






Differential population trends align with migratory connectivity in an endangered shorebird

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Abstract

Migratory connectivity describes the extent to which migratory species' populations are connected throughout the annual cycle. While recognized as critical for understanding the population dynamics of migratory species and conserving them, empirical evidence of links between migratory connectivity and population dynamics are uncommon. We analyzed associations between spatiotemporal connectivity and differential population trends in a declining and endangered migratory shorebird, the far eastern curlew (*Numenius madagascariensis*), with multiyear tracking data from across the Australian non-breeding grounds. We found evidence of temporal and spatial segregation during migration and breeding: curlew from southeast Australia initiated northward migration earlier, arrived at breeding sites earlier, and bred at lower latitudes than curlew from northwest Australia. Analysis of land modification intensity revealed that populations from southeast Australia face greater human impacts compared to those from northwest Australia at both the breeding and nonbreeding grounds, a pattern that aligns with steeper population declines in southeast Australia. This alignment between migratory

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connectivity, human impacts, and differential population change highlights the importance of a full annual cycle approach to conservation that includes mitigating threats on the breeding grounds and better protecting nonbreeding habitats in Australia where far eastern curlew spend over half of each year.

KEYWORDS

conservation, East Asian–Australasian flyway, far eastern curlew *Numenius madagascariensis*, full annual cycle ecology, habitat loss and modification, migration

1 | INTRODUCTION

Many migratory birds undertake an annual cycle that involves traveling thousands of kilometers from nonbreeding grounds to breeding grounds, and back again, often with stopovers along the way. The environmental conditions and threats that individuals experience at each stage, such as habitat loss, disturbance, and hunting, impact their survival and reproductive success, but not all individuals experience the same conditions. Distances and timing of migration can vary by age and sex (“differential migration”; e.g., Woodworth et al., 2016) and species vary in the extent to which populations mix or segregate across the annual cycle (“migratory connectivity”; e.g., Webster, Marra, Haig, Bensch, & Holmes, 2002), meaning different segments of a population can be exposed to different threats and conditions across their annual cycle. Consequently, understanding patterns of migratory connectivity and differential migration is recognized as critical for interpreting the population dynamics of migratory species, predicting their responses to environmental change, and, ultimately, conserving them (Martin et al., 2007; Runge, Martin, Possingham, Willis, & Fuller, 2014).

Migratory connectivity is understood for a growing number of species (Brown et al., 2017; Finch, Butler, Franco, & Cresswell, 2017; Knight et al., 2018, 2021; Lagassé et al., 2020; Trierweiler et al., 2014), which in turn is leading to an increase in empirical evidence of links between connectivity and population dynamics (Hewson, Thorup, Pearce-Higgins, & Atkinson, 2016; Kramer et al., 2018; Rushing, Ryder, & Marra, 2016). In a study of two migratory songbirds with partially overlapping breeding grounds in North America, breeding populations of both species that overwintered in Central America were stable, whereas populations of one species that overwintered in northern South America, where deforestation was greater, underwent steep declines (Kramer et al., 2018). In another example, differential survival of the common cuckoo (*Cuculus canorus*) was attributed to distinct migration routes between its western European breeding grounds and sub-Saharan Africa nonbreeding grounds (Hewson et al., 2016). Given rapid declines of many migratory species (Wilcove, 2008) and the widely

recognized implications of connectivity for their population dynamics (Marra, Norris, Haig, Webster, & Royle, 2006), expanding understanding of the prevalence and strength of relationships between migratory connectivity, threats, and broad-scale population dynamics is an important step for migratory species conservation.

The far eastern curlew (*Numenius madagascariensis*) is a large migratory shorebird endemic to the East Asian–Australasian flyway that has declined by two-thirds or more in Australia, where an estimated 70% of the population spends the nonbreeding season (Lilleyman, Woodworth, Clemens, Rogers, & Garnett, 2021). Consequently, the species is listed as endangered globally (BirdLife International, 2017) and critically endangered in Australia (Australian Government, 2015). Declines have been associated with rapid habitat loss and degradation at the species' primary migratory staging area in the Yellow Sea (Amano, Székely, Koyama, Amano, & Sutherland, 2010; Studds et al., 2017), with hunting at the breeding grounds and disturbance at nonbreeding grounds representing other known but poorly quantified threats (Dhanjal-Adams, Mustin, Possingham, & Fuller, 2016; Gallo-Cajiao et al., 2020; Klokov, Gerasimov, & Syroechkovskiy, 2019). Population changes, however, have not been even across the nonbreeding range, with continental- and local-scale analyses revealing steep declines in southeast Australia compared to stable and, in some places, increasing trends in northwest Australia (Clemens et al., 2016; Hansen, Menkhorst, Moloney, & Loyn, 2015; Lilleyman et al., 2020; Reid & Park, 2003; Rogers, Scroggie, & Hassell, 2020; Studds et al., 2017; Wilson, Kendall, Fuller, Milton, & Possingham, 2011). This raises the question of whether far eastern curlew from different nonbreeding regions are exposed to different threats across the annual cycle that have manifested in differential population trends.

To assess potential links between migratory connectivity and differential populations trends and their implications for conservation, we tracked the migration of far eastern curlew from four nonbreeding sites in southeast and northwest Australia over 3 years. We assessed the spatial connectivity and geopolitical distribution of the species across the annual cycle by identifying and mapping all stopover, staging, and breeding sites occupied, and

extracting the amount of time spent in different countries. We further mapped nonbreeding and breeding sites onto a layer of human modification (Kennedy, Oakleaf, Theobald, Baruch-Mordo, & Kiesecker, 2019) as a proxy for threat intensity. Lastly, we analyzed differences between populations from different nonbreeding regions in (a) breeding latitude, (b) migration timing (to assess whether patterns of spatial connectivity were reinforced by differences in phenology), and (c) human modification, to evaluate the potential for migratory connectivity to explain differential rates of population change.

2 | METHODS

2.1 | Tracking device deployments

We deployed tracking devices on far eastern curlew at two sites in northwest Australia (Broome $n = 8$

[-17.7513°N , 122.5528°E], Darwin $n = 3$ [-12.4867°N , 130.8927°E]) and two sites in southeast Australia (Moreton Bay $n = 8$ [-27.0335°N , 153.0925°E], Western Port $n = 3$ [-38.2321°N , 145.4820°E]) (Figure 1) over the course of two nonbreeding seasons, November–March 2017/2018 and November–March 2018/2019. A total of 22 individuals were fitted with either a solar-powered GPS-GSM transmitter (15 or 20 g Ornitrack, Ornitela, Lithuania) or an Argos solar-powered platform transmitter terminal (12 or 20 g PTT, Microwave Telemetry), weighing $1.79 \pm 0.13\%$ of the bird's body weight as measured in the field. All but three tracking devices (IDs 40961, 40964, 171332) were deployed on adults (i.e., individuals that had completed at least one previous northward migration). A tracker was attached to each bird's lower back via a Teflon ribbon leg-loop harness. PTTs were programmed to record location fixes on a duty cycle of 10 h on and 48 h off and the GPS-GSM devices were programmed to record two location fixes every 2–6 hr. One PTT in Moreton Bay

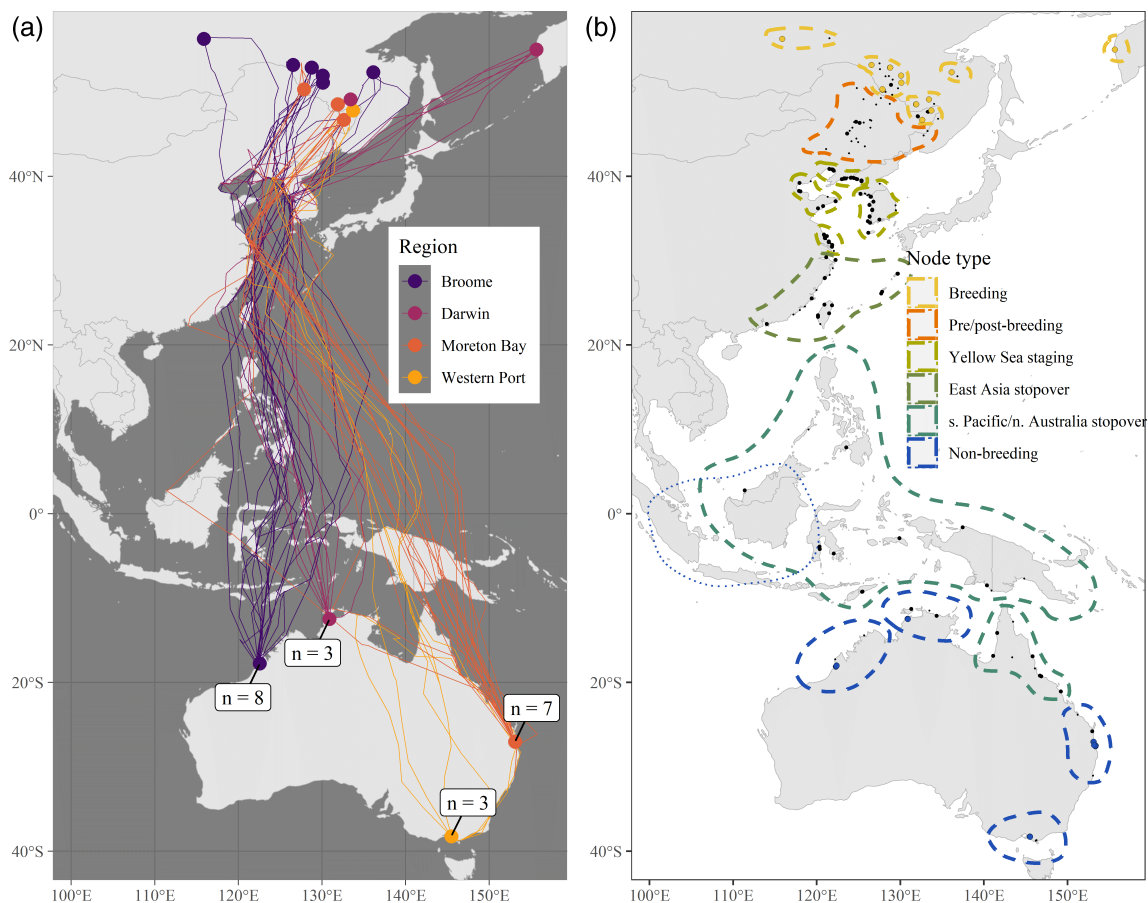


FIGURE 1 Migration routes and stages of the far eastern curlew revealed by satellite tracking. (a) Migration routes of 21 individuals tracked from four nonbreeding sites in Australia between 2017 and 2020. Points show nonbreeding sites where tracking devices were deployed (with sample sizes) and estimated breeding locations. Individual maps are provided in Figures S3–S23. (b) Polygons with dashed lines encompass different stages of the annual cycle extracted from the tracking data. The dotted polygon indicates a part of the nonbreeding range from which tracking data were not collected but where significant numbers of far eastern curlew have been recorded (Bamford et al., 2008)

stopped transmitting shortly after deployment, resulting in a sample of 21 tracked individuals.

2.2 | Extracting migration sites and timing

We analyzed tracking data collected up to November 18, 2020 (Lilleyman et al., 2021). We filtered the tracking data to retain all location fixes from the GPS-GSM devices and all PTT location fixes with an estimated error less than 1500 m (Argos location classes 3, 2, and 1). Migratory movements and sites were then extracted based on a simple set of criteria. We assumed that birds departed from a site (nonbreeding, breeding, stopover, staging), when they moved $>0.5^\circ$ (~ 50 km) from the previous site and did not return within 3 days. We assumed that individuals arrived at the breeding grounds when they no longer moved farther north and multiple successive fixes were recorded less than 0.5° of latitude apart, concluding their northward migration (Chan et al., 2019; Kuang et al., 2020). We considered individuals arrived at the nonbreeding grounds when they returned to the sites where they were first captured. During migration, we considered sites where birds remained for less than 72 hr as stopover sites and sites where birds remained for longer than 72 hr as staging sites (Ma et al., 2013; Warnock, 2010). The geographical position of a site was summarized as the arithmetic mean of all location fixes between the arrival and departure time from the site. We assigned the first recorded fix at a site as the time of arrival and the last recorded fix at the site as the time of departure (Cerritelli et al., 2020; Kuang et al., 2020).

To assess the geopolitical distribution of far eastern curlew across the annual cycle, all sites with associated durations of stay were intersected with a vector map of global exclusive economic zones (EEZ) (Flanders Marine Institute, 2020). Time spent within each country and outside EEZs was calculated for all individuals with at least one complete annual cycle. Time spent in each country was then averaged across individuals and years (in cases where curlew were tracked over multiple complete migrations) and divided by 365 days, to generate the average $\pm SE$ proportion of days spent within each country in a calendar year.

2.3 | Visualizing migratory connectivity and spatial representativeness

We visualized the year-round distribution and connectivity of far eastern curlew using a migratory network map (e.g., Knight et al., 2018), consisting of a set of “nodes”

representing clusters of sites (nonbreeding, stopover, staging, or breeding) connected by “edges” indicative of movements between sites. Edges were weighted by the number of tracked individuals that moved between nodes. We defined six node types based on the spatial distribution of staging, stopover, and breeding areas combined with existing knowledge of the species' migration ecology: breeding, noncoastal pre/postbreeding stopover and staging, Yellow Sea stopover and staging, southern East Asia stopover and staging, South Pacific/north Australia stopover and staging, and nonbreeding. The geographical position of each node was summarized as the arithmetic mean of all sites within the node.

We evaluated how spatially representative the 21 tracked individuals were of the broader species' population by comparing the distribution of stopover and staging sites within the species' primary staging area in the Yellow Sea (29.5°N , 117.5°E ; 42°N , 127°E) against in situ observations (eBird, 2019) and previously identified sites of importance (Bamford, Watkins, Bancroft, Tischler, & Wahl, 2008). From the eBird data, we mapped reporting rate (number of complete checklists in a cell that reported far eastern curlew divided by the total number of complete checklists in the cell; Strimas-Mackey et al., 2020). From the tracking data, we mapped the number of individuals that visited each cell as a proportion of the maximum number of individuals per cell. Both eBird data and tracking data were aggregated to a 50-km grid and the correlation between the two was assessed using Pearson's correlation coefficient (r). Whereas assessing spatial representativeness across all stages of the annual cycle would be the ideal scenario, we restricted our interpretation of spatial representativeness to the Yellow Sea region because little ground survey data were available from the breeding region.

2.4 | Statistical analysis of breeding latitude, human modification, and migration timing

We tested for differences between far eastern curlew from southeast and northwest nonbreeding regions in migration timing, breeding latitude, and human impacts at breeding and nonbreeding grounds. For analysis, we collapsed the four nonbreeding sites into northwest and southeast groups for both ecological and statistical reasons. First and foremost, previous analyses of far eastern curlew population trends have revealed declining populations in southeast Australia (encompassing Moreton Bay and Western Port study sites) compared to stable and, in some places, increasing trends in northwest Australia (encompassing Darwin and Broome study sites)

(Clemens et al., 2016; Hansen et al., 2015; Lilleyman et al., 2020; Reid & Park, 2003; Rogers et al., 2020; Studds et al., 2017; Wilson et al., 2011). Second, we had small sample sizes at two study sites, Western Port ($n = 3$, southeast Australia) and Darwin ($n = 3$, northwest Australia), so by clustering northwest and southeast sites, we increased the robustness of our statistical analyses. For the analysis of breeding latitudes and human modification, we supplemented our dataset with breeding locations from four individuals that were tracked from Moreton Bay to the breeding grounds in 1997–1999 (Driscoll & Ueta, 2002).

We analyzed differences in breeding latitude and migration timing between nonbreeding regions with linear mixed effects models. Response variables for the analyses of migration timing were time of departure from and arrival at the nonbreeding grounds; time of arrival, departure, and length of stay in the Yellow Sea during each migration direction; and time of arrival, departure, and length of stay at the breeding grounds. Units for all duration measurements were days and all arrival and departure dates were the day of the year (1–365). Year (2018–2020), sex (male/female; determined from bill length measurement), and age were included as fixed effects and treated as categorical variables, with age classified as “immature” (individual had not yet undertaken northward migration) and “adult” (individual had completed at least one previous northward migration). Repeated measures of migration timing and breeding latitude were accounted for by including individual ID in each model as a random variable.

For analyses and summaries of migration timing and duration, we included data from individuals with incomplete tracks ($n = 10$) and partial or aborted migrations ($n = 2$), in addition to data from individuals with complete migrations between the nonbreeding and breeding grounds ($n = 9$). For incomplete tracks, where tracking devices stopped transmitting part way through northward or southward migration, we used all available data up until the device stopped transmitting. Partial or aborted migrations represented two cases where individuals departed from and returned to the nonbreeding grounds but never reached the breeding grounds. For the curlew (ID = 17007) that migrated between the nonbreeding grounds and Yellow Sea but not to the breeding grounds, we analyzed departure from and arrival to the nonbreeding grounds and Yellow Sea, but not stopover duration in the Yellow Sea, which was atypically long because the individual never went to the breeding grounds. For the curlew (ID = 182229) that departed the southeast nonbreeding grounds and returned shortly thereafter without ever leaving Australia, we analyzed nonbreeding departure timing, but no other timing or duration metrics because the aborted migration was atypically short.

We evaluated human impacts at nonbreeding and breeding areas with a global human modification map (Kennedy et al., 2019). The human modification map combines 13 spatially explicit stressors, including human settlement and agriculture, into a 1-km² resolution metric of cumulative human modification of terrestrial lands (range = 0–1). To assess modification at breeding and nonbreeding areas, we generated minimum convex polygons around location fixes for each breeding and nonbreeding site, then added a 10 km buffer around each polygon to capture the broader breeding and nonbreeding landscapes, and third, conducted a spatial union to produce a set of non-overlapping polygons for both stages of the annual cycle. We then calculated the mean, median, and *SE* of human modification scores within each set of polygons and tested for differences between nonbreeding regions with *t* tests.

2.5 | Software

Data processing, analysis, and mapping were conducted using R version 4.0.2 (R Core Team, 2020) and ArcGIS version 10.7.1. Mixed-effects models were fitted using the “glmmTMB” R package (Brooks et al., 2017) and diagnostics were evaluated using the “DHARMA” R package (Hartig, 2020).

3 | RESULTS

Of the 21 far eastern curlew tracked during our study, nine were tracked for at least one complete migratory cycle to the breeding grounds and back, including six that were tracked for two or more complete migratory cycles (Figures 1 and S1, Supporting Information). Among the other 12 individuals, three migrated to the breeding grounds but had incomplete southward migration tracks, two undertook partial migrations, and seven had incomplete tracks that ended during northward migration. Of the two partial migrations, one individual migrated to the Yellow Sea, where it remained during the breeding period, before traveling back to Australia, and the other individual migrated overland from Western Port to northern Australia before circling back to Western Port via the east coast (Figures 1 and S3–S23).

3.1 | Description of the migratory network

The migratory network consisted of 41 edges linking 17 nodes during northward migration and 32 edges linking 16 nodes during southward migration (Figure 2). We

identified six node types. Breeding nodes encompassed broad spatial clusters of breeding sites (Figure 2, nodes 13–17). The prebreeding and postbreeding node consisted of inland stopover and staging sites north of the Yellow Sea, but south of the breeding grounds, where individuals spent an average of 3.5 ± 0.6 days (Figure 2, node 12). Yellow Sea nodes were primarily staging sites where birds remained for longer than 10 days (Figure 2, nodes 8–11). The southern East Asia node consisted mainly of short stopover sites in coastal southern China, Taiwan, and Japan, which were visited during northward migration before individuals continued northward to staging sites in the Yellow Sea (Figure 2, node 7). The South Pacific/north Australia node included a mix of stopover and staging sites used during both migration directions, including as the first points of landfall following direct flights from the Yellow Sea during southward migration (Figure 2, nodes 5–6). Finally, non-breeding nodes encompassed the broader areas where far

eastern curlew were tagged (Figure 2, nodes 1–4; Iwamura et al., 2013).

The distribution of tracked far eastern curlew in the Yellow Sea correlated well with previously identified sites of importance (Bamford et al., 2008) and eBird observations (Pearson's $r = .72$; Figure S2), providing confidence that our characterization of the year-round distribution and subsequent inferences about migratory connectivity were representative of the species more broadly.

3.2 | Migratory connectivity and human modification

We found differing degrees of population mixing across the annual cycle (Figures 2–4). Mixing occurred throughout most of the Yellow Sea, with three of the four nodes supporting curlew from both the northwest and southeast

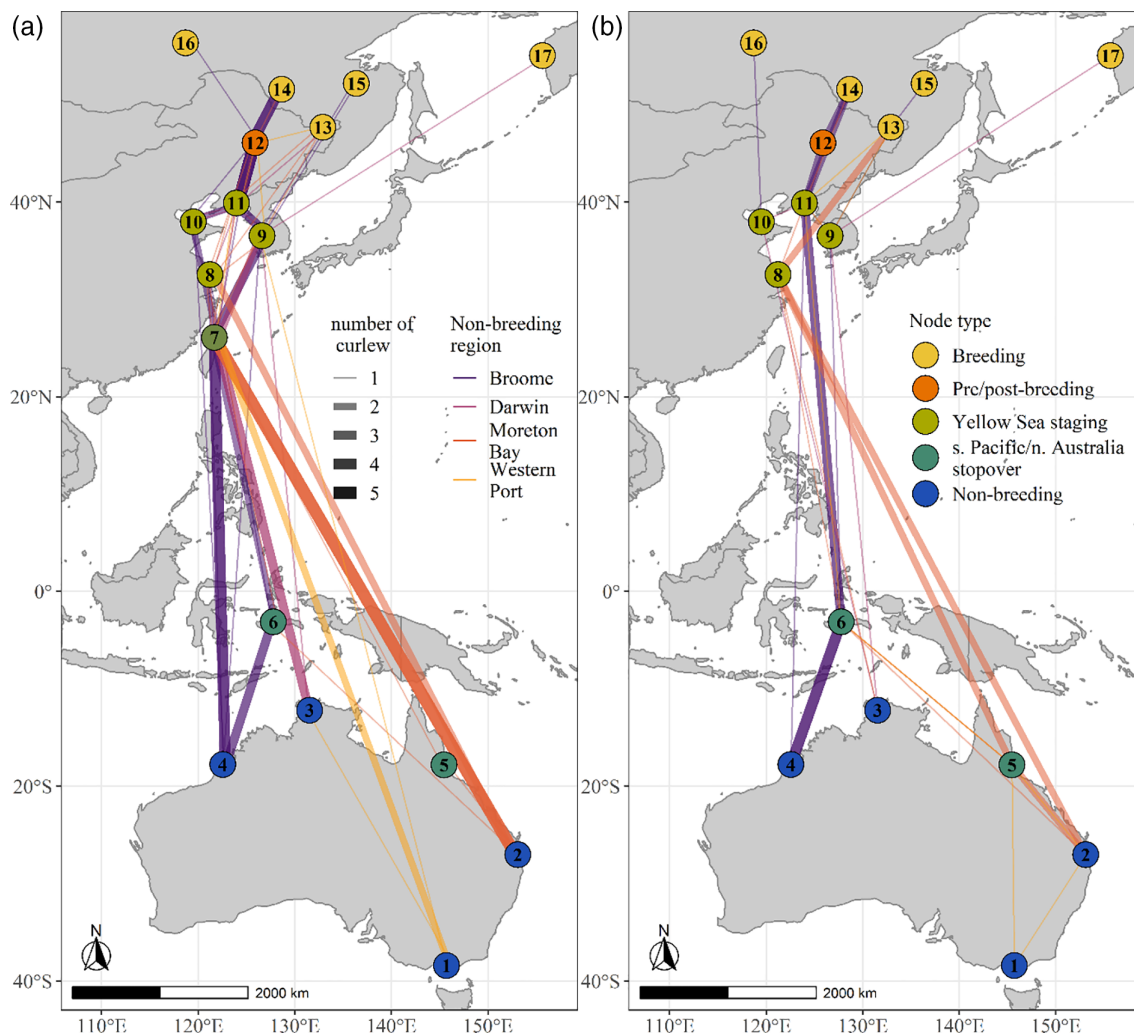
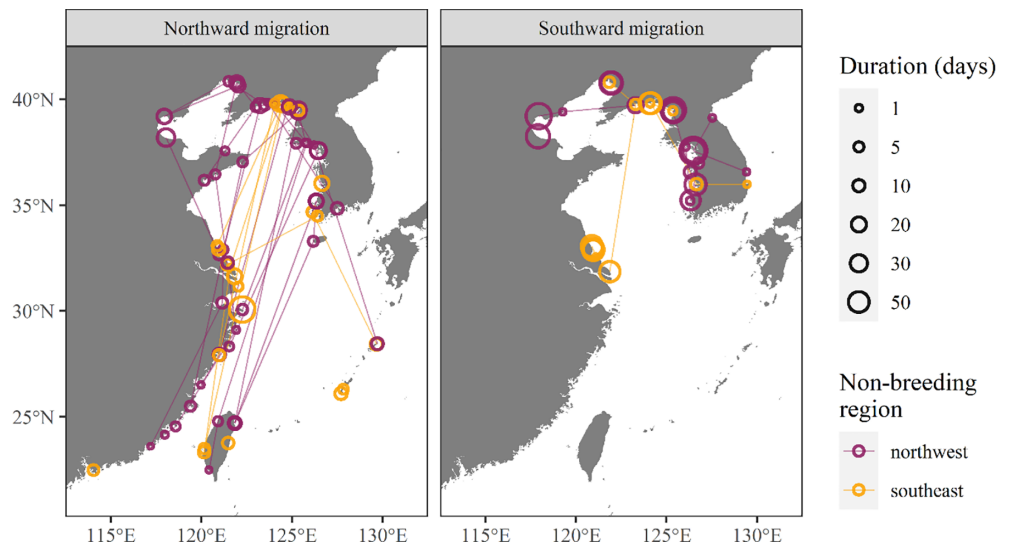


FIGURE 2 Northward (a) and southward (b) migratory network of the far eastern curlew. Nodes (points) represent broad clusters of staging, stopover, nonbreeding, and breeding sites used by tracked far eastern curlew across the annual cycle (see Figure 1b and results for node extents and definitions). Edges (lines) are colored by nonbreeding region and weighted by the number of individuals that moved between nodes

FIGURE 3 Mixing of far eastern curlew at stopover and staging sites in and around the Yellow Sea. Lines connect sites visited by an individual during each migration and the size of each point is scaled by time spent at the site (days), with larger points denoting longer visits



nonbreeding regions during northward migration and two of the four nodes supporting curlew from both nonbreeding regions during southward migration (Figure 2, nodes 9–11; Figure 3). By contrast, curlew from southeast Australia occupied breeding sites that were on average four degrees south of curlew from northwest Australia ($\beta \pm SE = -4.40 \pm 1.00^\circ$, $z = -4.41$, $p < .001$; Figure 4). Differences in breeding latitude between curlew from different nonbreeding regions translated into notable differences in human modification at both ends of the annual cycle (Figure 4). Human modification was significantly higher in landscapes occupied by curlew from southeast Australia compared to those occupied by curlew from northwest Australia at both the nonbreeding grounds (southeast: mean = 0.479, median = 0.464, $SE = 0.005$, $n = 2194$; northwest: mean = 0.175, median = 0.005, $SE = 0.008$, $n = 1308$; $t = -35.869$, $df = 2621.7$, $p < .001$) and breeding grounds (southeast: mean = 0.307, median = 0.186, $SE = 0.004$, $n = 4670$; northwest: mean = 0.045, median = 0.033, $SE = 0.001$, $n = 7443$; $t = -70.204$, $df = 5742.7$, $p < .001$).

3.3 | Migration timing

We found differences in the timing of annual cycle events between northwest and southeast nonbreeding populations that reinforced differences in breeding latitude (Figure 5 and Table S1). Specifically, the migration schedule of curlew from southeast Australia was ahead of curlew from northwest Australia by 2.5–3 weeks: they departed the nonbreeding grounds earlier ($\beta \pm SE = -17.5 \pm 4.7$ days, $z = -3.7$, $p < .001$), arrived in the Yellow Sea earlier ($\beta \pm SE = -22.3 \pm 3.6$ days, $z = -6.2$, $p < .001$), departed the Yellow Sea earlier ($\beta \pm SE = -23.0 \pm 5.3$ days, $z = -4.3$, $p < .001$), and arrived at the breeding grounds

earlier ($\beta \pm SE = -23.0 \pm 5.9$ days, $z = -3.9$, $p < .001$). Curlew from southeast Australia also spent less time staging in the Yellow Sea during northward migration ($\beta \pm SE = -7.9 \pm 3.1$ days, $z = -2.5$, $p = .011$). Differences in southward migration timing were similar in direction to northward migration but more variable (Figure 5 and Table S3).

3.4 | Time spent in each country

On average, individuals spent $57.9 \pm 3.8\%$ of the calendar year within the Australian exclusive economic zone, followed by mainland China ($15.0 \pm 3.3\%$) and Russia ($8.2 \pm 1.7\%$). The remaining 18.9% of the calendar year was distributed across nine countries (11.8%) and beyond national jurisdictions ($7.1 \pm 0.9\%$) (Table 1).

4 | DISCUSSION

This study provides a first evaluation of the migratory network of the far eastern curlew, a globally endangered and declining species. By deploying tracking devices at multiple sites across the species' nonbreeding range, we found spatiotemporal differences in breeding latitude and migration timing of nonbreeding populations from southeast and northwest Australia, with individuals from southeast Australia initiating northward migration earlier, arriving at the breeding grounds earlier, and breeding at more southerly latitudes. When coupled with steep population declines in southeast compared to northwest Australia (Clemens et al., 2016; Studds et al., 2017), these findings suggest an important association between migratory connectivity and differential population trends.

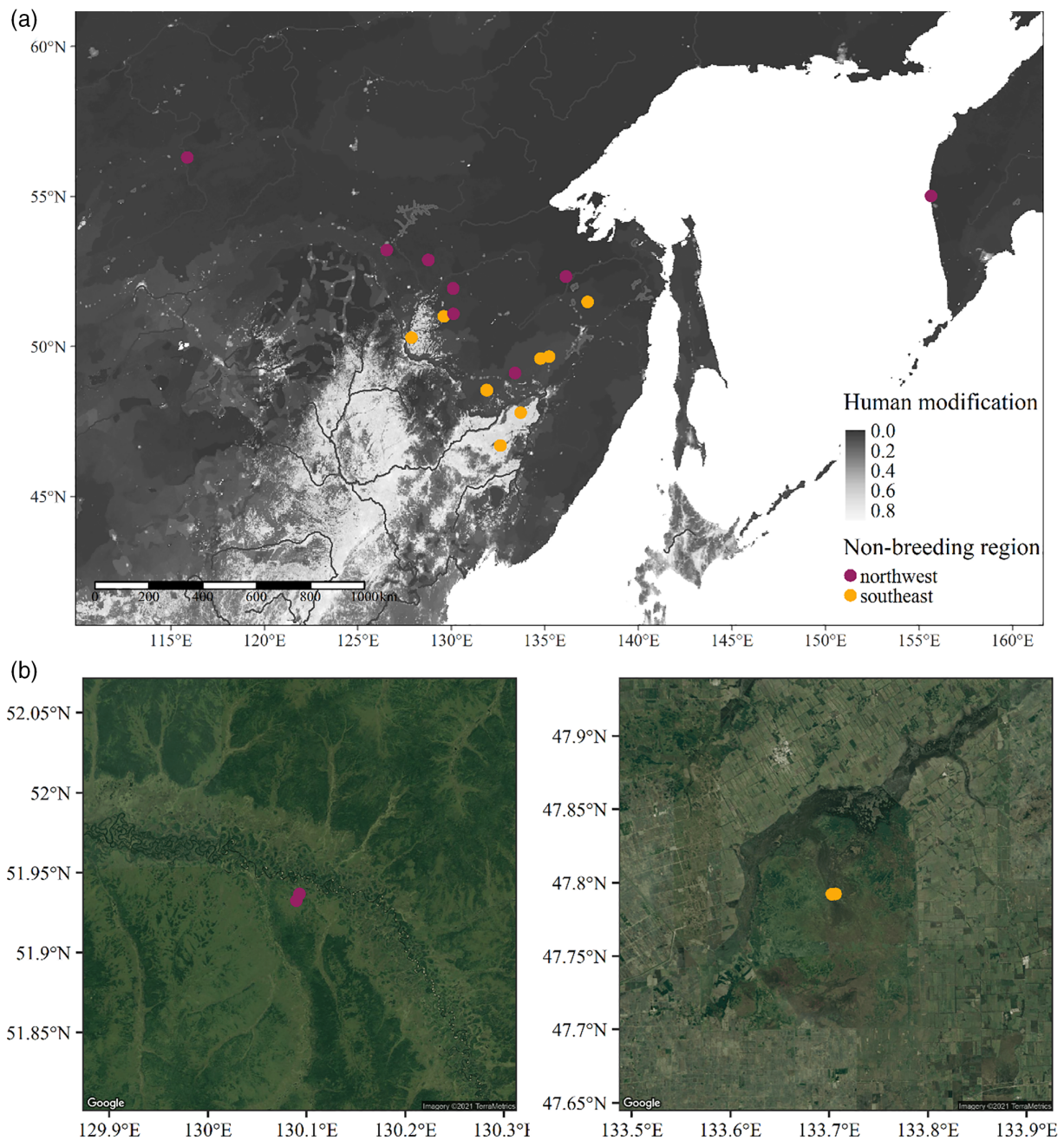


FIGURE 4 Differences in latitude and human impacts at breeding locations of far eastern curlew from nonbreeding regions in southeast and northwest Australia. (a) Breeding locations overlaid on a raster of human modification (Kennedy et al., 2019) revealing that curlew from southeast Australia breed at more southerly latitudes where they are exposed to more modified landscapes compared to curlew from northwest Australia that breed farther north. (b) Satellite imagery of example northern (left) and southern (right) breeding sites. See Figures S24–S37 for satellite imagery of all breeding and inland prebreeding/postbreeding stopover and staging sites

4.1 | Migratory connectivity and differential population trends

Varying degrees of interpopulation mixing across the annual cycle between southeast and northwest nonbreeding regions carries implications for interpreting the decline of the far eastern curlew and predicting the effectiveness of conservation actions. From 1993 to 2012, far

eastern curlew populations were estimated to decline by 5.2% (95% Bayesian credible interval = -6.9 to -3.5%) and 6.7% (95% BCI = -8.4 to -6.1%) per year across eastern and southeastern Australia, whereas populations in northwestern Australia showed no decline (-2.3% , 95% BCI = -6.5 , 2.0%) over the same period (Studds et al., 2017, fig. 3, table S2). This spatial variation in population change has been reinforced by another

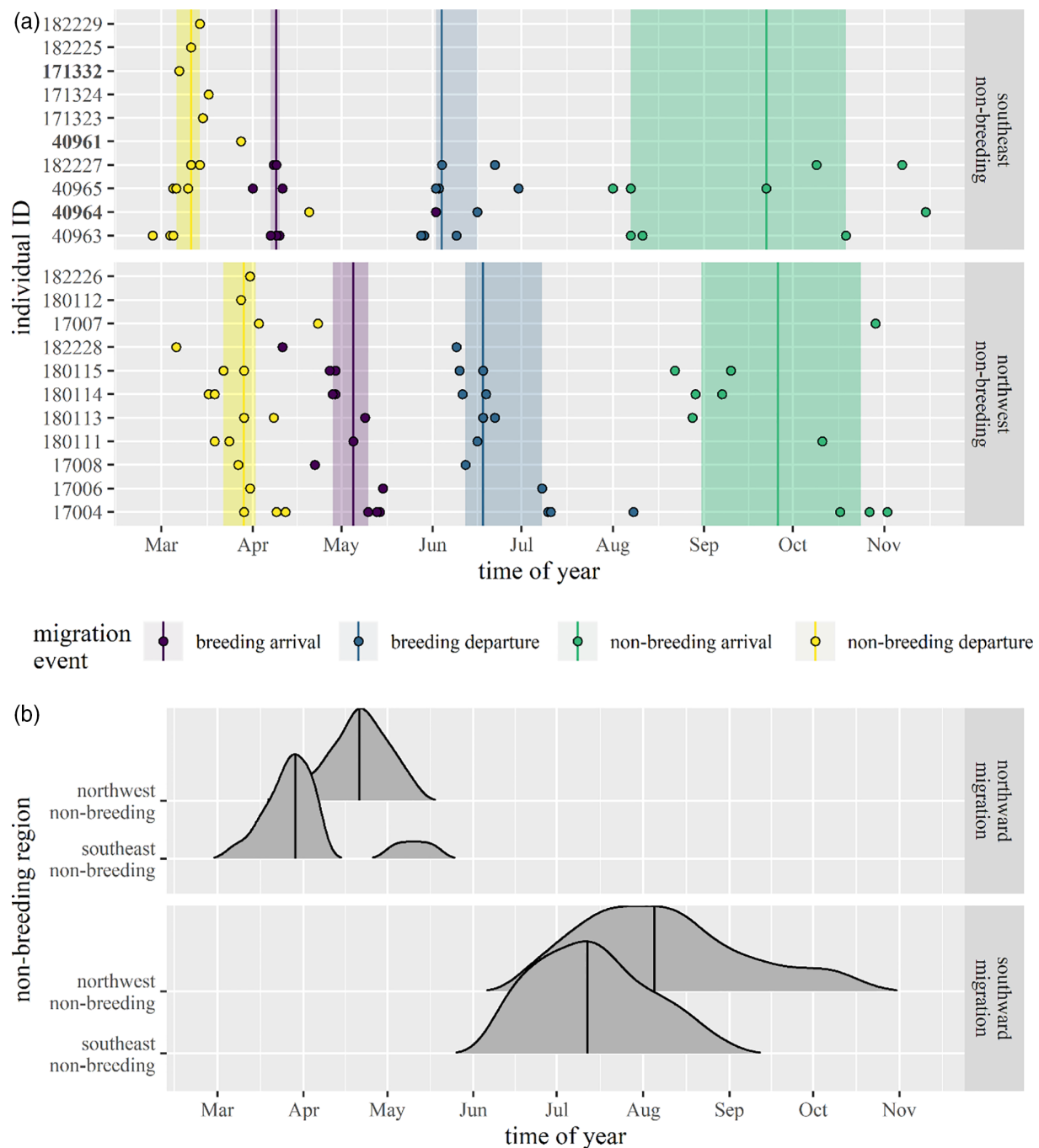


FIGURE 5 Migration timing of far eastern curlew from southeast and northwest Australia nonbreeding regions. (a) Timing of departure from and arrival at nonbreeding and breeding regions. Color bands show the interquartile range of dates for each migration event. IDs in bold text indicate individuals tagged as immatures. (b) Temporal occurrence of far eastern curlew in the Yellow Sea during southward and northward migration visualized with kernel density distributions (minimum height = 0.01) using R package ggridges (Wilke, 2020). Vertical lines show the median dates of (a) migration events and (b) occurrence in the Yellow Sea

continent-wide trend analysis (Clemens et al., 2016) and trend analyses conducted over various time periods at the four nonbreeding sites where tagging took place (Hansen et al., 2015; Lilleyman et al., 2020; Rogers et al., 2020; Wilson et al., 2011). When considered alongside the finding that curlew from southeast Australia bred farther

south in the Amur River basin of northeast China and eastern Russia compared to individuals from northwest Australia, this gradient in population change is significant for two reasons. First, habitat alteration and agriculture is more intensive in the southern breeding grounds (Figure 4) (Zhao et al., 2019). Second, the southeast

TABLE 1 Average amount of time that an individual far eastern curlew spent within the exclusive economic zone of each country during an annual cycle ($n = 22$)

Country	Time within a country (% \pm SE)	Time within a country (days/year \pm SE)
Australia	57.865 \pm 3.8	211.206 \pm 14.0
China mainland	15.043 \pm 3.3	54.908 \pm 12.2
Russia	8.218 \pm 1.7	29.995 \pm 6.1
South Korea	5.376 \pm 2.3	19.624 \pm 8.4
North Korea	3.820 \pm 1.7	13.944 \pm 6.2
Indonesia	1.382 \pm 0.4	5.046 \pm 1.6
Malaysia	0.450 \pm 0.5	1.643 \pm 1.6
Taiwan	0.428 \pm 0.2	1.563 \pm 0.8
Timor-Leste	0.187 \pm 0.1	0.682 \pm 0.5
Japan	0.123 \pm 0.1	0.451 \pm 0.5
Philippines	0.009 \pm 0.0	0.034 \pm 0.0
Papua New Guinea	0.002 \pm 0.0	0.006 \pm 0.0
Beyond EEZs	7.096 \pm 0.9	25.900 \pm 3.5

Australia nonbreeding grounds face considerably greater human pressure and coastal development (Kennedy et al., 2019). Therefore, while habitat loss in the Yellow Sea has been associated with migratory shorebird declines in the East Asian–Australasian flyway (Amano et al., 2010; Studds et al., 2017), more intense human pressure in the southern breeding range and southeast nonbreeding range could explain the steep declines of far eastern curlew in southeast Australia and relative stability of populations in northwest Australia.

The observed pattern of spatial connectivity between nonbreeding and breeding regions is strengthened when considered alongside differences in migration timing. The northward migration of individuals from southeast Australia was on average 2.5–3 weeks ahead of that of individuals from northwest Australia. Intraspecific spatial variation in migration timing has been found in other migratory shorebird species (Alves et al., 2013; Battley et al., 2005; Buehler & Piersma, 2008; Conklin, Battley, Potter, & Fox, 2010; van Bemmelen et al., 2019), including in bar-tailed godwit *Limosa lapponica* from New Zealand, where individuals occupying more southerly nonbreeding sites depart earlier than those occupying more northerly nonbreeding sites (Battley et al., 2020). While the specific causes of latitudinal variation in migration timing of far eastern curlew are not known, earlier migration is suggestive of southerly breeding areas because by breeding at more southern latitudes (closer to the equator), early arriving individuals can reduce their exposure to harsher climatic conditions that

occur farther north in spring (Smith, Gilchrist, Forbes, Martin, & Allard, 2010). Therefore, although inferences about differences in breeding latitude and their implications for understanding population declines are based on a sample of 26 breeding sites from 16 individuals, concurrent differences in migration timing suggest that differences in breeding latitude represent a genuine ecological pattern.

In contrast to the breeding grounds where we found evidence of separation among southeast and northwest nonbreeding populations, mixing occurred throughout most of the Yellow Sea, with the exception of the northern Bohai Sea region which was primarily visited by curlew from northwest Australia. Spatial overlap in this region implies that threats, such as habitat loss and degradation (Murray, Clemens, Phinn, Possingham, & Fuller, 2014), could impact broader segments of the far eastern curlew population, as opposed to a single subpopulation in isolation. Yet by the same logic, spatial overlap could also confer potential advantages. For example, management actions in the Yellow Sea, such as recent and forthcoming World Heritage migratory bird sanctuaries (UNESCO, 2019), could benefit a large proportion of the far eastern curlew population. Independent of observed levels of mixing in the Yellow Sea, individuals spent nearly one quarter of the annual cycle in the Yellow Sea region, second only to time spent at the Australian nonbreeding grounds (Table 1), reinforcing the responsibility the region bears for the species persistence (Barter, 2002; Melville, Chen, & Ma, 2016).

While the importance of the Yellow Sea as the primary staging area has long been known, our study revealed new information about stopover site use between the Australian nonbreeding grounds and the coast of the Yellow Sea. Sites in the Philippines, Indonesia, Papua New Guinea, and the South Pacific Islands were used during both migration directions, whereas East Asian sites outside the Yellow Sea and Japanese islands were used exclusively during northward migration. The amount of time curlew spent at these stopover sites made up a small proportion of the annual cycle (Table 1), but they likely provide critical short-term refuge when adverse weather events are encountered (Newton, 2007). Indeed, Lisovski, Gosbell, Minton, and Klaassen (2021) argue that differences in the number and spatial distribution of stopover sites may help to explain differential population trends of two other small migratory shorebird species in the East Asian–Australasian flyway. The more westerly migration routes of far eastern curlew from northwest Australia potentially provides these individuals with more emergency stopover opportunities compared to individuals from southeast Australia that take a more easterly migration route over the open ocean (Figure 1).

5 | CONCLUSIONS

Our results revealing alignment between patterns of migratory connectivity, differential population trends and human impact, suggest that threats to far eastern curlew at breeding and nonbreeding areas may be more impactful than previously thought. At the breeding grounds, hunting represents a potentially serious threat. Although efforts are underway to assess hunting pressure in parts of the breeding grounds (Klokov et al., 2019), coordinated assessment of the extent and population impacts of hunting remains a challenge (Gallo-Cajiao et al., 2020). In Australia, where the distribution and dynamics of the species are relatively well understood, improved protection of coastal habitats is needed, especially in the southeast where human pressure is most intense and is expected to increase with a growing human population (ABoS, 2018). Far eastern curlew spend nearly 60% of their annual cycle inside Australia's borders, the most of any country. Moreover, this proportion is even greater for immature birds that can spend multiple years at the nonbreeding grounds before migrating north for the first time (e.g., 40964 in Figure S1). Adopting a holistic, full annual cycle approach to research and conservation will help to improve the outlook for the endangered far eastern curlew and other similarly threatened species across the East Asian–Australasian flyway.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Zaine N. Morricks and Bradley K. Woodworth conceived and designed the study with input from Richard A. Fuller, Amanda Lilleyman, Jonathan T. Coleman, and Stephen T. Garnett. Amanda Lilleyman, Robert Bush, Jonathan T. Coleman, Grace Maglio, Roz Jessop, Clive D. T. Minton, and Bradley K. Woodworth collected the tracking data. Zaine N. Morricks and Bradley K. Woodworth analyzed the data and wrote the manuscript. All authors reviewed and edited the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The datasets generated and analyzed during the current study are available in the Movebank Data Repository, <https://doi.org/10.5441/001/1.v8r49083> (Lilleyman et al., 2021).

ETHICS STATEMENT

Tracking devices were deployed under the following approvals and permits: Charles Darwin University Animal Ethics Committee (project A16038), University of Queensland Native/Exotic Wildlife and Marine Animals Ethics Committee (project AE35173), Queensland Department of Agriculture and Fisheries Animal Ethics Committee (approval CA2018-02-1159), Northern Territory Parks and Wildlife permit 60882, and Australian Bird and Bat Banding Scheme permits 3090 (project 01) and 273 (project 01).

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SUPPORTING INFORMATION

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