

Movements and habitat connectivity of New Zealand forest birds: a review of available data

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Published online: 17 August 2022

Abstract: New Zealand's original forested landscape has been greatly fragmented since human arrival, limiting connectivity and habitat quality for forest-dependent fauna. We review the limited available information about forest bird movement behaviour, especially whole-year sociality and movement, natal dispersal, and pasture- and water-gap crossing. Most small insectivores (17 species) and North Island kōkako are territorial year-round, but frugivore-nectivores (three species), raptors (two species), and volant parrots (four species) can be highly mobile, presumably to find scattered food. Natal dispersal is the main behaviour by which birds find new habitats and mates, but natal dispersal distances are unknown for half the species we review. There is limited information about species' ability to cross gaps between forests, and more is known about movement over water than pasture. We classify four species (North Island kōkako, pōpokotea, South Island tīeke, and North Island brown kiwi) as strongly gap limited, defined as currently unknown to cross water or pasture gaps larger than 500 m. A further eight species (mohua, tītītipounamu, pīpīpi, weka, North Island tīeke, kakarūai, toutouwai, and miromiro) are moderately gap-limited, with maximum observed gap-crossing distances of less than 5 km. Pending new data, these twelve species have most need of corridors or translocations to enable them to establish in new, safe, ecosanctuary sites. Habitat connectivity can be increased by strategic planting, but this also risks decreasing populations if birds emigrate from safe to unsafe sites. Many managed ecosanctuaries are too small to accommodate natal dispersal distances expected in continuous forest, so pest control is required at larger scale in the long term to restore natural movement patterns.

Keywords: breeding dispersal, corridor, ecosanctuary, gap-crossing, natal dispersal, translocation

Introduction

In large areas of lowland New Zealand, forest birds can no longer disperse easily through continuous forest to find new habitat and unrelated mates. The New Zealand landscape was transformed by two waves of human colonisation that removed most indigenous forest cover (Walker et al. 2006; Sullivan et al. 2010). Indigenous forest now covers only 24% of New Zealand, compared with 82% at the time of human settlement (Ewers et al. 2006) and fragmentation is continuing (Ausseil et al. 2011; Monks et al. 2019). Since human arrival one-third of all New Zealand birds have become extinct. Extinction has occurred particularly on mainland New Zealand, where 47% (South Island) to 51% (North Island) of Holocene species have been lost (Holdaway et al. 2001). Today, 80% of extant native terrestrial birds are threatened with extinction (Robertson et al. 2021), due primarily to historical forest loss and ongoing pest mammal predation (Innes et al. 2010; Ruffell & Didham 2017).

Much recent conservation effort in New Zealand has focused on reducing mammalian predation, including the use of offshore islands or pest-fenced mainland ecosanctuaries to protect vulnerable species or populations (Pech & Maitland 2016; Innes et al. 2019). New Zealand conservation science has, since the 1990s, been dominated by studies of invasion ecology, crisis conservation, and threatened species management (Sullivan et al. 2010). While this need has been warranted to avert the imminent extinction of more of New Zealand's unique fauna, basic research needed to guide long-term conservation management has received less attention (Perry & McGlone 2021).

Movement, including dispersal, is an important behaviour that allows individual birds to find habitat throughout the year, despite environmental conditions changing by site, season, and year (Newton 1998). Natal dispersal, by which individuals move from where they were raised to where they first attempt to breed, is often the main dispersal type in birds (Baker 1978; Greenwood 1980; Richardson et al. 2015). Natal dispersal is

important to avoid resource competition (Juan et al. 1997), inbreeding (Jamieson et al. 2008; Szulkin & Sheldon 2008), and to locate habitat and mates. Birds may also disperse after translocation (post-release dispersal; Richardson et al. 2015).

High-quality habitat in fragmented landscapes is only useful if birds can reach it (Burge et al. 2017, 2021). Individuals may recolonise unoccupied sites by dispersal from intensively managed ecosanctuaries if the species can make the journey (e.g. Ortiz-Catedral & Brunton 2010; Burge et al. 2021), or by translocation if not (Miskelly & Powlesland 2013; Armstrong et al. 2015). Without connectivity, habitat may remain unoccupied despite other local restoration efforts (Taylor et al. 1993; Gilbert-Norton et al. 2010; Gregory & Beier 2014).

However, connectivity can also be detrimental to populations if natal or post-release dispersal enables translocated birds or their offspring to move from high- to low-quality habitat sites (Parlato & Armstrong 2012, 2013). That is birds may move from source habitat into surrounding sink habitat (Dunning et al. 1992). In New Zealand this is likely to be from pest-managed ecosanctuaries to surrounding unmanaged sites with poor habitat quality, including more introduced pest mammals (Andrews 2007; Bradley et al. 2012). Pest-managed ecosanctuary sites that in New Zealand have mean area c. 700 ha (Innes et al. 2019) may not adequately protect populations of highly mobile species at a landscape level.

Increased success with threatened species management and mammalian pest control now allows New Zealand conservation managers to shift attention towards landscape-level ecosystem restoration (Meurk & Swaffield 2000; Innes et al. 2010; Glen et al. 2013). Habitat connectivity will be vital to ensure that populations can persist long term and individuals can safely move throughout the landscape. Information on bird movements, including home range size, dispersal distances and movement capabilities, is needed to guide pest management, bird translocations, corridor creation, and landscape-scale habitat restoration. Knowing more about the movement of forest birds will also improve understanding of forest seed dispersal and regeneration, resource availability, and bird vulnerability to threatening processes.

Internationally, corridors for diverse fauna and flora have been widely discussed and studied, but few corridor proposals are actually implemented. A review of 162 publications about landscape connectivity from 2000 to 2013 "found no implementation of landscape connectivity proposals generated by the studies (e.g. potential corridors) into real landscape elements to ensure the permanence and functionality of ecosystems" (Correa Ayram et al. 2016). There is also considerable debate about corridor effectiveness (Simberloff et al. 1992; Beier & Noss 1998; Hodgson et al. 2009; Doerr et al. 2011), although a 2010 review (Gilbert-Norton et al. 2010) and other studies (e.g. Overmars et al. 1992; Haddad et al. 2003; Gillies & St Clair 2008) found strong support for corridors enhancing the movement of gap-limited fauna and flora.

Bird dispersal has previously been considered in New Zealand (1) in relation to the ability of birds to recover from population reduction (Spurr 1979), (2) in regard to island biogeography and reserve design (Williams 1981; Hackwell 1982; Diamond 1984; East & Williams 1984;), and only recently (3) as an element of mainland landscape connectivity (Zhang et al. 2021).

Here we review current knowledge of New Zealand forest bird movements relevant to establishing and maintaining populations in both intact and fragmented forest landscapes.

We sought information about bird movement and sociality from all published and grey literature known to us, and from species experts that we contacted. If they exist at all, movement data are typically scarce, and behaviour observed in detailed studies at one or a few sites may differ to that elsewhere. We focus on dispersal events recorded since 1920 because this reflects the existing dispersal potential of New Zealand forest birds following initial forest clearance and nationwide spread of the most serious introduced predators of arboreal forest birds (ship rats *Rattus rattus* and stoats *Mustela erminea*). Definitions of 'forest bird' and of key movement terms (breeding dispersal, dispersal, migration, natal dispersal, post-release dispersal), dispersion terms (dispersion, home range, territory) and landscape ecology terms (connectivity, corridor, gap-crossing, habitat) are provided in Appendix S1 in Supplementary Materials.

Forest birds, and their sociality, dispersion, and movements

We review the limited available movement data for 34 extant forest bird species, of which nineteen (54%) are either threatened with extinction or Naturally Uncommon, and 15 (44%) are Not Threatened (Table 1).

We classed nine of these species as small (< 30 g), 13 as medium-sized (30–175 g) and 12 as large (> 175 g). For each species in each size class, the following accounts summarise social behaviour through a year, because this underpins and explains most bird movement. To convert diverse published home range or territory areas into a standard distance parameter that enables comparison between species, we sometimes calculate home-range diameters assuming they are circular and present these as whole-year range lengths. We also present known data about gap-crossing movements over land or water between forest habitat patches. Sample sizes of observations are invariably small and are presented along with supporting references in the species accounts rather than in Tables 2–4.

Small forest birds

The nine predominately insectivorous or omnivorous species that are small (< 30 g; Table 2) include eight of New Zealand's 16 forest birds that are Not Threatened (Table 1). Tracking these species' movements is difficult because of their small size, as transmitters must weigh < 1 g to not affect individuals excessively. Therefore, detailed movement and dispersal information is scarce.

Tititipounamu / rifleman

Tititipounamu Acanthisitta chloris occupy year-round, loose, rarely defended territories as kinship groups that raise young cooperatively (Sherley 1990; Higgins et al. 2001; Withers 2013). At Kōwhai Bush, Kaikōura (42° 23' S, 173° 37' E), five sub-adults that dispersed between study areas crossed 300+ m of pasture containing small native forest copses; maximum dispersal was 1.7 km (Sherley 1990). Adult territories at various locations were 0.5–2 ha (typical movement 150 m; Higgins et al. 2001). *Tititipounamu* colonised Entry I., Breaksea Sound, Fiordland, which is a minimum 1.03 km water crossing from Resolution I. (Miskelly et al. 2021).

Pīpīwharau / shining cuckoo

Pīpīwharau Chrysococcyx lucidus breed parasitically in

Table 1. Conservation status according to the New Zealand Threat Classification System (NC = Nationally Critical, NE = Nationally Endangered, NV = Nationally Vulnerable, and Inc = Nationally Increasing are categories of Threatened; Dec = Declining, Rec = Recovering, NU = Naturally Uncommon and Rel = Relict are categories of At Risk; NT = Not Threatened; Robertson et al. 2021), size and vegetation use of extant New Zealand mainland forest bird species, in alphabetical order by scientific name. Weight and length data were compiled from www.nzbirdsonline.org.nz (accessed June 2020) and unpublished data from authors. We define small birds as mean weight < 30 g, medium as 30–175 g, large as > 175 g. NI = North Island, SI = South Island, NZ = New Zealand. Vegetation types are exotic forest (E), fragments in agricultural landscapes (F), native forest (N) and urban (U; from www.nzbirdsonline.org.nz, accessed October 2021).

Scientific name	Common name	Status	Weight (g)	Length (cm)	Size class	Vegetation used
<i>Acanthisitta chloris</i>	Tititipounamu, rifleman	NT	6–7	7–9	small	N
<i>Anthornis melanura</i>	Korimako, bellbird	NT	26–34	20	medium	E, F, N, U
<i>Apteryx australis</i> *	Tokoeka, southern brown kiwi	NU	2400–3100	45	large	N
<i>Apteryx maxima</i> *	Roroa, great spotted kiwi	NU	2200–3000	45	large	N
<i>Apteryx mantelli</i> *	Kiwi-nui, NI brown kiwi	Dec	2000–2700	40	large	E, F, N
<i>Apteryx owenii</i> *	Kiwi pukupuku, little spotted kiwi	Inc	1150–1350	30	large	N
<i>Apteryx rowi</i> *	Rowi	NE	1900–2600	40	large	N
<i>Callaeas wilsoni</i>	NI kōkako	Inc	180–280	38	large	N
<i>Chrysococcyx lucidus</i>	Pīpīwharau, shining cuckoo	NT	25	16	small	E, F, N, U
<i>Circus approximans</i>	Kāhu, swamp harrier	NT	650–850	50–60	large	E, F, N, U
<i>Cyanoramphus auriceps</i>	Yellow-crowned kākārīki	Dec	41–51	25	medium	N
<i>Cyanoramphus malherbi</i>	Orange-fronted kākārīki	NC	30–52	19–22	medium	N
<i>Cyanoramphus novaezelandiae</i>	Red-crowned kākārīki	Rel	50–100	25–28	medium	N
<i>Eudynamis taitensis</i>	Koekoeā, long-tailed cuckoo	NV	125	40	medium	N
<i>Falco novaeseelandiae</i>	Kārearea, NZ falcon	R	205–740	40–50	large	E, F, N
<i>Gallirallus australis</i> *	Weka	NT	730–1400	50–60	large	E, F, N, U
<i>Gerygone igata</i>	Riroriro, grey warbler	NT	5.5–6.5	11	small	E, F, N, U
<i>Hemiphaga novaeseelandiae</i>	Kererū	NT	630	50	large	E, F, N, U
<i>Mohoua albicilla</i>	Pōpokotea, whitehead	NT	12–20	15	small	E, N
<i>Mohoua novaeseelandiae</i>	Pīpipi, brown creeper	NT	11–13.5	13	small	E, F, N
<i>Mohoua ochrocephala</i>	Mohua, yellowhead	Dec	25–30	15	small	N
<i>Nestor meridionalis</i>	Kākā	Rec	340–575	34–44	large	N
<i>Ninox novaeseelandiae</i>	Ruru, morepork	NT	175	29	medium	E, F, N, U
<i>Notiomystis cincta</i>	Hihi, stitchbird	NV	24–45	18	medium	N
<i>Petroica australis</i>	Kakaruai, SI robin	Dec	35	18	medium	E, N
<i>Petroica longipes</i>	Toutouwai, NI robin	Dec	26–32	18	medium	E, N
<i>Petroica macrocephala</i>	Miromiro, tomtit	NT	11	13	small	E, N
<i>Philesturnus carunculatus</i>	SI tīeke	Rec	75–85	25	medium	N
<i>Philesturnus rufusater</i>	NI tīeke	Rel	60–90	25	medium	N
<i>Prothemadera novaeseelandiae</i>	Tūi	NT	90–125	30	medium	E, F, N, U
<i>Rhipidura fuliginosa</i>	Pīwakawaka, NZ fantail	NT	8	16	small	E, F, N, U
<i>Strigops habroptila</i> *	Kākāpō	NC	1000–4000	58–64	large	N
<i>Todiramphus sanctus</i>	Kōtare, NZ kingfisher	NT	55	23	medium	E, F, N, U
<i>Zosterops lateralis</i>	Tauhōu, silvereye	NT	13	12	small	E, F, N, U

*Flightless

New Zealand, laying in nests of riroriro and Chatham I. warbler *Gerygone albofrontata*. They are migratory and disperse between overwintering sites in Bismarck Archipelago (New Guinea) and Solomon I. (Higgins 1999), and breeding sites in New Zealand. They are highly mobile over both water and land and cover large distances during their dispersal (5000 km). Natal dispersal distance is unknown.

Riroriro / grey warbler

Riroriro *Gerygone igata* within Kōwhai Bush, Kaikōura, had a mean territory size of 0.68 ha ($n = 34$; whole-year range length 100 m) and a mean natal dispersal of 0.9 km ($n = 17$). Adults were sedentary in territories all year, although birds moved up to 100 m beyond summer ranges in winter outside the breeding season (Gill 1982). Their ability to cross pasture

Table 2. Diet and movement distances of small (< 30 g) New Zealand forest birds based on available studies, reports, and anecdotal observations, as explained in the following species accounts. Diet (fruit = Fr, invertebrates = I, nectar / flowers = N) is shown in order of importance for each taxon. Gap-crossing is the maximum distance of pasture and/or water known to have been crossed. Natal dispersal is mean or maximum juvenile dispersal from parent home range. Whole-year range length is the diameter of adult home ranges when assumed to be circular. Species are listed by Māori and common names in order as per Table 1. NI = North Island, SI = South Island, NZ = New Zealand.

Species	Diet	Gap crossing over land ^L or water ^W (km)	Natal dispersal (km)	Whole-year range length (km)
Tītīpounamu, rifleman	I	0.3 ^L , 1.03 ^W	1.7 (max.)	0.08–0.16
Pīpīwhararoa shining cuckoo	I	> 5000 ^W	unknown	migratory > 5000
Riroriro, grey warbler	I	105 ^W	0.9 (mean)	0.1–0.2
Pōpokotea, whitehead	I, Fr	0.1 ^L	0.65 (max.)	0.22–0.42
Pīpīpi, brown creeper	I, Fr	1.03 ^W	unknown	0.11 (mean)
Mohua, yellowhead	I, Fr	0.86 ^W	unknown	0.28–1.13
Miromiro, tomtit	I, Fr	3.5 ^W	unknown	0.11–0.27
Pīwakawaka, NZ fantail	I, Fr	105 ^W	unknown	0.1–0.21
Tauhou, silveryeye	I, Fr, N	800 ^W	0.16	unknown

gaps is undocumented, but ubiquity across fragmented forest landscapes in New Zealand suggests considerable capability. Riroriro reached Snares Is / Tini Heke from southern Stewart I. / Rakiura (105 km across water) on at least six occasions (Miskelly et al. 2001).

Pōpokotea / whitehead

Pōpokotea *Mohoua albicilla* at high density on Te Hauturu-o-Toi / Little Barrier I. (henceforth Hauturu) bred in small cooperative groups of two to eight individuals in territories as small as 1.3 ha, although year-round home ranges for males and females were 3.8–14.1 ha (Higgins & Peter 2002). In autumn and winter, after breeding, groups have larger home ranges, with a variable flock size up to 30 birds (Heather & Robertson 2015). Pōpokotea are the main lead species in mixed species flocks on Hauturu involving fantails, yellow- and red-crowned kākārīki, and riroriro (McLean et al. 1987). On Hauturu all 26 re-sighted banded young remained within 350 m of their natal site in their first year, and 10 stayed within 200 m of natal areas for up to 40 months, with the maximum dispersal being 650 m after 2–3 years (Higgins & Peter 2002). Winter flock movements may be much larger. Pōpokotea may cross pasture gaps of c. 100 m (KAP, pers. obs.) but are unlikely to cross gaps > 250 m. A translocation of pōpokotea to the Hunua Ranges in 2002, a highly connected large forest site, is assumed to have failed because of high post-release dispersal (T Lovegrove, Auckland Council, pers. comm.).

Pīpīpi / brown creeper

Pīpīpi *Mohoua novaeseelandiae* pairs defend territories all year. At Kōwhai Bush, Kaikōura, pair territories averaged 0.97 ha (s.d. 0.21, $n = 39$; whole-year range length 110 m), and locations changed little between years (Cunningham 1985; Higgins & Peter 2002). Natal dispersal distance is unknown, but in autumn and winter juveniles remain together as sibling groups and may coalesce with other juvenile groups to form large, non-territorial flocks, often associating with tauhou, kākārīki, riroriro and pīwakawaka (Cunningham 1985; Heather & Robertson 2015). Cunningham (1985) describes sub-adult sibling groups that were on average 620 m from their parental territories (range 0–1236 m; $n = 5$). Pīpīpi colonised Entry I., Breaksea Sound, Fiordland, which is a minimum 1.03 km water crossing from Resolution I. (Miskelly et al. 2021).

Mohua / yellowhead

Mohua *Mohoua ochrocephala* pairs, with or without helpers, raise young in 2–7 ha territories during October to January, after which family parties join to form feeding flocks that roam over 60–100 ha, sometimes moving from valley floors to mountainsides (Higgins & Peter 2002). They often lead mixed species feeding flocks, particularly with kākārīki (Higgins & Peter 2002; Heather & Robertson 2015). In Fiordland small flocks of mohua crossed water gaps of 90–300 m between islands, and the largest water crossing was 860 m (Miskelly et al. 2017). Mohua have been recorded on Tāmihau I., 300 m from a source population on Ulva I. (Oppel & Beaven 2004a; Miskelly et al. 2017). Natal dispersal distance is unknown.

Miromiro / tomtit

Breeding adult miromiro *Petroica macrocephala* remain on territories throughout the year, but juveniles and sub-adults may disperse tens of kilometres looking for mates and territories (Powlesland 2013a). A juvenile returned to its territory in the Hūnua Ranges after translocation to Tiritiri Matangi, over 56 km away (Parker et al. 2004). Miromiro are therefore probably strong dispersers, although there is little direct research on their movement (Parker et al. 2004). They colonised Rangitoto I. (3.5 km offshore and 30 km from nearest source); another reached Tiritiri Matangi I. (3.5 km offshore; Anderson 2003); and they colonised Moturoa I., Bay of Islands, 1.4 km offshore (Ralph et al. 2020). Miromiro are frequently encountered at Tāwharanui, most likely dispersers from Tamahunga (7 km straight-line distance), which must cross degraded habitat and multiple gaps (KAP, pers. comm.). Natal dispersal distance is unknown, but birds that reached Rangitoto I. were probably from the Hūnua or Waitākere Ranges 30 km away. Mean territory size in the Ōrongorongo River valley was 5.7 ha ($n = 5$; Brockie 1992) and elsewhere 1.2–4 ha (Higgins & Peter 2002), so with whole-year range length of 114–268 m.

Pīwakawaka / fantail

Breeding adult pīwakawaka *Rhipidura fuliginosa* are strongly territorial in the breeding season and remain on or near their territories outside it, while juveniles sometimes form loose flocks with other species such as pīpīpi, pōpokotea and tauhou (Powlesland 2013b; Heather & Robertson 2015). Movements have been little studied, despite pīwakawaka

being one of New Zealand's commonest birds. One banded individual crossed 150 m between islands in the Noises Is, Hauraki Gulf, and territories on Cuvier I. were at least 100 m across. Pīwakawaka are regarded as migratory in Australia, but generally not in New Zealand (Higgins et al. 2006). Powlesland (1982) monitored over 300 SI pīwakawaka over three breeding seasons at Kōwhai Bush, Kaikōura. Very few of the banded birds were observed again, probably due to predation. Three of 160 nestlings and seven of 88 adults bred within the 250 ha study area the following breeding season, while only three birds were found breeding outside it. Natal dispersal distances are unknown. Pīwakawaka colonised Snares Is / Tini Heke from southern Stewart I. / Rakiura, requiring a water crossing of 105 km (Miskelly & Sagar 2008).

Tauhou / silvereye

Breeding tauhou *Zosterops lateralis* pairs defend territories in the September to February nesting season, but in winter they form flocks that may be highly mobile (Heather & Robertson 2015). Tauhou colonised New Zealand late in the 19th century from Australia and have reached all major island groups, including Kermadec, Chatham, Snares, Auckland, Antipodes, Campbell, and Macquarie Is (maximum distance from New Zealand 1100 km; Diamond 1984), so they cross very large habitat gaps. Banding has verified travel between the South I. and North I. (Armitage 2013): a minimum of 22 km. There are no New Zealand natal dispersal studies of tauhou, one of our commonest birds, but in Australia mean natal dispersal on Heron I. was 160 m (Higgins et al. 2006). There are no published New Zealand accounts of territory size; working with banded silvereyes in Dunedin, Kikkawa (1962) wrote that "Nomadic birds probably moved over 50–100 acres [20–40 ha] while resident birds were restricted to only a few acres" and that "breeding density of silvereyes in the wooded part of Dunedin averaged 1.2 pairs per acre [2.5 pairs per ha] over the seasons 1958–61 (sample size, 20 acres [8 ha])."

Medium-sized forest birds

Nine of the 13 medium-sized forest birds (weighing 30–175 g)

are threatened with extinction. The group includes parakeets, honeyeaters, wattlebirds, and raptors (Table 1), and carnivorous (ruru *Ninox novaeseelandiae*, kōtare *Todiramphus sanctus*), seed-eating (kākāriki spp.), omnivorous (tīeke), and nectivorous (tūi *Prothemadera novaeseelandiae*, korimako *Anthornis melanura*, hihi *Notiomystis cincta*; Table 3) feeding guilds. Some species are frequently translocated and can be tracked more readily than smaller species. Despite this, dispersal information is variable, largely due to the high dispersal capability that has been recorded in many species, and the subsequent high mortality or disappearance of individuals from studies.

Korimako / bellbird

Korimako are territorial in the breeding season but nomadic and non-territorial outside it (Heather & Robertson 2015). On Tiritiri Matangi I. mean territory size for pairs was 201 m² around a central nest (Anderson & Craig 2003) but size will vary with density, and there are no reliable mainland data for either. Banded birds have moved up to 10 km (Sagar 2013). Korimako can be strong dispersers and cross large gaps of both sea and pasture. Adults and juveniles colonised Tāwharanui Open Sanctuary, which is 23 km across ocean from the source site, Hauturu (Brunton et al. 2008; Baillie et al. 2014). Korimako reached Campbell I. from Auckland Is, a 270 km flight over water (Miskelly et al. 2020). Birds translocated to Waiheke and Motuihe Is and Hamilton in 2010 had high post-release dispersal. Fourteen birds at each release ($n = 56$) were fitted with transmitters and monitored for a month. One adult male returned to the source location, Tiritiri Matangi, from the release site in Hamilton (140 km). Birds on average dispersed 6.5 km from release locations, but this varied significantly between sexes (male = 10 km, female = 3 km) and age (adult = 9 km, juvenile = 3 km). Birds released on Motuihe I. regularly crossed water to nearby Motutapu I. (2 km) and Waiheke I. (2.5 km; JI, NF, T Lovegrove, unpub. data). Poor success of all bellbird translocations (Miskelly & Powlesland 2013) can be explained by high dispersal tendencies.

There is no genetic differentiation in korimako across

Table 3. Diet and movement distances of medium size (30–175 g) New Zealand forest birds based on available studies, reports and anecdotal observations, as explained in the following species accounts. Diet (fruit/seed = Fr, invertebrates = I, nectar / flowers = N, vertebrates = V) is shown in order of importance for each taxon. Gap crossing is maximum distance of pasture and/or water known to have been crossed. Natal dispersal is mean or maximum juvenile dispersal from parent home range, where available. Whole-year range length is the diameter of adult home ranges when assumed to be circular. Species are listed by Māori and common names in order as per Table 1. NI = North Island, SI = South Island, NZ = New Zealand.

Species	Diet	Gap crossing over land ^L or water ^W (km)	Natal dispersal (km)	Whole-year range length (km)
Korimako, bellbird	N, I	270 ^W	23	0.05–20
Yellow-crowned kākāriki	Fr, N, I	370 ^W	unknown	0.5–2.5
Orange-fronted kākāriki	Fr, N, I	unknown	unknown	2
Red-crowned kākāriki	Fr, N, I	105 ^W	unknown	0.5–20
Koekoē, long-tailed cuckoo	I, V	> 6000 ^W	unknown	migratory, > 6000
Ruru, morepork	I, V	105 ^W	1 (mean)	0.21–0.31
Hihi, stitchbird	N, Fr, I	0.1–0.3 ^L , 20 ^W	0.9–1.7	3–4
Kakaruai, SI robin	I, Fr	1.7 ^W	4 (max.)	0.05–0.25
Toutouwai, NI robin	I, Fr	0.11 ^{LJ} , 3.5 ^W	20 (max.)	0.05–0.25
NI tīeke, saddleback	I, Fr, N	0.4 ^L , 1.3 ^W	0.8 (mean)	0.02–0.22
SI tīeke, saddleback	I, Fr, N	0.16 ^W	unknown	0.15–0.32
Tūi	N, Fr, I	20 ^L , 105 ^W	1.5 (max.)	5–35
Kōtare, NZ kingfisher	I, V	800 ^W	unknown	unknown

Cook Strait (22 km; Baillie et al. 2014), suggesting that birds frequently move between North I. and South I. Most long-distance dispersal is possibly by juveniles, with flocks of young birds arriving at Hauraki Gulf locations (Baillie et al. 2014). Although normally non-migratory, they have been observed foraging “tens of kilometres” from their breeding sites, especially in winter (Baillie et al. 2014).

Only 11 resightings of 475 korimako banded in Dunedin during 2009–2020 were > 1 km away from the banding site; maximum reported distance was 1.8 km (M Efford, pers. comm.).

Yellow-crowned kākārīki

Yellow-crowned kākārīki *Cyanoramphus auriceps* are considered resident in forests where they occur, but their seasonal movements are little known (Higgins 1999). There is possibly seasonal migration, with reports of large flocks invading lowland areas (Elliott et al. 1996), often over large distances, such as the width of the Canterbury Plains following mast events (T Greene, DOC, pers. comm.). In the Eglinton Valley males did not occupy small, well-defined home ranges when nesting. Of 21 radio-tracked male birds in the breeding season in Fiordland, one moved < 1 km, eight moved 1–2 km, and five moved > 2 km (Elliott et al. 1996). Ranges steadily increased with time, suggesting that males either have large home ranges or undertake regular random dispersal. All birds monitored only dispersed through forest (Elliott et al. 1996), and birds monitored on Hauturu also kept strongly to forest (Greene 1998), suggesting limited gap crossing. However, there have been several records of yellow-crowned kākārīki on the mainland near Mana I. (Wellington, where they were released in 2004), requiring a minimum water crossing of 2.5 km (records in eBird). Also, they reached Auckland Is 370 km offshore (T Greene, DOC, pers. comm.). Natal dispersal distance is unknown. Two fledglings observed in a Fiordland study were highly mobile and dispersed rapidly from the nest area (Elliott et al. 1996).

Orange-fronted kākārīki

Very little is known about the breeding and movement ecology of orange-fronted kākārīki *Cyanoramphus malherbi* (Kearvell 2002; Heather & Robertson 2015; Kearvell & Legault 2017). They were once widespread in the North and South Is (Heather & Robertson 2015), but are now highly restricted, occurring in only four beech forest valleys in the South I. Within this restricted area birds are distributed patchily, possibly suggesting low dispersal and gap-crossing ability. Banded individuals have been observed at artificial feeding sites c. 2 km apart, and two banded birds released into the south branch of the Hurunui were observed in the adjacent Poulter Valley, > 15 km away (post-release dispersal; T Greene, DOC, pers. comm.).

Red-crowned kākārīki

Red-crowned kākārīki *Cyanoramphus novaeseelandiae* pairs “remain within fairly distinct areas before and during breeding season” (Higgins 1999). They defend the area around their nests in the breeding season (October to January) and form mobile but not migratory small flocks outside this time (Heather & Robertson 2015). They can cross > 100 km of ocean (Greene 2013), and colonised the Chathams (645 km offshore) and other very remote islands (T Greene, DOC, pers. comm.). They have been recorded from the Snares Is / Tini Heke, which are 105 km from the nearest source population on islands off southern Stewart I. (Miskelly et al. 2001). One bird translocated

65 km to Motuihe I. from Hauturu returned within 50 days (Ortiz-Catedral 2010), and others were reported in Torbay and Glenfield, Auckland, 20–25 km from the source Tiritiri Matangi I. (Spurr 2012). They are “commonly seen moving about island archipelagos such as Mokohinau and Mercury particularly when flax is beginning to flower” (T Greene, DOC, pers. comm.). When flying over land they “seem to like dropping into cover if [avian] predators are near” (L Ortiz-Catedral, Massey University, pers. comm.). Natal dispersal distances of juveniles are unknown but subadults radio-tracked for 6 months from pest-fenced Zealandia ecosanctuary dispersed on average 1.34 km (males, range 0.15–3.95 km) or 0.63 km (females, range 0.18–1.33 km; Irwin et al. 2021). In a rare documentation of breeding dispersal, monogamous red-crowned kākārīki pairs at Zealandia moved on average 75 m ($n = 122$) between clutches, while divorced males moved 161 m ($n = 19$) and divorced females 62 m ($n = 30$; Irwin 2017).

Koekoeā / long-tailed cuckoo

Koekoeā *Eudynamis taitensis* breed only in New Zealand but overwinter up to 6000 km away on Pacific islands from Micronesia to French Polynesia (Gill & Hauber 2012). Failure to colonise sites such as Tiritiri Matangi I. and Zealandia where pōpokotea / whitehead have been successfully translocated suggests strong natal philopatry (Gill 2017).

Ruru / morepork

Ruru strongly defend territories of 3.5 to 7.8 ha (whole-year range length 210–315 m; Imboden 1975; Stephenson 1998; Seaton & Hyde 2013). Four sub-adults monitored during natal dispersal on Mokoia I. moved 500–1500 m and could not have moved further than that without leaving the island (Stephenson & Minot 2006). Maximum movements of ruru across pasture or water are unknown. They inhabit exotic and native forest and shrubland patches, including in farmland with shelterbelts, and in urban areas with parks and gardens (Higgins 1999). They have been recorded from the Snares Is / Tini Heke, which are 105 km from the nearest source population on islands off southern Stewart I. / Rakiura (Miskelly et al. 2001).

Hihi / stitchbird

Hihi occupy territories only during the breeding season, when adults chase conspecifics and other birds away from the nest site. Otherwise they are “...quite nomadic, travelling several kilometres in a day between good feeding sites” (Heather & Robertson 2015). On Kapiti I. hihi ranged widely (3–4 km) between feeding sites, especially along streams (Higgins et al. 2001). At Maungatautari and Ark in the Park ecosanctuaries, hihi crossed pasture gaps up to 100 m (Richardson et al. 2015). However, at Bushy Park / Tarapurui, near Whanganui, there is no evidence of hihi crossing pasture gaps of 90–300 m to reach adjacent forest fragments, and the 40 translocated birds, which were monitored for 6 weeks using radio telemetry, all stayed within the sanctuary. Since birds were reintroduced to Shakespear Regional Park in 2020, banded birds have been observed in the surrounding suburban landscape, including one at Little Manly Beach 6 km away, which would involve dispersing through relatively modified habitat. Mean natal dispersal at Maungatautari was 1.75 km for males and 0.88 km for females (Richardson et al. 2017). Over the year hihi “ranged all over” 135 ha Mokoia I. (maximum 1500 m across; Higgins et al. 2001), but they have small breeding territories. Breeding territories at Maungatautari are also small, with nests of some adjacent females 200–400 m apart (K Richardson, Massey University, pers. comm.).

Because of their likely high vulnerability to exotic predators and confinement to isolated island refuges, there are few data on hihi gap crossing. A hihi observed at Tāwharanui c. 2007 most likely came from Hauturu, requiring a 20 km ocean crossing (KAP, unpub. data). However, there have been no confirmed sightings of hihi crossing to the mainland from reintroduced populations on Tiritiri Matangi I. (3.5 km), Kapiti I. (5 km) or Mokoia I. (2.1 km). Based on these observations, and the fact that hihi have relatively well-developed wings, they may have reasonable dispersal capabilities even though dispersal may be relatively rare.

Kakaruai / South Island robin

Breeding adult kakaruai *Petroica australis* are territorial all year round, especially in the July to January breeding season (Heather & Robertson 2015). Territories were 1–5 ha at Kōwhai Bush, Kaikōura, where density was low, but 0.2–0.6 ha in dense island populations (Higgins & Peter 2002). Territories are 0.2–5 ha in area meaning whole-year range length of c. 50–250 m. Maximum natal dispersal at Kōwhai Bush, Kaikōura was 4 km (Flack 1973) and one juvenile Stewart I. robin (*Petroica australis rakiura*, a different subspecies) dispersed up to 16 km from its natal territory (Opell & Beaven 2004b). Kakaruai at Kōwhai Bush were “reluctant to cross even 100 m of open ground” (Flack 1979), but birds translocated to Anchor I., Dusky Sound, crossed water gaps > 1.4 km, recolonising 30 other islands within 15 years (Miskelly et al. 2017). Kakaruai in the Marlborough Sounds and Stewart I. / Rakiura have dispersed up to 1.7 km across water (Miskelly et al. 2017).

Toutouwai / North Island robin

Breeding adult toutouwai *Petroica longipes*, especially males, are territorial all year round, although juveniles are more mobile (Heather & Robertson 2015). In dense island or sanctuary populations there may be 4–6 territories per ha, but 0.2–1 elsewhere. Radio-tracked juveniles from forest fragments in the King Country preferred to disperse through woody vegetation and were unlikely to cross gaps between forest cover > 110 m (Richard & Armstrong 2010a); however, crosses of c. 300 m were known to occur (DPA, unpub. data). On Tiritiri Matangi I., dispersing juveniles moved readily through low, regenerating vegetation unsuitable for holding territories (Armstrong & Ewen 2002; Wittern & Berggren 2007). Juveniles dispersed up to 20 km in the King Country (Richard & Armstrong 2010b), and offspring of translocated toutouwai dispersing from Wenderholm Regional Park established two populations 15 km away (Andrews 2007; Richardson et al. 2015). A juvenile from Paengaroa Reserve near Taihape moved 8–14 km from its natal territory (Raeburn 2001). Adults rarely disperse from their territories once established, but they may do so to find mates. An adult male toutouwai from Tiritiri Matangi moved to Shakespear Regional Park, requiring a 3.5 km water crossing, but this is the only such observation despite toutouwai being banded on Tiritiri Matangi for 26 years (DPA, unpub. data).

North Island tīeke / North Island saddleback

Paired adult NI tīeke *Philesturnus rufusater* defend a territory throughout the year and from year to year, in which they do most of their foraging (Higgins et al. 2006). They are generally considered to have limited dispersal ability, are sedentary, and form territories whose size varies with density, from 0.03 to 4 ha (whole-year range length 20–225 m; Lovegrove 1996; Higgins et al. 2006). On the mainland, tīeke have not been recorded crossing a 90 m pasture gap to adjacent forest

fragments at Bushy Park / Tarapurui Forest Sanctuary. In the Hauraki Gulf, tīeke naturally colonised Coppermine I. from Whatupuke I. (150 m), and one individual was seen on Middle Stack I. (250 m from Lady Alice and Whatupuke I; Newman 1980). On Kapiti I. one locally bred juvenile dispersed up to 3 km, but eight of nine settled within 1 km of the core area of their natal territories (T Lovegrove, pers. comm.). Three juveniles dispersed > 1.6 km from the nearest breeding pairs at Tāwharanui (KAP, unpub. data). Following the translocation of tīeke to Motuihe I. in 2005, a single bird was sighted multiple times on Waiheke I. (2.5 km away, but with small Crusoe I. located halfway) before disappearing (ZLS, unpub. data).

One of the few studies that has tracked NI tīeke with transmitters was part of a translocation of wild-caught birds from Cuvier I. to Boundary Stream Mainland Island in 2006 (Sullivan 2006). From the 10 birds tracked, mean daily dispersal was 30 m, with significant differences between adult birds (42 m) and juvenile birds (16 m). Most pairs established territories within 307 m of the release location, and most territories were within calling distance of a neighbouring pair. The largest dispersal recorded was 1952 m, for a juvenile female. One individual crossed a 400 m pasture gap.

South Island tīeke / South Island saddleback

SI tīeke *Philesturnus carunculatus* defend breeding territories year-round (Heather & Robertson 2015). Territory size was 1.9–8.8 ha on 59 ha Motuara I. (whole-year range length 155–320 m; Pierre 1999). The longest water gap crossed by SI tīeke was where two birds flew 160 m from Erin I. to the easternmost of the Doubtful Islands in Lake Te Anau in 2003–2004, and there are several other observations of SI tīeke crossing water gaps up to 100 m between islands in Fiordland and off Stewart I. / Rakiura (Miskelly et al. 2017). SI tīeke may have strong breeding dispersal tendencies, as higher mortality in monitored birds has been observed at the start of the breeding season (Masuda & Jamieson 2012), which may be due to birds dispersing out of managed sanctuaries to find mates. Following translocation, SI tīeke dispersed widely across Motuara I., consistent with evidence from NI tīeke that post-release dispersal in connected habitats is high (Pierre 1999). We found no data on natal dispersal.

Tūi

During the breeding season, tūi pairs establish breeding territories but aggressively defend only the immediate vicinity of the nest and feeding sites. They are highly mobile and move as family groups 5–35 km in the winter when not breeding to access scattered nectar and fruit sources, including across pasture (Bergquist 1985, 1989; Stewart & Craig 1985; O'Connor 2006; Fitzgerald et al. 2021). Tūi form small flocks at high-density sites (e.g. Tiritiri Matangi, Kapiti I). Small flocks fly from Kapiti I. to the mainland (5 km), and from Hen I. to the mainland (12 km; KAP, pers. obs.). Tūi established themselves in Seatoun, Wellington, 8 km from a source population in the Karori / Zealandia wildlife sanctuary (Bell 2008), and colonised Hamilton City from forest fragments at least 10 km away (Fitzgerald et al. 2019). There were 769 re-sightings of 596 tūi banded in Dunedin during 2009–2020 that were > 1 km away from the banding site; maximum distances moved were 105 km southwards and 110 km northwards (M Efford, pers. comm.).

Maximum natal dispersal distance from six banded young in Auckland was 1.5 km (Bergquist 1985), but it can presumably be much larger. A juvenile tūi was recorded from

the Snares Is / Tini Heke, which are 105 km from the nearest source population on islands off southern Stewart I. / Rakiura (Miskelly et al. 2001).

Kōtare / kingfisher

Kōtare are said to be an “altitudinal migrant in New Zealand, moving to coast during winter” (Higgins 1999), based on surveys rather than marked birds (Taylor 1966; Ralph & Ralph 1977). Kingfishers also left the Ōrongorongo Valley near Wellington in winter, probably due to changes in food availability, and one bird banded there was found dead 11 km away 4 months later at Seatoun, across Wellington Harbour (Fitzgerald et al. 1986). Kingfishers breed as solitary territorial pairs and may disperse singly or in flocks outside this period (Higgins 1999). Territory size, natal dispersal distance, and typical whole-year movements in New Zealand are unknown. There are at least five records of kingfishers from the Chatham Islands, which are 800 km east of mainland New Zealand (Miskelly et al. 2006, 2019).

Large forest birds

Twelve species are large, weighing > 175 g, including many iconic species such as kiwi and kākāpō. New Zealand’s large forest birds are the most threatened and studied, with 9 out of 12 species classed as At Risk or Threatened (Table 1). Birds of this size, which are often flightless, can support larger tracking devices, but their rarity means that many aspects of natural dispersal patterns and movement ecology are uncertain. Most currently available dispersal information is limited to isolated populations in small sites and to post-release dispersal.

Tokoeka / South Island brown kiwi

Genetic analysis has revealed up to four distinct geographical forms of tokoeka *Apteryx australis*, from Haast, north Fiordland, south Fiordland and Stewart I. / Rakiura (Weir et al. 2016). While many aspects of their ecology are still unknown, all tokoeka occupy defended, non-overlapping territories (Marchant & Higgins 1990; Heather & Robertson 2015). Territories of Fiordland tokoeka average about 51 ha (Edmonds 2015; whole-year range length 800 m) and of Stewart I. / Rakiura tokoeka (Chew Tobacco Bay) averaged 5–6 ha (Marchant & Higgins 1990; whole-year range length 252–276 m). Chicks of Fiordland and Stewart I. / Rakiura tokoeka frequently remain in their natal territories to assist adults with raising subsequent broods. Dispersing Murchison Mountains sub-adults travelled at least 5 km after fledging (Edmonds 2015).

Roroa / great spotted kiwi

Breeding pairs of roroa *Apteryx maxima* occupy and defend territories all year round (McLennan & McCann 1991). In the Saxon River, northwest Nelson, territories averaged 23 ha ($n = 9$, range 10–42 ha; whole-year range length 357–722 m), and Kahurangi Point pairs ranged up to 40 ha ($n = 7$, McLennan & McCann 1991). Radio-tracking 10 birds in Hurunui (6000 ha) found nightly movement of 488–1701 m, with most birds moving 1050–1250 m in a single night. Mean home range area of adult roroa was 29.3 ha, range 19.6–35.4 ha (Keye et al. 2011; mean whole-year range length 541 m). In this study, a sub-adult female was observed dispersing 2 km from her original location to establish a new home range. Post-translocation monitoring of 44 roroa in Kahurangi National Park showed birds dispersed for 9–878 days before settling up to 9.8 km away from the release site, and mean annual home

ranges varied from 26 to 126 ha (Toy & Toy 2020).

Kiwi pukupuku / little spotted kiwi

On Kapiti I. where little spotted kiwi *Apteryx owenii* are at high density, “adults probably occupy the same 2–3 ha territory throughout their lives” (Marchant & Higgins 1990). On Red Mercury I., at much lower density, 11 radio-tracked pairs had an average territory size of 20 ha (range lengths 500–920 m; Robertson et al. 1993). We found no estimates of natal dispersal and pasture gap-crossing distances.

Kiwi-nui / North Island brown kiwi

North Island brown kiwi *Apteryx mantelli* routinely inhabit and move across rough pasture, especially in Northland, where forest fragments are numerous. In one Northland radio-tracking study, 83% of 23 monitored kiwi used forest remnants scattered over farmland (Potter 1990). The maximum distance walked by kiwi between forest remnants was 330 m, but movements up to 1.2 km were made using remnants as stepping stones. Juveniles disperse up to 22 km, and territories are 5–92 ha (whole-year range length 252–1082 m), depending on density (Basse & McLennan 2003; Miles et al. 1997; Robertson 2013). Young dispersed 0.5–2 km from the nest at Coromandel (Forbes 2009); minimum mean dispersal at Lake Waikaremoana was 5.2 km (Basse & McLennan 2003). Most long-distance dispersal occurs when birds are sub-adult (9 months).

Rowi

Very little is known about the movement ecology of rowi *Apteryx rowi*, which have a small population in a restricted distribution (Ōkārito) but are locally common there. Ōkārito is bordered by the Southern Alps to the east and wide braided river systems to the north and south. While kiwi in general have high dispersal ability, these topographic features may have limited the long-distance dispersal of rowi, creating divergence of this species from other kiwi (Burbidge 2003). Natal dispersal is unknown.

North Island kōkako

North Island kōkako *Callaeas wilsoni* that are established as breeding adults defend exclusive territories as pairs or singles all year round. Territories are 4–20 ha (whole-year range length 226–504 m). Juveniles are highly mobile, travelling up to 20 km (Higgins et al. 2006) before settling on average 1300 m away from their natal territory (Innes et al. 2013; $n = 174$, maximum = 5.4 km). Following translocation, kōkako are highly exploratory and may move up to 10 km before settling (Innes et al. 2013). Following translocation to Whirinaki Forest, birds moved on average 433 m per day, and breeding territories the following season were located on average 5.18 km from the release location ($n = 3$; Bradley et al. 2012). NI kōkako are poor fliers and struggle to gain height, but they may glide several hundred metres down valleys from tree-top start-points (Innes et al. 2013). They do not appear to fly across flat pasture gaps of > 40 m (R Burns, pers. comm.), but have been observed gliding over 120 m of pasture downhill (I Flux, pers. comm.).

Kāhu / swamp harrier

In the breeding season harriers *Circus approximans* have large, overlapping home ranges of c. 900 ha, and only c. 30 ha around the nest site is defended. However, in the non-breeding season home ranges are c. 3700 ha (whole-year range length 6.9 km) and they may join communal roosts of up to several

hundred birds (Baker-Gabb 1981; Higgins & Marchant 1993; Seaton et al. 2013). They are highly mobile, since individuals cross between the North I. and South I. and visit or breed on remote islands such as the Kermadec, Campbell, Snares and Auckland Is. Some may be migratory, since birds annually visit Kermadec Is, 1500 km northeast of New Zealand (Higgins & Marchant 1993). Juveniles may travel > 100 km from natal territories (Higgins & Marchant 1993).

Kārearea / New Zealand falcon

Most established kārearea *Falco novaeseelandiae* pairs remain in the same home ranges all year and between years. These are c. 900 ha in central North I. pine forests, c. 1500 ha in eastern South I., and larger again (c. 7500 ha) in native forest (whole-year range length 4.4–9.8 km), although the adults defend only 400–500 m around the nest (Heather & Robertson 2015; Higgins & Marchant 1993; Seaton 2007). Recoveries of 10 banded birds showed a mean travel distance of 4.4 km (maximum 10 km). Juveniles in Kaingaroa Forest dispersed 1.4–34.8 (mean 9.6 km, $n = 11$; Seaton 2007). Kārearea are occasional visitors to Hauraki Gulf islands and breed on Auckland Is 465 km from New Zealand (Higgins & Marchant 1993; Miskelly et al. 2020). This species reached Campbell I. from Auckland Is, a 270 km flight over water (Miskelly et al. 2020).

Weka

Weka *Gallirallus australis* are flightless and generally sedentary; breeding pairs remain on their territories all year. In Westland, adults moved on average c. 190 m ($n = 20$) and sub-adults 170 m ($n = 13$) between sightings on successive days (Higgins & Marchant 1993). Weka near Hokitika moved a maximum distance of 2.3 km within a two-week period, but movements were reduced at campsites ($n = 39$; Carpenter et al. 2019). Mean home range size was 2.0 ha (range 0.7–4.5 ha) on Kapiti I., 11.9 ha in Westland ($n = 13$; Coleman et al. 1983) and 3.5 ha ($n = 5$ females) to 10 ha ($n = 10$ males) at Gisborne (Bramley 1994; whole-year range length 94–389 m). Non-territorial sub-adults ranged over 70 ha at Double Cove (Marlborough Sounds; Higgins & Marchant 1993) and 105 ha at Motutapu Station, South I. ($n = 15$; Watts et al. 2017). Natal dispersal averaged 1.3 km (max. 5 km) on Kapiti I., 5+ km in the Marlborough Sounds, and 9 km in Westland (Higgins & Marchant 1993). Post-translocation dispersal averaged 7 km at Karangahake ($n = 2$; Bramley 1994) and 0.74 km at Motutapu Station, South I. ($n = 19$; Watts et al. 2017), but homing movements can be very large, up to 130 km (Higgins & Marchant 1993). They can swim at least 1 km (Wright 1981). All weka studied near Gisborne had some pasture in their home ranges (Bramley 1994), but there are no published accounts of the pasture gaps that weka will cross.

Kererū / New Zealand pigeon

Kererū *Hemiphaga novaeseelandiae* are one of the more studied birds in New Zealand in terms of movement, as they are a key frugivore and seed disperser of many large-seeded native plant species. While not territorial, individual kererū can spend weeks or months inside a few hectares, interspersed with long-distance flights to reach seasonal food sources (Clout et al. 1991; Powlesland 2013c; M Rayner, Auckland Museum, pers. comm.). Historically kererū were known to form large “mega-flocks” when feeding on toromiro (fruit of *Prumnopitys ferruginea*) or the foliage of kōwhai (*Sophora* spp; Lyver et al. 2008). Flocks have been recorded more recently within

ecosanctuaries where populations are recovering and when fruiting is high, or when birds are feeding on new leaves of willow (*Salix* spp.) or tree lucerne (tagasaste, *Chamaecytisus palmensis*).

Kererū were observed to range up to 102 km when followed via satellite tags near Invercargill, and some crossed Foveaux Strait (33 km) to Stewart I. / Rakiura (Powlesland et al. 2011). A kererū observed on Great King I. (Three Kings I, M Thorsen, pers. comm. to CMM) must have flown from the New Zealand mainland, a minimum distance of 56 km.

A study of daily movements of kererū in Taranaki ($n = 13$) and Canterbury ($n = 11$) found that birds displayed strong sedentary behaviour during the peak fruiting season, with relatively long stationary periods in single locations (Wotton 2007). Birds in Taranaki were more sedentary than those in Canterbury. Average flight distances were 77 m, with a maximum movement of 1457 m recorded.

Hill (2003) found that kererū home ranges at Whirinaki forest (55 000 ha) ranged from 13.9 ha to 704.2 ha (mean = 163.2 ha), compared to 1.8–22.2 ha in a more urban landscape at Banks Peninsula (Schotborgh 2005). Thirty-one of 53 birds tracked by Hill (2003) made short-term movements of > 1.5 km. During this study, eight individuals could not be detected using extensive helicopter searches across the site, suggesting they had dispersed at least 40 km from their original location. Most long-distance movement of kererū coincides with changes in fruit availability and/or unsuccessful breeding attempts. At Hinewai Reserve, Banks Peninsula, ranges averaged 15.9 ha, with core areas of only 2 ha (Campbell 2006), and ranges were larger when birds were eating fruit than when eating foliage. We have found no estimates of natal dispersal distance.

Kākā

Adult kākā *Nestor meridionalis* have relatively small, overlapping home ranges (e.g. mean 15 ha at Whirinaki, $n = 6$, Beaven 1996; c. 30 ha at Pureora, T Greene, DOC, pers. comm.), but will make occasional substantial excursions before returning to a core area (Greene et al. 2004). Juveniles from Hauturu travel 20–25 km (with one recorded at c. 400 km; Moorhouse & Greene 1995) to the North I. mainland and many Hauraki Gulf islands (e.g. Aotea / Great Barrier I., Waiheke I.), all over water (Higgins 1999). Kākā visit Hamilton, Rotorua, and other central North I. sites in early winter and have recently been tracked in spring flights over at least 180 km from Hamilton to Hauturu and Aotea Islands in the Hauraki Gulf (NF, JI, unpub. data). Unsurprisingly, there is little population structure between North and South Is (Dussex et al. 2015).

Kākā in the Eglinton Valley, South I., have large annual movements to feed on flowering tree fuchsia (*Fuchsia excorticata*) and southern rātā (*Metrosideros umbellata*) and fruiting podocarps, and “it also seems likely that there is considerable movement of kākā between islands and the mainland in some of the larger fiords such as Preservation and Dusky” (T Greene, DOC, pers. comm.).

Post-release monitoring of captive-reared and wild-caught kākā juveniles at Pukaha / Mt Bruce sanctuary showed that most birds remained close to the release location (Berry 1998). Captive-reared birds remained within 1 km of release locations, but wild-caught birds dispersed further, with one bird 39 km away from the release site. This individual was relocated back to the release site, after which it remained, suggesting that individual preference for dispersal fluctuates substantially. Multiple individuals crossed pasture to visit

trees 600–800 m away, suggesting daily movements of this distance may be common.

Birds from the population that was reintroduced to the fenced Zealandia ecosanctuary in Wellington in 2002 have been recorded 10–14 km away in various surrounding suburbs, including Mākara, Tawa, and Red Rocks (Charles 2012). One banded kākā from Zealandia flew to Pukaha, over 70 km away, where it stayed for 6 weeks before returning (GC Parker, Parker Conservation, pers. comm.). Juveniles from Hauturu moved to Aotea and to the North I. mainland (Higgins 1999) but natal dispersal distances are unknown.

Kākāpō

Kākāpō *Strigops habroptila* are now restricted to a few offshore islands, but were once common throughout mainland New Zealand (Miller et al. 2003). Due to their quick decline following human arrival (Dussex et al. 2018) few studies are available on natural dispersal in larger landscapes, but movements on refuges have been reasonably well studied. For most of the year kākāpō are highly solitary, with independent, overlapping home ranges (Powlesland et al. 2006). Despite being flightless, they are highly mobile and are capable of travelling considerable distances over short periods (Farrimond et al. 2005). On Hauturu, radio-tracked birds were recorded moving up to 1.7 km in a single night; elsewhere birds have been recorded moving up to 5 km in a single night (Best & Powlesland 1985).

Radio-tracked birds on Stewart I. / Rakiura, the last ‘mainland’ remnant population, had home ranges of 15–50 ha (Best & Powlesland 1985). Comparably, home ranges from their island refuges range from between 3 and 44 ha (Farrimond et al. 2005) or 1.4–33 ha (Whitehead et al. 2012) on Whenua Hou (depending on how home range is measured), and 15–34 ha on Hauturu (Moorhouse & Powlesland 1991). Home ranges were 0.81–29.22 ha and 0.75–11.4 ha on smaller Maud and Pearl I, respectively (Trinder 1998; Joyce 2008). Home ranges often remain permanent over time, and translocated birds have been recorded returning to the same home ranges after decades away (Stone et al. 2017).

As a lek breeding species, breeding males move kilometres to their display sites—often within an area separate from their winter home range—and remain there for the rest of the season (Powlesland et al. 1992). Females travel up to several kilometres to male display sites, and after mating return to build nests and raise young (Powlesland et al. 1992; Joyce 2008). On Whenua Hou females increase their home range during the breeding season and can travel several kilometres in search of good-quality food (Farrimond et al. 2005; Whitehead et al. 2012). This may be due to patchy distribution of rimu (*Dacrydium cupressinum*) on Whenua Hou, since ranges remain constant in more productive landscapes (Whitehead 2007; Whitehead et al. 2012).

Natal dispersal is probably high in kākāpō, but this has been difficult to study given the small islands where juveniles are raised. On Whenua Hou, juveniles generally stay within their natal range for 6–10 months, after which individuals have been recorded 3–5 km away (Powlesland et al. 2006).

Discussion

Current data (Tables 2–4) on forest bird gap crossing, natal dispersal, and whole-year movement are valuable but provisional, because sample sizes are mostly small, and maximum recorded dispersal distances will depend greatly on sample sizes. Many of the observations we collate here are previously unpublished. For many species we could not find any data; in particular, distances of gap crossing, natal dispersal, and whole-year movements are unknown for 7, 15, and 3 forest birds, respectively. The limited available data may be biased and may reflect unnatural movement patterns associated with the current reduced ranges and abundance of birds, or exceptional individuals and situations.

Gap crossing

There are many more reports of gap crossing over water than land (Fig. 1), perhaps because establishment on pest-free

Table 4. Diet and movement distances of large (> 175 g) New Zealand forest birds based on available studies, reports and anecdotal observations, as explained in the preceding species accounts. Diet (foliage = Fo, fruit = Fr, invertebrates = I, nectar / flowers = N, and vertebrates = V) is shown in order of importance for each taxon. Gap crossing is maximum distance of pasture and/or water known to have been crossed. Natal dispersal is the mean or maximum juvenile dispersal from parent home range to their first breeding site, where available. Whole-year range length is the diameter of adult home ranges when assumed to be circular. Species are listed by Māori and common names in order as per Table 1. NI = North Island, SI = South Island, NZ = New Zealand.

Species	Diet	Gap crossing over land ^L or water ^W (km)	Natal dispersal (km)	Whole-year range length (km)
Tokoeka, SI brown kiwi	I, Fr	unknown	5+	0.25–0.8
Roroa, great spotted kiwi	I, Fr	unknown	2	0.36–0.72
Kiwi pukupuku, little spotted kiwi	I, Fr	unknown	unknown	0.5–0.92
Kiwi-nui, NI brown kiwi	I, Fr	0.33 ^L	0.5–22	0.26–1.1
Rowi	I, Fr	unknown	unknown	unknown
NI kōkako	Fo, Fr, I, N	0.04 ^L	1.3 (mean)	0.25–0.5
Kāhu, harrier	V	1500 ^W	100+	6.9 (mean)
Kārearea, NZ falcon	V, I	270 ^W	1.6–34.8	4.4–9.8
Weka	I, Fr, V	1 ^W	1.3–9	0.09–0.39
Kererū	Fr, Fo, N	33 ^W	unknown	1–100
Kākā	N, I, Fr	25 ^W	unknown	100+
Kākāpō	Fo, Fr, N	unknown	3–5	1.7–5

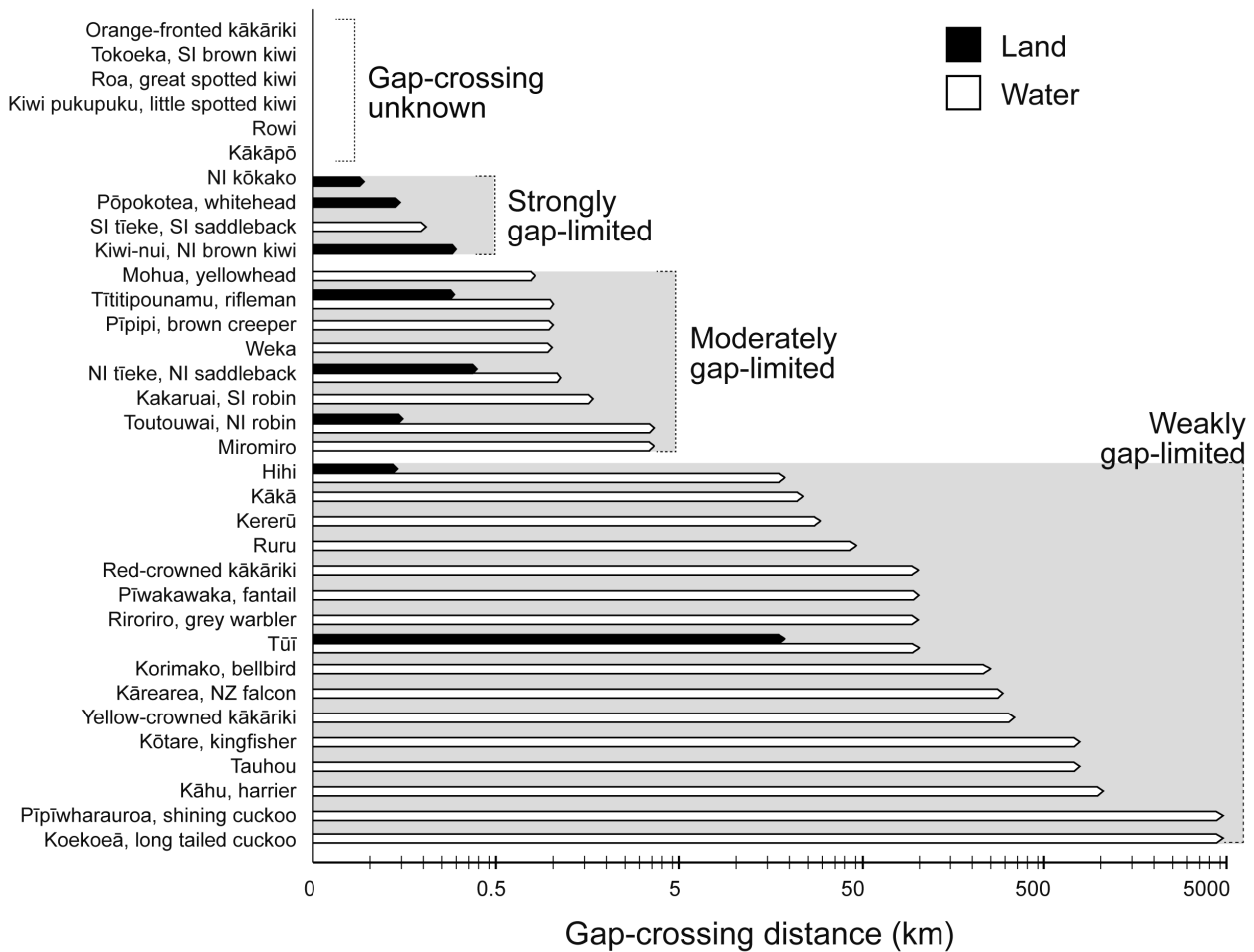


Figure 1. Apparent gap-crossing ability of New Zealand forest birds, ordered from top to bottom by species, with unknown gap crossing (six species), and the remaining species (28) by increasing maximum known gap-crossing distances. Note the logarithmic scale of the x axis to accommodate very short and long movement distances on the same axis. We present both land- and water-based gap-crossing distances for a species if both are known, but birds are ordered by whichever of the two measures is greatest. We classify birds not known to cross 500 m gaps as strongly gap-limited, not known to cross 5 km gaps as moderately gap-limited, and others as weakly gap-limited. Many values are based on small sample sizes, including single observations, and unpublished data from species experts (see species accounts). NI is North Island, SI is South Island.

islands is more likely than on a mainland fragment, or because such crossings are more likely to be noticed, or because high population densities on islands encourage dispersal. The paucity of information on gap-crossing distances over land (data for only eight of 34 taxa; Fig. 1) is probably due to the importance of this parameter not being recognised. Also, defining a ‘gap’ on land is harder than over water. Known water-crossing distances are on average 22 times larger than land-crossing distances for the five species with data for both. For hihi, the believed 20 km ocean crossing from Hauturu to Tāwharanui is 200 times greater than the maximum known pasture crossing (100 m), while for toutouwai, the (exceptional) 3.5 km ocean crossing from Tiritiri Matangi I. to Shakespear Regional Park is 32 times greater than the well-studied pasture-gap distance of 110 m (Richard & Armstrong 2010a). While limited, the data suggest that crossing land is a greater obstacle to dispersal than seemingly more hostile gaps over water or that obtaining bird arrival records on islands is simply easier than over land.

We could not find gap-crossing data for six species. Orange-fronted kākārīki, rowi, roroa, tokoeka and kākāpō are forest taxa that do not have populations near pasture. Kiwi

pukupuku are known to feed in pasture on islands to which they have been introduced.

We classified four species (NI kōkako, pōpokotea, SI tīeke and NI brown kiwi) as ‘strongly gap limited’, defined by us as not being reported to cross water or pasture gaps larger than 500 m. A further eight species (mohua, tītītipounamu, pīpipi, weka, NI tīeke, kakaruai, toutouwai and miomiro) have pasture or water gap-crossing distances of less than 5 km, of which pasture-crossing distances are always smaller. Provisionally, these twelve forest birds are least likely to establish by natural dispersal in new, safe sites that are separated from existing populations by 5 km of pasture or water, and so have most need for translocations or wildlife corridors. Conversely, they are also most likely to be contained inside isolated forests to which they have been translocated but achieving such isolation can be difficult. Nearly all juvenile toutouwai dispersed out of Wenderholm Regional Park, Auckland (Andrews 2007), while two NI kōkako translocated to Trounson Kauri Park dispersed c. 10 km northwest to Marlborough Forest (Gillies et al. 2003).

Loss of dispersal ability for New Zealand forest birds is correlated with a preference for forest interiors (e.g.

tītīpounamu, mohua, hihi, toutouwai; Spurr 1979) rather than edges or shrublands, and with greater endemism (MacArthur & Wilson 1967; Spurr 1979; Williams 1981; Diamond 1984). Forest specialist species are likely to face the greatest barriers to movement when forest is fragmented, while generalists may even respond positively to landscape heterogeneity (Devictor et al. 2008; Estavillo et al. 2013; Boesing et al. 2021). Therefore, specialist species are more sensitive than generalists to within-patch habitat quality (Ye et al. 2013). Forest birds endemic at levels of order (e.g. kiwi) or family (e.g. tītīpounamu, pōpokotea, pīpī, mohua, hihi, kōkako, tīeke) are most likely to be threatened with extinction and subject to restoration programmes (Parlato et al 2015; Walker & Monks 2017), but are also the weakest dispersers and so at greatest risk of non-recovery if reduced in numbers (Spurr 1979).

Sixteen species are only weakly gap limited (defined by us as being reported to cross water or pasture gaps larger than 5 km; Fig. 1). These include migratory cuckoos (pīpīwharaua and koekoeā), raptors (kāhu, kārearea, ruru), common frugivores (tūi, korimako, kererū), parrots except kākāpō, kōtare (which has a wide distribution in the southwest Pacific and Australia), and also some small-bodied, recent biogeographical immigrant species that are common and widespread (riroriro, pīwakawaka, tauhou). Our list agrees substantially with earlier classifications of “water-crossers” by Diamond (1984), and forest birds with “good dispersal” by Spurr (1979).

Most of lowland New Zealand is dominated by pastoral farmland, exotic forestry and urban development, and species that can breed in or safely traverse these landscape features are much less likely to be gap-limited than those that use just native forest. All 16 forest birds that use all four of these landscapes (Table 1) except weka are classified by us as weakly gap-limited; perhaps weka may be reclassified as weakly gap-limited when more data emerge. The scattered trees that exist across all of these landscapes are probably very important for enabling survival and movement of forest birds across them (Fischer et al. 2010; Waite 2012; Le Roux et al. 2017). The ability of forest birds to survive in and travel across human-altered matrix environments between native forest patches is undoubtedly a key determinant of their current conservation status; 15 of the 16 are classified Not Threatened by the NZ Department of Conservation (Table 1; Robertson et al. 2021).

Patterns of year-round sociality, territoriality and movement

The commonest social system (17 species) is year-round

territoriality, and these species are primarily insectivores, except for NI kōkako, whose main diet is foliage and fruit (Table 5). A further five species (pōpokotea, mohua, tauhou, red-crowned kākāriki and hihi) are territorial in the breeding season but more mobile outside it, sometimes forming mixed-species flocks that year-round territorial birds like pīwakawaka and riroriro may join. Winter flocks may offer protection from predators, or extra food because flocks disturb prey or are more efficient at finding scattered food than individuals (McLean et al. 1987; Goodale et al. 2020).

Frugivore–nectarivores (tūi, korimako, kererū), volant parrots (red- and yellow-crowned kākāriki, kākā) and raptors (kāhu and kārearea) defend small spaces around nests but otherwise overlap feeding sites with others, and in the non-breeding season they range widely. Raptors, parrots and frugivores benefit from large annual movements and gap crossing because their food is available at widely scattered sites at different times. The spatiotemporal variability of flower and fruit resources (Ogden 1985) requires nectivorous and frugivorous species to forage widely, as also seen in Australian Meliphagidae (Keast 1968).

These mobile taxa historically formed large intraspecific flocks that are absent today. Tūhoe (Urewera) informants described kererū flocks “passing overhead that would shade the sun” (Lyver et al. 2008). Irruptions of red- and yellow-crowned kākāriki occurred after beech (*Lophozonia* and *Fuscospora* spp.) seed masts in the northern South I., and “many thousands of them were killed” by settlers protecting crops (Oliver 1955). Behaviours and ecological roles of flocks reported historically are fascinating to contemplate, and they deserve research. Individuals can derive foraging benefit from group membership (Ligorio et al. 2020), and flock reductions can increase individual mortality through Allee effects (Gardner 2004).

Maximum whole-year range lengths of adult, year-round, territorial insectivores are smaller (150–320 m for passerines and ruru; 720–1100 m for kiwi) than those of species that are territorial when nesting but otherwise flock (range 210–35 000 m; Tables 2–4). Territory size in many bird species is smaller when densities are high e.g. korimako (Sagar & Scofield 2006), NI tīeke and NI kōkako (Higgins et al. 2006).

Alternative annual movement behaviours include koekoeā and pīpīwharaua, which undertake obligate migration (“hard-wired”, Newton 2012) between New Zealand and the central Pacific. Kākāpō are New Zealand’s only lek breeders; both males and females are solitary, but with overlapping ranges

Table 5. Social systems of New Zealand forest birds that have repercussions for their year-round movements. Species are presented in alphabetical order by Māori or common name. NI = North Island, SI = South Island, NZ = New Zealand.

Social system	Forest bird species
Occupy defended territories year-round	Kakaruai (SI robin), kārearea (NZ falcon), kiwi-nui (NI brown kiwi), kiwi pukupuku (little spotted kiwi), miromiro (tomtit), NI kōkako, NI tīeke, pīpī (brown creeper), pīwakawaka (NZ fantail), riroriro (grey warbler), roroa (great spotted kiwi), ruru (morepork), SI tīeke, tītīpounamu (rifleman), tokoeka (southern brown kiwi), toutouwai (NI robin), weka
Defend territories or nests in the breeding season but mobile outside it	Hihi (stitchbird), kāhu (swamp harrier), kākā, kererū, korimako (bellbird), mohua (yellowhead), pōpokotea (whitehead), red-crowned kākāriki, tauhou (silveryeye), tūi
Migratory	Koekoeā (long-tailed cuckoo), pīpīwharaua (shining cuckoo)
Lek	Kākāpō
Unknown	Kōtare (NZ kingfisher), orange-fronted kākāriki, rowi, yellow-crowned kākāriki

for most of the year, and then may move several kilometres to lek display sites in episodic breeding years (Powlesland et al. 2006). More basic research is required for many taxa (e.g. yellow-crowned and orange-fronted kākāriki, kākā and kōtare).

Natal and breeding dispersal

Natal dispersal is probably the main way that New Zealand forest birds find new habitat and mates, because most juveniles undertake natal dispersal, while breeding dispersal is rare, and because natal dispersal distances are generally much larger than whole-year movements. Natal dispersal distances are larger than maximum whole-year adult movement distances for 17 of the 19 forest birds we have provisional data for (Tables 2–4). Natal dispersal distances are unknown for 15 (44%) of 34 species, and we have little understanding of natural variation.

Forest birds regularly self-introduce to ecosanctuary sites (e.g. kārearea and kererū to Zealandia, Wellington; Miskelly 2018; NI kākā and korimako to Tāwharanui, Auckland; M Maitland, unpub. data; Brunton et al. 2008), perhaps by natal dispersal. It seems likely that many weakly gap-limited species are already dispersing widely but are unnoticed because few destinations have high-quality habitat for them.

Sub-adults can be extremely vulnerable during the natal dispersal stage, although there are few data on juvenile survival and mortality. Toutouwai juveniles at Tāwharanui Open Sanctuary suffer the highest mortality during the first weeks following fledging (Drummond et al. 2019). Juvenile mortality is density-dependent in some species, where higher mortality is observed under higher densities as populations approach carrying capacity (Armstrong et al. 2002).

Conservation objectives and roles for corridors, ecosanctuaries and translocations

Two objectives of conservation for New Zealand forest birds are to prevent taxon extinctions and then to increase abundance through as much as possible of former distributions. Reducing pest mammals and translocating native birds increases “indigenous dominance” and “species occupancy” and restoring populations across diverse environments improves “environmental representation”; all are components of “ecological integrity” (Lee et al. 2005).

The key cause of decline of New Zealand forest birds in large, intact, upland native forests is predation by pest mammals, although food supply is an important, interacting, secondary factor for some species (Innes et al. 2010). Limiting factors are more complicated in settled, fragmented environments because forest area itself may be limiting (Hackwell 1982; Innes et al. 2010; Ruffell & Didham 2017), and there are diverse additional threats, including vegetation change, dogs, cats, roads and vehicles. We suggest that absence of connectivity is likely to currently limit only a few populations of mainland forest birds, because few have yet reached carrying capacity based on densities observed in island populations (Armstrong et al. 2002). It is currently more important to increase the area of safe, pest-free sites on the mainland than to make connections between unsafe sites (Hodgson et al. 2009, 2011).

In the long term, vegetated corridors will enable gap-limited taxa to move between isolated populations, increasing genetic exchange and effective population size and allowing populations to expand by natal, breeding, or post-release dispersal (Overmars et al. 1992; Desrochers & Hannon 1997; Robertson & Radford 2009). Increasing the distributions of forest birds also increases their beneficial mutualisms, especially seed dispersal and pollination (Kelly et al. 2010; Iles

& Kelly 2014; Bombaci et al. 2021) and predation (Carpenter et al. 2021).

Conversely, increasing connectivity from excellent to poor habitat could reduce the viability of forest bird populations if emigrating individuals cannot breed or are killed at the new site, known as the source–sink paradigm (Dunning et al. 1992; McArthur et al. 2019). New sites destined for reconnection by corridors or for translocations need to be made safe for target taxa before the birds arrive there (Veitch 1994; Parker et al. 2022). In New Zealand, corridors or stepping-stones may not require high-level predator control to become effective short-term dispersal pathways, especially if birds are most vulnerable to predation as eggs or chicks rather than as sub-adults and adults (e.g. NI kōkako; Basse et al. 2003).

Corridor proposals have been discussed in New Zealand for many years (Thomas 1991; Overmars et al. 1992), and some are now being implemented, especially around Auckland. These include North-West Wildlink¹, Forest Bridge Trust², and Eastern Bays Songbird Project³. Other corridors are planned between Maungatautari and Pirongia ecosanctuaries in central Waikato, and between New Plymouth and Taranaki Mouna in Taranaki. Large-scale tree-planting proposals, such as the One Billion Trees Programme⁴, are valuable opportunities for restoring wildlife connectivity.

Some corridors have a species focus. There are plans to link separated (strongly gap-limited) NI kōkako subpopulations at Kaharoa–Onaia and Otanewainuku, near Rotorua (I Corkery, DOC, pers. comm.), and two corridors have already been implemented to connect parts of Mapara Wildlife Management Reserve, King Country (I Flux, pers. comm.). There is little understanding of details of vegetation used by forest birds for dispersal. Elsewhere, “agroforest woodlots” (Uezu et al. 2008) and scattered trees (Fischer et al. 2010; Prevedello et al. 2018) have been shown to assist biodiversity retention and birds’ gap crossing, dependent on landscape structure, tree size and predation risk (Le Roux et al. 2018; Silva et al. 2020).

Pest-fenced and unfenced ecosanctuaries, including marine islands, are key tools to restore forest birds in New Zealand, but they are frequently too small (mean c. 700 ha; Innes et al. 2019) to accommodate normal natal dispersal (Armstrong & Ewen 2002; Basse & McLennan 2003; Miskelly et al. 2005) or even annual home range movements, leading to “spillover” (e.g. Fitzgerald et al. 2019). Ecosanctuaries may eventually provide source individuals to colonise a mammal predator-free landscape (Parkes et al. 2017; Parker et al. 2022), but many ecosanctuaries have little high-quality habitat around them and poor connectivity to it. The extra isolation of peninsula-fenced ecosanctuaries that protects them against invading pests also isolates them from connected habitats suitable for dispersing gap-limited birds (Burge et al. 2021). Ecosanctuaries may benefit from isolation in the short term because emigration of threatened birds is limited, but connectivity to adjacent forests is desirable in the long term. On isolated marine islands where natal dispersal of strongly gap-limited birds is prevented by water, juvenile survival declines as populations increase and territories become rarely available (McLean & Miskelly 1988; Armstrong et al. 2005; Sagar & Scofield 2006).

Translocations can establish populations of species at sites they could not otherwise reach, but populations may

¹ <https://www.forestandbird.org.nz/projects/north-west-wildlink>

² <https://www.theforestbridgetrust.org.nz>

³ <https://songbird.org.nz/web>

⁴ <https://www.mpi.govt.nz/forestry/funding-tree-planting-research/one-billion-trees-programme/>

fail if post-release dispersal enables birds to leave safe, high-quality habitat for less suitable areas nearby (Parlato & Armstrong 2013; Richardson et al. 2015; Parker et al. 2022). At Taranaki Mouna, 70% of translocated toutouwai dispersed outside of the pest-managed release area, while 25% remained. Such outcomes cannot always be mitigated by releasing more individuals because these sites will probably also have high natal dispersal (Parker et al. 2022). There is increasing understanding that considering habitat in landscapes around release sites should be part of translocation planning (“integrated landscape management”; Richardson et al. 2015). Constraining post-release dispersal until the translocated species establishes might require delaying connection to adjacent habitat until it has excellent quality (e.g. few pest mammals).

Future research needs

The outcomes of forest bird restoration projects will be difficult to predict until more is known about bird movements, especially natal dispersal. This is unknown for 14 of the 34 species we reviewed, including common (e.g. pīwakawaka, miromiro) and threatened (e.g. mohua, all kākārīki) taxa. More basic studies of forest bird natural history, such as those undertaken at Kōwhai Bush, Kaikōura, in the 1970s (Hunt & Gill 1979) and in the Ōrongorongo River valley near Wellington from 1966 to 1990 (Brockie 1992), are required. We also need empirical studies of dispersal behaviour itself, including individuals’ timing, search paths, habitat selection, philopatry, and interactions with conspecifics (Doerr & Doerr 2005).

There are many fewer data on gap-crossing distances over land than water (Fig. 1), and further research is required into vegetation and other structure that different species will move through (e.g. Wittern & Berggren 2007). Continued research into the potential of corridors and stepping-stones as a method for restoring connectivity is required, along with practical attempts to create such pathways so that empirical evidence of their effectiveness can be collected. We also suggest that studies of the ecological functions and demographic outcomes of flocking will be rewarding, because historical accounts describe large flocks as being normal for some species in some seasons and years.

Conclusions

More research is needed on movement of New Zealand forest birds, and improving technology and tools should assist this. Our preliminary review suggests that about half the species for which there are gap-crossing data are only weakly gap limited, defined by us as being reported to cross 5 km of pasture or water between forest habitats. Efforts to increase habitat connectivity can therefore focus on the remaining birds that are strongly (< 0.5 km; NI kōkako, pōpokotea, SI tīeke and NI brown kiwi) or moderately (< 5 km; mohua, fītitipounamu, pīpipi, weka, NI tīeke, kakaruai, toutouwai, and miromiro) gap limited. Much more is known about birds crossing forest gaps over water than land; some species with known large, over-water flights may need to be reclassified in the future if their maximum over-pasture flights are found to be smaller.

Improving our understanding of bird dispersal is important as we consider more large-scale, mainland-focused conservation strategies. Habitat connectivity is a double-edged sword that can increase habitat availability, genetic exchange,

and species distributions, or it can facilitate population declines by enabling dispersal from source to sink sites. Translocations can valuably establish populations of featured species at new sites, but translocations can also be undermined by subsequent post-release and natal dispersal. The connectedness of a site to adjacent habitat should be considered as part of initial translocation planning (Richardson et al. 2015; Parker et al. 2022).

Ideally, pest-managed sites in New Zealand should be large enough to accommodate natal dispersal. However, the few estimates of such areas (10 000 ha for NI brown kiwi Basse & McLennan 2003; 50 000 ha for SI kākā, Leech et al. 2008) are vastly larger than the current mean ecosanctuary area (700 ha, Innes et al. 2019). In the long term, in intact forests we need new tools or strategies that control key mammal pests effectively at much larger scale. In fragmented lowland forest, however, establishing connecting corridors between remaining forest fragments will frequently be a valuable first step to increase habitat area. In the meantime, as a holding pattern, many threatened forest bird species can be maintained in isolated subpopulations in managed ecosanctuaries, with genetic exchange by translocation if required.

Acknowledgements

Andrew Digby, Ian Flux, Jo Carpenter, Kate Richardson, Maj de Poorter, Mandy Brooke, Matt Rayner, Murray Efford, Terry Greene, and Rhys Burns gave helpful advice about taxa or sites. Thanks to librarians Edward Doonerwind and Jamie Blackman, editor Ray Prebble, graphics designer Nicolette Faville and to Kate Boardman at Manaaki Whenua – Landcare Research for help sourcing literature, preparing Figure 1 and editing. Comments from Susan Walker, Jo Carpenter and Anne Schlesselmann, Manaaki Whenua – Landcare Research, and from two anonymous referees valuably improved a draft manuscript. We also thank James Brock and Tom Etherington for valuable editing and advice during the publication process. Strategic Science Investment Funding to Manaaki Whenua – Landcare Research enabled JI and NF to undertake this review. DPA, KAP and ZLS were supported by Endeavour funding from the Ministry of Business, Innovation and Employment for the More Birds in the Bush programme.

Author contributions

JI and ZS conceived and drafted the initial manuscript and final writing was led by JI. All authors assisted with acquisition and interpretation of data and provided editorial input.

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Received: 1 June 2021; accepted: 14 January 2022
 Editorial board member: Thomas Etherington

Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Glossary

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