. *American Naturalist* 115: 510–530.
- Holmes RT 1986. Foraging patterns of forest birds: male-female differences. *Wilson Bulletin* 98: 196–213.
- Jewell T, Brock PD 2002. A review of the New Zealand stick insects: new genera and synonymy, keys, and a catalogue. *Journal of Orthoptera Research* 11: 189–197.
- Johnsen A, Pärn H, Fossøy F, Oddmund K, Laskemoen T, Lifjeld JT 2008. Is female promiscuity constrained by the presence of her social mate? An experiment with bluethroats *Luscinia svecica*. *Behavioral Ecology and Sociobiology* 62: 1761–1767.
- Kelly JP, Wood C 1996. Diurnal, intraseasonal, and intersexual variation in foraging behavior of the Common Yellowthroat. *The Condor* 98: 491–500.
- Lee KE 1959. *The earthworm fauna of New Zealand*. Wellington, Government Printer.
- Lefebvre G, Poulin B, McNeil R 1992. Settlement period and function of long-term territory in tropical mangrove passerines. *The Condor* 94: 83–92.
- McGavin S 2008. A 2008 survey of North Island robins / toutouwai (*Petroica australis longipes*) in part of Karori Wildlife Sanctuary. Wellington, Karori Wildlife Sanctuary.
- Morton ES 1980. The ecological background for the evolution of vocal sounds used in close range. *Acta XVII Congressus Internationalis Ornithologici* Vol. 1. Pp. 737–741.
- Nakamura M, Atsumi T 2000. Adaptive significance of winter pair bond in male pintail, *Anas acuta*. *Journal of Ethology* 18: 127–131.
- Pasinelli G 2000. Sexual dimorphism and foraging niche partitioning in the Middle Spotted Woodpecker *Dendrocopos medius*. *Ibis* 142: 635–644.
- Powlesland RG 1980. Food storing behaviour of the South Island robin. *Mauri Ora* 8: 11–20.
- Powlesland RG 1981. Comparison of time-budgets for mainland and Outer Chetwode Island populations of adult male South Island robins. *New Zealand Journal of Ecology* 4: 98–105.
- Rodway MS 2007. Timing of pairing in waterfowl I: reviewing the data and extending the theory. *Waterbirds* 30: 488–505.
- Rowan MK 1966. Territory as a density-regulating mechanism in some South African birds. *Ostrich Suppl.* 6: 397–408.
- Small DR 2004. Survival, breeding success and habitat selection of North Island robins *Petroica Australis Longipes* translocated to the Karori Wildlife Sanctuary. Unpublished MSc thesis, Victoria University of Wellington, Wellington, New Zealand. 239 p.
- Sodhi NS, Paszkowski CA 1995. Habitat use and foraging behavior of four parulid warblers in a second-growth forest. *Journal of Field Ornithology* 66: 277–288.
- SPSS 2007. *SPSS for Windows Release 16.0.1*. Chicago, SPSS Inc.
- Steer J, Burns KC 2008. Seasonal variation in male-female competition, cooperation and selfish hoarding in a monogamous songbird. *Behavioral Ecology & Sociobiology* 62: 1175–1183.
- Van Horik J, Burns KC 2007. Cache spacing patterns and reciprocal cache theft in New Zealand robins. *Animal Behaviour* 73: 1043–1049.
- Vander Wall SB 1990. *Food hoarding in animals*. Chicago, University of Chicago Press.
- Yosef R, Pinshow B 1989. Cache size in shrikes influences female mate choice and reproductive success. *Auk* 106: 418–421.
- Yosef R, Pinshow B 2005. Impaling in true shrikes (*Laniidae*): A behavioral and ontogenetic perspective. *Behavioural Processes* 69: 363–367.

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