



# Where nothing stands still: quantifying nomadism in Australian arid-zone birds

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## Abstract

**Context** Nomadism is a movement strategy in response to non-seasonal environmental variability. Knowledge of nomadic species movements is poor but is necessary to understand life histories and develop appropriate conservation strategies.

**Objectives** We provide a first quantification of nomadism among Australia's arid bird community, which is presumed to be highly nomadic, by measuring variation in species' occurrence and abundance among years to determine whether there are clear nomadic and non-nomadic strategists.

**Methods** We surveyed birds annually from 2012 to 2016. We measured how many years each species was present at a site and estimated inter-annual variability in species abundance, using both measures to infer

species movement patterns. We used results to inform existing movement classifications.

**Results** Most arid species showed low site persistence, with species detected at the same site, on average, 1.8 out of the five survey years. Movement varied along a continuum rather than grouping into distinct nomadic and non-nomadic groups. Species classified as nomadic showed higher variation in abundance and lower site persistence than species classified as resident. Our method of quantifying nomadism closely replicated existing expert-derived movement classifications of arid zone bird species.

**Conclusions** Rather than a fixed attribute, movements of many species in our study can be heavily environment-dependent, and individuals of a single species can display a continuum of movements in different times and places. This complicates the conservation of species, but the growing recognition of the complexity of species movements offers opportunities for a more nuanced understanding of the relationship between species and environment.

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## Introduction

Mobile species are often classified into four distinct groups based on their strategies for acquiring resources: (1) residents, that inhabit a given locality year to year with some local movement; (2) migrants, that display predictable to-and-fro movement each year, with individuals relocating to areas with consistently available seasonal resources; (3) irruptive species, that exhibit resident behavior in years when resources are abundant and undertake long-distance movements outside of their normal range in years of low resource availability; and (4) nomadic species, that move with little or no seasonal regularity, tracking resources that fluctuate over space and time (Jonzén et al. 2011; Newton 2012; Teitelbaum and Mueller 2019). Of course, not all species movements are resource-driven (other drivers include social hierarchies, mate location, predation risk; Shaw 2020), and these four groups represent only a subset of all movement strategies (Mueller and Fagan 2008; Cottee-Jones et al. 2015). Furthermore, recent studies have found that species' movements are likely to be more complex than these simplistic classifications suggest (Cagnacci et al. 2016; Martin et al. 2018). In the case of partial migration, populations or individuals within a species may migrate or exhibit residency depending on environmental conditions (Chan 2001; Shaw 2020). Recent advances in tracking technology have revealed that many species thought to be migratory or resident display irregular movements (Wheat et al. 2017), thus nomadism may be more widespread than previously thought.

Nomadism represents the most extreme example of spatially and temporally dynamic distributions (Jonzén et al. 2011; Cornelius and Hahn 2012). This movement strategy functions to buffer species against extreme environmental variation (Lloyd 1999) and is the dominant form of movement for many southern hemisphere species where environmental conditions commonly result in unpredictable resource availability (Dean 2004). Nomadism occurs across a wide range of feeding guilds, from granivores and nectarivores that track seed and nectar production (Wyndham 1983; Eby et al. 1999), to herbivores that track post-rainfall vegetation growth (Nandintsetseg et al. 2019a), and raptors that track irruptions of prey populations (Pavey and Nano 2013). Resource pulses can also lead to opportunistic breeding, for example,

the swift parrot (*Lathamus discolor*) tracks ephemeral, nectar-producing flowers, and breeds wherever they are most abundant (Stojanovic et al. 2015). Changes in species abundance between years at sites with ephemeral resources could result from a combination of breeding success, mortality, and movement, which can complicate our understanding of nomadism and the conservation and monitoring of nomadic species.

The arid interior of Australia contains one of the highest proportions of nomadic bird species worldwide, with between 30 and 46% of the region's breeding species considered nomadic (Dean 2004). Irregular rainfall events in the region result in resource pulses that can trigger an influx of species, with some birds flying thousands of kilometres in a matter of days to make use of ephemeral resources (Pedler et al. 2014). The remainder of the arid bird assemblages in such regions are thought to comprise mainly residents (Dean 2004; Burbidge and Fuller 2007), which are arid-adapted and able to persist through harsh periods. This movement dichotomy has become conventional wisdom (Davies 1984), but whether there are nomadic versus non-nomadic strategists, or whether species vary along a continuum of movement types from fully resident to fully nomadic, remains unclear. Understanding the plasticity of species' movement patterns is important for predicting their distributions and developing appropriate conservation approaches (Runge et al. 2016). The classification of species as nomadic has been largely based on incidental historical records and expert opinion (e.g., Keast 1968; Schodde 1982; Pavey and Nano 2009) and there have been few attempts to quantify the extent of species movements (Griffioen and Clarke 2002; Webb et al. 2014; Jordan et al. 2017). A few studies have developed metrics to quantify nomadism (e.g., net squared displacement, Bunnefeld et al. 2011; using random-walk models, Abrahms et al. 2017); however, these approaches usually require knowledge of range extent or an individual's location in space and/or time, which is unfeasible for an entire assemblage. Citizen science projects have made available large quantities of data on arid zone bird species' distributions and movements (Reside et al. 2012; Runge et al. 2015) and response to rain (Burbidge and Fuller 2007; Pavey and Nano 2009). However, strong spatial and temporal biases in survey effort, for instance toward coastal areas or during cooler periods of the year, often result in sparse and localized data. Professional field studies

are often conducted at smaller spatial or temporal scales than that at which mobile species and weather dynamics typically operate. Repeated, systematic surveys across a broad area are needed to generate data on movement patterns that are comparable among species.

For the first time, we use empirical time series data to infer avian movement patterns across one of the most arid regions of central Australia in the years following an extreme rainfall event. We (i) quantify inter-annual variation in occupancy and abundance among a majority set of species in the arid zone assemblage, (ii) determine whether these data are consistent with the occurrence of two distinct mobility strategies: nomadism and residency, and (iii) compare our measures of nomadism with existing classifications of bird movement strategies. We measure variation in mean annual abundance for 64 species and explore site persistence of individual species (intended here as a species' rather than an individual trait) over the five-year survey period. We hypothesise that species previously classified as nomadic will display highly variable abundance, as nomadic populations often move as a group (Mueller and Fagan 2008). We also anticipate low site persistence of nomads relative to species classified as resident, as nomads are thought to track rain and resources that are unpredictable in space and time (Davies 1984; Teitelbaum and Mueller 2019)). Conversely, we expect previously identified resident species to show less variable inter-annual abundance and higher site persistence in our dataset.

## Material and methods

### Study region

The study area is located in the Lake Eyre Basin, a region of approximately 1.2 million km<sup>2</sup> (16% of the continent) of arid inland Australia and which has the greatest annual rainfall variability of any arid region globally (McMahon et al. 2008). About 83% of land in the region is grazed, with 15% managed for nature conservation (Land Use of Australia, Version 4, 2005–2006; [http://data.daff.gov.au/anrdl/metadata\\_files/pa\\_luav4g9abl07811a00.xml](http://data.daff.gov.au/anrdl/metadata_files/pa_luav4g9abl07811a00.xml)). Artificial boreholes provide year-round water on pastoral leases, and vegetation is dominated by chenopod shrublands,

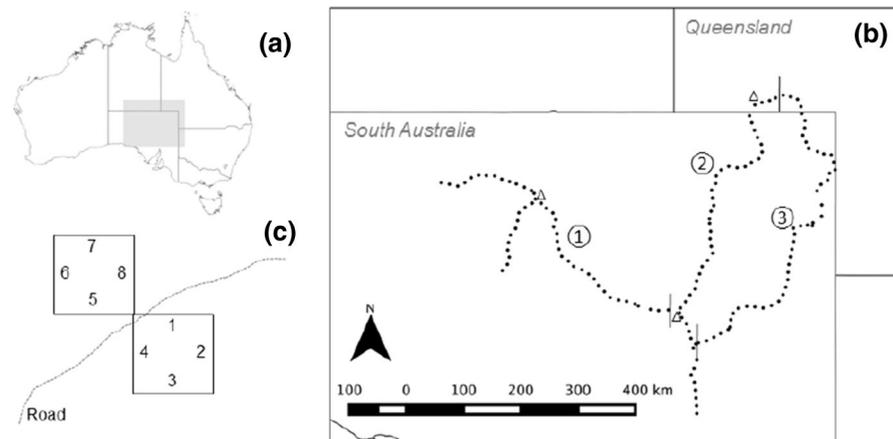
samphire shrublands and forblands, and tussock grassland (NVIS 4.2, Australian Government Department of Environment and Energy). The area experiences extended periods of drought interspersed with brief and irregular rainfall events (McMahon et al. 2008; Morton et al. 2011). Mean monthly temperatures for the region range from 14.5 to 29.5 °C (maximum) and mean annual rainfall is 186 mm, with an average intra-annual rainfall Coefficient of variation (CV) of 1.5 and an average inter-annual CV of 0.56 (Fig. 1). In 2010 and 2011, back-to-back rainfall events that greatly exceeded long-term averages occurred over much of central Australia, which marked both the wettest two-year period and the end of the longest dry period in Australia's recorded history (National Climate Centre, Bureau of Meteorology 2012).

### Bird surveys

Observers surveyed 150 sites, located an average of 16 kms apart, each year from 2012 to 2016 during winter–early spring (July–September) along the Birdsville, Oodnadatta, and Strzelecki tracks of South Australia and Queensland (Fig. 1b). Due to track closures resulting from flooding in years with heavy rain, observers were only able to survey 125 sites in all five years. Observers conducted eight 400-m line transect surveys and seven five-minute point counts at each site between sunrise and sunset (Fig. 1c) and used distance sampling techniques to account for undetected individuals (Buckland et al. 2001). Observers walked the transect line at a moderate, consistent pace and recorded the identity and group size of all birds detected by sight or sound between the start and stop points of the transect, and the perpendicular distance of a bird/group from the transect line upon first detection. Observers used laser range finders whenever possible to record distances from observers to birds (Bushnell Yardage Pro Sport 450). Observer teams followed a strict survey protocol, and comprised experienced ornithologists trained in the identification by sight and sound of all local species.

### Density estimation

We use bird abundance data to estimate individual species densities (birds/ha) using distance sampling methods, which model detection probability as a



**Fig. 1** **a** Study region (shaded rectangle) within Australia. **b** Survey sites (dots) along three drivable tracks ([1] Oodnadatta track, [2] Birdsville track [3] Strzelecki track). Long-term rainfall\* and temperature averages for the region are taken from three representative weather stations (indicated by triangles, clockwise from far left: Oodnadatta airport; Birdsville Police Station; Marree) from the 1961–1990 reference period used by the Australian Bureau of Meteorology ([www.bom.gov.au/climate/data](http://www.bom.gov.au/climate/data)). Vertical lines indicate where tracks begin or

end. **c** Orientation of the eight 400 m line transects at each census stop relative to the road. \*Intra-annual rainfall variability (coefficient of variation- CV) was calculated for each year (1961–1990) as the standard deviation of total monthly rainfall divided by the average total monthly rainfall, which was then averaged across the three weather stations. Inter-annual rainfall CV was calculated as the standard deviation of total annual rainfall across years divided by the average total annual rainfall across years

function of distance from the observer (Buckland et al. 2001). Line transects are better suited for surveying lower density, more mobile species in homogenous habitats and record more birds than point counts (Bibby et al. 1998), and we found this also. Therefore, although we collected bird observations using both line transects and point counts, we only use the line transects for our analyses. The exception was that we included point count data in our measure of species' site persistence as pooling the occurrence of species from line transect and point count methods ensured a more comprehensive species list at each site (see 'Estimating inter-annual distribution variability' of Methods). We obtained density estimates for each species at each site in each year by pooling counts and effort (i.e., transect length) of each of the eight transects conducted annually at a site. We excluded records of nocturnal and aquatic species from our analyses, as they were present at very few sites and our survey was not designed to estimate their density. We define an observation as a single detection event where at least one individual of a species is detected. Thus, there could be multiple observations of the same species along a single 400-m transect.

To ensure robust density estimates, we only calculated species-specific detection functions for species

with at least 60 observations ( $n = 51$  species), following Buckland et al. (2001). For nine species with fewer than 60 observations but that were not considered rare (present at  $> 10\%$  of sites), we used the detection probability of 'surrogate' species with similar detection characteristics to estimate density (Table 1) (Allredge et al. 2007; Fuller et al. 2008). We calculated detection probabilities for four species that lacked a surrogate equivalent, but which had similar detection characteristics by pooling observations of all four species (Table 1) (Allredge et al. 2007). Consequently, we estimated densities for 64 species in total, which comprised 95% of all observations and 95% of all individual birds detected in surveys.

Using the 'Distance' package in R (Miller 2015; R Core Team 2019), We evaluated the fit of different detection models using two functions (hazard rate and half normal), the shapes of which assume detection probability of birds at zero distance from the observer is 100% and decreases with distance from the observer (Thomas et al. 2010). For each species or species-group (using the pooling method discussed previously), we selected the best performing detection function model using Akaike's Information Criterion (AIC), and assessed adequate model fit visually by checking that detection function plots showed a

**Table 1** The 65 species included in our study, species codes referring to manuscript figures, average body mass from Garnett et al. 2015, detection probabilities (derived from detection functions- see Methods), and the method of density estimation used for species with fewer than 60 observations (either a surrogate species or species grouping approach; see Methods)

Species code	Common name	Scientific name	Body mass (g)	Detection probability	Average density (birds/ha) (Std dev)	Surrogate species (*)/ species group (**)
AUPI	Australasian Pipit	<i>Anthus novaeseelandiae</i>	25.7	0.31	0.039 (0.018)	
AUMA	Australian Magpie	<i>Cracticus tibicen</i>	280	0.33	0.004 (0.002)	
AURA	Australian Raven	<i>Corvus coronoides</i>	593	0.31	0.012 (0.003)	
BALA	Banded Lapwing	<i>Vanellus tricolor</i>	186	0.10	0.018 (0.010)	Wader**
BAWH	Banded Whiteface	<i>Aphelocephala nigricincta</i>	10.5	0.19	0.005 (0.002)	
BLHO	Black Honeyeater	<i>Sugomel niger</i>	9.3	0.30	0.002 (0.002)	Pied Honeyeater*
BLKI	Black Kite	<i>Milvus migrans</i>	847	0.11	0.021 (0.029)	
BFCS	Black-faced Cuckoo-shrike	<i>Coracina novaehollandiae</i>	115	0.28	0.003 (0.002)	
BFWO	Black-faced Woodswallow	<i>Artamus cinereus</i>	35.3	0.20	0.045 (0.014)	
BSKI	Black-shouldered Kite	<i>Elanus axillaris</i>	275	0.38	0.001 (0.001)	
BRFA	Brown Falcon	<i>Falco berigora</i>	574	0.34	0.003 (0.003)	
BRSO	Brown Songlark	<i>Cincloramphus cruralis</i>	53.2	0.62	0.012 (0.005)	
BUDG	Budgerigar	<i>Melopsittacus undulatus</i>	28.8	0.06	0.354 (0.318)	
CHWE	Chirruping Wedgebill	<i>Psophodes cristatus</i>	40.8	0.60	0.015 (0.005)	
CIQT	Cinnamon Quail-thrush	<i>Cinlosoma cinnamomeum</i>	56.1	0.42	0.021 (0.005)	
COCK	Cockatiel	<i>Nymphicus hollandicus</i>	92.4	0.06	0.013 (0.014)	
CRBE	Crested Bellbird	<i>Oreoica gutturalis</i>	63.4	0.42	0.001 (0.001)	
CRPI	Crested Pigeon	<i>Ocyphaps lophotes</i>	192	0.19	0.041 (0.015)	
CRCH	Crimson Chat	<i>Epthianura tricolor</i>	10.7	0.09	0.034 (0.029)	
DIDO	Diamond Dove	<i>Geopelia cuneata</i>	32.1	0.08	0.025 (0.028)	
EMU	Emu	<i>Dromaius novaehollandiae</i>	35,500	0.07	0.002 (0.002)	
FAMA	Fairy Martin	<i>Petrochelidon ariel</i>	10.8	0.03	0.026 (0.057)	
FLBR	Flock Bronzewing	<i>Phaps histrionica</i>	289	NA	NA	
GALA	Galah	<i>Eolophus roseicapillus</i>	306	0.04	0.052 (0.023)	
GIBB	Gibberbird	<i>Ashbyia lovensis</i>	17.5	0.22	0.005 (0.02)	
HORO	Hooded Robin	<i>Melanodryas cucullata</i>	19.3	0.22	0.002 (0.001)	Red-capped Robin*
HOBC	Horsfield's Bronze-cuckoo	<i>Chalcites basalus</i>	23.2	0.38	0.003 (0.003)	

**Table 1** continued

Species code	Common name	Scientific name	Body mass (g)	Detection probability	Average density (birds/ha) (Std dev)	Surrogate species (*)/ species group (**)
INDO	Inland Dotterel	<i>Charadrius australis</i>	79.2	0.10	0.029 (0.024)	Wader**
LIBQ	Little Button-quail	<i>Turnix velox</i>	45	0.10	0.02 (0.024)	Ground flusher**
LICO	Little Corella	<i>Cacatua sanguinea</i>	497	0.02	0.06 (0.042)	
LICR	Little Crow	<i>Corvus bennetti</i>	396	0.17	0.010 (0.009)	Whistling Kite*
LIEA	Little Eagle	<i>Hieraaetus morphnoides</i>	832	0.41	0.0002 (0.0002)	
MALA	Magpie-lark	<i>Grallina cyanoleuca</i>	88	0.41	0.002 (0.001)	
MAWO	Masked Woodswallow	<i>Artamus personatus</i>	34.7	0.03	0.066 (0.068)	
MIST	Mistletoebird	<i>Dicaeum hirundinaceum</i>	8.8	0.28	0.004 (0.003)	
NANKE	Nankeen Kestrel	<i>Falco cenchroides</i>	179	0.37	0.007 (0.004)	
ORCH	Orange Chat	<i>Epthianura aurifrons</i>	10.5	0.14	0.064 (0.041)	
PACU	Pallid Cuckoo	<i>Heteroscenes pallidus</i>	87.6	0.28	0.002 (0.002)	Black-faced Cuckoo-shrike*
PIHO	Pied Honeyeater	<i>Certhionyx variegatus</i>	26.4	0.30	0.009 (0.011)	
RBKI	Red-backed Kingfisher	<i>Todiramphus pyrrhopygius</i>	51.7	0.45	0.002 (0.002)	
RBPA	Red-browed Pardalote	<i>Pardalotus rubricatus</i>	10.1	0.49	0.001 (0.001)	
RCRO	Red-capped Robin	<i>Petroica goodenovii</i>	8.7	0.22	0.009 (0.003)	
RUFI	Rufous Fieldwren	<i>Calamanthus campestris</i>	14.5	0.31	0.010 (0.006)	
RUSO	Rufous Songlark	<i>Cincloramphus mathewsi</i>	29.7	0.34	0.008 (0.007)	
RUWH	Rufous Whistler	<i>Pachycephala rufiventris</i>	23.5	0.21	0.004 (0.003)	White-winged Triller*
SIHO	Singing Honeyeater	<i>Lichenostomus virescens</i>	24.3	0.41	0.037 (0.016)	
SOWH	Southern Whiteface	<i>Aphelocephala leucopsis</i>	12.4	0.19	0.005 (0.003)	Banded Whiteface*
SCHO	Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	44.7	0.36	0.011 (0.007)	
SPHA	Spotted Harrier	<i>Circus assimilis</i>	568	0.11	0.002 (0.002)	Black Kite*
STPA	Striated Pardalote	<i>Pardalotus striatus</i>	11.1	0.23	0.004 (0.002)	
STQU	Stubble Quail	<i>Coturnix pectoralis</i>	101	0.10	0.010 (0.015)	Ground flusher**
TBGR	Thick-billed Grasswren	<i>Amytornis modestus</i>	19.3	0.16	0.007 (0.003)	
TRMA	Tree Martin	<i>Petrochelidon nigricans</i>	16.6	0.03	0.062 (0.067)	

**Table 1** continued

Species code	Common name	Scientific name	Body mass (g)	Detection probability	Average density (birds/ha) (Std dev)	Surrogate species (*)/ species group (**)
VAFW	Variegated Fairy-wren	<i>Malurus lamberti</i>	8	0.08	0.028 (0.021)	
WTEA	Wedge-tailed Eagle	<i>Aquila audax</i>	3630	0.35	0.001 (0.0002)	
WHKI	Whistling Kite	<i>Haliastur sphenurus</i>	769	0.41	0.001 (0.001)	
WBSW	White-backed Swallow	<i>Cheramoeca leucosterna</i>	14	0.07	0.027 (0.013)	
WBWO	White-browed Woodswallow	<i>Artamus superciliosus</i>	35.3	0.03	0.061 (0.069)	Masked Woodswallow*
WFHO	White-fronted Honeyeater	<i>Purnella albifrons</i>	17.2	0.36	0.004 (0.005)	Spiny-cheeked Honeyeater*
WPHO	White-plumed Honeyeater	<i>Lichenostomus penicillatus</i>	18.3	0.20	0.032 (0.009)	
WWFW	White-winged Fairy-wren	<i>Malurus leucopterus</i>	7.5	0.20	0.199 (0.091)	
WWTR	White-winged Triller	<i>Lalage tricolor</i>	25.5	0.21	0.004 (0.003)	
WIWA	Willie Wagtail	<i>Rhipidura leucophrys</i>	20.7	0.37	0.017 (0.006)	
YTMI	Yellow-throated Miner	<i>Manorina flavigula</i>	57.4	0.17	0.013 (0.004)	
ZEFI	Zebra Finch	<i>Taeniopygia guttata</i>	11.1	0.07	0.538 (0.308)	

monotonically decreasing curve, indicating that detection probabilities were highest near the survey line and decreased with increasing distance (Buckland et al. 2001). We included observer team as a covariate in the detection function model for each species (to account for potential differences in observer ability), which can also serve as a proxy for any year-specific effects as observer teams were different in each survey year. We included time of day as an additional covariate (because a species' detectability may vary throughout the course of a day) only when it improved detection model fit as indicated by AIC (i.e., when AIC was at least two units lower than any competing model without time of day, Burnham and Anderson 2002). Time of day was a categorical variable with three levels: 'AM' = before 11:00; 'MD' = 11:00 to 15:00; 'PM' = 15:00 onwards. We tested species with an average flock size of > 4 within the relevant

truncation distance (the distance beyond which observations are excluded) for cluster-size bias, as larger clusters of species are sometimes more easily detected at longer distance. Potential cluster bias was assessed by regressing log-transformed group size against scaled detection probability. If cluster-size bias was present (as indicated by a significant regression), group size was included as an additional covariate in the detection function model. Distances were grouped into intervals with cut-points selected such that distances favored for rounding (e.g., 10 m, 20 m, etc.) fell midway between cut-points to avoid 'heaping' effects. We excluded detections beyond 145 m for most smaller-bodied species (body mass < 300 g; Table 1; Table S1) because, at this distance, detection probabilities tended to fall below the suggested minima of 15% required for robust density estimations (Buckland et al. 2001). Similarly, we excluded

detections beyond 500 m for most larger-bodied (body mass > 300 g) species.

### Estimating inter-annual distribution variability

To explore the inter-annual variability of each species' landscape-wide abundance across the region, we used the coefficient of variation (CV; e.g., Nimmo et al. 2015). To do this, we first calculated the mean density of each species in each year across all sites, so that each species,  $i$ , had five (2012–2016) annual density estimates across sites ( $\mu_{i,y}$ ):

$$\mu_{i,y} = \frac{1}{n_s} \sum_{s=1}^{n_s} x_{i,y,s}$$

where  $x_{i,y,s}$  is the density at site  $s$  in year  $y$  for species  $i$ , and  $n_s$  is the number of sites. Then we calculated the CV of each species' annual density estimates (hereafter referred to as 'CV of density';  $CV_i$ ) by dividing the standard deviation of annual density estimates by the average of annual density estimates for that species:

$$CV_i = \frac{\sigma_i}{\mu_i} = \frac{\sqrt{\sum_{i=1}^{n_y} (\mu_{i,y} - \mu_i)^2}}{\mu_i}$$

where  $\sigma_i$  is the standard deviation of annual densities of species  $i$  across sites,  $n_y$  is number of years, and  $\mu_i$  is the mean density of species  $i$  across sites and years:

$$\mu_i = \frac{1}{n_y n_s} \sum_{s=1}^{n_s} \left[ \sum_{y=1}^{n_y} x_{i,y,s} \right]$$

As CV is the percentage variation around the mean, higher values indicate more variable inter-annual abundance of a species. To explore how the density of a species varied at the site level across years, we first calculated the CV of density at each site ( $CV_{i,s}$ ) by dividing the standard deviation of annual site-level density estimates by the 5-year average of site-level density:

$$CV_{i,s} = \frac{\sigma_{i,s}}{\mu_{i,s}}$$

where  $\sigma_{i,s}$  is the standard deviation of annual densities of species  $i$  at site  $s$ , and

$$\mu_{i,s} = \frac{1}{n_y} \sum_{y=1}^{n_y} x_{i,y,s}$$

We then calculated the mean of these site CVs (hereafter 'site-level CV of density';  $\overline{CV_{i,s}}$ ):

$$\overline{CV_{i,s}} = \frac{1}{n_s} \sum_{s=1}^{n_s} CV_{i,s}$$

Species' persistence at a site (inter-annual 'site persistence') was calculated for species detected at > 10% of sites surveyed in all years (65 species and 125 sites in total, respectively) using line transect and point count data. Site persistence was calculated for each species as the number of years a species was detected at a site and then averaged across all sites so that each species had one mean site persistence value (theoretically ranging from 1 to 5;  $SP_i$ ):

$$SP_i = \frac{1}{n_s} \sum_{s=1}^{n_s} y_{i,s}$$

where  $y_{i,s}$  is the number of years species  $i$  is detected at site  $s$ . Species' site persistence may be influenced both by an observer's ability to detect a bird if it is present and by the size of the species' home range. Thus, to account for these factors we tested for significant relationships between species' site persistence and: (i) detection probability (values generated from detection function models) and (ii) body mass (as an indicator of range size; Garnett et al. 2015; see Table 1), using a Generalized linear model (GLM). Detection probability and body mass values can be found in Table 1. To explore variability of species persistence among sites, the CV was calculated by dividing the standard deviation of site persistence across sites by the species' average site persistence across sites. As species' biology could also influence movement behaviour (Woinarski 2006), we tested for significant relationships between species' site persistence and diet category (from the Elton Traits database; Wilman et al. 2014) and between inter-annual variation in density ( $CV_i$ ) and diet category using two separate GLMs.

## Comparison with existing movement classifications

We compared our results with species' mobility classifications from Garnett et al. (2015), which compiled and adapted data from the Handbook of Australian, New Zealand and Antarctic Birds (Marchant and Higgins 1990) and the Handbook of the Birds of the World (del Hoyo et al. 2014). Garnett et al. (2015) assigned binary scores (0/1) to species in one or more categories: local dispersal; partial migrant; total migrant; nomadic or opportunistic; and irruptive. We adapted this scheme so that each species was classified into a single movement classification. We considered nomadic species those whose movements are described by Garnett et al. (2015) as nomadic, irruptive, and/or opportunistic with no local dispersal ( $n = 11$ ; Table S2). We considered species with only local dispersal as resident ( $n = 20$ ), and those described as having local and nomadic, irruptive, or opportunistic dispersal as resident/nomadic ( $n = 16$ ). We considered species described by Garnett et al. as complete ( $n = 1$ ) or partial migrants ( $n = 16$ ) as migratory ( $n = 17$ ). As existing classifications for most migratory species are supported by banding records and/or seasonal changes in occurrence or abundance, albeit often from less-arid coastal areas (Marchant and Higgins 1990; del Hoyo et al. 2014), we do not attempt to classify these species in terms of nomadism or residency. Furthermore, we cannot confirm whether these species are migratory using our data because our surveys are conducted over a similar period each year (but start date can vary up to two months depending on year and track). Thus, depending on when our surveys fell relative to migratory movements, a migratory species could appear as resident or nomadic. We retain these species as a benchmark for comparison purposes as nomadism is thought to exist along a spectrum of movement frequency along with residency and migration (Teitelbaum and Mueller 2019).

## Results

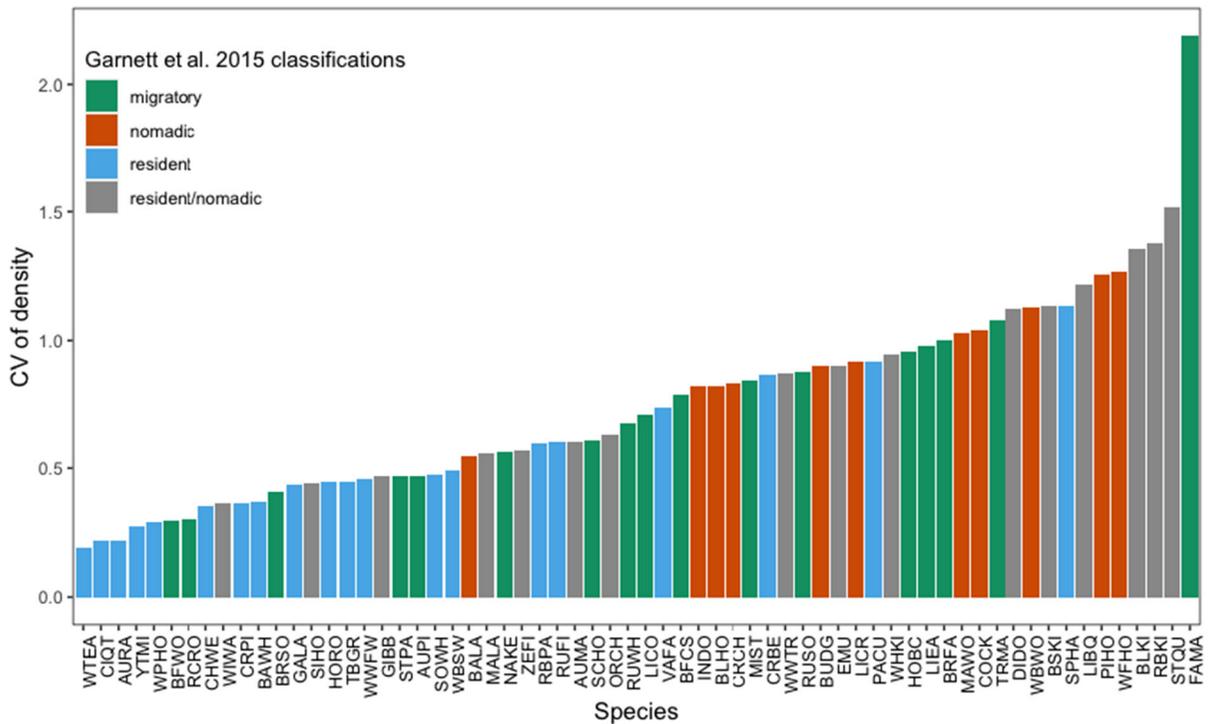
### Variation in species density and site persistence

Over the five years of annual bird surveys (2012 to 2016), we conducted 715 site-surveys. We surveyed

5713 400 m line transects and 5005 5-min point counts, and we detected 122 terrestrial species. Species' estimated densities ranged from 0.0002 birds/ha for little eagle (*Hieraaetus morphnoides*) to 0.54 birds/ha for zebra finch (*Taeniopygia guttata*), and detection probabilities ranged from 0.02 for little corella (*Cacatua sanguinea*) to 0.62 for brown songlark (*Cinchoramphus cruralis*; Table 1). Including time of day as a covariate significantly improved model fit for eight species and we detected cluster size bias for the flocking species budgerigar (*Melopsittacus undulatus*; Table S1).

Variability of inter-annual species abundance (CV of density,  $CV_i$ ) spanned a wide range of values, from 0.19 for wedge-tailed eagle (*Aquila audax*) to 2.2 for fairy martin (*Petrochelidon ariel*; Fig. 2; Table S2). A species that is found at the exact same density across years would have a  $CV_i$  equal to zero, whereas a species found at very different densities across years would have a  $CV_i$  greater than one. Most species (49 of 64 species for which we could estimate densities) had a  $CV_i$  of less than one and 15 had  $CV_i$  of greater than one. We found a continuum in  $CV_i$  values among the species rather a bimodal distribution, which would be observed if species behaved as classic nomadic and non-nomadic species (Fig. 2). In general, species classified by Garnett et al. as resident had lower  $CV_i$  values (blue bars in Fig. 2; Table S2), species classified as nomadic had higher  $CV_i$  values (red bars in Fig. 2; Table S2), and species classified as resident/nomadic and migratory were spread more evenly throughout (grey and green bars, respectively, in Fig. 2). We found higher variation of site-level densities (site-level CV of density,  $CV_{i,s}$ ) for all species across years, ranging from 0.98 in white-winged fairy-wren (*Malurus leucopterus*) to 2.2 in stubble quail (*Coturnix pectoralis*; Fig. S1), suggesting widespread species fluctuations in species abundance at a local level. Again, species classified as resident by Garnett et al. had relatively low  $CV_{i,s}$  values, those classified as nomadic had relatively high  $CV_{i,s}$  values, and species classified as migratory and resident/nomadic had  $CV_{i,s}$  values spread more evenly throughout (Fig. S1).

The number of years in which a species was detected at the same site ('site persistence') was tallied and the mean of this value calculated across all sites where a species occurred, for each of the 65 species. This ranged from 1.0 (i.e., rarely found at a site on  $> 1$



**Fig. 2** Overall variation in density across the entire study area between years ('CV of density',  $CV_i$ ) from 2012 to 2016 for 64 species. Colors represent existing movement classifications

adapted from Garnett et al. 2015 (see Table S2) and species codes can be found in Table 1

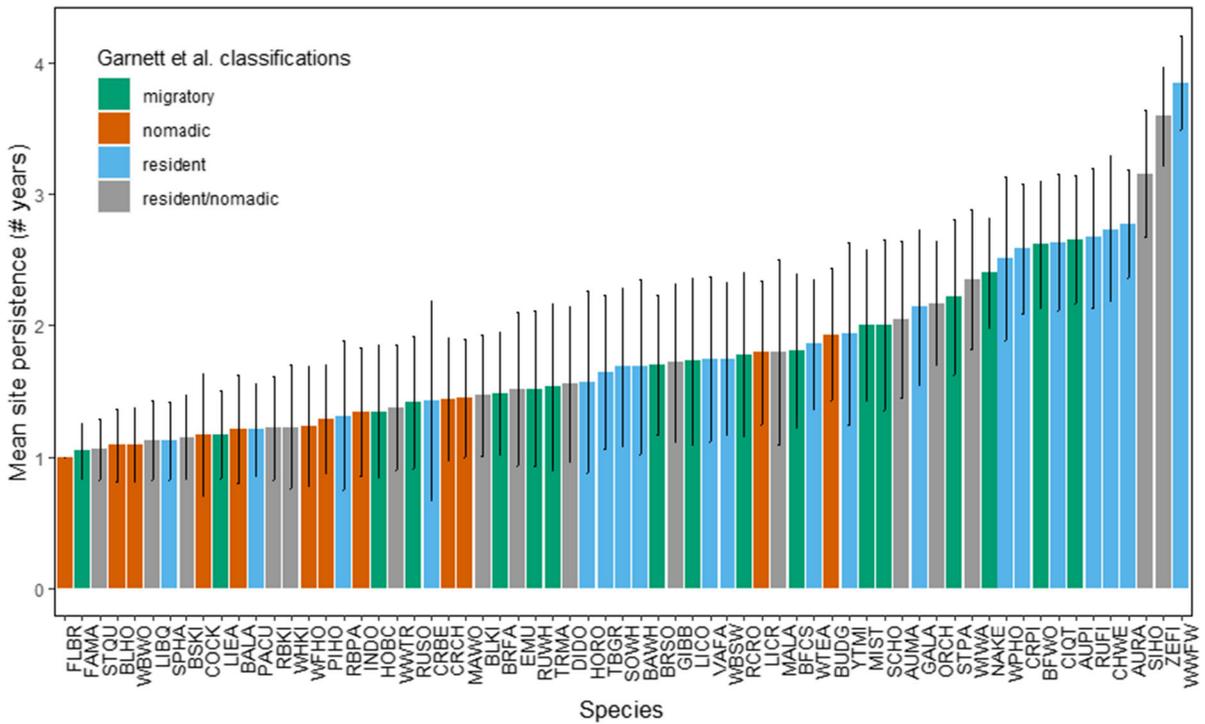
occasions) for flock bronzewing (*Phaps histrionica*) to 3.8 (i.e., typically found at an occupied site on circa 4 out of 5 visits) for white-winged fairy-wren (out of a maximum five years; Fig. 3), with an average of 1.8 years across all species. Overall, apparent site persistence was fairly low among species, with a majority of species (48 of 65 species) detected at the same site in two or fewer survey years. Site persistence followed a gradual continuum, with the exception of three species for which it was markedly higher than for the rest of the bird assemblage: singing honeyeater (*Lichenostomus virescens*) (3.2), zebra finch (3.6), and white-winged fairy-wren (3.8; Fig. 3). Among-site variation in individual species' site persistence was low (all CV values < 1; error bars in Fig. 3), suggesting that these estimates are robust to variations in the set of sites surveyed.

#### Movement classifications

Using our approach, species considered nomadic by Garnett et al. appeared to separate largely into

nomadic and resident groups, with nomads showing lower site persistence and higher  $CV_i$ , and residents showing higher site persistence and lower  $CV_{i,s}$  (Fig. 4). Fifteen out of the 20 species classified as resident by Garnett et al. formed a spatially distinct cluster relative to nomadic species (lower-right, Fig. 4), and nomadic species clustered relative to resident species, indicating general agreement with our method. However, six species showed marked differences from expert classifications. Five resident species overlapped in parameter space with nomadic species (crested bellbird *Oreoica gutturalis*, pallid cuckoo *Heteroscenes pallidus*, red-browed pardalote *Pardalotus rubricatus*, spotted harrier *Circus assimilis*, and variegated fairy-wren *Malurus lamberti*), one nomadic species overlapped with resident species (banded lapwing), and nomadic/resident species were interspersed amongst both nomadic and resident species groups (Fig. 4).

We did not find a significant relationship between species site persistence and detection probability (Poisson GLM: estimate = 0.03;  $t = 1.03$ ;  $P$ -value =



**Fig. 3** The mean number of years each species was detected at the same site (mean ‘site persistence’) from 2012 to 2016. Error bars are coefficient of variation. Species present at less than 10%

of sites were excluded. Colors represent existing movement classifications adapted from Garnett et al. 2015 (see Table S2) and species codes can be found in Table 1

0.31) or body mass (estimate =  $-4.0 \times 10^{-6}$ ;  $t = -0.37$ ;  $P$ -value = 0.71), suggesting that changes in site persistence reflected real changes in occurrence rather than detectability ‘noise’ due to observer error or limited sampling at a site. We did not find a significant relationship between species site persistence and any diet groups (invertebrate, omnivore, plant/seed, or vertebrate/fish/scavenger). We did find that variability in inter-annual density ( $CV_i$ ) was lower for invertebrate (Poisson GLM: estimate =  $-0.65$ ;  $t = -2.35$ ;  $P$ -value = 0.02) and omnivore diet groups (estimate =  $-0.70$ ;  $t = -2.24$ ;  $P$ -value = 0.029).

**Discussion**

This study took an empirical approach to assess movement strategies of an entire assemblage, testing the notion that Australian arid-zone species can be classified as either resident or nomadic. Our data suggest that the movement patterns of arid zone birds span a continuum of strategies rather than fitting a

binary classification and that most species are moderately mobile in our study region, as evidenced by changes in occurrence and abundance. Some species typically classified as resident showed variation in abundance and site persistence comparable to species usually classified as nomadic. Our findings closely mirror existing species movement classifications that resulted from years of fieldwork and synthesised expert knowledge, indicating that our method was largely successful in detecting nomadism and residency across this species assemblage. Our work complements existing knowledge by providing an objective way of classifying nomadism versus residency in a particularly arid part of species’ ranges where prior work does not exist.

Our results show marked similarities to the existing movement classifications of Garnett et al. (2015). The few inconsistencies we found (where nomadic and resident species overlap; Fig. 4) could arise when some populations or individuals within a species display nomadic movements while others remain resident (Lack 1943; similar to “partial migration”;



the idea that resident species tend to be predominantly insectivores or generalists (Burbidge and Fuller 2007; Tischler et al. 2013), while groups such as nectarivores and granivores are more likely to use nomadic movements to track availability of specialised food resources (Woinarski 2006; Ford 2013; Tischler et al. 2013). Considering that all of the species in our study inhabit a similar environment, it seems reasonable that species' diet would play an important role in driving differences in movement behaviour.

Most existing studies of arid Australian birds use a priori movement classifications or expert opinion when investigating species' responses to rainfall, with few assessing mobility and site persistence based on recorded changes in occurrence and abundance (Burbidge and Fuller 2007; Pavey and Nano 2009; Tischler et al. 2013 but see Wyndham 1983; Griffioen and Clarke 2002). However, a recent study at a single reserve in central Australia characterized temporal patterns of arid Australian birds as stable or fluctuating, based on the proportion of surveyed sites in which a species was recorded at 66 sites over six years (frequency of occurrence; Jordan et al. 2017). We found broad agreement between our results and the movement classifications of arid bird species from Jordan et al. (2017). Of the 23 non-migratory species in common between our studies, Jordan et al. classified all species that we found to have higher  $CV_i$  and lower site persistence (upper-left cluster of Fig. 4) as extremely or moderately irruptive (13/13 species: black honeyeater *Sugomel niger*; budgerigar; cockatiel *Nymphicus hollandicus*; crimson chat *Epthianura tricolor*; diamond dove *Geopelia cuneata*; little button-quail *Turnix velox*; masked woodswallow *Artamus personatus*; pallid cuckoo; pied honeyeater *Certhionyx variegatus*; red-backed kingfisher *Todiramphus pyrrhopygius*; spiny-cheeked honeyeater *Acanthagenys rufogularis*; white-fronted honeyeater *Purnella albifrons*; white-winged triller *Lalage tricolor*) except crested bellbird. Jordan et al. classified all but one (zebra finch) of the species with lower  $CV_i$  and higher site persistence as stable (8/9 species: banded whiteface *Aphelocephala nigricincta*; crested pigeon *Ocyphaps lophotes*; hooded robin *Melanodryas cucullata*; singing honeyeater; variegated fairy-wren; white-winged fairy-wren; willie wagtail *Rhipidura leucophrys*; yellow-throated miner *Manorina flavigula*). This difference could be attributable to our inclusion of site-level persistence as a measure of

movement, rather than variation in occurrence over a general study region as used by Jordan et al. Thus, species considered resident by Jordan et al. could still exhibit local movements beyond the site level, whereas our study's measure of site persistence meant a species persisted at the same site in multiple years. In addition to measuring species occurrence, our study incorporated fluctuating density as a measure of nomadism, which was not used by Jordan et al. As nomadic species are known to respond *en masse* to shifts in resource availability (Mueller and Fagan 2008; Pedler et al. 2014), changes in abundance and occurrence are both important indicators of movement.

Our results add to the growing body of knowledge that animal movement strategies are more labile than previously thought (Cagnacci et al. 2011; Mueller et al. 2011; Boyle 2017; Martin et al. 2018). This shift in thinking has important implications for our ability to predict species distributions as well as conservation approaches for mobile species globally, many of which are threatened (Wilcove and Wikelski 2008; Cottee-Jones et al. 2015; Runge et al. 2016). Currently, the development of conservation strategies for mobile and nomadic species is hampered by a lack of knowledge about their movements and movement cues. Many conventional conservation approaches, such as protected area designation, assume species distributions to be static. For species with dynamic distributions, such as nomads, this can lead to inadequate management strategies that do not overlap in space or time with species' occurrences (Runge et al. 2014; Nandintsetseg et al. 2019b). Our results solidified this as most species showed low site persistence. For a truly resident species, a static protected area may be more appropriate, while alternative management approaches are necessary for nomadic or opportunistic species. The latter could incorporate dynamic species distributions and include state- and time-dependent actions, such as creating temporary habitat for migratory species (Reynolds et al. 2017), altering human activities during peak movement periods to mitigate negative impacts on mobile animals and their habitats (Drewitt and Langston 2006; Grantham et al. 2008), or protecting numerous, small sites over a landscape-scale rather than one large area (Nandintsetseg et al. 2016). Our definition of site persistence is based on survey locations (spaced 16 km apart) and is therefore

scale-dependent. Adjusting this spatial scale such that a single ‘site’ includes groups of nearby individual survey locations could potentially result in increased site persistence values for species. Exploring the sensitivity of this measure was not an aim of our study; however, such an approach could be used to estimate the scale of species’ movements at the population level, which could be useful in protected area design.

Misclassifying species movements risks inaccurately assessing the degree of protection afforded to a species by conservation actions. For example, a nomadic species that has been misclassified as a resident might require management in very specific parts of its overall distribution, such as refugia. Conservation efforts that assume its distribution is static might over- or under-estimate the degree of protection afforded and potentially miss the important refugial sites that are more likely to be occupied in most years. For species falling toward the middle of the movement spectrum, such as white-browed woodswallow *Artamus leucorhynchus* or orange chat *Artamus persimilis*, misclassification as resident would have less serious negative implications but could still miss protecting the species more than half of the time (given an average site persistence of  $\sim 2$  years out of 5). Misclassifying such species as nomadic could risk prioritizing refugia over the broader landscape. However, management of nomadic species should ideally be closely tailored to the spatial and temporal patterns of species occurrence (Runge et al. 2016). Furthermore, treating species’ geographic range size as a fixed attribute when assessing extinction risk might underestimate extinction risk in nomadic species if range size is estimated by pooling occurrences over time (Runge et al. 2015). Indeed, spatial prioritization of protected areas can vary enormously depending on movement patterns of species; thus, improving our understanding of movement patterns is an essential first step toward making informed conservation decisions (Runge et al. 2016).

Our study has some limitations that could affect interpretation of our results. We cannot definitively attribute changes in species abundance to movement (immigration/emigration) or demographic processes (births/deaths) as information on the breeding response of many arid birds to rainfall and food resources is lacking. There is some evidence that breeding activity occurs within a couple of months of rainfall for certain species (Burbidge and Fuller 2007),

and a study on zebra finches found peak breeding activity four months following heavy rainfall (Zann et al. 1995). The possibility of breeding contributing to an increase in population rather than movement cannot be ruled out for some species, especially following significant rain events. This said, some studies have documented nomadic species arriving in areas from which they were previously definitely absent, or population increases within periods too short to be explained by a breeding response (Burbidge and Fuller 2007; Tischler et al. 2013; Jordan et al. 2017). Nonetheless, a conservative interpretation is necessary until demographic processes can be more convincingly ruled out. Tracking technologies present the best opportunity for teasing apart movement versus demographic processes and for better understanding the relationships between species movements and environmental conditions in arid regions (Pedler et al. 2014; Kays et al. 2015).

Our sampling methods are most useful for species with relatively high densities and/or moderate- to small-scale movements. Cryptic species, rare species, or species with large home ranges can be difficult to detect and could result in false absences, underestimating site persistence, and overestimating nomadism. However, very few species used in our analyses fit these profiles and species detected at 12 or fewer sites (10% of all sites) were excluded from analyses. Larger ranging species are inherently less likely to be present at the site-level given the scale of their territories. Thus, we cannot rule out that species with larger ranges may consistently occupy a territory and so may be less nomadic than indicated by our approach. Metrics of site persistence can also be inaccurate if all individuals of a species at a site are missed by observers. We argue that the likelihood of this occurring is very low given the spatial extent of our surveys at each site and that surveys were conducted by trained ornithologists in predominantly open, sparsely vegetated, and flat habitats. Although distance sampling methods do not account for false absences, they do account for missed individuals at sites where a species is detected and thus result in more accurate species density estimates. We conclude that distance sampling is a powerful tool for detecting nomadic movements across local populations for the majority of arid-zone bird species we observed.

We acknowledge that our study was not designed to specifically inform conservation interventions;

however, we suggest future research on spatially dynamic species prioritize effect of timing and intensity of disturbances on critical resources, such as grazing on seed eaters and insectivores, and predicting climate change impacts. For example, an increased number of days with temperatures exceeding 35 °C for more than a third of the year for Australia rangelands increases the risk of mass bird die-offs (e.g., McKechnie et al. 2012; CSIRO and BoM Climate Change in Australia website — <http://www.climatechangeinaustralia.gov.au>). Additionally, an increase in time spent in drought paired with a decline in winter rainfall over the next century reduces the probability of population recovery of arid species. These changes to climate are widespread and so the ability of species to move is unlikely to confer sufficient advantage to overcome the extended gaps in resource availability under climate change.

Our results highlight the variability that occurs in what are often considered binary classifications of resident and nomadic species, especially in highly dynamic ecosystems such as arid Australia. Agreement between our findings and species movement classifications sourced from arguably the most thorough compilation of species information in Australia to date (Garnett et al. 2015) is encouraging and suggests our systematic survey effort was capable of detecting different movement classifications. We further show that within-species mobility strategies are flexible and encourage further work to assess variation in movement patterns across the geographic range of species. In the case of to-and-fro migration, there are a number of cases from across the world where some species' populations are migratory, whilst others of the same species are sedentary ('partial migration'; Lack 1943; Chan 2001) – and we would expect the same thing for nomads. This suggests care is needed in using species-level classifications of movement strategy, and that for many local populations of a species, movements might be heavily environment-dependent. Accurate information on species movements is important to the design of conservation strategies for those species. Further, the use of a priori movement categories hinders objective assessment of arid bird ecological dynamics by restricting the interpretation of species ecologies through an unnecessarily narrow lens. We hope our findings encourage further empirical approaches to understanding animal movement strategies.

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**Author contributions** SGW and RAF initiated the monitoring, and MG, SGW, and RAF conceived the ideas; RAF and MG largely organised the fieldwork logistics. All authors except PAS collected field data, along with numerous field assistants. MG analysed the data, assisted by PAS and all other authors; MG led the writing under the guidance of CAR, RAF, SGW, and PAS.

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**Data availability** Raw species abundance data collected for this study are provided as a supporting file in this published article [Gibson\_etal\_surveydata.xlsx].

**Code availability** Code for species density models can be made available if requested upon acceptance by the journal.

#### Declarations

**Conflict of interest** The authors declare that they have no conflicts of interest.

**Research permit and ethical approval** Permission to conduct observational activities and collect data on wild bird species was given by the South Australia Department of Environment, Water and Natural Resources, No. E26001.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

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