

The influence of geographic variation in song dialect on post-translocation pair formation in North Island kokako (*Callaeas cinerea wilsoni*)

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Abstract: Following the translocation of North Is kokako (*Callaeas cinerea wilsoni*) to Kapiti I, southern North Is, New Zealand, Department of Conservation staff noted that most pairs were forming between individuals that came from the same source origin. This study investigated whether geographic variation in dialects influenced mate selection and, ultimately, pair formation on Kapiti I. Between Nov 1999 and Mar 2001 songs of male kokako that had paired and were resident at a single site were recorded. In addition, recordings were obtained from the Department of Conservation of birds in the source areas. Analysis of the songs indicated that kokako songs were typical of their areas of origin at the time of translocation and differed from songs of birds from different source areas. Translocated female kokako preferentially chose males whose repertoire was typical of the acoustic environment they experienced before translocation. Song analysis and pair formation of kokako born on Kapiti I indicates that the observed assortative mating was a temporary phenomenon in the years after translocation, which did not continue following juvenile recruitment.

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INTRODUCTION

The translocation of species to islands with fewer or no mammalian predators is an important conservation tool in New Zealand and has been used successfully to save several species, including kakapo (*Strigops habroptilus*), black robin (*Petroica traversi*), and South Is saddleback (*Philesturnus carunculatus carunculatus*) from possible extinction (Bell & Merton 2002). Ongoing monitoring of populations founded by translocation is necessary to determine factors affecting the success of species translocations (Lovegrove 1996). The North Is kokako (*Callaeas cinerea wilsoni*) is a threatened endemic New Zealand wattlebird (family Callaeatidae) listed both nationally and internationally as endangered

(BirdLife International 2000; Hitchmough 2002; Baillie *et al.* 2004). The taxon exists in c.15 isolated populations in the North Is, with the total population estimated to be < 500 pairs (Innes & Flux 1999). It will be necessary to establish viable populations of North Is kokako (hereafter kokako) on predator-free offshore islands to ensure its continued survival in case the mainland populations decline further (Brown & Innes 2004).

Between 1990 and 1997, the New Zealand Department of Conservation (DOC) translocated 32 kokako to Kapiti I to found a new population there. These kokako came from 4 mainland natural populations (Waikato, 5; Manawahe, 4; Taranaki, 2; Mapara, 5), a self-sustaining translocated offshore island population (Little Barrier I, 5) and a captive-rearing facility (National Wildlife Centre, Mount Bruce, 8) (Fig. 1; Brown *et al.* 2004). Since the initial



Fig. 1 Location of source populations from which North Is kokako (*Callaeas cinerea wilsoni*) were translocated to Kapiti I. Note that the population on Little Barrier I was itself established from an earlier translocation from mainland North Is populations.

translocations, monitoring each breeding season (Oct to Mar) revealed that the introduced kokako paired mostly with birds from the same area of origin, which resulted in fewer pairs forming than would have been expected from the number of birds present (unpubl. report, DOC). The assortative pairing suggested that a behavioural factor may have been inhibiting the formation of pairs between birds from different source populations.

Several dialect groups are often present in each mainland kokako population, but because these groups are relatively close, individuals can breed with birds from a neighbouring dialect group (McLeod 1998). Songs can differ significantly, however, between geographically isolated populations (Hughes 1981; McLeod 1998) and isolation-by-distance prevents interbreeding between populations. The translocation of kokako to Kapiti I provided an opportunity to study the role that behaviour might play in the success of translocation attempts and hence of overall conservation strategies. The unique dialects at each area of origin could, potentially, affect pair formation between birds from different populations.

On Kapiti I, kokako from previously isolated populations were artificially placed together in a new forest habitat of relatively limited extent. Several studies suggest that song dialects and geographic variation influence mate choice and can result in positive assortative mating (Baker & Mewaldt 1978; Tomback & Baker 1984; Baker *et al.* 1987; Chilton *et al.* 1990; Casey & Baker 1992), when females mate with males that sing the song type of their natal area, rather than with males singing alien song types (Baker & Mewaldt 1978; Tomback & Baker 1984). For some species, a distant conspecific dialect is no more stimulating than the dialect of a different subspecies (Baker 1983; Baker & Cunningham 1985). We investigated the influence of geographic variation in song dialect on pair formation in the North I kokako, and the resulting short- and long-term implications for the success of translocation management.

METHODS

Study site

Kapiti I (1965 ha, 40°50' S, 174°56' E) is 5.6 km from the southwestern coast of the North Is, New Zealand I and is 10 km long by 2 km wide (Esler 1967; Maclean 1999). Its forested eastern slopes have many ridges and gullies, whereas the western side has steep cliffs of up to 500 m (Maclean 1999). The highest point, Tuteremoana, is 520 m a.s.l. (Esler 1967; Maclean 1999).

Song tape recording

We recorded kokako songs on Kapiti I over 2 (southern) summer breeding seasons: Nov - Mar 1999/2000 and 2000/2001. The optimum time of day for recording song was between 0530 h and 0900 h (NZ Summer Time), on days with fine weather. Recordings were made on a Sony DAT TCD-8 digital recorder using Sony PDP-65C DAT tapes and a Sennheiser K6 directional microphone. On each occasion, the selected territory was entered at 0515 h (before sunrise) and the kokako pair was located by listening for song. When a bird was heard to sing, it was approached and males were identified by their colour band combinations. Recordings were made only of males singing spontaneously; playback was not used to induce singing. Individual kokako were numbered according to origin for identification purposes. Abbreviations for source areas are: KAP, Kapiti I; LBI, Little Barrier I; MAP, Mapara; NWC, National Wildlife Centre; TAR, Taranaki.

Other data

Tape recordings of kokako on Kapiti I made by DOC officers between Nov 1997 and Mar 1999 were made available for this study. We also used recordings made by DOC employees at Mapara and Little Barrier I in 1996, the year birds were transferred from these sites to Kapiti I. These recordings represent, therefore, syllables present

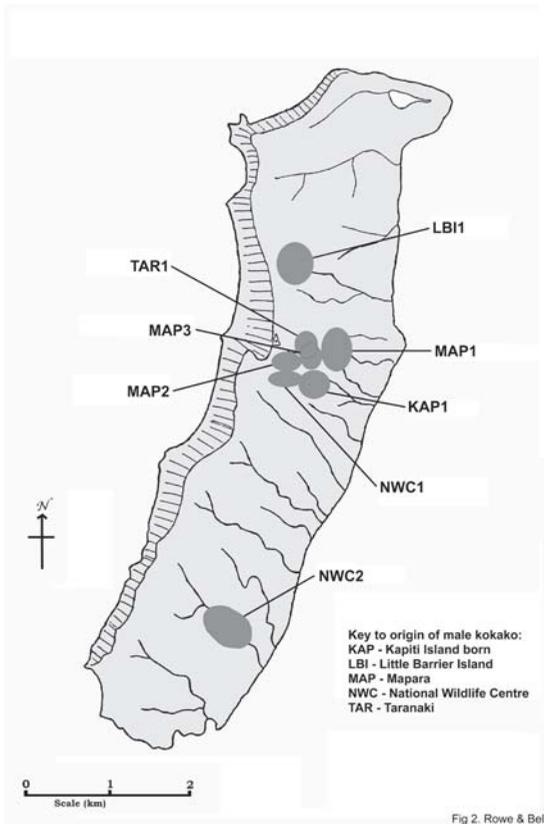


Fig. 2 Location of territories of male North Is kokako (*Callaeas cinerea wilsoni*) whose songs were recorded on Kapiti I between Nov 1999 and Mar 2001. The territories of TAR-1 and MAP-3 were separated temporally and did not overlap as indicated because TAR-1's partner (TAR-2) was removed from the island in May 2000 and TAR-1 remained alone in his territory until it was taken over by MAP-3 in Sep 2000.

at the source sites when the birds were removed. DOC records were searched to determine how long (months) each kokako was present on Kapiti I before it formed a pair, and how many birds from each origin were present in each season.

Song analysis

The same duration (45 min) of continuous song was analysed for each kokako so that results were comparable. Real-time sonograms of songs were produced using Avisoft™ SASLab Pro (Version 3.1b) software. Different syllables from the printed sonograms were assigned individual number codes, which allowed songs to be translated into representative sequences. Each kokako's song was then catalogued, listing the syllables sung and the proportion of each syllable type sung during the 45 min of continuous song.

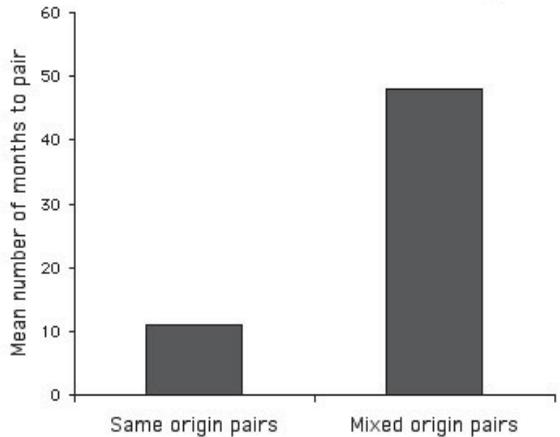


Fig. 3 Mean time (months) that individual North Is kokako (*Callaeas cinerea wilsoni*) translocated from natural populations (and 1 introduced population) were present on Kapiti I before they formed pairs.

All recordings were grouped into 2 recording periods (except for recordings from areas of origin), as not all birds were recorded in every season (between Nov 1997 and Mar 2001). The 1st recording period was Nov 1997 to Mar 1999, which included all DOC recordings taken over the 1997/98 and 1998/99 breeding seasons. The 2nd period was Nov 1999 to Mar 2001, which included all recordings made in this study during the 1999/00 and 2000/01 breeding seasons.

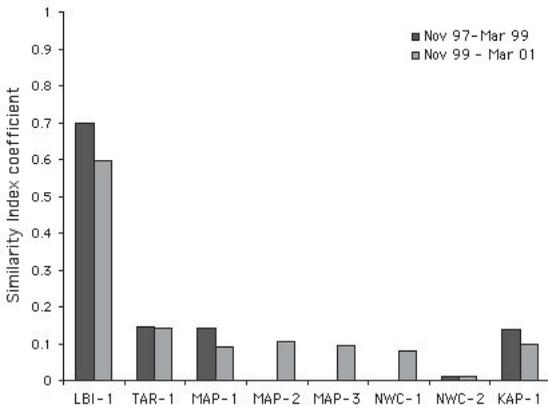
A similarity index (SI) was used to compare songs for similarity of syllable types and proportions, following Hay (1975). This index allowed comparison of 2 sets of data that were divided into similar groups (syllable types), and took into account the size of the respective groups (number of syllables) (Hay 1975). The SI was calculated using:

$$SI = 1 - 0.5 (\sum |a_i - b_i|),$$

where a_i = proportion of i th syllable in songs of bird a , and b_i = proportion of i th syllable in songs of bird b . A SI coefficient of 1 indicated syllable repertoires consisting of all the same syllables, but also sung in the same proportions, whereas 0 indicated that the 2-syllable repertoires shared no syllables.

Similarity index coefficients were used to compare each kokako's syllable repertoire with syllable samples from areas of origin (where applicable), and the syllable repertoires of all other kokako on Kapiti I, over the 2 recording periods. The percentage of syllables shared between individual male kokako and samples from the areas of origin was also determined, using Spearman's rank order coefficient to test for the significance of relationships.

a) Little Barrier Island



b) Mapara

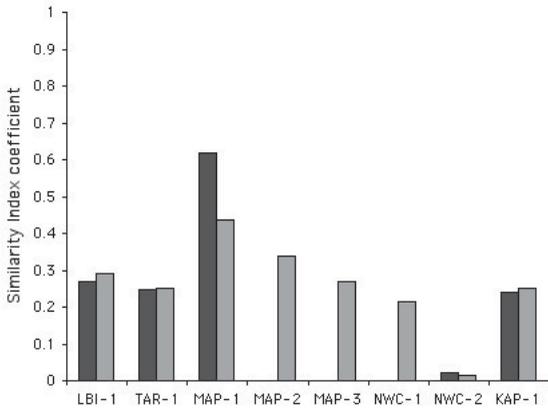


Fig. 5 Similarity index coefficients for the vocal repertoires of 8 male North Is kokako (*Callaeas cinerea wilsoni*) on Kapiti I in comparison with samples of repertoire from 2 areas of origin: (a) Little Barrier I; (b) Mapara.

Kokako on Kapiti I continued to share a high percentage of actual syllables (as opposed to syllable repertoires) with songs recorded where they came from. Over the 2 recording periods, all syllables performed by male LBI-1 were present in recordings made on Little Barrier I in 1996 (the year he was translocated). In comparison, the average percentage of syllables shared by non-LBI translocated kokako and the Little Barrier I samples was 37% and 38% over the 2 recording periods, respectively.

MAP-1 shared 77% (17 of 22 syllables) and 68% (13 of 19 syllables) of his repertoire with syllables present in Mapara recordings over successive recording periods. MAP-2 and MAP-3 shared 73% (11 of 15 syllables) and 53% (8 of 15 syllables) of their syllable repertoires with the range of syllables recorded at Mapara. Translocated kokako from areas

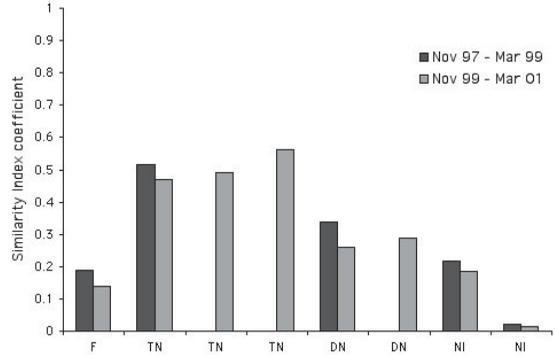


Fig. 6 Similarity index coefficients for the syllable repertoire of North Is kokako (*Callaeas cinerea wilsoni*) KAP-1 in comparison with the syllable repertoires of his father and all other kokako recorded on Kapiti I. F, father; TN, territorial neighbour; DN, distant neighbour; NI, no interaction.

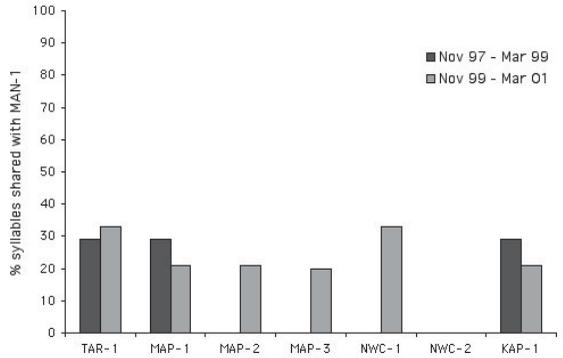


Fig. 7 The percentage of syllables shared by North Is kokako (*Callaeas cinerea wilsoni*) MAN-1 with other kokako on Kapiti I.

other than Mapara shared 38% and 36% of syllables with those in the Mapara syllable samples.

The length of time individual kokako were present on Kapiti I before pairing, was not correlated with neither syllable repertoire size ($r = 0.084$, $P = 0.794$), or the number of syllables an individual sang h^{-1} ($r = -0.429$, $P = 0.260$).

Kapiti I-bred kokako

Pair formation

Four kokako hatched on Kapiti I had paired by Mar 2001 and the origin of their parents and mates are given in Table 2. Two birds could not have paired with a bird from their parent's origin, as no birds from the same origin were left unpaired on Kapiti I by then.

Mate selection by female kokako hatched on Kapiti I

Two female kokako hatched on Kapiti I had paired there at the time of this study. To determine whether

Table 2 Origins of parents and mates of North Is kokako (*Callaeas cinerea wilsoni*) bred on Kapiti I, and whether potential mates from the parental source area were present at time of pairing. KAP, Kapiti I; MAN, Manawahe; NWC, National Wildlife Centre; LBI, Little Barrier I; MAP, Mapara (see Fig. 1 for location of source areas); Unpaired present?, indicates whether unpaired individuals from the parental area of origin were available at time Kapiti I-bred bird paired.

Kapiti I-bred kokako	Origin of parents	Origin of mate	Unpaired present?
KAP-1 ♂	MAN-MAN	NWC	No
KAP-2 ♀	LBI-LBI	NWC	No
KAP-3 ♀	NWC-KAP	MAP	Yes
KAP-4 ♂	NWC-KAP	LBI	Yes

Table 3 Comparative similarity index coefficients and percentage of syllables shared between each female North Is kokako's (*Callaeas cinerea wilsoni*) father and mate on Kapiti I, southern North I, New Zealand.

Kapiti I-bred female	Origin of father	Origin of mate	SI coefficient (father and mate)	% syllables shared by father and mate
KAP-2	LBI	NWC	0.2125	28%
KAP-3	NWC	MAP	0.4248	67%

Table 4 Number and percentage of syllables that male North Is kokako (*Callaeas cinerea wilsoni*) KAP-1 shared with his territorial neighbours and his father on Kapiti I, southern North Is, New Zealand. Song of father of kokako KAP-1 was recorded in 1993.

	Nov 1997 - Mar 1999		Nov 1999 - Mar 2001	
	No.	Percentage	No.	Percentage
Territorial neighbours				
TAR-1	9/14	64	7/19	37
NWC-1	-	-	11/19	58
MAP-3	-	-	11/19	58
Father				
MAN-1	4/14	29	4/119	21

females hatched on Kapiti I had chosen mates that share a high proportion of syllables with their father, we compared the syllable repertoires of their chosen mates and their fathers (Table 3). KAP-2's mate had a syllable repertoire that was dissimilar to that of her father whereas the syllable repertoires of KAP-3's mate and father were moderately similar.

Syllable composition of songs of male kokako bred on Kapiti I
KAP-1's syllable repertoire is more similar to that of his territorial neighbours than that of his father (Fig. 6). Comparison of the percentage of syllables shared in the repertoires of all kokako on Kapiti I and the syllable repertoire of MAN-1 reveals several other kokako share the same amount of syllables with MAN-1 as does KAP-1 in the Nov 1997 to 1999 recording period (Fig 7).

From Nov 1997 to Mar 1999, KAP-1 shared 64% of his repertoire with his territorial neighbour TAR-1 (Table 4). Of the 5 syllables not shared with TAR-1, a distant neighbour sang 1, and 4 were sung by no other kokako on Kapiti I. Table 4 also indicates that

KAP-1 sang 4 syllables that were sung by his father (MAN-1), but these syllables were also sung by 3 other kokako on Kapiti I. One syllable that KAP-1 shared with his father was also sung by TAR-1, which was MAN-1's territorial neighbour on Kapiti I.

KAP-1's repertoire had increased from 14 to 19 syllables by the Nov 2000 - Mar 2001 breeding season. Of the 19 syllables, 9 (47%) were shared with both his territorial neighbours (NWC-1; MAP-3), 2 (10.5%) were shared with only NWC-1, and 2 (10.5%) were shared with only MAP-3. Of the 6 (32%) syllables in KAP-1's repertoire not sung by his territorial neighbours, 2 were sung by distant neighbours, and the remaining 4 were sung by no other bird on Kapiti I, nor by his father.

DISCUSSION

Pair formation of translocated kokako

Few pairs were formed by the North Is kokako in the initial transfer to Kapiti I between 1991 and 1993, which may indicate that something inhibited pair

formation. The kokako translocated from remnant populations during the early 1990s may have been predominantly males, or birds too old to breed (Brown *et al.* 2004). However, kokako from 'healthy' populations (Little Barrier I, Mapara), and captive-reared birds released between 1994 and 1997 also exhibited low levels of pair formation until juvenile recruitment increased towards the end of the study period.

Most of the pairs that formed after the release on Kapiti I were between kokako moved from the same area. The 2 kokako translocated from natural populations that paired with juvenile Kapiti I birds, were the last known birds that had not found mates from their areas of origin. Over all breeding seasons, unpaired male kokako outnumbered unpaired females, which suggests that each female had several potential mates, but these were not necessarily from the same origin. The inability to find a mate from the same area appears to have hindered pair formation until more locally-bred juveniles were available.

Assortative mating according to dialect

Single male kokako can hold territories, which is behaviour typical of male birds that advertise either themselves or their territories to potential mates (Catchpole & Slater 1995). Females, however, are mobile and travel through numerous territories before selecting a mate (Innes & Flux 1999). Theories of sexual selection based on female choice depend on the assumption that females actively choose their mates (Bensch & Hasselquist 1992). Active female choice has been demonstrated in many studies (e.g., Alatalo *et al.* 1986; Dale *et al.* 1990; Bensch & Hasselquist 1992; Bell *et al.* 2004). Dale *et al.* (1990) demonstrated that a female pied flycatcher (*Ficedula hypoleuca*) visits up to 9 males before settling in a territory. Female great reed warblers (*Acrocephalus arundinaceus*) visit on average 6 male territories over 1-3 days before returning to mate with a male that supposedly offered the best breeding potential (Bensch & Hasselquist 1992). Our study suggests that female kokako moved through several territories following translocation and were attracted finally to localized males whose songs contained syllables typical of the songs of birds in their source area.

For dialectal differences to promote assortative mating, female kokako should choose males with vocal repertoires typical of their area of origin and distinct from other males' repertoires (Baptista & Morton 1982). Analysis of kokako repertoires revealed that after establishing territories on Kapiti I, translocated males performed syllables typical of their area of origin, which were dissimilar to the composition of songs of birds in different source areas. Whereas LBI-1 performed a syllable repertoire typical of those in his area of origin, males translocated from Mapara performed syllables less

typical of birds resident in the Mapara area. Three dialectal areas were present at the Mapara Reserve (McLeod 1998) and the syllable samples we used were taken from a variety of kokako throughout the Reserve. Hence, individual Mapara males translocated to Kapiti I would perform only 1 dialect, not all 3, which could account for the lower level of similarity with samples. However, the Little Barrier I population was itself founded recently by birds from mainland sources and hence more limited than in a residual "natural" population. Nevertheless, to a female from Mapara on Kapiti I, any 1 of the 3 Mapara dialects should have been more stimulating than a dialect from elsewhere, because juvenile females may range into other dialect areas during their dispersal period before they mate.

Evidently, differences in dialects allowed translocated females to recognise the familiar songs of males from the same natal area and to prefer them as mates over males performing songs they had not heard before. Studies have suggested that when females are choosing a mate, the dialect of a distant conspecific is no more stimulating than the dialect of a different subspecies (Baker 1983; Baker & Cunningham 1985). The songs a female hears during her early development may be more sexually stimulating than songs she hears when she is older, so that she will mate preferentially with males singing the natal dialect (Baker *et al.* 1981; Casey & Baker 1992). Female kokako that did not recognise, or respond to, dialects they had not heard before may explain the observed assortative mating on Kapiti I.

The distinct dialects in each area may not have been the sole factor influencing female mate choice. As females visit males' territories before selecting a mate, they are thought to base their choice of mate on indicators such as territory quality, or a male's physical characteristic or behaviour (Janetos 1980; Leonard & Zann 1998). Natal dialects may initially attract females, after which they may use other cues such as body size, plumage colour, territory quality, or even other aspects of calls on which to base their final choice. Female pied flycatchers are thought to use repertoire size, song versatility, and plumage colour as cues during mate selection (Lampe & Saetre 1995). Furthermore, where dialects exist in natural kokako populations, neighbouring males would share most syllables (McLeod 1998). Consequently, females in natural populations may use dialects as an initial indicator to ensure they mate within their preferred dialect group, but then make their final decision based on other characteristics that further signal an individual male's quality.

Kapiti I-raised kokako

Pairing history suggests that kokako hatched on Kapiti I showed no preference for the origin of prospective mates, as they have paired with

kokako from mainland populations and captive-reared birds. Of the kokako hatched on Kapiti I that had paired at the time of this study, the 2 females had paired 20 and 22 months, respectively, after fledging and the 2 males paired 12 and 14 months after fledging (DOC unpubl. data). The 2 birds whose parents had been translocated from natural populations were unable to choose a mate from their parent's origin, because all potential mates from their parent's source area had paired already. If there was a preference to pair with a bird singing a song similar to the parental song, kokako bred on Kapiti I should have taken much longer to pair, as did the 2 translocated birds that took 4 years to form pairs, in the absence of suitable potential partners.

Mate selection of females hatched on Kapiti I

Females hatched on Kapiti I did not necessarily choose mates whose songs had a high proportion of syllables in common with those of their fathers. KAP-2 paired with a male from the National Wildlife Centre (NWC-1), yet her father (LBI-1) came from Little Barrier I. Comparison of the syllable repertoires of NWC-1 and LBI-1 revealed that they shared only 28% of syllables, suggesting that KAP-2 had not chosen a mate whose song was similar to her father's song. The father (NWC-1) and mate (MAP-3) of KAP-3 shared 67% of their syllables, indicating that she may have chosen a mate that had a similar syllable repertoire to that sung by her father.

A female's song preference may develop in the 1st few months after fledging. The females translocated to Kapiti I from Mapara were <1 year old (unpubl. data DOC) and they paired with males from Mapara on Kapiti I, which suggests that their preference for that dialect may have already become fixed. That KAP-2 chose a mate whose syllable repertoire was very different to that of her father suggests that female mate choice may be based on songs they become familiar with post-fledging. Before they paired, the juvenile females KAP-2 and KAP-3 were seen in several established territories occupied by paired kokako (unpubl. data DOC), which would have allowed them to become familiar with local songs. The 2 males (MAP-3, NWC-1) they eventually paired with, shared 93% and 72%, respectively, of their syllables with other kokako on Kapiti I and, therefore, sang many syllables that the females reared on Kapiti I would have heard when moving about the island.

Song learning by males hatched on Kapiti I

Male kokako hatched on Kapiti I have not established territories next to the parental territories. We have found no published information on whether male kokako establish territories in alien or natal dialectal areas following dispersal. North Is kokako commonly occur in mixed podocarp-broadleaf

forest dominated by tawa (*Beilschmiedia tawa*), but may also inhabit shrublands and regenerating seral forest associations (Innes & Flux 1999). The territories established on Kapiti I suggest that the kokako have preferentially settled in, and more or less filled, the tawa-dominated forest at the heads of the Kahikatea and Rangatira catchments. Consequently, the observed settlement patterns of juvenile kokako could result from the restricted area of prime habitat on the island.

KAP-1 had not learnt his syllable repertoire from his father, but from his territorial neighbours, as has been reported in other passerines. Male corn buntings (*Miliaria calandra*) and song sparrows (*Melospiza melodia*) learn the song of their nearest neighbour, rather than inheriting or learning the song of their father, indicating that songs are learnt after dispersal (McGregor *et al.* 1988; Nordy *et al.* 1999). The level of similarity between KAP-1's syllable repertoire and his neighbours' repertoires indicated that he had learnt particular syllables from each of his neighbours, rather than selectively learning from 1 neighbour. He also learnt syllables that several neighbours sang, perhaps allowing him to conserve energy by being able to use those syllables to counter-sing with both neighbours. Young song sparrows select songs from 3 or 4 neighbouring adults and they preferentially learn song types that those neighbours share (Beecher *et al.* 1994). KAP-1 also sang 4 unique syllables that were not sung by any other kokako on Kapiti I. These syllables may have developed as a result of mistakes in learning.

Whether KAP-1 learnt any syllables before establishing his territory is not known because no songs of dispersing juveniles were recorded. KAP-1 was seen in the territories of 2 pairs before he established his own territory. Nordy *et al.* (1999) proposed that young song sparrows construct their songs by sampling the repertoires of several older birds in their 1st year. In the following year, they attempt to establish their territory next to those "tutors" and then preferentially learn precisely and perform the song types of tutors with which they continue to interact. Before establishing his territory, it is likely that KAP-1 became familiar with local syllables and then learnt and performed syllables that were useful in counter-singing with neighbours after establishing his territory.

Young birds may gain advantages by learning song types that they will share with their neighbours, as they may be able to defend their territories more efficiently. Experiments have shown that song sparrows selectively use their shared song types in singing interactions with neighbours, which may play a significant role in the establishment and maintenance of territorial relationships between neighbours (Nordy *et al.* 1999). For example, song

sparrows and indigo buntings (*Passerina cyanea*) that share more songs with their neighbours hold their territories longer (Payne 1982; Nordy *et al.* 1999; Beecher *et al.* 2000). Young males that learn their songs from neighbours may also gain reproductive benefits. First year male indigo buntings that mimic the song of an adult neighbour have significantly greater mating and breeding success than indigo buntings that retain an individualistic song (Payne 1982; Payne *et al.* 1988). Male kokako hatched on Kapiti I may therefore have gained advantages in territory defence or reproductive success by learning syllables from neighbouring adults.

As the syllable repertoire of only 1 male kokako hatched on Kapiti I could be analysed with respect to song learning, it is premature to suggest that all kokako learn their songs from neighbours. The only other male hatched on Kapiti I to have established a territory and paired was KAP-4, which was seldom heard to sing, so perhaps he had a very small repertoire. He established a territory in Mar 2000, so was in only his 1st full breeding season when recordings were attempted during the 2000/2001 breeding season. KAP-1 was the only male hatched on Kapiti I that was recorded, 1st in his 2nd breeding season when his repertoire included 14 syllables, and again in his 5th breeding season when his repertoire included 19 syllables. However, the size of KAP-1's repertoire in his 1st breeding season is unknown. Hence, KAP-4 may still have been learning syllables and his singing rate and repertoire size still had the potential to increase. Furthermore, KAP-4 had only 1 territorial neighbour whereas KAP-1 was in the densest population of kokako on Kapiti I. Consequently, KAP-4 may have taken longer to develop his full song because he had less "tutor" song available.

Implications for conservation management

Viable kokako populations on offshore islands are seen as a safeguard against possible extinction at mainland sites. Islands used for bird translocations in New Zealand are generally (and increasingly) free from mammalian predators, which makes them more economic to manage in comparison to large mainland populations for which ongoing, expensive predator control is necessary for their survival (Innes & Flux 1999). It is, therefore, important to ensure that populations translocated to islands are successful and that they yield information likely to increase the success rate of future translocations.

Knowing that a behavioural characteristic, such as dialectal variation, can act as a barrier to pair formation between kokako of different origins is obviously important information in planning future translocations. It seems unlikely that conservation managers will be able to prevent kokako from mating assortatively with birds from their natal population when they have been

moved to a new site. The assortative mating, while it may promote inbreeding in small populations, did result in the rapid formation of pairs followed by successful breeding (unpubl. data DOC). By reassessing the number of kokako sourced from each site, it should be possible to increase the likelihood and speed of pair formation in the years following translocation. The kokako that founded the present Kapiti I population came from 4 natural populations, an established restored population, and a captive-rearing facility. Only 2-7 individuals were taken from each natural population, so very few birds from the same origin were available for pairing. Future translocations would optimise pair formation by translocating 10-15 kokako from each of 2-3 populations to maximise the number of kokako available for pairing from each population. This would lead to faster pair formation and subsequent juvenile recruitment: after that, the progeny of the different original stocks would choose mates from a wider pool and hence limit the extent of in-breeding.

The behaviour of birds hatched on Kapiti I suggested that assortative mating was indeed a temporary phenomenon, an artefact of translocation, which became less important over time. Males hatched on Kapiti I learnt their syllable repertoires from neighbouring adults and similarly the females appeared to develop song preference in the initial years following fledging. This behaviour is important in light of the recommendations made here. Even if more kokako were translocated from each origin, and birds from the same origin paired preferentially, their offspring should show no original-dialect-based preference in pairing. Consequently, once juvenile recruitment increases, pair formation should also increase and any translocated kokako left unpaired will most likely pair with a juvenile, allowing founding populations to become self-sustaining much sooner.

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LITERATURE CITED

Alatalo, R. V.; Lundberg, A.; Glynn, C. 1986. Female pied flycatchers choose territory quality and not male characteristics. *Nature* 323: 152-153.

- Baillie, J.E.M.; Hilton-Taylor, C.; Stuart, S.N. 2004. *2004 IUCN Red List of Threatened Species: A Global Species Assessment*. City IUCN Species Survival Commission.
- Baker, M.C. 1983. The behavioural response of a female Nuttall's white-crowned sparrows to male song of natal and alien dialects. *Behavioural ecology and sociobiology* 12: 309-315.
- Baker, M.C.; Cunningham, M.A. 1985. The biology of bird-song dialects. *The behavioural and brain sciences* 8: 85-133.
- Baker, M.C.; Spittle-Nabors, K.J.; Bradley, D.C. 1981. Early experience determines song dialect responsiveness of female sparrows. *Science* 214: 819-821.
- Baker, M.C.; Mewaldt, L.R. 1978. Song dialects as barriers to dispersal in white-crowned sparrows, *Zonotrichia leucophrys nuttalli*. *Evolution* 32: 712-722.
- Baker, M.C.; Bjerke, T.K.; Lampe, H.U.; Espmark, Y.O. 1987. Sexual responses of female yellowhammers to differences in regional song dialects and repertoire size. *Animal behaviour* 35: 395-401.
- Baptista, L.F.; Morton, M.L. 1982. Song dialects and mate selection in montane white-crowned sparrows. *Auk* 99: 537-547.
- Beecher, M.D.; Campbell, S.E.; Stoddard, P.K. 1994. Correlation of song learning and territory establishment strategies in the song sparrow. *Proceedings of the National Academy of Sciences, USA* 91: 1450-1454.
- Beecher, M.D.; Campbell, S.E.; Nordby, J.C. 2000. Territory tenure in song sparrows is related to song sharing with neighbours, but not to repertoire size. *Animal behaviour* 59: 29-37.
- Bell, B.D.; Borowiec, M.; Lontkowski, J.; Pledger, S. 2004. Short records of marsh warbler (*Acrocephalus palustris*) song provide indices that correlate with nesting success. *Journal für Ornithologie* 145: 8-15.
- Bell, B.D.; Merton, D.V. 2002. Critically endangered bird populations and their management, pp. 105-138 In: Norris, K.; Pain, D.J. (ed.). *Conserving bird biodiversity: General principles and their application*. Cambridge, Cambridge University Press.
- Bensch, S.; Hasselquist, D. 1992. Evidence for female choice in a polygynous warbler. *Animal behaviour* 44: 301-311.
- BirdLife International. 2000. *Threatened birds of the World*. Barcelona and Cambridge, Lynx Edicions.
- Brown, K.; Innes, J. 2004. Kokako Recovery. pp. 97-102 In: Brown, K (ed.). *Restoring Kapiti: Nature's second chance*. Dunedin, Otago University Press. .
- Brown, K.P.; Empson, R.; Gorman, R.; Moorcraft, G. 2004. North Island kokako (*Callaeus cinerea wilsoni*) translocations and establishment on Kapiti Island, New Zealand. *Department of Conservation internal series* 172. Wellington, Department of Conservation ,
- Casey, R.M.; Baker, M.C. 1992. Early social tutoring influences female sexual response in white-crowned sparrows. *Animal behaviour* 44: 983-986.
- Catchpole, C.K.; Slater, P.J.B. 1995. *Bird song: biological themes and variations*. Cambridge, Cambridge University Press.
- Chilton, G.; Lein, M.R.; Baptista, L.F. 1990. Mate choice by female white-crowned sparrows in a mixed dialect population. *Behavioural ecology and sociobiology* 27: 223-227.
- Dale, S.; Amundsen, T.; Lifjeld, J.T.; Slagsvold, T. 1990. Mate sampling behaviour of female pied flycatchers: evidence for active mate choice. *Behavioural ecology and sociobiology* 27: 87-91.
- Esler, A.E. 1967. The vegetation of Kapiti Island. *New Zealand journal of botany* 5: 353-391.
- Hay, R. 1975. The vocal behaviour of the New Zealand robin *Petroica australis* and its local congeners. Unpubl. MSc thesis, University of Auckland, Auckland, New Zealand.
- Heather, B.D.; Robertson, H.A. 2000. *The field guide to the birds of New Zealand*. Auckland, Penguin Books (NZ) Ltd.
- Hitchmough, R. 2002. New Zealand threat classification lists – 2002. *Threatened species occasional publication* 23. Wellington, Department of Conservation, .
- Hughes, A.J. 1981. The vocal dynamics of the North Island kokako. Unpubl. MSc thesis, University of Auckland Auckland, New Zealand.
- Innes, J.; Flux, I. 1999. North Island kokako recovery plan, 1999-2009. *Threatened species recovery plan* 30. Wellington, Department of Conservation.
- Janetos, A.C. 1980. Strategies of female mate choice: a theoretical analysis. *Behavioural ecology and sociobiology* 7: 107-112.
- Lampe, H.M.; Saetre, G. 1995. Female pied flycatchers prefer males with larger song repertoires. *Proceedings of the Royal Society of London, Series B Biological sciences* 262: 163-167.
- Leonard, M.L.; Zanette, L. 1998. Female mate choice and male behaviour in domestic fowl. *Animal behaviour* 56: 1099-1105.
- Lovegrove, T. G. 1996. Island releases of saddlebacks *Philesturnus carunculatus* in New Zealand. *Biological conservation* 77: 151-157.
- McGregor, P.K.; Walford, V.R.; Harper, D.G.C. 1988. Song inheritance and mating in a songbird with local dialects. *Bioacoustics* 1: 107-129.
- McLeod, J. 1998. Song and territorial behaviour of male-male and male-female pairs of North Island kokako. Unpubl. MSc thesis, University of Waikato, Hamilton, New Zealand.
- Macleod, C. 1999. *Kapiti*. Wellington, Whitcombe Press.
- Nordy, J.C.; Campbell, S.E.; Beecher, M.D. 1999. Ecological correlates of song learning in song sparrows. *Behavioural ecology* 10: 287-297.
- Payne, R.B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in indigo buntings. *Ecology* 63: 401-411.
- Payne, R.B.; Payne, L.L.; Doehlert, S.M. 1988. Biological and cultural success of song memes in indigo buntings. *Ecology* 69: 104-117.
- Rowe, S.J. 2001. Song repertoire variation in kokako (*Callaeus cinerea wilsoni*) and saddlebacks (*Philesturnus carunculatus rufusater*) in relation to mate selection, song learning and the development of regional dialects following translocation to Kapiti Island. Unpubl MSc thesis, Victoria University of Wellington, Wellington, New Zealand.
- Tomback, D.F.; Baker, M.C. 1984. Assortative mating by white-crowned sparrows at song dialect boundaries. *Animal behaviour* 32: 465-469.