Australian Field Ornithology 2021, **38**, 87–98
http://dx.doi.org/10.20938/afo38087098

Malleefowl *Leipoa ocellata* breeding behaviour: Insights from citizen science camera surveillance

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Abstract. Observations on natural history are a useful but often overlooked branch of ecology. With the use of camera-traps, collection of data e.g. on breeding behaviour and success has never been easier, particularly when studying cryptic species. Additionally, camera-traps are well suited to citizen science because of their ease of operation and the ability to store and verify data. Malleefowl *Leipoa ocellata* breeding behaviour has previously been studied through direct observation or time-lapse photography, resulting in small sample sizes and potentially biased observations. Using camera-trap data collected by citizen scientists, we examined the breeding behaviour of this species. We quantified the timing and duration of mound-tending activities at 20 mounds using camera surveillance for >30,000 hours (1250 days) over six breeding seasons. Time spent at the mound during five mound stages and visit frequencies by the male and female during each stage are reported. Female involvement at the mound was consistent, although males spent three times as long at the mound compared with females during egg-laying. On egg-laying days, females spent longer uncovering the mound, compared with covering the mound post egg-laying. Our findings confirm that both male and female Malleefowl spend a substantial amount of time constructing and maintaining their mound throughout the year and, most notably, that the female consistently participates in mound-tending. These insights are particularly valuable as our surveillance was over markedly longer time spans than previous studies that relied upon direct observation.

Introduction

Observations on natural history extend our knowledge of the biology of a species and act as a basis for generating hypotheses that can be tested experimentally. However, despite their usefulness, particularly around breeding behaviour, they are often undervalued in ecology (Barrows *et al.* 2016). Quantitative data can be challenging to collect via direct observation because it is time-consuming and requires specific expertise, but remote motion-sensor cameras (camera-traps) are an increasingly useful and affordable tool (Meek *et al.* 2015). Breeding ecology is particularly suited to surveillance methods, especially when activity is centred around a fixed focal point such as a den, nest or hollow (Brandis *et al.* 2014). Furthermore, the use of camera-traps is often appropriate in projects involving volunteers or citizen scientists as camera operation does not require expert skills, and data can be stored and verified by a supervising expert. Stored camera data can potentially be applied to *ad hoc* research questions (in addition to the original intended purpose of surveillance), creating an even more valuable, multipurpose dataset.

The Malleefowl *Leipoa ocellata* (Megapodiidae) is a shy and elusive ground-dwelling bird that is difficult to observe in the Australian semi-arid mallee *Eucalyptus* spp. woodlands that it inhabits. It is one of 22 species of megapode, found across south-eastern Asia, Australia and the Pacific, that uniquely incubate their eggs using external heat sources (Jones & Birks 1992). Malleefowl incubate their eggs in large, conspicuous mounds and concentrate activity at these mounds for up to 11 months of the year (Frith 1959). They create a mound during winter by excavating a large depression and filling it with leaf-litter (Frith 1959), which starts to decompose and release heat after exposure to winter rainfall (Frith 1956). When the correct incubation temperature is reached, the female lays eggs in the centre of the mound, which is again covered with litter and sand. Studies from the 1950s to 1990s, using direct observations and time-lapse photography, suggest that Malleefowl spend considerable time constructing and maintaining mounds (Frith 1956, 1959; Weathers & Seymour 1998), but quantitative data are needed to confirm this and to provide more nuanced insights. As the only megapode that inhabits arid areas, it is expected that greater effort may be required by Malleefowl to maintain the correct incubation temperature than species in wetter areas (Jones & Göth 2008).

Within the megapode family, some species' incubation mounds are built and maintained solely by the male, whereas in other species the female and male spend equal amounts of time on mound-tending activities (Jones 1988; Palmer *et al*. 2000). The degree to which the male and female Malleefowl participate in mound-building and maintenance is unclear. Malleefowl form strong pair-bonds that span multiple breeding seasons (Immelmann & Böhner 1984; Böhner & Immelmann 1987; Weathers & Seymour 1998). The male and female of a pair both participate in the preparation and maintenance of an incubation mound, but the male is thought to ultimately control temperature regulation, and the extent of female involvement differs geographically (Frith 1959; Booth 1987; Weathers & Seymour 1998; Priddel & Wheeler 2003). Varying degrees of social interaction have been observed between the members of Malleefowl pairs, ranging from almost solitary birds in areas of New South Wales (Frith 1959) to highly social and interactive in the Murray Mallee of South Australia (Frith 1959; Booth 1987; Weathers & Seymour 1998).

Calperum Station (Australian Landscape Trust) and Gluepot Reserve (BirdLife Australia) are large ex-pastoral properties in South Australia now managed for conservation, with searching for, recording, and monitoring Malleefowl mounds a key volunteer activity since the mid 1990s. More recently, this activity has been formalised through the National Malleefowl Recovery Team annual monitoring protocol (National Malleefowl Recovery Team 2016). In 2012, mound surveillance with camera-traps was initiated by citizen scientists and continued at active mounds across six breeding seasons. At the time, the footage was used to make qualitative observations and engage other volunteers but, subsequently, the potential value of these data for quantitative analysis was realised.

Our objective was to gain insights into the breeding behaviour of Malleefowl using mound-surveillance data collected by citizen scientists. Specifically, we aimed to quantify the timing and duration of mound-tending activities, including the extent of female involvement. Finally, we highlight the benefits and limitations of engaging citizen scientists in studies of cryptic species, and detail considerations for future research into the role of Malleefowl in ecosystem processes.

Materials and methods

Site location

Our study took place at Calperum Station and Gluepot Reserve in the Murray Mallee region of South Australia (Figure 1). Calperum Station (238,638 ha) and Gluepot Reserve (54,390 ha) are owned and managed by the Australian Landscape Trust and BirdLife Australia, respectively. Both operated as pastoral leases from the mid 1800s but were destocked in the mid 1990s and subsequently managed for conservation purposes. This area experiences a semi-arid climate with average annual rainfall of 256 mm, although annual rainfall is highly variable (90–517 mm) and rainfall events are unpredictable and patchy. The landscape is a sand-dune system (the Woorinen formation), supporting a range of *Eucalyptus* mallee communities. The dominant overstorey tree species (Red Mallee *Eucalyptus socialis*, Giant Mallee *E. oleosa*, White Mallee *E. dumosa* and Yorrell *E. gracilis*) and associated understorey vary with changes in soil and topography. The understorey ranges from sparse *Zygophyllum* spp. to extensive areas of Porcupine Grass *Triodia scariosa*. Within the extensive mallee vegetation communities are patches of semi-arid woodland dominated by either Sugarwood *Myoporum platycarpum* or Black Oak *Casuarina pauper*.

Surveillance of mounds

Volunteers conducted annual surveys of known Malleefowl mounds at Calperum Station (North Calperum Volunteer Group and the Australian Landscape Trust) and Gluepot Reserve (Friends of Gluepot and BirdLife Australia). These surveys were conducted over 7 years (2012–2018) at varying times of the year, but typically from July through to November (winter–spring). Camera-traps were installed at mounds with signs of recent activity, such as sand or litter disturbance or recent Malleefowl tracks. At some mounds, multiple cameras were installed to extend the field of view. Mounds were revisited periodically to check for continued activity and for camera maintenance (i.e. change batteries and memory cards). Because of the voluntary nature of these activities, initiated by citizen scientists, timing and equipment did not follow pre-defined protocols, and surveillance sometimes occurred opportunistically and was dictated by volunteer availability. Gaps in camera operation occurred when memory cards were full or batteries were exhausted. Cameras were usually removed at the end of the breeding season in late January/early February. Overall, 14 active mounds at Calperum Station and six at Gluepot Reserve were under surveillance from 2012 to 2018 (Figure 1).

Each camera (either LTL-6210 or LTL-6310, Ltl Acorn, Guangdong, China) was mounted ~1.5 m above the ground on a tripod placed ~2 m from the edge of a mound and angled slightly downward to include a view into the centre of the mound. An entire mound (~25 m^2) was within the camera's field of view. Camera settings varied (still or video), but were always set to continuous, i.e. with no time delay. Other settings (e.g. sensitivity, video resolution, photo burst mode) and camera positions were not standardised for all mounds, possibly affecting how the cameras were triggered. However, trials have indicated that, at close range and across a range of camera models, large birds trigger cameras more consistently than do smaller animals (Randler & Kalb 2018).

Classification of camera footage

Camera footage was reviewed by a single observer (HN), who recorded the presence of Malleefowl and their activities, the duration of their visits, egg-laying events, and chick emergence at each mound stage. Mound stages were derived from descriptions of the mound 'construction' and 'maintenance' processes (Frith 1959; Jones & Göth 2008), but the number of stages was expanded to account for the distinct shifts in mound-tending behaviour that were observed within both the broader construction and maintenance categories.

As Malleefowl are sexually monomorphic and the male and female could not be reliably distinguished visually, behavioural indicators were used to determine sex, based on data collected over long-term studies, where banded individuals of known sex were observed (Priddel & Wheeler 2003). Priddel & Wheeler (2003) found that males are primarily responsible for the building and maintenance of mounds, and that females attend mounds to lay eggs and will assist with mound-tending in the presence of males, confirming the assumptions made in the seminal field observations of Frith (1956, 1959). In other Australian megapodes, the males are similarly responsible for mound-building and maintenance, with varying input from females (Jones & Göth 2008). In the present study, single Malleefowl present at mounds, and engaged in mound-tending, were assumed to be males. Single birds present at mounds but not engaged in mound-tending were classified as of unknown sex. Two birds present at a mound were assumed to be the male and female of a breeding pair, although the sex of the individual birds was not identifiable except when a female was laying an egg.

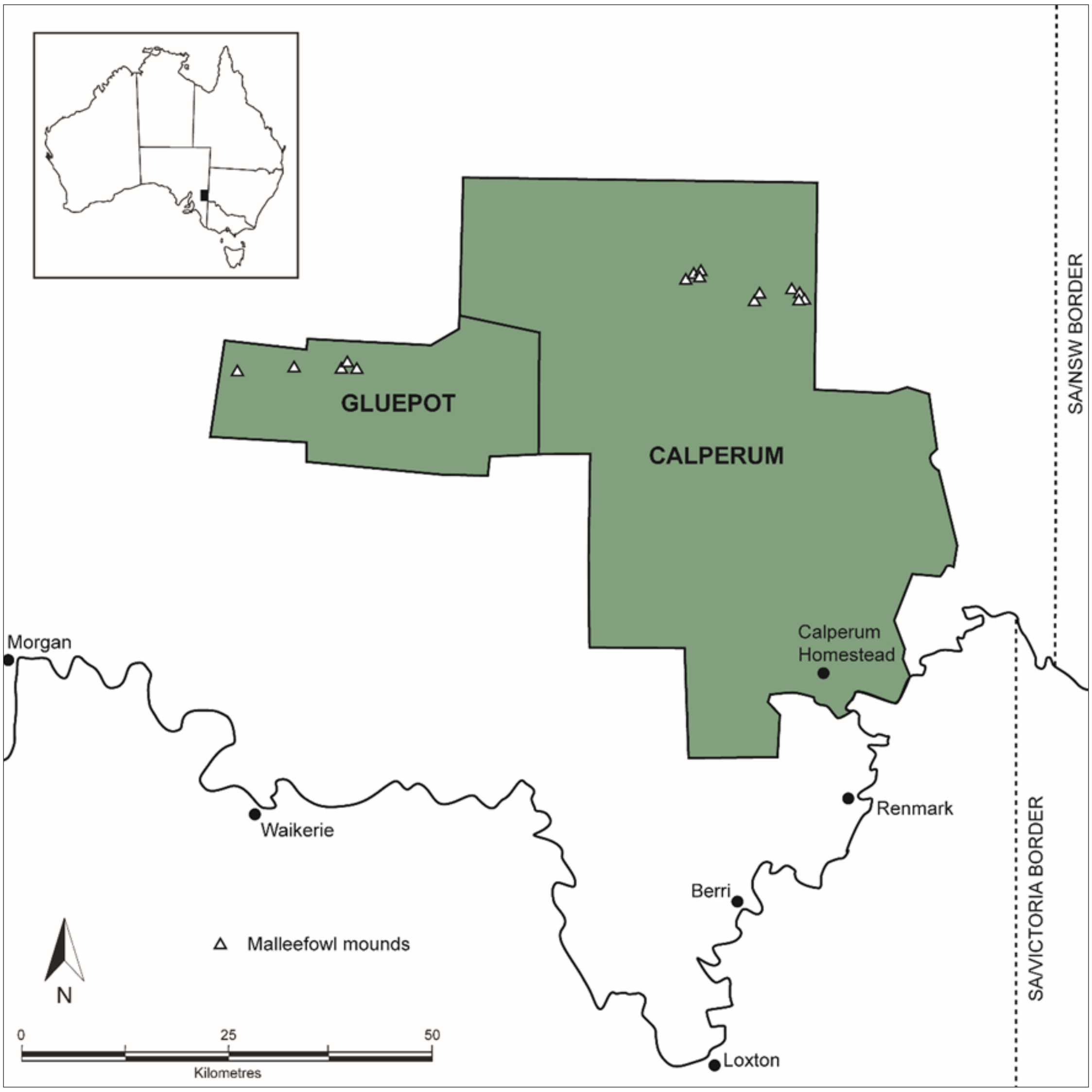


Figure 1. Calperum Station and Gluepot Reserve are adjacent properties in South Australia. The Malleefowl mounds used in this study are indicated by the white triangles. NSW = New South Wales, SA = South Australia.

Mound-tending was defined as the deliberate removal or addition of material to a mound. If a bird was engaged in non-mound-tending activities on the surface of the mound (e.g. standing, walking, or foraging), it was simply classified as being present. To simplify the classification of data, visits to mounds, and their duration, were treated as continuous if consecutive footage had breaks of ≤10 minutes; if >10 minutes, visits were recorded separately. Many of the data from one mound (GLU_2014, which was actively incubating eggs at an abnormal time, March–May) were omitted from detailed analysis because of concerns that they were not comparable.

Analysis of data

Because of the variable camera settings and differing durations and non-continuous nature of surveillance at the 20 Malleefowl mounds, analysis of data was completed with caution. When there appeared to be problems with camera operation or the camera angle did not provide a clear view of an entire mound, data were omitted. As individual Malleefowl were not marked, it was not possible to identify pairs across multiple breeding seasons. Therefore, behavioural data collected at each mound could not be considered strictly independent because it was not clear whether the same pairs or individuals were monitored multiple times across different breeding seasons. To overcome this problem, some variables were examined by year, with the assumption that each pair of Malleefowl was contributing to only one mound per breeding season. A single incidence of polygyny has been observed in Malleefowl, where a male mated with two females and divided his time between two nearby mounds (Weathers *et al.* 1990). However, in our study, it is highly unlikely that a male or female would have had multiple mates and be involved in multiple mounds (distance between the mounds monitored in a given year was at least 6.5 km) or impossible (because sometimes pairs were recorded simultaneously working at different mounds). Where we have compared the means of different groups (e.g. sex, mound stage), we used two-way Analysis of Variance (ANOVA) with type III sum of squares for unbalanced design and made pairwise comparisons using Tukey's HSD test. All analyses were completed in *R* (R Core Team 2018), with ANOVAs performed using *car* (Fox & Weisberg 2011) and *post-hoc* testing using *lsmeans* (Lenth 2016).

Results

In 2012–2018, 20 active Malleefowl mounds were monitored via camera surveillance for a total of 31,080.85 h (1295.04 days). Two mounds were active over consecutive seasons; GLU_2016 and GLU_2017b were the same mound, and CAL_2016b and CAL_2017 were the same mound. In August 2018, surveillance started at two additional mounds at Calperum Station but both these mounds were subsequently abandoned, and no breeding was observed during the 2018–2019 breeding season at any known mounds. Rainfall varied over the six breeding seasons and between Calperum Station and Gluepot Reserve, with annual rainfall lowest in 2018 and highest in 2016 at both locations (Table 1).

Mound stage timeline

We categorised mound activities into five stages (adapted from Frith 1959) *post hoc*.

1. Excavation was the stage where material was removed from the centre of existing mounds, increasing the depth of the central depression. We observed only the renovation of existing mounds and never recorded the creation of an entirely new mound. This is partly because areas were not comprehensively searched for mounds every year but, rather, existing mounds were revisited and monitored. Therefore, a new mound would be encountered only by chance.
2. Litter collection included the scraping of litter from around mounds into the excavated mound and arranging litter on mounds.
3. Construction of egg-chamber occurred after litter collection and before the first eggs were laid. It involved covering litter with sand, digging an egg-chamber in the centre of a mound, and a period of opening the mound, checking the temperature, and closing the mound before the first egg was laid. The final two stages were during the 'active' phase of the mound (defined as a mound being used by Malleefowl as an incubator for their eggs*:* National Malleefowl Recovery Team 2016).

The active phase was comprised of:

4. Egg-laying, the period during which females were laying eggs, and
5. Post egg-laying when egg-laying had ceased, but the mound was still incubating eggs and chicks were emerging.

The five mound stages were observed to varying degrees, depending on the timing and continuity of surveillance footage (Figure 2). Excavation was observed at two mounds from late March to mid May. Continuous footage captured the complete excavation stage at one mound in 2016 (GLU_2016: 25 March–11 May, 47 days) and the beginning of the excavation stage at one mound in 2017 (GLU_2017b: 20 April, and still going on 18 May when surveillance stopped). Litter collection was observed at four mounds from May to early September. At GLU_2016, it began on 12 May and was completed on 6 September 2016 (117 days), including a period of 30 days in July when the mound was not visited. At CAL_2013b and CAL_2017, litter collection ended on 4 September 2013 and 13 August 2017, respectively.

The beginning of egg-chamber construction was observed at CAL_2013b on 5 September 2013. The complete stage was observed at GLU_2016 (7–15 September 2016, 8 days) and CAL_2017 (14 August–21 September 2017, 38 days).

The earliest observation of egg-laying was at GLU_2013a on 2 September 2013, and the latest at GLU_2014 on 7 March 2015. Most eggs were laid from September to January (Figure 3). The earliest observation in any year of the post egg-laying stage was at CAL_2012b on 27 October 2012 and the latest chick emergence was at GLU_2014 on 11 May 2015 (Figure 3).

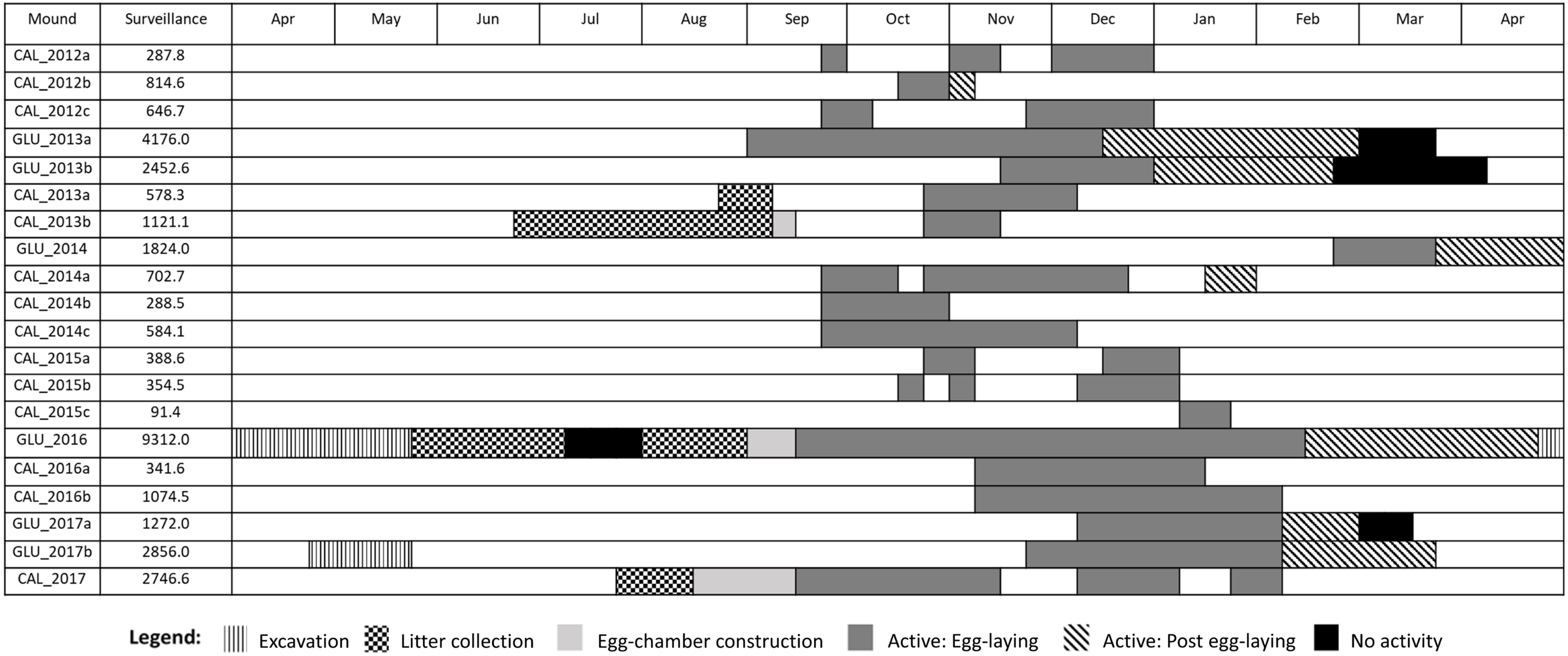
Activity at mound

Overall, 1050.87 h of male and 348.33 h of female mound-tending activity were recorded (Figure 4). When examining the mean percentage of total time spent in mound-tending, there was significant interaction between sex and mound stage (P <0.05). *Post-hoc* testing indicated that males spent significantly more time mound-tending during the egg-laying stage than during any other stage, but we found no significant difference among mound stages in the time that females spent mound-tending. During the egg-laying

Table 1. Winter (June–August) and annual rainfall totals (mm) in 2012–2018 at Calperum Station 'Oak Bore' rain gauge (within 12 km of Malleefowl mounds) and Gluepot Reserve 'Magpie' rain gauge (within 8 km of Malleefowl mounds), South Australia.

Year	*Winter*		*Annual*	
	Calperum	*Gluepot*	*Calperum*	*Gluepot*
2012	53.5	110.0	169.0	281.6
2013	57.0	85.0	208.0	187.9
2014	30.5	59.9	258.0	280.7
2015	61.5	56.0	226.0	222.0
2016	60.5	80.2	299.5	288.7
2017	39.0	32.0	237.0	194.3
2018	43.0	48.5	136.5	131.9

Figure 2. Malleefowl mound stages observed during camera-trap surveillance at Calperum Station and Gluepot Reserve, South Australia, in 2012–2018. Surveillance indicates the total time (h) that a camera was operational. Unshaded areas indicate when a camera was not operational.



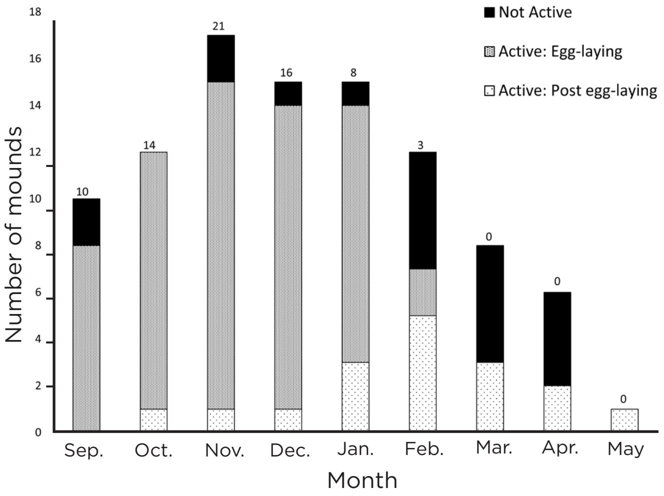


Figure 3. Number of observed Malleefowl mounds at Calperum Station and Gluepot Reserve during the active: egg-laying, and active: post-egg-laying stages in September–May, 2012–2018. The 'not active' category includes all mound stages where incubation was not occurring (i.e. excavation, litter collection, egg-chamber construction and no activity). Numbers at the top of the bars give the total number of laying events observed in each month at all mounds.

stage, males spent approximately three times more time mound-tending than did females, and approximately twice as much time during the post-egg-laying stage.

Frequency of visits

The mean frequency of male and female visits to mounds was calculated across the five mound stages for various mounds depending on the presence and continuity of surveillance footage (Table 2). During the egg-laying mound stage, the mean interval between egg-laying events ranged from 4.17 ± 0.48 (GLU_2013a) to 8.67 ± 1.67 days (GLU_2013b). Low standard errors indicated that females consistently laid at the same interval, i.e. there was no evident trend of increased or decreased laying frequency throughout the months of the egg-laying stage (September–February), although we could not statistically analyse this because of the low number of egg-laying events at each mound in a given month. Rather, inter-pair variation in laying frequency was observed (Table 2). During the egg-laying stage, males generally visited mounds daily, and females made visits to the mound in addition to their egg-laying visits (Table 2).

At mound GLU_2016, where we had the most continuous mound surveillance, we were able to perform meaningful statistical analysis. Mean interval between visits (number of days) corresponded to a significant interaction between visit type (male or female) and mound stage (two-way ANOVA, Type III sum of squares for unbalanced design, P <0.05). The male visited the mound more frequently than did the female during the egg-laying stage, whereas male and female visitation rates did not differ during the post-egg-laying, excavation and litter collection stages (Figure 5). Furthermore, in the active mound stages (egg-laying and post-egg-laying), the female visitation interval was significantly lower (i.e. visits were more frequent) after laying had ceased (Figure 5). The female of this pair consistently made visits to the mound in addition to her necessary attendance on egg-laying days and contributed to mound-tending alongside the male (Table 2).

Figure 4. Time spent at Malleefowl mounds (mean ± standard error) at Calperum Station and Gluepot Reserve, South Australia, as a percentage of the total camera surveillance time for a particular mound during a particular mound stage, by male and female at the five mound stages: excavation (n = 2), litter collection (n = 3), egg-chamber construction (n = 3), active: egg-laying (n = 17) and active: post-egg-laying (n = 7). Letters indicate significant differences from two-way ANOVA, Type III sum of squares for unbalanced design (P = 0.05). Pairwise comparisons were made using Tukey's HSD test.

Total bird-hours at active mound

Total bird-hours (i.e. number of hours × number of birds) spent mound-tending was calculated for days during the egg-laying and post-egg-laying stages, with the former stage further divided into days when an egg was laid and days when no egg was laid (Figure 6, Appendix 1). In every year, mean total bird-hours was higher on egg-laying days (ranging from 5.00 ± 0.46 in 2012 to 7.15 ± 0.68 in 2014), than on non-egg-laying and post-egg-laying days. This was attributed largely to the increased female involvement at the mound on egg-laying days. Mean total bird-hours on 'no-egg' and 'post-egg' days were similar, ranging from 0.93 ± 0.25 to 2.85 ± 0.40 h (no-egg days) and from 0.41 ± 0.13 to 3.74 ± 0.64 h (post-egg days).

Female participation in mound-tending

On egg-laying days, across all mounds, a mound was uncovered (material removed from the mound) and before every laying event the internal temperature was checked. Presumably, if the temperature was suitable the female laid her egg, and then the mound was again covered (material added to the mound). Across all years, females had greater involvement in uncovering a mound before laying, compared with covering the mound after the egg was laid (Figure 7). Females were involved in uncovering the mound between 67.1 ± 14.6 and 98.2 ± 1.8% of the time but were involved in covering the mound only between 0 and 15.0 ± 5.2% of the time.

Table 2. Mean interval (number of days ± standard error) between mound-tending visits by female (F) and by male (M) and egg-laying visits (E) by female to Malleefowl mounds during the five different mound stages at Calperum Station and Gluepot Reserve, South Australia. Sample size is shown in parentheses; a dash indicates insufficient data to calculate a mean visit interval for that mound and stage.

Mound no.	*Mound stage*									
	Excavation		*Litter collection*		*Egg-chamber construction*	*Active: Egg-laying*			*Active: Post egg-laying*	
	F	*M*	*F*	*M*	*M*	*E*	*F*	*M*	*F*	*M*
GLU_2016	1.67 ± 0.29 (21)	1.57 ± 0.18 (23)	2.15 ± 0.41 (14)	3.33 ± 0.95 (14)	–	5.64 ± 0.24 (11)	2.68 ± 0.16 (25)	1.13 ± 0.06 (60)	2.86 ± 0.70 (7)	1.00 ± 0.00 (11)
GLU_2017b	1.87 ± 0.29 (15)	1.65 ± 0.26 (17)	–	–	–	6.00 ± 0.00 (2)	2.80 ± 0.66 (5)	1.06 ± 0.06 (17)	1.43 ± 0.20 (13)	2.00 ± 0.35 (18)
GLU_2013a	–	–	–	–	–	4.17 ± 0.48 (6)	3.25 ± 0.25 (12)	1.11 ± 0.05 (47)	3.38 ± 0.47 (3)	1.76 ± 0.26 (17)
GLU_2013b	–	–	–	–	–	8.67 ± 1.67 (3)	4.67 ± 0.80 (6)	1.42 ± 0.16 (19)	4.38 ± 1.28 (10)	2.77 ± 0.81 (26)
CAL_2016b	–	–	–	–	–	5.00 ± 0.55 (5)	2.2 5± 0.14 (20)	1.13 ± 0.05 (40)	–	–
CAL_2017	–	–	2.00 ± 0.33 (6)	2.00 ± 0.33 (7)	2.15 ± 0.41 (13)	6.25 ± 0.16 (8)	3.71 ± 0.46 (14)	1.43 ± 0.09 (42)	1.50 ± 0.50 (4)	1.20 ± 0.20 (5)
GLU_2014	–	–	–	–	2.15 ± 0.41 (13)	7.33 ± 0.88 (3)	1.44 ± 0.18 (9)	1.00 ± 0.00 (22)	1.24 ± 0.08 (59)	1.24 ± 0.08 (59)
GLU_2017a	–	–	–	–		6.67 ± 0.33 (3)	3.63 ± 0.56 (8)	1.64 ± 0.20 (14)	4.33 ± 0.76 (6)	2.60 ± 0.52 (10)

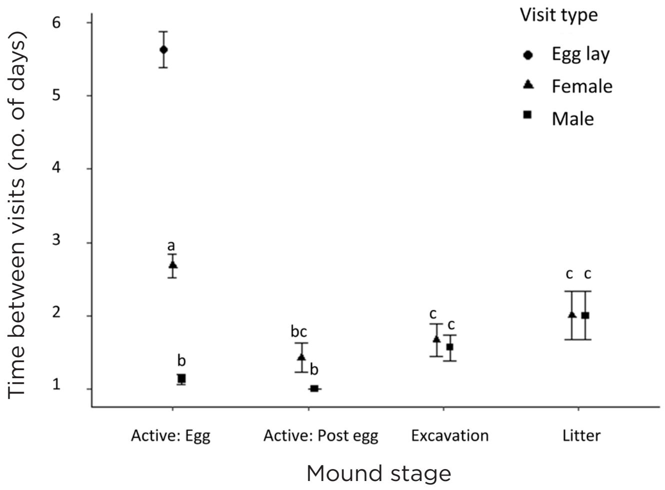


Figure 5. Interval between visits (mean ± standard error) at mound GLU_2016, Gluepot Reserve, South Australia, at four mound stages. Visit types are categorised as 'Male' (only male working the mound), 'Female' (female and male working together at the mound, including egg-laying events) and 'Egg lay' (relevant only to the active: egg-laying stage; female and male working together at the mound and an egg is laid). Letters indicate significant differences from two-way ANOVA, Type III sum of squares for unbalanced design ($P = 0.05$). Pairwise comparisons were made using Tukey's HSD test. 'Egg lay' was omitted from ANOVA as egg-laying events are included in the 'Female' visit category.

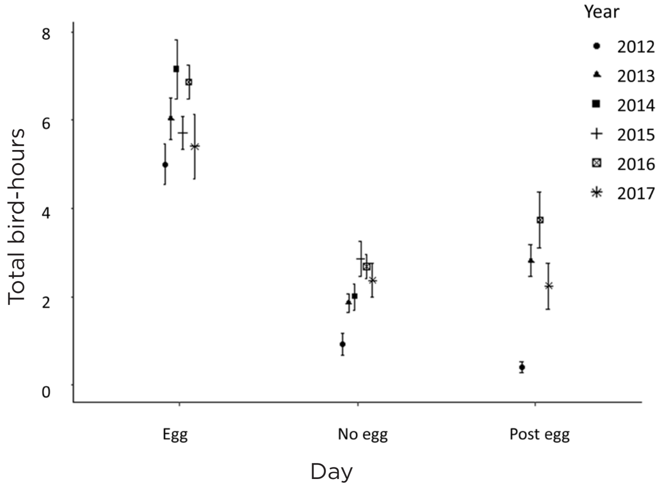


Figure 6. Total bird-hours (number of hours spent working the mound × number of birds; mean ± standard error) at active Malleefowl mounds at Calperum Station and Gluepot Reserve, South Australia, on days when an egg was laid (Egg), days when no egg was laid (No egg), and days when the mound was still active but egg-laying had ceased (Post-egg). Mound sample sizes per category per year are detailed in Appendix 1.

Reproductive outcomes at mounds

The total number of eggs laid and of chicks emerging was observed only at mound GLU_2016 during the 2016–2017 breeding season: 23 eggs were laid, and 13 chicks were observed emerging.

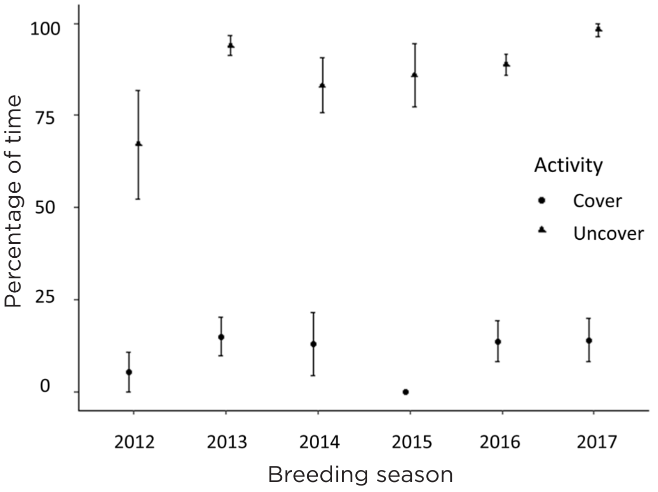


Figure 7. Percentage of time (mean ± standard error) spent by female Malleefowl uncovering and covering their mound on egg-laying days, during six breeding seasons at Calperum Station and Gluepot Reserve, South Australia. Mound sample sizes per year are detailed in Appendix 2.

Observations of behaviour

Although not quantified in the current study, we noted that for each pair of Malleefowl the two birds consistently greeted each other at their first daily meeting by raising their wings, bowing the head, and circling each other, and that the time spent on social interaction appeared to differ between pairs (as described in captivity by Böhner & Immelmann 1987; see Neilly *et al*. 2019 for video and images). Similarly, we observed that temperature checking occurred once a mound was fully opened, exposing the egg-chamber, but it was not possible to determine if male, female or both performed this behaviour because we could not identify individuals. As Frith (1957) described, this behaviour involved a Malleefowl inserting its head deep into the egg-chamber for *c*. 2–3 seconds. On three occasions, laying did not occur, despite the presence of all the behavioural indicators of an egg-laying event (time since last egg laid, female at mound). It is unclear if these were failed laying attempts, in contrast to the 72 successful laying attempts that were observed over the course of mound surveillance. In each of the three instances, a female returned the following day and laid an egg. On two separate occasions (one at GLU_2013a and one at GLU_2017a), a female arrived at the mound alone, dug a small hole in the side of the mound, laid an egg, and covered it with sand; it was unclear if the female belonged to that mound-pair or was an interloper.

Discussion

We found that Malleefowl invested up to an average of 7.15 bird-hours per day in mound-tending activities during the active phase of the breeding season. The time spent mound-tending during excavation and litter collection has not previously been quantified, but our data show that this was up to an average of 2.5% of the total surveillance time for males and females, although much of the litter collection occurs away from the mound and therefore was not recorded. The timing of the breeding season, duration of the egg-laying stage, interval between laying of successive eggs, clutch-sizes, and hatching success observed in our study fall within the ranges described by direct observation of Malleefowl in New South Wales and South Australia (Frith 1957, 1959; Booth 1987; Reichelt 1999; Priddel & Wheeler 2005; Jones & Göth 2008; Griffiths & Lewis 2014; Hedger 2016). The variation in the timing and duration of the breeding season have been attributed largely to patterns of winter rainfall (e.g. Priddel & Wheeler 2005; Benshemesh *et al*. 2020), although summer rainfall is also influential, and can truncate or extend the egg-laying period (Brickhill 1987).

Female involvement in mound-tending ranges from very little (although not quantified) in New South Wales (Frith 1956, 1957, 1959) to substantial in South Australia (Booth 1987; Weathers *et al.* 1993; Weathers & Seymour 1998). Weathers & Seymour (1998) quantified mound-tending in January and March at four Malleefowl mounds in South Australia using time-lapse photography and found that males and females tended the mound together on average 55% of the time on egg-laying days, and 68–86% of the time on post-egg-laying days. We found lower female involvement (~33% on egg-laying days and ~50% on post-egg-laying days), but our data generally support the findings of Weathers & Seymour (1998) and other South Australian studies, showing that females consistently participate in mound-tending. We also found that the time spent by females on mound-tending was constant throughout the year, whereas males spent more time tending mounds when these were active. An increased disparity in male and female involvement at the mound during the active stage was observed in studies in New South Wales, despite the lower overall female involvement (Frith 1957). During the egg-laying stage, females have the added energy burden of producing eggs, so our data suggest that energy expenditure increases during reproduction, in both the male and the female, although that energy is directed towards different tasks.

On egg-laying days, females were more likely to contribute to uncovering mounds. The female needs the mound to be uncovered before she can lay her egg, so the purpose of her involvement may be to speed up the uncovering process. Alternatively, Frith (1957) suggested that females help determine a suitable location in the mound for eggs. If this is the case, female involvement during the mound-uncovering process is imperative, but is less important after the egg is laid. Either way, this is not the sole purpose of female participation in mound-tending because females were regularly observed closing mounds after eggs were laid and opening and closing mounds on non-egg-laying days.

Intervals between the laying of eggs have been observed to increase, decrease or not change throughout the breeding season (Benshemesh 1992; Priddel & Wheeler 2005). We found these did not vary throughout the breeding season, but there was variation between pairs of Malleefowl. Although not the focus of our study, it was noted that the relationships between members of a pair appeared to be quite different: some pairs spent considerable time interacting through greeting displays and vocalising whereas others did not. Further research is required to determine whether pair interactions relate in any way to the strength of a pair-bond and potentially to reproductive success (Neilly *et al*. 2019).

The failed breeding season in 2018 coincided with the lowest annual rainfall over the study period. Malleefowl breeding success is closely linked to rainfall, not only because higher rainfall increases food availability and can extend the egg-laying period, but winter rain is also required to initiate litter decomposition in the mound (Booth & Seymour 1984; Brickhill 1987; Harlen & Priddel 1996; Priddel & Wheeler 2005). Interestingly, in 2018, winter rainfall was not the lowest during the study period, so it is likely that the size and timing of winter rainfall events, the antecedent conditions, and the rainfall during the egg-laying period all influence breeding success, rather than total winter rainfall alone. Despite moderate winter and annual rainfall in 2012, egg-laying began at one of the Calperum Station mounds but abruptly stopped at the end of October. The outlier mound GLU_2014 was active from March to May 2014 after February rainfall of 93.8 mm, more than quadruple the long-term February average. This supports the view that triggers for the breeding season are complex (Priddel & Wheeler 2005). Because of our lack of continuous surveillance at most mounds, we could not examine in any detail the relationships between clutch-size, subsequent breeding success and rainfall. Considering the predicted change in rainfall timing and event size with climate change (Garnaut 2008), it is particularly important to understand Malleefowl breeding triggers for the conservation of this species.

Just over half the Megapodiidae species build incubation mounds. However, although the three Australian species have been the subjects of numerous studies, very little is understood about the species in the South-East Asian and Pacific regions. In Australia, the Australian Brush-turkey *Alectura lathami* and Orange-footed Scrubfowl *Megapodius reinwardt* are found in subtropical and tropical climates (Jones & Birks 1992). Our results confirm that, of the Australian megapodes, pairs of Malleefowl appear to spend the most time manipulating their mounds once they are incubating eggs (Jones & Göth 2008). Australian Brush-turkey mounds are constructed and maintained exclusively by males, which spend large parts of their day on mound-related activities during construction and maintenance (Jones 1988). Conversely, members of pairs of Orange-footed Scrubfowl share mound-tending duties evenly, with males and females spending a maximum of only 0.8% of daylight hours on mound-tending (Palmer *et al*. 2000). This superior effort by the Malleefowl is likely because of the harsh, arid conditions and unpredictable rainfall experienced over this species' range. Without the reliability of rainfall to facilitate consistent microbial decomposition and generate warmth for incubation, Malleefowl need to devote more of their time to mound-tending than do the subtropical and tropical megapode mound-builders (Jones & Göth 2008).

Limitations and future directions

There are several limitations of this study (as detailed in Methods), but these data, with cautious analysis and interpretation, not only expand our knowledge of Malleefowl activity at incubation mounds but provide direction for future research. A major consideration, and one that limited statistical analyses, was the incomplete coverage of data collected at different mounds. The continuity of mound surveillance proved important, especially when considering the inter-pair behavioural variations observed. Likewise, for an accurate record of clutch-size, continuous surveillance was necessary. In this study, breeding success as measured by chick emergence was unreliable. Chick emergence did not always trigger cameras and, even when recorded, it could be easily overlooked when reviewing camera footage because of the chicks' small size, and their tendency to emerge at night when photograph or video clarity is low. To optimise the capture of egg-laying and chick emergence, overhead cameras, mounted on tripods with extendable horizontal arms, are being trialled at the study location. Behavioural observations from video footage tended to be more insightful than still images, but there are considerations of memory capacity and battery life when recording videos.

We assumed that a single bird undertaking mound-tending activity was a male based on observations from studies where birds were banded and from the collective understanding of the behaviour of Malleefowl and other megapodes (Jones & Göth 2008). Although this assumption does not affect many of the results of this study (e.g. Figures 2, 3 and 6), we cannot unequivocally rule out the possibility that we have underestimated female activity when we have treated male and female activity separately. Without capturing, sexing and banding individuals, we cannot be sure that females never undertook mound-tending alone. Although our assumption is well supported by other studies, in the absence of definitive sex determination, the data presented as 'male' and 'female' activity could be strictly classified as 'lone mound work', and 'pair mound work'.

Although there are limitations, observational studies by citizen science can undoubtedly provide valuable ecological data. The Malleefowl is an engaging species in the communities where it occurs, with many volunteers participating in the annual Malleefowl Monitoring Program (National Malleefowl Recovery Team 2016; Benshemesh *et al.* 2020) and Malleefowl Adaptive Management project (Walsh *et al*. 2012a,b; Hauser *et al*. 2019). Community observations have also been used to track Malleefowl populations in Western Australia (Parsons *et al*. 2008, 2009). Furthermore, the video and still footage captivate the general public and may encourage further public involvement (Griffiths & Lewis 2014), which is likely to be relevant for engaging communities in the study and conservation of a range of cryptic species worldwide. Projects capturing information on cryptic species can be even more valuable with scientific input at the beginning, allowing data collection methodology to be designed to meet specific objectives and to answer pre-defined research questions from the citizen science.

Observations on natural history are a crucial component of modern field ornithology, not only as a tool to assist with conservation but also to generate hypotheses about species' biology and their role in ecosystem processes (Callaghan *et al.* 2018). As we have observed, during the building and maintaining of an incubation mound, Malleefowl collect large amounts of litter and shift tonnes of dirt (Frith 1962). A redistribution of resources may influence soil function, vegetation dynamics and fauna communities at and around Malleefowl mounds, which has great significance in depauperate, arid ecosystems like the mallee woodland (Neilly *et al*. 2021). Up to this point, research on Malleefowl has understandably focused on the species' biology and conservation, particularly considering its threatened status. However, the potential role of these birds as soil-disturbing ecosystem engineers should not be overlooked. Mammalian ecosystem engineers are often considered in the context of ecosystem function and restoration (McCullough Hennessy *et al*. 2016; Valentine *et al*. 2017), and further research should consider the role of the Malleefowl in the restoration of degraded mallee woodlands.

Acknowledgments

We thank the many volunteers from the North Calperum Volunteer Group, Friends of Gluepot and staff from Australian Landscape Trust and BirdLife Australia for assisting with data collection. Special thanks go to Shirly Wells. We are grateful to Rebecca Boulton for providing useful feedback on a draft of the manuscript. This study was funded through The Ian Potter Foundation Early Career Researcher Fellowship, the Margaret Middleton Fund and Birds SA project fund.

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Received 4 January 2020, accepted 1 December 2020, published online 3 June 2021

Appendix 1. Mound sample size per category per year for the total bird-hours (number of hours spent working the mound × number of birds) at active Malleefowl mounds at Calperum Station and Gluepot Reserve, South Australia, on days when an egg was laid (Egg), days when no egg was laid (No egg), and days when the mound was still active but egg-laying had ceased (Post egg). Mean total bird-hours ± standard error are displayed in Figure 6.

Year	*Mound no.*	*Egg*	*No egg*	*Post egg*
2012	CAL_2012a	2	3	0
	CAL_2012b	1	4	5
	CAL_2012c	2	16	0
2013	CAL_2013a	0	2	0
	CAL_2013b	3	6	0
	GLU_2013a	11	27	15
	GLU_2013b	5	14	26
2014	CAL_2014b	1	5	0
	CAL_2014c	3	10	0
	GLU_2014	3	0	0
2015	CAL_2015a	3	11	0
	CAL_2015b	0	8	0
	CAL_2015c	1	0	0
2016	CAL_2016a	2	7	0
	CAL_2016b	7	20	8
	GLU_2016	13	33	14
2017	CAL_2017	7	11	4
	GLU_2017b	3	12	11

Appendix 2. Mound sample size per year for the percentage of time spent by female Malleefowl uncovering and covering their mound on egg-laying days during six breeding seasons at Calperum Station and Gluepot Reserve, South Australia. Mean percentage of time ± standard error is displayed in Figure 7.

Year	*Mound*	*No. days sampled (n)*
2012	CAL_2012a	4
	CAL_2012b	2
	CAL_2012c	4
2013	CAL_2013b	6
	GLU_2013a	22
	GLU_2013b	10
2014	CAL_2014b	2
	CAL_2014c	6
	GLU_2014	6
2015	CAL_2015a	6
	CAL_2015c	2
2016	CAL_2016a	4
	CAL_2016b	14
	GLU_2016	26
2017	CAL_2017	14
	GLU_2017b	6