- 1 Title: Where nothing stands still: quantifying nomadism in Australian arid-zone birds
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24 Abstract

25 Context: Nomadism is a movement strategy in response to non-seasonal environmental variability.
26 Knowledge of nomadic species movements is poor but is necessary to understand life histories and

27 develop appropriate conservation strategies.

28 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

- 30 among years to determine whether there are clear nomadic and non-nomadic strategists.
- Methods: We surveyed birds annually from 2012–2016. 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.
- 39 Conclusions: Rather than a fixed attribute, movements of many species in our study can be heavily 40 environment-dependent, and individuals of a single species can display a continuum of movements in 41 different times and places. This complicates the conservation of species, but the growing recognition of 42 the complexity of species movements offers opportunities for a more nuanced understanding of the 43 relationship between species and environment.
- 44 Key words: Australia, bird, distance sampling, movement ecology, nomadic species, sedentary species.

45

46 Introduction

47 Mobile species are often classified into four distinct groups based on their strategies for acquiring 48 resources: (1) residents, that inhabit a given locality year to year with some local movement; (2) 49 migrants, that display predictable to-and-fro movement each year, with individuals relocating to areas 50 with consistently available seasonal resources; (3) irruptive species, that exhibit resident behavior in 51 years when resources are abundant and undertake long-distance movements outside of their normal 52 range in years of low resource availability; and (4) nomadic species, that move with little or no seasonal 53 regularity, tracking resources that fluctuate over space and time (Jonzén et al. 2011; Newton 2012; 54 Teitelbaum and Mueller 2019). Of course, not all species movements are resource-driven (other drivers 55 include social hierarchies, mate location, predation risk; Shaw 2020), and these four groups represent 56 only a subset of all movement strategies (Mueller and Fagan 2008; Cottee-Jones et al. 2015). 57 Furthermore, recent studies have found that species' movements are likely to be more complex than 58 these simplistic classifications suggest (Cagnacci et al. 2016; Martin et al. 2018). In the case of partial 59 migration, populations or individuals within a species may migrate or exhibit residency depending on 60 environmental conditions (Chan 2001; Shaw 2020). Recent advances in tracking technology have 61 revealed that many species thought to be migratory or resident display irregular movements (Wheat et 62 al. 2017), thus nomadism may be more widespread than previously thought.

63 Nomadism represents the most extreme example of spatially and temporally dynamic distributions 64 (Jonzén et al. 2011; Cornelius and Hahn 2012). This movement strategy functions to buffer species 65 against extreme environmental variation (Lloyd 1999) and is the dominant form of movement for many 66 southern hemisphere species where environmental conditions commonly result in unpredictable 67 resource availability (Dean 2004). Nomadism occurs across a wide range of feeding guilds, from 68 granivores and nectarivores that track seed and nectar production (Wyndham 1983; Eby et al. 1999), to 69 herbivores that track post-rainfall vegetation growth (Nandintsetseg et al. 2019a), and raptors that track 70 irruptions of prey populations (Pavey and Nano 2013). Resource pulses can also lead to opportunistic 71 breeding, for example, the swift parrot (*Lathamus discolor*) tracks ephemeral, nectar-producing flowers, 72 and breeds wherever they are most abundant (Stojanovic et al. 2015). Changes in species abundance 73 between years at sites with ephemeral resources could result from a combination of breeding success, 74 mortality, and movement, which can complicate our understanding of nomadism and the conservation 75 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 81 residents (Dean 2004; Burbidge and Fuller 2007), which are arid-adapted and able to persist through 82 harsh periods. This movement dichotomy has become conventional wisdom (Davies 1984), but whether 83 there are nomadic versus non-nomadic strategists, or whether species vary along a continuum of 84 movement types from fully resident to fully nomadic, remains unclear. Understanding the plasticity of 85 species' movement patterns is important for predicting their distributions and developing appropriate 86 conservation approaches (Runge et al. 2016). The classification of species as nomadic has been largely 87 based on incidental historical records and expert opinion (e.g. Keast 1968; Schodde 1982; Pavey and 88 Nano 2009) and there have been few attempts to quantify the extent of species movements (Griffioen 89 and Clarke 2002; Webb et al. 2014; Jordan et al. 2017). A few studies have developed metrics to 90 quantify nomadism (e.g. net squared displacement, Bunnefeld et al. 2011; using random-walk models, 91 Abrahms et al. 2017); however, these approaches usually require knowledge of range extent or an 92 individual's location in space and/or time, which is unfeasible for an entire assemblage. Citizen science 93 projects have made available large quantities of data on arid zone bird species' distributions and 94 movements (Reside et al. 2012; Runge et al. 2015) and response to rain (Burbidge and Fuller 2007; 95 Pavey and Nano 2009;). However, strong spatial and temporal biases in survey effort, for instance 96 toward coastal areas or during cooler periods of the year, often result in sparse and localized data. 97 Professional field studies are often conducted at smaller spatial or temporal scales than that at which 98 mobile species and weather dynamics typically operate. Repeated, systematic surveys across a broad 99 area are needed to generate data on movement patterns that are comparable among species.

100 For the first time, we use empirical time series data to infer avian movement patterns across one of the 101 most arid regions of central Australia in the years following an extreme rainfall event. We (i) quantify 102 inter-annual variation in occupancy and abundance among a majority set of species in the arid zone 103 assemblage, (ii) determine whether these data are consistent with the occurrence of two distinct mobility 104 strategies: nomadism and residency, and (iii) compare our measures of nomadism with existing 105 classifications of bird movement strategies. We measure variation in mean annual abundance for 64 106 species and explore site persistence of individual species (intended here as a species' rather than an 107 individual trait) over the five-year survey period. We hypothesise that species previously classified as 108 nomadic will display highly variable abundance, as nomadic populations often move as a group 109 (Mueller and Fagan 2008). We also anticipate low site persistence of nomads relative to species 110 classified as resident, as nomads are thought to track rain and resources that are unpredictable in space 111 and time (Davies 1984; Teitelbaum and Mueller 2019)). Conversely, we expect previously identified 112 resident species to show less variable inter-annual abundance and higher site persistence in our dataset.

113 Material and methods

114 Study region

115 The study area is located in the Lake Eyre Basin, a region of approximately 1.2 million km² (16% of 116 the continent) of arid inland Australia and which has the greatest annual rainfall variability of any arid 117 region globally (McMahon et al. 2008). About 83% of land in the region is grazed, with 15% managed 118 for nature conservation (Land Use of Australia, Version 4, 2005-2006; 119 http://data.daff.gov.au/anrdl/metadata_files/pa_luav4g9abl07811a00.xml). Artificial boreholes provide 120 year-round water on pastoral leases, and vegetation is dominated by chenopod shrublands, samphire 121 shrublands and forblands, and tussock grassland (NVIS 4.2, Australian Government Department of 122 Environment and Energy). The area experiences extended periods of drought interspersed with brief 123 and irregular rainfall events (McMahon et al. 2008; Morton et al. 2011). Mean monthly temperatures 124 for the region range from 14.5 °C (minimum) to 29.5 °C (maximum) and mean annual rainfall is 125 186mm, with an average intra-annual rainfall coefficient of variation (CV) of 1.5 and an average inter-126 annual CV of 0.56 (Fig. 1). In 2010 and 2011, back-to-back rainfall events that greatly exceeded long-127 term averages occurred over much of central Australia, which marked both the wettest two-year period 128 and the end of the longest dry period in Australia's recorded history (National Climate Centre, Bureau 129 of Meteorology 2012).

130 Bird surveys

131 Observers surveyed 150 sites, located an average of 16 kilometres apart, each year from 2012 to 2016 132 during winter-early spring (July-September) along the Birdsville, Oodnadatta, and Strzelecki tracks of 133 South Australia and Queensland (Fig. 1b). Due to track closures resulting from flooding in years with 134 heavy rain, observers were only able to survey 125 sites in all five years. Observers conducted eight 135 400-metre line transect surveys and seven five-minute point counts at each site between sunrise and 136 sunset (Fig. 1c) and used distance sampling techniques to account for undetected individuals (Buckland 137 et al. 2001). Observers walked the transect line at a moderate, consistent pace and recorded the identity 138 and group size of all birds detected by sight or sound between the start and stop points of the transect, 139 and the perpendicular distance of a bird/group from the transect line upon first detection. Observers 140 used laser range finders whenever possible to record distances from observers to birds (Bushnell 141 Yardage Pro Sport 450). Observer teams followed a strict survey protocol, and comprised experienced 142 ornithologists trained in the identification by sight and sound of all local species.

143 Density estimation

We use bird abundance data to estimate individual species densities (birds/ha) using distance sampling methods, which model detection probability as a 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 148 also. Therefore, although we collected bird observations using both line transects and point counts, we 149 only use the line transects for our analyses. The exception was that we included point count data in our 150 measure of species' site persistence as pooling the occurrence of species from line transect and point 151 count methods ensured a more comprehensive species list at each site (see 'Estimating inter-annual 152 distribution variability' of Methods). We obtained density estimates for each species at each site in each 153 year by pooling counts and effort (i.e., transect length) of each of the eight transects conducted annually 154 at a site. We excluded records of nocturnal and aquatic species from our analyses, as they were present 155 at very few sites and our survey was not designed to estimate their density. We define an observation 156 as a single detection event where at least one individual of a species is detected. Thus, there could be 157 multiple observations of the same species along a single 400-m transect.

158 To ensure robust density estimates, we only calculated species-specific detection functions for species 159 with at least 60 observations (n= 51 species), following Buckland et al. (2001). For nine species with 160 fewer than 60 observations but that were not considered rare (present at >10% of sites), we used the 161 detection probability of 'surrogate' species with similar detection characteristics to estimate density 162 (Table 1) (Alldredge, Pollock, Simons, & Shriner, 2007; Fuller, Warren, Armsworth, Barbosa, & 163 Gaston, 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) 164 165 (Alldredge et al. 2007). Consequently, we estimated densities for 64 species in total, which comprised 166 95% of all observations and 95% of all individual birds detected in surveys.

167 Using the 'Distance' package in R (Miller 2015; R Core Team 2019), we evaluated the fit of different 168 detection models using two functions (hazard rate and half normal), the shapes of which assume 169 detection probability of birds at zero distance from the observer is 100% and decreases with distance 170 from the observer (Thomas et al. 2010). For each species or species-group (using the pooling method 171 discussed previously), we selected the best performing detection function model using Akaike's 172 Information Criterion (AIC), and assessed adequate model fit visually by checking that detection 173 function plots showed a monotonically decreasing curve, indicating that detection probabilities were 174 highest near the survey line and decreased with increasing distance (Buckland et al. 2001). We included 175 observer team as a covariate in the detection function model for each species (to account for potential 176 differences in observer ability), which can also serve as a proxy for any year-specific effects as observer 177 teams were different in each survey year. We included time of day as an additional covariate (because 178 a species' detectability may vary throughout the course of a day) only when it improved detection model 179 fit as indicated by AIC (i.e. when AIC was at least 2 units lower than any competing model without 180 time of day, Burnham and Anderson 2002). Time of day was a categorical variable with three levels: 181 'AM' = before 11:00; 'MD' = 11:00 to 15:00; 'PM' = 15:00 onwards. We tested species with an average 182 flock size of >4 within the relevant truncation distance (the distance beyond which observations are 183 excluded) for cluster-size bias, as larger clusters of species are sometimes more easily detected at longer

- 184 distance. Potential cluster bias was assessed by regressing log-transformed group size against scaled
- 185 detection probability. If cluster-size bias was present (as indicated by a significant regression), group
- 186 size was included as an additional covariate in the detection function model. Distances were grouped
- 187 into intervals with cut-points selected such that distances favored for rounding (e.g., 10m, 20m, etc.)

fell midway between cut-points to avoid 'heaping' effects. We excluded detections beyond 145 metres

- 189 for most smaller-bodied species (body mass < 300g; Table 1; Table S1) because, at this distance,
- 190 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 metres for most
- **192** larger-bodied (body mass > 300 g) species.

188

193 Estimating inter-annual distribution variability

194 To explore the inter-annual variability of each species' landscape-wide abundance across the region,

195 we used the coefficient of variation (CV; e.g., Nimmo et al. 2015). To do this, we first calculated the

196 mean density of each species in each year across all sites, so that each species, *i*, had five (2012-2016)

197 annual density estimates across sites $(\mu_{i,y})$:

198
$$\mu_{i,y} = \frac{1}{n_s} \sum_{s=1}^{n_s} x_{i,y,s}$$

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:

203
$$CV_i = \frac{\sigma_i}{\mu_i} = \frac{\sqrt{\sum_{i=1}^{n_y} (\mu_{i,y} - \mu_i)^2}}{\mu_i}$$

where σ_i is the standard deviation of annual densities of species *i* across sites, n_y is number of years, and μ_i is the mean density of species *i* across sites and years:

206
$$\mu_i = \frac{1}{n_y n_s} \sum_{s=1}^{n_s} \left[\sum_{y=1}^{n_y} x_{i,y,s} \right]$$

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 sitelevel density estimates by the 5-year average of site-level density:

211
$$CV_{i,s} = \frac{\sigma_{i,s}}{\mu_{i,s}}$$

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

213
$$\mu_{i,s} = \frac{1}{n_y} \sum_{y=1}^{n_y} x_{i,y,s}$$

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

215
$$\overline{CV_{i,s}} = \frac{1}{n_s} \sum_{s=1}^{n_s} CV_{i,s}$$

216 Species' persistence at a site (inter-annual 'site persistence') was calculated for species detected at >10% 217 of sites surveyed in all years (65 species and 125 sites in total, respectively) using line transect and point 218 count data. Site persistence was calculated for each species as the number of years a species was 219 detected at a site and then averaged across all sites so that each species had one mean site persistence 220 value (theoretically ranging from 1 to 5; *SP_i*):

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

222 where $y_{i,s}$ is the number of years species *i* is detected at site *s*. Species' site persistence may be influenced 223 both by an observer's ability to detect a bird if it is present and by the size of the species' home range. 224 Thus, to account for these factors we tested for significant relationships between species' site 225 persistence and: i) detection probability (values generated from detection function models) and ii) body 226 mass (as an indicator of range size; Garnett et al. 2015; see Table 1), using a generalized linear model 227 (GLM). Detection probability and body mass values can be found in Table 1. To explore variability of 228 species persistence among sites, the CV was calculated by dividing the standard deviation of site 229 persistence across sites by the species' average site persistence across sites. As species' biology could 230 also influence movement behaviour (Woinarski 2002), we tested for significant relationships between 231 species' site persistence and diet category (from the Elton Traits database; Wilman et al. 2014) and 232 between inter-annual variation in density (CV_i) and diet category using two separate GLMs.

233 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 241 with no local dispersal (n = 11; Table S2). We considered species with only local dispersal as resident 242 (n = 20), and those described as having local and nomadic, irruptive, or opportunistic dispersal as 243 resident/nomadic (n = 16). We considered species described by Garnett et al. as complete (n = 1) or 244 partial migrants (n=16) as migratory (n=17). As existing classifications for most migratory species are 245 supported by banding records and/or seasonal changes in occurrence or abundance, albeit often from 246 less-arid coastal areas (Marchant and Higgins 1990; del Hoyo et al. 2014), we do not attempt to classify 247 these species in terms of nomadism or residency. Furthermore, we cannot confirm whether these species 248 are migratory using our data because our surveys are conducted over a similar period each year (but 249 start date can vary up to two months depending on year and track). Thus, depending on when our 250 surveys fell relative to migratory movements, a migratory species could appear as resident or nomadic. 251 We retain these species as a benchmark for comparison purposes as nomadism is thought to exist along 252 a spectrum of movement frequency along with residency and migration (Teitelbaum and Mueller 2019).

253 Results

254 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
5,713 400m line transects and 5,005 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 (*Cincloramphus 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).

262 Variability of inter-annual species abundance (CV of density, CV_i) spanned a wide range of values, 263 from 0.19 for wedge-tailed eagle (Aquila audax) to 2.2 for fairy martin (Petrochelidon ariel; Fig. 2; 264 Table S2). A species that is found at the exact same density across years would have a CV_i equal to 265 zero, whereas a species found at very different densities across years would have a CV_i greater than 266 one. Most species (49 of 64 species for which we could estimate densities) had a CV_i of less than one 267 and 15 had CV_i of greater than one. We found a continuum in CV_i values among the species rather a 268 bimodal distribution, which would be observed if species behaved as classic nomadic and non-nomadic 269 species (Fig. 2). In general, species classified by Garnett et al. as resident had lower CV_i values (blue 270 bars in Fig. 2; Table S2), species classified as nomadic had higher CV_i values (red bars in Fig. 2; Table 271 S2), and species classified as resident/nomadic and migratory were spread more evenly throughout 272 (grey and green bars, respectively, in Fig. 2). We found higher variation of site-level densities (site-273 level CV of density, CV_{i,s}) for all species across years, ranging from 0.98 in white-winged fairy-wren 274 (Malurus leucopterus) to 2.2 in stubble quail (Coturnix pectoralis; Fig. S1), suggesting widespread 275 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).

279 The number of years in which a species was detected at the same site ('site persistence') was tallied and 280 the mean of this value calculated across all sites where a species occurred, for each of the 65 species. 281 This ranged from 1.0 (i.e., rarely found at a site on >1 occasions) for flock bronzewing (*Phaps* 282 histrionica) to 3.8 (i.e., typically found at an occupied site on circa 4 out of 5 visits) for white-winged 283 fairy-wren (out of a maximum five years; Fig. 3), with an average of 1.8 years across all species. 284 Overall, apparent site persistence was fairly low among species, with a majority of species (48 of 65 285 species) detected at the same site in two or fewer survey years. Site persistence followed a gradual 286 continuum, with the exception of three species for which it was markedly higher than for the rest of the 287 bird assemblage: singing honeyeater (Lichenostomus virescens) (3.2), zebra finch (3.6), and white-288 winged fairy-wren (3.8; Fig. 3). Among-site variation in individual species' site persistence was low 289 (all CV values < 1; error bars in Fig. 3), suggesting that these estimates are robust to variations in the 290 set of sites surveyed.

291 Movement classifications

292 Using our approach, species considered nomadic by Garnett et al. appeared to separate largely into 293 nomadic and resident groups, with nomads showing lower site persistence and higher CV_i, and residents 294 showing higher site persistence and lower $CV_{i,s}$ (Fig. 4). Fifteen out of the 20 species classified as 295 resident by Garnett et al. formed a spatially distinct cluster relative to nomadic species (lower-right, 296 Fig. 4), and nomadic species clustered relative to resident species, indicating general agreement with 297 our method. However, six species showed marked differences from expert classifications. Five resident 298 species overlapped in parameter space with nomadic species (crested bellbird Oreoica gutturalis, pallid 299 cuckoo Heteroscenes pallidus, red-browed pardalote Pardalotus rubricatus, spotted harrier Circus 300 assimilis, and variegated fairy-wren Malurus lamberti), one nomadic species overlapped with resident 301 species (banded lapwing), and nomadic/resident species were interspersed amongst both nomadic and 302 resident species groups (Fig. 4).

303 We did not find a significant relationship between species site persistence and detection probability 304 (Poisson GLM: estimate = 0.03; t = 1.03; P-value = 0.31) or body mass (estimate = -4.0 x 10^{-6} ; t = -305 0.37; P-value = 0.71), suggesting that changes in site persistence reflected real changes in occurrence 306 rather than detectability 'noise' due to observer error or limited sampling at a site. We did not find a 307 significant relationship between species site persistence and any diet groups (invertebrate, omnivore, 308 plant/seed, or vertebrate/fish/scavenger). We did find that variability in inter-annual density (CV_i) was 309 lower for invertebrate (Poisson GLM: estimate = -0.65; t = -2.35; *P*-value = 0.02) and omnivore diet 310 groups (estimate = -0.70; t = -2.24; *P*-value = 0.029).

311 Discussion

312 This study took an empirical approach to assess movement strategies of an entire assemblage, testing 313 the notion that Australian arid-zone species can be classified as either resident or nomadic. Our data 314 suggest that the movement patterns of arid zone birds span a continuum of strategies rather than fitting 315 a binary classification and that most species are moderately mobile in our study region, as evidenced 316 by changes in occurrence and abundance. Some species typically classified as resident showed variation 317 in abundance and site persistence comparable to species usually classified as nomadic. Our findings 318 closely mirror existing species movement classifications that resulted from years of fieldwork and 319 synthesised expert knowledge, indicating that our method was largely successful in detecting nomadism 320 and residency across this species assemblage. Our work complements existing knowledge by providing 321 an objective way of classifying nomadism versus residency in a particularly arid part of species' ranges 322 where prior work does not exist.

323 Our results show marked similarities to the existing movement classifications of Garnett et al. (2015). 324 The few inconsistencies we found (where nomadic and resident species overlap; Fig. 4) could arise 325 when some populations or individuals within a species display nomadic movements while others remain 326 resident (Lack 1943; similar to "partial migration"; Chan 2001; Shaw 2020). With the exception of 327 spotted harrier, all the resident species that overlapped with nomadic species were woodland species 328 (crested bellbird, pallid cuckoo, red-browed pardalote, and variegated fairy-wren; species list from 329 Fraser et al. 2019); however, woodland habitat made up a very small proportion of our study sites, so 330 incomplete sampling effort in woodland could explain the large variation in inter-annual abundance and 331 site persistence for these species. Thus, surveying a limited number of sites will not accurately capture 332 movement strategies of species with geographically vast and environmentally varied ranges. For 333 example, species previously reported as resident from less arid regions might be more likely to behave 334 as nomads in our study, located in the most arid region of Australia. Similarly, surveying over a limited 335 time period can lead to biased species movement classifications, especially if conducted only during 336 extreme wet or dry times. The idea that many mobile species are able to move opportunistically rather 337 than being constrained to discrete movement strategies is accepted for migratory species (partial 338 migration; see Berthold 2001; Cagnacci et al. 2011), but partial nomadism has not been explored for 339 species that exhibit both resident and nomadic behaviours in different locations or at different times. It 340 is possible that individuals behave as nomads while, at the population level, species may appear less 341 nomadic. For example, a ringing study of zebra finch in southeastern Australia found individuals 342 dispersed between permanent breeding colonies each year (Zann and Runciman 1994) but low recapture 343 rates indicated high turnover and thus high levels of individual mobility. Disparities between our results 344 and Garnett et al.'s classifications highlight that movement strategy is not a species-level attribute, but 345 rather an interaction between species and environment (Newton 2012; Martin et al. 2018), and 346 highlights the need for an agreed upon, objective typology of strategies.

Similar to previous studies, we found that species with invertebrate-dominant or omnivorous diets fluctuated less in abundance year-to-year. This supports 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 2002; 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.

354 Most existing studies of arid Australian birds use *a priori* movement classifications or expert opinion 355 when investigating species' responses to rainfall, with few assessing mobility and site persistence based 356 on recorded changes in occurrence and abundance (Burbidge & Fuller, 2007; Pavey & Nano, 2009; 357 Tischler et al., 2013 but see Wyndham, 1983; Griffioen & Clarke, 2002). However, a recent study at a 358 single reserve in central Australia characterized temporal patterns of arid Australian birds as stable or 359 fluctuating, based on the proportion of surveyed sites in which a species was recorded at 66 sites over 360 six years (frequency of occurrence; Jordan et al. 2017). We found broad agreement between our results 361 and the movement classifications of arid bird species from Jordan et al. (2017). Of the 23 non-migratory 362 species in common between our studies, Jordan et al. classified all species that we found to have higher 363 CV_i and lower site persistence (upper-left cluster of Fig. 4) as extremely or moderately irruptive (13/13) 364 species: black honeyeater Sugomel niger; budgerigar; cockatiel Nymphicus hollandicus; crimson chat 365 Epthianura tricolor; diamond dove Geopelia cuneata; little button-quail Turnix velox; masked 366 woodswallow Artamus personatus; pallid cuckoo; pied honeyeater Certhionyx variegatus; red-backed 367 kingfisher Todiramphus pyrrhopygius; spiny-cheeked honeyeater Acanthagenys rufogularis; white-368 fronted honeyeater Purnella albifrons; white-winged triller Lalage tricolor) except crested bellbird. 369 Jordan et al. classified all but one (zebra finch) of the species with lower CV_i and higher site persistence 370 as stable (8/9 species: banded whiteface Aphelocephala nigricincta; crested pigeon Ocyphaps lophotes; 371 hooded robin Melanodryas cucullata; singing honeyeater; variegated fairy-wren; white-winged fairy-372 wren; willie wagtail Rhipidura leucophrys; yellow-throated miner Manorina flavigula). This difference 373 could be attributable to our inclusion of site-level persistence as a measure of movement, rather than 374 variation in occurrence over a general study region as used by Jordan et al. Thus, species considered 375 resident by Jordan et al. could still exhibit local movements beyond the site level, whereas our study's 376 measure of site persistence meant a species persisted at the same site in multiple years. In addition to 377 measuring species occurrence, our study incorporated fluctuating density as a measure of nomadism, 378 which was not used by Jordan et al. As nomadic species are known to respond en masse to shifts in 379 resource availability (Mueller and Fagan 2008; Pedler et al. 2014), changes in abundance and 380 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

383 shift in thinking has important implications for our ability to predict species distributions as well as 384 conservation approaches for mobile species globally, many of which are threatened (Wilcove and 385 Wikelski 2008; Cottee-Jones et al. 2015; Runge et al. 2016). Currently, the development of conservation 386 strategies for mobile and nomadic species is hampered by a lack of knowledge about their movements 387 and movement cues. Many conventional conservation approaches, such as protected area designation, 388 assume species distributions to be static. For species with dynamic distributions, such as nomads, this 389 can lead to inadequate management strategies that do not overlap in space or time with species' 390 occurrences (Runge et al. 2014; Nandintsetseg et al. 2019b). Our results solidified this as most species 391 showed low site persistence. For a truly resident species, a static protected area may be more 392 appropriate, while alternative management approaches are necessary for nomadic or opportunistic 393 species. The latter could incorporate dynamic species distributions and include state- and time-394 dependent actions, such as creating temporary habitat for migratory species (Reynolds et al. 2017), 395 altering human activities during peak movement periods to mitigate negative impacts on mobile animals 396 and their habitats (Drewitt and Langston 2006; Grantham et al. 2008), or protecting numerous, small 397 sites over a landscape-scale rather than one large area (Nandintsetseg et al. 2016). Our definition of site 398 persistence is based on survey locations (spaced 16km apart) and is therefore scale-dependent. 399 Adjusting this spatial scale such that a single 'site' includes groups of nearby individual survey locations 400 could potentially result in increased site persistence values for species. Exploring the sensitivity of this 401 measure was not an aim of our study; however, such an approach could be used to estimate the scale of 402 species' movements at the population level, which could be useful in protected area design.

403 Misclassifying species movements risks inaccurately assessing the degree of protection afforded to a 404 species by conservation actions. For example, a nomadic species that has been misclassified as a 405 resident might require management in very specific parts of its overall distribution, such as refugia. 406 Conservation efforts that assume its distribution is static might over- or under-estimate the degree of 407 protection afforded and potentially miss the important refugial sites that are more likely to be occupied 408 in most years. For species falling toward the middle of the movement spectrum, such as white-browed 409 woodswallow Artamus superciliosus or orange chat Artamus superciliosus, misclassification as resident 410 would have less serious negative implications but could still miss protecting the species more than half 411 of the time (given an average site persistence of ~ 2 years out of 5). Misclassifying such species as 412 nomadic could risk prioritizing refugia over the broader landscape. However, management of nomadic 413 species should ideally be closely tailored to the spatial and temporal patterns of species occurrence 414 (Runge et al. 2016). Furthermore, treating species' geographic range size as a fixed attribute when 415 assessing extinction risk might underestimate extinction risk in nomadic species if range size is 416 estimated by pooling occurrences over time (Runge et al. 2015). Indeed, spatial prioritization of 417 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 conservationdecisions (Runge et al. 2016).

420 Our study has some limitations that could affect interpretation of our results. We cannot definitively 421 attribute changes in species abundance to movement (immigration/emigration) or demographic 422 processes (births/deaths) as information on the breeding response of many arid birds to rainfall and food 423 resources is lacking. There is some evidence that breeding activity occurs within a couple of months of 424 rainfall for certain species (Burbidge and Fuller 2007), and a study on zebra finches found peak breeding 425 activity four months following heavy rainfall (Zann et al. 1995). The possibility of breeding contributing 426 to an increase in population rather than movement cannot be ruled out for some species, especially 427 following significant rain events. This said, some studies have documented nomadic species arriving in 428 areas from which they were previously definitely absent, or population increases within periods too 429 short to be explained by a breeding response (Burbidge and Fuller 2007; Tischler et al. 2013; Jordan et 430 al. 2017). Nonetheless, a conservative interpretation is necessary until demographic processes can be 431 more convincingly ruled out. Tracking technologies present the best opportunity for teasing apart 432 movement versus demographic processes and for better understanding the relationships between species 433 movements and environmental conditions in arid regions (Pedler et al. 2014; Kays et al. 2015).

434 Our sampling methods are most useful for species with relatively high densities and/or moderate- to 435 small-scale movements. Cryptic species, rare species, or species with large home ranges can be difficult 436 to detect and could result in false absences, underestimating site persistence, and overestimating 437 nomadism. However, very few species used in our analyses fit these profiles and species detected at 12 438 or fewer sites (10% of all sites) were excluded from analyses. Larger ranging species are inherently less 439 likely to be present at the site-level given the scale of their territories. Thus, we cannot rule out that 440 species with larger ranges may consistently occupy a territory and so may be less nomadic than 441 indicated by our approach. Metrics of site persistence can also be inaccurate if all individuals of a 442 species at a site are missed by observers. We argue that the likelihood of this occurring is very low 443 given the spatial extent of our surveys at each site and that surveys were conducted by trained 444 ornithologists in predominantly open, sparsely vegetated, and flat habitats. Although distance sampling 445 methods do not account for false absences, they do account for missed individuals at sites where a 446 species is detected and thus result in more accurate species density estimates. We conclude that distance 447 sampling is a powerful tool for detecting nomadic movements across local populations for the majority 448 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 & 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.

460 Our results highlight the variability that occurs in what are often considered binary classifications of 461 resident and nomadic species, especially in highly dynamic ecosystems such as arid Australia. 462 Agreement between our findings and species movement classifications sourced from arguably the most 463 thorough compilation of species information in Australia to date (Garnett et al. 2015) is encouraging 464 and suggests our systematic survey effort was capable of detecting different movement classifications. 465 We further show that within-species mobility strategies are flexible and encourage further work to 466 assess variation in movement patterns across the geographic range of species. In the case of to-and-fro 467 migration, there are a number of cases from across the world where some species' populations are 468 migratory, whilst others of the same species are sedentary ('partial migration'; Chan, 2001; Lack, 1943) 469 - and we would expect the same thing for nomads. This suggests care is needed in using species-level 470 classifications of movement strategy, and that for many local populations of a species, movements 471 might be heavily environment-dependent. Accurate information on species movements is important to 472 the design of conservation strategies for those species. Further, the use of *a priori* movement categories 473 hinders objective assessment of arid bird ecological dynamics by restricting the interpretation of species 474 ecologies through an unnecessarily narrow lens. We hope our findings encourage further empirical 475 approaches to understanding animal movement strategies.

476

477 Declarations

- 478 *Data availability:* Raw species abundance data collected for this study are provided as a supporting479 file in this published article [Gibson etal surveydata.xlsx].
- 480 *Funding:* This project arose from a CSIRO Distinguished Visiting Scientist Fellowship to SGW. The

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- 484 *Conflict of interest statement:* Authors have no conflicts of interest to declare.

485 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

487 field data, along with numerous field assistants. MG analysed the data, assisted by PAS and all other

- 488 authors; MG led the writing under the guidance of CAR, RAF, SGW, and PAS.
- 489 *Research permit & ethics approval:* Permission to conduct observational activities and collect data
- 490 on wild bird species was given by the South Australia Department of Environment, Water and Natural
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- 492 *Consent to participate:* Not applicable.
- 493 *Consent for publication:* Not applicable.
- 494 *Code availability:* Code for species density models can be made available if requested upon
- 495 acceptance by the journal.
- 496

Tables

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	Anthus novaeseelandiae	25.7	0.31	0.039 (0.018)	
AUMA	Australian Magpie	Cracticus tibicen	280	0.33	0.004 (0.002)	
AURA	Australian Raven	Corvus coronoides	593	0.31	0.012 (0.003)	
BALA	Banded Lapwing	Vanellus tricolor	186	0.10	0.018 (0.010)	Wader**
BAWH	Banded Whiteface	Aphelocephala nigricincta	10.5	0.19	0.005 (0.002)	
BLHO	Black Honeyeater	Sugomel niger	9.3	0.30	0.002 (0.002)	Pied Honeyeater*
BLKI	Black Kite	Milvus migrans	847	0.11	0.021 (0.029)	
BFCS	Black-faced Cuckoo-shrike	Coracina novaehollandiae	115	0.28	0.003 (0.002)	
BFWO	Black-faced Woodswallow	Artamus cinereus	35.3	0.20	0.045 (0.014)	
BSKI	Black-shouldered Kite	Elanus axillaris	275	0.38	0.001 (0.001)	
BRFA	Brown Falcon	Falco berigora	574	0.34	0.003 (0.003)	
BRSO	Brown Songlark	Cincloramphus cruralis	53.2	0.62	0.012 (0.005)	
BUDG	Budgerigar	Melopsittacus undulatus	28.8	0.06	0.354 (0.318)	
CHWE	Chirruping Wedgebill	Psophodes cristatus	40.8	0.60	0.015 (0.005)	
CIQT	Cinnamon Quail-thrush	Cinclosoma cinnamomeum	56.1	0.42	0.021 (0.005)	
COCK	Cockatiel	Nymphicus hollandicus	92.4	0.06	0.013 (0.014)	
CRBE	Crested Bellbird	Oreoica gutturalis	63.4	0.42	0.001 (0.001)	
CRPI	Crested Pigeon	Ocyphaps lophotes	192	0.19	0.041 (0.015)	

CRCH	Crimson Chat	Epthianura tricolor	10.7	0.09	0.034 (0.029)	
DIDO	Diamond Dove	Geopelia cuneata	32.1	0.08	0.025 (0.028)	
EMU	Emu	Dromaius novaehollandiae	35500	0.07	0.002 (0.002)	
FAMA	Fairy Martin	Petrochelidon ariel	10.8	0.03	0.026 (0.057)	
FLBR	Flock Bronzewing	Phaps histrionica	289	NA	NA	
GALA	Galah	Eolophus roseicapillus	306	0.04	0.052 (0.023)	
GIBB	Gibberbird	Ashbyia lovensis	17.5	0.22	0.005 (0.02)	
HORO	Hooded Robin	Melanodryas cucullata	19.3	0.22	0.002 (0.001)	Red-capped Robin*
HOBC	Horsfield's Bronze-cuckoo	Chalcites basalis	23.2	0.38	0.003 (0.003)	
INDO	Inland Dotterel	Charadrius australis	79.2	0.10	0.029 (0.024)	Wader**
LIBQ	Little Button-quail	Turnix velox	45	0.10	0.02 (0.024)	Ground flusher**
LICO	Little Corella	Cacatua sanguinea	497	0.02	0.06 (0.042)	
LICR	Little Crow	Corvus bennetti	396	0.17	0.010 (0.009)	
LIEA	Little Eagle	Hieraaetus morphnoides	832	0.41	0.0002 (0.0002)	Whistling Kite*
MALA	Magpie-lark	Grallina cyanoleuca	88	0.41	0.002 (0.001)	
MAWO	Masked Woodswallow	Artamus personatus	34.7	0.03	0.066 (0.068)	
MIST	Mistletoebird	Dicaeum hirundinaceum	8.8	0.28	0.004 (0.003)	
NANKE	Nankeen Kestrel	Falco cenchroides	179	0.37	0.007 (0.004)	
ORCH	Orange Chat	Epthianura aurifrons	10.5	0.14	0.064 (0.041)	
PACU	Pallid Cuckoo	Heteroscenes pallidus	87.6	0.28	0.002 (0.002)	Black-faced Cuckoo- shrike*
PIHO	Pied Honeyeater	Certhionyx variegatus	26.4	0.30	0.009 (0.011)	
RBKI	Red-backed Kingfisher	Todiramphus pyrrhopygius	51.7	0.45	0.002 (0.002)	
RBPA	Red-browed Pardalote	Pardalotus rubricatus	10.1	0.49	0.001 (0.001)	
RCRO	Red-capped Robin	Petroica goodenovii	8.7	0.22	0.009 (0.003)	

RUFI	Rufous Fieldwren	Calamanthus campestris	14.5	0.31	0.010 (0.006)	
RUSO	Rufous Songlark	Cincloramphus mathewsi	29.7	0.34	0.008 (0.007)	
RUWH	Rufous Whistler	Pachycephala rufiventris	23.5	0.21	0.004 (0.003)	White-winged Triller*
SIHO	Singing Honeyeater	Lichenostomus virescens	24.3	0.41	0.037 (0.016)	
SOWH	Southern Whiteface	Aphelocephala leucopsis	12.4	0.19	0.005 (0.003)	Banded Whiteface*
SCHO	Spiny-cheeked Honeyeater	Acanthagenys rufogularis	44.7	0.36	0.011 (0.007)	
SPHA	Spotted Harrier	Circus assimilis	568	0.11	0.002 (0.002)	Black Kite*
STPA	Striated Pardalote	Pardalotus striatus	11.1	0.23	0.004 (0.002)	
STQU	Stubble Quail	Coturnix pectoralis	101	0.10	0.010 (0.015)	Ground flusher**
TBGR	Thick-billed Grasswren	Amytornis modestus	19.3	0.16	0.007 (0.003)	
TRMA	Tree Martin	Petrochelidon nigricans	16.6	0.03	0.062 (0.067)	
VAFW	Variegated Fairy-wren	Malurus lamberti	8	0.08	0.028 (0.021)	
WTEA	Wedge-tailed Eagle	Aquila audax	3630	0.35	0.001 (0.0002)	
WHKI	Whistling Kite	Haliastur sphenurus	769	0.41	0.001 (0.001)	
WBSW	White-backed Swallow	Cheramoeca leucosterna	14	0.07	0.027 (0.013)	
WBWO	White-browed Woodswallow	Artamus superciliosus	35.3	0.03	0.061 (0.069)	Masked Woodswallow*
WFHO	White-fronted Honeyeater	Purnella albifrons	17.2	0.36	0.004 (0.005)	Spiny-cheeked Honeyeater*
WPHO	White-plumed Honeyeater	Lichenostomus penicillatus	18.3	0.20	0.032 (0.009)	
WWFW	White-winged Fairy-wren	Malurus leucopterus	7.5	0.20	0.199 (0.091)	
WWTR	White-winged Triller	Lalage tricolor	25.5	0.21	0.004 (0.003)	
WIWA	Willie Wagtail	Rhipidura leucophrys	20.7	0.37	0.017 (0.006)	
YTMI	Yellow-throated Miner	Manorina flavigula	57.4	0.17	0.013 (0.004)	
ZEFI	Zebra Finch	Taeniopygia guttata	11.1	0.07	0.538 (0.308)	

Figures



Figure 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). Vertical lines indicate where tracks begin or end. c) Orientation of the eight 400m 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



Figure 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



Figure 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



Figure 4. Scatterplot of site persistence values (from Fig. 3) versus variability of species' mean annual densities (CV of density, CV_i, from Fig. 2). Colours represent existing movement classifications adapted from Garnett et al. 2015 (see Table S2). Species present at less than 10% of sites were excluded. Species codes can be found in Table 1

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