ANIMAL CULTURE

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

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The emergence, spread, and establishment of innovations within cultures can promote adaptive responses to anthropogenic change. We describe a putative case of the development of a cultural adaptation to urban environments: opening of household waste bins by wild sulphur-crested cockatoos. A spatial network analysis of community science reports revealed the geographic spread of bin opening from three suburbs to 44 in Sydney, Australia, by means of 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 parrots. Bin opening is directly linked to human-provided opportunities, highlighting the potential for culture to facilitate behavioral responses to anthropogenic change.

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

Identifying persistent cultures in animal species—that is, 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, as community science allows for a wide spread of observations (*3*). Additionally, many urban resources are standardized (e.g., waste disposal) (*4*). Urban environments may also 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*), although direct evidence of this is lacking (*9*). However, if innovations spread through populations via social learning, they can lead to emergent adaptive cultures (*8*, *10*)—socially learned behaviors that are beneficial for urban living and that differ between sites.

The cultural intelligence hypothesis predicts that animal culture has coevolved 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 also exhibit vocal cultures (*13*). However, there is a paucity of evidence for social learning or culture in the foraging behavior of large parrots. 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 throughout our 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. We used a large-scale community

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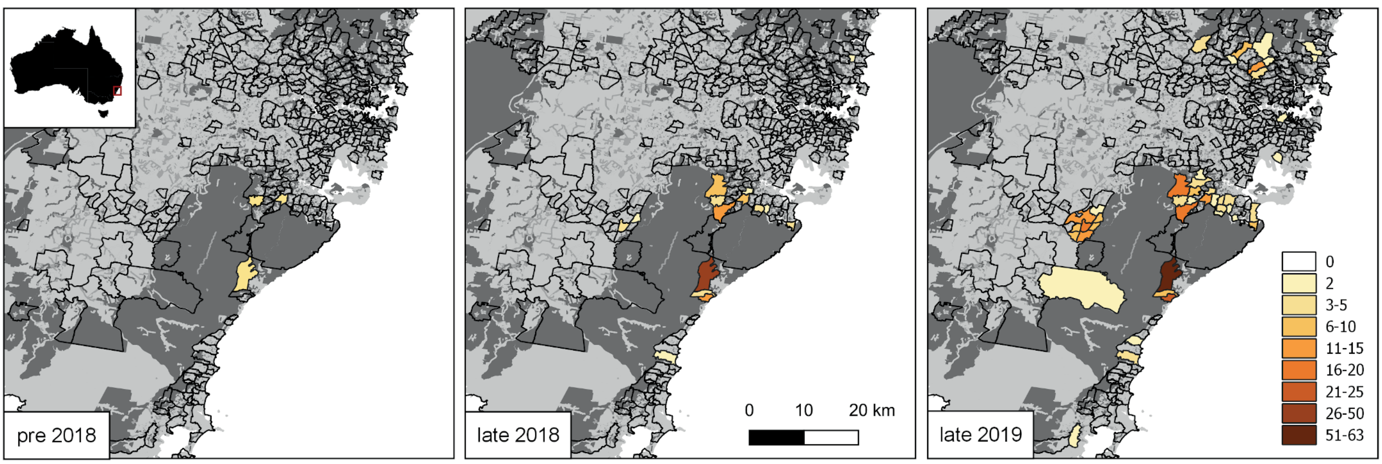


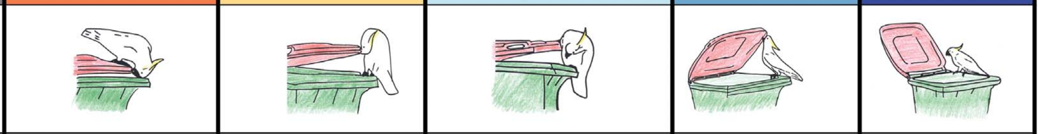
Fig. 2. Spread of bin opening across the Sydney and Wollongong regions. Reported in only three suburbs before 2018, bin-opening behavior had spread to 44 suburbs by late 2019. Suburbs outlined with black returned only negative reports, whereas suburbs with at least two positive reports for the respective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

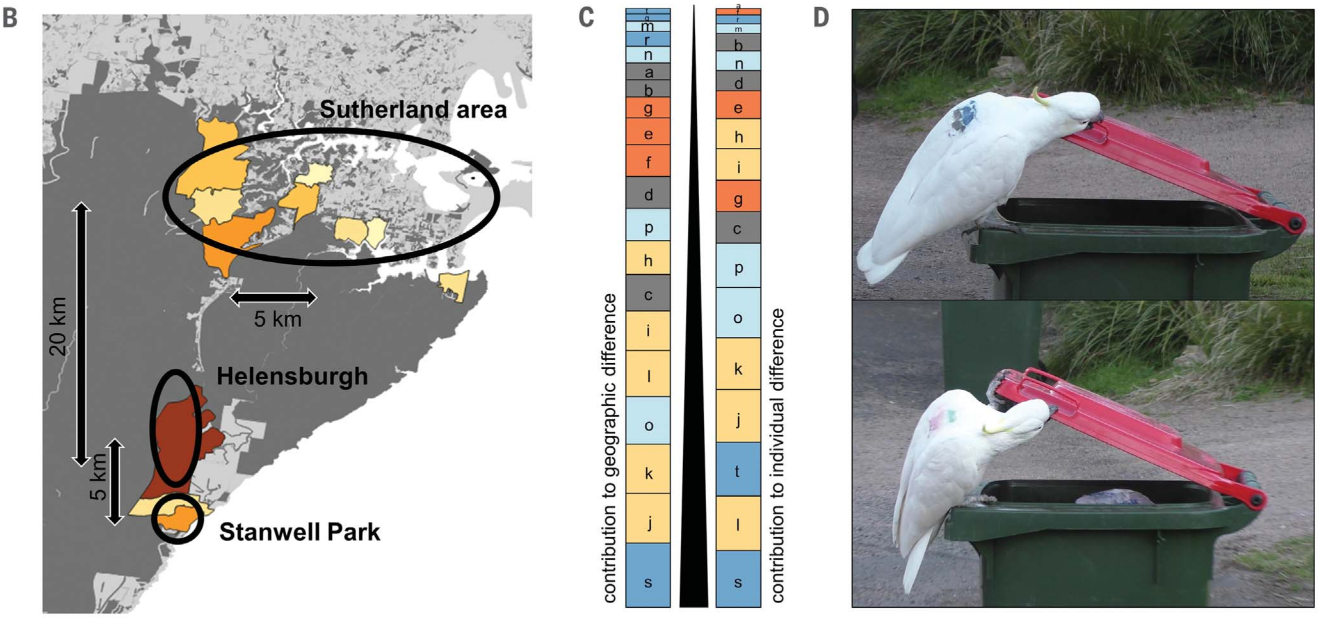
science survey to map bin opening across the Sydney and Wollongong regions combined with direct observations at multiple sites to identify possible individual or site-level differences.

To map occurrence, we collected data via an online survey over two consecutive years (2018 and 2019). We asked whether residents had observed cockatoos opening lids of household bins and, if so, when and where (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 the ample

A

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 the movies for each stage (for details, see tables S2 and S3). (**B**) Study areas for direct observations. (**C**) Relative contribution of each behavioral variable to geographic (left) and individual differences (right); most to least important, bottom to top, cumulative to 100%. Colors and letters are matched to those in (A). (**D**) Marked individuals holding the lid with the bill at the handle (top) and with bill and foot at the rim (bottom).

opportunities for birds 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 on the basis of 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 analysis assumes that if cumulative uptake in suburbs is due to social learning, new occurrences are more likely in suburbs closer to and within dispersal distance to where the behavior is established (*14*). Three suburbs in which bin opening was observed prior to 2018 were included as likely sites of origin. We included three suburb-level variables: (i) number of survey participants to control for reporting rate, (ii) suburb size (square kilometers) as an imperfect proxy for cockatoo population size, and (iii) number of dwellings as a 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% confidence interval 86.5 to 97.3%) of suburbs where it occurred. The models also revealed a secondary innovation of bin opening in the far north of Sydney (Narraweena) in late 2018, as shown by Fig. 2. From this, the behavior subsequently spread by social learning. The estimated 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. 3, B and D, and fig. S2). Movie analysis of 160 successful opening sequences revealed that bin opening is a complex, multistep foraging behavior, consisting of five stages with several options at each stage (Fig. 3A and tables S2 and S3).

Several components of the opening sequences, such as walking direction (possibly related to laterality) and whether or not the lid was pried open (possibly related to experience as prying is not necessary for successful bin opening), were strongly associated with individual cockatoos. Other components—e.g., those associated with the opening stage—differed more between sites (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 identity, dissimilarity between sequences increased with increasing geographic distance between observations (partial Mantel test: $r = 0.21$, $P = 0.002$; Fig. 4 and Movie S1), suggesting the formation of local subcultures 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 the 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, 9 cockatoos were successful (n = 112 complete sequences) and 27 attempted but were unsuccessful (n = 94 sequences) in opening bins. Both adults and juveniles opened bins [cumulative link model (CLM) testing age bias: $\chi^2 = 0.86$, $P = 0.35$, $n = 84$],

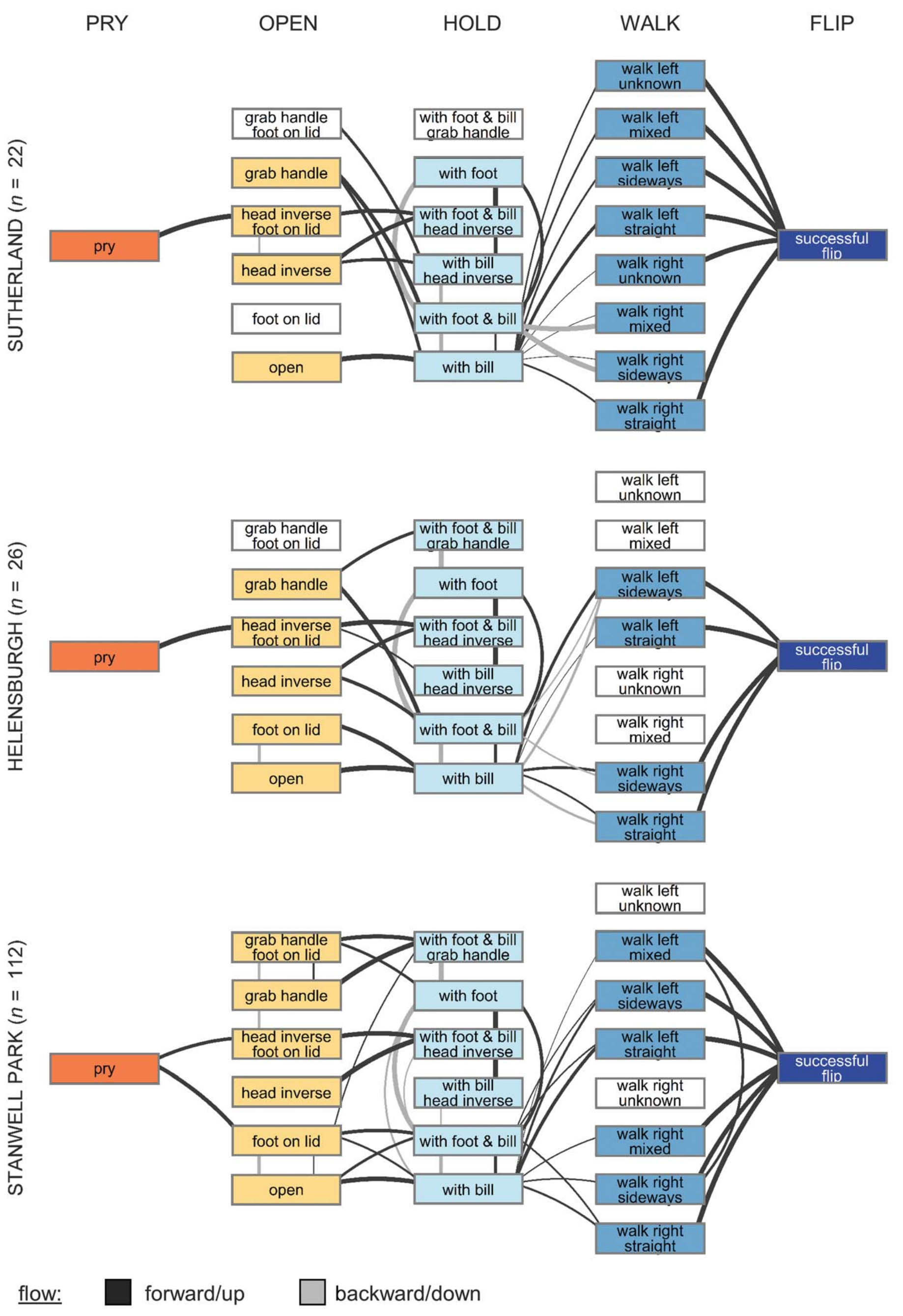


Fig. 4. Behavioral sequences of successful openings across sites. Bin-opening stages are depicted from left to right. Connections are colored by direction: advance to the next stage or upward within a stage (black), regress to the previous stage or downward within a stage (gray). The thickness of a connection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

suggesting social transmission between age classes. Of cockatoos with 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: $\chi^2 = 7.68$, $P = 0.006$, $n = 37$; fig. S3). Finally, there was a nonsignificant tendency for heavier males to attempt bin opening (generalized linear model: $\chi^2 = 3.12$, $P = 0.08$, $n = 20$), although a small sample size for males with known weight precluded full analysis of potential interactions between rank and weight.

Males tend to be heavier and more dominant than 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); we frequently observed cockatoos displacing conspecifics off of bins. Our results contrast other studies suggesting that younger and lower-ranking individuals have a higher probability of social learning [e.g., (*18*)] but demonstrate 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 difficult, however, as 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 attempting or 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 higher similarity 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: $est = 0.97$, $P = 0.010$, $n = 34$). Although 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 the spread of innovation can not only result in establishment of culture, but can also further lead to emergent geographically distinct subcultures. Our study area is characterized by suburbs and forests. Data from color-marked birds suggest that forests may serve as barriers, as little movement through such areas was observed. 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 complex multistep traits, as observed here, could potentially further enhance this effect. This behavior has emerged in direct response to land-use change. It illustrates 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

science.sciencemag.org/content/373/6553/456/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S5
Tables S1 to S5
References (*25*–*50*)
MDAR Reproducibility Checklist
Movie S1
Data S1 to S3

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Birds in the bin

It is by now well accepted that humans are not the only animal to have complex culture, and we have also found that ecological novelty can lead to cultural innovation. Klump *et al.* documented the emergence of an evolving set of behaviors in response to human-generated resources, specifically garbage bins, in sulphur-crested cockatoos. This finding both documents the existence and spread of complex foraging culture among parrots, a lineage known for high-level cognitive function, and illuminates how the spread of a cultural innovation can lead to regional distinct variations.

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