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Title: Innovation and geographic spread of a complex foraging culture in an urban parrot

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Abstract:

The emergence, spread, and establishment of innovations as cultures is an important mechanism promoting adaptive responses to anthropogenic change. We describe a putative case of the development of a cultural adaptation to urban environments: opening household-waste bins by wild sulphur-crested cockatoos. A spatial network analysis of community science reports revealed the geographic spread of bin-opening from 3 to 44 suburbs, in Sydney, Australia, via social learning. Analysis of 160 direct observations revealed individual styles and site-specific differences. We describe a full pathway from the spread of innovation to emergence of geographic variation, evidencing foraging cultures in parrots and indicating the existence of cultural complexity in this group. Bin-opening is directly linked to human-provided opportunities, highlighting potential for culture to facilitate behavioral responses to anthropogenic change.

One Sentence Summary: Bin-opening by urban sulphur-crested cockatoos reveals cultural complexity in parrots.

Main Text:

Identifying persistent cultures in animal species – population-specific behaviors acquired via social learning from knowledgeable individuals (*1*) – remains challenging. The behavior in question may be rare or hard to observe, and it is difficult to exclude genetic and ecological variables as alternative explanations for population-level differences (*1*, *2*). Urban habitats provide opportunities to overcome these challenges – the 'many-eyes' of community science allows for a wide spread of observations (*3*), and many urban resources are standardized (e.g.

waste disposal) (*4*). Additionally, urban environments may promote innovation (an asocially learned solution to a problem (*5*)) by providing novel resources and foraging opportunities (*4*, *6*). Innovations by wild animals living in cities are well documented, and comparative analyses suggest that innovativeness may enable behavioral flexibility to anthropogenic changes (*7*). Observations of multiple individuals engaging in a novel behavior are often assumed to result from the spread of innovation (*5*, *8*), yet direct evidence is lacking (*9*). However, if innovations spread through populations via social learning, they can lead to emergent adaptive cultures (*8*, *10*), i.e. socially-learned behaviors that are beneficial for urban living and differ between sites.

The cultural intelligence hypothesis predicts that animal culture has co-evolved with larger brain size, high sociality, and slower life history (*11*). Supporting this, extensive cultures across multiple domains have been identified in social species with relatively complex cognition (e.g., primates, cetaceans, and corvids (*2*, *10, 12*)). Large parrots share many life history traits with these groups, and exhibit vocal cultures (*13*). Yet, there is a paucity of evidence for social learning or culture in their foraging behavior. Sulphur-crested cockatoos, *Cacatua galerita* (henceforth: cockatoos), are a large-brained, long-lived, and highly social parrot native to eastern Australia. They are increasingly common in cities (*3*) and occur across our entire study area. In recent years, there have been isolated reports of cockatoos opening the lids of household-waste bins to scavenge food (henceforth: ‘bin-opening’, Fig. 1). This foraging innovation exploits a widely available resource, but little else is known about it. Here, we combined a large-scale community science survey to map bin-opening across the Sydney and Wollongong regions with direct observations at multiple sites to identify possible individual or site-level differences.

To map occurrence, we collected data via an online survey in two consecutive years (2018/19) asking residents whether, where, and when they had observed cockatoos opening lids of household bins (supplementary text). We collected 1396 reports by 1322 participants across 478 suburbs, of which 338 reports from 44 suburbs described bin-opening. Multiple cockatoos were present in 93.3% of the observed cases, highlighting cockatoos' ample opportunity to observe bin-opening. In 88.8% of cases, birds opened general waste bins (identifiable by red lids).

To investigate spatial-temporal dynamics, we assigned the data to seven discrete time periods, based on survey reports (Fig. S1; see supplementary text for sensitivity analysis on discretization of continuous data). We then created a spatial network of geographic distance (in meters) between suburbs, informed by knowledge of cockatoo dispersal distances, and ran a spatial 'network-based diffusion analysis' (*14*). This assumes that if cumulative uptake by suburbs is due to social learning, new occurrences are more likely in suburbs closer and within dispersal distance to where the behavior is established (*14*). The only three suburbs in which bin-opening had been observed prior to 2018 were included as likely sites of origin. We additionally included three suburb-level variables: 1) the number of survey participants to control for reporting rate, 2) suburb size (km^2) as an imperfect proxy for cockatoo population size, and 3) the number of dwellings as proxy for resource availability (number of bins). Network models with social transmission received overwhelming support (summed Akaike weight, indicating relative support $\sum w_i > 0.99$). In the best model, bin-opening was estimated to have spread by social learning to 93.9% (95% CI 86.5-97.3%) of suburbs where it occurred. The models additionally revealed a secondary innovation of bin-opening in the far north of Sydney (Narraweena in late 2018, Fig. 2), from which the behavior subsequently spread by social learning. The estimate of social learning rate was negatively influenced by the number of dwellings ($\sum w_i = 0.87$) and positively by the number of survey participants ($\sum w_i > 0.99$), but no other suburb-level variable influenced learning rates (all $\sum w_i < 0.5$; Table S1).

To evaluate the complexity of bin-opening behavior, we temporarily color-marked 486 cockatoos across three hotspot sites identified from the online survey (Fig. 3B/D, Fig. S2). Video analysis of 160 successful opening-sequences revealed that bin-opening is a complex, multi-step foraging behavior, consisting of five stages with several options at each stage (Fig. 3A, Table S2, S3).

Several components of the opening sequences by cockatoos were strongly associated with individuals, e.g. walking direction (possibly related to laterality), and whether the lid was pried open (possibly related to experience as prying is not necessary for successful bin-opening). Other components differed more between sites, e.g., those associated with the opening stage (Fig. 3C). Overall, sequences by the same individual were more similar than sequences by different individuals (Partial Mantel test, accounting for geographic distance: r=0.16, p<0.001). Controlling for individual ID, dissimilarity between sequences increased with increasing geographic distance between observations (Partial Mantel test: r=0.21, p=0.002; Fig. 4, Movie S1), suggesting the formation of local sub-cultures of the behavior (for a similar example in chimpanzees, see (*15*)).

To assess the importance of individual and social characteristics on bin-opening ability, we marked >90% of birds at one hotspot site (Stanwell Park, Fig. 3B), and collected data on sex, age, weight, dominance rank and social associations (*16*). Out of 114 identifiable individuals, nine cockatoos were successful (n = 112 complete sequences) and 27 attempted unsuccessfully to open bins (n = 94 sequences). Both adults and juveniles opened bins (cumulative link model [CLM] testing age bias: χ^2=0.86, p=0.35, n=84), suggesting social transmission between age classes. Of cockatoos of known sex, most successful bin-openers (89%) and most birds that attempted to open bins (84%) were male (Table S4). Individuals higher in the male dominance hierarchy were also more likely to attempt and succeed at bin-opening (CLM: χ^2=7.68, p=0.006, n=37; Fig. S3). Finally, there was a non-significant tendency for heavier males to attempt bin-opening (generalized linear model: χ^2=3.12, p=0.08, n=20), although small sample size for males with known weight precluded full analysis of potential interactions between rank and weight.

Males tend to be heavier and dominant over females (*17*), and males might have a strength advantage if bin-opening is physically demanding. Alternatively, high-ranking males might have preferential access to resources (bins) – indeed we frequently observed cockatoos displacing conspecifics off bins. Our results contrast other studies suggesting that younger and lower ranking individuals have a higher probability of social learning (e.g. (*18*)), but demonstrates how resource distribution can influence social dynamics of social learning and culture (*19*). In the only other bird known to open bins, the New Zealand kea (*Nestor notabilis*), it was also only males that opened lids (*20*). Further comparisons are however difficult; kea bin-opening was only observed at one location and with low success rates.

Finally, social network analysis revealed a tendency for males (permutating within bin-opening status, linear model [LM]: t_{78}=2.54, p=0.018) and attempted/successful bin-openers to have a higher eigenvector centrality in the association network (permutating within sex, LM: t_{78}=1.07, p=0.001, Fig. S4). As expected, the likelihood of being more similar in bin-opening status was most strongly affected by sex (multiple regression quadratic assignment procedure [MRQAP]: *est*=0.13, p<0.001, n=89). However, when males were considered separately, there was a significant tendency for bin-openers to associate more (controlling for rank, MRQAP: *est*=0.97, p=0.010, n=34). While directionality cannot be ascertained from these data (supplementary text), these patterns are consistent with those expected from social learning, with associated and more socially-central individuals having better access to social information, and therefore a greater likelihood of learning (for a similar finding in primates, see (*21*)).

Our study combines the two classic approaches to the study of animal culture, namely mapping the spread of an innovation over space and time (*6*, *10*), and observing geographic variation in behavior (*2*). Our results show that spread of innovation cannot only result in establishment of culture, but further lead to emergent geographically distinct sub-cultures. Our study area is characterized by two different habitats – suburbs and forests. Data from our color-marked birds suggest little movement through forested areas, functionally making forests barriers to regular movement. This in turn might trap behaviors in suburban areas (within which they can spread). Founder effects and drift may then give rise to local behavioral variants at relatively small geographic scales; cultural evolutionary theory would predict that multi-step, complex traits, as observed here, could potentially further enhance this effect. This behaviour has emerged in direct response to land-use change. It is a powerful illustration of how, in the Anthropocene, animal culture can allow urban populations to access novel resources, potentially facilitating local adaptation (*22*, *23*).

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Supplementary Materials:

Materials and Methods

Supplementary Text

Figures S1-S5

Tables S1-S5

References (24-50)

Movie S1

Data S1-S3

Fig. 1. A paint-marked sulphur-crested cockatoo opening a household bin.

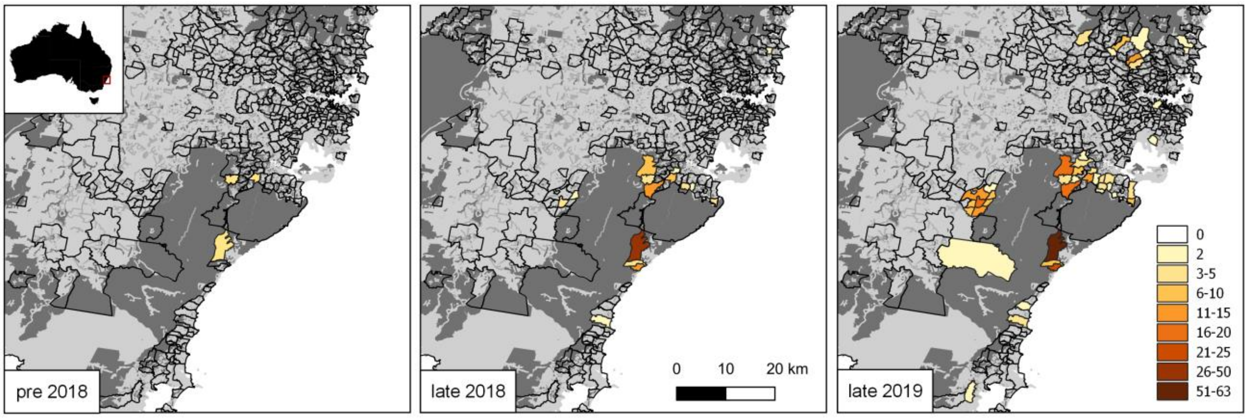
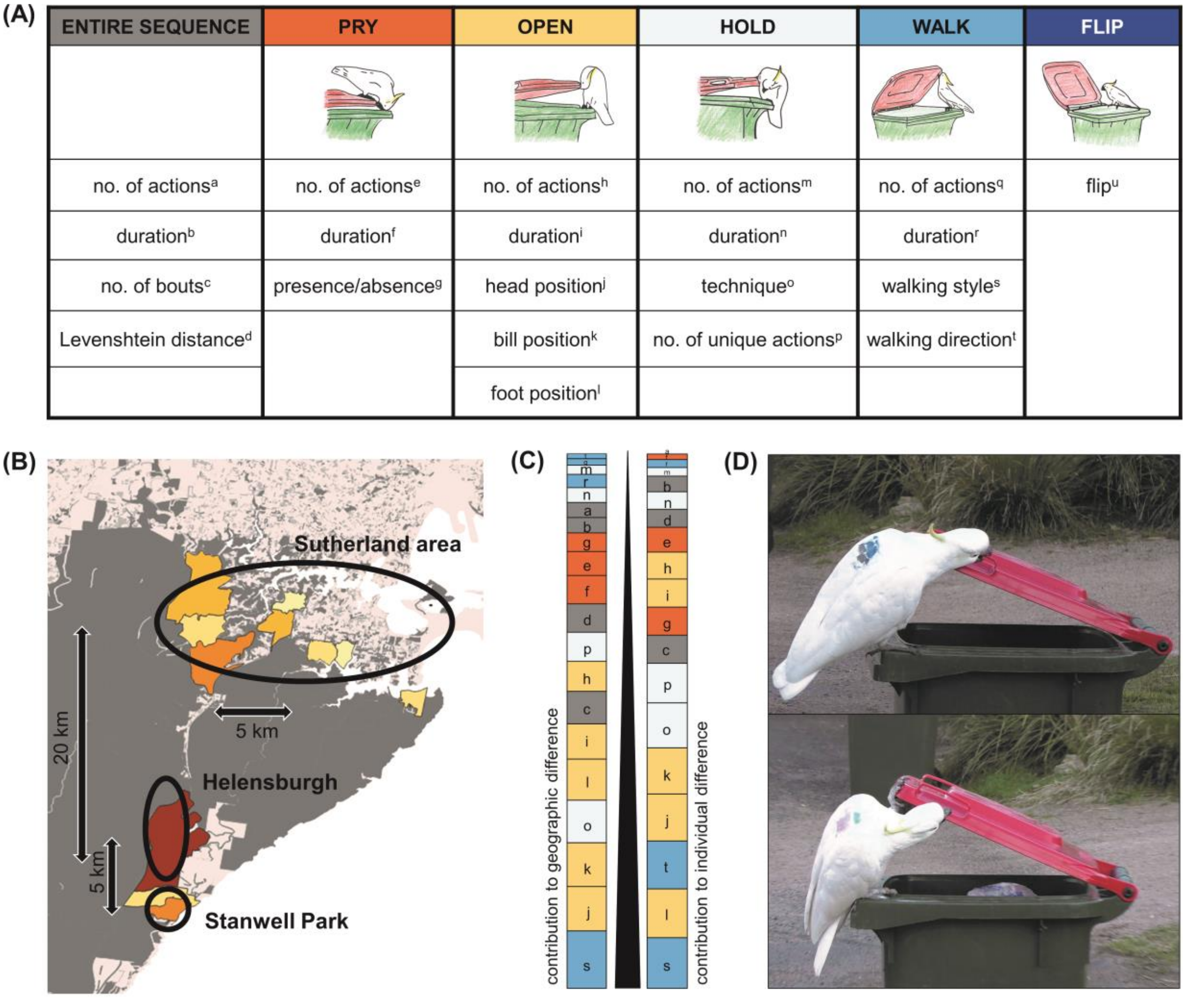


Fig. 2. Spread of bin-opening across the Sydney and Wollongong Region. Reported in only three suburbs before 2018, bin-opening behavior spread to 44 suburbs by late 2019. Suburbs outlined with black only returned negative reports, suburbs with at least two positive reports for the respective time period are colored (cumulative over time). Forested areas (trees 10-15 m high > 9.6%) are shown in dark grey. For all time periods, see Fig. S1.



ENTIRE SEQUENCE	PRY	OPEN	HOLD	WALK	FLIP
no. of actions[a]	no. of actions[e]	no. of actions[h]	no. of actions[m]	no. of actions[q]	flip[u]
duration[b]	duration[f]	duration[i]	duration[n]	duration[r]	
no. of bouts[c]	presence/absence[g]	head position[j]	technique[o]	walking style[s]	
Levenshtein distance[d]		bill position[k]	no. of unique actions[p]	walking direction[t]	
		foot position[l]			

[a] cumulative no. of actions in the sequence
[b] cumulative duration of the sequence
[c] no. of the successful bout within one engagement period
[d] Levenshtein distance of the sequence
[e] no. of actions in the prying stage
[f] duration of the prying stage
[g] whether prying occurred
[h] no. of actions in the opening stage
[i] duration of the opening stage
[j] position of the head during the opening stage
[k] position of the bill during the opening stage
[l] position of the feet during the opening stage
[m] no. of actions in the holding stage
[n] duration of the holding stage
[o] how the lid is held during the holding stage
[p] no. of unique actions in the holding stage
[q] no. of actions in the walking stage
[r] duration of the walking stage
[s] how the bird walks along the rim
[t] direction in which the bird walks along the rim
[u] the lid is completely flipped over

Fig. 3. Individual and geographic variation in bin-opening behavior. (A) The five stages of bin-opening. Columns list the variables scored from video for each stage (for details see Table S2, S3). **(B)** Study areas for direct observations. **(C)** Relative contribution of each behavioral variable to site (left) and individual differences (right); most to least important, bottom to top, cumulative to 100%. Colors and letters are matched to panel (A). **(D)** Marked individuals holding the lid with the bill at the handle (top) and with bill and foot at the rim (bottom).

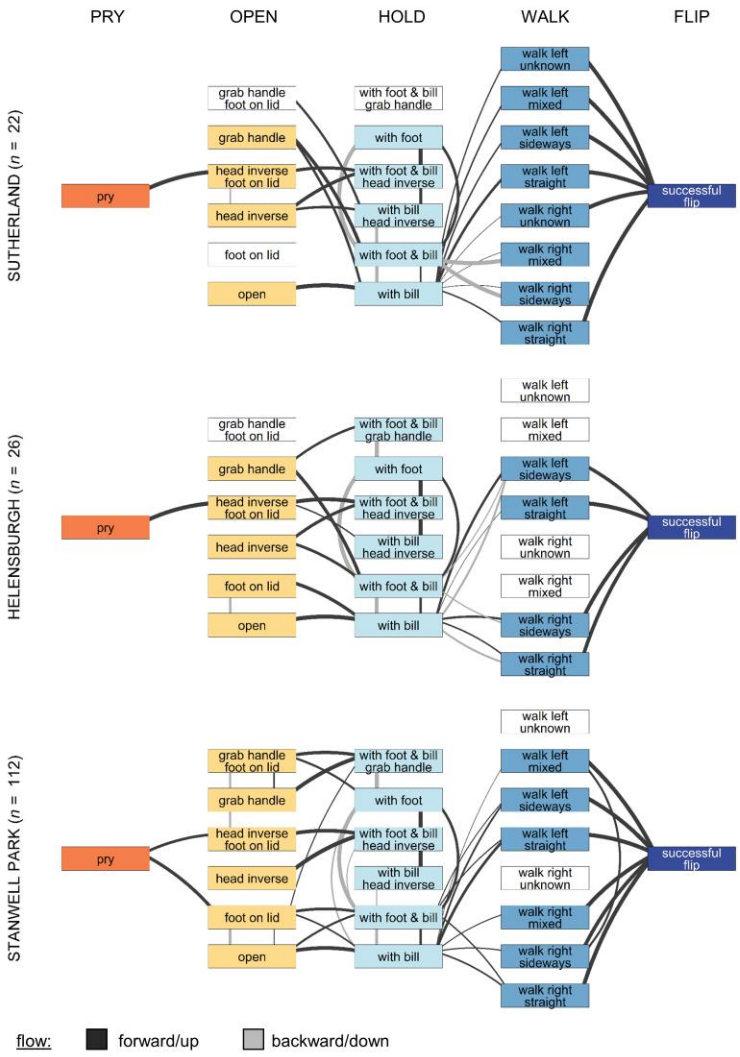


Fig. 4. Behavioral sequences of successful openings across sites. Bin-opening stages are depicted from left to right. Connections are colored by direction: advance to the next stage or upwards within a stage (black), regress to the previous stage or downwards within a stage (grey). The thickness of a connection represents the percent occurrence of this transition (for details, see Table S2, S3).

Supplementary Materials for

Innovation and geographic spread of a complex foraging culture in an urban parrot

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This file includes:

- Materials and Methods
- Supplementary Text
- Figs. S1 to S5
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- Captions for Movie S1
- Captions for Data S1 to S3

Other Supplementary Materials for this manuscript include the following:

- Movie S1
- Data S1 to S3

Materials and Methods

1. Survey

In 2018 and 2019 we conducted an online survey running between 24 August and 24 December, asking residents in the Sydney and Wollongong Region to report whether or not they had observed cockatoos accessing household bins by lifting and flipping lids. The survey was publicized through traditional and social media, and through organizational email and newsletter lists (e.g. Australian Museum, Royal Botanic Garden, Sutherland Shire Council) reaching subscribers across the region.

Through the survey, after asking consent, we collected data on the residency of participants (suburb level). For positive reports (direct observation of successful bin-openings), we additionally collected information on the location at the suburb level, the time period of observation (< 3 months ago, between 3-6 months ago, between 6-12 months ago, > 12 months ago), bin type, lid color, and whether other cockatoos were present. We only used reports from New South Wales, and excluded reports of direct bin-opening that: (i) were not from ‘wheelie’ bins (n = 25), (ii) where we could not assign a location (n = 6), and when comments stated that (iii) the bird did not successfully open the bin (n = 6), or (iv) the lid was partly open to begin with (n = 19). Duplicated data were deleted. The final dataset consisted of 1396 reports by 1322 participants across 478 suburbs.

To determine the time when bin-opening behavior originated in a given suburb, we assigned all positive reports to seven distinct time periods based on the time period of observation as ascertained in the online survey: pre 2018, early 2018, mid 2018, late 2018, early 2019, mid 2019, late 2019. We excluded all reports from the 2019 survey that stated the bin-opening had occurred more than 12 months ago (n = 39), since we could not attribute these data to a particular time period. Furthermore, we only considered the behavior to be occurring in a suburb if we had received at least two positive reports for the suburb in a given time period.

2. Analysis of spatial diffusion dynamics

To identify and describe the potential spread of bin-opening behavior, we first subset the survey dataset to all suburbs within 80 km of the likely origin of the behavior (Helensburgh – based on survey data and newspaper articles). This distance was chosen because it is well outside the usual dispersal distance of sulphur-crested cockatoos (see below), and the resulting area is bordered to the east by the Pacific Ocean, to the west by the Great Dividing Range, and to north and south by two major river systems (Hawkesbury River in the north and Shoalhaven River in the south). However, the results were robust to variation in this boundary distance (50 and 100 km). We then created a distance network of all suburbs in this area, with edge weights represented by the reciprocal distances in km between the centroids of all suburbs as a network. Our investigation of six years of community science reports of 120 wing-tagged cockatoos tagged in central Sydney (*3*, *24*) revealed that the average for the maximum distance between any two reports of a given bird was 12.8 km. Apart from 3 outliers who moved 32 km, 33.3 km, and 65.6 km, the distribution of movements ranged from 0.7 - 24.8 km (117 birds). This suggests that dispersal movements further than 25 km were very unusual. In order to make the distance network realistic to the spatial movements of cockatoos, we therefore identified all pairs of suburbs that are more than 25km apart and set their edge weights to 0.

We then employed a spatial network-based diffusion analysis (NBDA) using the NBDA package v0.9.4 (*25*) in R v4.0.2 (*26*). NBDA tracks the spread of a behavior through a network and infers that it is socially learned if the diffusion follows the network connections (*27, 28*). In this case, a spread through the spatial network of suburbs would be consistent with the hypothesis that the behavior has spread across cockatoo populations through a pattern of social learning, dispersal and further social transmission (*29*). We used the discrete 'time of acquisition diffusion analysis' (disTADA) variant of NBDA (*28*), which grouped suburbs where the first positive reports of bin-opening occurred during the same time window into discrete time steps. It assumes no social transmission between suburbs within each time step (see above). We included three suburbs in which bin-opening was reported as occurring before 2018 (Barden Ridge, Helensburgh, Sutherland) as 'demonstrators'. These suburbs are therefore not included in the diffusion, but others can acquire the behavior from them.

We included three additional suburb-level variables that we thought might affect the likelihood of the behavior occurring and/or people observing the behavior: i) number of participants, ii) suburb area (km^2), and iii) number of dwellings. The participant number (reflecting both negative and positive reports) was included to control for variation in local community interest in observing cockatoo behavior. Suburb-level participant number will also reflect the total suburb-level human population size, and as expected, was correlated with dwelling number ($r = 0.2$). Participant number was further treated as a time-varying suburb-level variable, distinguishing between the number of participants in the 2018 survey and those in the 2019 survey. Suburb area may affect the possible local population size of cockatoos, as – all else being equal – population size should correlate with habitat area. Finally, the number of dwellings will directly correspond to the number of bins, and thus affect the availability of this resource. All suburb-level variables were standardized, which resulted in a more stable parametrization of the models, and more easily interpretable estimates for the social transmission parameter s.

The parameter s estimates the strength of social transmission per unit connection with already informed individuals (here: suburbs where the behavior has been previously reported) relative to a baseline rate of asocial learning (*28*). Here, the baseline rate was calculated for a suburb of average size with an average number of participants and number of dwellings. We fitted unconstrained models (*29*) in which individual-level variables can influence social and asocial rate independently with/without social transmission and in all possible combinations with/without the individual-level variables. This resulted in 72 models. We then used the Akaike Information Criterion corrected for sample size to obtain relative model support (*30*), and used model averaging methods to provide a more stabilized inference about the strength of social transmission and the influence of individual-level variables on the social and asocial learning rate (Table S1). The observed effect of dwelling and participant number on the social learning rate is unsurprising, given that a) lower dwelling number will result in a higher density of cockatoos per bin and hence increased social learning opportunities, and b) bin-opening is more likely to be reported in suburbs with more participants. Importantly, participant number alone did not sufficiently explain the spread and when controlling for it, the large effect of social learning remained. We found that reliable standard errors could not be obtained – likely due to asymmetrical likelihoods of key parameters (*31*) – and instead derived 95% confidence intervals using profile likelihood techniques (*32*) based on the best performing model.

Discretization of continuous data – here the spread of bin-opening through Sydney's suburbs – can be problematic as the results may be sensitive to the choice of the length and number of discrete time steps. Ideally, such data would therefore be analyzed in a hierarchical statistical modelling framework (*33*), which, however, cannot (yet) be implemented in the current version of NBDA. To ensure robustness of our results, we therefore performed a sensitivity analysis (see Data S1) using the alternative 'order of acquisition diffusion analysis' (OADA) variant of NBDA (*14*). OADA uses the order in which individuals (here suburbs) acquired a behavior – and not the time – as diffusion data. Given how our data were collected, we had knowledge about the time steps during which bin-opening first occurred in a given suburb, but not about the exact time or order within each time step.

In our sensitivity analysis, we first randomized the order of acquisition within each of our 7 time steps, creating 1000 alternative orders of acquisition. For each randomized order of acquisition, we then ran an OADA model based on the best performing model obtained from the discrete TADA analysis, i.e. with the number of dwellings and the number of survey participants as suburb-level variables influencing the social learning rate. We then compared AICcs between a model with social learning and a model without social learning. For each model, we also extracted estimates for the social learning parameter s (as percentage of acquisition events through social learning), as well as parameter estimates for the two included suburb-level variables.

In all 1000 models with randomized orders of acquisition, the social model clearly outperformed the asocial model (all with deltaAICc of >4). All parameter estimates (percentages of acquisition events through social learning; number of dwellings and number of participants influencing the social learning rate) fell well within the 95% profile likelihood confidence interval that we had extracted from the best model obtained from the discrete TADA analysis (Fig S5). Based on our sensitivity analysis, we conclude that our results remain robust despite the discretization of continuous data.

To ensure that the spread of the behavior followed the spatial network – and not some other, unmeasured network – we additionally ran NBDA on the best performing model using a homogenous network with entries of all 1s and compared model performance based on AICc values between a model including the spatial and a model using the homogenous network (*14*). The model including the spatial network clearly outperformed the alternative model including the homogenous network (deltaAICc>29), indicating that the spread indeed followed the spatial network. Dataset and code for all NBDA analyses: (*34*).

3. Individual Marking

Based on preliminary analyses of the survey reports (in late 2018) as well as direct observation of one the authors (REM) who lives in the area, we identified four presumed geographic hotspots of bin-opening (Sutherland, Campbelltown, Helensburgh and Stanwell Park). Between 26 June and 12 August 2019, we made a concerted effort to temporarily habituate and mark cockatoos in three of these areas with uniquely identifiable color combinations (Sutherland, Helensburgh and Stanwell Park, Campbelltown was excluded for logistical reasons). At a set time per day over a period of 2-3 weeks, cockatoos were attracted to the ground in local public parks by scattering sunflower seeds. The observer (BCK) and/or an assistant would remain as close as possible to the foraging flock until birds were willing to forage nearby and could be lightly touched on the back without eliciting a strong adverse response. A unique combination of non-toxic fabric dye (Marabu Fashion Spray, MARABU GmbH) was then applied on their back. No capture or restraints were necessary for the marking procedure, and paint marks remained for approximately 3-6 months (until next molt), see Fig. S2 for examples.

In total, almost 500 cockatoos were marked in: Sutherland n = 230, Helensburgh: n = 143, and Stanwell Park: n = 113 (plus one morphologically identifiable bird). In Stanwell Park (a suburb with a relatively closed population), we achieved a marking rate of over 90% of the local population based on daily counts of marked *vs* unmarked cockatoos that were present at the marking site. For this population, we additionally collected feather samples from individuals (for DNA-sexing) and sexed, aged (based on eye color) and weighted birds (by letting them hop onto a balance) when possible (see Table S4 for confirmed bin-openers and birds that attempted to open bins).

4. Direct observations of bin-opening behavior

Pilot study

Based on preliminary analyses of the 2018 online survey, as well as direct observations, we initially identified four geographic hotspots of bin-opening (Sutherland, Campbelltown, Helensburgh and Stanwell Park, see above). Between 07 and 30 October 2018, BCK and JKH attempted to film ‘bin-opening’ *in situ* in these areas on bin-collection days – afternoon before and morning of collection day – when suburban bins were positioned on the street curb. Initial observations suggested that cockatoos were very fast at opening bins, leading to many ‘missed openings’. We therefore also ‘staged’ opportunities, where we placed a few sunflower seeds or small pieces of bread (a preferred food for urban cockatoos) inside full, but not overfull bins (so that the lid still completely closed), when wild cockatoos were present. We then filmed opening attempts using a Panasonic HD camcorder. After successful openings, we closed the lids again to give cockatoos the opportunity to open the lid again. It also proved more feasible to work in a team of two, with one person filming and the second taking notes, and explaining the research to residents. We filmed 41 successful openings at two locations (Sutherland: n = 14, Stanwell Park: n = 27). This data was used for the establishment of the video scoring scheme (see below) and for inter-observer reliability testing, but did not allow for detailed analyses, since all birds were unmarked.

Direct observation of bin-opening, video coding and analysis of sequence data

Between 04 and 23 August 2019, up to four teams of two fieldworkers each simultaneously covered as much area as possible on bin-collection days in Sutherland, Helensburgh and

Stanwell Park, following the established protocol from 2018 (see above). We filmed and analyzed 160 successful openings (only instances where the entire sequence was visible) across the three hotspot locations. Sutherland: $n = 22$, all by unmarked birds; Helensburgh: $n = 26$, of which 13 were by 2 marked birds (3 and 10 openings, respectively); Stanwell Park: $n = 112$, all by marked birds, openings per individual: 12.44 ± 10.65 [mean ± SD], range 2 - 29. In Stanwell Park, we additionally filmed and analyzed 94 unsuccessful opening attempts by 27 marked birds.

For successful bin-openings, we scored from video: (i) the number of attempts (bouts) until successful opening, (ii) the duration of the successful opening sequence (last bout), (iii) the number of behavioral actions of the last bout and (iv) the number, identity, and duration of actions in each of the five main stages of bin-opening (see Fig. 3A and Table S2, S3 for details). All durations were scored to the nearest 0.2 seconds. We additionally recorded the geographic location (lat/lon) and the ID of the bird opening. All videos were scored in random order by BCK using 'Solomon Coder' software (http://solomoncoder.com). While the premise of the video scoring was to analyze individual- and site-specific differences, at the time of scoring, BCK had no knowledge as to which of the variables scored could be affected (the 2018 dataset was too small to allow for a formal analysis). To further limit observer bias, eight randomly selected successful openings from the 2018 data set (20%) were re-scored by JKH (who was hypothesis-naïve) to assess inter-observer agreement, which was excellent ($r \geq 0.99$, $p < 0.001$, Table S5). All analyses are based on BCK's original scores. For unsuccessful bin-openings in Stanwell Park, we scored from video: (i) the number of attempts (bouts) until the bird gave up, (ii) the stage at which the bird failed (best per engagement period), and (iii) the ID of the bird. Videos were scored in random order by Tim Jäger (who was hypothesis-naïve) and birds identified subsequently by BCK.

To compare similarity of bin-opening sequences between individuals and sites, we first normalized each of the 20 behavioral variables scored from video. We then calculated the overall dissimilarity between each pair of sequences using the '*dist*' function (Euclidian distance) in *R* (*26*), to create a behavioral dissimilarly matrix of all successful bin-opening events. We additionally created a matching individual matrix as well as a geographic matrix (in meters) based on the location where the opening-sequence had been observed. For unmarked individuals, identity was assumed to be the same within a single video, or if noted by the observer, and different between videos. We assessed correlations between the geographic, individual, and behavioral distance matrices using Partial Mantel tests (*35*) in the R package '*vegan*' (*36*), with the Pearson correlation method. Partial Mantel tests control for the effect of a third matrix when assessing whether the residuals of two matrices are correlated. We controlled for individual ID of the bin-opener when assessing the effect of geographic distance (square rooted) on behavioral dissimilarity and for geographic distance (square rooted) when assessing the effect of individual ID. We also calculated the relative contribution of each of the 20 behavioral variables to individual and site differences. Dataset: (*34*).

5. Social data and analysis

At one site, Stanwell Park, we additionally recorded social data on association and aggressive interactions. First, we measured social associations on nine days between 08 and 18 July 2019.

At a public park nearby to the birds' communal roost site, birds were attracted to begin ground foraging (a natural part of their behavioral repertoire) by scattering a few sunflower seeds across an area of approximately 350 m^2. Once individuals were foraging, BCK conducted group scans every 10 min for ca. 3 hours per day recording overall number and ID of individuals present, giving n = 112 scans of n = 114 marked individuals. We excluded individuals that were observed less than 5 times, resulting in a final data set of n = 89 individuals, of which 78 were of known sex (42M, 36F). Scans were then converted into a dyadic social network using the gambit of the group (*16*), with association strengths calculated with the simple ratio index. Here, social association ranged between 0 (never observed foraging together in the same scan) to 1 (always observed foraging together) (*37*). All social network analyses were conducted in *R* package '*asnipe' (38, 39)*.

Of the 89 birds present in the social network, 5 birds had been observed to successfully open bins (4M, 1F), 25 had been observed attempting to open bins (20M, 4F, 1 unknown sex), and 59 hadn't been observed engaging in this behavior (18M, 30F, 11 unknown sex). As we did not know the order in which birds first began to acquire the behavior, we did not perform a NBDA to investigate whether this acquisition was via social learning. Instead, we examined the indirect evidence for social learning in two ways. First, birds that are more central in the social network should have more access to social information, and so should have had a greater opportunity to socially learn the behavior. Second, if bin-opening is socially transmitted, then birds that are more associated to other bin-openers should be more likely to also be bin-openers. Importantly to note, while a positive correlation in both/either test is consistent with this interpretation, we can't conclusively determine directionality. It is also possible that bin-opening increases the social attractiveness of birds (therefore increasing centrality), or that 'bin-foragers' preferentially increase their association strength with similarly behaving birds (an effect of homophily, as recently demonstrated in dolphins (*40*)).

To test our first prediction, we compared eigenvector centrality in a linear model (LM) against bin opening status (attempted/successful *vs* not attempted). Eigenvector centrality was calculated in the R package '*sna'(41, 42)* . This measures both the connectedness of an individual and the connectedness of its associates, and is a particularly useful measure of centrality when considering variation in access to information (*43*). Individual-level network measures are not independent, and so significance was determined with 10,000 data stream permutations of the group-by-individual matrix using the *network_permutation* function in the R package '*asnipe' (38, 39).* Significance was assigned if the observed value for the coefficient of variation fell outside of the 95% range of estimates for models run on permutated networks. The results showed that males were more likely to be bin-openers, but also had a tendency to be more social than females (response variable = eigenvector centrality; permutating only within bin-opening status - LM: t_{78}=2.54, p=0.018). To control for this, permutations were restricted to within each sex.

To test our second prediction, we ran a multiple regression quadratic assignment procedure (MRQAP) in the R package '*asnipe' (38, 39)*, comparing a matrix of similarity in bin-opening status (successful, attempted, not attempted) against the social network while including age- and sex-similarity matrices as co-variates. Given the strong effect of sex (as the large majority of bin-openers were male), a second model was run limiting the dataset to males only. Significance was assigned by randomizing the residuals from the regression on each fixed effect as per standard MRQAP procedure (*39*).

To construct a dominance hierarchy for this group, we collected aggressive interaction (winner/loser) data on 14 days between 08 July and 02 October 2019. Interactions were recorded a) opportunistically in-between group scans (see above), and b) by placing a small handful of sunflower seed in a pile on the ground every two minutes (outside of group scan hours). This resulted in *n* = 1407 aggressive interactions. However, since most birds attempting and succeeding at opening bins were male (see Table S4) and males tend to be higher in the hierarchy in cockatoos, we limited our analysis to male-male interactions. We furthermore excluded individuals with unknown age, as well as individuals with fewer than five interactions. The final dataset included 625 interactions by 37 individuals. We obtained a dominance hierarchy using randomized Elo-rating procedure (1000 randomizations (*44*)), which accounts for the temporal sequence of interactions. Randomized Elo-scores were highly repeatable: 91.6%. We calculated ranks using the '*elo_scores'* function in the '*aniDom*' *R* package (*45*). Rank was not influenced by the number of interactions an individual had (LM: F (1,35)=3.01, *p*=0.09).

Finally, to assess whether individual-level variables influenced the likelihood of being a bin-opener, we ran: (i) For age (juvenile or adult) an ordinal cumulative link model (CLM, *'ordinal'* package (*46, 47*)), with the response variable ordered as: has not attempted bin-opening > attempted bin-opening > successful opening for all individuals with known age. (ii) For rank (in hierarchy) a CLM (as (i)) for all males with known age and at least five interactions. (iii) For weight a generalized linear model (GLM) with a binomial error structure ('*lme4*' package (*48*), response: binomial not attempted *vs* attempted/successful for males with known age and weight (removing one outlier) and at least five interactions. We assessed the significance of main effects with likelihood ratio tests (best model against null model, at α=0.05). Model assumptions were checked using the packages '*ordinal*' (*47*) and '*DHARMa*'(*49*). All analyses were done in *R* (*26*).

Supplementary Text

Ethics:

Research was approved by the Ethics Council of the Max Planck Society, Germany (application no. 2018_12) and the Animal Care and Ethics Committee, NSW Department of Industry, Australia (application no. 19/2107), and covered under a Scientific License by the NSW National Parks & Wildlife Service, Office of Environment & Heritage (license number: SL100107).

Extended list of acknowledgements

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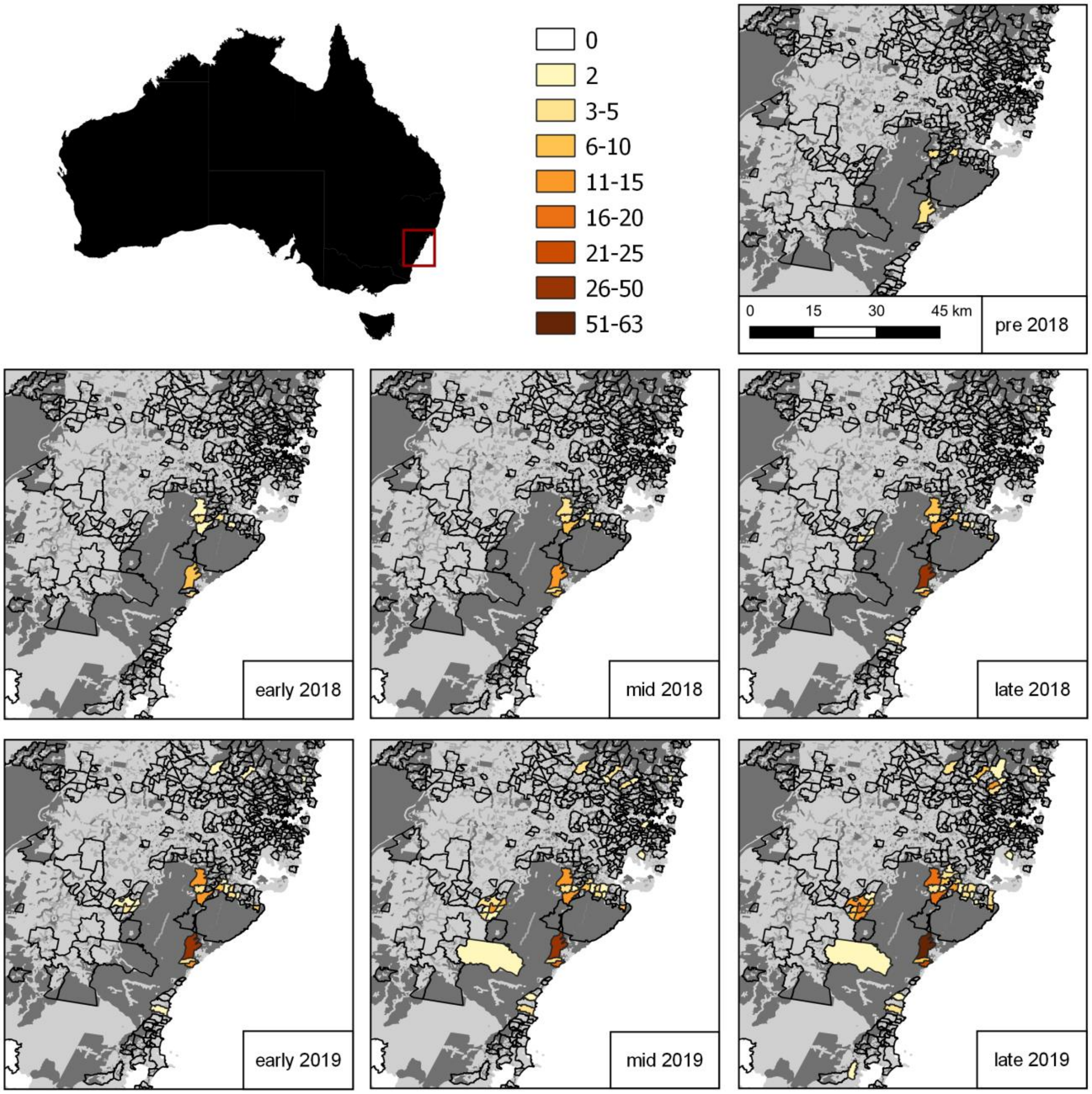


Fig. S1. Spread of bin-opening across the Sydney and Wollongong regions across seven time periods. Community reports were received via an online survey August-December 2018 and August-December 2019. Suburbs outlined in black only received negative reports (no direct observation of bin-opening), suburbs with at least two positive reports for each respective time period are colored. Higher numbers of positive reports are shown in darker colors (cumulative over time). Areas with high tree coverage (trees 10-15 m high > 9.6%) are depicted in dark grey, areas with low tree cover (< 9.6%) in light grey.

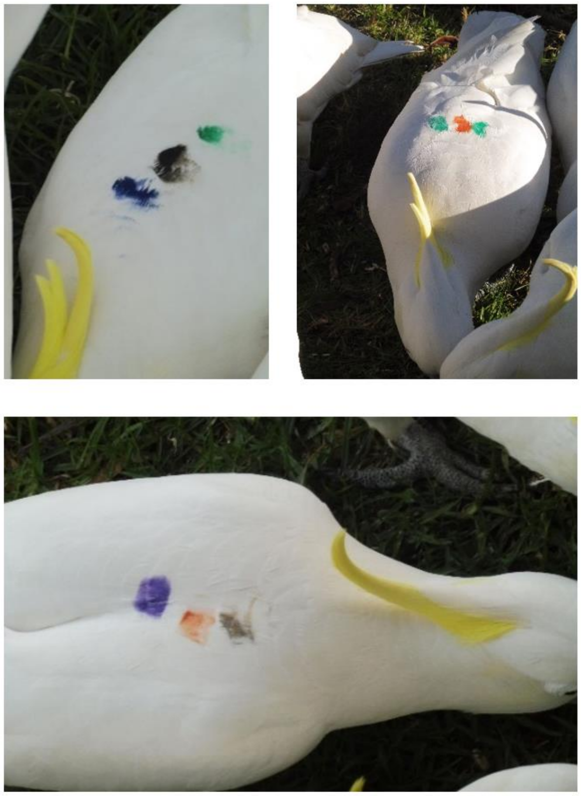


Fig. S2. Color-marked sulphur-crested cockatoos. Three examples of color-marked sulphur-crested cockatoos. Birds were marked with two to four colored dots of non-toxic paint, either vertically or horizontally, to allow for individual identification.

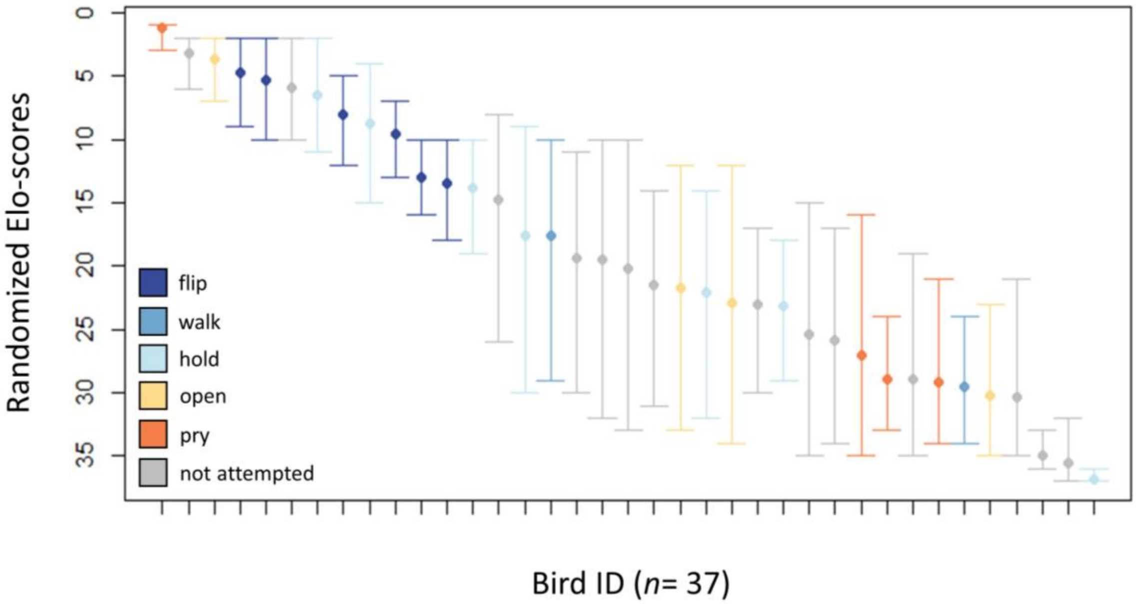


Fig. S3. Dominance hierarchy of male sulphur-crested cockatoos in Stanwell Park. Dominance rank calculated by the randomized Elo-rating procedure, using interactions at a clumped food source. Since males are generally dominant over females in sulphur-crested cockatoos, and most cockatoos that attempted to or successfully opened bins were male, analysis of interactions was limited to those where both partners were male, age was known, and individuals had at least five interactions. Colors indicate the best stage a bird reached during bin-opening attempts.

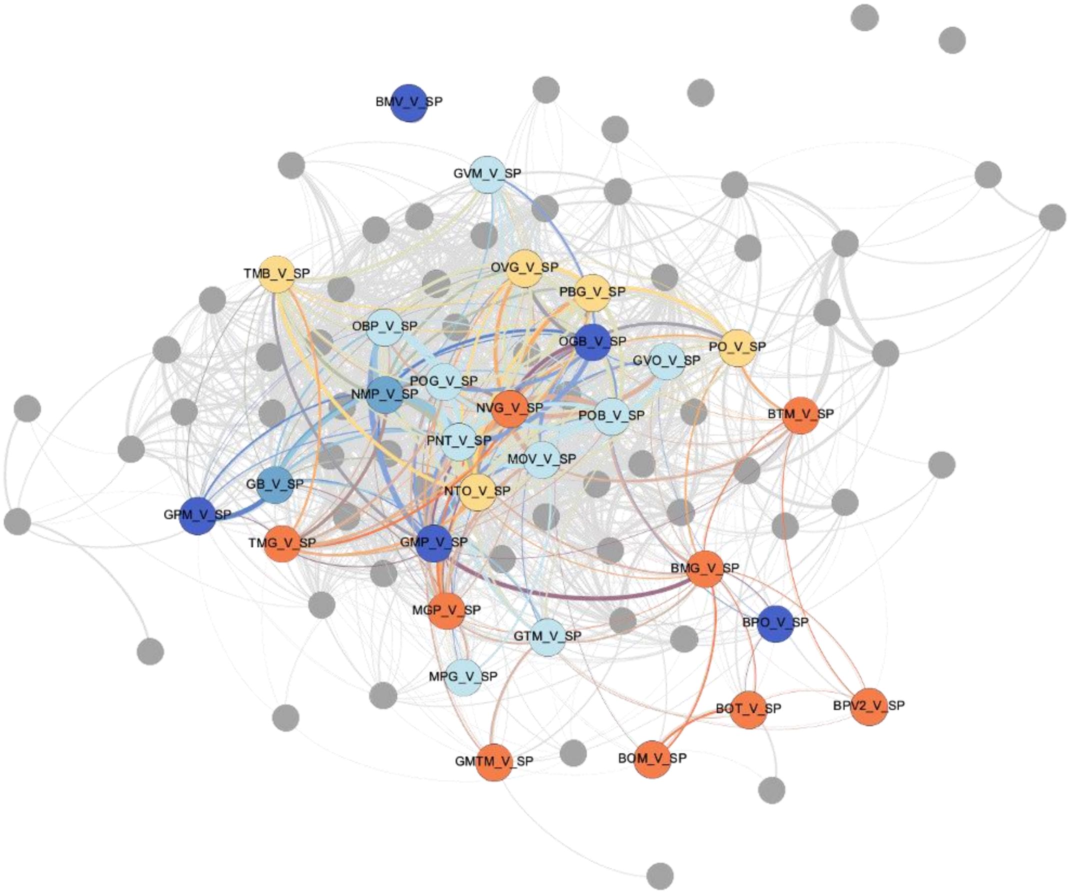


Fig. S4. Social network of sulphur-crested cockatoos in Stanwell Park. Networks recorded over nine days for 89 individuals. Node size represents the sum of an individual's association strengths. Association strength between dyads is represented in edge weights. Successful and unsuccessful bin-openers are labelled, all others are in grey. Within bin-openers, nodes are colored, with successful bin-openers in dark blue, birds that attempted to open in orange to medium blue depending on behavioral state (see Fig. 3A, main text, Fig. S3).

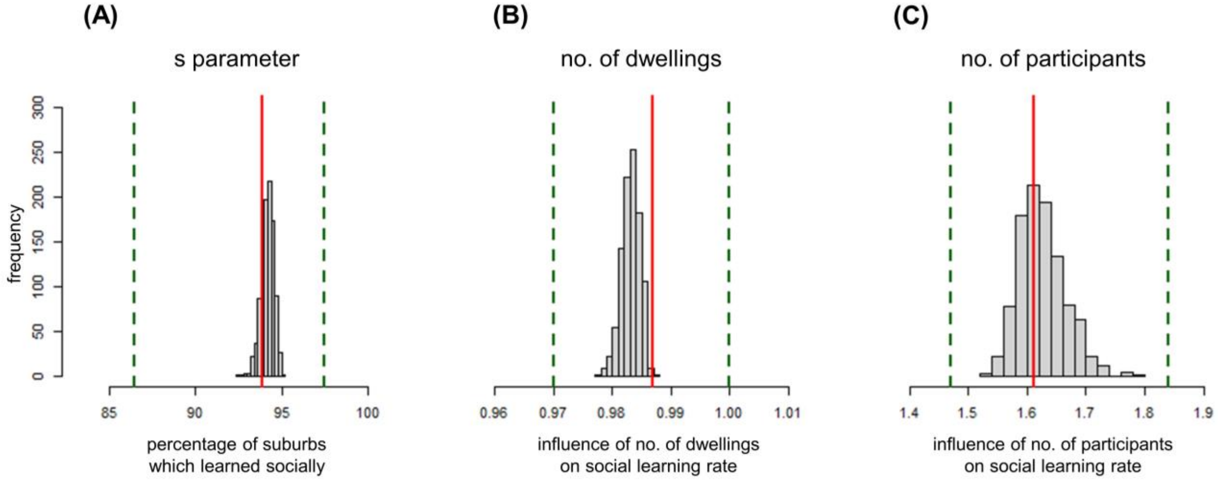


Fig. S5. Parameter estimates from sensitivity analysis using OADA with randomized order of acquisition within each time step. Parameter estimates for **(A)** the strength of social transmission; **(B)** the number of dwellings and **(C)** the number of survey participants influencing the social learning rate. Parameter estimates fall well within the 95% profile likelihood confidence interval (upper and lower level indicated by green dashed lines) based on the best performing model from discrete TADA. Red lines indicate the model averaged estimates for each parameter resulting from the discrete TADA analysis (reported in the main text), averaged across all models.

Table S1. Support for Individual-Level Variables on learning rates with model average estimates stated as summed Akaike weights.

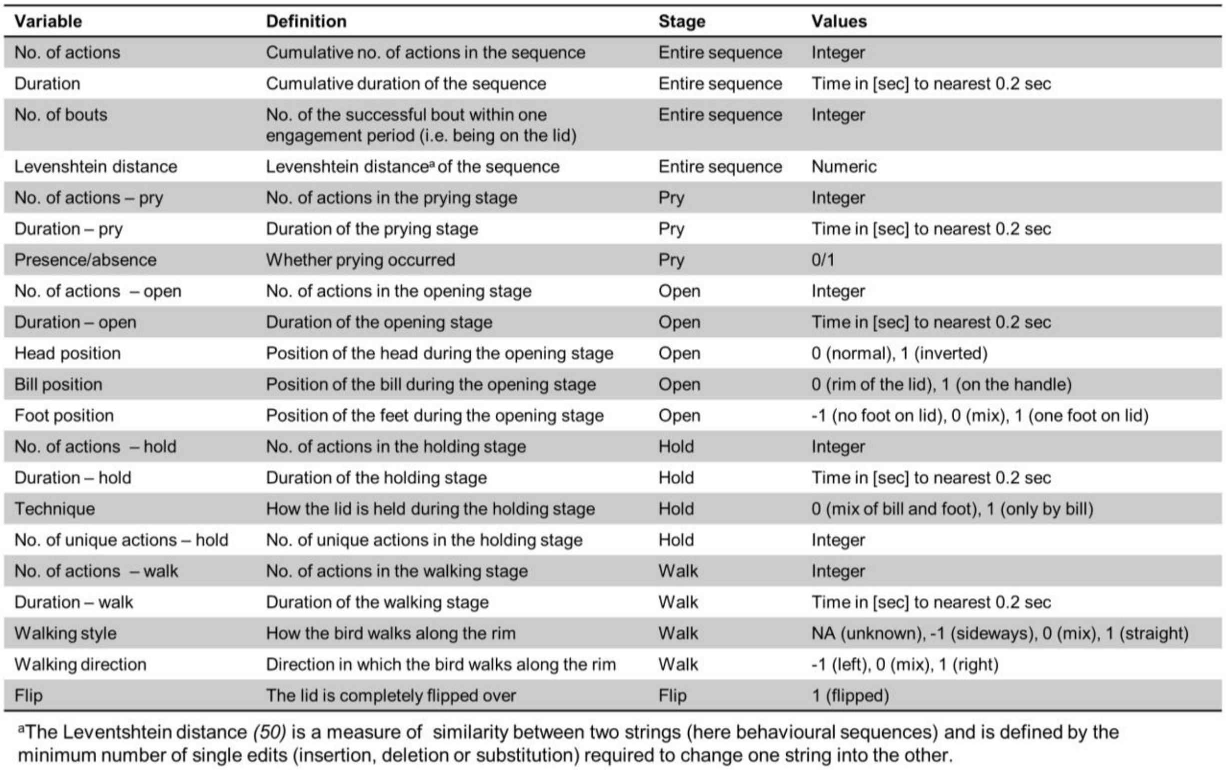
ILV	**Size (km^2)**	**No. of dwellings**	**No. of participants**
Relative support for effect on social learning	0.27	**0.87**	**>0.99**
Model averaged estimate (mean; back-transformed)	-	0.99 per dwelling	1.61 per participant
Profile likelihood confidence interval conditional on the best model	-	0.97-1 per dwelling	1.47-1.84 per participant
Relative support for effect on asocial learning	0.22	0.26	0.36
Model averaged estimate (mean; back-transformed)	-	-	-
Profile likelihood confidence interval conditional on the best model	-	-	-

Table S2. Definitions of behavioral actions used for video scoring.

Action	Definition
Pry	The bird pries open the lid while either standing on the lid with one or both feet or by standing on the rim. The bill and the rim of the bin are in constant contact.
Open lid	The bird opens the lid with the bill, grabbing the lid at the rim .
Open lid – foot on lid	The bird opens the lid with the bill, grabbing the lid at the rim while having one foot on the lid.
Open lid – head inverted[a]	The bird opens the lid with the bill, grabbing the lid at the rim while having the head inverted.
Open lid – head inverted[a] – foot on lid	The bird opens the lid with the bill, grabbing the lid at the rim while having the head inverted and with one foot on the lid.
Open lid – grab handle	The bird opens the lid with the bill, grabbing the lid at the handle.
Open lid – grab handle – foot on lid	The bird opens the lid with the bill, grabbing the lid at the handle while having one foot on the lid.
Hold lid with bill	The bird holds the lid with the bill, grabbing the lid at the rim.
Hold lid with foot and bill	The bird holds the lid simultaneously with one foot and the bill, grabbing the lid at the rim.
Hold lid with bill – head inverted[a]	The bird holds the lid with the bill, grabbing the lid at the rim while having the head inverted.
Hold lid with foot and bill – head inverted[a]	The bird holds the lid simultaneously with one foot and the bill, grabbing the lid at the rim while having the head inverted.
Hold lid with foot	The bird holds the lid with one foot.
Hold lid with foot and bill – grab handle	The bird holds the lid simultaneously with one foot and the bill, grabbing the lid at the handle.
Walk along the rim – left	The bird walks along the rim towards the left.
Walk along the rim – right	The bird walks along the rim towards the right.
Walking style – straight	The bird walks along the rim by putting one foot in front of the other.
Walking style – sideways	The bird walks along the rim by putting one foot next to the other.
Flip	The lid is completely flipped over.

[a] The cockatoo is holding the head upside down. For an example, see Fig. 3A – opening stage.

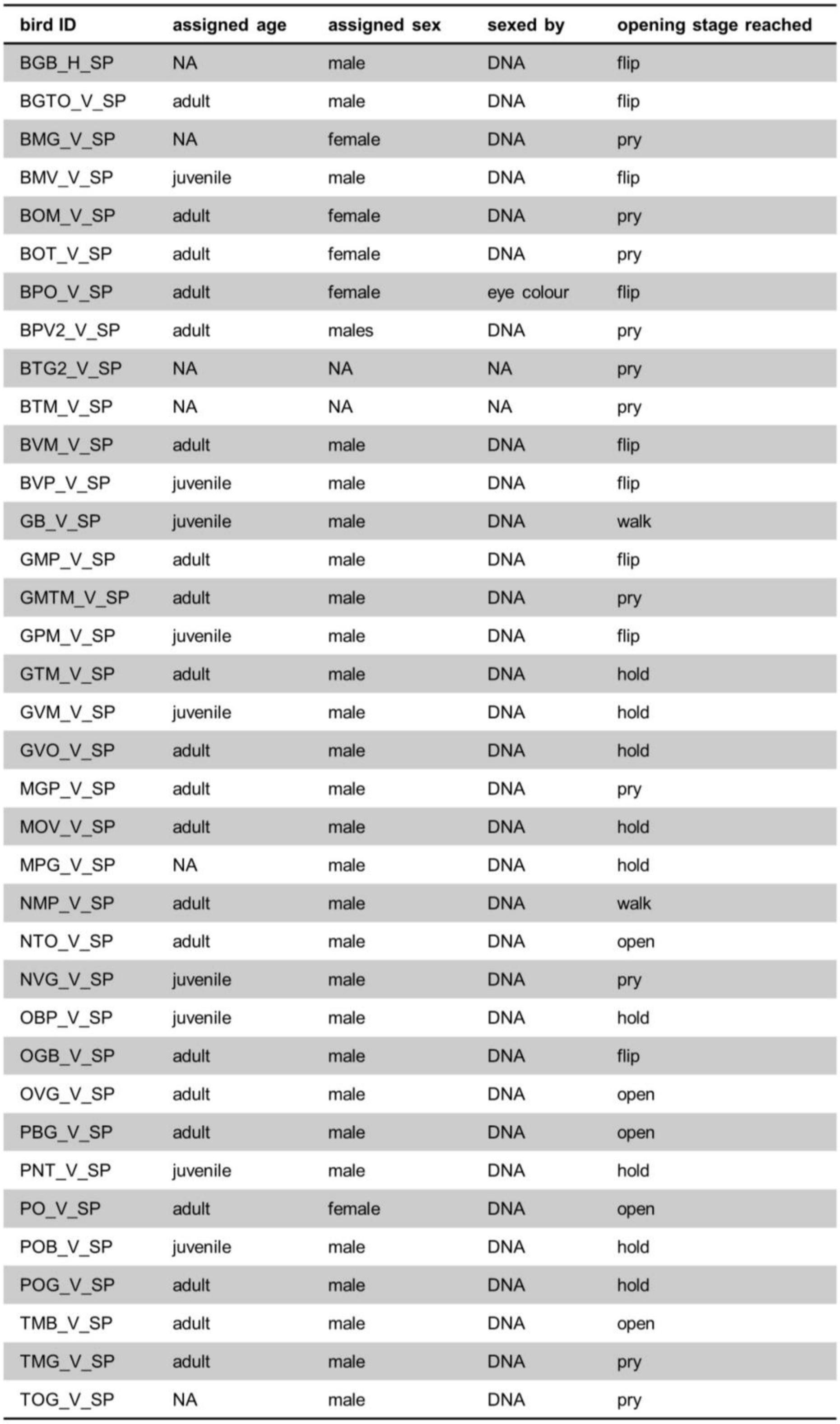
Table S3. Behavioral variables used for analysis of geographic and individual differences in bin-opening by sulphur-crested cockatoos.



Variable	Definition	Stage	Values
No. of actions	Cumulative no. of actions in the sequence	Entire sequence	Integer
Duration	Cumulative duration of the sequence	Entire sequence	Time in [sec] to nearest 0.2 sec
No. of bouts	No. of the successful bout within one engagement period (i.e. being on the lid)	Entire sequence	Integer
Levenshtein distance	Levenshtein distance[a] of the sequence	Entire sequence	Numeric
No. of actions – pry	No. of actions in the prying stage	Pry	Integer
Duration – pry	Duration of the prying stage	Pry	Time in [sec] to nearest 0.2 sec
Presence/absence	Whether prying occurred	Pry	0/1
No. of actions – open	No. of actions in the opening stage	Open	Integer
Duration – open	Duration of the opening stage	Open	Time in [sec] to nearest 0.2 sec
Head position	Position of the head during the opening stage	Open	0 (normal), 1 (inverted)
Bill position	Position of the bill during the opening stage	Open	0 (rim of the lid), 1 (on the handle)
Foot position	Position of the feet during the opening stage	Open	-1 (no foot on lid), 0 (mix), 1 (one foot on lid)
No. of actions – hold	No. of actions in the holding stage	Hold	Integer
Duration – hold	Duration of the holding stage	Hold	Time in [sec] to nearest 0.2 sec
Technique	How the lid is held during the holding stage	Hold	0 (mix of bill and foot), 1 (only by bill)
No. of unique actions – hold	No. of unique actions in the holding stage	Hold	Integer
No. of actions – walk	No. of actions in the walking stage	Walk	Integer
Duration – walk	Duration of the walking stage	Walk	Time in [sec] to nearest 0.2 sec
Walking style	How the bird walks along the rim	Walk	NA (unknown), -1 (sideways), 0 (mix), 1 (straight)
Walking direction	Direction in which the bird walks along the rim	Walk	-1 (left), 0 (mix), 1 (right)
Flip	The lid is completely flipped over	Flip	1 (flipped)

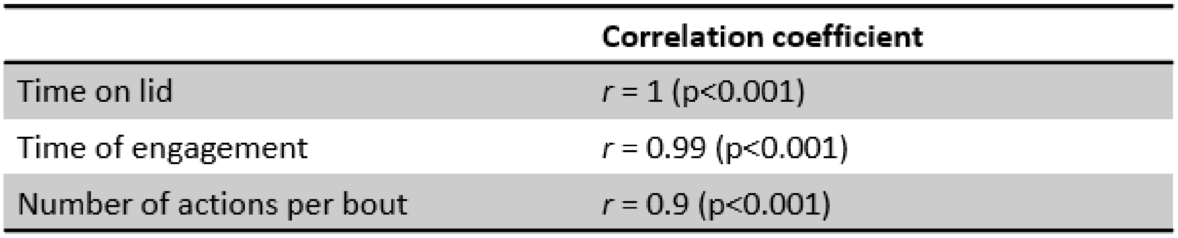
[a] The Leventshtein distance *(50)* is a measure of similarity between two strings (here behavioural sequences) and is defined by the minimum number of single edits (insertion, deletion or substitution) required to change one string into the other.

Table S4. Sex and age attributes for color-marked birds at Stanwell Park that attempted to open bins with opening stage reached.



bird ID	assigned age	assigned sex	sexed by	opening stage reached
BGB_H_SP	NA	male	DNA	flip
BGTO_V_SP	adult	male	DNA	flip
BMG_V_SP	NA	female	DNA	pry
BMV_V_SP	juvenile	male	DNA	flip
BOM_V_SP	adult	female	DNA	pry
BOT_V_SP	adult	female	DNA	pry
BPO_V_SP	adult	female	eye colour	flip
BPV2_V_SP	adult	males	DNA	pry
BTG2_V_SP	NA	NA	NA	pry
BTM_V_SP	NA	NA	NA	pry
BVM_V_SP	adult	male	DNA	flip
BVP_V_SP	juvenile	male	DNA	flip
GB_V_SP	juvenile	male	DNA	walk
GMP_V_SP	adult	male	DNA	flip
GMTM_V_SP	adult	male	DNA	pry
GPM_V_SP	juvenile	male	DNA	flip
GTM_V_SP	adult	male	DNA	hold
GVM_V_SP	juvenile	male	DNA	hold
GVO_V_SP	adult	male	DNA	hold
MGP_V_SP	adult	male	DNA	pry
MOV_V_SP	adult	male	DNA	hold
MPG_V_SP	NA	male	DNA	hold
NMP_V_SP	adult	male	DNA	walk
NTO_V_SP	adult	male	DNA	open
NVG_V_SP	juvenile	male	DNA	pry
OBP_V_SP	juvenile	male	DNA	hold
OGB_V_SP	adult	male	DNA	flip
OVG_V_SP	adult	male	DNA	open
PBG_V_SP	adult	male	DNA	open
PNT_V_SP	juvenile	male	DNA	hold
PO_V_SP	adult	female	DNA	open
POB_V_SP	juvenile	male	DNA	hold
POG_V_SP	adult	male	DNA	hold
TMB_V_SP	adult	male	DNA	open
TMG_V_SP	adult	male	DNA	pry
TOG_V_SP	NA	male	DNA	pry

Table S5. Correlation coefficients for inter-observer agreement of video scoring.



	Correlation coefficient
Time on lid	r = 1 (p<0.001)
Time of engagement	r = 0.99 (p<0.001)
Number of actions per bout	r = 0.9 (p<0.001)

Movie S1. Individual and geographic variation in bin-opening behavior.

Data S1. R Code for NBDA models.

Data S2. Dataset for NBDA models.

Data S3. Dataset for analysis of bin-opening sequences