

Setting conservation priorities for migratory networks under uncertainty

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Abstract

Conserving migratory species requires protecting connected habitat along the pathways they travel. Despite recent improvements in tracking animal movements, migratory connectivity remains poorly resolved at a population level for the vast majority of species, hampering conservation prioritisation. In the face of these data limitations, we develop a novel approach to spatial prioritisation based on a model of potential connectivity, derived from empirical data on species abundance and distances travelled between sites while on migration. Applying this approach to migratory shorebirds using the East Asian-Australasian Flyway, we demonstrate that conservation strategies that prioritise sites based on connectivity and abundance together, outperform strategies that only prioritise sites based on the abundance of birds. The conservation value of a site is therefore dependent on both its capacity to support migratory animals and its position within the migratory pathway, with the loss of crucial sites leading to partial or total population collapse. We suggest that strategies prioritising conservation action at sites supporting large populations of migrants should, where possible, be augmented using data or models on the spatial arrangement of sites.

Introduction

Conservation plans often assume that species are static in time and space (e.g. Pressey et al. 2007), yet many species undertake seasonal, cyclic or dispersive movements throughout their life cycle, with migratory species travelling some of the longest distances (Block et al. 2011). Migratory journeys take animals across continents and oceans, to exploit seasonal pulses in resource availability (Alerstam et al. 2003) or to avoid inhospitable conditions (Runge et al. 2014). For instance, many migratory species time their breeding or migration to coincide with peaks in food abundance to maximise their chances of survival, as well as that of their offspring (Klaassen et al. 2006). Many individuals can concentrate at a small number of sites during a migratory journey, and

in some cases an entire population may congregate in a single location, during the breeding season (Matthiopoulos et al. 2005), the stationary non-breeding season (Richter & Cumming 2008), or while moving between the two (Runge et al. 2014). Such sites form migratory bottlenecks, and habitat degradation or loss at such sites may result in disproportionately large decreases in abundance or survival (Iwamura et al. 2013). The location of sites relative to others (i.e. the network structure), is therefore an important determinant of the number of individuals that will successfully migrate between these sites (i.e. connectivity).

Understanding migratory connectivity at a population level is essential to conserving migratory species (Bauer et al. 2016). Indeed, conservation plans that account for connectivity have repeatedly been shown to outperform plans that do not (Hermoso et al. 2012; Nicol et al. 2015; Sheehy et al. 2011). However, connectivity is rarely incorporated into conservation plans due to a paucity of population-level connectivity measures. For example, more than 90% of the world's migratory birds are inadequately protected across their annual cycle, with connectivity between breeding, stopover and non-breeding habitats overlooked in the planning process (Runge et al. 2015). Yet many migratory species are in urgent need of strategic conservation action, with populations declining at much greater rates than non-migratory species' populations worldwide (Wilcove & Wikelski 2008).

Recent advances in animal tracking have revolutionised the study of migratory connectivity, with lightweight devices able to accurately track migrations over thousands of kilometres (Block et al. 2011), and the development of expansive citizen science networks that report sightings of individually marked animals (Silvertown 2009). Such methods are beginning to show promise for describing migratory pathways in a comprehensive manner to permit formal spatial prioritisation. Yet our knowledge is presently very patchy, with many migrants having never been formally studied, and with only sparse data from those that have. Despite the increasing sophistication of the technology, tracking animal movements remains difficult and expensive, and animals are often only tagged or banded at a small number of locations (e.g. Block et al. 2011), limiting inference at a

population level (Lisovski et al. 2016). Resightings or recaptures are needed to track animals that have been colour tagged or fitted with geolocators respectively, causing bias toward areas with many observers (e.g. Minton et al. 2006). Though the resulting data are important for mapping connectivity, it is unclear how well they represent population-level connectivity patterns. With many migratory animals in severe decline (Wilcove & Wikelski 2008), methods that make best use of the available data are crucial in setting appropriate conservation priorities in migratory networks.

Here, we use available tracking data to parameterise a model of migratory connectivity for migratory species and prioritise site protection for the conservation of seven migratory shorebird species in the East-Asian Australasian Flyway (EAAF). We use tracking data to estimate the frequency of migratory movements of different distances, and calculate the likelihood of movements between any two sites within the migratory network. We estimate the effect of site loss on overall population flow through the migratory network to identify conservation strategies to minimise population loss. We compare our spatially-explicit prioritisation with an approach based on prioritising sites that support large numbers of individuals, revealing that abundance-based measures can deliver better conservation outcomes when augmented with connectivity-based measures.

Methods

To model potential connectivity between all sites within a migratory network, we use a maximum-flow approach. In the following sections, we describe how we: (i) formulated the maximum-flow problem, (ii) tailored it to migratory species (iii) prioritised sites for conservation, and (iv) applied our approach to migratory shorebirds in the EAAF before (v) conducting a sensitivity analysis.

Formulating the maximum-flow problem

The maximum-flow problem is a widely used approach for modelling movement and migration of animals within a network of non-contiguous habitat patches or sites (Minor & Urban 2007; Urban & Keitt 2001). The approach models the population as a whole as it flows through a network of sites, similar to modelling water flowing through pipes, rather than accounting for the behaviours and decisions of individuals. Each pair of sites has a pre-defined capacity, which can be expressed in an ecologically meaningful way based on, for example, carrying capacity, site type (breeding, stopover or non-breeding) or distance between sites. This method allocates similar numbers of animals to migratory routes with similar capacities. In contrast, a greedy approach would allocate all animals down one route, but none down a minutely poorer route (e.g. Dijkstra 1959).

Mathematically, the maximum-flow problem is formulated as follows. Let $G(V, E)$ be a directed graph or network, defined by a set of nodes V and edges E . Nodes represent important migratory habitat (i.e. discrete habitat patches used for breeding, non-breeding or stopover). An edge (u, v) represents connectivity between nodes u and v . Each edge (u, v) in E has a capacity c_{uv} , the maximum number of animals that can migrate along edge (u, v) . Let G have a source node s and sink node t in V which represent the start and end of the migratory cycle (respectively the breeding and non-breeding grounds, for example). Every node u in V other than s and t can have multiple edges entering and exiting u . Thus breeding s and non-breeding t nodes are defined differently from stopover nodes u .

However, if we consider a case where there are multiple breeding or non-breeding nodes, it is possible to create supersource and supersink nodes s' and t' respectively. Thus, directed edges (s', s_j) go from supersource node s' to all source nodes s_j , where $j \in \{1, 2, \dots, m\}$ and m is the total number of start nodes. Each edge (s', s_j) has an unlimited capacity to enable the population to flow into the s_j nodes unconstrained (i.e. conceptually, to pre-allocate animals to nodes before starting migration). However, we may also add a capacity to the s_j nodes to ensure no more than the number of individuals the site can support will be present at that site to start migration. A similar approach can

be used for the supersink node t' with directed edges (t_k, t') from all sink nodes t_k where $k \in \{1, 2, \dots, n\}$ and n is the total number of sink nodes, with a capacity of infinity. Unlike s_j , the number of animals entering t_k will already have been allocated, and there is no need to constrain (t_k, t') edges.

The objective of the maximum-flow problem is then to maximise the flow between supersource node s' and supersink node t' , without exceeding the edge capacities. Representing the flow between edges (u, v) in E with x_{uv} , we can formulate the maximum-flow problem as:

$$\text{Maximize: } f(x) = \sum_{(u,v) \in E(s)} x_{uv},$$

$$\text{Subject to: } \sum_{\{v: (u,v) \in E\}} x_{uv} - \sum_{\{v: (v,u) \in E\}} x_{vu} = 0 \quad \forall u \in V\{s,t\},$$

$$0 \leq x_{uv} \leq c_{uv} \quad \forall (u,v) \in E.$$

The first constraint ensures that the number of birds entering and exiting a node must be the same; the second constraint ensures that the number of birds migrating along each edge cannot exceed the edge capacity. For migratory species, maximum flow can measure how local changes to node capacity will affect population-level migratory connectivity (Iwamura et al. 2013; Minor & Urban 2007; Urban & Keitt 2001). The maximum-flow problem is a linear programming problem, which we solve using Gurobi 6.0.0 (Gurobi Optimization 2012).

Defining a migratory network using tracking data

We use two simple rules of thumb to parameterise the edge capacities within our network (i.e. the numbers of individuals migrating between all pairs of nodes). Firstly, we assume that animals are more likely to migrate to sites where large numbers have been counted. Secondly, we assume that animals have preferential travel distances (some for instance may prefer to make multiple short journeys, while others might prefer to make fewer longer distance journeys), and are more likely to

migrate to sites within this preferred distance. Thus it is possible to estimate edge capacities using (i) a list of sites with known count data, and (ii) a small sample of tracking data.

More specifically, by using individual animal tracks (start and end latitude and longitude for example), it is possible to estimate the probability density distribution for migratory movements between nodes using the function “density” in R (R Core Team 2015). By fitting a density distribution around the available tracks, we measure the likelihood that an animal can travel a given distance, accounting for uncertainty in the tracking process. Indeed, tracking data and notably geolocator data are variable in accuracy, ranging from $495.5 \text{ km} \pm 1031.2$ (Rakhimberdiev et al. 2016) to 20 km (Lisovski et al. 2012) depending on environmental conditions and calibration method. Furthermore, the data are spatially-biased, with all individuals tagged in the same location. Many individuals are therefore potentially migrating similar distances along similar routes. To deal with these uncertainties, the function fits a distribution to the data by trading off “over-fitting” which produces multiple peaks, and “over-extrapolating”, which produces flat distributions that predict similar probabilities for all distances. A good fit (*adjust* = 2 in the *density* function in R) was found by manual adjustment and visual inspection of the curves. Thus, the density distribution gives the probability P_{uv} of migration along edge (u,v) according to distance (Fig. 1), and is used to parameterise edge weights w_{uv} :

$$w_{uv} = P_{uv} N_v A_{uv},$$

where N_v represents the proportion of the population using node v and $A_{uv} = |\cos(\phi_{uv})|$ represents the absolute cosine of the azimuth angle ϕ between nodes u and v in radians. A_{uv} weights northerly or southerly nodes more heavily than easterly or westerly nodes, specifically for species which undertake North-South migrations, to prevent them from “zigzagging” northward and southward.

For species that do not undertake directional migrations, A_{uv} can be set to 1. w_{uv} weights nodes with many migrants and within likely travel distances more heavily than nodes supporting few migrants

that are within an unlikely travel distance (according to the density distribution ; Fig. 1). These assumptions approximate the observed pattern of migratory journeys, and it is likely that migratory routes with larger carrying capacities and with stopover nodes within preferential migratory distances will support a larger proportion of the population.

We use w to determine the proportion of each species population migrating between each set of nodes. w_{uv} is used to parameterise the capacity c_{uv} , or number of animals moving along each edge (u,v) in E , such that $c_{uv} = x_u (w_{uv} / \sum_{\{v: (u,v) \in E\}} w_{uv})$, where x_u represents the number of animals which has flowed into node u . The capacity calculation is initiated from start node s where x_s is equal to the known population size of the species. Finally, we determine the proportion of the population migrating through each graph $G (V, E)$ as per the maximum flow problem formulation above.

Our methods allow migratory animals to go anywhere in the network, although the majority of the population utilises edges with the greatest capacity going in the correct direction (N, NE and NW when migrating to breeding grounds, and S, SE and SW when migrating to non-breeding grounds), with few individuals utilising other edges.

Full code can be found in the Supporting Information.

Prioritising nodes for conservation

Our prioritisation objective was to identify nodes that maximised the expected migratory population flow. We used a reverse-greedy approach for the prioritisation, sequentially removing nodes least likely to deliver our objective. In practice, this approach delivers similar results to more complex optimisation algorithms (Polasky et al. 2000; Pressey et al. 1997).

We used three prioritisation strategies, based on: (i) flow, (ii) maximum count and (iii) random. For the population flow and maximum count strategies, we iteratively removed the node that

contributed least to the prioritisation criteria (i.e. population flow or maximum count as per Bamford *et al.* 2008) through the network until no nodes remained (the approach of Conklin *et al.* 2014). Thus when a site is lost, this methodology assumes that the individuals using the site die. This has previously been observed in some migratory species such as great knots (*Calidris tenuirostris*; Moores *et al.* 2016; Rogers *et al.* 2010) and monarch butterflies (*Danaus plexippus*; Flockhart *et al.* 2015) where habitat loss has directly resulted in population declines.

We compared the ranking of sites between the flow and maximum count prioritisation strategies using Spearman's rank correlation. We also compared the prioritisations to a family of random samples. To do so, we iteratively removed nodes from the network at random, and repeated this process 1000 times (Fig. 2).

Migratory shorebird case study

We constructed directional graphs representing migration for seven EAAF shorebird species: bar-tailed godwit (*Limosa lapponica baueri*), eastern curlew (*Numenius madagascariensis*), great knot (*Calidris tenuirostris*), grey-tailed tattler (*Tringa brevipes*), red knot (*Calidris canutus*), ruddy turnstone (*Arenaria interpres*) and sanderling (*Calidris alba*). These species (i) have been tracked, albeit in small numbers, (ii) have mapped breeding, stopover and non-breeding sites (Bamford *et al.* 2008) which can be used as nodes within a maximum flow framework, (iii) have an estimate of overall population size (Bamford *et al.* 2008), and (iv) are known to migrate directionally northward and southward (Alerstam *et al.* 2001). Each species took different north and south migratory routes, and utilised different stopover nodes (Bamford *et al.* 2008) .

We used tracking data collected from a literature review and provided by the Victorian and Queensland Wader Study Groups to parameterise migration through the network of sites. We

classified tracks into northward or southward migration to account for the different distances birds are possibly capable of flying before and after breeding, which is energetically demanding (Battley et al. 2012). We acquired tracks for bar-tailed godwits (number of individually tracked birds $n=16$, total number of records of flights made during north migration $nm=32$, and south migration $sm = 0$; Battley et al. 2012), eastern curlews ($n=9$, $nm=34$, $sm=21$; Driscoll & Ueta 2002), great knots ($n=4$, $nm=13$, $sm=14$; Victorian Wader Study Group), grey-tailed tattlers ($n=3$, $nm=18$, $sm=10$; Queensland Wader Study group <http://waders.org.au/studying-waders/banding-shorebirds/satellite-transmitters-and-geolocators/>), red knots ($n=3$, $nm=7$, $sm=15$; Victorian Wader Study Group), ruddy turnstones ($n=48$, $nm=162$, $sm=162$; Minton et al. 2010; Minton et al. 2011; Minton et al. 2013) and sanderlings ($n=13$, $nm=50$, $sm=75$; Lisovski et al. 2016; Minton et al. 2013). The accuracy of all Wader Study Group data was estimated as per Lisovski et al. (2016).

Sensitivity analysis

We used ruddy turnstone, the species with the most data, to investigate how the flow prioritisation strategy changed with 10, 20 or 40 fewer birds tracked, and finally with only one bird tracked. For each scenario, we randomly removed 10, 20 and 40 birds from our tracking dataset and carried out the prioritisation 1000 times. For the scenario where we only used one tracked bird, each bird was used once. The resulting prioritisation was extremely stable at the different sample sizes (Supporting Information). This is consistent with previous research showing that even small numbers of tracks can make a significant contribution to a spatial conservation planning (Mazor et al. 2016).

Results

The density distribution of recorded flight lengths varied markedly among species (Fig. 1). Some were very narrow (eastern curlew, grey-tailed tattler and sanderling) and others broad (bar-tailed godwit and red knot). For species with narrow distributions, the probability density distribution generally peaked and receded before 5,000 km (eastern curlew, great knot, grey-tailed tattler and sanderling). Species with broader distributions varied more substantially. For instance, bar-tailed godwits had a similar probability of migrating between 5,000 and 10,000 km, but were unlikely to migrate less than 5,000 km. In contrast, red knots and ruddy turnstones were most likely to migrate less than 5,000 km, although birds were still capable of making long-distance (>10,000 km) flights with a small probability.

These probability distributions drove the structure of network connectivity for each species, and therefore the outcomes of the prioritisation strategies. The flow strategy outperformed the maximum count strategy, which generally outperformed the random strategy (Fig. 2). However, there were some marked differences among species. For some, the difference between the strategies diminished as nodes/sites were removed (great knot and red knot). For others, the difference remained large (bar-tailed godwit, eastern curlew, grey-tailed tattler and ruddy turnstone). Surprisingly for two species, there was substantial overlap between the maximum count and random prioritisation strategies (great knot and sanderling). Species with large networks (e.g. bar-tailed godwit, 53 sites as per Bamford et al. 2008; ruddy turnstone, 69) therefore lost population flow gradually as sites were lost, while species with smaller numbers of sites available to them (e.g. great knot, 33; red knot, 30; sanderling, 35) experienced a population collapse when the number of sites crossed a critical threshold, around 50% of the sites (Fig. 2 and Supporting Information).

The importance of network structure was apparent when comparing site rankings between the maximum count and flow prioritisation strategies (Supporting Information). Indeed, species with large networks and gradual population loss showed the highest agreement between maximum count and flow prioritisation rankings (Supporting Information; Spearman's rank correlation: bar-

tailed godwit $r_s = 0.73$, $p = 1.8e^{-9}$), while species with smaller numbers of sites and experiencing sudden population collapses showed much lower levels of agreement between maximum count and flow prioritisation rankings (Supporting Information; sanderling $r_s = 0.49$, $p = 2.9e^{-3}$; great knot $r_s = 0.43$, $p = 1.4e^{-2}$). Overall, the levels of agreement between the maximum count and flow prioritisation strategies were intermediate (red knot $r_s = 0.78$, $p = 1.63e^{-6}$; eastern curlew $r_s = 0.68$, $p = 8.61e^{-7}$, grey-tailed tattler $r_s = 0.64$, $p = 9.8e^{-8}$, and ruddy turnstone $r_s = 0.57$, $p = 8.2e^{-7}$). When comparing individual ranks between the maximum count and the flow prioritisations, the majority did not shift markedly in rank (circled sites in Fig. 3 and Supporting Information). However, some sites greatly increased in rank (upward facing arrows in Fig. 3 and Supporting Information) while others decreased (downward facing arrows in Fig. 3 and Supporting Information). Sites that increased in rank were removed later in the flow prioritisation than the maximum count prioritisation, and vice versa. Sites that were not well connected, or that only supported birds during southward or northward migration were removed earlier in the flow prioritisation than the maximum count prioritisation (Fig. 3 and Supporting Information). A few key sites are therefore fundamental in driving the efficiency of the flow prioritisation strategy.

Discussion

Despite tracking devices becoming smaller, cheaper and more accurate, and the availability of tracking data increasing rapidly, much remains unknown about species' migratory routes, hampering conservation planning. Here, we have shown that limited tracking data can be used to parameterise a simple model of migratory connectivity to aid decision-making for migratory species.

We showed that prioritising the protection of sites with the largest counts of individuals was not as efficient as using migratory connectivity, and in some cases, maximum count strategies performed as poorly as randomly selecting sites for conservation (Fig 2). This might seem counterintuitive, since

sites supporting large numbers of birds would be expected to have a higher conservation priority than sites supporting smaller numbers of birds. In fact, this is a widely used approach for setting conservation priorities (e.g. Conklin et al. 2014; Convention on Wetlands 1999). However, groupings of sites with small numbers of birds act as a unit if they are highly connected, whereby the loss of one of these sites will compromise the flow of migrants through the other sites, thus making it more beneficial to conserve a grouping of small connected sites over one larger site (Fig. 3). Indeed, the relative conservation value of small patches of habitat is increasingly recognised (Tulloch et al. 2016).

Similarly, there were trade-offs between conserving non-breeding, stopover and breeding sites. Different types of sites contributed very differently to population flow through the network, with population flow particularly sensitive to the removal of breeding sites. In our case study, the breeding site was always removed last because it acted as both a supersource and supersink node (Supporting Information). Yet, for a different case study with a different network structure, a non-breeding or breeding site could be removed in the reverse-greedy algorithm before a stopover site (Supporting Information). This is because groupings of connected non-breeding, stopover and breeding sites are always prioritised over individual less-connected sites; regardless of whether the site supports a large number of animals, or is a breeding site. The trade-offs between conserving sites with smaller or larger number of birds, which are more or less connected, are therefore complex and difficult to predict without mathematically formulating a maximum-flow problem.

Network structure played a key role in the prioritisation. We observed that the flow maximisation strategy was more effective for some species (e.g. bar-tailed godwit and great knot), than for others (e.g. red knot; Figs. 2 and S2 in supporting information). The distribution of migration distances for these species hints at the mechanisms involved. For example, bar-tailed godwits can fly long distances and have many sites available to them (53 sites as per Bamford et al. 2008). The effect of removing one site on population flow was therefore low. The cumulative effect of removing sites

remained incremental until the population suddenly declined rapidly. This decline occurred once stopover sites were no longer available and non-breeding sites began to be removed (Supporting Information). Beyond that point, the population declined stepwise as non-breeding sites were removed until no birds remained (Supporting Information). No site strongly outweighed another in terms of its contribution to population flow, however, a critical mass of sites was required to maintain the flyway.

In contrast, the migration of great knots depended on a few key sites, and the population collapsed when these were lost (Supporting Information). This was partly because great knots preferred to fly shorter distances than bar-tailed godwits (Fig. 1) and were dependent on stopover sites to complete both their northward and southward migration (Moore et al. 2016). Furthermore, they had relatively few sites available (33). Losing stopover habitat, which birds can exploit during both north and south migration, and that are highly connected to non-breeding sites, resulted in rapid population declines. Unlike bar-tailed godwits, where non-breeding habitats were prioritised (Supporting Information), for great knots the flow maximisation strategy prioritised non-breeding and stopover habitat alike (Supporting Information). In fact, non-breeding and stopover habitats were prioritised at similar rates for all species except bar-tailed godwit (Supporting Information).

Tracking data are therefore very important in shaping network structure. Yet tracking data also provide their own set of challenges. Though small samples of tracking data do not adversely impact the prioritisation (Supporting Information), better estimates could be achieved by tracking single individuals from numerous locations (Mazor et al. 2016), as opposed to numerous individuals from a single location. Furthermore, tracking devices used in earlier studies were much bulkier than today, and are likely to have impacted migration. With eastern curlew for instance, some individuals did not migrate to the breeding grounds, returning instead to the non-breeding grounds (Driscoll & Ueta 2002).

Additional tracking data could refine our modelled connectivity estimates, however given the limited data availability, the pattern of migratory connectivity among sites remains impossible to fully validate at the population level. It would therefore be interesting to develop more biologically meaningful mechanistic (e.g. population growth, density-dependence) or eco-physiological models (e.g. energetics, starvation risk, predation risk, stopover duration) of the migration itself (Aharon-Rotman et al. 2016; Bauer & Klaassen 2013; Bauer et al. 2008; Taylor & Norris 2010). Indeed, the approach we develop here is not intended to replace such models, but to provide insight across a large number of sites when data are sparse. Mechanistic approaches are data hungry, computationally complex, and limited in their spatial accuracy. In the face of ongoing population declines and data paucity, estimates of connectivity patterns that make best use of existing data are urgently needed to inform coordinated protection for migratory species.

The proposed connectivity model should not be viewed as a method of determining which sites can be lost before others, but as a means of measuring the benefit of conserving a site. Using the approach, it is not only possible to rank internationally important sites based on connectivity criteria, in the same way as has previously been done using abundance criteria in Bamford et al. (2008) or Conklin et al. (2014), but most importantly, it is possible to quantify the benefit of including additional sites into conservation priorities for migratory species. Indeed, using our approach, some sites that are currently not considered internationally important due to the relatively small number of animals they support, appear to be important for maintaining flow through the network as a result of their strategic location. We have also highlighted how the loss of a single site can result in sudden population collapse (Fig. 2). It therefore follows that the creation or protection of strategically located habitat has the potential to result in increases in abundance. Given the current declines experienced by migratory species (Wilcove & Wikelski 2008), targeted conservation investment is urgently required.

In conclusion, our results suggest that limited tracking data can be used to develop estimates of population connectivity and improve conservation prioritisation. Indeed, we show that selecting sites for conservation based on connectivity and abundance simultaneously, could maintain larger populations than assessments based solely on abundance. Clearly, for many species, a migratory network is more than the sum of its parts. Loss of some sites can lead to partial or even total population collapse. Some species are especially vulnerable when migratory connectivity is not taken into account, and clear thinking on this issue is needed to avoid making poor protection decisions. Managing sites that support large numbers of individuals will not always deliver the most efficient conservation outcomes.

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Fig. 1. Density distribution of flight distances for a) bar-tailed godwit, b) eastern curlew, c) great knot, d) grey-tailed tattler, e) red knot, f) ruddy turnstone and g) sanderling.

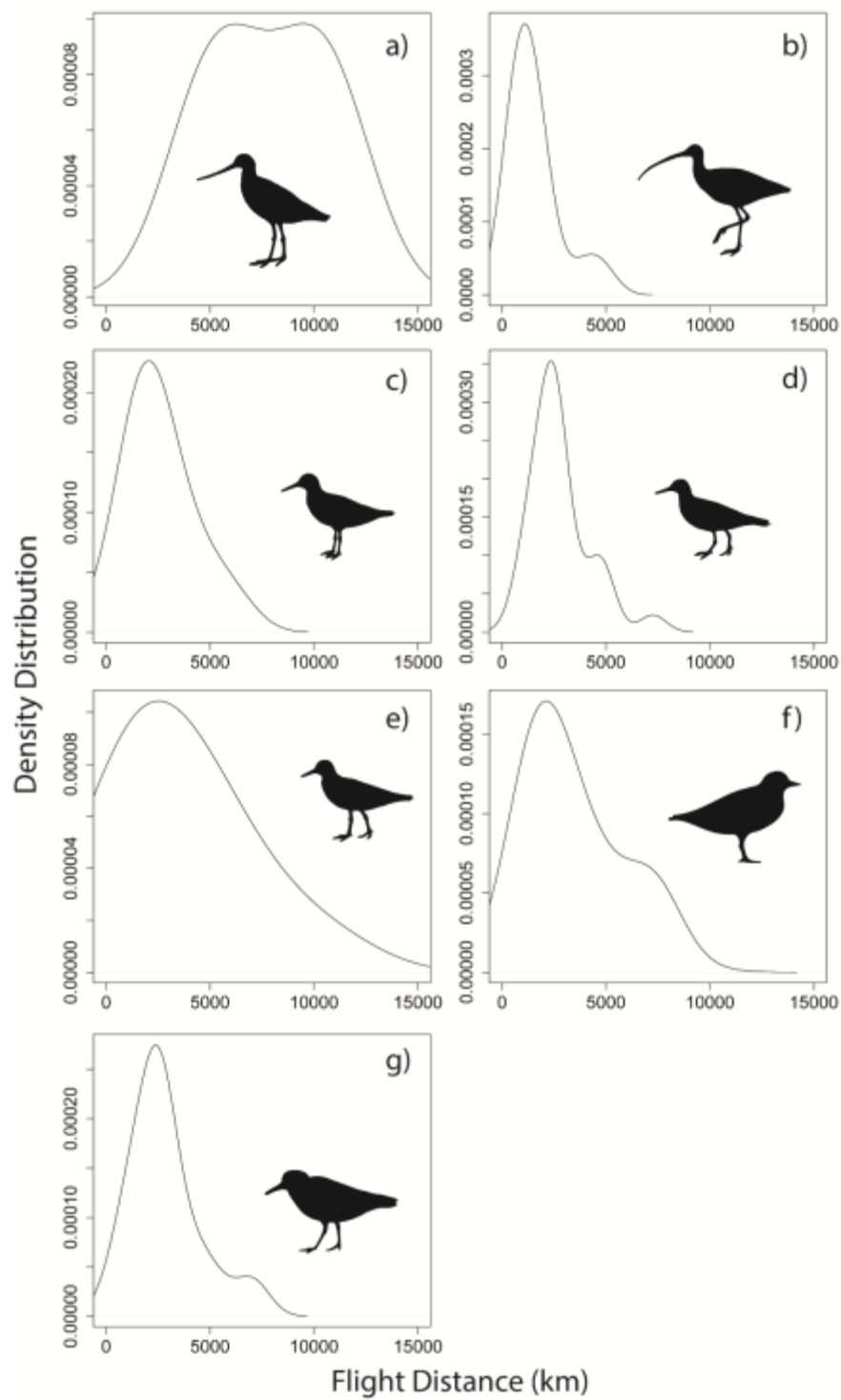


Fig. 2. Remaining population flow as sites are removed, according to the flow prioritisation strategy (black triangles), the maximum count prioritisation strategy (grey squares), and the random

prioritisation strategy (black circles; \pm 95% quantiles), for a) bar-tailed godwit, b) eastern curlew, c) great knot, d) grey-tailed tattler, e) red knot, f) ruddy turnstone and g) sanderling.

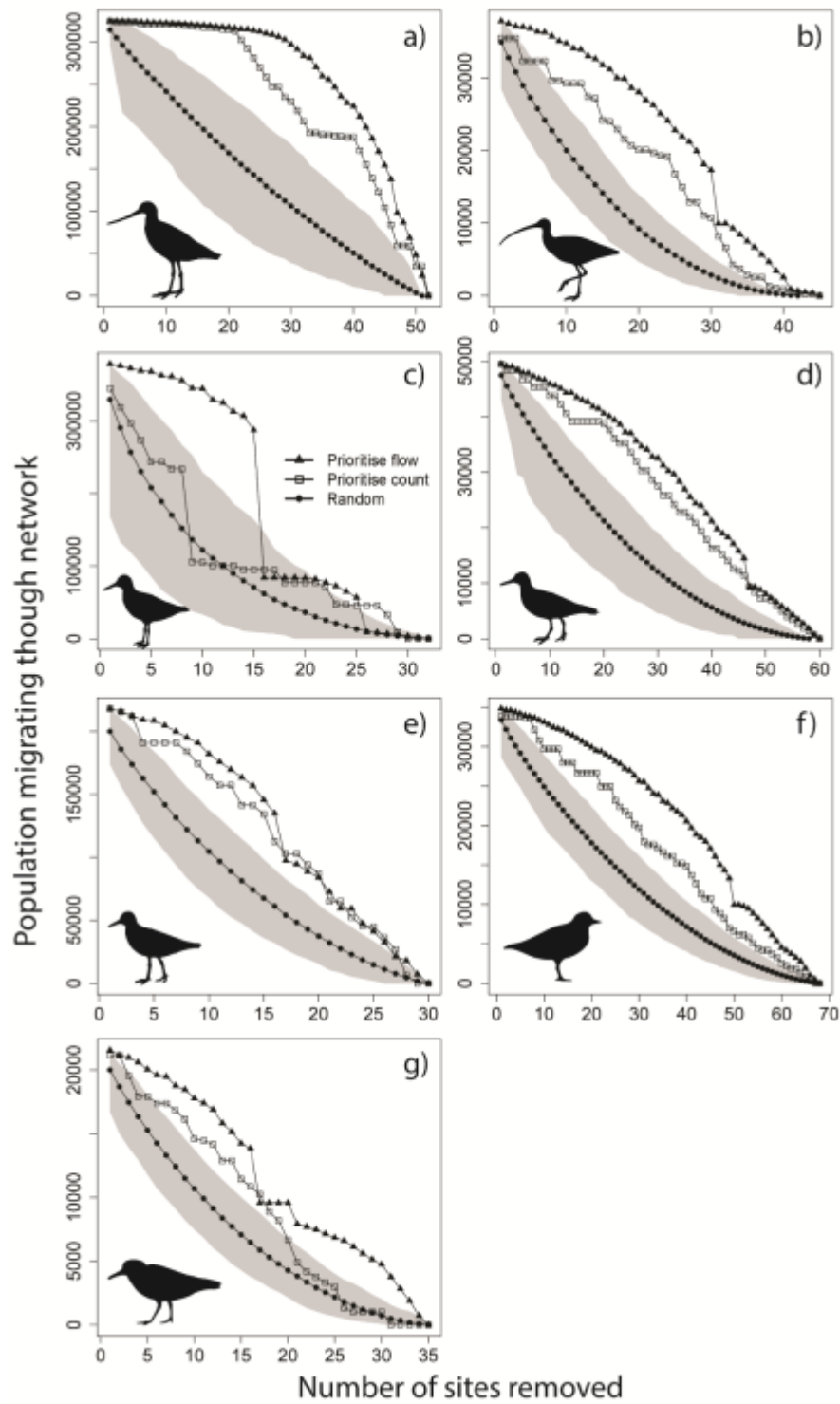


Fig. 3. Geographical distribution of rank changes between maximum count prioritisation and flow prioritisation strategies for a) bar-tailed godwit, b) eastern curlew, c) great knot, d) grey-tailed tattler, e) red knot, f) ruddy turnstone and g) sanderling. Downward facing arrows indicate false positives, where sites are high ranked in the count prioritisation strategy, but are lower ranked in the flow prioritisation strategy. Circles represent a change in rank of less than 5 positions. Upward facing arrows represent false negatives, where sites are low ranked in the count prioritisation strategy, but are higher ranked in the flow prioritisation strategy.

