Intraspecific adoption and foster feeding of fledglings in the North Island robin

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Abstract: Intraspecific foster feeding and adoption has rarely been observed in birds, with the exception of waterfowl. In this study, I document for the first time the existence of intraspecific foster feeding and adoption of fledglings by adult passerines with their own young. During a three-year study of the North Island robin (*Petroica longipes*), a species with very low levels of extra-pair paternity, eight fledglings (4% of the fledglings in the population the study years) were fed by adults other than their parents, with four of these being adopted. In cases of foster feeding and adoption in this species: 1) adopted fledglings came from parents with lower feeding rates than the population average; 2) the territories of adopting/foster parents were of higher quality than the fledglings original parents' territories; 3) in all cases the adopting/foster-feeding parent was a male; 4) adoption of a fledgling was associated with a very low survival of the foster parent's own fledglings; 5) the original parents of the adopted fledglings had a higher reproductive output than the general population. Although the frequency of adoption/foster-feeding was very low, the findings suggest that both the original parents and the fledglings may have a fitness payoff from this behaviour with the fledgling most likely being the active participant. Foster parents appear to be victims of this phenomenon, with it reducing their life-time reproductive output. This begs the question of why selection does not act to improve recognition of one's own young. One possibility is that males are trapped in a situation where better discrimination of offspring is more costly than any benefits it may bring. To better understand the complex phenomenon and possible adaptive explanations for adoption, the perspective of all participants, juveniles, original parents and the foster parents, need to be considered.

Keywords: foster parenting; North Island robin; adoption; fledgling; reproductive output; intergenerational conflict; passerine; *Petroica longipes*

Introduction

Foster feeding occurs when young are fed by adults outside of the social family unit. Foster feeding becomes adoption when one of these adults takes over the parental role and feeds the young as if it was their own. Intraspecific foster feeding and adoption is well documented in mammals, but less so in birds with the exception of waterfowl (Riedman, 1982; Eadie and Lyon, 1998). In birds, much of the focus has been on brood parasitic species and the majority of reports and studies have examined interspecific foster feeding and adoption (e.g. Shy, 1982; Sealy and Lorenzana, 1997).

Theories put forward to explain post-hatch foster-parenting are numerous and many have focused on the foster parents. The suggested causes for adults to feed young other than their own are: (1) altruism, where environmental constraints promote co-operation in caring for young (Riedman, 1982); (2) kin selection, when there is a high degree of kinship between foster parent and fostered young (Poole, 1982; Riedman, 1982); (3) situations where the male might be the fledgling's biological parent as a result of extrapair matings (Meek and Robertson, 1991); (4) increased opportunities for fathering offspring with the young's mother in the future due to acquiring her as a new mate and/or by increasing the chances of her re-nesting (Stutchbury and Ogden, 1996); (5) moulding the young into a helper-at-the-nest to increase future breeding success (Heinsohn, 1991; Connor and Curry, 1995); (6) a reproductive error in the fostering parent, e.g. due to high nesting density (Riedman, 1982; Eadie *et al.*, 1988); and (7) a reduced predation risk per chick with an enlarged brood which would increase reproductive success (Eadie *et al.*, 1988), and/or the family becoming more dominant and gaining better access to food (Lepage *et al.*, 1998; Loonen *et al.*, 1999). There are also situations when the original parent might benefit from having their young adopted as a salvage strategy: (1) when rearing habitat is limited and can not be acquired (Eadie *et al.*, 1988); or (2) as an energetic trade-off in the female, when leaving young with others might increase her life-time fitness (Eadie *et al.*, 1988).

By examining the phenomenon from the offspring's perspective, there are times when it is an advantage for the young to leave its parents to be fed or adopted by other adults. There would be an incentive to move if the young: (1) could increase its survival chances in the new family because the original parents were poor food-providers (Kenward *et al.*, 1993; Brown *et al.*, 1995; Roulin, 1999); (2) were fleeing from adverse competition conditions to enter a brood with young that they can compete with more successfully for food (Poole, 1982; Bustamante and Hiraldo, 1990; Morris *et al.*, 1991; Kenward *et al.*, 1993; Roulin, 1999); (3) could increase survival chances from additional feeding (i.e. prolonging the period of parental care) when having difficulty in finding food after independence (Roulin, 1999); (4) would be part of a family in which circumstances offered better protection against predators (Roulin, 1999); or (5) could increase their probability of acquiring a future breeding site (Roulin, 1999).

The negative consequences for the fostering parents taking in another fledgling seem obvious: an increased feeding effort expended on a potentially unrelated juvenile. This could result in a reduction in fitness for the adults because of a decreased survival of their own young (Brown *et al.*, 1995). Seeing it from the offspring's perspective, the risk of the tactic may be low (Poole, 1982; Pierotti *et al.*, 1988; Kenward *et al.*, 1993), though this is not always the case (Brown, 1998; Eadie and Lyon, 1998) as its survival may rely upon finding parents that supply it with enough food. Selection pressures are expected to result in an intergenerational conflict: where young benefit from being foster fed and adopted by non-related adults, while the adults should adapt to avoid foster feeding and adoption if it occurs frequently enough (Pierotti, 1991). While this phenomenon may be an important factor in population dynamics for some species, few studies have been carried out to examine the frequencies and mechanisms behind it.

During a population study of New Zealand's North Island robin (*Petroica longipes*), a small number of fledglings were found to be adopted by paired adult males. This is an unreported phenomenon in this species and the close monitoring of this population provided a good opportunity to study its occurrence. Detailed individual and territorial data provided the opportunity to study foster feeding and adoption in this species and allowed the testing of many of the above-mentioned hypotheses as to its cause.

Methods

The species and study population

The North Island robin is an insectivorous endemic New Zealand passerine (Fleming, 1950). Adults weigh 26–32 g and are weakly dimorphic with females being slightly smaller and having a lighter plumage than males (Higgins and Peter, 2002). The robin is long-lived (12+ years) and sedentary, with dispersal mainly occurring when juveniles move out of their parents' territory to establish their own territories. North Island robins are socially and genetically monogamous (Arndern *et al.*, 1997) with long-term bonds and year round territories (Armstrong *et al.*, 2000). Offspring care is biparental and both one-year-old males and females breed successfully. Robin pairs can raise up to three successful broods of one to three fledglings each per season. Chicks fledge at approximately 17 days after hatching and are reliant on parental feeding for an average of another 29.3 ± 1.4 days (Å. Berggren, unpubl. data). Parents usually divide their feeding effort so that each parent is responsible for feeding a specific fledgling if there is more than one. If three chicks survive to fledging, then one parent will feed two of the fledglings. Initially, fledglings are immobile and must wait for parents to return to them, but after the first week, fledglings begin to follow the parents while begging and start to search for food for themselves. At independence, parents will fly away, peck, chase or attack the fledglings to discourage them. Adults aggressively defend their territories from both other adults and dispersing juveniles (Berggren *et al.* 2004). A small number of dispersing independent juveniles have previously been observed being fed by unpaired males (Armstrong *et al.*, 2000); however, adoption has never been reported. The North Island robin is generally fearless of people and this enables close observations of individual behaviour to be made.

The study population is located on Tiritiri Matangi Island (36°36'S, 174°53'E), a 220-ha island reserve in the Hauraki Gulf, 3.5 km east of Whangaparaoa Peninsula and 28 km north of Auckland. The population is geographically closed; robins are not expected to fly the 3.5 km necessary to reach the adjacent mainland and none have ever been seen there since the reintroduction. Due to the small size of the island and resident nature of the species, greater than 90% of the robins present are detected in any survey (Armstrong and Ewen, 2002). Consequently, survival can be estimated accurately.

Robins were translocated to the island in 1992 and due to ongoing population monitoring over 95% of the birds are individually colour-banded. The population was intensively studied during three breeding seasons from September 2000 to June 2003 when these data were collected. The population had a mean of 30 breeding pairs each year and 198 fledglings were produced during the three years.

Individual data and censuses

Chicks were banded in the nest at 11 ± 0.3 days (mean ± SE) after hatching using a unique combination of one numbered metal band and three coloured plastic bands. At this time they were weighed (± 0.5 g) and had their tarsometatarsus measured (± 0.05 mm). In the breeding seasons of 2000/2001 and 2001/2002, a small pin-feather was taken from chicks for DNA sexing using a standard PCR–RFLP test. All territories on the island were visited at an average of every four days during the breeding season (September–March). A series of surveys was used to obtain data on behaviour and survival (see also Armstrong and Ewen 2002; Berggren *et al.*, 2004); these involved walking in transects through each forest patch searching for robins. The number and length of transects in a patch was related to patch size, with the aim to cover the entire area within the patch. Care was taken to spend an equal amount of time per area to minimize the risk of some areas being more heavily surveyed than others. While walking between fragments, any individuals and their behaviour were also recorded. Additional surveys were carried out every two weeks from the time the first young reached independence (early to late November) until the end of the breeding season; subsequent surveys were undertaken in March, April, July and September. This resulted in a total observation effort of 338 field days for the population. While parental and juvenile feeding behaviour was monitored for all broods, if foster feeding was observed, the active individuals were monitored more frequently. The feeding rates from the adults were calculated for all fledglings as the total number of times the fledgling was fed relative to the number of territory visits; thus, if the fledgling was seen being fed on half the occasions the territory was visited, its feeding rate was 50%. This index of parental provision gave an estimation of feeding-rate ranging between 0–100%. Because surveys involved going through each territory in transects, all fledglings of a pair were equally likely to be observed. Care was taken to not spend time observing some fledglings more than others.

Playback calls were used to aid in the censuses, as a tool to maximise the encounter rate of individuals. Binoculars were always used to avoid any mistakes in identification, and therefore in all observations data on age and sex of the birds were collected. Due to the intense monitoring of the pairs in the population, all broods, the number of chicks produced, hatching and fledging dates, and length of fledgling feeding periods were known for the majority of the pairs during the three years.

The terminology used in studies on foster feeding and adoption is not consistent or clear which reduces the ability to compare findings. In this study I will use the following terms and definitions. Foster feeding was defined as a fledgling being fed by an adult other than its own parent. A fledgling was deemed 'adopted' if it satisfied three criteria: (1) it was foster fed before it gained feeding independence; (2) it remained in the foster parent's territory and was fed as if it was a fledgling from the foster parents' own brood; and (3) it never returned to its original parents. A fledgling was deemed 'post-dependant foster-fed' (PDFF) if it was observed being foster fed after it had gained feeding independence from its original parents.

Approval to band birds was provided by the Department of Conservation. The Department of Conservation gave permission for the research to be done on Department of Conservation Estate.

Territory data

In 1971 the island consisted of pasture and small forest remnants. Since then a revegetation programme has covered large parts of the remainder of the island with regenerating native forest. Utilising knowledge of robin habitat usage, a simple measure of habitat quality was derived from two variables. One variable was calculated from the fact that the robins prefer old forest to regenerating forest, indicating that territories in older forest areas are of higher quality than younger forest areas (Armstrong and Ewen, 2002). Territories in forested areas, where the forest was older than 20 years (forest remnants), were given the value of 1, while territories in young regenerating forest (< 20 years old) were given the value of 0. There is a relatively large area of forest-edge habitat on the island because of forest fragmentation by grasslands and heathlands, both of which appear to be hostile matrix to the robin. These edge habitats may combine a higher predation risk from the interior of the forest by the native owl (*Ninox novaeseelandiae*) (Brown *et al.*, 1998) and from the matrix by the Australasian harrier (*Circus approximans*) (Baker-Gabb, 1981; Gardner, 1998). In addition, edge habitats are more affected by adverse abiotic conditions such as strong winds (Saunders *et al.*, 1991), which are common on Tiritiri Matangi Island. Because of these considerations, a second quality variable was derived. Territories that incorporated the edge areas of forest were classified as being of a lower quality (given a value of 0) than territories away from the edge (given a value of 1). These two variables were summed and gave a score ranging from 0 to 2 for every territory. The distances between territories were calculated from digitised maps of the island and were measured from the centre of the original parents' territory to the centre of the foster parents' territory.

Analyses

Due to the non-normal distribution of the majority of the data, most statistical analyses were carried out using a Mann-Whitney *U* test, where *n*-statistics show sample sizes of the groups. A paired sign test was used to examine differences between body sizes (weight and tarsometatarsal length) and feeding rates (before and after adoption) in adopted fledglings and their old and new siblings. The age of the adopted chicks and their siblings when they were measured (median 9 days), did not differ significantly from the age at measurement of other chicks in the population (median 11 days) to which they were compared (Mann-Whitney U, $Z = 1.64$, $n_1 = 7$, $n_2 = 106$, $P = 0.102$). A two-tailed Fisher's exact test was used to investigate differences between re-nesting frequencies in pairs that had their fledgling adopted and the pairs that adopted one. Sample sizes varied among tests as data could not be obtained for all individuals. Data on means are shown ± 1 SE.

Results

During the three-year study, 149 foster feeding observations from eight fledglings were recorded. Four fledglings were adopted during their normal feeding-dependant period and moved into the territory of the adopting parents. These fledglings never returned to their original parents. The remaining four fledglings were foster fed but were not adopted, and this occurred only after their 29 days of fledgling feeding by their own parents: hereafter called PDFF (post-dependant foster-fed). Fledglings were adopted at a mean age of 38.2 ± 4.1 days old, which is approximately 21 days out of the nest and entering the last quarter of their dependant-feeding period. Of the PDFF fledglings, one fledgling was fed by a foster parent for the equivalent of a second feeding period (35 days) after becoming independent from its own parents. In the other three cases, PDFF fledglings were fed by foster parents in whose territories they resided for more than one observation period, but were only observed being fed on one occasion. The four PDFF fledglings were 71.5 ± 5.9 days old when fed by their foster parents, corresponding to more than twice the length of the normal feeding-dependant period.

Only one fledgling per brood of either original parents or foster parents was adopted or post-dependant foster-fed. One pair had two fledglings adopted—each from a separate nesting attempt—while adoption or foster feeding occurred only once for the other original pairs. One pair adopted a fledgling on two occasions and post-dependant foster-fed a fledgling on one occasion; other pairs post-dependant foster-fed or adopted only once. The PDFF observations occurred during the 2000/2001 and 2001/2002 breeding seasons and the adoptions occurred the 2001/2002 and 2002/2003 breeding seasons. When all occasions were pooled and the total numbers of individuals in the population for all years were used, the yearly frequency of pairs adopting fledglings was 4.4% as was for pairs only foster feeding. This represents 2% of the fledglings being adopted and 2% being post-dependant foster-fed.

The fledglings

Brood size and morphometrics

Of the eight fledglings in this study, three were male, four were female and one was of unknown sex. Of the adopted birds, all came from first broods with a median brood size of (including themselves) 2 fledglings, which was the same size (not including themselves) as the broods they entered. These brood sizes did not significantly differ from brood sizes in the general population (median 2) (Mann-Whitney U test, $Z = 0.41$, $n_1 = 4$, $n_2 = 73$, $P = 0.686$). Once the adopted fledgling was added to the brood of the adopting parents, this raised their median brood size to 3 fledglings and reduced their parent's median brood size to 1 fledgling. Adopted fledglings tended to be smaller as chicks (median: weight 23.0 g, tarsus length 31.6 mm) than other chicks in the population (median: weight 27.0 g, tarsus length 34.6 mm), but not significantly so (weight, Mann-Whitney U, $Z = 1.67$, $n_1 = 3$, $n_2 = 78$, $P = 0.096$, tarsus, Mann-Whitney U, $Z = 1.74$, $n_1 = 3$, $n_2 = 92$, $P = 0.081$). Adopted fledglings were also not significantly different in size when compared to their original siblings (paired sign test, weight, $n = 7$, $P = 0.250$, tarsus length $n = 7$, $P > 0.99$) or their new siblings (paired sign test, weight $n = 8$, $P = 0.250$, tarsus length, $n = 8$, $P = 0.250$). The median age of all foster-fed fledglings relative to their new siblings differed depending on whether they were adopted or post-dependant foster-fed. The adopted fledglings were not of a significantly different age (median 40 days) to their new siblings (median 45 days) (Mann-Whitney U, $U = 6.0$, $n_1 = 4$, $n_2 = 4$, $P = 0.564$); whereas PDFF fledglings were older (median 76 days) than their new siblings (median 41.5 days) (Mann-Whitney U, $U = 0$, $n_1 = 4$, $n_2 = 4$, $P = 0.021$). In all cases when the adopted fledglings left their original parents, their siblings continued to be fed by their parents.

Feeding rates

The PDFF fledglings all came from first broods, and were initially fed by their original parents for a period similar to that of the general population (median 35.5 days vs. 32 days) (Mann-Whitney U, $Z = 1.05$, $n_1 = 4$, $n_2 = 112$, $P = 0.293$). Their ability to elicit a feeding

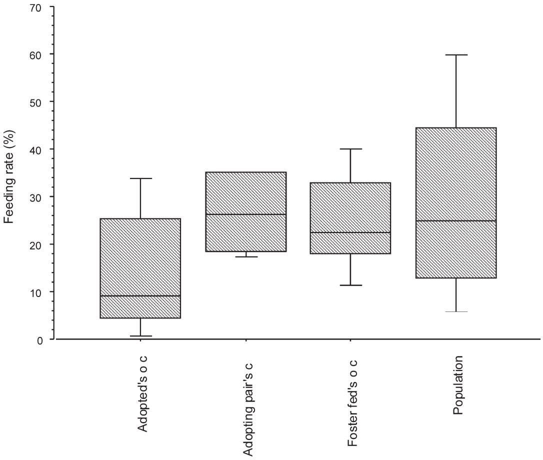

Figure 1. Boxplot of adult feeding rates of fledged young (times fed / times territory visited) for four clutch types; (1) the original clutches (o.c.) of the adopted fledglings (n = 8), (2) adopting pair's clutches (c) (n = 8), (3) PDFF's original clutches (foster fed's o.c.) (n = 8), and (4) the general population (n = 80). The line dividing the boxes represents the median, the end of the boxes represents the first and third quartiles, and the lines (whiskers) represent the extreme values found within 1.5 times the length of the box.

response from an adult resulted in them acquiring extra food when approximately twice the age (median 60.5 days) of that when feeding had generally stopped. Observed adult feeding rates of offspring from territories where a fledgling was adopted from (median 9.1% of the territory visits) were significantly lower than observed feeding rates in the rest of the population (median 25.0% of the territory visits) (Mann-Whitney U, $Z = 2.03$, $n_1 = 7$, $n_2 = 80$, $P = 0.042$) (Fig.1). There were no differences between feeding rates of young from broods in which fledglings later were post-dependant foster-fed (median 22.5%) and fledglings in the general population (25.0%) (Mann-Whitney U test, $Z = 0.54$, $n_1 = 8$, $n_2 = 80$, $P = 0.586$), nor were there any differences between the feeding rates at sites which adopted fledglings (median 26.3%) and the general population (Mann-Whitney U test, $Z = 0.14$, $n_1 = 5$, $n_2 = 80$, $P = 0.859$) (Fig.1.).

Despite the apparent gain in feeding rates for the adopted fledglings as suggested by these data, when the feeding rate of the adopted fledgling in its original brood were compared to its feeding rate in the new brood, no significant difference was found (paired sign test, $n = 4$, $P = 1.0$). Neither did the feeding rate for the adopted's original siblings change after it had left (paired sign test, $n = 3$, $P = 0.5$). With the adoption of the new fledgling, the foster parents' own fledglings suffered a reduced feeding rate (median 0.833 vs. 0.422), but this difference was not significant (paired sign test, $n = 4$, $P = 0.25$).

Territory quality

Though not significant, the average distance an adopted fledgling moved tended to be shorter (median 105 m) than the PDFF fledglings (median 255 m) (Mann-Whitney U, $U = 2.0$, $n_1 = 4$, $n_2 = 4$, $P = 0.081$); in three of the four cases the adopted bird moved to an adjacent territory. The foster-feeding adults' territories were ranked significantly higher in quality (median = 2) than the original parents' territories (median = 1) (Mann-Whitney U, $U = 9.0$, $n_1 = 8$, $n_2 = 8$, $P = 0.009$). Surviving foster-fed fledglings did not establish territories in the same forest patch as their adopted parents. Three of the foster-fed fledglings were seen in territory conflicts with other individuals, but were never seen in aggressive interactions with their foster parents or new siblings.

Survival

Adopted fledglings and their original siblings had a 50% survival rate to the next breeding season. Post-dependant foster-fed fledglings and their original siblings had a survival rate of 25% and 50% respectively. None of the offspring from the parents who adopted or post-dependant foster-fed chicks survived to the following breeding season. When compared to the survival of juveniles in the general population over the same period (35.5%), the survival of fledglings for the original parents (adopted = 50% and PDFF = 37.5%) was not significantly different (adopted, Fisher's exact, $\chi^2 = 0.49$, $n = 175$, $P = 0.484$; PDFF, Fisher's exact, $\chi^2 = 0$, $n = 175$, $P = 1.0$). This is in contrast to the lower survival of fledglings (not including the foster-fed individuals) from parents who adopted or fed post-dependant fledglings that were not their own (0%). For parents that adopted a fledgling, the reduction in survival of their own offspring was on the margin of significance when compared to the general population (Fisher's exact, $\chi^2 = 4.71$, $n = 175$, $P = 0.052$); for parents that fed the PDFF fledglings, their offspring's survival was significantly lower (Fisher's exact, $\chi^2 = 4.14$, $n = 174$, $P = 0.05$).

The parents

In all cases, the adults that engaged in foster feeding were male (see also Armstrong *et al.*, 2000) and had their own fledglings that they were feeding in addition to the new fledgling. In none of the cases was the foster-feeding male closely related (a son, father or sibling) to either of the original parents. The departure of a fledgling meant a 54.2 ± 6.9% reduction in the brood size of the adopted's original parents. The arrival of the new fledgling resulted in a 60.4 ± 8.9%

increase to the size of the brood for the parents adopting the fledgling.

Of the pairs that had a fledgling adopted, three of the four (75%) successfully re-nested; this can be compared to the pairs that adopted the fledgling, where only one of the four (25%) re-nested that year (Fisher's exact, $\chi^2 = 0.5$, $n = 8$, $P = 0.486$). The adopting parents that re-nested had an inter-clutch period of 76 days (an inter-clutch period is defined as the time between the hatching of the first clutch and the hatching of the second clutch). Pairs that had one of their fledglings adopted had a median inter-clutch period of 72 days, which did not differ from the general population (median 58 days) (Mann-Whitney U, $U = 19.0$, $n_1 = 3$, $n_2 = 17$, $P = 0.491$).

Discussion

The frequency of adoption in the North Island robin is similar to the barn owl (*Tyto alba*) (2.7%; Roulin, 1999) and the black kite (*Milvus migrans*) (1.1%; Bustamante and Hiraldo, 1990). Higher figures have been found in the red kite (*Milvus milvus*) where 10.8% of the fledglings were adopted (Bustamante and Hiraldo, 1990), in goldeneye ducks (*Bucephala islandica*) (16% of broods; Eadie and Lyon, 1998), and in the colony living ring-billed gull (*Larus delawarensis*) where 72.3% of the fledglings were adopted (Brown *et al.*, 1995). In spite of the low number of observed foster feeding in this study, its effects are measurable and, thus, have potential fitness consequences for the three groups of individuals involved: the original parents, the foster parents and the fledglings themselves. Selection may be operating in conflict between the three groups and thus to better understand the phenomenon, fitness impacts and the factors driving selection on all three participants must be fully considered.

The fledglings

It is likely that the robin fledgling is the primary active participant in any adoption or foster-feeding situation. Robin fledglings actively follow and beg for food during the feeding-dependant period. This begging can be intense and involves persistent begging calls, chasing and pecking at the parents (pers. obs.). Fledglings may be encouraged to move to another area if their parents are not adequately feeding them, especially if this is combined with the sound of begging fledglings from an adjacent territory (Poole, 1982; Kenward *et al.*, 1993). Even with no extension of the feeding period, switching territory might offer an improved food intake if the adopted fledgling is fed as much as the foster parents' own young (Bustamante and Hiraldo, 1990; Roulin, 1999). In this study, the brood size of the original parents was no larger than average. Thus it is unlikely that the behaviour was caused by abnormally high food competition. However, feeding rates in these territories were lower than normal, with adopted fledglings possibly attempting to improve their food intake by moving to a higher quality territory, and (along with PDFF fledglings) lengthening their feeding period. The new areas might also have provided a lower predation risk for the fledglings, which is vital during this time when the fledgling is young and naïve. However, to be adaptive, these benefits need to outweigh the increased competition they faced from an increased number of siblings. This competition was probably minimal for PDFF fledglings, as they were competing with fledglings that were of a significantly younger age. The extra feedings that PDFF fledglings received did not enhance their survival chances compared to the general population. Possibly, these fledglings were having difficulty in finding food and resorted to begging from adults. Such behaviour might have resulted in the small number of feedings that were recorded.

Because foster-fed juveniles moved into higher quality territories, another possible explanation is that future territory acquisition may be the motivation behind their moving. However, in the next breeding season no adopted fledglings had established themselves in the same forest patch as their adopted parents, indicating that territory acquisition was unlikely to be the driving force behind adoption.

Shifting territories is not without its risks; in some species aggression from the new siblings or parents may be directed at the intruding fledgling (Pierotti *et al.*, 1988; Donazar and Ceballos, 1990; Brown, 1998; Eadie and Lyon, 1998; but see Poole, 1982; Kenward *et al.*, 1993). However, the risks to robin fledglings when moving to new parents appear small, as confrontations with adults can be avoided through retreat (pers. obs.), and if the territory transition is unsuccessful, fledglings can always return to their own parents. As has been observed in the black and red kite (Bustamante and Hiraldo, 1990), adopted and PDFF robin fledglings were never attacked by members of their new family.

The adopting parents

It is interesting that all birds that foster fed and adopted fledglings were male (see also Armstrong *et al.*, 2000). This could be a result of fledglings only begging from males or only males accepting them. Males may be more inclined to feed fledglings from other nests if there is a good chance that they are their own. Adoptions in the black and red kite were between neighbouring nests (Bustamante and Hiraldo, 1990; Stutchbury and Ogden, 1996), suggesting that extra-pair paternity may have been a source of motivation to adopt. In the hooded warbler (*Wilsonia citrina*) this was also considered, though genetic analyses showed that this was not the case (Stutchbury and Ogden, 1996). In the robin, it was a trend that adopted fledglings had lower median distances between the original and foster parents' territories than the PDFF fledglings, with most adoptions occurring between adjacent territories. A probable explanation being that older PDFF juveniles were more mobile and could disperse further than the adopted juveniles. No genetic evidence for extra-pair fertilisations in the North Island robin has been found (Ardern *et al.*, 1997), but occasionally unpaired females have raised broods alone when there were no floater males in the population (Å. Berggren unpubl. data). Considering this lack of significant extra-pair sexual activity and the difficulty facing a male in recognising exactly where a random fledgling came from (not to mention his relationship to it), suggests that any explanation for adoption that relies on genetic relatedness is suspect. Robins have clearly defined territories and defend them vigilantly; nests are not near each other and pairs that end up adopting or feeding new fledglings are breeding themselves. This, combined with the lack of reciprocity resulting from adoption makes the hypothesis of altruism, as is seen in some colonial species, unlikely. Kin selection can similarly be excluded as an explanation as the banding records show that none of the parent birds were closely related. Cases of adoption in this species are unlike those seen in the hooded warbler, where adoption was only observed when the original male in the pair had died or disappeared and a new male came in and fed the fledglings (Stutchbury and Ogden, 1996). Male robins that adopt a fledgling are also breeding, and it is unlikely that they adopt another fledgling to gain breeding experience, as has been suggested in other species. Adoption in the red kite is believed to be a maladaption due to breeding at unnaturally high densities (Bustamante and Hiraldo, 1990). This explanation is not appropriate in this case as the robins on Tiritiri Matangi Island are breeding at similar densities as mainland sites with intensive exotic-predator control (Powlesland *et al.*, 2000), with an ongoing range expansion on the island (new pairs establish in either vacated or new areas). Reduction in predation risk or influencing dominance at feeding sites are not credible explanations because the parents feed each fledgling at different sites within the territory and individuals do not move around in groups searching for food. In species with helpers-at-the-nest caring for unrelated young, it has been suggested that this feeding behaviour is an unselected by-product from the strong selection on birds for parental feeding (Jamieson and Marshall, 1999). Thus, the male robins may be faced with a situation of simply being unable to resist feeding the begging young. The behaviour of a foster feeding adult should be regarded species by species and will be a result of its evolutionary history and the specific selective pressures that are at work (Wright, 1999).

The fledglings of fostering adults that adopted or fed fledglings in addition to their own had a lower than expected survival rate; a correlation also seen in the red kite (Bustamante and Hiraldo, 1990) and the common tern (Morris *et al.*, 1991). The adopting parents' fitness most likely suffered from stretching their resources to accommodate an extra offspring, which negatively impacted on their own fledglings' survival and their ability to re-nest. Such an impact on fitness would be expected to select for adults to recognize their own young and avoid unrelated offspring. However there may be costs associated with reducing the number of false positive errors, the most common being an increase in the number of false negatives – the mistaken rejection of one's own offspring as being foreign. Thus, the possibility needs to be considered that the adults, or at least the males, cannot fine-tune their offspring recognition any further than it is currently set, as this would increase costs (as they reject their own young) in excess of the benefits it would bring (as they reject young not their own).

All of the foster-fed fledglings entered new broods when their new siblings were nearing the end of their feeding period. It is difficult to understand why the adopted fledglings survived better than their new siblings, as they were in the same environment and the new siblings were close to independence. Because the frequency of foster feeding in the study was low, it is difficult to know whether this effect on fledgling survival is a general result, or simply an artifact of the sample size. To fully understand why the foster-fed fledglings were more successful than their new siblings requires further investigation. Despite this uncertainty, there is no evidence to support the notion that the adopting parents benefit in any way; this suggests that they are unwilling participants in this phenomenon.

The original parents

While adoption obviously affects the fledgling and adopting parents, it can also have an impact on the original parents and siblings. In this study, adoption reduced the number of fledglings to feed at the original nest site. This was a probable contributing factor to the improved survival chances of the siblings left behind and the likelihood of re-nesting by the original parents. Any increase in fledgling survival or fledgling output as a result of shifting the burden of offspring care to an unrelated individual would be favoured by selection, assuming that the adult had some measure of control regarding this decision. This suggests that, at least under certain circumstances, there is an incentive to send young out for adoption. This is thought to be an important driving force behind adoption in waterfowl

(Eadie and Lyon, 1998; Åhlund and Andersson, 2001). The active players, as well as the selective forces, still remain to be determined in the North Island robin.

Conclusion

Typically, the frequency of foster feeding and adoption is very low in most bird populations, thus, preventing robust analyses of the behaviour. Despite this difficulty in studying the phenomenon, a number of conclusions can be drawn and more focussed questions posed from a limited data set. It is extremely unlikely that the behaviour in the North Island robin can be explained as an adaptive strategy employed by the adopting parents as their fitness is consistently lower than the general population when they engage in this behaviour. Another consistency identified in this study (and reinforced by Armstrong *et al.*, 2000) is that the phenomenon of foster feeding appears to be limited to the adult male in this species. This raises the question of why males, but not females, are duped into feeding offspring that are not their own. Can females better recognise their offspring because of their longer contact with the chicks in the nest? Or is the difference related to the fact that females, but not males, must disengage from feeding first-brood fledglings and invest in their second brood. Thus, are females better able to resist the persistent begging of juveniles at the time of renesting or are they simply more careful in whom they invest because the time spent feeding fledglings is generally shorter than for males (Armstrong *et al.*, 2000, pers. obs.), thereby making every feeding day invested more valuable?

Regardless of the reasons for the existence of foster feeding and adoption in the North Island robin, this study shows that it is important to consider the selection pressures acting on all three participants involved: the fledglings, as well as the original and adopting parents. It seems likely that in this case, the males who feed other birds' fledglings are the victims of an intergenerational conflict where the fledglings are the active driving force.

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