3. Vannette, R.L., Gauthier, M.-P.L., and Fukami, T. (2013). Nectar bacteria, but not yeast, weaken a plant–pollinator mutualism. Proc. R. Soc. B *280*, 20122601.

4. Rering, C.C., Beck, J.J., Hall, G.W., McCartney, M.M., and Vannette, R.L. (2018). Nectar-inhabiting microorganisms influence nectar volatile composition and attractiveness to a generalist pollinator. New Phytol. *220*, 750–759.

5. Dharampal, P.S., Carlson, C., Currie, C.R., and Steffan, S.A. (2019). Pollen-borne microbes shape bee fitness. Proc. R. Soc. B *286*, 20182894.

6. Russell, A.L., and Ashman, T.-L. (2019). Associative learning of flowers by generalist bumble bees can be mediated by microbes on the petals. Behav. Ecol. *30*, 746–755.

7. Roulston, T.H., and Cane, J.H. (2000). Pollen nutritional content and digestibility for animals. Plant Syst. Evol. *222*, 187–209.

8. Christensen, S.M., Munkres, I., and Vannette, R.L. (2021). Nectar bacteria stimulate pollen germination and bursting to enhance microbial fitness. Curr. Biol. *31*, 4373–4380.

9. Álvarez-Pérez, S., and Herrera, C.M. (2013). Composition, richness and nonrandom assembly of culturable bacterial-microfungal communities in floral nectar of Mediterranean plants. FEMS Microbiol. Ecol. *83*, 685–699.

10. Pozo, M.I., Herrera, C.M., Lachance, M.-A., Verstrepen, K., Lievens, B., and Jacquemyn, H. (2016). Species coexistence in simple microbial communities: unravelling the phenotypic landscape of co-occurring *Metschnikowia* species in floral nectar. Environ. Microbiol. *18*, 1850–1862.

11. Pozo, M.I., and Jacquemyn, H. (2019). Addition of pollen increases growth of nectar-living yeasts. FEMS Microbiol. Lett. *366*, fnz191.

12. Álvarez-Pérez, S., Tsuji, T., Donald, M., Assche, A.V., Vannette, R.L., Herrera, C.M., Jacquemyn, H., Fukami, T., and Lievens, B. (2021). Nitrogen assimilation varies among clades of nectar- and insect-associated Acinetobacters. Environ. Microbiol. *81*, 990–1003.

13. Schmitt, A., Roy, R., and Carter, C.J. (2021). Nectar antimicrobial compounds and their potential effects on pollinators. Curr. Opin. Insect Sci. *44*, 55–63.

14. Lievens, B., Hallsworth, J.E., Pozo, M.I., Belgacem, Z.B., Stevenson, A., Willems, K.A., and Jacquemyn, H. (2015). Microbiology of sugar-rich environments: diversity, ecology and system constraints. Environ. Microbiol. *17*, 278–298.

15. Eisikowitch, D., Lachance, M.A., Kevan, P.G., Willis, S., and Collins-Thompson, D.L. (1989). The effects of the natural assemblage of microorganisms and selected strains of the yeast *Metschnikowia reukaufii* in controlling the germination of pollen of the common milkweed *Asclepias syriaca*. Can. J. Bot. *68*, 1163–1165.

16. Álvarez-Pérez, S., Baker, L.J., Morris, M.M., Tsuji, K., Sanchez, V.A., Fukami, T., Vannette, R.L., Lievens, B., and Hendry, T.A. (2021). *Acinetobacter pollinis* sp. nov., *Acinetobacter baretiae* sp. nov. and *Acinetobacter rathckeae* sp. nov., isolated from floral nectar and honey bees. Int. J. Syst. Evol. Microbiol. *71*, 004783.

17. Cullen, N., Fetters, A., and Ashman, T.-L. (2021). Integrating microbes into pollination. Curr. Opin. Insect Sci. *44*, 48–54.

18. Muth, F., Breslow, P.R., Masek, P., and Leonard, A.S. (2018). A pollen fatty acid enhances learning and survival in bumblebees. Behav. Ecol. *29*, 1371–1379.

19. Yang, M., Deng, G.-C., Gong, Y.-B., and Huang, S.-Q. (2019). Nectar yeasts enhance the interaction between *Clematis akebioides* and its bumblebee pollinator. Plant Biol. *21*, 732–737.

20. Vannette, R.L., and Fukami, T. (2018). Contrasting effects of yeasts and bacteria on floral nectar traits. Ann. Bot. *121*, 1343–1349.

Animal behavior: Innovation in the city

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Behavioral innovations may help animals cope with new environments, but how such behaviors start is hard to capture. A new study reports the innovation and transmission of a new foraging culture in an urban parrot.

British tits opening milk bottles[1], dolphins foraging from prawn trawlers[2] or crows making use of vehicles to crack walnuts[3] — these are just a few examples of the many behavioral innovations that animals use to profit from human civilization. Innovation — that is a new or modified learned behavior not previously known in a population[4] — allows animals to exploit new resources and to cope with environmental change[4]. Such new behaviors can spread through a population by social transmission from informed individuals to uninformed individuals via social learning[5] and potentially lead to adaptive cultures[6]. In recent decades, studies of animal social learning, information spread and arising culture have increased rapidly, spanning a great variety of behavioral domains and species[7,8]. Nevertheless, the identification of cultures in wild populations remains difficult. This is because behavioral innovations often arise unpredictably, are usually difficult to track across space and time and alternative explanations for local variation in the novel behavior, such as genetic or ecological factors, can be difficult to eliminate[8,9]. In a new study[6], Barbara Klump, Lucy Aplin and colleagues report in detail the development of a novel cultural adaptation to an anthropogenic resource by Sulphur-crested cockatoos (*Cacatua galerita*).

Sulphur-crested cockatoos are long-lived and highly social parrots, native to eastern Australia. These curious and intelligent birds increasingly inhabit urban environments and adapt well to city life. Klump and colleagues[6] document the social spread of a new foraging behavior of these parrots in Sydney, Australia: the opening of household-waste bins (Figure 1). The new study maps the diffusion of this novel behavior across suburbs of Sydney by collecting reports of 'bin-opening' through a large-scale citizen-science survey and combines this with detailed observations of the behavior by specific cockatoos of known identities within specific sites. Researchers used a web-based survey to collect 1396 reports across 478 suburbs in the Sydney and Wollongong regions about whether residents had witnessed birds opening household bins. By the end of the study, 338 reports from 44 suburbs had reported the behavior, despite being observed in just three suburbs initially.

If a behavior is socially transmitted, we would expect its spread to follow the social network, with individuals being more likely to gain the new information from their informed close associates, and then subsequently pass it on to their uninformed close associates[10]. However, collecting information about individual cockatoos' social connections across such a large geographical scale (over 150 km in diameter) is difficult to achieve. Therefore, a spatial 'network' of geographic distance between suburbs was created and fed with information about the cockatoo dispersal ranges, which are usually under 25 km. The assumption was made that if bin-opening is socially learned, new occurrences should be more likely in suburbs close to the area where the behavior originated, and subsequently spread from the new areas that the behavior was observed within.

Using spatial network-based diffusion analysis[11], Klump and colleagues[6] tracked the geographical spread of this new behavior and showed that transmission was strongly linked to the spatial proximity of suburbs, suggesting that the behavior was passed on through social learning as informed individuals dispersed into naive areas and took the behavior with them. Interestingly, as cockatoos appeared to avoid movement through forested areas and preferred other routes[6], this additionally suggests that it would now be beneficial for future work to examine how the distribution of habitat types across a landscape shapes the spread of new innovations.

In addition, the large-scale citizen-science approach utilized by Klump and colleagues[6] demonstrates how

Figure 1. Urban innovators.
Sulphur-crested cockatoo opening a household-waste bin while surrounded by flock members. (Photo: Barbara Klump.)

public engagement in scientific work increasingly makes important contributions to ecological research, and is at the same time a fantastic tool to engage the public[12]. Indeed, citizen science data are incorporated in many diverse research fields ranging from biodiversity to astronomy[13,14]. While Klump and colleagues[6] demonstrate here how direct citizen science can also be used to study animal behavior, other examples are beginning to emerge in other areas of behavioral ecology, such as using passively generated data from internet activity by individuals (termed 'iEcology'[15]) to provide insights into ecology. The internet holds a vast amount of accessible digital data, such as pictures from social media posts, and now this kind of passively generated data may perhaps provide another useful tool for researchers[15], especially when studying rare phenomena such as behavioral innovations.

Klump and colleagues[6] also combine their findings from the citizen-science data (which document behavioral spread across the landscape) with direct observations of individually-identified birds at multiple suburbs to identify the finer-scale mechanics of this socially learnt behavior. At three hotspots, video recordings of bin-opening revealed a complex, multi-step behavior involving five stages with various options: pry, open, hold, walk and flip. Several components of the behavioral sequence were location-specific, and dissimilarity in behavioral sequences increased with increasing geographic distance between sites. Site-specific differences in behavior indicate the formation of local cultures within sites, similar to as reported in foraging behavior of chimpanzees[16]. Finally, at one focal site, the authors measured various traits of 90% of birds to examine the effect of different characteristics in bin-opening behavior (Figure 2). Out of 114 individuals, nine opened a bin successfully and 27 attempted unsuccessfully. Successful bin-openers were mostly males ranking high in the dominance hierarchy. Social network analysis revealed that successful individuals had more extended social connections and occupied more central social network positions, which follows the common assumption that socially connected individuals may be the most likely to gain new information[10,11]. Furthermore, among males, bin openers were more closely associated to one another, as expected from social learning. These insights into how individual characteristics may shape innovation and behavioral spread within sites (Figure 2) now provide a foundation of examining this across sites too. Specifically, if future developments allow researchers to track individuals' social connections across suburbs, this will provide a bridge between the two components of this work, and will further knowledge about the transmission pathways, the role of

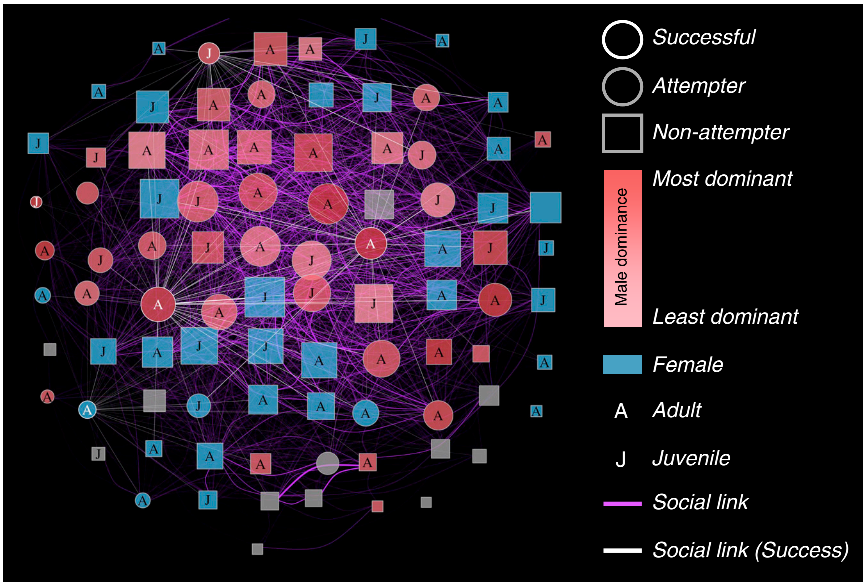

Figure 2. Cockatoo social network.
Each point represents an individual sulphur-crested cockatoo in Stanwell Park, with point shape denoting bin-opening activity (white circle = successfully opened, grey circle = attempted opening, grey square = no attempt at opening), point size showing social network centrality (larger = higher eigenvector centrality), point color showing sex (blue = female, red = male, grey = unknown) and shading indicating the dominance of males (darker = more dominant), and letters showing age (A = adult, J = juvenile). The edges between points show the social associations between individuals, and social associations with successful bin openers are highlighted in white.

dispersal, and the emergence of local behavioral variants.

Urban environments provide a whole range of novel resources for wildlife and may promote innovation[17]. A major attraction luring wildlife into cities is often considered as the availability of waste. Leftover food in bins or just a few breadcrumbs on the street make a great meal for the many city animals living among us. Just like the milk-drinking tits, prawn-trawling dolphins and the crows using cars as nut-crackers, the cockatoos of Sydney have taken urban scavenging behavior to the next level by learning to access anthropogenic resources in an entirely new way, and spreading this across their social networks. Once a waste bin has been successfully opened, birds will explore the content and — to the annoyance of the bin owners — leave a mess behind. In fact, the cockatoos' novel foraging technique bothers humans so much that they have started developing anti-cockatoo devices to thwart their access to bins. Humans are excellent innovators and social learners. The usage of bin protection, and particularly what type of protection, may also spread socially within and across suburbs. This interaction between humans and cockatoos hence has the potential to be a case of human–animal cultural co-evolution, where cultural adaptations in one species lead to the cultural adaptations in another species. As such, the conflict between humans and cockatoos may provide an interesting case of a cultural arms-race. Although time will show whether humans are continually outsmarted or if they manage to put an end to this novel cockatoo foraging behavior, we can continue to expect to see new innovations arising and spreading through various urban animal social networks as many different urban-dwelling species attempt to profit from our activities.

REFERENCES

1. Fisher, J.B., and Hinde, R.A. (1949). The opening of milk bottles by birds. Br. Birds *42*, 347–357.
2. Chilvers, B.L., and Corkeron, P.J. (2001). Trawling and bottlenose dolphins' social structure. Proc. R. Soc. Lond. B *268*, 1901–1905.
3. Nihei, Y., and Higuchi, H. (2001). When and where did crows learn to use automobiles as nutcrackers. Tohoku Psychol. Folia *60*, 93–97.
4. Reader, S.M., and Laland, K.N. (2003). Animal Innovation (Oxford: Oxford University Press).
5. Hoppitt, W., and Laland, K.N. (2013). Social Learning (Princeton University Press).
6. Klump, B.C., Martin, J.M., Wild, S., Hörsch, J.K., Major, R.E., and Aplin, L.M. (2021). Innovation and geographic spread of a complex foraging culture in an urban parrot. Science *373*, 456–460.
7. Whiten, A., Ayala, F.J., Feldman, M.W., and Laland, K.N. (2017). The extension of biology through culture. Proc. Natl. Acad. Sci. USA *114*, 7775–7781.
8. Whiten, A. (2021). The burgeoning reach of animal culture. Science *80*, 372.
9. Whiten, A., and Mesoudi, A. (2008). Establishing an experimental science of culture: animal social diffusion experiments. Philos. Trans. R. Soc. B Biol. Sci. *363*, 3477–3488.
10. Firth, J.A. (2020). Considering complexity: animal social networks and behavioural contagions. Trends Ecol. Evol. *35*, 100–104.
11. Hasenjager, M.J., Leadbeater, E., and Hoppitt, W. (2021). Detecting and quantifying social transmission using network-based diffusion analysis. J. Anim. Ecol. *90*, 8–26.
12. Pocock, M.J.O., Tweddle, J.C., Savage, J., Robinson, L.D., and Roy, H.E. (2017). The diversity and evolution of ecological and environmental citizen science. PLoS One *12*, e0172579.
13. Theobald, E.J., Ettinger, A.K., Burgess, H.K., DeBey, L.B., Schmidt, N.R., Froehlich, H.E., Wagner, C., HilleRisLambers, J., Tewksbury, J., and Harsch, M.A. (2015). Global change and local solutions: Tapping the unrealized potential of citizen science for biodiversity research. Biol. Conserv. *181*, 236–244.
14. Lintott, C.J., Schawinski, K., Slosar, A., Land, K., Bamford, S., Thomas, D., Raddick, M.J., Nichol, R.C., Szalay, A., and Andreescu, D. (2008). Galaxy Zoo: morphologies derived from visual inspection of galaxies from the Sloan Digital Sky Survey. Mon. Not. R. Astron. Soc. *389*, 1179–1189.
15. Jarić, I., Correia, R.A., Brook, B.W., Buettel, J.C., Courchamp, F., Di Minin, E., Firth, J.A., Gaston, K.J., Jepson, P., and Kalinkat, G. (2020). iEcology: harnessing large online resources to generate ecological insights. Trends Ecol. Evol. *35*, 630–639.
16. Boesch, C., Kalan, A.K., Mundry, R., Arandjelovic, M., Pika, S., Dieguez, P., Ayimisin, E.A., Barciela, A., Coupland, C., and Egbe, V.E. (2020). Chimpanzee ethnography reveals unexpected cultural diversity. Nat. Hum. Behav. *4*, 910–916.
17. Lee, V.E., and Thornton, A. (2021). Animal cognition in an urbanised world. Front. Ecol. Evol. *9*, 120.