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Red-necked avocets disperse at continental scales and breed following high rainfall in distant locations

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Nomadic species present conservation challenges due to their dynamic use of habitats at broad spatial scales. We carried out the first tracking of Red-necked Avocets (*Recurvirostra novaehollandiae*), a nomadic waterbird, to document their movements as they dispersed from the Coorong (a coastal refuge that regularly supports > 5% of the global population) to core breeding areas in central Australia. Dispersal from the Coorong to wetlands in the Lake Eyre Basin was most likely soon after high seven-day rainfall in that basin (departure odds diminished 5.24% per additional day post-rainfall event), whereas dispersal to wetlands in the Murray-Darling Basin was not significantly associated with any local or distant rainfall patterns. Tracking revealed ten nesting attempts (from six individuals) spread across three Australian states. Only four attempts showed evidence of hatching. The three individuals tracked for > 1 year all returned to the Coorong, suggesting high site fidelity to this wetland. Consequently, long-term Coorong census data is likely to be a genuine index of Red-necked Avocet population abundance rather than reflecting flux of birds visiting only once. This work supports the conservation of a connected habitat network for this nomadic species, as site-based conservation measures are less effective if broader landscape context is ignored.

Waterbirds occupy highly dynamic environments, with wetland availability and condition influenced by rainfall and groundwater patterns at local and catchment scales[1–3]. In response to the dynamism of their habitat, waterbirds have evolved some remarkable movement strategies, with some species amongst the most mobile animals on Earth[4]. Well-known examples are the annual migrations of waterbirds targeting reliable seasonal changes in habitat condition at global scales[4]. By contrast, waterbirds that occupy less predictable environments tend to use a nomadic movement strategy[3,5,6]. Nomadic waterbird movements are often opportunistic and can involve long distance flights between multiple wetland habitats in response to resource conditions[5–8], even within a single season[9]. For these species, movements may be driven by the availability of suitable habitat elsewhere, a decline in local habitat quality, or both[10–12]. It is unclear what environmental cues, and what scales, drive these nomadic movements, although heavy local rainfall has been shown to trigger long distance night time flights in Pacific Black Duck (*Anas superciliosa*)[6]. In some nomadic species, there is clearly a highly directional response upon departure, whereas for other cases there can be a more exploratory pattern[6,8,13].

Expansive movements make managing and monitoring waterbird populations challenging, and this is especially so for nomadic species[14,15]. For example, waterbirds' dependence on a network of wetlands means that management carried out at one location may be ineffective if population size is limited by the conditions experienced at other locations in the wetland network[16]. Similarly, monitoring at a site may indicate that habitat quality is high, but if the birds are occupying another part of their range at the time, they are unable to capitalise on the favourable habitat conditions[10,17]. Therefore, it is vital to understand patterns of wetland use tocorrectly interpret how monitoring is likely to reflect population-wide demography[14].

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Much of our understanding of waterbird population status is derived from count data[18–20]. For sedentary species the interpretation of count data can be relatively straightforward[21]. However, for mobile species, particularly those with unpredictable movement strategies, deciphering population trends from local count data, in the absence of information at broader scales, can be challenging or even lead to incorrect conclusions[22,23]. For example, if individuals are moving across the landscape, they may be counted at multiple sampling sites leading to artificially inflated population estimates[24]. Similarly, counts at a single location may indicate population decline, but emigration may mean that some individuals are missed during the population census leading to underestimation of the true population size[25].

Australia is a vast continent characterised by an arid and dynamic interior and more mesic and relatively stable coastal regions. Wetlands in central Australia are typically ephemeral, remaining dry for years at a time before being filled when sporadic rainfall events deluge over inland areas. The movements of many Australian waterbirds are strongly influenced by prevailing cycles of wet and dry across the continent[15,17]. Individuals move inland during wet periods before contracting their range back towards the coast when conditions are dry[12,26,27]. Inland movements can also be accompanied by mass breeding events, which may be important for maintaining population size, especially for species that rarely breed in coastal parts of their range[5,7,17]. Maintaining a network of wetlands between the coast and inland breeding sites should therefore be an important component of management to support these species.

The Coorong, a Ramsar-listed coastal wetland in southern Australia, is a waterbird drought refuge. It can support upwards of 90% of the waterbirds in the Murray-Darling Basin during drought[28]. It provides habitat for species including Grey Teal (*Anas gracilis*), Banded Stilt (*Cladorhynchus leucocephalus*), and Red-necked Avocet (*Recurvirostra novaehollandiae*) that have nomadic movement ecology and key breeding sites scattered across inland Australia[3,7,9]. The size of the Coorong population of Red-necked Avocets regularly exceeds 5% of the global population[29]. However, the number of Red-necked Avocets using the Coorong fluctuates widely (e.g., from 163 to 6,030 individuals during January counts between 2000 and 2007[30]. This variability poses challenges for interpreting trends. It is unclear whether individuals return to the Coorong following nomadic movements out of the wetland (i.e., display site fidelity) or whether variation is driven by individuals that visit the wetland only once. The latter would limit the applicability of Coorong time series data for monitoring global population trends.

To better understand the movement patterns of Red-necked Avocets from the Coorong, we tracked 16 individuals using GPS devices. We analysed patterns of site use along nomadic dispersal routes and identified nesting attempts to demarcate areas that support population maintenance. We also assessed site fidelity to the Coorong. Our study provides much-needed information on long-distance dispersal of a nomadic waterbird on a continent where such movement patterns are relatively unstudied despite many waterbird species exhibiting nomadic movement ecology. This work also yields new insights into wetland use and breeding ecology in remote areas that are relatively inaccessible to ecologists[31].

Methods

Capture and tracking device deployment

Red-necked Avocets (n = 19) were captured in the Coorong (Fig. 1) at night with a hand net by using a bright spotlight to temporarily dazzle individuals and facilitate a close approach[32]. Captured birds were aged and sexed using plumage characteristics (e.g. number of white-tipped inner primary feathers and extent of white around the base of the bill) and bill morphology[29,33]. Only adult individuals were fitted with a tracking device. GPS tracking devices were fitted to 16 Red-necked Avocets (n = 11 Ornitela UAB, Vilnius Lithuania; n = 5 Cellular Tracking Technologies, New Jersey USA) using a Teflon leg-loop harness[34]. The tracking devices and attachment weighed < 15 g, representing a mean of 3.99% (range: 3.23–4.74%) of the birds' body mass. These solar powered devices transmitted data via the 3G and 4G telecommunications network and were programmed to record a GPS location every 15 min (Ornitela devices) or 2 h (Cellular Tracking Technologies devices). These differences in programming were due to different battery performance of the two device types. Capture and tracking were carried out under University of Adelaide Animal Ethics Committee (approval number 34788) and Department for Environment and Water Scientific Research (Y27036-1 and Y27036-2) permits, and all experiments were performed in accordance with relevant guidelines and regulations. We report our study in accordance with ARRIVE guidelines.

Data Preparation

We checked for erroneous locations using the McConnell et al.[35] speed filter using the 'vmask' function of the R package *argosfilter*[36] with a speed threshold of 105 km.h^{-1}. This value was chosen based on a Cleveland dot plot of the speed of movement between successive tracking points, which indicated that movement speeds of up to our chosen threshold frequently occurred in the dataset (Figure S1).

Departures in relation to rainfall

Australian Gridded Climate Data[37]were used to identify periods of anomalously high rainfall in drainage basins. Daily total precipitation values at 0.05° resolution were summed within the boundaries of each drainage basin[38]to generate a time series of basin-specific daily rainfall. We also computed a rolling seven-day total of rainfall in each drainage basin to consider whether Red-necked Avocets were responding to rainfall events that lasted several days. We selected these two accumulation periods because the former represents the finest grained temporal resolution in the available dataset, and the latter represents an easily intuitable period consistent with that used in other meteorological research in Australia[e.g.,39]. Given the relatively small sample size of individuals in our study, our aim was not to identify an exact accumulation window that results in the strongest relationship for our relatively small sample size because this may be overly prescriptive and not generalise to the entire

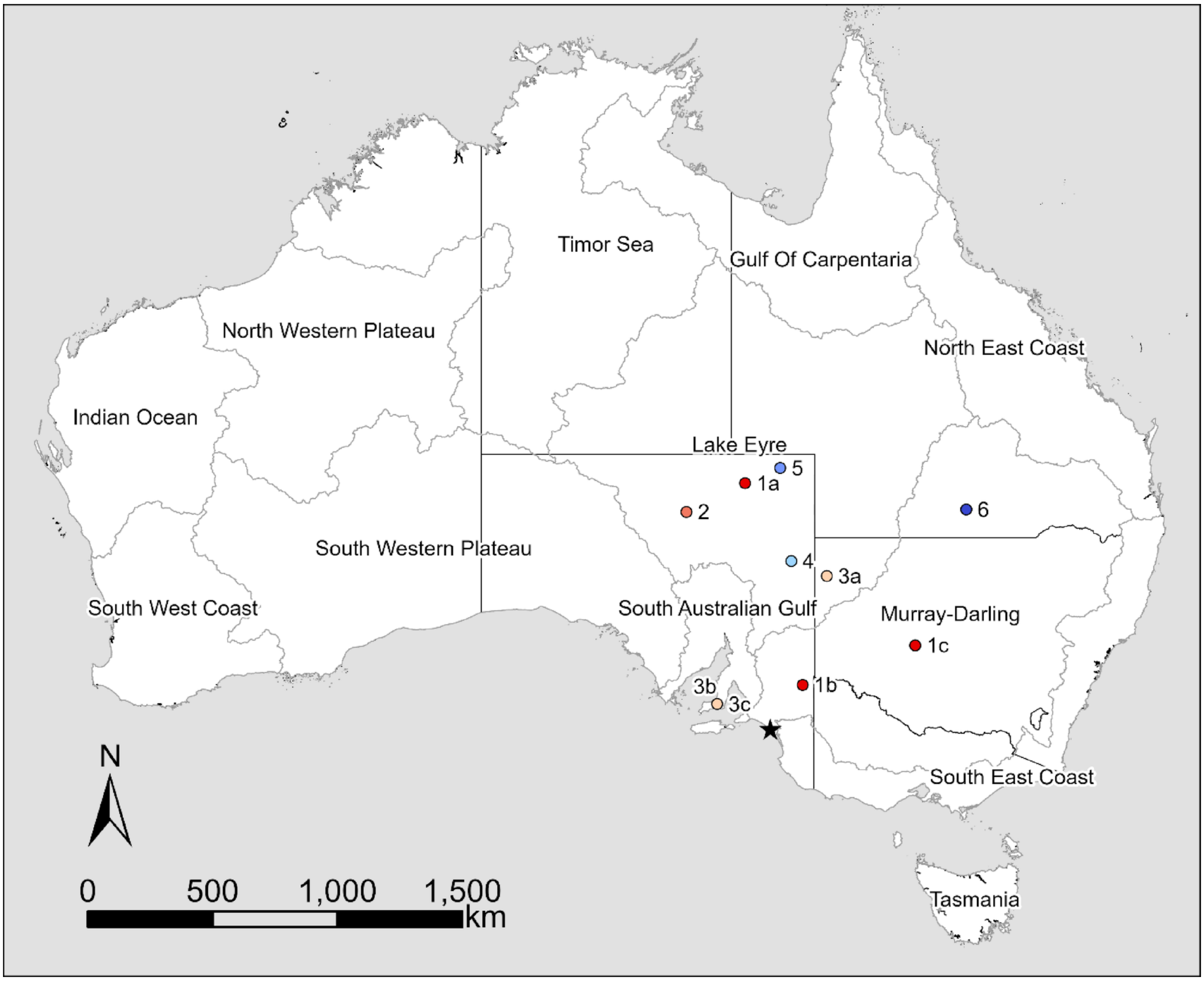

Fig. 1. Location of the Coorong (black star) in relation to major drainage basins (grey lines and text labels) and state borders (black lines). Red-necked Avocet nesting sites identified from the tracking data are shown by coloured circles. Each circle represents the location of an individual nesting attempt, with the colour of the circle denoting a unique individual (i.e., circles with the same colour indicate repeated nesting attempts by the same individual). Nesting attempts are also labelled with an alphanumeric code (the number represents individual and each letter a distinct breeding attempt by that individual) to discriminate cases where two nests occur in very close proximity. Grey shading indicates ocean. This map was created using ArcGIS Pro 3.0.3 (https://www.esri.com/en-us/arcgis/products/arcgis-pro).

population. Although it is possible that stronger responses may be observed for other rainfall accumulation periods, the nested nature of increasingly larger and larger accumulation periods means that cumulative rainfall will be highly correlated across a range of accumulation window sizes. We therefore consider single-day and seven-day cumulative rainfall totals to be a useful indicator for the effects of short-term and longer-term rainfall patterns on Red-necked Avocet departures. In addition to these distant rainfall patterns, we also calculated daily and seven-day rainfall in the local Coorong region (within 10 km of the wetland). These basin and local daily and seven-day time series were then used to identify respective periods of anomalously high rainfall, which we defined as being 1.5 times the interquartile range greater than the 75 th percentile of the rainfall data for each basin or the local Coorong region[40]. The number of days between the beginning of a period of anomalously high rainfall and the time of each Red-necked Avocet departure from the Coorong was calculated to infer whether individuals were responding to rainfall events in a particular basin as well as local rainfall patterns.

We ran generalised linear models to investigate the relationship between Red-necked Avocet departures from the Coorong and rainfall events. The input data for these models consisted of rainfall parameters associated with true departures and a random sample of 1000 pseudo-departure dates for each true departure. The random sample of pseudo-departure dates for each true departure was drawn from the dates that the corresponding tracking device was active. Prior to modelling, predictor variables were screened to ensure there were no unacceptable levels of correlation (|Pearson r| > 0.7[41]). Generalised linear models were fitted with the *stats* package[42] with a binomial error distribution and were of the form:

$$Departure \sim Basin_{Daily} + Basin_{Seven} + Local_{Daily} + Local_{Seven} + 1.$$

Where *Departure* is binary indicating whether a departure occurs, $Basin_{Daily}$ is the number of days after an anomalously high single-day rainfall event in a particular drainage basin, $Basin_{Seven}$ is the number of days since the beginning of a seven-day period of anomalously high rainfall in a particular drainage basin, $Local_{Daily}$ is the number of days after an anomalously high single-day rainfall event locally in the Coorong, $Local_{Seven}$ is the number of days since the beginning of a seven-day period of anomalously high rainfall locally in the Coorong. A separate model was constructed for each drainage basin, with departures and their corresponding pseudo-departures included in each basin-specific model only if the Red-necked Avocet used that drainage basin in the 30-day period following that departure. Parameter significance values from this saturated model were used to identify simpler model structures that may explain relationships more parsimoniously than the full model. The performance of the reduced model was then compared to the saturated model and a null model containing only an intercept term using Akaike's Information Criterion corrected for small sample sizes (AICc) using the package *MuMIn*[43]. Smaller AICc values were considered indicative of better model performance, with AICc values differing by > 2 indicative of strong support for one model having better performance than alternative models. Partial response plots were then generated to visualise the influence of explanatory variables on probability of departure.

Detecting periods of wetland use

To distinguish periods of wetland use from periods of flight, we generated a Cleveland dot plot of the speed of movement between successive tracking points. This enabled us to visually identify a point of inflexion consistent with a switch between wetland use and flight (Figure S2). This inflexion occurred at a speed of 2 km.h^{-1}. Red-necked Avocets were deemed to be using wetlands if their speed of movement remained below this threshold for at least 1 h.

Wetland importance

Preliminary work[44]using Digital Earth Australia's Waterbodies dataset[45] identified that many locations consistent with wetland use occurred outside of mapped wetlands. This was the case even when locations up to 50 m away from a mapped wetland were considered to be within that wetland. The Digital Earth Australia dataset represents Landsat pixels classified as having standing water present > 5% of the time (see Krause et al.[46] for a complete description of this dataset). Hence, this preliminary work demonstrated that Red-necked Avocets were using ephemeral wetlands that rarely held water. Therefore, to avoid overlooking the importance of these sites in the present analysis we used a grid-based approach across the entire range used by tracked individuals. We divided the entire area used by tracked Red-necked Avocets into 5 × 5 km grid cells. The number of individual Red-necked Avocets using each grid cell, as well as the cumulative number of use days, were used as indicators of the importance of that location. Cumulative use days were calculated by summing the number of days a grid cell was used across all individuals. For example, if one individual used the grid cell for two days and another individual used the grid cell for one day, that grid cell had three cumulative use days. We ran these analyses separately on data for wetland use only, and periods of flight and wetland use.

Similarly, whether an individual returned to a grid cell that it had previously used was also used to indicate wetland importance. For a return to a cell previously used to be considered a re-visit, a period of ≥ 30 days must have elapsed between departure and return (i.e., if the cell was used twice within a one-month window, that was considered the same period of use and not a revisit).

Detection of nesting attempts

To detect periods of nesting by tracked individuals, we used the *nestR* package[47]. The 'find_nests' function uses patterns of revisits to a location to detect nesting behaviour. Nesting Red-necked Avocets share incubation duties[29], and incubation changeovers for congeneric species occur frequently (e.g., mean < 1 hour [48]; mean < 1.5 hours Hamilton 1975). Therefore, identifying nesting attempts based on frequent site revisits should be reliable regardless of the sex of the tracked bird. The incubation period of Red-necked Avocets is ~ 25 days from the time the first egg is laid[29]. Chicks are precocious and leave the nest shortly after hatching[29]. Consequently, we used central place movements lasting > 23 days to infer a successful nesting attempt (i.e., an attempt where eggs were successfully reared to hatching). Behaviours with similar movement characteristics (e.g., returning to a favoured roosting site) were ruled out by specifying a small return radius (20 m) and requiring the individual to visit the 20 m radius on at least five consecutive days and spend > 40% of a single 24-hour period at the site at least once. To enable computation within computer memory limits, tracking data were split into four periods per year and each period was analysed separately. To avoid missing nesting attempts that spanned the boundary of one of these artificial periods, this analysis was repeated with each split in the tracking dataset brought forward by 45 days. Duplicated nesting attempts identified in each of these runs were subsequently removed.

Results

Tracking data were obtained from 12 individual Red-necked Avocets (ten Ornitela devices and two Cellular Tracking Technologies devices). Of the four tracking devices that did not return useable data, three devices failed to transmit any data and one device returned stationary location data within hours of deployment. Neither the device or the bird could be found despite searching, suggesting device detachment.

The dataset included a total of 147,434 locations, with the number of locations per individual ranging from 58 to 44,220 (Table 1). During the tracking period, individuals travelled up to 20,454 km, venturing up to 1,310 km from the point of capture in the Coorong (Table 1). All but one individual left the Coorong for at least some of the time that it was tracked (Table 1). Individuals that spent a high proportion (> 0.9) of the tracking period in the Coorong were tracked for only a short duration (≤ 64 d; Table 1) before data transmission ceased (e.g., device failure).

ID	Sex	Capture date	*n* points	Last date	Duration (d)	Travel dist. (km)	Max dist. (km)	Prop. In Coorong
1	M	7/12/2021	43,036	21/06/2023	561	20454.0	1238.3	0.25
2	M	24/01/2022	8229	20/04/2022	86	3775.6	1018.6	0.02
3	M	27/01/2022	38,980	8/04/2023	436	18410.5	916.9	0.05
4	M	24/01/2022	6998	7/04/2022	73	1816.1	909.7	0.03
5	F	7/12/2021	27,445	5/10/2022	302	13479.6	1309.5	0.43
6	F	26/01/2022	44,220	5/05/2023	464	15910.6	1199.2	0.00
7	M	2/12/2021	5555	28/01/2022	57	1557.0	458.1	0.93
8	F	25/01/2022	382	29/01/2022	4	332.4	241.4	0.98
9	M	26/11/2021	6208	29/01/2022	64	2279.2	590.3	0.95
10	F	26/01/2022	8825	28/04/2022	92	4212.9	1004.4	0.10
11	F	14/04/2021	58	19/04/2021	5	70.0	34.3	1.00
12	M	13/04/2021	530	31/05/2021	48	2277.7	176.7	0.95

Table 1. Summary of the tracking dataset for each Red-necked Avocet. Columns indicate the individually assigned study identifier (ID) and characteristics including most recent date of data acquisition (Last date), the number of days over which tracking data were collected (Duration), the minimum curvilinear distance travelled by each individual over the tracking period (Travel dist.), the maximum straight line distance that the individual reached from the point of capture in the Coorong (Max dist.) and the proportion of all tracking data that were obtained while the individual was within the Coorong (Prop. In Coorong). ID codes correspond to the numeric component of the alphanumeric codes given in Figs. 1 and 4 and Table 4 relating to nest attempts.

Basin	Model	df	AICc	ΔAICc
Lake Eyre	Departure ~ $Basin_{Seven}$ + 1	2	121.40	0.00
	Departure ~ $Basin_{Daily}$ + $Basin_{Seven}$ + $Local_{Daily}$ + $Local_{Seven}$ + 1	5	127.05	5.65
	Departure ~ 1	1	128.53	7.13
Murray-Darling	Departure ~ 1	1	128.53	0.00
	Departure ~ $Basin_{Daily}$ + $Basin_{Seven}$ + $Local_{Daily}$ + $Local_{Seven}$ + 1	5	132.00	3.46

Table 2. Comparison of AICc values of different models constructed to identify important rainfall parameters related to Red-necked Avocet departures from the Coorong.

Thirteen discrete departures from the Coorong were observed (Table S1; Figure S3 and S4). For six departures, wetland use occurred in two drainage basins in the 30 days after the departure. Eight departures were followed by wetland use in the Lake Eyre Basin, and eight departures were followed by wetland use in the Murray-Darling Basin (Table S1). Departures to wetlands in the South Australian Gulf and South East Coast Basins were recorded only once each (hence these two basins were not included in modelling) (Table S1). Seven-day rainfall patterns in the Lake Eyre Basin had a significant effect on departure probability to the Lake Eyre Basin (Tables 2 and 3). Single-day rainfall in that basin and single-day and seven-day rainfall in the local Coorong region did not affect departure probability significantly and were omitted from the final model based on AICc (Table 2 and S1). For Red-necked Avocets that departed for the Lake Eyre Basin, the odds of a departure occurring were greatest soon after anomalously high seven-day rainfall in that basin (Fig. 2; Table 3). Exponentiating the beta coefficients from the generalised linear model indicated that with every additional day after anomalously high seven-day rainfall in the Lake Eyre Basin the odds of a Red-necked Avocet departure occurring diminished by 5.24% (Fig. 2; Table 3). No rainfall parameters were found to have a significant effect on departure probability for Red-necked Avocets that departed for the Murray-Darling Basin (Table 2 and S1).

The vast majority of grid cells where wetland use occurred were used by only a single tracked Red-necked Avocet (93% of 369 cells). Only seven grid cells were used by three or more individuals (Fig. 3A, Figure S5, Table A1). Six of these were associated with use of the Coorong South Lagoon (Fig. 3A, Figure S5, Table A1). The remaining grid cell was associated with wetland use at Berri Basin Wetland (−34.2963, 140.5655) within the Murray-Darling Basin in the South Australian Riverland (Fig. 3A, Figure S5, Table S2).

Twenty-four grid cells had cumulative use values ≥ 30 days when considering only periods of wetland use (Fig. 3B, Table S3). Nine of these were in the Coorong South Lagoon, with a further two cells immediately south of the southern end of the Coorong South Lagoon (one in the South-East Coast Drainage Basin) (Fig. 3B). Elsewhere in the Murray-Darling Basin, high cumulative use cells included sites connected to major rivers such as the Murray River (Berri Basin Wetland, and wetlands between Chowilla Island and Lake Merreti) and the Darling River (Well Lake on the floodplain between Menindee and Wilcannia), as well as on the extremities of the floodplain of the Warrego River (Fig. 3B). In the Lake Eyre Basin, five cells had cumulative use values ≥ 30 days (e.g., Lake Callabonna, Big Salt Lake, and ephemeral wetlands immediately west of Kati Thanda/Lake Eyre) (Fig. 3B, Table S3). The only other Drainage basin where cumulative wetland use values ≥ 30 days occurred was

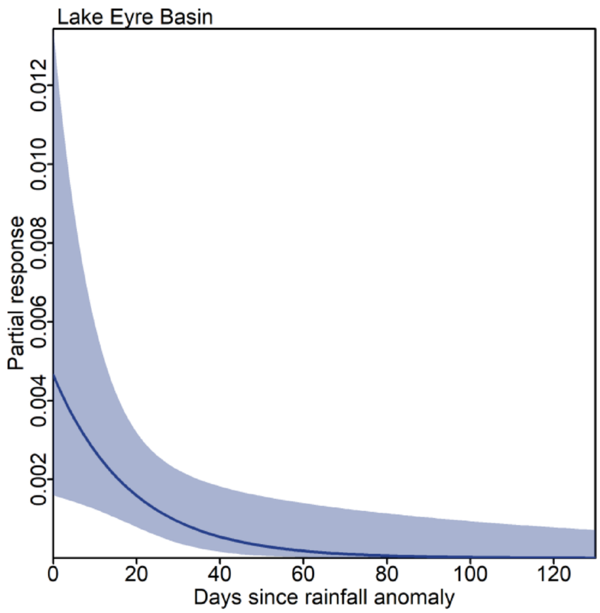

Fig. 2. Partial response plots of the predicted probability of a Red-necked Avocet departure to wetlands in the Lake Eyre Basin occurring as a function of the number of days since anomalously high seven-day rainfall in the Lake Eyre Basin. The shaded area indicates the 95% confidence interval of the prediction. The y-axis is plotted on the probability scale (i.e., the plogis of the prediction from the logit scale beta coefficients). Note: the absolute values of the y-axis should not be interpreted as true probabilities because the curve will be shifted along the y-axis depending on the ratio of pseudo-departures to true departures in the modelled dataset.

Parameter	Coefficient	s.e.	z	*p*-value
Intercept	−5.368	*0.547*	*−9.818*	*< 0.001*
$Basin_{Seven}$	−0.054	*0.023*	*−2.327*	*0.02*

Table 3. Generalised linear model output for the best performing model for Red-necked Avocet departures to the lake Eyre basin.

the South Australian Gulf Basin, with wetlands on the Yorke Peninsula (surrounding Warooka and Honiton) used for > 30 days (Fig. 3B).

When these analyses were run to include periods of flight as well as wetland use, the same general patterns were observed (Fig. 3C and D). They revealed a tendency for individuals to use flight corridors along the Murray and Darling River corridors, before veering north-west and entering the Lake Eyre Drainage Basin (Fig. 3C and D).

Grid cells in the Coorong South Lagoon were revisited by three individual Red-necked Avocets (Fig. 3F). Similarly, one Red-necked Avocet made three visits to grid cells associated with Berri Basin Wetland in the South Australian Riverland (Fig. 3E). There was also a cluster of cells in the east of the Lake Eyre Drainage Basin that were re-visited multiple times, and two individuals also made re-visits to a grid cell associated with Yantara Lake in this drainage basin (Fig. 3E and F).

Movements consistent with nesting were detected for six individual Red-necked Avocets. These events occurred across three states (South Australia, New South Wales, and Queensland) and three basins (the Lake Eyre Basin, Murray-Darling Basin, and South Australian Gulf Basin) (Figs. 1 and 4). Two individuals appeared to make three nesting attempts during the tracking period, with each of the remaining birds making only a single nesting attempt while tracking data were being collected (Fig. 1; Table 4). Only four of the ten nesting attempts involved central place movements lasting the known incubation period of ~ 25 days (Table 4). One of the re-nesting attempts (for individual 3) occurred just nine days after the previous nesting period had finished, suggesting that the chick from the first of these two nesting attempts did not survive to fledging age.

Discussion

We documented long-distance dispersal of Red-necked Avocets soon after anomalously high rainfall over seven-day periods in the Lake Eyre Basin. Conversely, the influence of rainfall in the Murray-Darling Basin was not evident in our dataset. It is possible that these two types of dispersal were associated with different dispersal stimuli. A range of stimuli operating at various spatial and temporal scales have been proposed as triggers for waterbird dispersal[6,8,50]. Substantial rainfall over multiple days in the core breeding range in central Australia

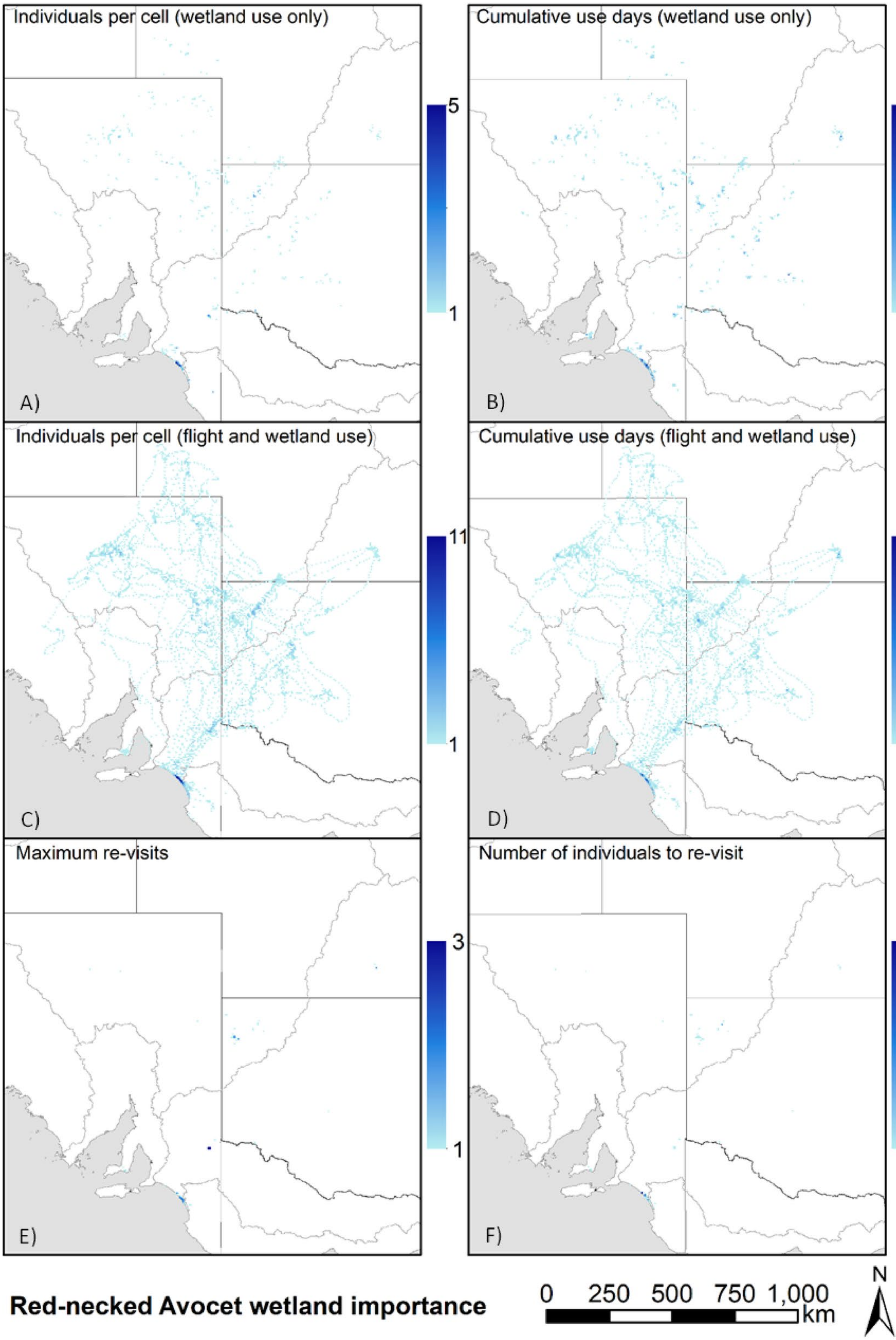

Fig. 3. Patterns of grid cell use by tracked Red-necked Avocets. The number of individuals per grid cell where wetland use (**A**) and flight and wetland use (**C**) occurred, with darker blues indicating use by a greater number of tracked individuals. The cumulative use days values of each grid cell for wetland use (**B**) and flight and wetland use (**D**) are also shown. The bottom left panel (**E**) depicts the maximum number of times a grid cell was re-visited by an individual across all individuals. The bottom right panel (**F**) depicts the number of individuals that made a re-visit to a grid cell. Grey lines indicate the boundaries of major drainage basins. Black lines indicate state boundaries. Grey shading indicates ocean. This map was created using ArcGIS Pro 3.0.3 (https://www.esri.com/en-us/arcgis/products/arcgis-pro).

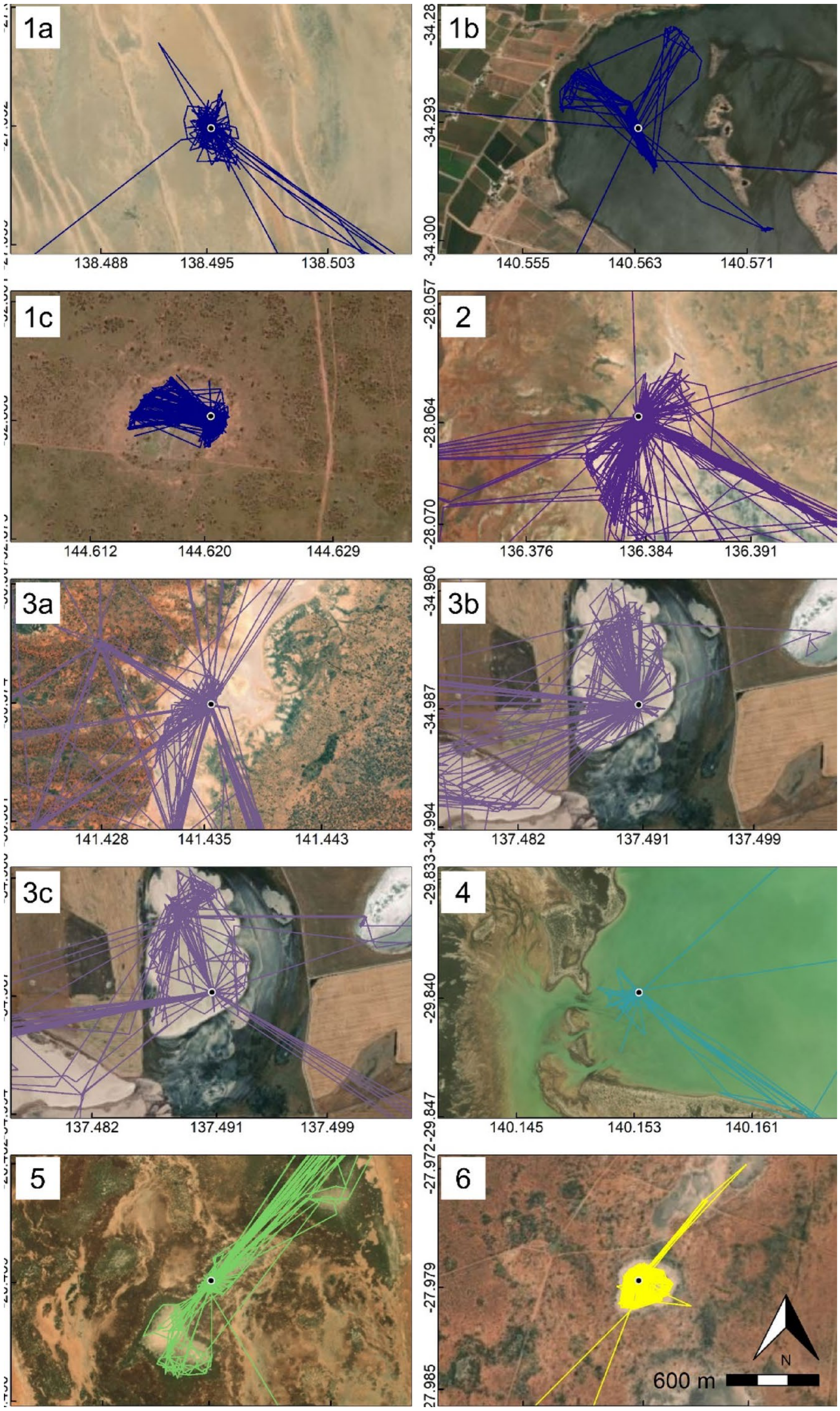

Fig. 4. Tracking data relating to periods of purported nesting activity of Red-necked Avocets. The location of the nest in each case is indicated by the black circle. Each panel displays the data for a single period of nesting activity (i.e., repeated nesting attempts by the same individual are displayed in separate panels). Tracking lines with the same colour represent data for the same individual (six individuals had movements consistent with nesting activity). Alphanumeric codes in the top left of panels (the number represents individual and each letter a distinct breeding attempt by that individual) are the same as those displayed in Fig. 1. The same scale is used for all panels. This figure was created in R 4.2.2 (https://www.R-project.org/).

(and the Lake Eyre Basin specifically) appears to be strongly related to their movement to those locations, whereas other stimuli that we did not investigate may be associated with dispersal to wetlands in the Murray-Darling Basin. Our research suggests that dispersal stimuli used by Red-necked Avocets are complex. Further investigation of the role of stimuli that manifest after several days of rain in distant wetlands (e.g., olfactory

Nest ID	Longitude	Latitude	Start date	Attempt duration	Maximum attendance
1a	138.4953	−27.0321	2/02/2022	9	79.17
1b	140.5632	−34.2934	5/06/2022	7	42.71
1c	144.6205	−32.8678	28/10/2022	24	84.38
2	136.3835	−28.0636	7/02/2022	24	76.04
3a	141.4355	−30.3741	3/03/2022	17	67.71
3b	137.4907	−34.9867	13/07/2022	24	51.58
3c	137.4907	−34.9868	15/08/2022	16	47.42
4	140.1533	−29.8397	30/03/2022	8	76.04
5	139.7621	−26.4889	14/02/2022	10	70.83
6	146.4507	−27.9786	30/10/2022	24	72.92

Table 4. Summary of nesting attempt attributes for the ten likely nesting events that occurred during the tracking period. Columns are as follows: nest id = the identity of the individual Red-necked Avocet (numeric value) and any renesting attempts by that individual (letter following numeric value) which corresponds to the alphanumeric codes given in Figs. 1 and 2; longitude and latitude = the coordinates of the presumed nest; start date = the date of the start of movements consistent with nesting activity; attempt duration indicates the number of days for which movement was consistent with central place foraging; and maximum attendance = the maximum value for the percentage of locations recorded at the nest site on a given day.

cues associated with wetland rehydration[13,50] is warranted to more fully understand the triggers for Red-necked Avocet long-distance dispersal.

The Red-necked Avocets that dispersed from the Coorong in January and early February 2022 all departed northward. Their movements coincided with heavy rains across large parts of central Australia that resulted in widespread flooding (Figure S7). The departure of the tracked birds coincided with a rapid decline in the number of Red-necked Avocets present in the Coorong after this rain event[51]. Therefore, it seems likely that the majority of the Coorong population of Red-necked Avocets departed to capitalise on favourable conditions brought about by widespread inland rainfall. Analysis of long-term observation data from south-east Australia more broadly indicates mass emigration of Red-necked Avocets occurs when there is high water availability across the Australian continent[26,27]. Consequently, the movements our tracking data document are not an isolated occurrence. Hence, our data provide an insight into key sites for these mobile waterbirds when commuting between one of their most reliable population strongholds, the Coorong, and key breeding sites in central Australia. Rainfall in the study region is generally projected to decrease as a result of climate change[52]. Hence, these typical movement patterns may be disrupted in the future.

The unique hydrological regime of the Coorong enables it to function as a major drought refuge for Red-necked Avocets and other Australian waterbirds[28]. However, Red-necked Avocets rarely breed in the Coorong[53,54]. Therefore, maintaining linkages between the Coorong, where large numbers of Red-necked Avocets may persist when conditions are not conducive to breeding, and core breeding areas in central Australia is an important management action to safeguard this species. The wetlands of central Australia have an important role in the maintenance of many functional groups of waterbirds[17]. Pedler et al. (2014) tracked Banded Stilts that moved between the Coorong and central Australia. Those movements followed a coastal route to the top of the Spencer Gulf before moving north into the Eyre Basin[5]. By contrast, the Red-necked Avocets tracked in our study used a movement corridor that followed the Murray and Darling Rivers followed by north-westerly movement to similar areas used by the Banded Stilts in Pedler et al.'s (2014) study. These contrasting movement strategies suggest management of a wetland network for one of these species will not provide the same degree of benefit for the other species despite them being in the same family and having somewhat similar ecologies.

The route used by Red-necked Avocets along the Murray and Darling Rivers included use of the Berri Basin Wetland in the South Australian Riverland by multiple birds. This wetland was also re-visited three times by one individual. Such high visitation among our small sample of tracked birds suggests that this wetland may play a crucial stepping-stone role in enabling Red-necked Avocets to move between the Coorong and central Australia. Degradation of key staging areas has been implicated in the dramatic population declines of long-distance migratory shorebirds[55,56]. This effect is particularly evident in species that use fewer sites along the migratory path[57]. If Berri Basin Wetland is one of the few available stopping sites for Red-necked Avocets at this point in their movement corridor, then the condition of this wetland should be monitored to ensure it provides habitat for Red-necked Avocets to enable the completion of movements between coastal and inland regions. Management actions may include maintaining appropriate water levels[31,58]and salinity[58], ensuring sufficient feeding habitat in the surrounding region[59], and maintaining consistent landcover surrounding the wetland[60].

The three Red-necked Avocets with the longest tracking time series returned to the Coorong after venturing to central Australia. One of these individuals returned to the Coorong on two occasions. This has important implications for interpreting long-term census data for this species. High site fidelity suggests that population census data collected at the Coorong is likely to sample the same individuals over time. Therefore, any population trend derived from long-term monitoring data at the Coorong is likely to reflect a genuine signal of change in abundance for the Coorong population rather than characterising a flux of individuals that may be using the Coorong for only a single occasion in their life. However, high rates of movement into and out of the Coorong mean that change from year-to-year may not reflect true population change[22]. Consequently, this species will require a longer time series of census data to detect robust population trends than species whose census data are subject to less dispersal-induced variability. This may be a contributing factor to recent work that found no significant population trend for the Coorong Red-necked Avocet population across nine sampling years, but a multidecadal analysis of data pooled at the national scale indicated a significant decline has occurred[61]. Likewise, population trends are likely to be more accurate if comparisons are made only between years with similar rainfall conditions across central Australia.

We detected nesting attempts of Red Necked Avocets at sites spread widely across the continent. Breeding information for Red-necked Avocets is scant due to the remote location of the core breeding areas[29]. Although the species does regularly breed in colonies, which can make detecting breeding events easier, the remoteness of central Australia means that most breeding attempts are never observed, making our documentation of nesting attempt sites from tracking data particularly valuable. Comparing the nesting locations we report with breeding data contained in The Atlas of Australian Birds[62]and the eBird dataset[63], seven (70%) of the breeding locations we report occur in areas (grid cells spanning 1° of longitude and 1° of latitude) where breeding has not previously been reported (Figure S6). Conversely, some breeding locations we report reinforce the importance of some wetlands already known for their importance to other Australian waterbirds. Pedler et al. (2017) used aerial surveys to locate breeding attempts for Banded Stilts in the Lake Eyre Basin. They found Banded Stilts breeding at Lake Callabonna, which was one of the locations at which nesting by a Red-necked Avocet was detected in the present study. This site is known to have supported breeding by Banded Stilts multiple times in the early 1900s[9]. The repeated use of this site for breeding by recurvirostrids indicates its value in the national wetland network.

Our movement data for nesting Red-necked Avocets suggested that only 40% of nesting attempts resulted in successful hatching. Furthermore, chick mortality is likely for one of the four nests that are believed to have hatched. Altricial birds (those with young that require parental care) have a mean hatching success of 60%[64]. Nesting success of other waterbirds in Australia at the time our tracking study was high (e.g., 63% of eggs resulted in a fledged chick in Straw-necked Ibis (*Threskiornis spinicollis*) in the Macquarie Marshes[65]. Conversely, Pedler et al. (2017) monitored nesting attempts of Banded Stilts in central Australia between 2011 and 2016. They found hatching occurred in only 31% of nesting colonies. Nest predation by Silver Gulls (*Chroicocephalus novaehollandiae*) and drying of the wetlands surrounding the breeding colony were identified as drivers of low reproductive success. Together with our observations, this suggests that low reproductive success may be an important limitation on the rate of population increase of recurvirostrids in Australia. In other recurvirostrid species around the world, hatching success ≥ *c.* 60% is common[66,67], except where nest predation by gulls is implicated in reducing nest success[68]. Reducing Silver Gull abundance during Banded Stilt breeding events has been a successful management strategy to increase breeding success for that species[69], and could also be an important strategy for Red-necked Avocets.

Long-term monitoring is particularly important for nomadic species because their movements are likely to vary from year to year[70]. Our tracking data included two summer periods for four individuals. Summer is the time of year when count data indicate movements of Red-necked Avocets from central Australia to coastal locations frequently occur[26,27]. Therefore, our dataset was able to capture inter-annual variation for a limited number of individuals. However, it would be beneficial to conduct further tracking of this species to confirm whether the movement corridors and sites identified as important by our work are maintained under a range of rainfall regimes because there is some evidence of interannual variation in movement strategies in other species when they were tracked over longer periods[71].

Data availability

Data and analysis code used in this study are available on the Open Science Framework (https://osf.io/sw8en/?view_only=778fc36c958b40e09099517346b65 d8b).

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Author contributions
R.M. wrote the main manuscript text. R.M. and T.P. conducted statistical analysis. R.M., T.P., J.B. and P.C. conceived the study design. R.M., M.J., and S.S.G. carried out the fieldwork. A.B., J.O., D.R. sat on the project steering committee and contributed expertise to project implementation. All authors reviewed the manuscript.

Declarations

Competing interests
The authors declare no competing interests.

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