Distinctive and highly variable bird migration system revealed in Eastern Australia

Highlights

- Weather radar network reveals a structured bird migration system in East Australia
- Sequential migration peaks move latitudinally, and directions reverse seasonally
- Magnitude is smaller than in the Northern Hemisphere but with larger daytime activity
- Direction, timing, and magnitude vary more between years than in North America

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In brief

Shi et al. show that a structured migration system with seasonal peaks and contrasting flight directions exists in Eastern Australia. Unlike in the Northern Hemisphere, Australian migrations show a significant proportion of diurnal movement, with lower intensity and greater variability in timing, direction, and magnitude across years.







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Distinctive and highly variable bird migration system revealed in Eastern Australia

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SUMMARY

Our understanding of bird migration is heavily biased toward long-distance movements in the Northern Hemisphere,¹⁻³ with only fragmented knowledge from the Southern Hemisphere.^{4,5} In Australia, while some species migrate, 4,6-8 the timing and direction of large-scale, multi-species seasonal movements remain critically understudied due to the complexity of movement in this region and a lack of research personnel and infrastructure. 7,9 It is still unclear whether there are pronounced and structured mass movements resembling those in the Northern Hemisphere. 10-12 Here, we analyze data from a latitudinal transect of weather radars spanning the entire coastline of Eastern Australia to determine the magnitude, directions, timing, and variability of bird migration compared to that of Northern Hemisphere migration systems. Bird movements exhibited sequential seasonal peaks along a latitudinal gradient with seasonally contrasting flight directions, confirming that a structured bird migration system exists. Three features were distinct from Northern Hemisphere migrations. First, distinct movements occurred around sunrise with comparable magnitudes to nocturnal migration, likely representing a strong diurnal component to the bird movements. Second, migration intensity averaged 0.06 million birds km⁻¹ in autumn, much lower than Northern Hemisphere migrations. 11-13 Finally, flight directions were more dispersed, and the timing and amount of migration were highly variable between years compared to Northern Hemisphere migration systems, perhaps in response to variable climate. This first quantification of continental-scale movements in Australia revealed a distinctive migration system, and it suggests that much remains to be discovered about the ecological and evolutionary factors shaping animal migrations in the Southern Hemisphere.

RESULTS

Seasonal flows of billions of avian migrants transport huge amounts of energy and nutrients, and they impact ecosystem processes and functions over large geographical scales. 14,15 Recent global declines in migratory birds present acute challenges for managing their ecosystem services relevant for human economy and health. 16,17 To evaluate magnitudes of declines and conserve their ecosystem functions and services, we need long-term (e.g., years to decades) and continent-wide quantification of migration flows. Detailed quantification of migration flow has advanced rapidly in the Northern Hemisphere, specifically in the United States (US) 10,13,18 and Europe, 11,12,19 with initial assessments underway in East Asia 20, however, these efforts focus largely on birds breeding in the Northern Hemisphere. Quantification of migration flows of birds within the Southern Hemisphere 4,5 is still lacking.

In this study, we aim to detect, for the first time, whether a seasonal migration flow exists in Eastern Australia and report the direction, phenology, and magnitude of such movement. We analyzed data from 10 weather radars from Tasmania to northern Queensland in Eastern Australia, covering a period of 6 to 16 years (STAR Methods). Most weather radar-based migration studies consider only the nocturnal period during migration seasons, since these periods are dominated by birds in terms of radar returns.3 With the development of a new method that improves the filtering of insect-produced signals from the weather radar returns,²¹ and considering previous observations that diurnal migration may be a common strategy in Australian landbirds, 4,7,22,23 we here investigate the pattern of avian movement in time and vertical space across the full 24-h cycle. We quantify diurnal and nocturnal movements throughout the entire year and make comparisons with migration systems in other parts of the world.



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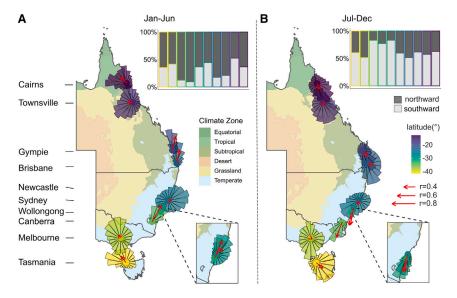
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Seasonally contrasting flight directions

Bird flight direction showed a clear seasonal pattern in Eastern Australia (Figure 1, detailed statistics for each site are given in Table S1): all sites showed mean directions with a northward component in January-June (first half of the year, i.e., southern autumn) and a southward component in July-December (second half of the year, i.e., southern spring), except for Townsville in Jan-Jun (mean direction = 268° from north). Across all locations, northward movements comprised 69% (± 15%) of all movement during Jan-Jun, and southward movements comprised 65% (± 12%) of all movement during Jul-Dec. Seasonal contrast was largest in Canberra, with 88% of movements northward in Jul-Dec and 83% southward in Jul-Dec. Most sites showed a significant difference in the proportions of northward movement in Jan-Jun compared with Jul-Dec (mean increase = 35%, p < 0.01, t test paired for each year at each site from 2018 to 2022), except for Townsville, which was not significant (p = 0.25). The level of directional concentration varied across sites: mean r was 0.40 (± 0.24) in Jan-Jun and 0.30 (± 0.19) in Jul-Dec.

Comparable diurnal and nocturnal movement peaks

Spatial-temporal patterns of potentially migratory movements within each day and night showed variation among sites (Figure 2). All sites showed highest movement in the lowest altitudinal band, and most movement occurred below 600 m above ground level. Movement above 1,000 m was rare in the mid-latitude sites but proportionally more frequent in the most southerly site (Tasmania) and the two most northerly sites (Townsville and Cairns), possibly an effect of residual meteorological signals in the C band radars. Most sites showed the highest movement intensities in the nocturnal period. For Canberra, Wollongong, and to a lesser extent Newcastle and Sydney, another peak movement occurred around civil dawn, from the last 2-3 deciles of night to the first 2-3 deciles of day, which reached up to around 1 km above ground. Such dawn peaks were not observed in likely non-migratory movements at these four sites (movement with southward component in the first half of the year and northward in the second half, Figure S1).

Figure 1. Flight direction distributions at each site during two periods

Flight direction distributions at each location during (A) January to June and (B) during July to December, aggregated with data from 2018 to 2022, with climate zones illustrated in the background. A Red arrows represent mean direction of flight and strength of concentration (r). Proportions of northward and southward flights are given in the top-right corner of each plot. Flight directions at Wollongong and Sydney are illustrated in the inset box to reduce overlap.

See also Table S1.

We found a wide range of movement intensities among sites (Figures 3A and 3B), with the amount of nocturnal movement often higher than diurnal movement, except for Canberra and Wollongong. The highest diurnal peak in Jan–Jun was

 $0.61 \times 10^4 \text{ cm}^2 \cdot \text{km}^{-1} \cdot \text{day}^{-1}$ near Canberra on 13 April (day 101 converted to a calendar date of a common year), and in Jul-Dec it was $0.31 \times 10^4 \text{ cm}^2 \cdot \text{km}^{-1} \cdot \text{day}^{-1}$ near Newcastle on 18 September. The highest nocturnal peak was $1.25 \times 10^4 \text{ cm}^2 \cdot \text{km}^{-1} \cdot \text{night}^{-1}$ near Brisbane on 3 April, and in Jul-Dec, it was $0.86 \times 10^4 \text{ cm}^2 \cdot \text{km}^{-1} \cdot \text{night}^{-1}$ near Gympie on 14 September. Combining diurnal and nocturnal trends, many sites showed two clear peaks of movement intensity across the year (Figure 3C). The highest peak traffic was $1.56 \times 10^4 \text{ cm}^2 \cdot \text{km}^{-1}$ per day and night near Brisbane on 10 April and $1.00 \times 10^4 \text{ cm}^2 \cdot \text{km}^{-1}$ per day and night near Gympie on 13 September, for each half of the year. Notably, Sydney, Newcastle, and Melbourne recorded much higher combined peaks in the second half of the year than the first.

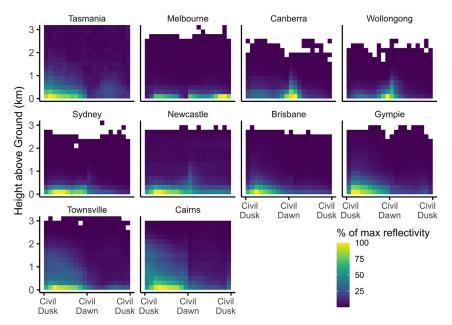
There were weak, non-significant relationships between latitude and median passage date in both Jan-Jun (slope = 0.20. $r^2 = -0.10$, p = 0.70; Figure 3D) and in Jul-Dec (slope = -0.47, $r^2 = 0.12$, p = 0.16; Figure 3D). When excluding the two most northerly sites, the relationship between latitude and median passage date strengthened slightly in Jan-Jun (slope = 0.79, $r^2 = -0.05$, p = 0.45; Figure 3D), while becoming significantly more negative in Jul–Dec (slope = -1.64, $r^2 = 0.89$, p < 0.01; Figure 3D). Mean time interval between Jan-Jun and Jul-Dec median passage dates was 175 ± 17 days, with Tasmania exhibiting the shortest difference (143 days) and Wollongong the longest difference (200 days). The median date intervals showed positive relationships with latitude (all sites: slope = 0.67, $r^2 = -0.01$, p = 0.36; excluding two northmost sites: slope = 2.44, $r^2 = 0.33$, p = 0.08), with later spring and earlier autumn (hence shorter intervals) at southern sites and longer intervals at northern sites.

Greater variation in Australia compared with the US

Standard deviations in median passage date were much higher in Australia than in the US in spring (Figure 4A, mean = 7.42 for Australian radars, 3.40 for all US radars, and 3.46 for East Coast subset) and in autumn (mean = 7.06 for Australian radars, 3.84 for all US radars, and 3.81 for East Coast subset; $\rho < 0.01$ for both seasons between Australian and US subset data; t test). Coefficients of variation in migration traffic were also much higher in

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Australia than in the US in spring (Figure 4B, mean = 0.32 for Australian radars, 0.19 for all US radars, and 0.19 for East Coast subset) and in autumn (mean = 0.35 for Australian radars, 0.17 for all US radars, and 0.15 for East Coast subset; p = 0.03 for spring and p < 0.01 for autumn). The level of directional concentration was much lower in Australia than in the US in spring (Figure 4C, mean = 0.30 for Australian radars, 0.87 for all US radars, and 0.90 for East Coast subset) and in autumn (mean = 0.40 for Australian radars, 0.87 for all US radars, and 0.91 for East Coast subset; p < 0.01 for both seasons).

DISCUSSION

This study is the first large-scale characterization of bird migration in the Southern Hemisphere based on direct quantified data. Using weather radar spanning a large continental area and a broad latitudinal extent, we revealed the overall patterns of avian movements and quantified migration flows in Eastern Australia. Without prior knowledge or assumption on when and where to expect bird movements in Eastern Australia, we explored movement patterns for day and night and across the whole year. Most bird movements occurred in the autumn and spring and showed seasonally contrasting flight directions and sequential phenology along the latitudinal gradient, together constituting strong evidence of a migration system reminiscent of those found in the temperate Northern Hemisphere. Previous studies summarizing ringing, tracking, and observational data only qualitatively assessed whether individual species are (partially) migratory, ^{4,7} and they often fell short of revealing the timing, routes, and amounts of migration. Such studies are complicated by the short-distance and partial migrations that seem commonplace in Australia and which are less perceptible than long-distance to-and-fro migrations; variable timing and routes as well as admixture with other types of movement further complicate detecting an underlying pattern.⁶ By analyzing radar data, we were able to confirm the presence of a pronounced migration system and to quantify

Figure 2. Spatial and temporal distribution of bird movement throughout the day and night

Temporal resolution is one-tenth of the day (between civil dawn and dusk) and night (between civil dusk and dawn). Spatial resolution is 200 m up to 3 km above ground. Movement intensities in every time-altitude cell are scaled to the max reflectivity value in all the cells of each radar to facilitate comparison between radars, averaging data from 2018 to 2022. Bird movements are limited to northward flights in the first half of the year and southward flights in the second half.

See also Figure S1.

its major characteristics for the first time in the Southern Hemisphere.

Most weather radar-based research on bird migration has focused on the nocturnal period during migration seasons, when bird radar reflectivity often far exceeds insect radar reflectivity (i.e., in the Northern Hemisphere for US and

Europe). By adopting new methods that strengthen our capacity to separate birds and insects, we extended the typical nocturnal study period to the full 24-h cycle and built more comprehensive profiles of bird migration. We found that diurnal movement peaks were the dominant process in Canberra and Wollongong, reaching a comparable magnitude to nocturnal peaks from other sites in the whole migration system. Diurnal migration, therefore, may constitute a significant proportion of all movement at the mid-latitude sites, potentially a distinctive aspect of Australian land bird migration and perhaps of austral migrants in general. Australia lacks a diverse group of diurnal avian predators, and short migration distances may reduce the necessity for nocturnal migration,^{4,7} which capitalizes on cooler temperatures and calmer winds that facilitate long-distance flight.³

Many honeyeater species (family Meliphagidae) observed during daylight hours move in seasonally explicit directions, and studies in captivity have also shown early morning restlessness in several species during the migration season, which coincides with the daily and seasonal timing of our study. 22,25,26 These dawn movements could indicate diurnal migrants taking off around sunrise and rising to hundreds of meters above ground to gain orientation or weather cues. We recognize our limited knowledge regarding where and which species may be nocturnally/diurnally migrating or mobile and furthermore which species fly high enough to be detected by radar in Australia. Additionally, the reason for an absence of dawn peaks at both ends of the latitudinal range remains unclear, possibly related to the distribution and extent of migration among diurnally migrating species. Given that GPS-tracking and acoustic monitoring studies of nocturnal migration for Australian passerines are still rare, definitive evidence is needed to confirm the extent of nocturnal/diurnal migration for many Australian species.

By combining nocturnal and diurnal movements, we quantified the complete set of movements occurring along the east coast of Australia. Without prior knowledge of the species



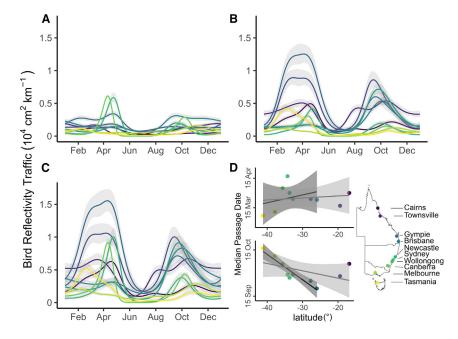


Figure 3. Magnitude and median passage dates of bird movement along the east coast of Australia

(A) Smoothed trend of diurnal bird reflectivity traveling across a 1 km transect per day for each radar location.

(B and C) (B) Smoothed trend of nocturnal bird reflectivity and (C) combined trend summing diurnal and nocturnal trends.

(D) Linear regression of median passage Julian date as in combined smoothed trends with latitude for each half of the year. Lighter gray regression lines represent analysis of all sites, while darker gray lines represent those excluding the two northmost sites. Shaded areas in all plots indicate 95% confidence intervals of regression model. Data from 2018 to 2022, filtering for northward movements in the first half of the year and southward in the second half.

density in the continental US¹³ and in Southern Europe, ^{11,12} and they are perhaps more comparable to high-latitude migration in the Northern Hemisphere. ¹²

Australia lacks a diverse group of small body-sized passerine migrants (e.g., Sylviid and Parulid warblers from Palearctic and Nearctic systems, respectively); thus, it is not surprising that the amount of bird migration is much lower compared with the temperate Northern Hemisphere. Eastern Australia (east of the Great Dividing Range) is a narrow band of relatively humid and forested landscapes; thus the total flow of biomass and population size of migrants in Eastern Australia are also likely much lower than those of Europe or North America.

composition and average size of migrants, we did not assume a mean radar cross section (RCS) to translate reflectivity into the number of birds. If we use the same mean RCS of passerine-sized birds (11 cm²) that has been assumed in temperate Northern Hemisphere studies of bird migration, we would arrive at 870 birds km⁻¹ per circadian cycle, or 0.16 million birds km⁻¹ for the first half of the year for Brisbane (the highest site), and 0.06 million birds km⁻¹ for all sites averaged. These estimates are likely an order of magnitude lower than autumn migration

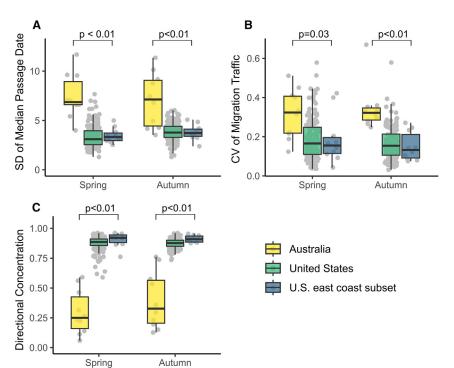


Figure 4. Comparison of level of variation of migration characteristics in Australia and the United States

(A) Comparison of the standard deviation in median passage dates.

(B and C) (B) Comparison of coefficient of variation in migration traffic and (C) comparison of degree of concentration in flight direction, separately for each season. t tests were performed, and p values are annotated between the mean values of each parameter of Australian data and the US East Coast subset that has equal sample size (n = 10).



Many characteristics in the bird movement patterns reflect Australia's unique landscape and climate. The observation that seasonal movement seems most structured from Tasmania to South East Queensland aligns with previous studies that many Australian species migrate across limited latitudinal spans, as far north as southern Queensland, ^{6,7} similar to austral migrations in other southern continents.⁵ Most Australian land bird species travel relatively short distances, and the sequential movement peaks observed in southeastern sites may be waves of shortdistance migrants rather than long-distance migrants, driven by local seasonality and environmental stimuli. 4,7,28 Directional concentration is low at our sites compared to Northern Hemisphere migration systems. 12 These observations also agree with⁶ that birds emigrating from Tasmania and Victoria in autumn move in a broad, multi-directional front rather than uniformly heading toward the eastern coastline and then northward. Migrants can either head toward New South Wales in the northeast or toward South Australia in the northwest during autumn and vice versa in spring. The movement of birds between coastal and inland regions further contributes to the overall low directional concentration observed, while still following a general pattern of seasonal reversal in direction.

The observed variability in bird migration phenology and magnitude in Australia is considerably larger than that observed in the US, perhaps attributable to several factors inherent to the Australian climate and to the nature of austral migration in general. Australia's climate is marked by variable rainfall patterns and diverse environmental conditions, with a vast arid interior and relatively narrow humid, vegetated regions along the east coast, ranging from temperate to tropical climates.^{24,29} In contrast, North America, particularly the eastern US and Canada, has extensive temperate regions, offering more predictable climatic conditions. Such climatic heterogeneity likely plays a significant role in shaping the migratory behaviors of avian species.²⁸ Additionally, Australia lacks the high-latitude environments where migration is primarily obligatory due to the strong seasonality and coordinated by relatively consistent environmental cues (e.g., photoperiod). Instead, migration in Australia is dominated by facultative migrants that may adjust their decision, timing, and the distance of migration in response to environmental cues, such as food availability and meteorological and climatic conditions, leading to increased variability in the migration phenology and magnitude from year to year. These factors highlight the need for further research to discover the ecological and evolutionary mechanisms driving the observed variability in Australian bird migration, which is crucial for informing conservation efforts and management strategies for preserving a variable migration system in the face of environmental change.

Conclusions

This study provides the first direct quantification of avian movement patterns in the Southern Hemisphere, demonstrating the capacity of a weather radar network as a surveillance tool across a large continental area with a sparse human population for understanding avian movements. Our work also highlights a wealth of research opportunities; with so little information about avian migration in Australia, our results could serve as a reference point for tracking and acoustic recording studies to reveal

more species-specific migration patterns. The ongoing expansion and upgrade of the Australian weather radar network, especially in the arid interior, will enable researchers to capture transient movements of nomadic species, look into how they track temporal resources over long distances, and to link extreme climate events to their movement dynamics. 30 Climate and anthropogenic changes are also heavily impacting Australia's wildlife and ecosystems. The growing radar archive is a unique source of information to explore whether we are experiencing a similar trend of avifauna decline in Eastern Australia, as witnessed elsewhere, 17 and what the drivers are of any changes. Most importantly, our work is a call for ecologists to use weather surveillance radar to study avian movement outside of the European and North American continental land masses. Such research is essential to addressing growing threats (e.g., light pollution and wind energy infrastructure) to migrants and more broadly to biodiversity in regions where conservation is in urgent need of more information and tools.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Xu Shi (xu.shi@student.uq.edu.au).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- All radar data used in this study are publicly accessible through the Australian weather radar archive: https://www.openradar.io/ operational-network.
- Processed radar data and R code have been deposited at Figshare (DOI: https://doi.org/10.6084/m9.figshare.26946520).
- All additional information required to reanalyze the data reported in this
 paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

X.S., J.S., R.A.F., and J.W.C. conceived the study. X.S., J.S., J.M., and A.M.D. contributed to data curation. X.S. analyzed the data, with A.M.D. and J.S. providing crucial support. X.S., J.S., R.A.F., and J.W.C. wrote the first draft of the paper, and all authors made significant contributions to the final draft.

DECLARATION OF INTERESTS

The authors declare no competing interests.





STAR*METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR*METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Australian weather radar level-1 data	Soderholm et al.31	https://www.openradar.io/operational-network
ERA5 hourly wind data on pressure levels	Hersbach et al.32	https://doi.org/10.24381/cds.bd0915c6
U.S. migration phenology data	Horton et al.33	https://doi.org/10.6084/m9.figshare.10062239.v1
Australian climate zone map	Stern et al. ²⁴	http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications/index.jsp?maptype=kpngrp#maps
Processed radar data	This paper	Figshare: https://doi.org/10.6084/m9.figshare.26946520
Original R code to analyze the data and generate the plots	This paper	Figshare: https://doi.org/10.6084/m9.figshare.26946520
Software and algorithms		
R v.4.1.2	R core team ³⁴	https://www.r-project.org/
"MistNet" algorithm	Lin et al. ³⁵	https://github.com/darkecology/wsrlib
"bioRad" R package	Dokter et al. ³⁶	https://cran.r-project.org/web/packages/bioRad/index.html
"mgcv" R package	Wood ³⁷	https://cran.r-project.org/web/packages/mgcv/index.html

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Data sources

We analyzed weather radar data from Eastern Australia along a latitudinal span of 24 degrees from Tasmania to northern Queensland. This region is characterized by a temperate climate in the south and tropical climate in the north, with forested and cultivated land-scapes. The Australian weather radar network consists of ~69 operating radars as of 2023. Most radars survey the airspace in 5-10 min intervals with a 3 dB beam angle of 1° width at multiple elevation angles (0.5° above horizontal, 0.9°, 1.8°, ... 32°). Radar data products include reflectivity, and when available, radial velocity, spectrum width, and dual-polarization moments. We obtained the level-1 dataset from the Australian National Computational Infrastructure (NCI), 31 for 10 Doppler radars along the east coast of Australia with 6-16 years of data available (Figure 1, see Table S2 for more details of the radars and years of data used for each radar). The reflectivity data were calibrated by matching collocated information with Tropical Rainfall Measuring Mission (TRMM) and Global Precipitation Measurement (GPM) satellite passes. 38

Notably, the Melbourne, Sydney and Brisbane radars underwent an upgrade from single-polarization to dual-polarization in late 2017, which has increased the effectiveness of identifying and removing non-meteorological signals. Therefore, we used data from 2018 to 2022 for all analyses to keep the methodology consistent for each of the ten radars within the period, except for the phenological variation calculation. Phenology estimates do not require estimates of the absolute magnitude of migration ^{33,39} and therefore the impact of systemic changes related to the radar upgrade is expected to be minimal. For comparing phenological variation with other continents, we used the full period of data to maximize the sample size.

METHOD DETAILS

Radar data screening and processing

We extracted vertical profiles of bird reflectivity (η , cm²·km⁻³) using the vol2bird algorithm available in the R package "bioRad" designed for separating bird signals from other meteorological returns. ^{27,36} We analyzed a total of 37,785 radar days of available Australian weather radar data, representing 98% of all the radar days during the study period. Contamination from slow-moving targets such as hydrometeors and insects was initially removed based on standard deviation of radial velocity (sd_vvp) in single-polarized radars. Bird migration typically causes higher standard deviation in velocity than insects and a lower correlation coefficient than precipitation. ^{27,36} In dual-polarization radars, removal of precipitation was enhanced by also using the correlation coefficient (ρ_{HV}), where a value greater than 0.95 indicates likely precipitation and is subsequently removed. ⁴⁰ We further applied the MistNet model to exclude meteorological contamination in the S band radars. ³⁵ The MistNet model was developed with U.S. WSR-88D data, we evaluated its compatibility with Australian weather radar data prior to application. we selected data from three dual-polarized radars (Brisbane, Sydney, Melbourne, see also Table S2 for detail) in March and October 2021, and further used the lowest scans from polar volumes within one hour after sunset and one hour before sunrise, the presumed period likely to have co-occurring biological and meteorological signals. This resulted in 1107 scans in total. We applied the MistNet model on each scan and then rendered the



resulting scan to 360^*360 raster image of each parameter. These parameters include the original radar measurements (reflectivity factor DBZH, radial velocity VRADH, correlation coefficient ρ_{HV} , differential reflectivity Z_{DR} , differential phase ϕ_{DP}) and MistNet segmentation results CELL. Pixels with CELL > 1 would be classified as weather. We calculated the pixel-level confusion matrix of CELL with dual-pol-based rule (e.g. True Positive would be pixels with CELL>1 and $\rho_{HV}>0.95$) and evaluated the performance of MistNet model with different intensity of weather events. We found an overall good performance of MistNet model on Australian data (Precision = 76.4, Recall = 96.9, F-score = 85.2). MistNet performed better with increasing amount of weather pixels, while being less consistent with small-scale weather events (Figure S2). Compared to the evaluation results with US weather radar data (Precision = 99.1, Recall = 96.7, F-score = 97.9, note that the original model is evaluated against manually labelled scans), MistNet performance is relatively lower with Australian data. This could be due to the fact that MistNet is trained on three radar products (DBZH, VRADH and spectrum width WRADH), while WRADH is missing in the Australian data, and that the elevation angles in the US radar system is slightly different to the Australian ones. Nonetheless, MistNet model would be a valuable complement to the vol2bird algorithm analyzing single-polarized data in the Australian S band radars, and readily enable many years of historical data for analysis. More dedicated approach, such as training a new model with Australian data would likely achieve even better results, but we argue that MistNet is sufficient for our current study design.

We manually reviewed the resulting vertical profiles to exclude unfiltered meteorological events and ground clutter by viewing the time-series plots of reflectivity factor.³⁶ Old world flying-foxes (Pteropodidae) roost in large colonies and appear in radar imagery during post-sunset departure from and pre-dawn return to roosts.⁴¹ Flying-fox patches would achieve DBZH values unrealistically high for bird migration (usually > 30) in the S band radar due to their large body size and high density, and subsequently segmented as weather by the MistNet model. For C band radars without applying the MistNet model, we also excluded reflectivity with DBZH > 20 to reduce flying-fox and meteorological contamination. We also manually identified segments from their peak emergence for known colonies near one C band radar (Weipa radar, longitude: 141.92, latitude: -12.66, elevation: 43m, only used for flying-fox evaluation) and one S band radar (Gympie radar, see Table S2) respectively, calculated mean DBZH and excluded signals above this value for three hours after sunset and three hours before sunrise, the period when flying-foxes are most active and up to 400 m above ground, above which very few flying-foxes occur, ⁴² see also Figure S3. The exemplar flying-fox segments and mean DBZH value are in Figure S4. In total, quality control processes removed 8% of the data.

The sd_vvp threshold has shown satisfactory results in removing insect-dominated movement in C band radars, although its performance has not been thoroughly examined with S band radars, ³⁶ or when birds and insects co-occur in comparable reflectivities in the air. In the latter case, the weather radar will detect a reflectivity-weighted average radial velocity for birds and insects, and the resulting estimation of airspeed will therefore fall below the expected value for bird airspeeds (e.g. around 8 m·s⁻¹). ⁴³ In the temperate Northern Hemisphere, previous studies have demonstrated that birds are the dominant source of reflectivity during peak migration season at night, however in the Southern Hemisphere this has not been evaluated. We investigated the potential insect-bird composition in our data by examining the airspeed of the vertical profiles. Airspeed was computed by taking the ground speed obtained from weather radar and subtracting the wind speed provided by the ERA5 hourly data on pressure levels, ³² linearly interpolated to the location of each radar and to the hour and altitude in the vertical profile.

We found that airspeeds in our vertical profiles were much lower than those found in European and North American studies^{43,44} with highly right-skewed distributions (Figure S5, reflectivity weighted median airspeed = 3.6 m·s⁻¹ across all sites and vears. 5 -95th percentiles: 1.6 - 8.0 m·s⁻¹), suggesting a mixture of birds and insects. We developed the following analytical procedures to estimate the proportion of birds in the mixture. We assume that: birds fly at an average self-powered airspeed of a m·s⁻¹ in a self-maintained heading direction, meanwhile insects move primarily downwind with an average self-powered airspeed of b m·s⁻¹. The vector sum of their airspeeds, weighted by their proportions in the reflectivity would result in the observed airspeed. These parameters are used to solve for the potential proportion of birds in the mixture and their heading direction. Detailed documentation of the analytical procedure and application onto exemplar vertical profiles, as well as the consequences and limitations of this approach can be found in Shi et al.²¹ We used $a = 10 \text{ m} \cdot \text{s}^{-1}$ to represent the average airspeed of birds⁴⁵ and $b = 1 \text{ m} \cdot \text{s}^{-1}$ to represent the migrant insect community, considered to consist of a large proportion of numerous micro-insects with very slow self-powered airspeeds (<1 m·s⁻¹), plus smaller numbers of larger migrants with airspeeds around 2-4 m·s⁻¹.46,47 Bird reflectivity in the mixture was eventually calculated by multiplying the mixture's reflectivity with the proportion of birds in each time-altitude bin. Bird ground speed and direction was solved by adding the heading vectors to the wind vectors. Bird proportions were firstly averaged in every hourly timestamp and subsequently averaged for each year, weighted by reflectivity. Following this, we calculated the mean and standard deviation of bird proportion for the years spanning from 2018 to 2022. Bird proportions among sites averaged about 45% ± 11% (SD) in the biological reflectivities from the seven S-band radars and 39% ± 10% in the three C band radars (Figure S6).

QUANTIFICATION AND STATISTICAL ANALYSIS

Spatial-temporal patterns of bird movement

To investigate whether seasonally explicit flight directions exist in Eastern Australia, we illustrated the distribution of bird ground speed direction from the above analytical procedure, summarized in 20° segments of rose diagrams, weighted by reflectivity. Since Australian birds might not fly or migrate with a preferred direction of movement or common orientation, 6 we also reported the





proportion of northward and southward movement in each half of the year to reveal the underlying pattern of seasonal flight directions. To aid interpretation of the climate types at each site, We incorporated the climate zones of Australia following Australia Bureau of Meteorology's climate classification.²⁴

We further investigated the spatial-temporal distributions of bird movement within each day/night, as well as on a seasonal scale throughout the year. We selected northward movements in the first half of the year (1 January to 31 June) and southward movements in the second half of the year (1 July to 31 December) to focus on potential migratory movements. We summarized the bird reflectivities from their original resolution of 5-10 min intervals to ten intervals each for day and night (deciles) to facilitate comparison throughout the year when day and night lengths vary, 48 and up to 3000 m above ground in 200 m bands. We examined whether bird movement exhibited seasonal variations throughout the year, particularly if peak movements exist during potential migration seasons. Initial assessment showed that in some sites diurnal movement peaks lasted several hours before and after civil dawn,21 so we subsequently defined diurnal/day as 1 hour prior to civil dawn to civil dusk to better capture the extent of diurnal movement, and nocturnal/night as civil dusk to 1 hour prior to civil dawn. We generated daily/nightly bird reflectivity traffic (cm²·km⁻¹, see Dokter et al. 36), defined as the amount of bird reflectivity passing through a theoretical 1-km transect during each day and night. Reflectivity traffic was calculated by multiplying bird reflectivity densities with bird ground speed and the time difference between radar profiles (in units of hours, see Dokter et al. 13), summed through all altitude bins up to 3 km above ground. To illustrate the seasonal patterns, we generated year-long smoothed phenology curves for each radar station using GAM models with the R package "mgcv" with cyclic cubic regression splines and a quasi-Poisson distribution, 37 using the reflectivity traffic as a response variable and day of year as a predictor variable. Diurnal and nocturnal trends are summed to create combined trends to reveal the overall patterns. We extracted the median passage date from the combined trend at each radar, defined as the Julian date by which 50% of summed reflectivity traffic had been recorded, 33 separately for first and second half of year, and analyzed the relationship between median passage date with latitude using linear regression. All analyses were done in R 4.1.2.34

Comparison of migration metrics between Australia and the United States

As a final step, we compared the level of variation between three metrics of migration between Australia and the United States, namely the level of variation in median passage date, the total migration traffic, and concentration of flight direction. We used the complete dataset spanning all available years for the ten Australian radars (Table S2) for median passage date comparison. We used median passage dates spanning 24 years for 143 radars from the United States.³³ In the United States phenological data, seasons were defined as 1 March to 15 June for spring and 1 August to 15 November for autumn. To facilitate comparison, we defined spring as 1 Aug to 15 Nov in Australia and autumn as 1 Feb to 15 May, adjusting to the main window of migration in Australia while maintaining the same temporal durations. We subsequently calculated the standard deviation in median passage dates of each radar from the two countries.

We further compared the level of variation in the migration traffic between years, using the Coefficient of Variation (CV; standard deviation divided by the mean) of seasonally summed migration traffic. For Australian radars, we calculated the CV using five years of data (2018 to 2022). For U.S. radars, we calculated the CV using data from the same 143 radars from 2017 to 2021 (as data from 2022 was not processed yet at the time of analysis), following the methodology described in Dokter et al. ¹³ We compared the level of concentration in flight direction by calculating the length of the mean direction vector weighted by reflectivity (r, r = 0 means uniform distribution and r = 1 means all directions are same), using the same years of data as the CV comparison. To account for the significant difference in the number of Australian and U.S. radars, we conducted an additional comparison of the same metrics using t-test between Australian radars and a subset of 10 U.S. east coast radars (east of 90 °W) that have distances to the coast closest to the Australian average (20.1km, U.S. subset:19.3km, latitude span: 25.6° - 43.8°N).