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To cite this article: Inka Veltheim, Simon Cook, Michael A. McCarthy, Grant C. Palmer & F. A. Richard Hill (2022) Partial migration of Brolgas (*Antigone rubicunda*) within a restricted range is revealed by GPS tracking, *Emu - Austral Ornithology*, 122:1, 39-50, DOI: [10.1080/01584197.2022.2036196](https://doi.org/10.1080/01584197.2022.2036196)

To link to this article: <https://doi.org/10.1080/01584197.2022.2036196>

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## Partial migration of Brolgas (*Antigone rubicunda*) within a restricted range is revealed by GPS tracking

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### ABSTRACT

No quantitative information exists on the movement patterns of Brolga, *Antigone rubicunda* (Gruidae) although the species is considered to undertake seasonal movements between breeding and non-breeding areas, and has been also described as both non-migratory and partly migratory. Information on this species' movement behaviour is required to understand its basic ecology and inform conservation management across its range. Thus, we sought to investigate whether Brolgas in southern Australia undertake seasonal movements, to define routes travelled by individuals, and to clarify the species' migratory status. Here, for the first time for this species, we quantified the distances travelled, timing of movements between breeding and non-breeding areas, and individual-level differences in movement patterns. We deployed GPS transmitters on five adults, six juvenile and 12 unfledged 6–9 week chicks in Victoria, Australia. Individuals were monitored for 71–646 days. These Brolgas showed partial migratory behaviour, with the south-west Victorian population including resident and migrating individuals, moving 6–30 km and 96–111 km between breeding and non-breeding areas respectively and some remaining resident throughout the year. Brolgas moved 1.6 km from roost to foraging areas on average throughout the year, the majority (95%) of these movements were within 5.2 km and overall Brolgas moved shortest distances during the non-breeding season. We discuss the main potential drivers for these movement patterns. These findings may assist local conservation planning and add to our understanding of Australian waterbird movements more broadly.

### ARTICLE HISTORY

Received 22 August 2020  
Accepted 10 December 2021

### KEYWORDS

Movement behaviour;  
waterbird; GPS tracking;  
threatened species; Gruidae

## Introduction

Our knowledge of movement patterns of a range of bird species has been enhanced by advances in animal tracking technology (e.g. Kanai *et al.* 2002; McCulloch *et al.* 2003; Ueta *et al.* 2003; Krapu *et al.* 2011; Battley *et al.* 2012). Migration and seasonal movements of birds have been extensively studied in the northern hemisphere (Johnson *et al.* 2010; Klaassen *et al.* 2010; Köppen *et al.* 2010; Burnham and Newton 2011), where latitudinal patterns of migration are relatively predictable due to distinctive seasonal temperature variation. Much less is known about seasonal movements of Australian species, particularly waterbirds, partly because their movements can be less predictable due to the stochastic nature of the continent's weather patterns and resulting resource availability (Dorfman and Kingsford 2001; Kingsford and Norman 2002; Roshier *et al.* 2008a).

Migratory movements are a response to seasonal changes in quality or abundance of resources within animals' range (Shaw and Couzin 2013). A greater

density of resource patches should favour a resident strategy (Grovenburg *et al.* 2011; Shaw and Couzin 2013), whereas smaller habitat patches and highly seasonal environments should favour a migration strategy (Shaw and Couzin 2013). When both resource patch types are present within a species' range, and where variation in seasonality occurs across the species' distribution, resident and migratory individuals can be present, which is referred to as partial migration (Kaitala *et al.* 1993; Chan 2001; Shaw and Levin 2011).

The ecology and movement patterns of Gruiformes (cranes, rails, crakes and gallinules) are amongst the poorest known of all waterbirds in Australia (Kingsford and Norman 2002; Yarwood *et al.* 2019), in contrast to our understanding of other crane species (family: Gruidae) in Europe, Asia and northern America (e.g. Higuchi *et al.* 2004; Alonso *et al.* 2008; Qian *et al.* 2009; Krapu *et al.* 2011; Ivey *et al.* 2015; Pearse *et al.* 2018). The Brolga (*Antigone rubicunda*, family: Gruidae) is

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 Supplemental data for this article can be accessed at <https://doi.org/10.1080/01584197.2022.2036196>.

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a wetland-dependent crane common in northern Australia (50,000 (Kingsford *et al.* 2012) to 100,000 (Meine and Archibald 1996) individuals), but is threatened with extinction in southern Australia (Bransbury 1991; DuGuesclin 2003) (1,000 individuals (Meine and Archibald 1996)) with no published quantitative research on the species' movement behaviour. The Brolga in Victoria is listed under the *Flora and Fauna Guarantee Act 1988* and has recently been reclassified from vulnerable to endangered due to apparent decline in numbers since the 1980s and due to ongoing threats to its long-term population persistence (DELWP 2021a), particularly from ongoing wetland habitat loss (DuGuesclin 2003).

Brolgas in southern Australia breed in shallow, seasonally inundated, freshwater wetlands between July and November (Arnol *et al.* 1984; Herring 2001) during the austral winter. The drying of these wetlands in the late spring and early summer drives individual movements to non-breeding areas where Brolgas congregate in flocks of up to 200–300 individuals at permanent freshwater and saline water bodies throughout the summer and autumn (December–June) (Arnol *et al.* 1984; White 1987; Marchant and Higgins 1993; Sheldon 2004; SWIFFT 2021).

Brolgas have been described as 'non-migratory' (Meine and Archibald 1996; DuGuesclin 2003), 'partly migratory'; with 'some dispersive movements' (Marchant and Higgins 1993), 'resident' (Arnol *et al.* 1984; Marchant and Higgins 1993) and undertaking 'seasonal movements' (DuGuesclin 2003). These varied definitions reflect limited understanding of individual Brolga movement behaviour and possible drivers for these movements. This lack of fundamental knowledge on Brolga movement patterns limits effective conservation planning, such as land-use management, habitat protection and restoration; processes that need to include information on the species' movement patterns and habitat requirements. Consequently, our study aimed to address knowledge gaps regarding landscape scale movement patterns of Brolgas, in southern Australia. Here, we undertake the first investigation of Brolga movement patterns with the aim of: (1) determining distances, timing and routes between breeding and non-breeding areas; (2) identifying individual differences in movement patterns in an attempt to identify the potential demographic and local landscape patterns related to movement; and consequently (3) resolve the definition of the Brolga's migration status.

## Methods

### Capture sites and movement data

We conducted our study in south-west Victoria, Australia (Figure S1 supplemental material). We captured adult and juvenile (<12 months old) Brolgas at two main non-breeding sites and pre-fledged chicks at 17 breeding sites across the region (Table S1; Figure S1 supplemental material) (Veltheim *et al.* 2015). We captured 32 Brolgas to study their movements and fitted 23 individuals with a Global Positioning System (GPS) platform transmitter terminal (PTTs) and colour bands (five adults, six juveniles and 12 pre-fledged chicks), and 10 with colour bands only (one adult, and nine pre-fledged chicks). One of the chicks fitted with a colour band only was recaptured as a juvenile and fitted with a GPS PTT (Table S1, supplemental material). We deployed backpack (85–90 g) or leg-band mounted (30 g) PTT (Veltheim *et al.* 2015) on adults and juveniles, representing 1.00–1.25% and 0.34–0.67% of their body weight respectively of the individuals captured in this study. Pre-fledged chicks carried leg-band mounted PTTs, which were 0.71–0.91% of their body weight at capture.

We downloaded GPS PTT location data from the Argos satellite system website (<http://www.argos-system.org/>) and decoded them using North Star's software PTT Tracker (Veltheim 2018). We recorded resighting of colour banded individuals with a GPS unit (Garmin eTrex Legend, Olathe, Kansas, USA) (Veltheim 2018). All colour-banded chicks were seen at least once after fledging and we had breeding site dispersal data for six of them (Table S1, supplemental material). One adult and two juveniles with a GPS PTT died before undertaking movements between breeding and non-breeding areas (Veltheim *et al.* 2015); we excluded data for these individuals from the analyses.

We used GPS data of 20 individuals for analysis and visualisation of movements: data of 19 Brolgas from April 2010–August 2012 and one captured opportunistically outside of the main study period with data from October 2012 to March 2013. These data included adults, juveniles and chicks, post-fledging (Table S1, supplemental material). Fledged crane chicks fly to non-breeding sites with their parents (Alonso *et al.* 2008) and their movements can thus be considered as movements of family groups – consisting of breeding adults and their fledged chicks – and have been interpreted as such here, to investigate movement distances between breeding and non-breeding areas.

GPS fix accuracy was between <25 m and 100 m, calculated by Argos. We further filtered our data using the Douglas Argos-filter (DAF) (Douglas *et al.* 2012) to ensure location fix accuracy prior to analysis, after

noticing several implausible location fixes for pre-fledged chicks (Veltheim 2018). Distance between some fixes was further than expected from a flightless chick and often within another chick's home range (Veltheim 2018). The DAF is commonly used for low quality Argos Doppler location data (Douglas *et al.* 2012). It marks suspect locations using a set of algorithms, with user-defined parameter thresholds for maximum distance within a given time, rate of movement and angle of movement (Douglas *et al.* 2012).

The maximum plausible distance moved by Brolgas between fixes was determined from birds with PTTs acquiring 13 fixes a day (IDs 91406\_2, 91409, 91413; Table S1, supplemental material). These data showed that movements of up to 20 km within a 4-hour period were possible. We used the same rate of movement as Krapu *et al.* (2011) for Sandhill Cranes (*Antigone canadensis*) and chose an acute turning angle of 10°, as Brolgas exhibit a high level of angular movements departing from roosts in the morning, often returning to the same roost in the evening (I. Veltheim unpublished data). We thus set the maximum distance between fixes (MAXREDUN, km, see Douglas *et al.* 2012) to 20 km, rate of movement (MINRATE, km/hr, see Douglas *et al.* 2012) to 100 km/hr and angle of movement (RATECOEF, see Douglas *et al.* 2012) to 10°, resulting in DAF identifying locations to be filtered that exceeded these distances and rates and were below 10° for turning angles (Veltheim 2018).

Individual points marked as filtered by the DAF were examined in ArcMap 9.2. Location fixes marked for filtering but upon visual inspection were supported by other, nearby, fixes in the individual's schedule were retained if the habitat, movement distance and latitude and longitude were realistic (similar to the approach used by Krapu *et al.* (2011)). The DAF marked 119 out of a total of 22,753 fixes as filtered (0.005% of all fixes). A further 117 (0.005%) fixes were duplicates or otherwise improbable due to location and habitat – e.g. fixes over the sea or in forested habitat with no nearby wetlands (Veltheim 2018). Of all these DAF marked errors, duplicates, and other errors, 127 location fixes were removed following visual inspection. After removing errors, the total number of GPS fixes acquired during the study (up to 25 August 2012) was 22,626. Once we removed fixes other than 8:00, 12:30, 15:30, and 23:00 for the three PTTs that acquired 13 fixes a day (to be consistent with PTTs collecting four fixes a day), and excluded three birds that died, our final data set consisted of 18,822 fixes; 2,155 for four adults; 2,535 for four juveniles; and 14,132 for 12 birds captured as pre-fledged chicks (Table S1, supplemental material). These tracking data have been submitted to the

Department of Environment, Land, Water and Planning Victorian Biodiversity Atlas (submitted to DELWP in 2017) and are available through the atlas (DELWP 2021b) or NatureKit (DELWP 2021c). We sub-sampled the GPS data for two different analyses, described further in the following sections. Additionally, we used all the data for visualising the tracks (including fixes additional to 8:00, 12:30, 15:30, and 23:00 for the three PTTs that acquired 13 fixes a day).

### **Defining non-breeding and breeding areas of Brolgas**

To understand and calculate movement distances in relation to breeding and non-breeding areas, we defined non-breeding and breeding areas in south-western Victoria in the following way. We collated all Brolga occurrence records from the South West Victorian Brolga flocking database (BFD) (Sheldon 2004), the Victorian Department of Environment, Land, Water and Planning Biodiversity Atlas (VBA) and the BirdLife Australia atlas (Blakers *et al.* 1984; Barrett *et al.* 2003) up to 2009. We used records from December to May for all years to represent non-breeding records as per Sheldon (2004). Records prior to 1950 and duplicates were omitted. To be consistent with Sheldon's (2004) definition for flocking (non-breeding) sites, we also omitted records with counts of less than 10 individuals. Furthermore, we used 28 of the 29 non-breeding sites identified by Sheldon (2004) to define non-breeding areas in our study. Sheldon (2004), selected sites based on five criteria: records since 1990; recorded in more than one year; direct association of record with wetland;  $\geq 1$  record of counts of 10 or more individuals and recorded in more than one month. We excluded Lake Florence (wetland ID 182 in Sheldon 2004) using these criteria. We added post-2004 records that fitted Sheldon (2004) criteria from: BirdLife Australia atlas (Blakers *et al.* 1984; Barrett *et al.* 2003), the Victorian Biodiversity Atlas, and the current study at: Edenhope, Peshurst, Streatham, Darlington, Lake Bolac and Pura Pura (Veltheim 2018).

We mapped non-breeding areas using the above-described data, by creating 100% Minimum Convex Polygons (MCPs) with Hawth's tools extension in ArcMap 9.2 (Figure S1 supplemental material). We used MCPs due to the small number of database records for many known non-breeding areas resulting in insufficient data for using other home range estimators. The non-breeding areas consisted of at least three presence records within five kilometres of each other, which represents realistic Brolga foraging ranges from roost



sites (Herring 2001). We used confirmed breeding records from all our data sources to define breeding locations and areas (using data from VBA, BirdLife, ecological consultants, landholders, aerial surveys (I. Veltheim unpublished data)).

### **Sampling and analysis of movements – movement distances between non-breeding and breeding; and roost and foraging areas**

We investigated timing, distance and direction of Brolga movements between breeding and non-breeding areas using GPS and colour band resighting data for individuals with available data for these analyses. We used subsequent relocation GPS fixes or colour-band re-sightings between the non-breeding MCP locations and breeding locations (determined from chick capture locations or database records) to map tracks in ArcMap 9.2 and to calculate all movement distances using Hawth's Tools extension.

We also calculated daily distance moved from roost to foraging areas for the 20 individuals fitted with GPS transmitters, as the distance between the night fix (23:00) and morning fix (8:00 or 9:30 depending on PTT schedule), and compared adult and juvenile movement distances for all the months of available data for each individual. We excluded days where one or both of these fixes were missing in the individuals' schedules.

### **Sampling and analysis of movements – timing and distance of monthly movements**

Preliminary mapping revealed different movement patterns between adults and juveniles as well as between capture locations, west (Willaura and Penshurst) and east of Hopkins River (see Figure S1 & Table S1, supplemental material for capture locations) (Veltheim 2018). We investigated these patterns further in the following way. We used the GPS data from adults and juveniles, which included post-fledging data for juveniles that were captured as chicks. The fledging date for these individuals was determined using behavioural change point analysis (Gurarie *et al.* 2009) as described in Veltheim *et al.* (2019) and data after the fledging date for these individuals were used as inputs in the analyses.

We calculated movement distances as the distance between monthly centroids, where a centroid was the centre of the monthly GPS location fixes, calculated as an average latitude and longitude for each month for each

bird. We used the Hawth's Analysis Tools extension for ArcMap and 'R' version 3.0.1 (R Core Team 2013) to calculate movement distances and summary statistics, in kilometres. As the data were heavily skewed towards short movement distances, we log transformed the distance values for further analysis to meet model assumptions of a normal distribution of the response variable (mean distance). We excluded data from the Brolga captured near Kaladbro in this model (ID 76389; Table S1, supplemental material), as it was the only individual captured at this location (Veltheim 2018) and 76387\_1 due to insufficient amount of data post-fledging.

We used a random effects model to test the effect of age, capture location and month on centroid movement distance (Veltheim 2018). The response variable was the log of distance moved ( $d_i = \ln(D_i)$ ), which was assumed to be drawn from a normal distribution with a residual standard deviation ( $\sigma$ ) that was estimated. The mean of the log distance for observation  $i$  ( $m_i$ ) was modelled as a linear function of the age class of the bird (adult and juvenile) associated with observation  $i$ , the effect of capture location (two different locations: Willaura/Penshurst and east of Hopkins River), and the month of year (as a categorical variable with 12 levels). The model also included a random effect for individual to account for variation in the distance moved among individuals:

$$m_i = \alpha + \beta_1 \times A_{j[i]} + \beta_2 \times L_{j[i]} + \beta_{3,M_i} + \varepsilon_{j[i]}$$

where  $\alpha$  is the intercept,  $j[i]$  is the identity of the individual associated with data point  $i$ ,  $\beta_1$  is the effect of the age of the individual associated with observation  $i$ ,  $\beta_{2,j}$  is the effect of the location at which individual  $j$  was captured,  $\beta_{3[j]}$  is the effect of month  $j$  of data point  $i$ , and  $\varepsilon_j$  is the random effect for individual  $j$  associated with the observation. The categorical variable of month was modelled by setting movement in January as the reference class ( $\beta_3[1] = 0$ ), and estimating the other parameters ( $\beta_3[2]$ ,  $\beta_3[3]$ , ...,  $\beta_3[12]$ ). Thus, the parameters  $\beta_3$  reflect the difference in movement distance relative to the average distance moved in January. Age was expressed as  $A_j = 1$  when individual  $j$  was an adult, and  $A_j = 0$  when individual  $j$  was a juvenile. Thus,  $\beta_1$  represents the difference in distance moved between adults and juveniles. Individuals captured at Willaura/Penshurst were coded as  $L_j = 1$ , and individuals captured at sites east of Hopkins River were coded as  $L_j = 0$ . Thus,  $\beta_2$  represents the difference in distance moved between individuals captured at the two locations. The random effect was modelled as being drawn from a normal distribution with a mean of zero and a standard deviation that was estimated (Veltheim 2018). We

also estimated the mean distance moved for juveniles for each month, with  $\beta_2 = 0$ , (i.e. for the sites east of the Hopkins River – the reference class).

$$meandist_j = \exp(\alpha + \beta_{3,M_i})$$

We were unable to estimate mean monthly distances for adults using the model, due to a small sample size of four individuals and some months having only a single centroid distance value for this age class.

We undertook modelling within the Bayesian framework, using OpenBUGS (version 3), with flat priors (Veltheim 2018). Priors for regression coefficients were normal distributions with a mean of 0 and standard deviation of 1000. Priors for the standard deviations were uniform distributions between 0 and 100. We ran the model with three chains with convergence of the Markov chains occurring within 20,000 iterations. We also used the Brooks-Gelman-Rubin statistic to assess convergence. We then continued to take a further 100,000 samples from each chain, providing 300,000 samples in total to characterise the posterior distributions of the parameters (Gelman and Hill 2006).

## Results

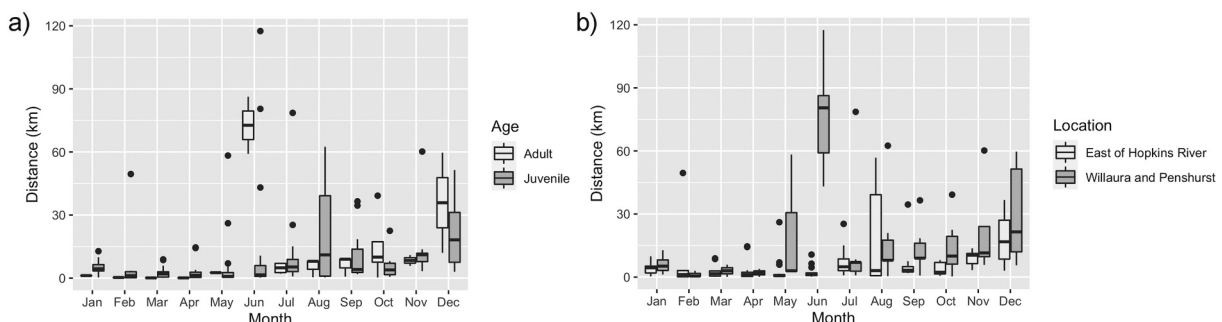
The 23 PTTs transmitted for 4–646 days, with an average of 174 (SD = 134) days for adults, 168 (SD = 159) for juveniles and 453 (SD = 227) for fledged chicks (classed as juveniles post-fledging). Of all the GPS fixes, 42% were within the accuracy class of < 25 m, 40% had an accuracy of 26–50 m, 14% were within 51–75 m and 4% were within 76–100 m. The average PTT GPS acquisition rate was 64% (SD = 12%) (range 41%–89%; n = 23).

## Movement distances

Of all the night roost to morning foraging area movements, throughout the annual life cycle (breeding and non-breeding season), for all Brolgas, 95% were within 5.2 km, with 94.7% of fixes within <5 km, 4.7% within 5–9.9 km and 0.5% within >10 km, with maximum movement from night roost to foraging area of 25.9 km (n = 3539 GPS fixes), and an average movement distance of 1.6 km (SD = 1.84). Adults moved 0.69 km on average from night roost (range: 0–16.1 km, SD = 1.27, n = 455) with 50% of movements within 0.2 km and 95% within 2.3 km. Juveniles moved further than adults from roost: 1.8 km on average from night roost to foraging areas (range 0–25.9 km, SD = 1.87, n = 3084) with 50% of movements within 1.2 km and 95% within 5.4 km.

Monthly distances moved by Brolgas, between non-breeding and breeding areas, varied greatly between individuals (Table S2, Table S3, supplemental material), age (Figure 1(a)), capture locations (Figure 1(b)), and months (Figure 1(a,b)), though there was little difference in distances moved from breeding to non-breeding areas and non-breeding to breeding areas overall (Table 1). Individuals captured at Willaura and Penshurst tended to move further than individuals captured east of Hopkins River (posterior mean of  $\beta_2 = 1.35$ , 95% CI: [0.52, 2.14]) (Table S2, supplemental material), equivalent to a factor of  $\exp(1.35) = 3.9$  times further (Figures 1(b) and 2) and adults moved shorter distances (Figure 1(a)) on average than juveniles (posterior mean of  $\beta_1 = -1.10$ , 95% CI: [-2.10, -0.07], equivalent to  $\exp(-1.10) = 0.3$  times the distance of juveniles (Table S2).

Juvenile Brolgas undertook the longest distance movements in November ( $meandist_j[11] = 8.20$  km, 95% CI: [3.10, 17.71]) and December ( $meandist_j$



**Figure 1.** (a) Boxplot of all centroid distances (km) moved by adult (white) and juvenile (grey) Brolgas each month. Distance (km) is the distance between monthly centroids (January is the centroid distance moved from December to January; February the centroid distance moved from January to February, and so on for each month shown). (b) Boxplot of all centroid distances (km) moved by Brolgas captured at east of Hopkins River (white) and Willaura and Penshurst (grey). The horizontal bars represent the median distance moved (km) (distance between centroids); the horizontal edges of the boxes represent the hinges (25<sup>th</sup> and 75<sup>th</sup> percentiles); the vertical lines represent the boxplot whiskers, which extend to values within 1.5 times the interquartile range of the hinge; and the points beyond the whiskers are outliers, which in this case indicate individuals undertaking particularly long-distance flights.

**Table 1.** Distances Brolgas moved into and out of non-breeding areas. These movements were generally between known non-breeding areas (identified from literature and database records) and breeding areas (identified by breeding records or chick capture locations). In some cases the location flown from was not able to be confirmed as a breeding area (i.e. the location had no known breeding sites), but nonetheless considered representative of movements between non-breeding and breeding areas.

Capture location	Age	n	Into non-breeding areas (km) mean (SD; range)	Out of non-breeding areas (km) mean (SD; range)
<b>Migratory</b>				
Willaura/Penshurst	Adult	4	96.3 (29.4; 58–124)	110.6 (12.1; 93.9–123.0)
Willaura/Penshurst	Juvenile	4	95.5 (58.7; 13–145.1)	103.4 (17.9; 78–119)
<b>Resident/Sedentary</b>				
East of Hopkins River/Kaladbro	Juvenile	7	17.2 (2.5–42)	
East of Hopkins River/Kaladbro	Juvenile	4		5.7 (3.7; 1.3–9.8)
East of Hopkins River/Kaladbro/ Macarthur/Penshurst	Juvenile	19	30.4 (15.2; 8.5–61.9)*	

\*These movements represent natal dispersal of fledged chicks from breeding sites, and can be considered as movements of family groups consisting of breeding pairs with their offspring. These included two pairs of chicks: one pair colour-banded only and captured near Penshurst, and one pair with one colour-banded only and one fitted with GPS PTT.

[12] = 11.57 km, 95% CI: [4.33, 25.26]) (Table S3), and similar pattern was evident in adults (Figure 1(a)), though we were not able estimate adult distances due to lack of replicate monthly centroid data. Brolgas are expected to move from breeding to non-breeding areas at this time of the year (Arnol *et al.* 1984). The greatest variation in movement distances occurred in these months (Table S3). Juveniles moved shortest distances with the least amount of individual variation between January and May, with shortest distances moved in February ( $meandistj[2] = 0.76$  km, 95% CI: [0.30, 1.60]) (Figure 1(a), Table S3), when individuals gather in flocks over the driest periods of the year (Arnol *et al.* 1984). During the non-breeding season, mixed-age flocks roost and move to forage together and these can be considered largely representative of adult and juvenile non-breeding average movements.

Juveniles moved longer distances and showed more individual variation on average from June to December compared to other months of the year (Table S3). Brolgas generally move from non-breeding to breeding areas in June, and from breeding areas to non-breeding areas in December and juveniles may accompany breeding adults until pairs begin nesting (Arnol *et al.* 1984). Once adults nest, juveniles are likely to move from breeding sites and roam in the landscape (Figure S2, supplemental material), which could drive such variability.

When considering only the distances moved between non-breeding and breeding areas – juveniles and adults captured at Willaura and Penshurst moved over 65 km further from breeding into non-breeding areas (96–111 km) than juveniles (captured as pre-fledged chicks) east of Hopkins River and Kaladbro (Table 1) (6–30 km). The average distances moved by Willaura and Penshurst

juveniles (mean = 95.5 km) and adults (mean = 96.3 km) were similar, although distances moved by juveniles were more variable than those of adults (Table 1) (Veltheim 2018). Distances moved by fledged chicks dispersing from breeding sites were also highly variable (Table 1, Figure S3a, S3b, supplemental material).

### Timing of movements between non-breeding and breeding areas

Brolgas undertook longer distance movements in May–August (non-breeding to breeding areas) and in November–December, though timing was variable between age classes (Figure 1(a)). Adults moved from non-breeding to breeding areas between May–June, whereas most juveniles moved between May–August, roamed around the landscape more frequently and had less directed movement paths than adults throughout the year (Figure 1(a), Figure S2, supplemental material) (Veltheim 2018).

Timing of chick natal dispersal was highly variable. These represent movements of family groups, adult breeders and their young, from breeding sites to non-breeding sites. Chicks colour-banded in 2009–10 dispersed from breeding areas between January and May, 2–5 months after capture and one was still at a breeding site in July, 7 months after capture. No dispersal was recorded for one individual, which remained near the breeding site five months after capture. The 12 chicks fitted with PTTs in 2010–11 and 2012 dispersed 2–10 months after capture, between June and December. These Brolga families thus remained resident at or near their breeding areas for the duration of the non-breeding season (December to June).

## Discussion

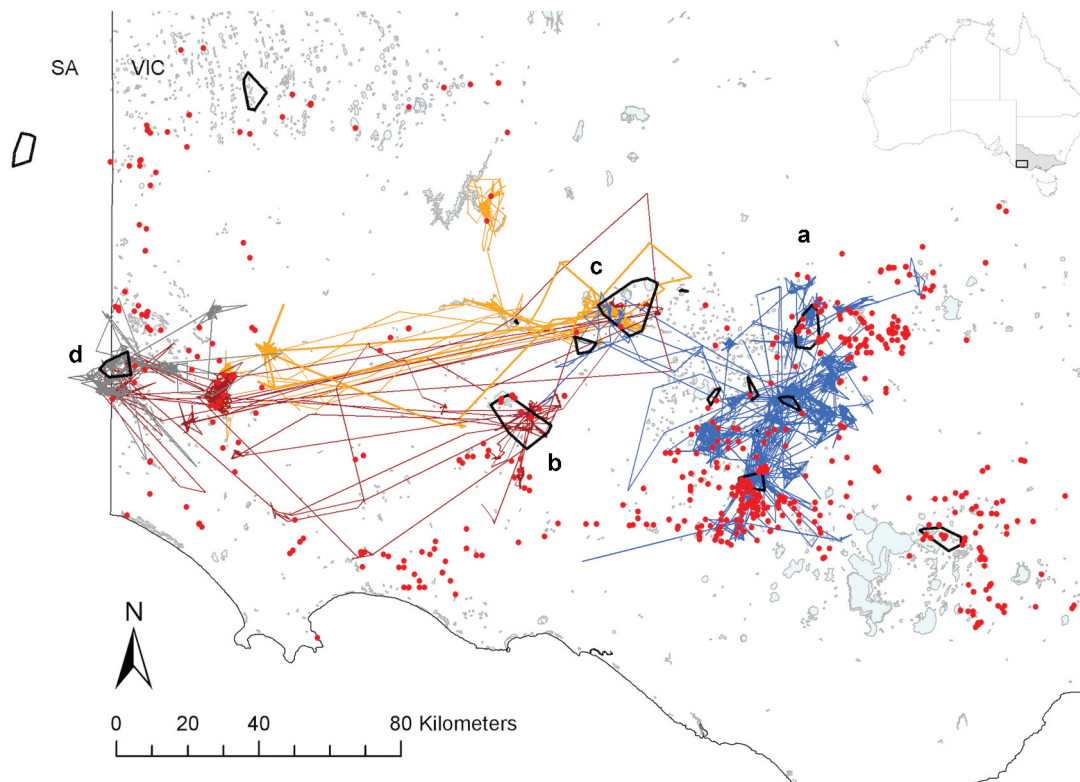
GPS tracking of Brolgas in south-west Victoria showed evidence of partial migration, with migratory and resident individuals present within the same population. Brolga movement patterns from the Willaura and Penshurst non-breeding areas fit Dingle and Drake's (2007) definition of migration: 'movement paths were persistent and straight; resulted in a relocation on a greater scale than daily movements; seasonal movements between regions, which alternate in favourable or unfavourable conditions and including a breeding region; and movements that lead to a redistribution of the population' (Velthim 2018). Other individuals using breeding and non-breeding areas East of Hopkins River moved short distances and remained locally resident.

### Breeding and non-breeding movements

Overall, juveniles moved further on average and the distances they moved varied more between individuals from June to December, compared with adults. This is when adult pairs would be expected to be on breeding territories (Arnol *et al.* 1984).

Adult and juvenile Brolgas in south-western Victoria moved the shortest distances during the non-breeding season, between January–May, suggesting their distribution is most stable at this time of the year. Brolgas roost in wetlands (Marchant and Higgins 1993; DuGuesclin 2003), many of which dry and become scarcer over summer in southern Australia, during the non-breeding season. Shorter movements and restricted distribution of Brolgas is thus likely due to limited wetland habitat availability during the drier months of the year and Brolgas are likely to select suitable wetland roost sites in proximity to food resources such as crops and shallow freshwater wetlands.

Throughout the year, including the breeding and non-breeding seasons, Brolgas moved 1.6 km from roost to foraging areas on average, and the majority (95%) of these movements were within 5.2 km. Thus, Brolgas appear to forage at similar distance from wetland roosts in south-west Victoria, compared to northern Victoria and southern New South Wales where flocks have been observed feeding within 3–5 km of their wetland roosts (Herring 2001, 2005). Similarly to Brolgas in our study, 95% of Greater Sandhill Crane (A.



**Figure 2.** Movements of GPS-tracked Brolgas in south-western Victoria, showing resident and migratory movement patterns: individuals captured (a) east of Hopkins River (blue,  $n = 10$ ), (b) Penshurst (red,  $n = 4$ ), (c) Willaura (yellow,  $n = 5$ ) and (d) Kaladbro (grey,  $n = 1$ ). Note also that some individuals moved between non-breeding areas (between areas east of Hopkins River (A); A & C; and B & C). Black polygons depict non-breeding areas, identified with 100% MCP database occurrence records from VBA, BFD and BirdLife and red circles are occurrence records defined as 'breeding' in BirdLife and VBA databases (see Methods). Major rivers are shown in light grey and wetlands in light blue. State of Victoria is denoted by 'VIC' and state of South Australia by 'SA'. For individuals 91406\_2, 91409 and 91413 programmed to acquire 13 fixes per day, all fixes were used to map tracks.



*c. tabida*) daily movements were within 5 km of roost sites during the non-breeding season, while wintering in the Sacramento-San Joaquin Delta of California, USA (Ivey *et al.* 2015). Their average roost to foraging area commuting distances were  $1.9 \pm 0.01$  km (mean  $\pm$  SE), comparable to Brolgas. Like Brolgas, the Sandhill Cranes spend their non-breeding season within agricultural areas, roosting in wetlands and moving out to feed during the day where the roosts are centrally located in relation to the agricultural fields they use for foraging (Ivey *et al.* 2015). Although our results include both breeding and non-breeding season movements, and Ivey *et al.* (2015), Herring (2001) and Herring (2005) reported on non-breeding movements, our findings suggests that the movement behaviour of these crane species in agricultural areas is comparable. Brolgas, like other cranes, are prone to anthropogenic disturbance at their roosts and powerline collisions (DuGuesclin 2003; Végvári *et al.* 2011; Luo *et al.* 2012) so knowledge of distances moved from roosts can help in designing disturbance and infrastructure-free habitat protection areas and may also aid in conserving and restoring wetland, roosting, and foraging habitat.

### **Movements between breeding and non-breeding areas**

Most Brolgas moved out of non-breeding areas in May–August. After the breeding season, most individuals moved back into non-breeding areas in October–January (Figure 1(a,b)). This followed known seasonal movement patterns of Brolgas (Arnol *et al.* 1984; Herring 2001), although there were exceptions (Veltheim 2018). Use of known non-breeding areas and the arrival of individuals from breeding areas can vary between years (Harper 1990; Herring 2001; Veltheim 2018).

In general, juveniles departed non-breeding areas later and returned earlier than adults (Veltheim 2018). Juveniles do not have the pressure to breed or seek suitable breeding sites, and adults likely depart before juveniles to secure breeding territories. Later return of pairs from breeding to non-breeding areas and an extended breeding season may occur in wet years, as breeding and foraging resources can remain suitable at breeding sites (Arnol *et al.* 1984; Herring 2001) if rainfall is high and occurs throughout late spring and summer. This may explain the variability and late natal dispersal of Brolgas in 2011 in our study (Veltheim 2018). In late 2010–early 2011, the south-western Victorian region had record-breaking rainfalls (Imielska 2011), which would have increased availability

of roosting and foraging wetland habitat for Brolgas throughout the region and their breeding and non-breeding areas (Veltheim 2018).

Individuals using the Willaura and Peshurst non-breeding area migrated within a defined movement corridor, which approximately followed the Wannon River, in a south-westerly to north-easterly direction with mean distances of 95.5 km to 110.6 km (Table 1) (Veltheim 2018). This suggests a learnt route and possible use of landscape features, such as rivers and wetlands to navigate to breeding areas. Some juveniles deviated from this path, while moving between breeding and non-breeding areas (Veltheim 2018). Similarly, Sandhill Cranes and White-naped Cranes (*Antigone vipio*) migrate along defined corridors (Higuchi *et al.* 2004; Krapu *et al.* 2011) and juvenile cranes may deviate from main migratory paths (Alonso *et al.* 2008; Mueller *et al.* 2013).

In contrast to the Brolgas moving from Willaura and Peshurst, individuals east of Hopkins River did not exhibit strong directionality when moving between breeding and non-breeding areas. Additionally, Brolgas captured east of Hopkins River and Kaladbro were resident rather than migratory, moving 5.7–30.4 km on average in and out of non-breeding areas and many pairs with chicks stayed at or near their breeding areas through the non-breeding season (Veltheim 2018). Arnol *et al.* (1984) and White (1987) also report Brolga breeding pairs in south-west Victoria staying resident near breeding sites throughout the year in some years.

Adult Brolgas likely remain faithful to their breeding sites and follow the same annual routes to breeding sites, like other crane species (Alonso *et al.* 2008; Krapu *et al.* 2011). In contrast, immature cranes fly with their parents from breeding to non-breeding areas in their first year of life (Alonso *et al.* 2008) or switch to a different route in following years (Alonso *et al.* 2008), learning movement routes through social facilitation (Mueller *et al.* 2013), which could explain the wider-ranging and longer distance movements of the juvenile Brolgas in our study (Veltheim 2018).

### **Brolga movement patterns are comparable to some other Australian waterbird species**

Brolga movement patterns varied greatly between individuals, similar to other Australian waterbird species that have been tracked across temperate, arid and tropical regions (Kingsford and Norman 2002; Roshier *et al.* 2006; Traill *et al.* 2010; McEvoy *et al.* 2015; Pedler *et al.* 2018; Veltheim 2018; Corriveau *et al.* 2020). Furthermore, Brolga movement behaviour was

most similar to tropical Magpie Goose (*Anseranas semipalmata*) movement patterns (Veltheim 2018). Movements of Brolgas (Veltheim 2018) and Magpie Geese (Traill *et al.* 2010) were more predictable, seasonally driven, geographically restricted and movement distances were shorter (up to about 100 km for both species) compared with movements of arid and colonially nesting waterbird species, which can exceed 1000 km and are undertaken in response to unpredictable weather events (Kingsford and Norman 2002; Roshier *et al.* 2008b; McEvoy *et al.* 2015; Pedler *et al.* 2018).

GPS tracking revealed Brolgas were partially migratory (Veltheim 2018), similarly to 36% of 472 Australian non-aquatic landbirds (Chan 2001). It is possible that partial migration is also more prevalent in Australian temperate and tropical waterbirds, given the similarities in movement behaviour of Brolgas (Veltheim 2018) and Magpie Geese (Traill *et al.* 2010). This could particularly be true in areas where inter- and intra-annual weather conditions may render some, but not all, breeding areas suitable throughout the year, reducing the need to move to non-breeding areas for some individuals (Veltheim 2018). It appears some Brolgas, in some years, remain resident at breeding sites while others move from breeding sites as these sites dry out, and become unsuitable for roosting or foraging, as Arnol *et al.* (1984) has suggested (Veltheim 2018). In comparison, more recent GPS tracking of Magpie Geese showed this species can move up to 565 km and exhibits variable and opportunistic movement behaviour, fitting descriptions of seasonal nomadism and partial migration and possibly responding to spatially and temporally fluctuating resource availability (Corriveau *et al.* 2020).

Resident behaviour can arise when resource patch density is high (Grovenburg *et al.* 2011; Shaw and Couzin 2013). High annual variability in climate and resource availability conditions result in partial migration persisting (Chan 2001). Distribution of breeding and non-breeding resources particularly within, and in proximity to, wetlands throughout their annual lifecycle may influence whether Brolgas are migratory or resident (Veltheim 2018). Residency may reflect high resource availability (Alonso *et al.* 2008). For example, migratory Common Cranes (*Grus grus*) now spend the non-breeding season in greater numbers in France rather than moving further south to Spain, as in the past, due to increased food availability from agriculture (Alonso *et al.* 2008). The two movement patterns we describe here for Brolgas have probably evolved in such a geographically small area due to the dynamic nature of wetland availability across the species' range and the distances between suitable breeding and non-breeding

wetland habitats (Veltheim 2018). This wetland availability can vary annually and across the landscape that Brolgas occupy, which may influence movement patterns. The differing resource requirements of Brolga during the breeding and non-breeding seasons necessitates movements between wetland habitats as their availability changes (Veltheim 2018). Areas with high densities of wetlands with presumably high resource availability within them, and short distances between suitable breeding and non-breeding habitats are likely to have favoured the evolution of resident strategy. In other parts of the Brolga's range, greater distances between habitat with important breeding and non-breeding season resources and more marked seasonal and annual change in the quality and abundance of resource availability is likely to have favoured selection for a migratory strategy (Veltheim 2018). It also appears that adoption of resident or migratory strategy can be influenced by rainfall, with breeding pairs remaining resident in high rainfall years (Veltheim 2018), as has been suggested by Arnol *et al.* (1984). The potential influence of wetland density and variation in resource availability in driving resident and migratory movement patterns in Brolgas warrants further investigation.

This study has clearly demonstrated that Brolgas adopt a wide range of movement patterns and that partial migration exists within a small geographic area, indicating that the species has a flexible movement strategy and can adapt to variability in habitat and environmental conditions (Veltheim 2018). The findings clarify the varying descriptions of Brolga movement patterns ('non-migratory' (Meine and Archibald 1996; DuGuesclin 2003); 'partly migratory' (Marchant and Higgins 1993); 'some dispersive movements' (Marchant and Higgins 1993), 'resident' (Arnol *et al.* 1984; Marchant and Higgins 1993) and undertaking 'seasonal movements' (DuGuesclin 2003) and it is likely Brolgas are partly migratory across their entire Australian range (Veltheim 2018).

## Conclusion

Much of the Brolga's wetland habitat in south-eastern Australia has been lost or modified, mainly for agricultural purposes (Bransbury 1991; DuGuesclin 2003); ongoing habitat loss continues to threaten the species (DuGuesclin 2003) and is reflected in the recent upgrade of its status in Victoria from 'vulnerable' to 'endangered' (DELWP 2021a). Understanding landscape scale movement patterns and migratory behaviour of animals are important steps in identifying conservation and management actions (e.g. Higuchi *et al.* 1996; Chan 2001; Kanai *et al.* 2002; Russell *et al.* 2013; Runge *et al.* 2014; Pearse *et al.* 2016), such as areas for habitat protection

and restoration, for the Brolga in southern Australia. The lack of evidence for movements between southern and northern Victoria, and northern Australia, strongly suggest that conservation management actions for the southern Australian threatened population should be focused on ensuring the long-term viability of the Brolga population within its core range in southern Australia (Victoria and South Australia), and protecting and restoring habitats required throughout the species' annual lifecycle and distributional range.

## Acknowledgements

This study was funded by the Commonwealth Department of Environment, Victorian Department of Sustainability and Environment (DSE), Sustainability Victoria, Bird Observation and Conservation Australia (BOCA), the Clean Energy Council, Origin Energy, Meridian Energy Wind Macarthur, Union Fenosa Wind Australia, Pacific Hydro, Biosis Research, Wind Prospect, Holsworth Wildlife Research Endowment, Birds Australia Victoria research grant, and a postgraduate scholarship to IV from Federation University Australia and DSE. The Australian Research Council Centre of Excellence for Environmental Decisions provided additional support. Additional funding to attend conferences was provided by the Birds Australia Stuart Leslie Award and The Waterbird Society. We thank all volunteers for field assistance and landholders for access. Thanks to David Roshier and David Brandt for help and advice on the Douglas Argos-filter. John Weiss and Matthew Malishyev provided helpful comments on an earlier version of the manuscript. The project was approved by the Federation University Australia Animal Ethics Committee, approval number 08-006; Australian Bird and Bat Banding Scheme, approval number 2489; and conducted under scientific permits from DSE, permit numbers 10004758 and 10006195.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

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