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Numbers, distribution and behaviour of Australian Sarus Cranes *Antigone antigone gillae* and Brolgas *A. rubicunda* at wintering roosts on the Atherton Tablelands, far north Queensland, Australia

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Abstract. The Atherton Tablelands in far north Queensland is the only currently known concentrated flocking area for Australian Sarus Cranes *Antigone antigone gillae*. Brolgas *A. rubicunda* also flock there in the non-breeding season, offering a unique opportunity to survey numbers, distribution and roost-sites for both species and their interactions. We searched for dry-season roosts every year from 1997 to 2017, and conducted an annual volunteer count simultaneously at multiple sites from late afternoon to dark as cranes flew in to roost. From one to several thousand cranes winter annually on the Tablelands, with Sarus Cranes highly concentrated in the Atherton Tablelands Key Biodiversity Area (KBA) and Brolgas concentrated to the north-west and south-west of the KBA. No population trends were detected in the context of 21 years of highly variable annual counts, a substantial proportion of birds not identified to species in failing light, and a change in monthly timing of the annual count. Notwithstanding these caveats, we provide the first systematic minimum estimate of 826–3255 Australian Sarus Cranes wintering on the Tablelands, up to 19.5% of the global population. The corresponding estimate for Brolgas is up to 3469 individuals or 4.9% of the global population. These are likely to be underestimates, particularly for Sarus Cranes, which arrived at roosts on average much later than Brolgas, so were more likely to be unidentified. The species shared many roosts and, except at one large shared roost, family groups of the two species intermingled rather than occupying separate parts of the site, an uncommon relationship at mixed-species wintering crane roosts. Further study of these behavioural findings could extend understanding of sympatry in these closely related species. Conducting counts in a consistent month may improve trend detection within the limits imposed by strong fluctuations in annual numbers.

Introduction

After breeding, many populations of the world's 15 crane species move short or long distances to flocking (wintering) grounds, where they feed and roost communally in varying types of shallow wetlands (Mirande & Harris 2019). Counts at communal roosts are a useful technique to estimate populations of flocking birds (Bibby *et al.* 1992). In the United States of America, for example, the first simultaneous roost counts at multiple sites to support regional crane population estimates began in 1974 (Lewis 1979). Communal winter roosts typically contain only one crane species and, where two and rarely up to four species share a roost, they usually form separate flocks, occupying different parts of the site (Sauey 1985; Pae & Won 1994; Jia *et al*. 2019).

The Sarus Crane *Antigone antigone* is listed as globally Vulnerable because of population declines and habitat change in Asia, with an estimated global population of 13,550–20,650 (Mirande & Harris 2019). The Australian population, *A. a. gillae*, is internationally important, but the estimate of 5000–10,000 birds is unreliable (Mirande & Harris 2019). The Brolga *A. rubicunda* is classified as Least Concern, with an estimated national and global population of 50,000–100,000 (Mirande & Harris 2019), but there is no regional estimate for far north Queensland where Brolgas and Sarus Cranes both occur.

Brolgas have been recorded in the dry season on the Atherton Tablelands since at least the 1930s (Anon. 1935), only decades after significant forest clearing and the expansion of agriculture in the region (Nevard *et al*. 2019a). Sarus Cranes were first recognised in Australia in 1966 (Gill 1969) and, in July 1967, 23 Sarus Cranes were identified feeding amongst 80 Brolgas in a wetland near Atherton (Bravery 1969). By 1972, >300 Sarus Cranes had been recorded in visits to various roost-sites on the Tablelands (Gill 1971; Smith 1971; Archibald 1981). Brolgas and Sarus Cranes were observed using different roosts or occupying mostly separate areas at shared roosts (Crowhurst 1968; Lavery & Blackman 1969; Archibald 1981; Swaby 1983). The first detailed count at a Tablelands roost was in 1983, with 300 Sarus Cranes and 750 Brolgas flying in to roost at Bromfield Swamp (Swaby 1983), a perennial swamp within an extinct volcanic crater used for cattle grazing. By 1997, the Atherton Tablelands was recognised as an important flocking location for both crane species (MacGregor 1952; Marchant & Higgins 1993) but had not been censused, and little was known about mixed-species roosts. In 1997, BirdLife Northern Queensland (as it is now known) commenced an annual volunteer Crane Count centred on the Atherton Tablelands in the non-breeding tropical dry season, with simultaneous surveys at multiple evening roosts used by either or both species.

The aims of our study (see also Scambler 1997a,b) were to: estimate numbers of flocking Brolgas and Sarus

Cranes using the Tablelands, identify trends in populations, establish whether and to what extent the species share communal roosts, and to examine the species composition and timing of flocks flying in to roosts. In this paper, we report the results of 21 years of annual counts in relation to these objectives and consider some of the factors that may influence counts and year-to-year variation in them.

Key Biodiversity Areas (KBAs) are an international program of the International Union for Conservation of Nature (IUCN 2016) to recognise key areas for biodiversity conservation, including birds. A further objective of our study was to review the Atherton Tablelands KBA, which was established in 2009 based on the preliminary results of our study, showing that an area of the central Tablelands (Figure 1) regularly supported at least 1% of the estimated global population of the Vulnerable Sarus Crane (BirdLife International 2018; IUCN 2018). Brolgas and Sarus Cranes are closely related and very similar in appearance (Marchant & Higgins 1993; Krajewski *et al*. 2010), and at roost counts in failing light it can be difficult to identify them to species. We address time of arrival at roosts as a factor in species identification and estimation of numbers, and suggest a technique enabling unidentified cranes in this continuing program to be included in analyses and to benefit conservation planning (Brouwer *et al*. 2003; Wetlands International 2006).

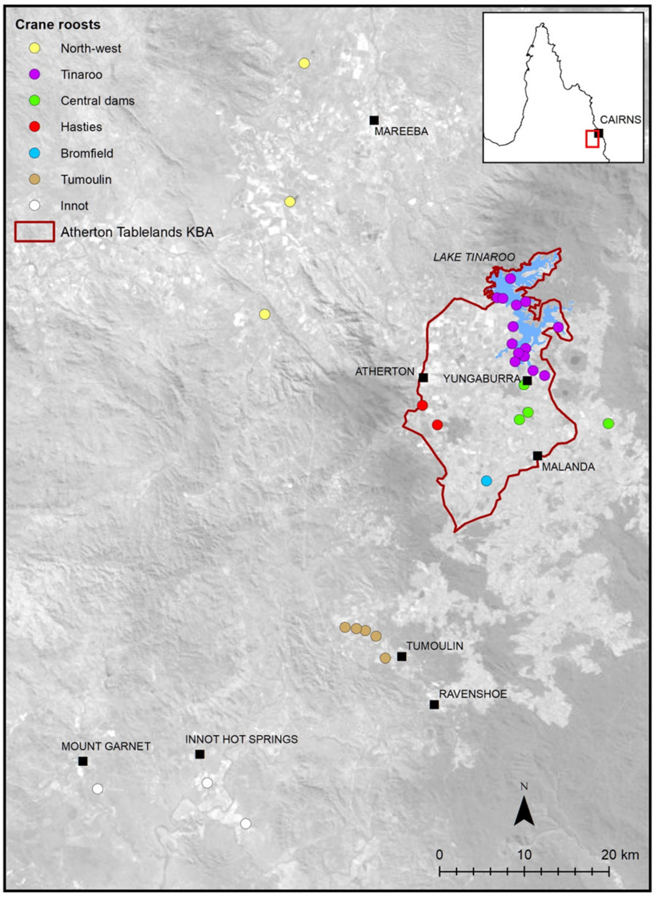

Figure 1. Study area on the Atherton Tablelands, far north Queensland, showing the 32 crane roosts (circles) counted during this study, with eco-geographic roost clusters. Clusters are a descriptive tool, grouping roosts with similar characteristics to aid analysis (see Methods). KBA = Key Biodiversity Area.

Methods

Study area

The study area of ~3300 km^2 is centred on the towns of Mareeba [16°99′S, 145°25′E; 405 m above sea level (asl)], Yungaburra (17°16′S, 145°34′E; 698 m asl) and Ravenshoe (17°36′S, 145°29′E; 943 m asl) in the northern, central and southern Atherton Tablelands, respectively, in far north Queensland (Figure 1). The climate is upland tropical with mean annual rainfall varying across the study area from 850 to >2000 mm, concentrated from November to April, but with higher-rainfall portions receiving some rain throughout the year (Bureau of Meteorology undated). Much of the Tablelands comprise a fertile elevated red-soil plain of volcanic origin, extensive areas of which have been cleared for grazing, cropping (mainly Maize *Zea mays* and Sugarcane *Saccharum officinarum*) and horticulture including Avocadoes *Persea americana* and Mangoes *Mangifera indica* (Tablelands Futures Corporation 2019). Waterbodies with shallow edges suitable for crane roosts are impoundments or wetlands that range from highly modified to semi-natural. The roosts vary significantly in extent and include the shores of Lake Tinaroo (3500 ha), and the Mareeba Wetlands (120 ha), Bromfield Swamp (60 ha), Hasties Swamp (20 ha) and numerous small farm dams.

Preparation for surveys

Simultaneous counts were conducted at multiple roosts on one evening per year from 1997 to 2017 (details below). Active roosts were located during the month before the survey by searching past roosts and likely habitat and by following crane flocks in late afternoon (by vehicle). Roosts were confirmed as still in use by follow-up searches in the week before the counts. At each roost, one or more vantage points were selected to maximise views of the roost without deterring birds from landing or disturbing landed birds, and with regard to landowner requirements and observer safety.

During searches in the final week before the count, crane numbers were estimated at each roost to assist in composing teams of observers with appropriate numbers, skill level, and equipment. Observers were recruited from BirdLife Australia members, birdwatchers, landowners and other members of the public, using a range of media. Experienced counters led teams of (usually) 2–6 observers and allocated the roles of data recorder, timekeeper, counter and identification checker. Participants were provided with datasheets and used their own optical equipment; those with telescopes were allocated to the most appropriate roosts. Materials and advice on the method and species identification were provided beforehand and during the survey, and, to further minimise the risk of misidentification, observers were encouraged to use the category ‘Unidentified’ in case of doubt. Watches were synchronised before the count. Counts began in the late afternoon (nominally 1700 h but this varied considerably) and ended when it was too dark to count numbers.

Data recorded

Cranes present at the roost at commencement were counted and identified. Those arriving subsequently were counted in flight, identified (or recorded as unidentified), and the time of their arrival (to 1 minute) and number landing noted. Birds leaving the roost after landing were entered as a negative number. Observers noted comments, including crane behaviour and any factors potentially disturbing the survey. From 1997 to 2008, to gauge the possibility that cranes could be missed because they arrivied at roosts after dark, observers were specifically asked whether any cranes arrived after it became too dark to count them. Datasheets were examined immediately after the count and queries discussed with team leaders before data entry.

Differences in surveys between years

The 1997 survey took place in early November, surveys from 1998 to 2009 in early October, and those from 2010 to 2017 in early September. The 2009 survey was confined to only six roosts in the central Tablelands, and the 2010 survey to the same six roosts plus one in the southern Tablelands. In all districts in all other years, one or two known roosts with small numbers of cranes (estimated <4 birds) were not counted, because of insufficient observers. New southern Tablelands locations were discovered and counted from 2003 (Kaban) and 2007 (Tumoulin). In the central Tablelands, one roost (Curry Wilson: Tinaroo cluster) was counted in 1998–2016, and in 1997 data for this roost were estimated from birds recorded flying over an adjacent roost. In the Innot Hot Springs (Innot) district of the southern Tablelands, a large roost (General Plains Swamp) was discovered in 1999 (Reardon 2007) and has been counted in most years since then. Additional roosts in the Innot district were discovered in 2004 and 2013 but appear to have been unavailable (because dry) or not used in most years. Until 2012, counts in the Innot district took place on the same day as elsewhere on the Tablelands, but from 2013 they were held 3–21 days later. For these reasons, and especially because the number of active roosts varied markedly from year to year, the number of roosts counted varied from as few as six (2009) to 20 (2008). The mean number of roosts counted was 13.3 (14.1 when 2009 and 2010 were excluded).

Analysis of data

Except where explicitly stated, Innot district roosts have not been included in the analysis because roost usage there was assessed only intermittently and counts were not always conducted on the same day as elsewhere. Unqualified generic statements about patterns across the Tablelands therefore do not include these roosts.

We examined annual totals by species with unidentified birds as a category for all roosts combined, and for each of seven eco-geographic roost clusters (six on the Tablelands plus the Innot cluster: Table 1). Roost clusters are employed as a descriptive tool. Each had a characteristic proportional composition of crane species generally maintained over time, were neighbouring (Figure 1), and roosts within a cluster occurred in similar landscape settings (Table 2). In an additional analysis, unidentified cranes were attributed to species for each roost cluster in proportion to the totals counted across all years in that cluster (see Discussion).

We examined trends over time in total crane numbers, evaluating the effects of year and time of survey (early October cf. early September), discarding the 1997 data (counted in early November) and the incomplete counts of 2009 and 2010. We did so in the DISTLM module of PERMANOVA+ (Anderson *et al.* 2008), evaluating alternative models using the Akaike Information Criterion corrected for small sample sizes. PERMANOVA+ evaluates models by permutation rather than assumed statistical distributions, and is thus robust for non-normal distributions and unequal variances.

Times of sunset and end of evening civil twilight were obtained from Geoscience Australia (2015). These terms are defined precisely by Geoscience Australia (undated) and we defined ‘twilight’ as the period between them. Using those counts for which cranes were present and data on the time of arrival are available (214 of 260 counts), we examined time of arrival relative to sunset. These analyses were complicated by variation in the time of commencement and conclusion of the survey, so we have considered these with subsets of the data in several ways (see Results).

To test (in part) the possibility of cranes being missed because of their moving from known active roosts to new, undiscovered roosts before the count, we used Google

Table 1. Number of crane roosts counted from 1997 to 2017 by eco-geographic clusters and years on the Atherton Tablelands, far north Queensland. Clusters are as shown in Figure 1 and detailed in Table 2.

Cluster	*Year (19– or 20–)*																				
	97	*98*	*99*	*00*	*01*	*02*	*03*	*04*	*05*	*06*	*07*	*08*	*09*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*
Bromfield	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Central dams	1	1	1	1	1	1	1	3	2	2	2	3	0	0	0	0	1	0	1	1	1
Hasties	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2
North-west	1	1	2	2	1	1	1	1	1	1	1	2	0	0	1	1	1	1	1	0	1
Tinaroo	7	6	8	8	9	11	5	7	7	8	8	8	4	4	4	6	8	6	6	6	0
Tumoulin	0	0	0	0	0	0	1	2	2	2	3	4	0	1	2	4	4	2	4	3	3
Innot	0	0	1	0	1	1	1	2	2	2	2	1	0	0	0	1	2	1	1	1	1
Total	**11**	**10**	**14**	**13**	**14**	**16**	**11**	**17**	**16**	**17**	**18**	**20**	**6**	**7**	**9**	**14**	**18**	**12**	**15**	**13**	**9**

Table 2. Characteristics of seven eco-geographic clusters of crane roosts on the Atherton Tablelands, far north Queensland. Table 1 shows the number of roosts counted in each cluster in each year. KBA = Atherton Tablelands Key Biodiversity Area, as shown in Figure 1.

Cluster	*No. roosts*	*No. roosts in KBA*	*Characteristics*
Bromfield	1	1	Wetland in crater, surrounded by pasture. Major roost, counted every year.
Central dams	4	3	Private dams in farmland, Yungaburra area.
Hasties	2	2	Hasties Swamp, historically a major wetland roost, counted every year; nearby Willetts Swamp, used and counted in 2017.
North-west	3	0	A cluster of roosts in the drier north-west of study area including Mareeba Wetlands, the latter counted most years.
Tinaroo	14	14	Shoreline of Lake Tinaroo, a large impoundment whose levels fluctuate markedly. Roost usage varied with water levels.
Tumoulin	5	0	A cluster of farm dams and a wetland near the village of Tumoulin on the inland side of the Evelyn Tableland. Discovered and first counted in 2003.
Innot	3	0	A cluster around an isolated agricultural irrigation area. The major roost (General Plains Swamp) used and counted in most years from 1999.

Table 3. Total numbers of cranes (Sarus Cranes, Brolgas and unidentified cranes) counted on the Atherton Tablelands, far north Queensland, across all years for each roost cluster and the attribution of unidentified birds to species. Total excludes Innot cluster.

	Counts				*Attribution of unidentified birds*	
Roost cluster	*Sarus*	*Brolga*	*% Sarus*	*Unidentified*	*To Sarus*	*To Brolga*
Bromfield	6962	1604	81.3	6084	4945	1139
Central dams	805	7	99.1	2603	2581	22
Hasties	1862	324	85.2	1263	1076	187
North-west	490	1662	22.8	2385	543	1842
Tinaroo	7776	14	99.8	4401	4393	8
Tumoulin	493	6360	7.2	2217	159	2058
Innot	869	13,136	6.2	6462	401	6061
Total	**18,388**	**9971**	**64.8**	**18,953**	**13,697**	**5256**

Earth Pro to estimate the distance from roosts where no cranes were recorded (despite being registered as active during searches) to the nearest occupied site. We estimated crane flight times between these sites based on measured speeds of Tablelands cranes flying to roosts (80 kph: Scambler 1997a). Unoccupied roosts were classified as 'adjacent' to occupied roosts (<2 km distance, <1 min. crane flight time), 'local' (2–5 km, 1–4 min.) or 'remote' (>5 km, >4 min.) from them.

To compare actual and estimated numbers of Brolgas and Sarus Cranes with national and global population ranges, we used the geometric means of population ranges (Wetlands International 2012; Mirande & Harris 2019) and calculated rounded 1% thresholds: Sarus Crane—national: range 5000–10,000, mean 7071, 1% = 70; global: range 13,550–20,650, mean 16,727, 1% = 170; Brolga—national and global: range 50,000–100,000, mean 70,711, 1% = 710.

Results

Annual totals

Excluding the years with incomplete counts (2009, 2010), the number of cranes counted (Innot cluster excepted) ranged from 1170 to 3735 (mean 2306), the percentage unidentified from 20.1 to 65.5% (mean 39.5%) and Sarus Cranes as a percentage of identified cranes from 37.0 to 92.7% (mean 66.2%) (Figure 2a). With attribution of unidentified birds (Table 3), the estimated number of Sarus Cranes ranged from 826 to 3255 (mean 1539) and the estimated number of Brolgas from 308 to 1613 (mean 767) (Figure 2b).

Both Sarus Cranes and Brolgas were recorded in all seven roost clusters but with strong geographic differentiation in relative abundance among those cranes identified (Table 3, Figure 3). Sarus Cranes predominated in the

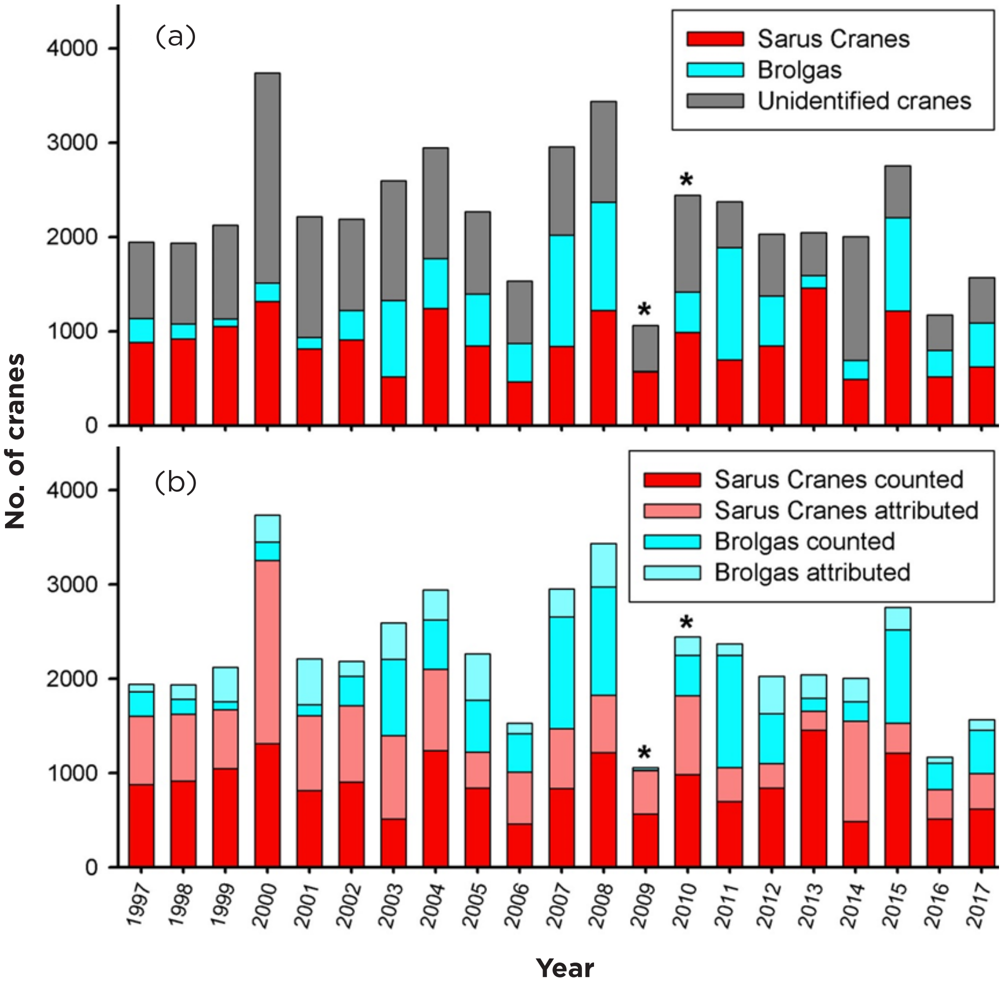

Figure 2. Number of cranes counted in annual roost counts on the Atherton Tablelands, far north Queensland: (a) raw counts, (b) with unidentified birds attributed to species. Innot cluster roosts are not included. Asterisks indicate years with incomplete counts not based on a prior assessment of roosts at which cranes were present; these have been excluded from most analyses.

central Tablelands clusters [Bromfield, Central dams, Hasties (2017 excepted), Tinaroo] corresponding with the Atherton Tablelands KBA, whereas Brolgas predominated outside the KBA in the north-west cluster, the south-west Tumoulin cluster and the Innot cluster. The number of Sarus Cranes counted in the KBA ranged from 458 to 1313 (mean 834) and estimated in the KBA from 826 to 3189 (mean 1444) (Figure 4a), and the estimated number of Sarus Cranes on the Atherton Tablelands within the KBA ranged from 79.9 to 100% (mean 94.1%) (Figure 4b).

In years when one or more roosts in the Innot cluster were counted, from 276 to 2586 (mean 1364) cranes were counted there, with 93.8% of identified cranes being Brolgas, and 31.6% of cranes unidentified (Figure 3g). In years when Innot was counted on the same day as other Tablelands roosts, it contributed from 485 to 2586 additional cranes, with a combined maximum total of 3469. In 2013 (when it was not counted simultaneously), it contributed 1204 more counted Brolgas than the entire counted plus attributed total of Brolgas for the rest of the Tablelands.

The effect of month of survey on total cranes counted was marginally non-significant (Pseudo-$F_{2, 16}$ = 3.38, P = 0.09) and that of year less so (Pseudo-$F_{2, 16}$ = 2.19, P = 0.16). There was no clear support for the addition of year to a model with time of year alone (ΔAIC_c = 2.9). On average, 546 more cranes were counted in early October (1998–2008) than in early September (2011–2017) (Figure 5). The 1997 count fell within the range of subsequent counts though outside the 95% confidence interval for the mean of counts from 1998 to 2008 (Figure 5).

Based only on numbers of identified Sarus Cranes, the main Tablelands recorded ≥1% of both the national and global populations in all 21 years (Table 4), up to ~21% of the national population (mean 12.38%) and up to 8.69% of global population (mean 5.23%). Based on identified Brolgas counted, the main Tablelands reported ≥1% of the global population in 5 years (mainly in the Tumoulin cluster) and the Innot cluster reported ≥1% in 8 years.

Time of arrival at roosts

The majority of cranes counted (54.1%) arrived at roosts after sunset (Figure 6), with 14.5% arriving after the end of civil twilight (Figure 7a) but these rates varied with the identification. Identified Brolgas were present at or arrived on average earlier than identified Sarus Cranes, and

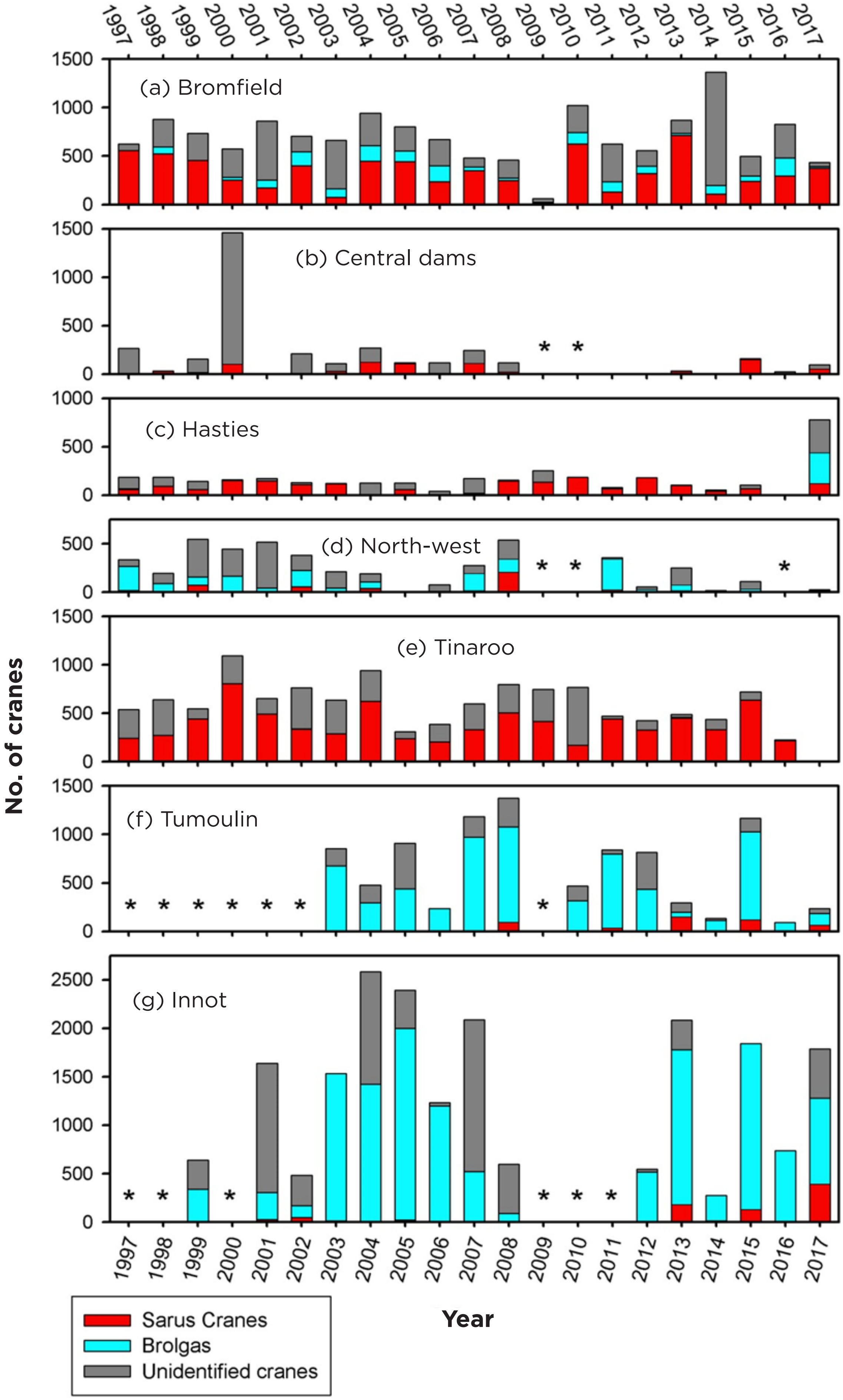

Figure 3. Number of cranes counted by species in annual roost counts in seven eco-geographic clusters of roosts on the Atherton Tablelands, far north Queensland. Asterisks indicate years when the cluster was not counted; other absences mean that no cranes were present.

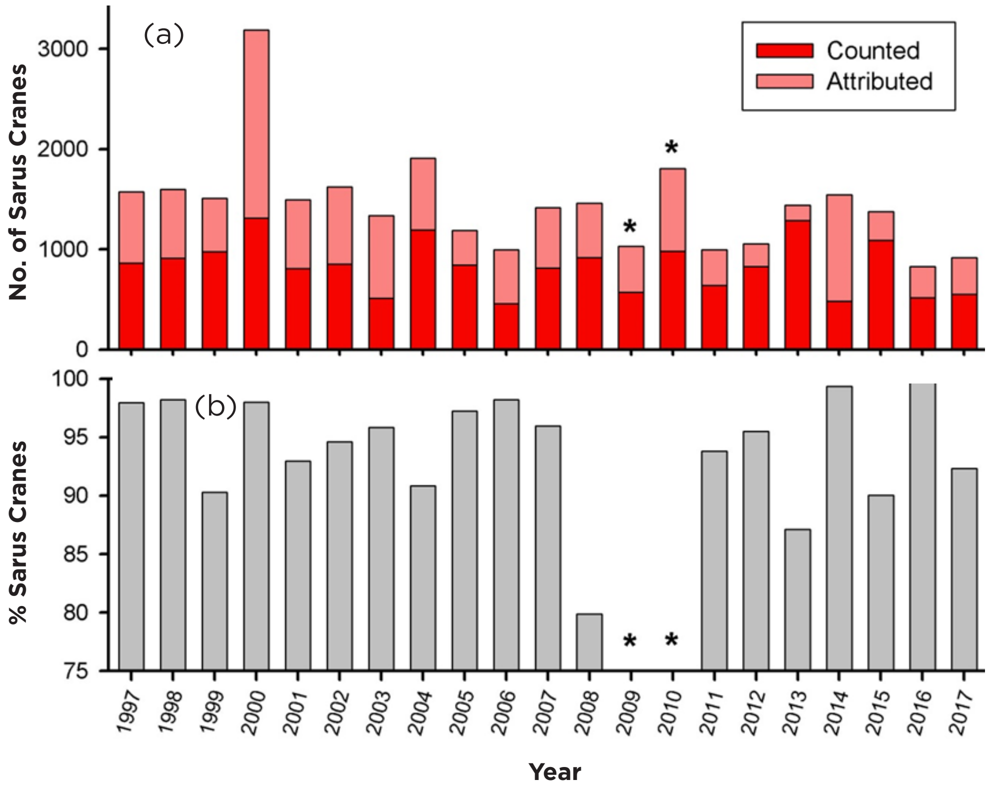

Figure 4. Sarus Cranes on the Atherton Tablelands KBA: (a) counted and attributed, and (b) as a percentage of those estimated (counts plus attributions) on the Tablelands (Innot cluster excepted). Asterisks indicate years with incomplete counts not based on a prior assessment of roosts at which cranes were present, and thus for which calculation of the percentage is not appropriate.

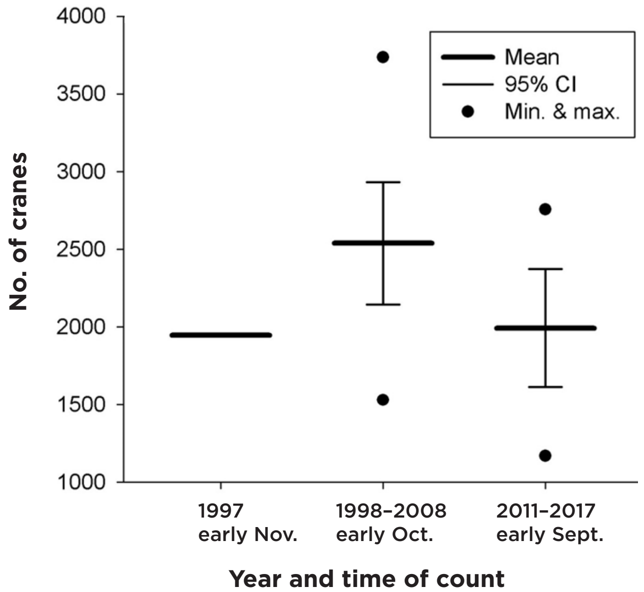

Figure 5. Difference between years in the total number of cranes counted on the Atherton Tablelands, far north Queensland, with years grouped according to the time of year at which they were counted. CI = Confidence interval.

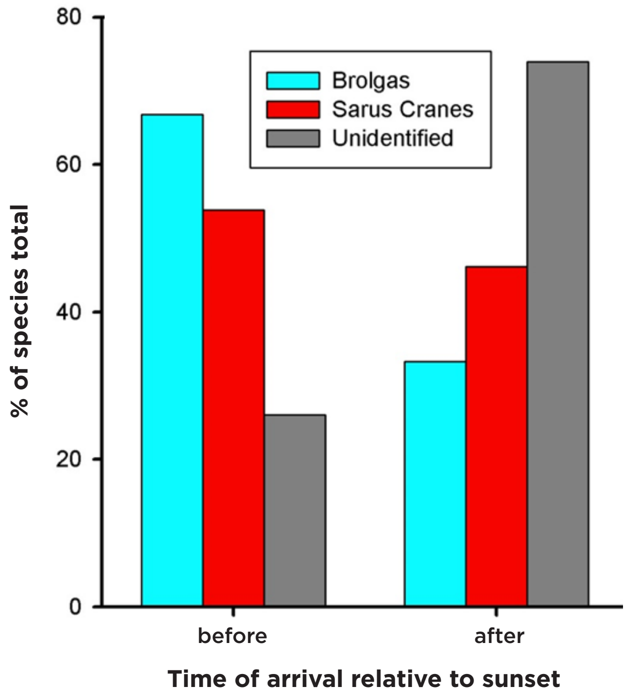

Figure 6. Presence or arrival of Brolgas and Sarus Cranes at roost-sites on the Atherton Tablelands, far north Queensland, before and after sunset. Cranes that arrived exactly at sunset are scored as 'after'. Sample sizes are: 214 roost counts, 5558 flocks (flocks containing both species, or with some unidentified, are counted as more than one flock) and 44,453 cranes.

Table 4. Actual (A) and estimated (E) numbers of Brolgas and Sarus Cranes, Atherton Tablelands, far north Queensland, as percentages of national and global population ranges. Percentages and 1% thresholds are calculated using the geometric means of population ranges (see Methods). All estimated numbers include unidentified cranes attributed to species.

	No. years ≥1%		*% population*		*Mean % population*	
	A	*E*	*A*	*E*	*A*	*E*
Sarus Crane (main Tablelands)						
National	21	21	6.5–20.6	11.6–46.0	12.38	21.6
Global	21	21	2.8–8.7	4.9–19.5	5.23	9.1
Brolga						
Main Tablelands	5	8	0.01–1.7	0.04–2.3	0.67	1.0
Innot	8	10	0.1–2.8	0.4–3.6	1.24	1.8

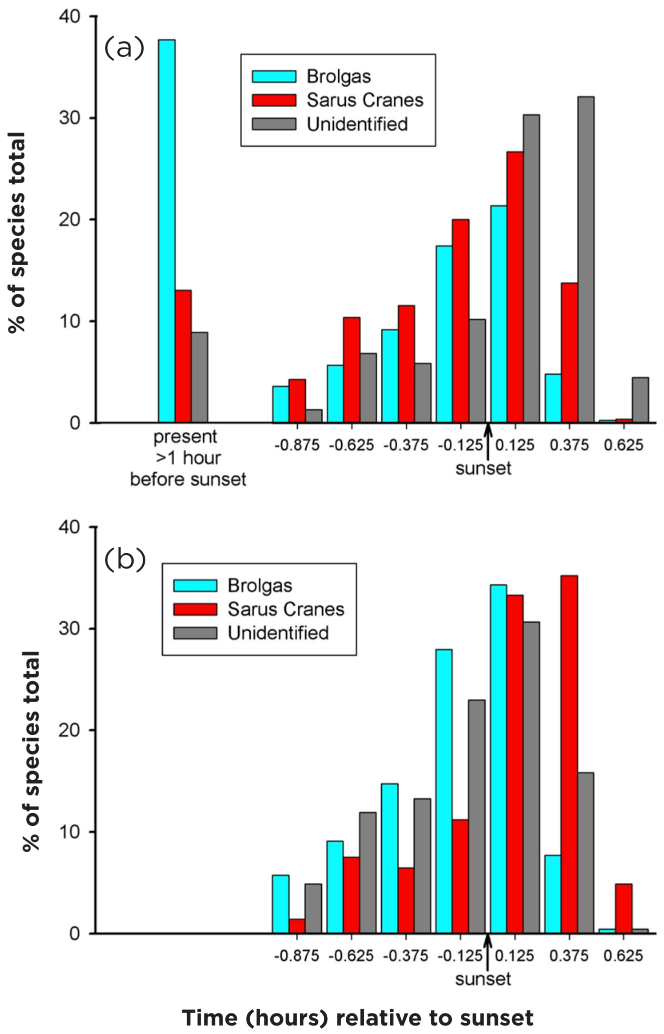

Figure 7. Presence or arrival of Brolgas and Sarus Cranes at roost-sites on the Atherton Tablelands, far north Queensland, in time intervals relative to sunset using only counts that commenced ≥1 hour before sunset: (a) all cranes, (b) recalculated using only those cranes that arrived <1 hour before sunset. Cranes that arrived exactly at sunset are scored as arriving in the interval immediately after it. Sample sizes are: 158 roost counts, 3823 flocks (flocks containing both species, or with some unidentified, are counted as more than one flock), and 30,381 cranes. Twilight lasted from 21 to 23 minutes after sunset.

birds that arrived after sunset were much less likely to be identified. These trends are elaborated when considering only those counts that commenced >1 hour before sunset (Figure 7a), with identified Brolgas very much more likely to be present or arrive at the roost >1 hour before sunset. When only those that arrived <1 hour before sunset are considered (Figure 7b), identified Brolgas still tended to arrive earlier than identified Sarus Cranes but the trend was weaker. For the 163 counts for which observers were asked whether cranes arrived after it was too dark to count them, 71.1% responded 'no', 20.3% responded 'yes' and 8.6% did not provide an answer.

Flock size and composition

Most cranes flew in to roosts but observers reported them walking in on 34 occasions (0.7%). Of these, 25 were Brolgas, three were Sarus Cranes and the cranes of six flocks were not identified. Flocks flying in to roosts contained from one to an estimated 300 birds and 49.9% of flocks contained 2–4 birds, with a median flock size of four, and a mean of 7.7 (Figure 8). Median flock size of Brolgas was identical to that of Sarus Cranes and the mean flock sizes were similar, but the small number of flocks containing both species were considerably larger

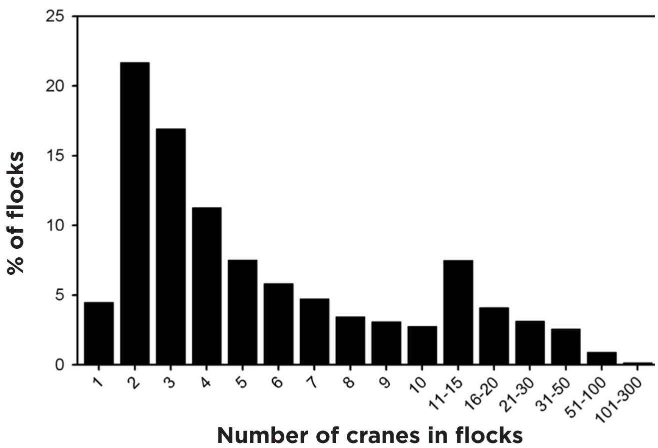

Figure 8. Crane flocks (*n* = 5185) arriving at roosts on the Atherton Tablelands, far north Queensland: percentages of different-sized flocks.

Table 5. Features of 5185 crane flocks arriving at roosts on the Atherton Tablelands, far north Queensland, according to their composition

Composition	*% of flocks*	*No. of cranes*	
		Mean	*Median*
Brolgas	19.7	6.6	4
Sarus Cranes	44.4	6.3	4
Brolgas & Sarus Cranes	1.5	21.8	11
Unidentified	33.3	9.5	5
Mixed identified & unidentified	1.1	11.6	9

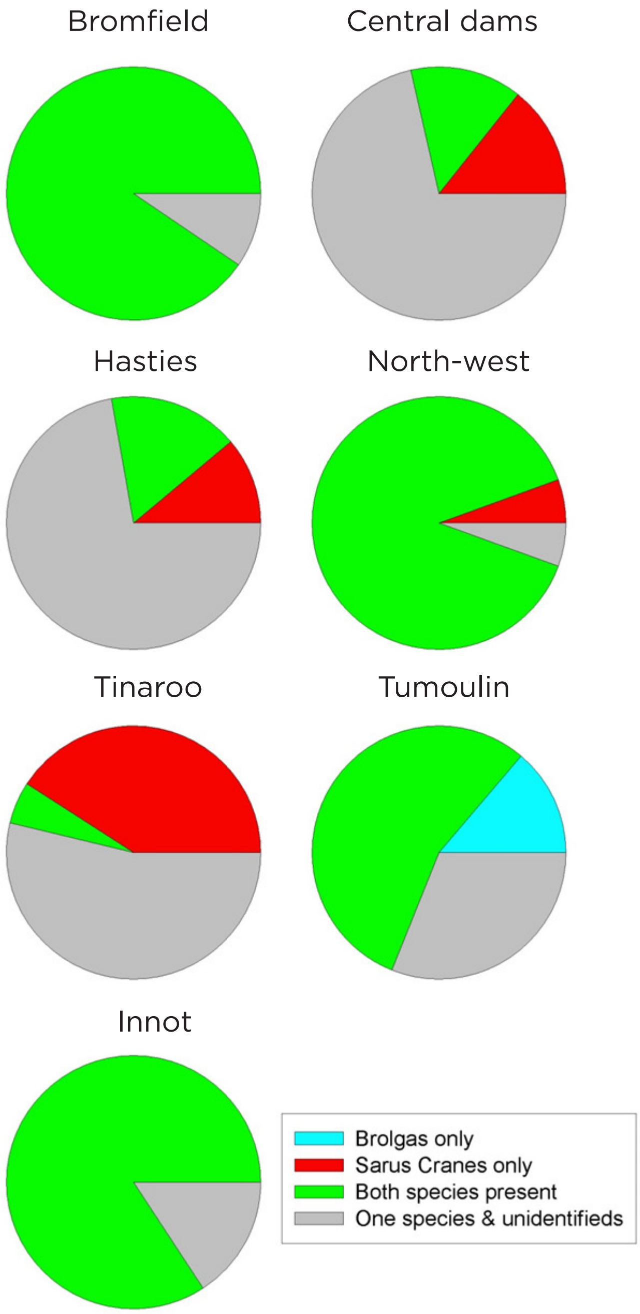

Figure 9. Crane species composition of roosts in seven roost clusters on the Atherton Tablelands, far north Queensland, using counts in which at least 10 cranes were identified. Sample sizes (roost counts) are: Bromfield 21, Central dams 14, Hasties 18, North-west 18, Tinaroo 93, Tumoulin 29 and Innot 19.

(Table 5). However, these calculations are confounded by the substantial portion of flocks that contained unidentified birds, these also having higher means and medians than for single-species flocks, so should be interpreted with caution.

Sharing of roosts

Overall, 31.6% of roost counts in which at least 10 cranes were identified included both species, with 2.1% including Brolgas alone, 22.3% including Sarus Cranes alone and a further 44.0% including one identified species plus unidentified cranes. However, this pattern varied markedly between roost clusters (Figure 9), with single-species roosts demonstrably outnumbering mixed-species roosts only in the Tinaroo cluster where 99.8% of all identified cranes were Sarus Cranes (Table 3). At shared roosts, both species roosted in family parties but these were intermingled with parties of the other species. An exception was a major roost in the Innot cluster where the two species occupied different parts of the site.

Unoccupied roosts

Of 260 roosts counted in all clusters but Innot, 22 (8.5%) recorded no cranes landing despite being classed as active in the preceding week. Nineteen of these had from one to four ‘adjacent’ or ‘local’ occupied roosts nearby. The remaining three unoccupied roosts (1% of those counted) were ‘remote’ from the nearest occupied site (11–38 km, 8–38 min. crane flight time away). Most unoccupied roosts were in the Tinaroo cluster and cranes were recorded flying over without landing. In 9 years, no unoccupied roosts were reported; in 11 years, 1–3 roosts; and in 1 year (2016), seven recently active roosts were found to attract no cranes. No unoccupied roosts were recorded in the Innot cluster.

Discussion

Using an annual volunteer count at roosts, we have demonstrated that the Atherton Tablelands has provided non-breeding habitat over many years for significant numbers of Australia’s two species of cranes. We have also demonstrated sharing of roosts by the two species and even mixed-species flocks arriving at them, but also marked differences between species in their spatial use of the Tablelands and in their time of arrival at roosts. This we have done notwithstanding high year-to-year variation in counts, and substantial problems with identification of the species especially as many individuals arrived at roosts after sunset, and even in the dark so late that they could not even be counted. Here, we explore these issues.

The Atherton Tablelands as crane habitat

At a minimum, more than a thousand cranes use the Atherton Tablelands as an overwintering site each year. The figure is likely to be, and is often demonstrably, much higher. In 2000, 3735 cranes were counted on the same day. Furthermore, the Innot area contributed about an additional 500–2600 cranes when counted simultaneously with the rest of the Tablelands; similar counts at Innot in years with a 3–21-day disjunction in timing suggest that these too are additional to the main Tablelands counts.

The Atherton Tablelands is nationally and internationally significant for both crane species. For Sarus Cranes, the main Tablelands supported ≥1% of the national and global population (respectively 70 and 170 birds, population ranges 5000–10,000 and 13,550–20,650: Mirande & Harris 2019) in all years based on birds identified to species alone, and up to 46% of the estimated national population and 19.5% of global Sarus Cranes including unidentified birds attributed to species. If Australian Sarus Crane numbers are as low as 5000 adults (Mirande & Harris 2019), then the majority of the population (3250, or 3052 excluding 6.1% first-year birds: Grant 2005) was present on the Tablelands in the year 2000. Both Lake Tinaroo and Bromfield Swamp, a nationally important wetland (Department of Environment and Science, Queensland 2019), were nationally and internationally significant based on counts of Sarus Cranes over 21 years.

For Brolgas, the Innot cluster supported ≥1% of the global Brolga population (710 birds, population 50,000–100,000: Mirande & Harris 2019) in 10 years, including birds attributed to species, and even the Sarus-dominated main Tablelands supported ≥1% of global Brolgas in some years, mainly in the Tumoulin cluster. In 2007, when the main Tablelands and Innot cluster were counted simultaneously, the combined Brolga total was 3469, including birds attributed to species, ~4.9% of the global population. This figure gives the first minimum population estimate for Brolgas in the Tablelands wintering region.

The high count of 3250 Sarus Cranes (including birds attributed to species) in the year 2000 provides for the first time a survey-based minimum baseline for estimating the population of Australian Sarus Cranes, but we are unable to suggest a revision of the estimated population range (Mirande & Harris 2019) based on this study alone. The Atherton Tablelands is the only currently known concentrated wintering location for Australian Sarus Cranes: other Sarus Cranes are assumed to spend the non-breeding season dispersed in the Gulf Plains and Cape York Peninsula (Marchant & Higgins 1993; Barrett *et al*. 2003), where there are no systematic counts and even incidental records are sparse. Our counts include all age classes. Except for limited data on the proportion of first-year Sarus Cranes on the Tablelands (Grant 2005), there are no metrics for age classes in Sarus Cranes or Brolgas in the migrating populations, which would enable our estimates to be refined to report the numbers of breeding adults.

The strong, though far from absolute, spatial segregation of the species by roost clusters was consistent across years and corresponds with the spatial pattern observed by Nevard *et al.* (2019a) for crane feeding sites on the Tablelands. Sarus Cranes preferred roosts in the central area of the Tablelands around Atherton and Lake Tinaroo, where soils are volcanic and fertile, but most Brolgas roosted in outlying areas to the north-west and south-west, feeding in areas with mostly alluvial soils. This partly corresponds with a preference for crops as feeding sites by Sarus Cranes and pasture and wetlands by Brolgas (Nevard *et al.* 2019b) but the feeding-site preferences are nowhere near as strong as the spatial segregation suggests. The tendency for Sarus Cranes to be more folivorous than Brolgas (which consume more corms and invertebrates), at least at their Gulf breeding sites (Sundar *et al.* 2019), may mean that Sarus Cranes need more-fertile soils to maintain positive energy balance. It is also possible that this spatial pattern is accentuated by Sarus Cranes being physically dominant at richer food sources, though the evidence for this is at best equivocal (Nevard *et al*. 2019a).

In all years, almost all Sarus Cranes surveyed were concentrated in the Atherton Tablelands KBA, which confirms the KBA boundaries set in 2009. At least 1% of the estimated global population of the Vulnerable Sarus Crane occupies the KBA every year, which meets the criteria for a trigger species (IUCN 2016). BirdLife Northern Queensland monitors Sarus Cranes in the KBA annually using numbers from the count. Despite caveats (see below), the technique that we have developed to attribute unidentified cranes to species will enable monitoring reports to include numbers of attributed birds, which enhances the value of count data for conservation planning (Brouwer *et al*. 2003; Wetlands International 2006).

Our data do not strongly suggest a trend in numbers of cranes on the Tablelands over 21 years, though interpretation is strongly confounded by year-to-year fluctuation in numbers as well as change to the timing of counts. For Sarus Cranes, lack of trend is consistent with the view of Garnett & Crowley (2000) that the population is stable, rather than increasing as suggested by Archibald & Swengel (1987). However, the latter paper precedes our study and might accurately reflect the earlier initial colonisation of the Tablelands by Sarus Cranes.

Reasons for the extreme fluctuations in total counts from year to year are not apparent from our data. However we suggest two reasons for them: resource-driven variation in movements (as demonstrated for Common Cranes *Grus grus* in Spain: Alonso *et al.* 1994) and variation in the source breeding populations because of differences in survival and recruitment. Tablelands cranes are assumed to be short-distance migrants (Nevard *et al*. 2020), breeding in the nearby Gulf Plains during the wet season (Sundar *et al.* 2019), giving them potentially greater flexibility than may be available to long-distance migrants. Though (as above) some remain in the Gulf throughout the year, some might migrate elsewhere, movement patterns which might vary from year to year. The feeding sites used by cranes on the Tablelands, primarily grain stubble, pasture and crops sown early (Grant 2002; Nevard *et al*. 2019a), are subject to seasonal conditions and spatial and long-term variation in cropping patterns (see also Nevard *et al*. 2019b). Breeding by cranes in the Gulf Plains is synchronised with the onset of seasonal rainfall (Sundar *et al*. 2019), the timing of which varies from year to year (Bureau of Meteorology undated). Thus, early, late or unseasonal rains might draw cranes away from the Tablelands to breeding sites earlier or later than usual.

There is no information on annual recruitment or survival for the migrating population of Brolgas. Annual recruitment in Sarus Cranes assessed on the Tablelands was relatively constant at an average of 6.6% over a 6-year period (Grant 2005) although exceptionally low and high recruitment rates have been observed more recently (J.D.A. Grant pers. comm.). There is no significant within-year mortality in first-year Sarus Cranes on the Tablelands (Grant pers. comm.) but nothing is known of mortality rates outside our study area. Very high numbers of Sarus Cranes counted in 2000 coincided with a below-average recruitment rate of 6.21% (Grant 2005), although search effort was consistent with other full-search years, and an average number of roosts (13) was occupied.

Crane behaviour

Flock sizes arriving at roosts in this study are comparable with those in many other crane populations with similar numbers at roosts (Walkinshaw 1973), and the prevalence of two-, three- and four-member flocks is consistent with the family-based social structure of all crane species (Johnsgard 1983). Larger flocks may comprise non-family cranes and family groups aggregating as they approach or leave roosts (Lovvorn & Kirkpatrick 1981), so to an extent reported flock sizes may well reflect the distance from the roost when the flocks are counted. Groups combining on approach to roosts may explain the larger size of the few mixed-species flocks that we recorded. Smith (1971) and Swaby (1983) noted only single-species flocks of cranes flying into roosts.

We identified a marked difference in time of arrival between sympatric crane species sharing communal roosts, with Sarus Cranes arriving much later. We can only speculate about the reasons for this. As discussed above, a more-folivorous diet in Sarus Cranes may necessitate more time spent feeding than Brolgas. Roosts and feeding sites of Brolgas are at times more-or-less identical and might at times preclude the need for flights between them. On the Tablelands, Sarus Cranes frequently forage further from roost-sites than do Brolgas (Nevard *et al*. 2019a). Both Smith (1971) and Swaby (1983) reported that Sarus Cranes arrived at roosts before Brolgas, which suggests an (unexplained) behavioural change before 1997. These results also suggest that, proportionally, the population of Sarus Cranes based on identified birds is more severely underestimated than that of Brolgas.

Intermingled sharing of roosts by Sarus Cranes and Brolgas was reported in all eco-geographic clusters but was most notable at Bromfield Swamp in the KBA, and in all three clusters outside the KBA. TDN (pers. obs.) typically noted intermingling of Sarus Cranes and Brolgas at the Mareeba Wetlands roost. Earlier Tablelands records noted spatial separation at shared roosts (Bravery 1969; Swaby 1983), suggesting another change in behaviour over time. Species mingling at shared communal roosts is apparently rare among cranes, with spatial separation the norm where several species share a roost. However, we note as a possible qualifier that despite Berg's (1924) account of separation at mixed roosts of Common Cranes and Demoiselle Cranes *Grus virgo* in Egypt, at exceptionally large mixed roosts of these species in India (K.S.G. Sundar pers. comm.) it is not possible to differentiate the species because of their similarity and/or their late arrival and early departure from the roost when light is poor.

Challenges in counting cranes

Our study necessarily comes with a number of caveats that reflect both inherent challenges and changes over time to counting methods.

It is possible that, despite extensive searches, some smaller active roosts remained undiscovered. In most cases, roost shifting immediately before the count was localised and is unlikely to have affected the counts, but it is plausible that during the 1-month search period before the count some cranes shifted roosts to sites not identified as active, and thus were missed. The effect, if any, will have been to count fewer cranes than were actually present, but quantifying its extent would require an impossibly large effort because patterns of change are likely to be roost- and time-specific. Underestimation might also be caused by the arrival of cranes at roosts after dark, too late to be counted.

The limited number of observers has often prevented the Innot cluster of roosts from being counted on the same day as the main count. Comparison of counts conducted simultaneously or not does not suggest that there has been significant double-counting or under-counting as a result. This has likely been facilitated by the Innot cluster of roosts being relatively remote from other roosts, thus reducing the risk of movements between them in the interval.

The substantial proportion of cranes that could not be identified derives both from arrival of cranes at roosts in poor light and the difficulty of distinguishing these species. Participants inevitably had varying levels of experience, but even experienced observers can struggle with crane identification at a distance and in poor light. Incomplete evening counts typically cannot be repeated next morning (e.g. Alonso *et al*. 1985; Allan 1995) because of morning mist, which persists until many cranes have departed (Swaby 1983). Population studies need to report unidentified birds and treatment of these needs to be explicit (Brouwer *et al*. 2003; Wetlands International 2006). Attribution to species may be based on the ratio of those identified to species in the same or a related survey, provided account is taken of habitat homogeneity or differences, and detectability (Day 2011). Our extrapolation based on the observed proportion within eco-geographic clusters of roosts takes habitat into account but does not account for the later arrival at roosts of Sarus Cranes often when light is failing. It is likely, therefore, that the number of Sarus Cranes has been somewhat underestimated and the number of Brolgas somewhat overestimated, but the extent of the problem is unclear and varies from year to year.

Initial uncertainty about the best time of year to conduct the surveys triggered a 2-month shift in their annual timing and this has hindered identification of population trends. With continued counting in early September, long-term trends may become clearer though year-to-year variation is likely to remain a substantial confounding factor.

Our key recommendations for future surveys are: to always conduct them in early September; to conduct all surveys on the same day if possible or, if not, to count the most distant sites (e.g. Innot area) on a day as close as possible to the main count; and to continue and if possible enhance training of observers in identification and recording skills. One avenue for enhancing identification of species in poor light without changing method could be the use of night-vision binoculars and telescopes, as recommended by Allison & Destefano (2006) for roosting Sandhill Cranes. A formal trial could be conducted if an initial field test suggests such equipment may be helpful in Tablelands conditions. As the reason for later arrival at roosts by Sarus Cranes is unknown, and because this behaviour might have changed and may change again over time, it would assist future analysis of time of arrival at roosts to always begin counts at least 1 hour before sunset.

Sympatry between such closely related crane species is rare (Mirande & Harris 2019). Further studies of the behavioural differences that we have reported in roost-site selection and time of arrival at roosts would extend knowledge of both species' ecology, and their interactions that enable such sympatry. For example, documenting crane behaviour after arrival to record the extent to which Brolgas spend time feeding (compared with comfort and social behaviours) could extend the finding of Nevard *et al*. (2019a), that Brolgas feed more often in wetlands during the day than do Sarus Cranes, to include a preferential selection by Brolgas of roost-sites with food resources. Mingling by Brolgas and Sarus Cranes at most roost-sites was observed throughout this study but is largely undocumented. To explore this apparently rare behaviour at multi-species wintering crane roosts, details of proximity and activities could be recorded during roost arrival and also throughout the night-roosting period using equipment such as sensor cameras or thermal drones.

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