



# 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, thus conservation prioritization is hampered. To address this data limitation, we developed a novel approach to spatial prioritization based on a model of potential connectivity derived from empirical data on species abundance and distance traveled between sites during migration. We applied the approach to migratory shorebirds of the East Asian-Australasian Flyway. Conservation strategies that prioritized sites based on connectivity and abundance metrics together maintained larger populations of birds than strategies that prioritized sites based only on abundance metrics. The conservation value of a site therefore depended on both its capacity to support migratory animals and its position within the migratory pathway; the loss of crucial sites led to partial or total population collapse. We suggest that conservation approaches that prioritize sites supporting large populations of migrants should, where possible, also include data on the spatial arrangement of sites.*

**Keywords:** Charadriiformes, connectivity, conservation planning, decision making, maximum flow, migratory species, prioritization, shorebirds

Establecimiento de Prioridades de Conservación para las Redes Migratorias bajo Incertidumbre

**Resumen:** *Conservar a las especies migratorias requiere de proteger al hábitat conectado a lo largo de los caminos que recorren. A pesar de las mejoras recientes en el rastreo de los movimientos de animales, la conectividad migratoria sigue siendo resuelta pobremente a nivel de población para la mayoría de las especies, por lo que la priorización de la conservación está obstaculizada. Para tratar esta limitación de datos desarrollamos una estrategia novedosa para la priorización espacial con base en un modelo potencial de conectividad derivado de los datos empíricos sobre la abundancia de las especies y la distancia recorrida entre los sitios durante la migración. Aplicamos la estrategia a las aves costeras migratorias de la Ruta Migratoria Asiática-Australoasiática. Las estrategias de conservación que priorizaron los sitios con base en la conectividad y medidas de abundancia juntas mantuvieron poblaciones más grandes de aves que las estrategias que priorizaron los sitios solamente con base en las medidas de abundancia. El valor de conservación de un sitio por lo tanto dependió tanto de su capacidad para mantener animales migratorios como de su posición dentro de la vía migratoria; la pérdida de sitios cruciales llevó al colapso total o parcial de la población. Sugerimos que las estrategias de priorización de la conservación aplicadas a sitios que mantienen poblaciones grandes de migrantes deberían, cuando sea posible, incluir también datos sobre los arreglos espaciales de los sitios.*

**Palabras Clave:** aves costeras, Charadriiformes, conectividad, especies migratorias, flujo máximo, planeación de la conservación, priorización, toma de decisiones

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## Introduction

Conservation plans are often based on the assumption 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, and none more so than migratory species (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 maximize 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. In some cases, an entire population may congregate in a single location during the breeding season (Matthiopoulos et al. 2005), the stationary nonbreeding season (Richter & Cumming 2008), or when conditions become unsuitable throughout the rest of their range (Runge et al. 2014). These 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 sites (i.e., connectivity).

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

New lightweight devices are able to accurately track migrations over thousands of kilometers (Block et al. 2011) and have revolutionized the study of migratory connectivity. This has led to the development of extensive citizen science networks, the members of which report sightings of individually marked animals at a global scale (Silvertown 2009). Such methods show promise for providing comprehensive descriptions of migratory pathways that can be used in formal spatial prioritization. Yet, knowledge is presently very patchy. Many migrants have not been formally studied, and for those that have,

data are sparse. 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), which limits inference at a population level (Lisovski et al. 2016). Resightings or recaptures are needed to track animals that have been color-tagged or fitted with geolocators, respectively. This requirement leads to bias toward areas with many observers (e.g., Minton et al. 2006). Although 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 available data are crucial in setting appropriate conservation priorities in migratory networks.

We used tracking data to parameterize a model of migratory connectivity to prioritize site protection for the conservation of 7 migratory shorebird species in the East-Asian Australasian Flyway (EAAF). We used tracking data to estimate the frequency of migratory movements of different distances and calculated the likelihood of movements between any 2 sites within the migratory network. We estimated the effect of site loss on overall population flow through the migratory network to identify conservation strategies that minimize population loss. We compared our spatially explicit prioritization with an approach based on prioritizing sites that support large numbers of individuals, to determine whether abundance-based measures delivered better conservation outcomes when augmented with connectivity-based measures.

## Methods

To model potential connectivity between all sites within a migratory network, we used a maximum-flow approach. We formulated the maximum-flow problem, tailored it to migratory species, prioritized sites for conservation, and applied our approach to migratory shorebirds in the EAAF before conducting a sensitivity analysis.

### Formulating the Maximum-Flow Problem

The maximum-flow problem is widely used to model movement and migration of animals within a network of noncontiguous habitat patches or sites (Urban & Keitt 2001; Minor & Urban 2007). The approach models the population as a whole as it flows through a network of sites, similar to modeling water flowing through pipes, rather than accounting for the behaviors and decisions of individuals. Each pair of sites has a predefined capacity, which can be expressed in an ecologically meaningful way based on, for example, carrying capacity, site type (breeding, stopover, or nonbreeding), or distance

between sites. This method allocates similar numbers of animals to migratory routes with similar capacities. In contrast, a greedy approach can allocate all animals to one route, despite the availability of another route of similar (yet slightly smaller) capacity (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, nonbreeding, 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 the edge  $(u, v)$ . Let  $G$  have a source node  $s$  and sink node  $t$  in  $V$  that represent the start and end of the migratory cycle (for example, the breeding and nonbreeding grounds, respectively). Every node  $u$  in  $V$  other than  $s$  and  $t$  can have multiple edges entering and exiting  $u$ . Thus, breeding  $s$  and nonbreeding  $t$  nodes are defined differently from stopover nodes  $u$ .

However, if one considers a case where there are multiple breeding or nonbreeding nodes, it is possible to create super-source and super-sink nodes  $s'$  and  $t'$ , respectively. Thus, directed edges  $(s', s_j)$  go from super-source 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. This enables the population to flow into the  $s_j$  nodes unconstrained (i.e., conceptually, to preallocate animals to nodes before starting migration). However, one 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 super-sink node  $t'$  with directed edges  $(t_k, t')$ . This approach represents movement into  $t$  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 maximize the flow between super-source node  $s'$  and super-sink node  $t'$  without exceeding the edge capacities. Representing the flow between edges  $(u, v)$  in  $E$  with  $x_{uv}$ , one can formulate the maximum-flow problem as follows:

$$\begin{aligned} &\text{maximize } f(x) = \sum_{(u,v) \in E(s)} x_{uv}, \\ &\text{subject to} \\ &\sum_{\{v:(u,v) \in E\}} x_{uv} - \sum_{\{v:(v,u) \in E\}} x_{vu} = 0, \text{ where } \forall u \in V \setminus \{s, t\}, \\ &\text{and } 0 \leq x_{uv} \leq c_{uv}, \text{ where } \forall (u, v) \in E. \end{aligned} \quad (1)$$

The first constraint ensures that the number of birds entering and exiting a node is the same. The second constraint ensures that the number of birds migrating along each edge does not exceed the edge capacity. For migratory species, maximum flow can be used to measure

how local changes to node capacity affect population-level migratory connectivity (Urban & Keitt 2001; Minor & Urban 2007; Iwamura et al. 2013). The maximum-flow problem is a linear programming problem that we solved using Gurobi 6.0.0 (Gurobi Optimization 2016).

### Defining a Migratory Network with Tracking Data

We used 2 simple rules of thumb to parameterize the edge capacities within our network (i.e., numbers of individuals migrating between all pairs of nodes). First, we assumed animals are more likely to migrate to sites where large numbers have been counted. Second, we assumed animals have preferential travel distances (e.g., some make multiple short journeys and others make a few long-distance journeys) and are more likely to migrate to sites within this preferred distance. Thus, it was possible to estimate edge capacities based on a list of sites with count data and a small sample of tracking data.

More specifically, by using individual animal tracks (e.g., start and end latitude and longitude), we estimated the probability “density” distribution for migratory movements between nodes with the function density in R (R Core Team 2015). By fitting a density distribution around the available tracks, we measured the likelihood that an animal can travel a given distance while accounting for uncertainty in the tracking process. Accuracy of tracking data and notably geolocator data is variable, ranging from 495.5 km (Rakhimberdiev et al. 2016) to 20 km (Lisovski et al. 2012), depending on environmental conditions and calibration method. Furthermore, the data were spatially biased. Groups of individuals were often tagged in the same location. Many individuals were therefore potentially migrating similar distances along similar routes. To deal with these uncertainties, the function fits a distribution to the data by trading off overfitting, which produces multiple peaks, and overextrapolating, 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 yielded the probability  $P_{uv}$  of migration along edge  $(u, v)$  according to distance (Fig. 1) and was used to parameterize edge weights  $w_{uv}$ :

$$w_{uv} = P_{uv} N_v A_{uv}, \quad (2)$$

where  $N_v$  is the proportion of the population using node  $v$  and  $A_{uv} = |\cos(\phi_{uv})|$  is the absolute cosine of the azimuth angle  $\phi$  between nodes  $u$  and  $v$  in radians. Thus,  $A_{uv}$  weights northerly and southerly nodes more heavily than easterly and westerly nodes, specifically to prevent species that undertake north-south migrations from zigzagging northward and southward. For species that do not undertake directional migrations,  $A_{uv}$  can be set to 1. Nodes with many migrants and within likely travel distances were weighted more heavily using  $w_{uv}$ ,

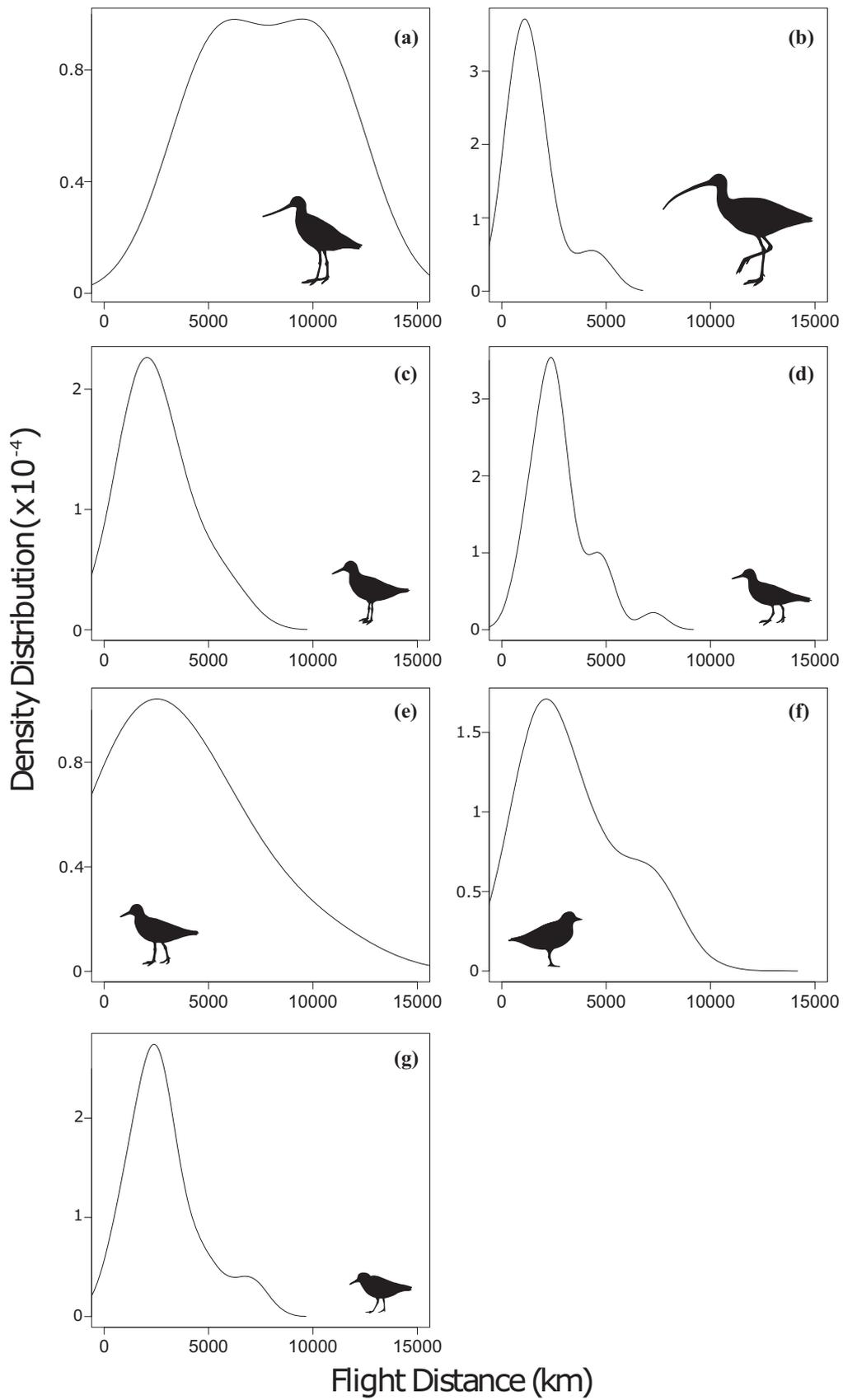


Figure 1. Density distribution of flight distances for (a) Bar-tailed Godwit, (b) Eastern Curlew, (c) Great Knot, (d) Grey-tailed Tattler, (e) Red Knot, (f) Ruddy Turnstone, and (g) Sanderling.

than nodes supporting few migrants that were within an unlikely travel distance (according to the density distribution [Fig. 1]). These assumptions approximated 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 used  $w$  to determine the proportion of a population migrating between each set of nodes and  $w_{uv}$  was used to parameterize the capacity  $c_{uv}$  (i.e., the 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  $x_u$  is the number of animals that flowed into node  $u$ . The capacity calculation was initiated from start node  $s$ , where  $x_s$  is equal to the known population size of the species. Finally, we determined the proportion of the population migrating through each graph  $G(V, E)$  based on the maximum-flow problem formulation above.

Migratory animals were allowed to go anywhere in the network with this approach, although the majority of the population used edges with the greatest capacity going in the correct direction (north, northeast, and northwest when migrating to breeding grounds and south, southeast, and southwest when migrating to nonbreeding grounds); few individuals used other edges. Full code is given in the Supporting Information.

### Prioritizing Nodes for Conservation

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

We used 3 prioritization strategies based on population-flow, maximum population-count, and random. For the population-flow and maximum population-count strategies, we iteratively removed the node that contributed least to the prioritization criteria (i.e., the node with the least population flowing through it and the node where the maximum number of birds were counted [Bamford et al. 2008], respectively) until no nodes remained (approach of Conklin et al. [2014]). Thus, when a site is lost, it is assumed individuals using the site die. This has been observed in some migratory species such as Great Knots (*Calidris tenuirostris*) (Rogers et al. 2010; Moores et al. 2016) 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 population-flow prioritization and the maximum population-count prioritization strategies with Spearman's rank correlation. We also compared the prioritizations with a family of random samples. To do so, we

iteratively removed nodes from the network at random and repeated the process 1000 times (Fig. 2).

### Migratory Shorebird Case Study

We constructed directional graphs representing migration for 7 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 have been tracked (albeit in small numbers); have mapped breeding, stopover, and nonbreeding sites (Bamford et al. 2008) that can be used as nodes in a maximum flow framework; have an estimated overall population size (Bamford et al. 2008); and migrate directionally northward and southward (Alerstam et al. 2001). Each species took different north and south migratory routes and used different stopover nodes (Bamford et al. 2008).

We used tracking data collected from a literature review and from the Victorian and Queensland Wader Study Groups to parameterize migration through the network of sites. We classified tracks into northward or southward migration to account for the different distances birds could fly 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 northern migration [nm] = 32, and southern migration [sm] = 0 [Battley et al. 2012]); Eastern Curlews ( $n = 9$ , nm = 34, and sm = 21 [Driscoll & Ueta 2002]); Great Knots ( $n = 4$ , nm = 13, and sm = 14 [Victorian Wader Study Group]) and Grey-tailed Tattlers ( $n = 3$ , nm = 18, and sm = 10 [Queensland Wader Study group]) (wader study group data available from <http://waderns.org.au/studying-waders/banding-shorebirds/satellite-transmitters-and-geolocators/>); Red Knots ( $n = 3$ , nm = 7, and sm = 15 [Victorian Wader Study Group]); Ruddy Turnstones ( $n = 48$ , nm = 162, and sm = 162 [Minton et al. 2010; Minton et al. 2011; Minton et al. 2013]); and Sanderlings ( $n = 13$ , nm = 50, and sm = 75 [Minton et al. 2013; Lisovski et al. 2016]). The accuracy of all Wader Study Group data was estimated as per Lisovski et al. (2016).

### Sensitivity Analyses

We used Ruddy Turnstones, the species with the most data, to investigate how the flow prioritization strategy changed with 10, 20, or 40 fewer tracked birds and with 1 tracked bird. For each scenario, we randomly removed 10, 20, and 40 birds from our tracking data set and carried out the prioritization 1000 times. For the scenario with one tracked bird, each bird was used once. The resulting prioritization was extremely stable at the different

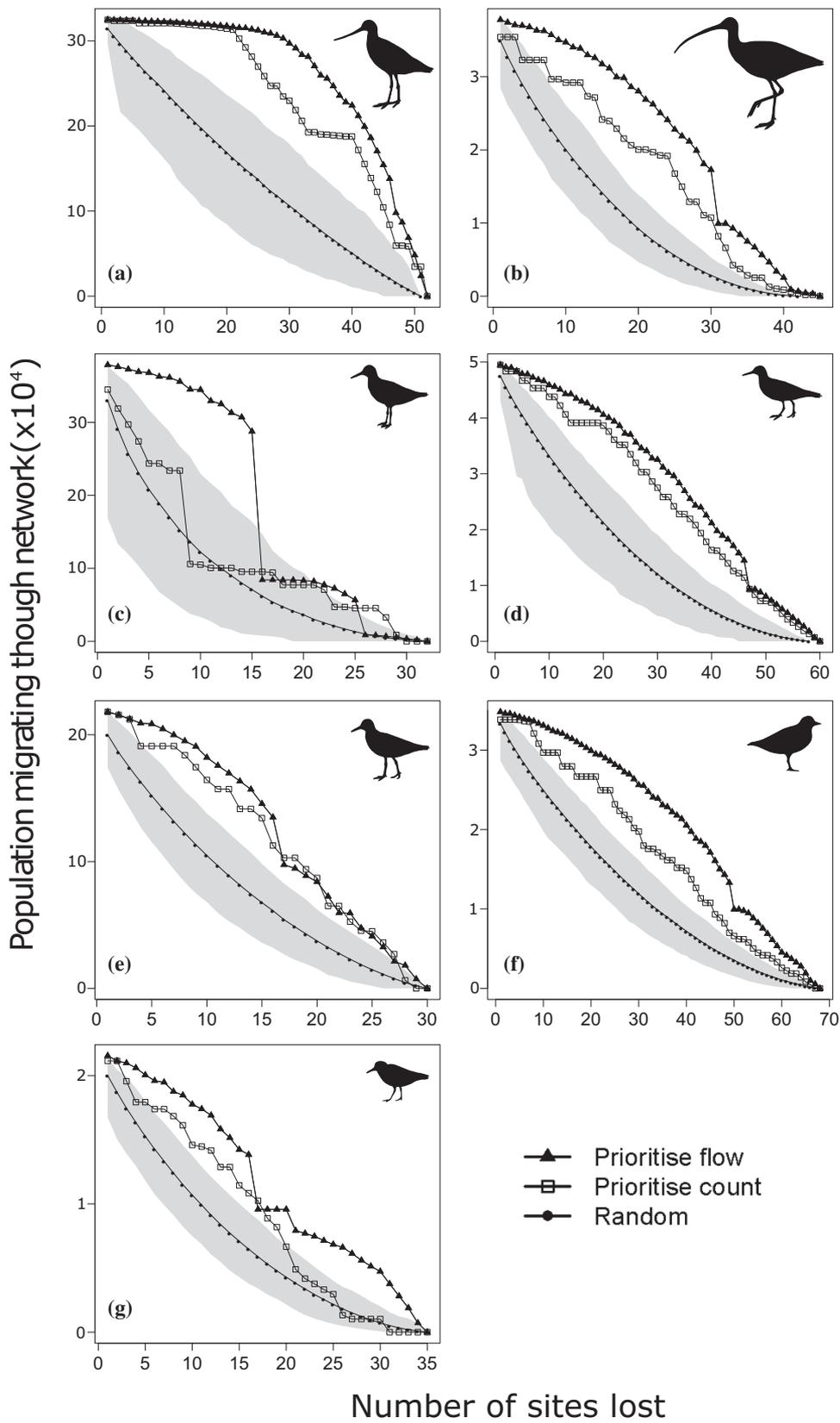


Figure 2. Flow of the population through the migratory network as sites are removed according to the population-flow prioritization strategy (black triangles), the maximum population-count prioritization strategy (gray squares), and the random prioritization strategy (black circles) (gray shading, 95% 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.

sample sizes (Supporting Information). This is consistent with previous research showing that even small numbers of tracks can make an important contribution to 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 5000 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 5000 and 10,000 km but were unlikely to migrate <5000 km. In contrast, Red Knots and Ruddy Turnstones were most likely to migrate <5000 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 prioritization strategies. The population-flow strategy outperformed the maximum population-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 or 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). Two species showed substantial overlap between the maximum population-count and random prioritization strategies (Great Knot and Sanderling). Species with large networks (e.g., Bar-tailed Godwit 53 sites [Bamford et al. 2008] and Ruddy Turnstone 69 sites) therefore lost population flow gradually as sites were lost, whereas populations of species with smaller numbers of sites available to them (e.g., Great Knot, 33; Red Knot, 30; and Sanderling, 35) collapsed when the number of sites crossed a critical threshold (around 50% of the sites) (Fig. 2 & Supporting Information).

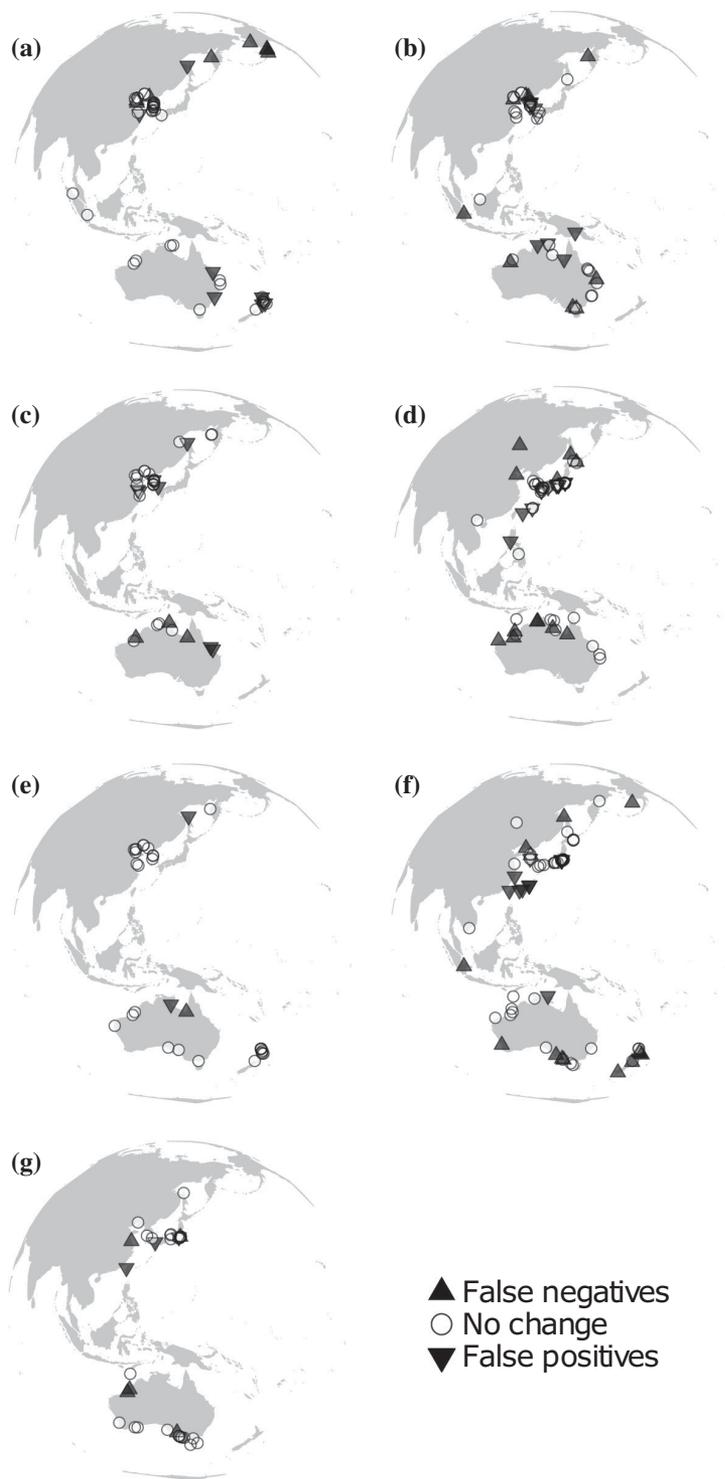
The importance of network structure was apparent when comparing site rankings between the maximum population-count and population-flow prioritization strategies (Supporting Information). Species with large networks and gradual population loss showed the highest agreement between maximum population-count and population-flow prioritization rankings (Spearman's rank correlation: Bar-tailed Godwit  $r_s = 0.73$ ,  $p = 1.8e^{-9}$ ) (Supporting Information), whereas species with smaller numbers of sites and sudden population collapses showed much lower levels of agreement between

maximum population-count and population-flow prioritization rankings (Sanderling  $r_s = 0.49$ ,  $p = 2.9e^{-3}$ ; Great Knot  $r_s = 0.43$ ,  $p = 1.4e^{-2}$ ) (Supporting Information). Overall, the levels of agreement between the maximum population-count and population-flow prioritization 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 population count and the population flow prioritizations, the majority did not shift markedly in rank (Fig. 3 [circled sites] & Supporting Information). However, some sites greatly increased in rank (Fig. 3 [upward-facing arrows] & Supporting Information), whereas others decreased (Fig. 3 [downward-facing arrows] & Supporting Information). Sites that increased in rank were removed later in the population-flow prioritization than in the maximum population-count prioritization, and vice versa. Sites that were not well connected or that supported birds only during southward or northward migration were removed earlier in the population-flow prioritization than in the maximum population-count prioritization (Fig. 3 & Supporting Information). A few key sites were therefore fundamental in driving the efficiency of the population-flow prioritization strategy.

## Discussion

Despite tracking devices becoming smaller, cheaper and more accurate, and tracking data becoming increasingly available, much remains unknown about species' migratory routes. This lack of knowledge hampers conservation planning. To overcome this hurdle, we have demonstrated how limited tracking data can be used to parameterize a simple model of migratory connectivity to aid decision making for migratory species.

Migratory connectivity plays a key role in maintaining large populations of migratory species. Indeed, prioritizing the protection of sites with the largest counts of individuals was not as efficient as using migratory connectivity, and in some cases maximum population-count strategies performed as poorly as randomly selecting sites for conservation (Fig. 2c). This may seem counterintuitive because sites supporting large numbers of birds would be expected to have a higher conservation priority than sites supporting small numbers of birds. In fact, this is a widely used approach for setting conservation priorities (e.g., Conklin et al. 2014; Ramsar Convention Bureau 2014). However, groupings of sites with small numbers of birds act as a unit if the sites are highly connected, whereby the loss of one of the sites compromises the flow of migrants through the other sites. Thus, it is more beneficial to conserve a group of small, connected sites than one larger site (Fig. 3). Indeed,



*Figure 3. Geographical distribution of changes in site ranks between maximum population-count and population-flow prioritization 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 (false positives, sites ranked higher in the maximum population-count prioritization strategy than in the population-flow prioritization strategy; no change, a change in rank of <5 positions; false negatives, sites ranked lower in the maximum population-count prioritization strategy than in the population-flow prioritization strategy).*

the relative conservation value of small patches of habitat is being increasingly recognized (Tulloch et al. 2016).

Similarly, there were trade-offs between conserving nonbreeding, stopover, and breeding sites. Different types of sites contributed very differently to population flow through the network; population flow was 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 super-source and a super-sink node (Supporting Information). Yet, for a different case study with a different network structure, a nonbreeding or breeding site could be removed in the reverse-greedy algorithm before a stopover site (Supporting Information). This is because groupings of connected nonbreeding, stopover, and breeding sites are always prioritized 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 relatively small or large numbers of birds, which are more or less connected, are therefore complex and difficult to predict without mathematically formulating the maximum-flow problem.

Network structure played a key role in the prioritization. We observed that the flow maximization strategy was more effective for some species (e.g., Bar-tailed Godwit and Great Knot) than for others (e.g., Red Knot) (Fig. 2 & 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 [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 nonbreeding sites began to be removed (Supporting Information). Beyond that point, the population declined stepwise as nonbreeding 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 fly shorter distances than Bar-tailed Godwits (Fig. 1) and depend on stopover sites to complete both 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 northern and southern migration and which is highly connected to nonbreeding sites, resulted in rapid population declines. Unlike Bar-tailed Godwits, for which nonbreeding habitats were prioritized (Supporting Information), for Great Knots the population-flow maximization strategy prioritized nonbreeding and stopover habitat alike (Supporting Information). In fact, nonbreeding and stopover habitats were prioritized at similar rates for all species except Bar-tailed Godwit (Supporting Information).

Tracking data are therefore very important in understanding network structure. Yet, tracking data also provide their own set of challenges. Although small samples of tracking data do not adversely affect the prioritization (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's and are likely to have affected migration. With Eastern Curlew for instance, instead of migrating to the breeding grounds, some individuals returned to the non-

breeding grounds without completing a full migration (Driscoll & Ueta 2002).

Additional tracking data could refine our modeled 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 be interesting to develop more biologically meaningful mechanistic (e.g., population-growth and density-dependence) or eco-physiological models (e.g., energetics, starvation risk, predation risk, and stopover duration) of the migration itself (Bauer et al. 2008; Taylor & Norris 2010; Bauer & Klaassen 2013; Aharon-Rotman et al. 2016). The approach we developed is not intended to replace such models; rather, it can be used 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 the best use of existing data are urgently needed to inform coordinated protection for migratory species.

Our connectivity model should not be used to determine which sites can be lost before others; rather, it can be used to measure the benefit of conserving a site. With this approach, it is possible to rank internationally important sites based on connectivity criteria, as has been done previously with abundance criteria (Bamford et al. 2008; Conklin et al. 2014), and most importantly to quantify the benefit of including additional sites into conservation priorities for migratory species. With 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 also found that 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.

Our results suggest that limited tracking data can be used to develop estimates of population connectivity and improve conservation prioritization. We showed 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 may 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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## Supporting Information

Model R code (Appendix S1), data for Eastern Curlew used in R code (Appendix S2), and figures describing the sensitivity analysis, proportional population loss, rank changes between prioritization scenarios, and site types used in the prioritization (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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