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Research Article

Migration strategy as an indicator of resilience to change in two shorebird species with contrasting population trajectories

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Abstract

1. Many migratory birds are declining worldwide. In line with the general causes for the global biodiversity crisis, habitat loss, pollution, hunting, over-exploitation and climate change are thought to be at the basis of these population declines. Long-distance migrants seem especially vulnerable to rapid anthropogenic change, yet, the rate of decline across populations and species varies greatly within flyways. We hypothesize that differences in migration strategy, and notably stopover-site use, may be at the basis of these variations in resilience to global change.

2. By identifying and comparing the migration strategies of two very closely related shorebird species, the Curlew sandpiper *Calidris ferruginea* and the Red-necked stint *Calidris ruficollis*, migrating from the same non-breeding site in Australia to similar breeding sites in the high Russian Arctic, we aimed to explain why these two species express differential resilience to rapid changes within their flyway resulting in different population trajectories in recent times.

3. Based on 13 Curlew sandpiper and 16 Red-necked stint tracks from light-level geolocator tags, we found that individual Curlew sandpipers make use of fewer stopover areas along the flyway compared to Red-necked stints. Furthermore, and notably during northward migration, Curlew sandpipers have a higher dependency on fewer sites, both in terms of the percentage of individuals visiting key stopover sites and the relative time spent at those sites. While Curlew sandpipers rely mainly on the Yellow Sea region, which has recently experienced a sharp decline in suitable habitat, Red-necked stints make use of additional sites and spread their relative time en-route across sites more evenly.

4. Our results indicate that differential migration strategies may explain why Curlew sandpipers within the East Asian-Australasian Flyway are declining rapidly (9.5%–5.5% per year) while Red-necked stints remain relatively stable (−3.1%–0%). We consider that more generally, the number of sites per individual and among a population, the spatial distribution across the flyway, as well as the relationship between the time spent over sites may prove to be key variables explaining populations and species' differential resilience to environmental change.

1 | INTRODUCTION

Many migratory species are declining and are at risk of extinction (Wilcove & Wikelski, 2008). As for non-migrants, habitat loss, pollution, hunting, over-exploitation and climate change are considered one of the leading causes of these population declines (Flockhart et al., 2015; Gallo-Cajiao et al., 2020; van Gils et al., 2016; Robinson et al., 1995; Sutherland et al., 2012). However, animals that move long distances, such as many migratory birds, may be especially vulnerable to these rapid anthropogenic alterations (Both, 2010; Sillett et al., 2000). Migratory animals rely on a range of widely separated sites distributed along the routes connecting their breeding and non-breeding locations. Such sites are considered to have disproportionate importance in terms of area and site use. Quantitative models indicate (Aharon-Rotman et al., 2016; Iwamura et al., 2013; Pettifor et al., 2000; Sheehy et al., 2011) and empirical data suggest (Piersma et al., 2016) that the quantity and quality of such stopover sites can limit population abundance and effect individual survival.

Millions of shorebirds migrate annually from their Russian and Alaskan Arctic breeding habitats to the coasts of Southeastern Asia and Australasia through the East Asian-Australasian Flyway (EAAF; Bamford et al., 2008; Minton et al., 2011). Many of these birds interrupt their journeys to rest and refuel in intertidal habitats at staging sites across eastern Asia (Buehler & Piersma, 2008; Clemens et al., 2016; Myers, 1984). These sites are close to large human populations, which has led to habitat loss due to land reclamation and otherwise intensive exploitation affecting the food resources for shorebirds. The Yellow Sea region, which hosts a large proportion of migratory shorebirds during the migration period, is the EAAF's most rapidly degrading area. Over 50% of its tidal mudflats are already destroyed for coastal development (Ma et al., 2014), leading to widespread concern (Larson, 2015) and empirical evidence (Piersma et al., 2016; Studds et al., 2017) that collapse of this particular ecosystem is driving declines in the migratory species that rely on it.

However, the rate of decline for the different species and populations using this flyway varies greatly. Some species, such as the Curlew sandpiper *Calidris ferruginea*, have shown an unprecedented annual decline of 7.5% (9.5–5.5; 95% CRI), whereas other closely related species, such as the Red-necked stint *Calidris ruficollis*, have had no or only a very slow 1.6% (3.1–0.0; 95% CRI) annual population decline (Studds et al., 2017). These differences are remarkable given the apparent ecological and spatial overlap between the two species. Within the EAAF, Curlew sandpiper and Red-necked stint share the same non-breeding and breeding habitats and have greatly overlapping foraging ecologies, and both species require relatively equal amounts of resources to achieve their equally similar migratory distances. However, they seem to differ in one notable aspect and that is their reliance on the Yellow Sea during migration. In the absence of tracking data, for Curlew sandpiper and Red-necked stint it was estimated by an expert panel that the proportion of birds in the flyway population relying on the Yellow Sea was 90% and 35%, respectively (Studds et al., 2017). But can this contrasting reliance of a population on a single site along their flyway make all the difference or may there be additional differences in their migration strategies that explain the widely different population dynamics and apparent susceptibility to environmental change?

In this study, we used light-level geolocators to track these two species from a single non-breeding site in south-eastern Australia to their high Arctic breeding sites. Aside from using these unique recordings to evaluate the species' use of the Yellow Sea, we also used these tracks to study any other differences in the birds' migration strategy potentially explaining the species' differential population trajectories. More specifically, we hypothesized that the Red-necked stint, being the apparently most resilient of the two species to environmental change, would use more sites on both the individual and population levels, distributing the fuelling for migration across more sites. Such strategy would not only spread the risk of habitat loss but also for potential other disturbances such as predation, pollution, hunting and food scarcity at specific sites.

2 | MATERIALS AND METHODS

2.1 | Geolocator deployment

Fieldwork was conducted at Western Port Bay, in south-eastern Australia between 2016 and 2020. To deploy light-level geolocators, birds were captured in cannon nets at high tide roosts at Yallock Creek (38°13′54.3″S 145°28′55.8″E). A total number of 61 geolocators (Migrate Technology Intigeo W30A9, 0.3 g) were deployed on Red-necked stints in April 2016. In March 2018, 55 geolocators were deployed on Red-necked stints (Intigeo W30A9, 0.3 g) and 60 units on Curlew sandpipers (Intigeo W65A9, 0.7 g). Between January and March 2019, another 53 geolocators were deployed in Curlew sandpipers (Intigeo W65A9, 0.7 g). The units were mounted on plastic leg-flags (made from a Darvic PVC sheet) using Kevlar thread reinforced with Araldite resin cement.

2.2 | Geolocation

Light-intensity data were recorded at 5-min intervals and analysed using a threshold method (Lisovski, Bauer, et al., 2020). Sunrise and

sunset events (twilight events) were identified on log-transformed light data and a threshold of 1 log lux, using the R package TwGeos (Lisovski et al., 2015). Twilight events recorded at the known deployment site during periods after deployment and before recapture were used for calibration, that is, to estimate the error distribution of twilight events and the individual reference sun elevation angle (position of the sun when twilight events were detected). Migratory movements were identified as sudden and directed changes of consecutive sunrise or sunset events (for details on the methods, see Lisovski, Bauer, et al., 2020). Periods of residency with a minimum of three consecutive twilight events were then identified as periods surrounded by migratory movements. Individual breeding sites were estimated, except for Red-necked stints with tags deployed in 2016 that did not record the required full light pattern, using the R package PolarGeolocation (Lisovski, 2018). We used a two-step approach to estimate the breeding sites. First, a rough search for the location was performed on a low spatial resolution of 100 km and a radius of 3,000 km centred around 150°E and 65°N. Next, the estimation was repeated using finer resolution of 50 km and a radius of 1,500 km around the cell (location) with the highest likelihood from the first iteration (for details on geolocation during 24 hr daylight, see Lisovski, 2018). For the final track estimation, we used a Bayesian approach from the R package SGAT (Wotherspoon et al., 2013) allowing to incorporate the twilight events, their error distribution (gamma density distribution), the information on periods of movement and residency, a spatial probability mask was use, an expected flight speed distribution (gamma distribution with shape = 2.2 and rate = 0.08) and the estimated breeding location. Altogether and via Markov chain Monte Carlo (MCMC) simulations, the method aims to refine tracks, providing most likely paths with credibility intervals. The *groupedThresholdModel*, providing a single location estimate for periods of residency, was chosen. For periods of defined movements, no mask to spatially restrict location estimates. For periods of residency, location estimates were spatially directed according to a relative likelihood with a probability of 1 for inland locations, −10 for locations at sea and 5 for locations within a 75 km distance to a coastline. During the MCMC simulation, the first and last site of residency (in case the logger was still recording light on return) and the breeding site were fixed to the deployment or the estimated breeding site. We first ran a *modifiedGamma* model (relaxed assumptions) for 1,000 iterations to initiate the model, before tuning the model with final assumptions/priors with three runs each containing 300 iterations. Finally, the model was run for 2,000 iterations to ensure convergence. Median location estimates and 95% CrI were calculated using the entire final MCMC chain (i.e. each location estimate was based on 2,000 estimates from within the MCMC chains).

2.3 | Phenology

Based on the analysis of stationary periods, we extracted the departure and arrival dates at the deployment site. The arrival and departure dates at the breeding sites were identified as the dates at which the birds entered 24-hr daylight. The latter might have an error of up to a couple of days. However, we expect birds to migrate straight to their breeding areas and back without stopping in the Arctic taiga/tundra for longer periods.

2.4 | Stopover sites

Stopover periods were identified prior to the MCMC simulation and based on changes in the sunrise and sunset times (see geolocation). The *groupedThresholdModel* in SGAT estimates one location for each stationary period, based on all twilight times within that period, and one location for each twilight during movement. Locations from the most likely track were used for plotting and further analyses. A hierarchical cluster analysis based on the geographical distance between all stopover sites and for both migratory seasons (i.e. northward and southward migration) was applied to identify potential regions used by multiple individual birds. The function *hclust* in R was used to create the hierarchical cluster and *cutree* to extract the cluster id for each site at different hierarchical levels. It was expected that the number of stopover sites within a population increases with number of tracked individuals. To investigate whether this increase is different across the two species, not biased by sample size, and independent of the hierarchical level of the cluster analysis, we performed a randomized analysis across individuals using a range of different clustering levels. To this end, for each species separately, with 100 randomized orders across individuals and for clustering levels ranging from 25 to 45, we calculated the cumulative number of stopover sites over individuals. A linear model with log-transformed number of individuals was used to present the relationship (with 95% CrI) and illustrate the difference between the two species.

2.5 | Individual site use

To investigate the difference in the number of stopover sites and their proportional use, we ranked the sites for each individual according to time spent relative to the entire time at stopover sites within each migratory season. A linear mixed model was then applied using log-transformed percentages over ranked sites and individual id as random factor for intercept and slope.

3 | RESULTS

3.1 | Geolocator retrieval

In January–April 2017, a total number of 17 geolocators were retrieved from Red-necked stints. Eight geolocators provided complete tracks of the northward and southward migration, one individual did

not migrate and eight geolocators recorded no data due to failure of the protective coating and corrosion of the units. In early 2019, one faulty geolocator was retrieved from a Red-necked stint and eight from Curlew sandpipers, which all provided full migration tracks. In 2020, a total number of 9 units were retrieved from Red-necked stints (one individual did not migrate and one tag did not provide data) and 8 from Curlew sandpipers (one individual did not migrate, one unit did not provide data and one tag that was deployed in 2018 provided data for almost two migration cycles). Thus, a total number of 16 Red-necked stint and 14 Curlew sandpiper tracks spanning both northward migration to the breeding grounds and southward migration, back to the Australian non-breeding grounds, were used in this analysis.

3.2 | Phenology

On average, Curlew sandpipers left the deployment site in south-eastern Australia 1 month earlier than Red-necked stints (Figure 1, cs: median = Mar 26, min = Mar 08, max = Apr 03; rns: median = Apr 23, min = Apr 03, max = May 21). The migration duration was, however, longer in Curlew sandpipers (median = 69 days, min = 52 days, max = 85 days) compared to Red-necked stints (median = 52 days, min = 38 days, max = 66 days), leading to a smaller difference in the species' arrival at the Arctic breeding sites (cs: median = May 31, min = May 25, max = June 11; rns: median = June 12, min = June 03, max = July 09). Start of southward migration was slightly earlier in Curlew sandpipers (cs: median = July 09, min = July 02, max = Aug
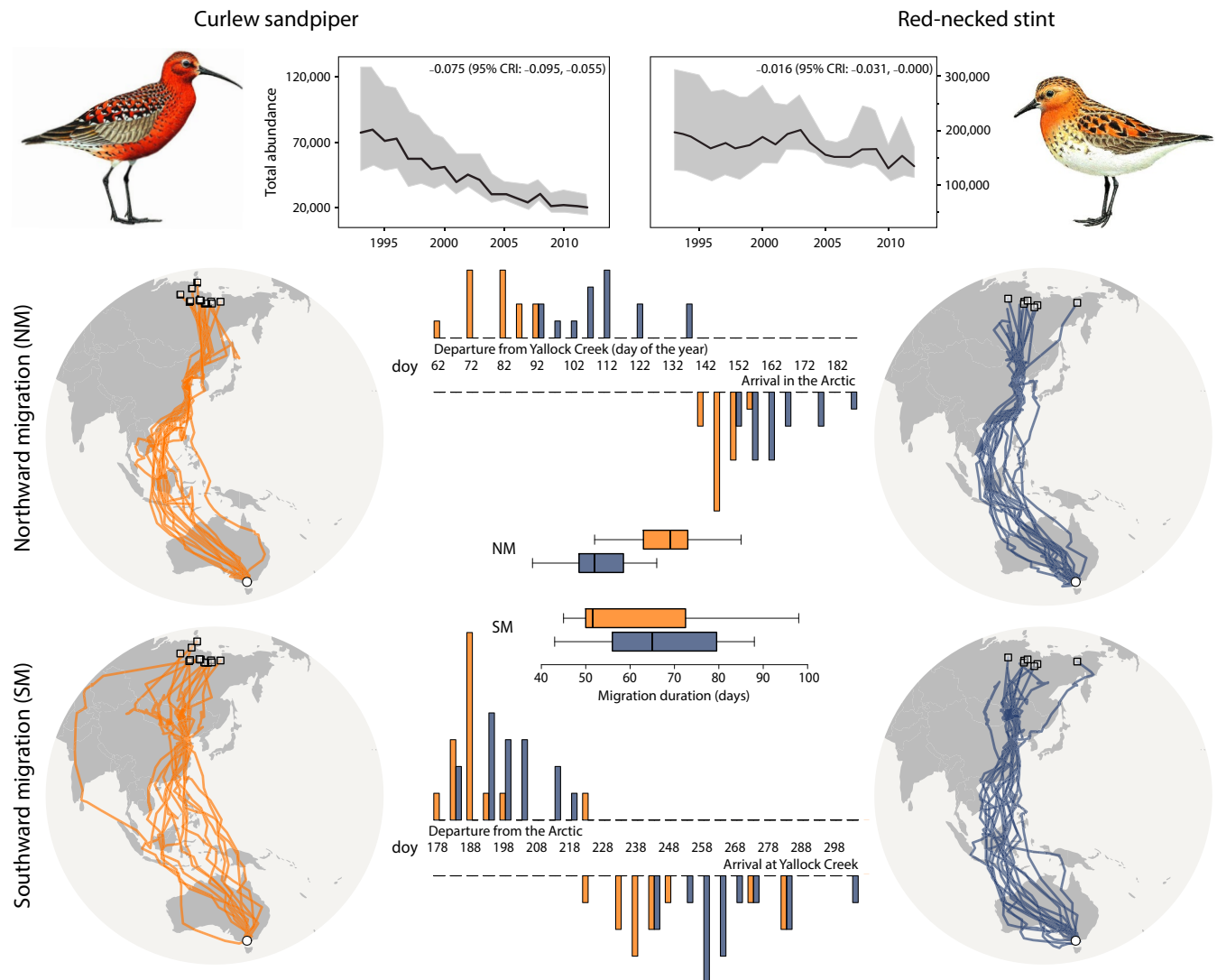

FIGURE 1 Contrasting population trajectories and general migration routes and timing between Curlew sandpipers (left; orange) and Red-necked stints (right; blue). Top panels show estimated Australian wide changes in absolute abundance for both species (data derived from Studds et al., 2017). The four globes depict the migration tracks for northward (top) and southward (bottom) migrations of all successfully tracked individuals. White circle in Australia indicates the non-breeding site at Yallock Creek where light-level geolocators were deployed and retrieved. Bar charts in the center show the departure and arrival frequencies for northward (top) and southward (bottom) migration for both species. The horizontal boxplots show migration durations in the two species for both migration seasons, defined as the time period between departure from Yallock Creek and arrival in the Arctic and vice-versa. Bird pictograms reproduced with permission of Lynx Edicions

08; rns: median = July 19, min = July 04, max = Aug 10). Mainly due to a relatively shorter migration period in Curlew sandpipers (cs: median = 51.5 days, min = 45 days, max = 98 days; rns: median = 65 days, min = 43 days, max = 88 days), Red-necked stints arrived almost 1 month later at the deployment site in south-eastern Australia (rns: median = Aug 31, min = Aug 16, max = Oct 15; rns: median = Sep 21, min = Sep 09, max = Nov 01).

3.3 | Migration routes and stopover sites

The northward and southward migrations of both species generally followed similar routes, from south-eastern Australia due north-west towards Indonesia and the east-Asian coastlines of Vietnam and China before heading into the Russian Arctic towards their breeding sites (Figure 1). Despite a clear outlier, Curlew sandpiper BQ877 that migrated south via central Asia (probably stopping in Kazakhstan) and Sri Lanka, all other individuals from both species took similar routes during south- to northward migration. After the first breeding season, Curlew sandpiper BJ573 did not migrate all the way back to Australia but remained in north-western Borneo (Malaysia) before starting the second recorded migration loop to the Arctic and then back to the deployment site in south-eastern Australia. For this individual, the second loop and the arrival and departure dates at Borneo were excluded from all phenology and stopover site analyses. The estimated breeding areas cover a wide range from Taymyr in the west to Chukotka in the east. However, breeding sites for most individuals of both species were estimated west of 140°E with only one Red-necked stint in the Chukotka region at around 163°E. Major differences were recorded in stopover-site distribution and use across the two species (Figure 2a).

During northward migration and in contrast to only one Curlew sandpiper, all Red-necked stints had at least one stopover on inland or coastal regions in Australia. Both species made use of several equatorial regions with sites in Indonesia, Malaysia and the Philippines with major aggregations of tracked individuals on the Island of Java (46% Curlew sandpiper, 25% Red-necked stint) and southern Borneo (15%, 50%). Further north, both species had stopover sites on the southern Chinese coastline (Hainan region, Taiwan region). However, these sites were used for longer periods by Curlew sandpipers. A cluster, centred close to Shanghai, appeared to be of major importance for the tracked Red-necked stints. This cluster that contains known sites of importance to shorebirds (Bamford et al., 2008; e.g. Chongming Dongtan Natural Nature Reserve, Yancheng NNR, Xuwei Saltworks) was visited by 69% of the tracked Red-necked stints for a period of 1–6 days. The Yellow Sea cluster, the next cluster to the north, was the cluster with by far the highest percentage of tracked Curlew sandpipers and the cluster this species used most extensively (4–26 days) during northward migration. Sites known to harbour large numbers of Curlew sandpipers within the region are North-west Bo Hai Wan, North Bo Hai Wan, Shi Jiu Tuo and the Nanpu saltpans (Lei et al., 2018). And while a large percentage of Red-necked stints visited this cluster too (87%), they spend considerably less time (1–13 days) within this region. Only a few Curlew sandpipers made another stop between the Yellow Sea cluster and their breeding sites while all Red-necked stints stopped at least once in covering the distance. Here, the Torey Depression cluster was visited by 68% of tracked individuals staying between 2 and 11 days. Sites between the breeding area and the Yellow Sea were visited by both species during southward migration (Figure 2b). However, only the Torey Depression cluster harboured more than 50% of
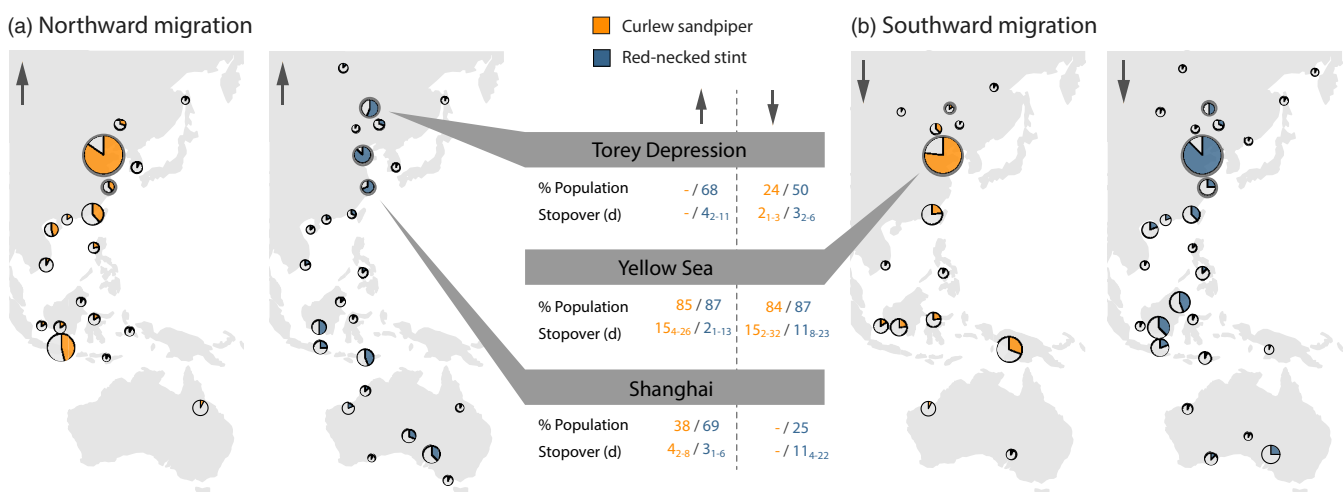

FIGURE 2 Spatial clusters of stopover locations and their use by Curlew sandpipers (orange) and Red-necked stints (blue) during northward (a) and southward (b) migration. The size of the circles scales with the cumulative time spent on each site across individuals and the pie chart indicates the percentage of tracked individuals that visited each site during northward or southward migration. Three clusters were identified that were visited by more than 50% of the tracked individuals in a species during one or both seasons. In the center numbers show the percentage of tracked individuals visiting these three clusters and the median time they spent there (including range across individuals) in each season (arrow up for northward and arrow down for southward migration)

Red-necked stints and they stayed for a much shorter period (2–6 days) compared to northward migration. For both species, the Yellow Sea was the by far most prominent cluster, both in terms of percentages visited and time spent. From there southwards, the Curlew sandpiper made use of nine clusters while the Red-necked stint used 18 clusters before arrival at the deployment site. None of these clusters were visited by more than 50% of the individuals of either species. During both migratory seasons, the cumulative number of stopover sites with increasing number of tracked

individuals (accounting for hierarchical cluster level) was consistently lower for Curlew sandpipers compared to Red-necked stints (Figure 3).

3.4 | Individual site use

During northward migration, on average Red-necked stints stopped at six sites (median = 6, min = 4, max = 10), two sites more than the majority of Curlew sandpipers used (median = 4, min = 3, max = 6; Figure 4). The same pattern was found during southward migration with individual Red-necked stints having more stopover sites (median = 5, min = 4, max = 8) compared to Curlew sandpipers (median = 4, min = 2, max = 5). During both northward (nm) and southward migration (sm), Curlew sandpipers spent a larger proportion of time at the site with the longest stay (nm; median = 42.37%, min = 29.82%, max = 65.5%, sm; median = 50.41%, min = 40.39%, max = 89.51%) than Red-necked stints (nm; median = 31%, min = 18.71%, max = 44.86%, sm; median = 41.26%, min = 19.23%, max = 57.18%).

Also, during both migratory seasons, the percentage of time spent at the lower ranked sites showed a stronger exponential decay in Curlew sandpipers (Figure 4).
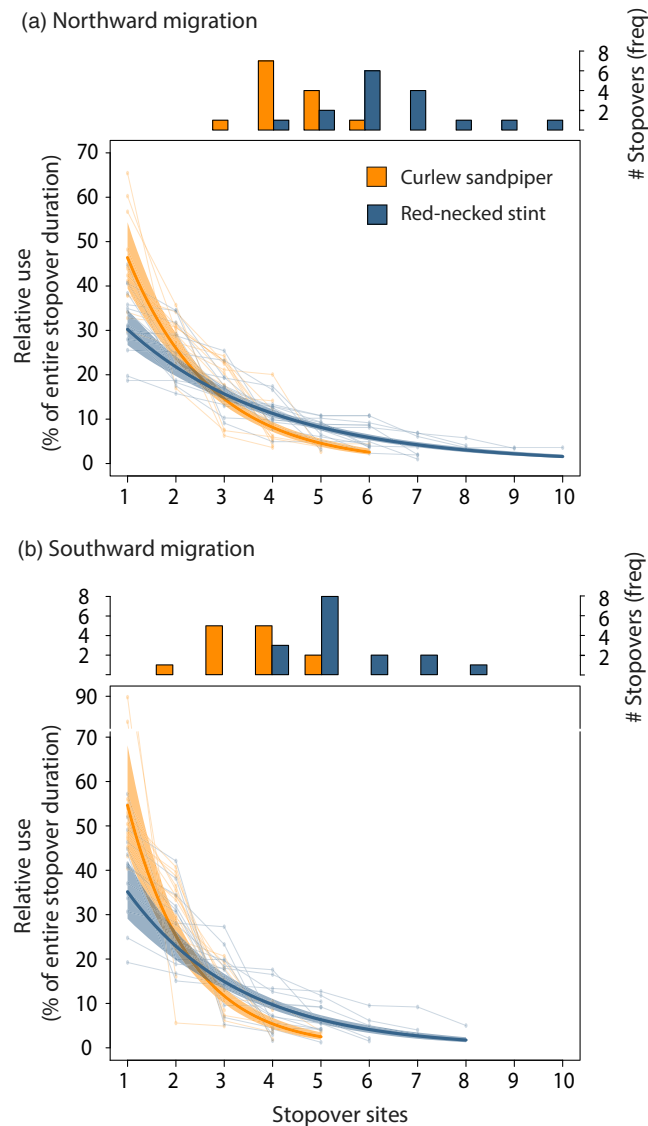

FIGURE 3 Stopover site use of tracked Curlew sandpipers (orange) and Red-necked stints (blue) during northward (a) and southward (b) migration. In each panel, the line graphs depict individual and average (with 95% CrI) reliance on stopover sites for the two species (as % of total time across all stopover sites; stopover sites along x-axis ranked from most to least used site for each individual), the bar plot at the top of each panel shows the frequency of the number of stopover sites across tracked individuals. Collectively, these graphs show that during both northward and southward migration Red-necked stints make use of more sites in a more even fashion than Curlew sandpipers
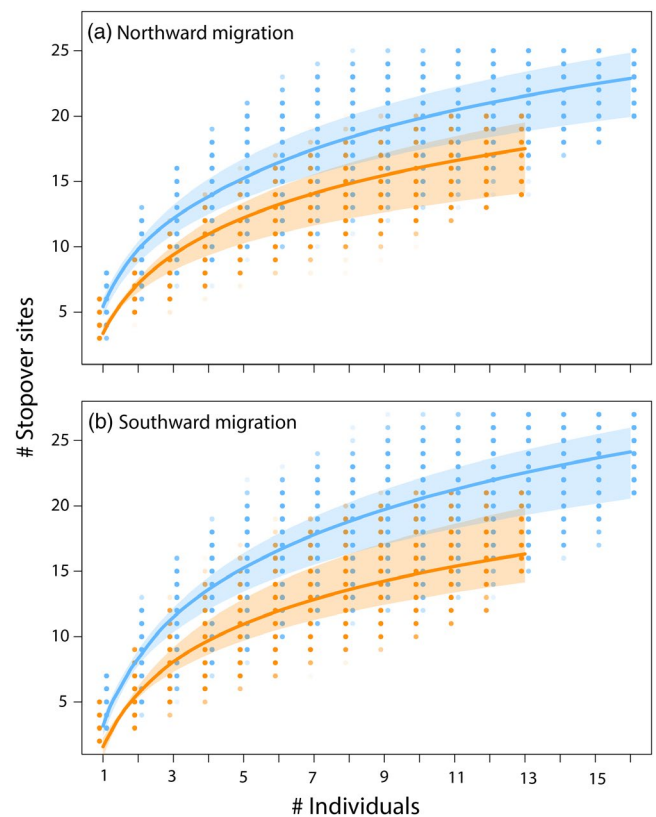

FIGURE 4 The number of stopover sites in relation to tracked individuals for Curlew sandpipers (orange) and Red-necked stints (blue) for (a) northwards and (b) southward migration. The modeled relationship (solid line) with the 95% CrI (colored area) is based on 100 randomized simulations with changing orders across individuals and over a range of hierarchical cluster levels of individual stopover sites (see Section 2 for details)

4 | DISCUSSION

Migratory animals are highly mobile, which could make them more resilient to change if they are able to shift their ranges and their phenology to track suitable climate or if they avoid areas that are becoming unfavourable or even dangerous due to human impacts (Robinson et al., 2009). Yet, migrants seem to be more vulnerable than non-migrants and a species' magnitude of migratory movements tends to act as an indicator of their vulnerability to environmental change (Wilcove, 2008). However, such a simple classification discounts potentially large within-species variation in migratory movements that has been shown to correlate positively with resilience to environmental change (Gilroy et al., 2016). Moreover, some species with overlapping ecological niches and populations that migrate via essentially identical routes and disperse similar distances between their non-breeding and breeding range are nevertheless experiencing widely different population trends that we have so far failed to explain. One such example concerns Curlew sandpiper and Red-necked stint from the East Asian-Australasian Flyway. By comparing individual movements of individuals from both species spending the non-breeding season at the very same location and migrating to similar areas in the high Arctic, we could identify several differences in their migratory strategies that may explain why Curlew sandpiper may be more vulnerable and thus less resilient than Red-necked stint to the massive changes within their flyway, that includes the loss of habitat to land reclamation, habitat degradation through aquaculture and harvesting, as well as gross pollution and invasion of exotic fauna, all of which have negatively affected shorebird foraging, roosting and breeding sites (Melville et al., 2016; Murray et al., 2014).

The first obvious difference between the two species is the number of stopover sites on which individuals typically rely (Figure 2). On average, Red-necked stints made use of more stopover sites during both northward and southward migration. Moreover, the number of regions that appeared suitable for stopover at the population level was also larger for the Red-necked stint compared to the Curlew sandpiper (Figure 3). Finally, Red-necked stint showed a more homogeneous use across their selected stopover sites (Figure 4), contrasting starkly with the Curlew sandpiper, showing a heavy reliance on a single site and using fewer sites generally. These characteristics are important identifiers for a species' migration strategy.

Piersma (1987) proposed three general and alternative strategies for avian migrants to adopt: the *hop*, *skip* and *jump* strategies. The hop strategy is where individuals *hop* between successive stopover sites that are short distances apart, where the birds accumulate small stores of fuel to make it to the next site. Alternatively, in the skipping strategy, they move longer distances and accumulate intermediate amounts of fuel storage. Finally, at the extreme of this spectrum, you have the *jump* strategy where birds accumulate large stores of fuel to enable long non-stop migratory flights between distant sites. Geographical properties and resource distribution along a flyway, as well as

the physiological capacity of a migrant may determine which of these strategies are being employed. To be able to perform a *jump* (usually a long flight over a barrier such as an ocean or a desert), migrants require sites or areas with abundant, predictable food resources to prepare for an energetic challenge requiring substantial fuel stores (Warnock, 2010). For shorebirds, the number of sites across the world that have allowed species to evolve a skip or jump strategy are limited. Only areas like the Yukon Delta in Alaska (Gill & Handel, 1990; Lindström et al., 2011), Delaware Bay in eastern USA (Clark et al., 1993), the Wadden Sea in Europe (Meltofte et al., 1994), the Banc d'Arguin in West Africa (Smit & Piersma, 1989) and the Yellow Sea (Barter, 2006) in East Asia allow hosting exceptionally large numbers of individuals that use jumping or skipping strategies to their subsequent destinations. Extreme examples involve Bar-tailed godwits *Limosa lapponica* of the *baueri* subspecies departing from the Yukon Delta in Alaska on a 12,000 km non-stop flight to their New Zealand non-breeding grounds, from where they make a 10,000 km non-stop flight to the Yellow Sea where they fuel up to perform another 6,000 km flight to their Alaskan breeding sites (Battley et al., 2012).

On a migratory route with few, highly productive and predictable sites, a jumping strategy might be the most successful way to cover the distance between the non-breeding and the breeding site (Gill et al., 2009). Yet, such strategy may also be more prone to failure if conditions deteriorate on one or more stopover sites. This is notably true if changes occur at a pace that does not allow for adaptive change as seen in the Yellow Sea region. At the individual level, migratory birds tend to be conservative, showing high site-faithfulness to migratory stopover sites across years (Vardanis et al., 2011; Yamamoto et al., 2014; but see: Dias et al., 2013), visiting the same sites even if their quality becomes less favourable or even unsustainable as observed in the Yellow Sea region. Transgenerational shifts in stopover site use have recently been observed in shorebirds (Verhoeven et al., 2018) but appear to happen slowly. What further hampers a change in site use and moving to alternative sites is the observation that highly productive and predictable stopover sites seem to diminish spatial variation in stopover site use within a population. The *baueri* Bar-tailed godwit mentioned earlier provides a prime example of this, with almost all individuals from the EAAF using the Yukon Delta and the Yellow Sea as their prime stopover sites during southward and northward migration, respectively. Adopting a skip or jump strategy with strong reliance on a single site will thus make a species more vulnerable to change if these sites deteriorate.

In Curlew sandpiper and Red-necked stint, migration strategies do not differ to the extreme in which the hop, skip and jump strategies differ. Nevertheless, the tracked Curlew sandpipers are further to the right on the continuum from hopping to jumping than the Red-necked stints are. For both, the Yellow Sea region represents a migratory bottleneck with the majority of birds visiting the area during northward and southward migration. Yet, and especially during northward migration, when birds are presumably under higher time constraints and selective pressure is higher compared to southward migration

(Kokko, 1999; Zhao et al., 2017), almost all tracked Curlew sandpipers spent a disproportional time in the Yellow Sea area compared to other stopover sites visited throughout the journey. These results are in line with the high percentage (90%) of Yellow Sea reliance presented by Studds et al. (2017) and Hassell et al. (2013) who reported 61,890 individual Curlew sandpipers on a day during northward migration within a single pond of the Nanpu Saltpans in Bohai Bay, which comprised approximately 69% of the flyway population (Hansen et al., 2016; Lei et al., 2018). And while our tracks indicate that a high percentage of Red-necked stints may also rely on the Yellow Sea, contrasting the 39% presented in Studds et al. (2017), the importance of the region seems lower compared to Curlew sandpipers. Within the flyway, Red-necked stints have at least two other sites that are extensively used in terms of time and relative number of tracked individuals. Most interestingly, Red-necked stints make use of several inland sites in Australia and between the Yellow Sea and their Arctic breeding grounds. The Torey Depression (Daursky Wetlands and Hulan Lakes) at the border between eastern Mongolia and Russia seems especially important in terms of tracked individuals using the site and relative amount of time spent during northward migration. Red-necked stint is known to be the most numerous shorebird in this region with about 30% of the species' world population making landfall here on the way to their breeding sites (Bamford et al., 2008). This very last stopover before migrating to the Arctic might play an important role since it not only provides the fuel required for the last flight bout but also energy stores to engage in courtship upon arrival, when food availability may still be limited and uncertain at best (Schmidt et al., 2019). Not relying on the Yellow Sea region as the last stopover site before departure to the breeding grounds may have become a crucial advantage for Red-necked stints over Curlew Sandpipers in the last few decades of rapid environmental change.

While we here focus on the effects of habitat loss and deterioration on population trajectories in migratory birds, we should not ignore potential interactions with climate change effects on shorebirds (e.g. van Gils et al., 2016). Climate change is likely to interact with a range of existing pressures and can exacerbate their effects through, for example, increasing susceptibility to disease (Munson et al., 2008; Wille et al., 2019). Species like the Curlew sandpiper that are already declining due to non-climate change related pressures such as habitat destructions are therefore likely to be more sensitive to climate change (Foden et al., 2019) and potentially associated with higher extinction risk (Pearson et al., 2014).

Although this study is limited to a comparison between two species, we consider the framework provided a potentially promising avenue in evaluating species' resilience to environmental change along their flyways. Specifically, we considered an unbiased estimate of stopover site richness and spatial distribution as well as the skew in stopover site use as key proxies for improved understanding of the relation between migration strategy and the resilience of populations and species to rapid changes in their environment. Notably in combination with the proxies proposed earlier by Wilcove (2008) and Gilroy et al. (2016) increased understanding of the bottlenecks that migratory birds are facing under rapid global change may be key

to the development and prioritization of effective mitigating plans that will help to turn the tide in the rapid population decrease of so many migratory species.

AUTHORS' CONTRIBUTIONS

S.L., K.G., C.M. and M.K. conceived the study; C.M., K.G. and M.K. organized and participated in data collection; S.L. and K.G. analysed the data; S.L. and M.K. wrote the manuscript with input from K.G.

DATA AVAILABILITY STATEMENT

Raw light recordings from geolocators, annotated twilight tables, location estimates and R code are available in the Movebank Data Repositories https://doi.org/10.5441/001.1.g2n3ps20 (curelw sandpiper; Lisovski et al., 2020a), https://doi.org/10.5441/001/1.s07tk38d (red-necked stint; Lisovski, Bauer, et al., 2020; Lisovski et al., 2020b).

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