

REVIEW

Conservation challenges in mobile birds: What do we know and need to know for effective conservation of endemic inland migrants?

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Abstract: In New Zealand, intensive, site-based conservation management of bird species is often focused on controlling threats from invasive species at a local scale. Such management may benefit species resident within the site but may be insufficient for mobile taxa whose movements extend beyond it through annual migrations, irregular nomadic movements, or exchanges of dispersing individuals in metapopulation networks. Here we highlight challenges in the conservation management of mobile species, and argue that information on population trends, vital rates (recruitment, survival, and immigration or emigration), movements, and population connectivity is required to understand whether threats at a particular time or place result in population limitation, and to evaluate different management options. We review and synthesise current knowledge on the vital rates of a group of migratory wading birds endemic to New Zealand: pohowera/banded dotterel (*Charadrius bicinctus*), tarāpunga/black-billed gull (*Larus bulleri*), tarapirohe/black-fronted tern (*Chlidonias albostratus*), tōrea/South Island pied oystercatcher (*Haematopus finschi*), and ngutu parore/wrybill (*Anarhynchus frontalis*). We identify knowledge gaps for these species about population trends, connectivity, and movement, and show that information on egg and chick survival is available for all species, but information on adult survival rates is scarce and only available for three species. Because dispersal and migration dynamics link geographically distant sites, greater recognition of population dynamics dependent on the full annual cycle is required to improve conservation actions and robustly assess management outcomes. We discuss how ecological understanding and conservation of mobile species can be advanced by technological developments coupled with new integrative modelling frameworks that incorporate existing data.

Keywords: *Anarhynchus frontalis*, animal movement, *Charadrius bicinctus*, *Chlidonias albostratus*, conservation ecology, *Haematopus finschi*, *Larus bulleri*, migratory networks, population dynamics, wildlife management

Introduction

For many decades the conservation management of vertebrate species in New Zealand has focused pragmatically on managed sites at scales from tens to tens of thousands of hectares (Saunders & Norton 2001; Towns et al. 2013; Elliott & Kemp 2016; Innes et al. 2019; Fea et al. 2021). Site-based suppression of invasive mammals as part of habitat protection is an appropriate response to the poor adaptation of island endemic species to these novel predators (Doherty et al. 2016) and has been highly effective in protecting a wide range of resident taxa on offshore and nearshore islands (Towns et al. 2013), and on the mainland (Binny et al. 2021). However, site-scale management may be insufficient to protect populations of mobile species whose movements extend beyond the site and management umbrella (Baillie et al. 2000; Schaub et al. 2012; Runge et al. 2014).

Mobile animals show a wide range of movement

behaviours across a range of spatial scales (Newton 2008; Table 1). Routine movements are local in scale and include movement associated with nesting, roosting, and feeding. Larger-scale, less frequent movement events may occur due to dispersal once or a few times during a lifespan (e.g. natal or breeding dispersal), annually as part of seasonal migration, or irregularly through nomadism. Individuals of the same species can undertake several types of movement during different life stages. For example, young birds in migratory populations must find a suitable location during the non-breeding season and are often nomadic across several sites for extended periods before they enter the breeding population and settle into more predictable migratory movements (Battley et al. 2020; Cresswell 2014).

Movement may expose individuals to threats away from focal conservation sites, which affect vital rates such as recruitment and survival, drive population declines, and inhibit recovery despite management at focal sites. New Zealand has a

Table 1. Descriptions of terrestrial bird movements, following Newton (2008).

Scale of movement	Movement type	Definition
10 ¹ km	Routine	Typically, routine movements include flights from nesting or roosting sites to feeding sites, or from one feeding site to another.
10 ¹ –10 ² km	Dispersal	Natal: a directed, one-way movement away from the natal site that occurs once during an individual's lifetime until an individual settles on a breeding site. Individuals returning to natal sites exhibit natal philopatry. Breeding: breeding adults may change nesting locations from year to year depending on environmental conditions or territory availability. Breeding dispersal generally spans shorter distances compared to natal dispersal. Species where individuals return to breeding sites consistently exhibit high breeding site fidelity. Non-breeding: individuals may also change non-breeding locations from year to year depending on environmental conditions. Species where individuals return to non-breeding sites consistently exhibit high non-breeding site fidelity.
10 ² km	Nomadism	Year-round: individuals move frequently between sites with irregular timing and or direction, leading to both within- and between-year variability in location and movement patterns. No one site is necessarily used every year, and some areas may be used only at intervals of several years when conditions permit. Phase: nomadic movement can be experienced only during certain life stages (e.g. juvenile) and is distinct from dispersal in that movement occurs multiple times and/or does not result in the establishment of a new territory. This is also called phase nomadism. Seasonal: nomadic movement can also be restricted to certain times of the year when individuals are nomadic, but they may be resident for the remainder of the year.
10 ² –10 ⁴ km	Migration	Individuals carry out regular return movements at about the same time each year, often to specific destinations, producing within- but not between-year variability in location and movement patterns. Compared to dispersal movements, migrations are often longer, and are carried out in a more restricted and fixed direction Seasonal changes in food availability are thought to be the fundamental evolutionary driver of the life histories and behaviours of migratory species.

significant number of threatened or declining mobile vertebrate species, and it is increasingly recognised that processes and threats beyond managed sites can compromise the outcomes of site-based intensive management. For example, a recent review found that 57% of New Zealand's threatened terrestrial bird species and 100% of threatened bat species (totalling 46 species) could be considered mobile and require conservation actions beyond current actively managed sites to ensure their persistence across forest, wetland, river, alpine, and urban ecosystems outside public conservation land (Williams et al. 2021).

Burge et al. (2021) found limited potential for many ecosanctuaries to augment forest bird populations “outside the fence” and warned that surrounding unmanaged areas could act as “habitat traps” for species with high natal dispersal or post-translocation dispersal (see examples in Richardson et al. 2015). Of New Zealand forest birds, most small insectivores and North Island kōkako (*Callaeas wilsoni*) are territorial year-round, but three species of frugivore-nectivores, two species of raptors, and four volant parrot species are highly mobile and natal dispersal distances are unknown for half of forest bird taxa (Innes et al. 2022).

Mobile threatened species present a complex problem for conservation managers wanting to reverse population declines and protect ecosystem processes (Scheele et al. 2018). The full range of factors that limit populations of mobile species are rarely known and can be difficult to identify when multiple biotic and abiotic processes are operating across large spatial scales (Webb et al. 2017). In Table 2 we describe three major

challenges that we suggest primarily set the conservation of mobile terrestrial species apart from that of less mobile species. All three challenges illustrate that factors beyond a focal management site may fundamentally alter or undermine the outcomes of management of a population at that focal site.

Our review is framed using four steps that distinguish the categories of information needed to determine the best conservation management actions for mobile species, taking both annual and life-cycle movement patterns into account. We show that information on population trends, vital rates (recruitment, survival, and immigration or emigration), movement, and population connectivity are required to evaluate different management options for mobile species. We review what information exists to guide conservation management of five endemic inland migrant bird species (a distinct group which undertake annual migrations between New Zealand inland breeding and coastal non-breeding sites, and back again). We summarise what relevant information is already available for those focal species in each step and identify priorities for further data collection. Finally, we suggest how the understanding and conservation of mobile species, such as inland migrants, could be advanced by technological developments coupled with new integrative modelling frameworks that incorporate existing data.

Table 2. Three challenges that set the conservation management of mobile species apart from that of less-mobile species. These challenges illustrate that factors beyond a focal management site may fundamentally alter or undermine the outcomes of management at that particular site.

Challenge	Explanation	Example
Population at a focal conservation site is sustained by immigrants	Dispersal can be a main driver of temporal variation in local population growth rates across a wide array of demographic and spatial contexts (Millon et al. 2019). Populations of mobile species can be part of a network of populations for all or part of their annual cycle with reciprocal exchange of dispersers (Doncaster et al. 1997) or source-sink metapopulation dynamics (Hanski 1999). If the population at a focal site is connected to a network of populations in such a way that it is sustained by immigration, the spatial scale of conservation management needs to extend beyond the local scale to ensure that neighbouring populations are included and exchange of individuals is maintained (Baillie et al. 2000).	A drop in immigration can lead to rapid local population extinctions even when local recruitment and survival remain unchanged, as was shown for a population of the woodchat shrike (<i>Lanius senator</i>) in Germany (Schaub & Ullrich 2021). Similarly, immigration can mask population sinks as large populations may appear to be sources without understanding the underlying processes as shown for Greenland white-fronted geese (<i>Anser albifrons flavirostris</i>) at non-breeding sites (Weegman et al. 2016).
Survival is restricted at sites away from the focal site due to migration or nomadism throughout the annual cycle	Individuals of migratory and nomadic species are exposed to multiple diverse environmental conditions and specific threats during periods of movement and residency (Faaborg et al. 2010; Nandintsetseg et al. 2019). Threats that may affect survival during migration or at non-breeding sites include risks of collision, habitat quality and quantity, novel diseases and competitors, as well as predators, and may result in population limitation (McGowan et al. 2017). If survival during the non-breeding period or during movement is low and not offset by recruitment (e.g. Hewson et al. 2016; Woodworth et al. 2017), any conservation management during the breeding season targeted at increasing recruitment or survival during breeding will be wasted effort, as conservation management across the annual cycle encompassing large-scale movements is required (Nater et al. 2023).	Human modification of Dutch coastal estuaries in 1986–1987 resulted in a 33% reduction in tidal area used for foraging by the majority of Eurasian oystercatchers (<i>Haematopus ostralegus</i>) as a non-breeding site. As a result, the survival of oystercatchers was reduced across the entire European continental population for at least 12 years (Duriez et al. 2012). Strong declines in seasonal survival of three shorebird species (red knot <i>Calidris canutus piersmai</i> , great knot <i>Calidris tenuirostris</i> , bar-tailed godwit <i>Limosa lapponica menzbieri</i>) using the East Asian-Australasian Flyway indicated that habitat loss at refuelling sites during migration in the Yellow Sea explains declining shorebird numbers at focal non-breeding sites in Australia (Piersma et al. 2016).
Carry-over effects at different sites across seasons decrease recruitment at focal conservation sites	Carry-over effects (i.e. conditions experienced during one period that continue to influence the fitness of individuals, and ultimately the health of populations during subsequent periods) have been identified in a range of migratory species (Ryan et al. 2005; Harrison et al. 2011; Marra et al. 2015). The influence of such carry-over effects on population demography depends on the relative connectivity between breeding and other sites used during the annual cycle. If breeding populations are spread across a range of other sites during their annual cycle, the population should be more buffered against carry-over effects compared to breeding populations that are closely linked to a small number of staging and/or non-breeding sites throughout the year (Runge et al. 2014; Nater et al. 2023).	For American redstarts (<i>Setophaga ruticilla</i>), changes in population abundance across North America were linked to different migration routes and use of different non-breeding sites of populations (Wilson et al. 2011). Experimental reduction of winter food availability for American redstarts delayed migration, which in turn reduced reproductive success (Cooper et al. 2015; Rushing et al. 2016).

Steps to guide conservation management of mobile species

We suggest that the information needed to guide mobile species conservation can be organised into the four following steps:

Step 1. Confirm whether the national abundance or distribution of the species is declining, increasing, or stable.

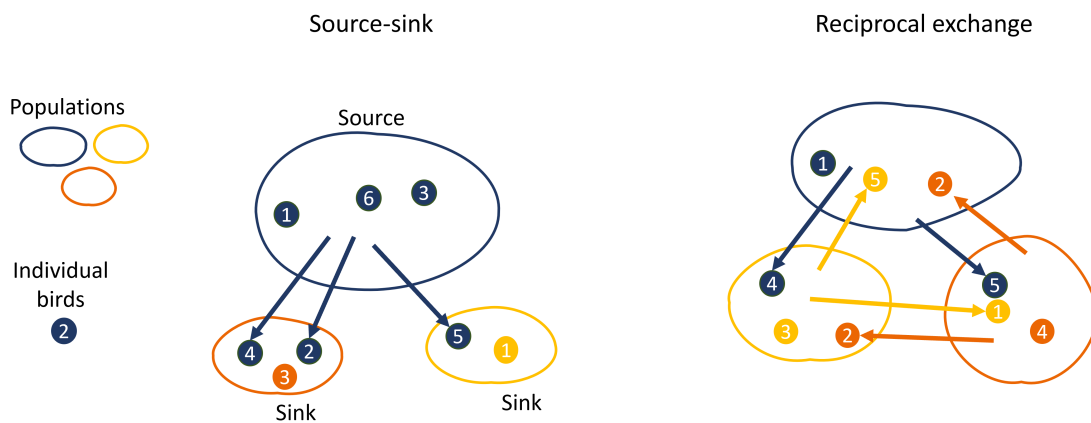
Understanding interannual changes in species' abundance and distribution is the foundation for conservation monitoring and management. However, range-wide information on distribution and abundance, and how they change (state and trend), is particularly challenging to obtain for species moving across large scales (Hortal et al. 2015; Chandler et al. 2017; Webb et al. 2019). Migratory species often have broad ranges, with different proportions of the population (e.g. depending on age class or phenotype) occupying parts of the range throughout the annual cycle. As a result, data collection on population

abundance may inadvertently introduce biases by non-randomly sampling across space (e.g. focusing only on part of the breeding habitat) or among ages and life-stages within a population (e.g. excluding non-breeders). In addition, because stochastic annual variation in numbers at a site is to be expected with mobile species, regular counts covering multiple major sites spread over time periods appropriate for the species in question are required (typically over at least 10 years).

Step 2. Determine connectivity between populations and sites.

Conservation planning can be undermined by limited knowledge of movements (sometimes called the "movement shortfall"; Cottee-Jones et al. 2016). Populations of mobile species are often spatially structured and can be part of a network of populations with different rates of immigration, emigration (Millon et al. 2019; Fig. 1a), and interaction between sites depending on migratory connectivity and fidelity throughout

a) Dispersal



b) Migration

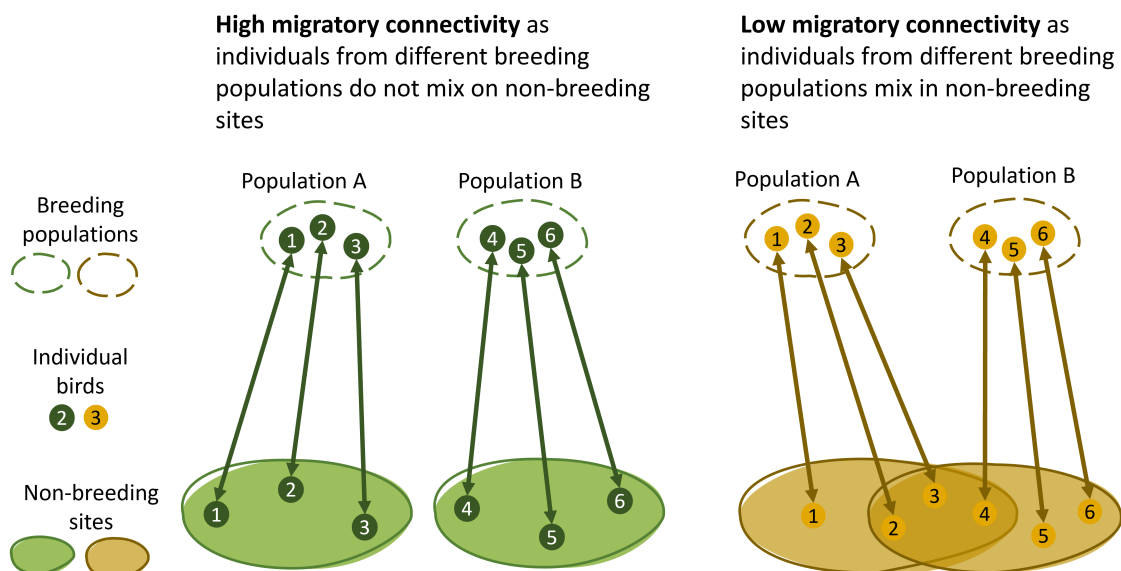


Figure 1. Populations and sites of mobile species can be connected through (a) dispersal or (b) seasonal migration resulting in different spatially structured populations depending on movement dynamics. Migratory connectivity is defined in terms of site fidelity and the degree of mixing of individuals from different breeding populations at other sites (e.g. Moore et al. 2019).

the annual cycle (Taylor 2019; Fig. 1b). By identifying dispersal networks, conservation management may become targeted towards key populations (Swift et al. 2021) or increase to include the entire network (Schaub et al. 2012). When a species uses a network of sites during the annual cycle but there is high migratory connectivity between breeding populations and non-breeding populations, there will be little mixing of individuals from different breeding subpopulations at non-breeding sites (Fig. 1b). If different breeding subpopulations have high migratory connectivity to different non-breeding sites, differing subpopulation trends across the range may be explained by the use of different sites and fidelity to those. This may justify managing subpopulations separately (Morrison et al. 2021). When a species uses a network of sites and mixing of individuals from different breeding sites occurs across non-breeding sites (Fig. 1b), migratory connectivity may moderate the effects (beneficial or otherwise) at any given site; this is because subpopulations are spread across a range of sites (Ellis et al. 2021). Nevertheless, visualisation of a network by itself is generally not sufficient to identify the best options for targeted conservation measures, because these systems are likely to be dynamic, depending on both extrinsic factors (e.g. habitat availability) and those factors that are intrinsic (e.g. dispersal behaviour) to the species (Taylor 2019). Importantly, the amount of information on connectivity needed will be species-dependent but should be sufficient to understand the underlying population processes such as migratory connectivity that may drive changes in abundance.

Step 3. Investigate population dynamics across space and time to determine limiting factors and the life stages they influence.

To target conservation management at the right stage of the annual cycle and the appropriate spatial scale it is important to identify the main drivers of population dynamics (Table 2) and quantify their effects. For mobile species, local and range-wide data on demographic parameters are required to develop mechanistic full-annual-cycle models (Fig. 2), which then allow for a process-oriented approach to evaluate population trends and drivers of population dynamics (e.g. Rushing et al. 2017).

Step 4. Assess which management actions, at what scales, are required for maximum population increase.

Once the limiting factors and the life stages they influence are understood, appropriate conservation management actions can be proposed, designed, and implemented, and their effectiveness tested (Williams et al. 2020). Strong inferences about the effectiveness of a management action can be made by measuring and analysing both outcomes over time and management effort (e.g. through before-after, control-impact or combined before-after-control-impact experimental designs; Innes et al. 1999), and by validating predictions based on these measurements and analyses (Hone et al. 2023).

Population viability analysis (PVA) is a useful approach for comparing outcomes of different potential management

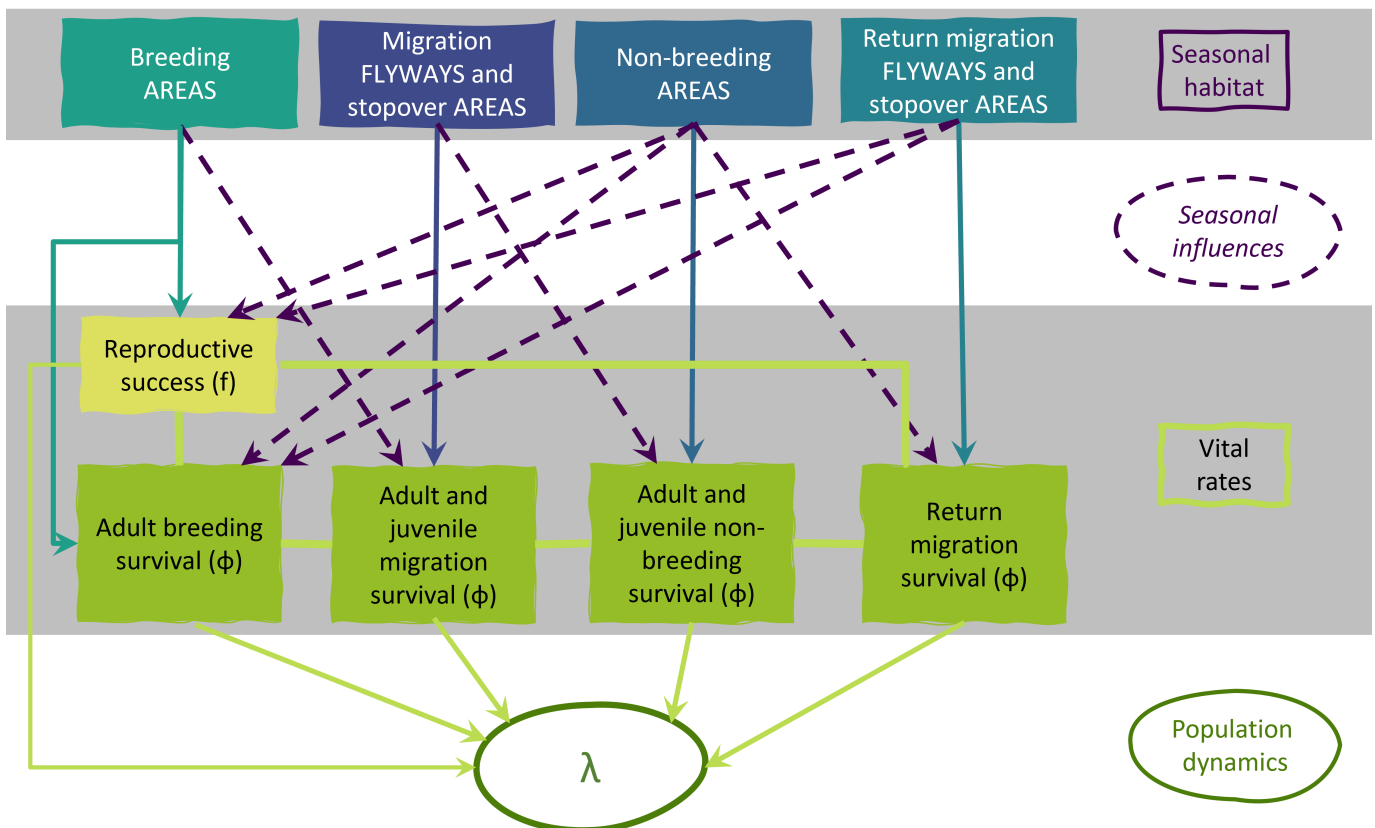


Figure 2. Seasonal habitat and influences combine to drive population dynamics. Purple and blue arrows indicate direct influences of seasonal habitat on different vital rates and green arrows indicate the contribution of these vital rates to overall population dynamics. Green lines connecting vital rates show interdependence of vital rates. Φ = survival rates; λ = population growth.

options relative to baseline conditions, assessing uncertainty of outcomes, and determining optimal strategies for achieving a set goal (Beissinger & Westphal 1998). Such analyses allow us to forecast population sizes in ‘what-if’ scenarios through simulation, and account for uncertainty and stochasticity of the demographic processes (births, deaths, immigration, etc.; Keedwell 2004).

Although there are only a handful of examples of full-annual-cycle assessments of population persistence and management actions, full-annual-cycle models can be used as a more spatially complete information base for PVAs. For example, Brown et al. (2017) used a full-annual-cycle PVA to determine whether the delisting from the U.S. Endangered Species Act of the Kirtland’s warbler (*Setophaga kirtlandii*) was appropriate, and which long-term management option on breeding grounds was required for persistence of the species, including accounting for variable environmental conditions experienced at non-breeding sites. Through their PVA they were able to determine that the population was stable with current levels of management, consisting of habitat provision through planting and predator reduction.

What information do we have to guide conservation management of New Zealand’s inland migrant bird species?

We reviewed what information exists to guide conservation management of five endemic inland migrant species (Appendix S1 in Supplementary Material): ngutu parore/wrybill (*Anarhynchus frontalis*), tarāpunga/black-billed gull (*Larus bulleri*), tarapirohe/black-fronted tern (*Chlidonias albstriatus*), tōrea/South Island pied oystercatcher (*Haematopus finschi*), and pohowera/banded dotterel (*Charadrius bicinctus*, the only one of this group that also undertakes annual international migration; Pierce 1999).

Information on their population status and trends, movements, and vital rates was collated from the published and unpublished literature (reports or theses) and by contacting relevant species experts or managers; we provide details of the methods and material used in Appendix S2. The findings of our review are summarised below under each of our four suggested steps.

Step 1. Most inland migrant species are likely to be in decline.

For New Zealand’s inland migrants, some information on state and trend is available through biannual counts around coastal sites covering 200 roost sites of waders, carried out since 1984 (Riegen & Sagar 2020), and regular bird counts along braided river breeding sites (e.g. O’Donnell & Hoare 2011; O’Donnell & Monks 2020). For most species, data on population size and trends are available only for part of the annual cycle, being counts from either non-breeding sites or braided rivers (Table 3). Those counts suggest that three inland migrant bird species are likely to be in decline and one increasing, while for one species (black-billed gull) the trend is unknown. Banded dotterel is the only species for which population counts have been analysed from both coastal (non-breeding) sites and from its key nesting areas in braided rivers (O’Donnell & Monks 2020). While declines have been detected in both breeding and non-breeding populations of banded dotterels in New Zealand, there is considerable variation between data

sources on the magnitude of those declines, possibly because trends from Australian non-breeding populations are unknown (O’Donnell & Monks 2020; Table 3). Overall, this suggests that most species are in need of conservation actions.

Step 2. Connectivity between inland migrant and non-breeding populations is poorly understood.

Natal dispersal of New Zealand wader species between different catchments has been observed through resighting of banded birds of four species, while breeding dispersal is common for colony-nesting black-billed gulls and black-fronted terns, but less common in the solitary-nesting species (banded dotterel, wrybill, South Island pied oystercatcher; Table 4). Full flyways between breeding and non-breeding populations have yet to be described for endemic migrants, but the Waikato coastline has been shown to be part of the flyway for the banded dotterel, South Island pied oystercatcher, and wrybill (Table 4). Migratory connectivity is best understood for the banded dotterel, with some knowledge on the other solitary nesting species, but little understood for the two colony-nesting species (Table 4).

Step 3. Knowledge on vital rates does not cover the full annual cycle.

Our literature search found that almost all information on demographic rates for New Zealand’s endemic migrants has been collected at breeding sites, especially South Island braided riverbeds (Fig. 3; Appendices S3, S4, S5). Of 326 observations of vital rates, 45% are of egg survival and 53% of chick survival, with only 2% relating to adult survival (Fig. 3). No information was available at all regarding adult survival of black-billed gulls or banded dotterels (Fig. 3). There is now considerable evidence that predation by introduced mammals and native avian predators is an important threat to nest, chick, and (in some instances) adult survival in these species at breeding grounds (Hay 1984; Rebergen et al. 1998; Sanders & Maloney 2002; Keedwell 2005; Norbury & Heyward 2008; Steffens et al. 2012; Cruz et al. 2013; Schlesselmann et al. 2018). However, individuals in these bird populations can spend as much as 70% of the year away from the breeding grounds (Appendix S1), and face a range of other, seasonally specific threats (O’Donnell et al. 2016). The alteration of habitat, climate change, and direct mortality during non-breeding seasons and migration may also have important population consequences, but these are still not well understood. Overall, we currently do not know what factors affect mortality outside breeding sites and when it occurs for any species.

Step 4. Evaluation of conservation actions is required.

Preliminary PVAs to test different management outcomes for banded dotterels, black-fronted terns, and South Island pied oystercatchers in the Mackenzie Basin were developed in the early 2000s (Keedwell 2004). These models highlighted that research needs to better understand seasonal effects on bird populations as well as inter-relationships between different threats at breeding grounds to further develop the PVA models. Data were not adequate to develop similar PVAs for wrybills and black-billed gulls at the time.

Predator trapping at various intensities or scales around nesting sites has been implemented, but its benefits for species recovery are not well understood because the outcomes of management are not fully measured (e.g. comparable estimates of productivity at a managed site compared with a control site

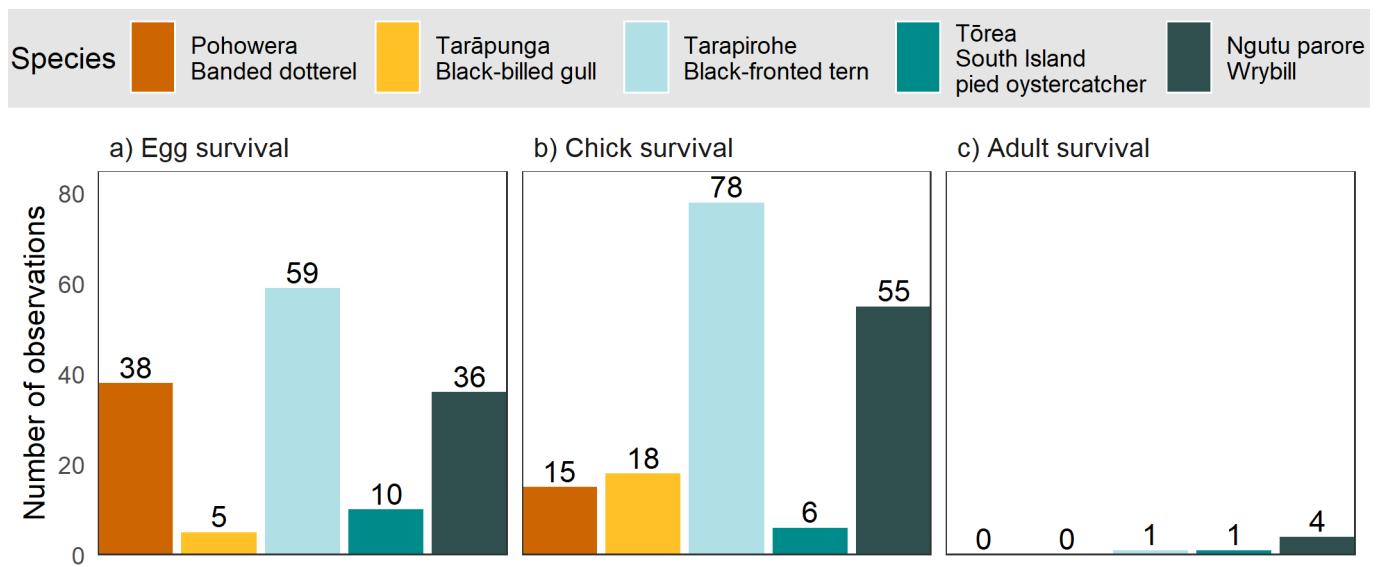


Figure 3. Overview of current information on demographic rates of New Zealand's endemic inland migrant bird species. Egg survival here is defined as at least one egg of a clutch hatching as all species are precocial. Chick survival is survival from hatching to fledging, and adult survival is of breeding birds. Each observation (detailed above each bar) stems from a single study system in a certain year, unless only averaged values across multiple years were available. Number of studies used for egg survival: $n = 34$; chick survival: $n = 32$; adult survival: $n = 4$.

Table 3. Overview of current information on the status and trend of New Zealand's endemic inland migrant bird species. For scientific names of species, see main text. p.a. = per annum.

Species	Threat classification ^a	Population size	Population trend	Reference
Pohowera Banded dotterel	At Risk (Declining)	13 000 birds (sum of most recent river counts before 2017) 19 000 birds (estimated)	-3.7% p.a. (estimated from braided river counts 1962–2017) -1.4% p.a. based on national wader counts 1984–2018 27% decrease ^b (ca. -1.15% decrease p.a.)	Hansen et al. 2016; O'Donnell & Monks 2020; Riegen & Sagar 2020
Tarāpunga Black-billed gull	At Risk (Declining)	121 000 birds (sum of ground-based nest counts and nest counts from aerial photographs during nesting; 2014–2016)	Unknown	Mischler 2018
Tarapirohe Black-fronted tern	Threatened (Nationally Endangered)	8000 birds (sum of most recent river counts before 2008)	50% decline over 25 years (estimated from braided river bird counts 1962–2008)	O'Donnell & Hoare 2011
Tōrea South Island pied oystercatcher	At Risk (Declining)	79 000 birds (winter wader counts 2019)	-1.2% p.a. since 2005 (winter wader counts)	Riegen & Sagar 2020
Ngutu parore Wrybill	Threatened (Nationally Increasing)	5000 birds (winter wader counts 2019)	33% increase ^b (c. 1.4% p.a.)	Riegen & Sagar 2020

Note: ^aBased on New Zealand Threat classification (Robertson et al. 2021); ^bcomparing winter wader counts 1983–1994 with winter wader counts 2005–2019.

Table 4. Overview of current information on connectivity between sites and populations of New Zealand's endemic inland migrant bird species.

Species	Dispersal networks	Flyways	Migratory Connectivity
Pohowera Banded dotterel	Partially known Natal dispersal appears to be high, but breeding dispersal appears to be low (Pierce 1989).	Partially known Full flyways not known, but surveys of the Waikato west coast suggest that part of the population passes on north- and south-bound migrations parallel to the coast, overland and offshore (Craig et al. 2015).	Partially known The majority of inland breeding birds in the southern South Island migrate to southern and eastern Australia (including Tasmania), coastal southern South Island birds stay sedentary, and inland breeding birds north of Canterbury generally move to the North Island (Pierce 1999).
Tarāpunga Black-billed gull	Mostly known All re-sighted second-year birds exhibited natal dispersal and 70% left their natal catchment (McClellan 2009), dispersing over hundreds of kilometres. Genetic research suggested local movements between nearby colonies (Mischler et al. 2018).	Unknown Most birds migrate to coastal areas at the end of the breeding season, although movements are poorly known (McClellan 2009).	Unknown
Tarapirohe Black-fronted tern	Mostly known Natal and breeding dispersal is occurring, based on banding within the Mackenzie basin, with only 9 of 169 fledglings resighted, 58% of breeding adults seen at other colonies, and 23% in other catchments (Keedwell 2005). Genetic and morphometric data suggests local dispersal between colonies, but not range-wide breeding dispersal (Schlesselmann et al. 2020).	Partially known Individuals move from inland breeding sites to coastal areas, and tracking data from the Mackenzie Basin suggest movement along rivers (Gurney 2022).	Unknown
Tōrea South Island pied oystercatcher	Mostly known. High natal dispersal but very low breeding dispersal based on banding (Sagar & Veitch 2014).	Partially known Full flyways not known, but surveys of the Waikato west coast suggest that a large proportion of the population passes on north- and south-bound migrations close to the coastline (Craig et al. 2015).	Mostly known Strong breeding site philopatry, but probably mixing at coastal non-breeding sites (Sagar et al. 2002).
Ngutu parore Wrybill	Unknown	Partially known Full flyways not known, but surveys of the Waikato west coast suggest that a large proportion of the population passes on north- and south-bound migrations parallel to the coast, overland and offshore (Craig et al. 2015).	Partially known Strong concentration at coastal non-breeding sites and considered to have high breeding philopatry (Hay 1984).

or before treatment), and the mobile nature of the species and lack of survival data complicate such assessments (Stojanovic et al. 2020). Two alternative management approaches to predator control have been tested at breeding sites. First, habitat modification (clearing islands of introduced vegetation to make them less likely to be occupied by introduced predators; Schlesselmann et al. 2018) resulted in no difference in nest survival of black-fronted terns due to high predation by avian predators across cleared and vegetated islands. Second, predator behaviour was manipulated through scent, and resulted in a 1.7-fold increase in nest survival of banded dotterels and wrybills (Norbury et al. 2021).

Ways forward: new technology and statistical approaches.

Despite data gaps concerning the connectivity between sites and the shortcomings in current understanding of population dynamics identified above, recent advances in tracking technology (Wilmers et al. 2015) and new statistical methods (Zipkin & Saunders 2018) can assist conservation biologists to start to take a full-annual and life-cycle approach. We suggest that adopting these tools and approaches could help us better understand and overcome the challenges of mobile species conservation.

Tracking technology.

Recent advances in tracking technology have revolutionised the ability to map movements of animals year-round for extended periods (e.g. several years) and over large spatial scales with high spatial and temporal resolution (Wilmers et al. 2015; Nathan et al. 2022). A wide range of high-throughput wildlife tracking systems have been developed, including devices that communicate through automated receiver networks (Taylor et al. 2017), store fine-scale data on-board (global positioning system (GPS) logger; Fraser et al. 2017), or communicate data in real time (e.g. GPS devices that communicate through the mobile phone network; Kämpfer et al. 2023). The utility of tracking tags has increased through the miniaturisation of devices; GPS tags with remote data shrank from 250 to 20 g between 2005 and 2015, and 1 g tags are now available. This miniaturisation has enabled researchers to track smaller species at increasing temporal resolution, with an order of magnitude increase in number of fixes every five years, while minimising the effects of tracking on animal behaviour or survival (Kays et al. 2015). Simultaneously, analytical tools and data management platforms have been developed to best leverage the volume and variety of the movement data generated (Kays et al. 2022).

Tracking technology has enabled an understanding of animal movements throughout the annual cycle and has elucidated the spatial and temporal migratory connectivity of migratory species (Knight et al. 2021). Through generating connectivity profiles, it is possible to direct research and conservation actions if differential population trends are apparent for populations that follow separate migration pathways and occupy separate non-breeding areas. Furthermore, migration pathway bottlenecks (places that most individuals pass through) can be identified as important sites to implement protection (Thaxter et al. 2019; Beal et al. 2021). Finally, tracking technology can improve our understanding of the survival and movement of juvenile or non-breeding

life stages and provide new understanding of whether lack of recruitment into a population is caused by mortality or dispersal (Irwin et al. 2021). For example, Gurney (2022) recorded unexpected movements of breeding black-fronted terns that were not incubating to separate night roosts during the breeding season. Such insights highlight the scale of movement and can guide conservation efforts accordingly. However, while modern tracking units generally have high GPS fix success and data transfer rates, performance of devices is strongly influenced by species and unit characteristics as well as environment (Hofman et al. 2019). Technological failures may still end unit deployments prematurely and as a result it may not be possible to distinguish whether an animal dispersed or died.

Integrated population modelling.

Various full-annual-cycle models for migratory species have been developed, which range in complexity and data requirements (from single-season counts combined with year-round environmental data to individual-based models; Hostetler et al. 2015). One of the most promising methods has been integrated population models (IPMs), which combine multiple data types into a single analysis (Zipkin & Saunders 2018). Such models provide a foundation for determining demographic drivers that have thus far rarely been studied (Figs. 2, 3) and can be difficult to study, such as dispersal (Schaub et al. 2012), seasonal survival (Rushing et al. 2017), or range-wide, large-scale drivers (Nater et al. 2023).

In New Zealand, IPMs have already been used to, for example, understand the population dynamics of forest birds such as hihi/stitchbirds (*Notiomystis cincta*; Parlato et al. 2021). They have also been used in combination with expert elicitation and structured decision-making to assess management options for seabirds such as the kuaka/Whenua Hou diving petrel (*Pelecanoides whenuaensis*) (Fischer et al. 2022).

IPMs have several advantages. Being flexible, they can be adapted to the primary question and data available, and thus can range in complexity (Schaub & Kéry 2021). It is possible to use sparse or fragmentary data on different population processes. Discrepancies between population trends from different data sources at different times of the annual cycle (e.g. breeding versus non-breeding counts) can be addressed by combining both data sources in an IPM (Saunders et al. 2019). Finally, such models can be extended into PVAs, based on information covering the spatial extent of the full annual cycle of the species to test different management scenarios. In one example, Davis et al. (2023) developed a PVA within an IPM of a black tern (*Chlidonias niger*) population in the Upper Midwestern United States. They showed projected population trends under current conservation management conditions during the breeding season, and compared these to projected population trends using interventions aimed at increasing adult and juvenile survival during migration and non-breeding periods.

We suggest that New Zealand's existing data from different scales can potentially be combined in an IPM to improve understanding of the challenges faced by inland migrant species (Fig. 4). For example, existing count data and mark-resight data could be combined to better understand survival throughout the annual cycle. As it becomes available, new data (e.g. from tracking individuals) could be incorporated to further inform estimates of survival and migratory connectivity (Rushing et al. 2021).

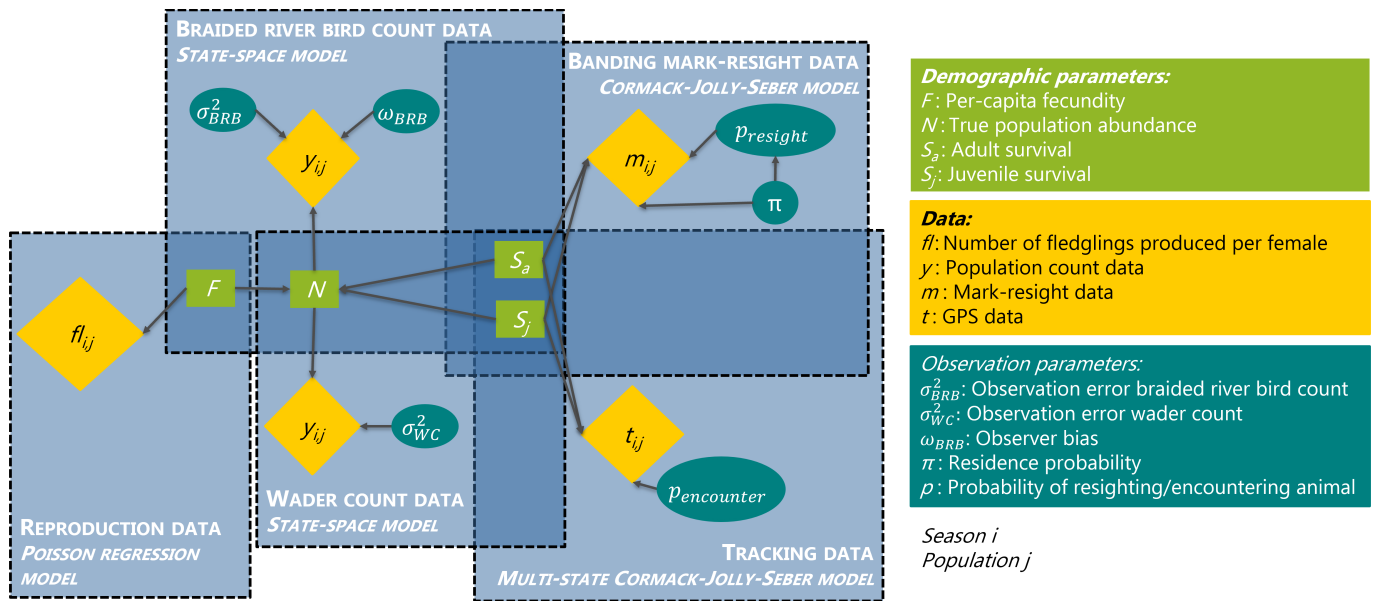


Figure 4. How existing data could be linked in an integrated population model to provide inferences about demographic parameters and population abundance. Not all data types are required, and other data types can be integrated if available. Demographic parameters are in yellow-outlined boxes, data are shown as blue-outlined diamonds, and observation parameters are in green ovals. Sub-models are represented by dotted yellow rectangles and titled with typical data and model structure (based on Zipkin & Saunders 2018).

Discussion

Inland migrant species in New Zealand have been studied at a range of different spatial scales: detailed information on egg or chick survival has been collected at local breeding sites; bird counts in braided rivers span regions but may not cover the entire breeding area; and national wader counts have a national range (Table 3, Fig. 3). However, understanding of the spatial structure of inland migrant populations is in its infancy. Dispersal among local breeding populations has been observed through some banding records and inferred through genetic work, but it is generally uncertain how frequent such dispersal is and how it influences local population dynamics (Table 4). Flyways and migratory connectivity are generally not well understood (Table 4). Vital rate information is biased towards productivity, and the focus on breeding sites closely mirrors international patterns across major vertebrate taxa (Roodbergen et al. 2012; Marra et al. 2015). Consequently, it is currently difficult to assess the local and nationwide population trends of these species and determine the benefit of conservation management actions at breeding sites or elsewhere (Hone et al. 2023).

Many examples from outside New Zealand illustrate a full-annual-cycle approach to mobile species conservation (but note that full-annual cycle approaches have already been adopted in New Zealand for seabirds such as Antipodean albatross (*Diomedea antipodensis*); Convention on Migratory Species 2020). These examples show that designing and evaluating effective conservation strategies for mobile species can be achieved through understanding drivers of population dynamics at local and range-wide scales. Here we have suggested how existing data could be combined to make a start with a full-annual-cycle approach for inland migrant bird species. New technology and new population modelling approaches offer the potential to better understand processes driving population dynamics in New Zealand’s mobile species at different spatial scales and to better assess management options.

It is likely that new data will need to be collected to reduce uncertainty, improve inference, and better target management to ensure the persistence and recovery of mobile species. Often there will be a need for conservation management to proceed despite knowledge gaps. However, planning to evaluate the effectiveness of conservation actions in comparison to species trajectories in the absence of management will enable management to become more informed and effective in the longer term. Successful application of full-annual-cycle approaches will also require coordination between different groups (iwi, private landowners, citizen scientists, researchers) and organisations (Department of Conservation, councils, Land Information New Zealand, universities, Crown Research Institutes, non-government organisations) across New Zealand.

Despite these challenges, we suggest that a full-annual-cycle approach offers many benefits. It could (1) forge a link between individual movement data and population-level processes; (2) reveal links between environmental factors and species demography; and (3) identify conservation actions locally and/or regionally with the greatest population impact nationally (Zipkin & Saunders 2018; Schaub & Kéry 2021; McClintock et al. 2022). Overall, adopting a full-annual-cycle approach would enable New Zealand to better understand the difference made by its present conservation management and better protect its mobile fauna.

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Supplementary Material

Additional supporting information may be found in the online version of this article:

Appendix S1. Overview of breeding habitats, non-breeding habitats, and timing of migrations of New Zealand's endemic inland migrant species.

Appendix S2. Description of methods and materials for the literature review of knowledge on vital rates of New Zealand's endemic inland migrant species.

Appendix S3. Excel file containing collated nest survival rates of New Zealand's endemic inland migrant bird species, study details, and source.

Appendix S4. Excel file containing collated chick survival rates of New Zealand's endemic inland migrant bird species, study details, and source.

Appendix S5. Excel file containing collated adult survival rates of New Zealand's endemic inland migrant bird species, study details, and source.

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