



Wild sulphur-crested cockatoos match human activity rhythms to access food in the urban environment

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Abstract

Urban areas are growing rapidly across the globe. Such environments present specific challenges to wildlife. Resources can be highly fragmented in space and time, accompanied by specific risks and opportunities that can emerge from proximity with humans. Overall, these have been shown to lead to specific activity patterns in wildlife, which tend to restrict their space use accordingly to avoid encounters with humans. Yet, some foraging opportunities supplied by humans can also attract wildlife. Urban-dwelling species would therefore benefit from learning when and where to exploit human derived food. Here, we investigate how birds exploit areas of different degrees of urbanization and if they do so with specific time patterns. We used the example of feeding sulphur-crested cockatoos (*Cacatua galerita*) in Sydney, Australia. We combined tracking birds to identify key resources, and a citizen science approach to investigate human-wildlife interactions in the urban landscape. Our data suggest that SCC do not use all parts of their home range equally, but use green spaces as roosting and foraging areas, while facultatively using more urbanized areas at specific times when they are the most rewarding. This implies a role for sophisticated time and place learning, with birds matching activity to human patterns. This study builds on the literature investigating human-animal interactions, expanding our understanding of animals' exploitation of human behavior. Our results highlight the unique opportunity that studies on urban wildlife have for understanding urban biodiversity establishment, maintenance, and cognitive ecology.

Keywords Episodic memory · Urban adaptation · Time-place learning · Sulphur-crested cockatoo · *Cacatua galerita* · Human-wildlife interaction

Introduction

Urbanization represents one of the most drastic changes that humans can impose on the environment (Vitousek et al. 1997; McDonnell and Hahs, 2015). Yet a growing body of literature highlights how species have adapted and thrive in this highly modified environment (Fehlmann et al. 2021; Ritzel and Gallo 2020; Sol et al. 2013). Indeed, the urban environment can offer new opportunities to wildlife, such as food, reduced climatic variation, and lower predation pressure (Shochat et al. 2006). As urban areas continue to grow rapidly around the globe, understanding how species exhibit behavioural adaptations that enable them to live successfully alongside humans is crucial for efforts to increase biodiversity in urban spaces.

For wildlife, adapting to the urban environment is not a given (Major & Parsons 2010; Fehlmann et al. 2021; Sol et al. 2013, 2014); finding space to sleep, forage and reproduce can be challenging due to the degradation of natural habitats

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(Sol et al. 2014; Callaghan et al. 2019). In streetscapes, the lack of trees or low vegetation is reducing bird and mammals' richness (Campos-Silva and Piratelli 2021; Kays & Parsons, 2014; Pena et al., 2023). The presence of vegetation is essential for several species and plays a role as cover or refuge, as well as sources of food, nesting area. Parks and gardens are then important for the maintenance of biodiversity (Grafius et al. 2017; Kays & Parsons, 2014; Pena et al., 2023; Reynolds et al. 2017). As city landscapes are divided in a mosaic of small properties individually managed by different landowners, urban spaces are also characterized by a lack of continuum in resources or corridors to reach them (Aronson et al. 2017).

In addition to the physical environments, the presence of large populations of humans and the accumulation of individual routines result in large-scale flows of people, including high traffic when people commute to work and high frequentation of parks during weekends. Such patterns strongly shape the ecology of urban wildlife that may have to adjust to these artificial rhythms. Shifts in diel activities are frequently reported in response to negative interactions with people (Ritzel and Gallo 2020; Sol et al. 2013). For example, coyotes (*Canis latrans*) in Alberta, Canada, were found to be more likely to survive when active around midnight rather than at dusk leading to urban coyotes becoming more nocturnal (Murray and Clair 2015).

Yet, human presence can also attract wildlife, by creating new easily accessible or more predictable foraging opportunities (for example household waste, outdoor dining, deliberate provisioning) (Ducatez et al. 2013; Flint et al. 2016; Klump et al. 2021). Because human supplied foraging opportunities can be more energetically rewarding than wild alternatives (Fehlmann et al. 2021; Soriano-Redondo et al., 2021; Støstad et al. 2017), they can act as a strong motivator to exploit the specific time and place where they

are available. This should be particularly emphasized with short-lived resources (Barrett et al. 2018; Fehlmann et al. 2017; Klump et al. 2021). As a result, wildlife exploiting such resources and facing time restrictions based on artificial cycles such as weeks or working schedules, may learn the time and place to benefit from human derived short-lived foraging opportunities (Barrett et al. 2018; Lee and Thornton 2021). If so, such positive direct human-wildlife interactions can lead to synchronicity in activity. As many urban-dwelling species foraging on human provided resources are likely to be confronted with such tasks, exploring such mechanism can become essential as to maximize or reduce (in case of conflicts) such interactions.

To explore one such positive human-wildlife interaction, we use the example of human provisioning of sulphur-crested cockatoos (*Cacatua galerita*; hereafter SCC); a species that appears to thrive in urban environments such as Sydney, Australia (Kirksey et al. 2018). SCC are large (700–1200 g), relatively slow-breeding and long-lived parrots (Smeele et al., 2022). SCC form stable roosting groups of 50–500 individuals that collectively exploit a home-range centered on their roost site, which is usually a cluster of large trees (Penndorf et al. 2023). They forage on a variety of food sources including shoots, roots, seeds, nuts and fruits (Birdlife Australia, 2023). In urban areas, their diet also includes bird seed and nuts (e.g., almonds) that are voluntarily provisioned by people in parks or at their homes (e.g. balconies) via direct feeding (Fig. 1A). Such opportunities are therefore temporally restricted (Fig. 1) (Kirksey et al. 2018).

We studied one population of SCC in central Sydney to test how this large parrot exploits different degrees of urbanization, and if the short-lived nature of such direct feeding could lead to synchrony between humans and wildlife. SCC have been the subject of a long-running citizen science

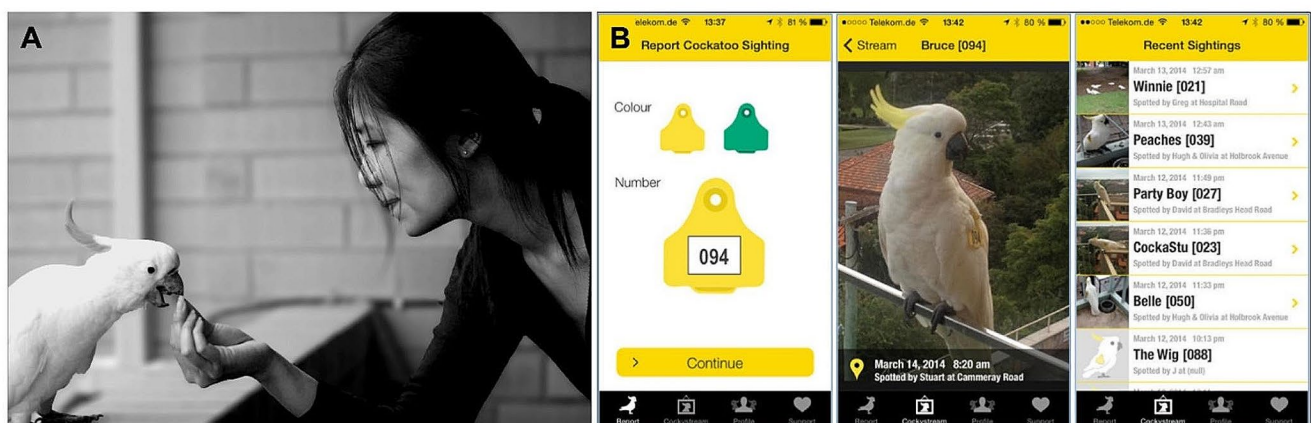


Fig. 1 (A) Local resident provisioning a wild sulphur-crested cockatoo with sunflower seed. Photo taken on a balcony in Potts Point, Sydney, used with permission from Mariangel Lezama. (B) Screenshots

from the citizen science smartphone application “Wingtags”, showing a report of bird 094 “Bruce”, along with recent sightings. Figure partly reproduced from Aplin et al. 2021

program since 2010, where people report sightings of 144 individually wing-tagged SCC through a smart-phone application ('Big City Birds App.'; Aplin et al. 2021; Davis et al. 2017). We equipped eight wing-tagged SCC with GPS and matched this active tracking data with citizen-science data on human provisioning. We identified sites where birds would spend time and investigated which habitats the SCC exploited. We then explored the timing of the visits of the GPS tracked individuals to the different habitat types, hypothesizing that birds would synchronize their exploitation of the most urbanized areas to match the spatio-temporal patterning of human supplementary feeding.

Methods

Study population and area

We focused on two roosting groups close to central Sydney, one in the Royal Botanic Garden (S -33.864377, E 151.214693, approx. 70 birds) and one in Clifton Gardens (S -33.837209, E 151.251112, approx. 100 birds), at 1.5 km and 5.3 km from Sydney's central business district, respectively. Roosting sites were located in parks with remnant old-growth eucalypt trees. Based on the observed maximum distance travelled from the roost (average $\pm$ sd: 3858 m $\pm$ 1654 m), we characterized the environment within a radius of 4 km from each roost. Within the area around the Botanic Garden, the land cover was characterized by 27.3% trees, 6.7% grass, 2.2% bare earth, and 57.5% built environment. Around Clifton Gardens, trees represented 39.9% of the land cover, 6.6% grass, 3.7% bare earth, and 43.8% the built environment.

We equipped nine birds with solar powered GPS receivers (e-Obs GmbH). We targeted birds that had already been caught and wing-tagged (see Aplin et al. 2021). Bird seed was used to attract SCC to forage on the ground close to the researchers and individual birds were then caught by hand with leather gloves. They were then moved a short distance ($\sim$ 500 m) for processing, with GPS receivers attached using a teflon harness (see Aplin et al. 2021). Nine birds were chosen as an initial assessment of the usefulness of this method as studies have reported challenges tracking parrots (see Cope et al., 2024). One bird removed its tag shortly after deployment, resulting in three tagged birds roosting in Clifton Gardens (two adult males and one adult female), and five in the Botanic Garden (three adult males, one adult female and one juvenile male).

Transmitters were programed to record GPS locations every 5 min in 2016 and 2017 from 5:00 to 21:00 local time. However, data acquisition was uneven across the year due to lower battery during winter and autumn. We therefore

focused our analysis on spring-summer (September–February) when the tags had the higher performance rate with an average of 61 ($\pm$ 45) fixes a day (min = 5, max = 169) (Table S1). Over the two years, this resulted with 206 days of recordings on average per bird (min = 62, max = 312).

Quantifying bird feeding activities

We documented recreational feeding of SCC using the citizen science project called 'Wingtags' (Davis et al. 2017). Launched in 2012, this project encourages local Sydney residents to report observations of wing-tagged SCC through a smart-device application, submitting a photograph of the observed bird(s) along with their identity (defined by a wing-tag number, Fig. 1B). The application then adds a location and timestamp to the observation.

The dataset available for this study included 95,631 reports across Sydney. Unfortunately, we could not retrieve photographs from March 2014 to January 2017 due to a data error. The remaining dataset included 13,652 reports that had attached photographs and were from within 4 km of one of the two roosting sites. Of these photographs, 2,344 had been annotated by volunteers as part of the Australian Museum 'DIGIVOL' scheme (<https://australianmuseum.net.au/digivol>), recording the behavior of the bird in the picture. Each image was analyzed by a citizen scientist at the Australian Museum and verified by one of five expert citizen scientists chosen for their attention to detail and accuracy in scoring the images. The expert citizen scientists were verified by the researchers (JMM). Our previous research showed that citizen scientist reports of wing-tagged SCC contained an $\sim$ 1.9% error rate. For the purposes of this study, GF pre-screened all the remaining 11,308 photographs to identify potential foraging events. That is, if the bird was holding a foot up, leaning forward, standing next to a feeder, with a person (Ex. Figure 1A) or inside a building. This resulted in 2,902 reports. GF annotated photographs using the same scheme as the 'DigiVol' dataset. She considered birds being fed by people if the bird was observed eating, holding, or standing next to manufactured food items, nuts or loose seeds. Importantly, we did not include reports when birds were standing next to a bird feeder, focusing only on direct recreational feeding (Ex. Figure 1A). Since people can submit several reports for the same feeding event (when several birds were foraging), we only considered feeding events reported by the same person if they were more than 20 min apart. This resulted in 1657 reports between April 2012 and July 2021. We assigned each feeding event to the closest roosting site (either the Botanic Garden area or Clifton Gardens).

Space use

Definition of exploited areas

We used first-passage time (FPT) to identify areas that were exploited more intensely in opposition with areas used for travelling (pathways or corridors). Traditional FPT studies are based upon the assumption that foraging animals engage in more tortuous and slower movements (Area of Restricted Search: ARS, (Fauchald and Tveraa 2003), resulting in animals staying within a certain radius longer than when traveling. We used this method to identify where birds were stationary considering that the GPS signal of a stationary bird will result in a local Brownian movement pattern within the range of GPS error (around 30 m). FPT analysis requires GPS tracks with regular sampling. For each bird, we therefore considered missing locations. If time gaps between two successive locations were less than 30 min, we linearly interpolated locations with a time lag of 5 min. When time gaps were longer than 30 min, we split the track into distinctive sections or bursts to compute FPT on regular section of data. We discarded all bursts that lasted less than 1.5 h to reach a minimum number of locations to perform the following analysis.

We identified distinctive phases in the birds' movements, i.e., sedentary vs. travelling behaviors, by plotting FPT against time. We used the Lavielle segmentation to partition each burst (Barraquand and Benhamou 2008). This segmentation process is used to identify the location and the number of change points in the time series data, breaking the signal in bouts of homogeneous means and variances (Lavielle 2005). For each segment, we identified the location of the maximum FPT, where the animal stayed longest (Fig. 2). The location was considered as a potential exploited site if FPT was above 15 min, based on behavioral observations

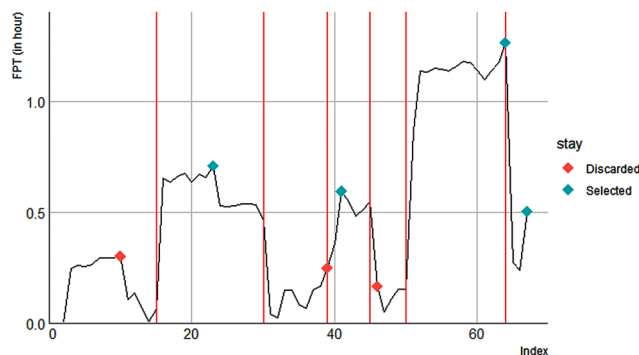


Fig. 2 Example of one GPS burst segmented with Lavielle segmentation, FPT (in hours) is plotted against time (as index). The result of Lavielle segmentation is represented with vertical red lines. Within each segment, we identified the locations at which the maximum FPT occurred with a diamond, i.e., where the animal stayed the longest, and selected it as an ARS if FPT was higher than 15 min and below 6 h

of birds at a feeding site. We discarded sites exploited for more than 6 h as these would be most probably resting sites (minimum duration of nights over the study period: 6 h and 7 min).

Recursive visits

Most ARS resulting from the above analysis were clustered within a radius of 30 m (GPS error rate), suggesting recursive visits to the same site. We decided to average the position of the clustered ARS to identify with more reliability the location of the revisited site. We projected the location of each ARS identified on to a raster with a 30 m grid cell. We then iteratively considered local maxima to identify clusters of ARS. Within each iteration, we selected the cell containing the most ARS and its eight neighboring cells. We averaged the location of all ARS contained within these nine cells and added a buffer of 45 m around this point to account for GPS error. Finally, we considered all ARS falling within this circle as revisits to the same site, we removed these from the list of ARS before starting a new iteration. Sites that were visited less than three times over the entire duration of the spring and summer were not considered for later analysis.

Environmental sampling

We described the urban environment with a 2m resolution land cover map obtained in 2019 from the publicly available dataset “Buildings, Surface Cover, Trees © Geoscape Australia” (2019, PSMA). This dataset is based on satellite imagery, details on surface cover such as roads, buildings, built-up areas, swimming pool, bare earth, grass, trees, low vegetation, and water. We combined ‘roads’ and ‘built up areas’ as ‘urban features’, including roads, parking lots made of human-made substrate, built up areas smaller than 9m², and other human-made environments. For each revisited site, we calculated the proportion of the area within a radius of 30m, covered by grass, trees, low vegetation, buildings, other urban features, and assigned to each site the dominant habitat feature (5 classes, see Fig. 3B). When buildings were present, we calculated the average building height and area and the proportion of residential buildings located at each site (Fig. S1).

Statistical analysis

We compared the timings of bird visits to buildings versus the timing of their visits to any of the other habitat types using a logistic regression. For each visit to an exploited site (ARS), as indicated by the GPS tagged birds, we used the habitat classified as 1 for buildings and 0 for any of the

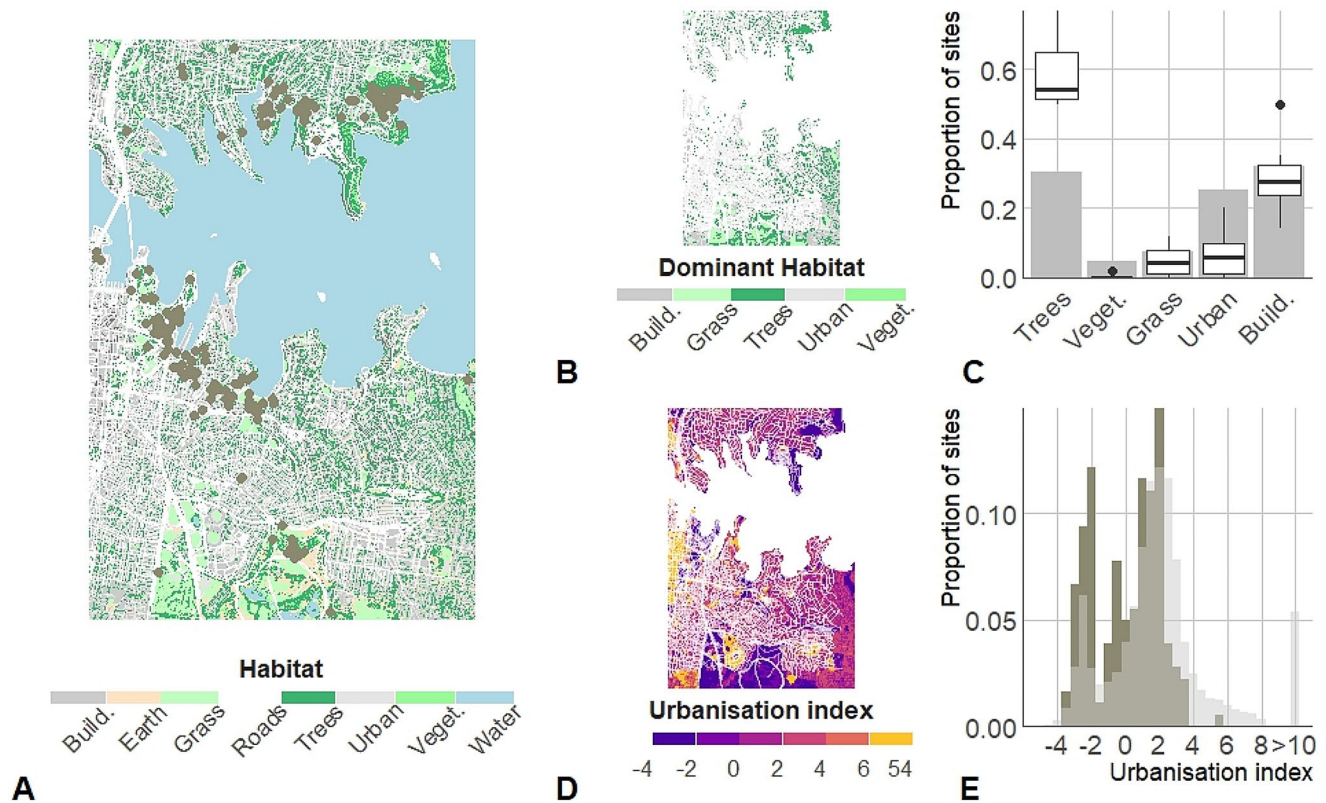


Fig. 3 (A) The SCC equipped with a GPS ($N=8$) in the city center of Sydney revisited specific locations indicated by grey points. (B) We characterized these sites and the study area by considering the dominant habitat within 30×30 m cells, and (C) compared each bird's use of the different habitats (boxplot) versus the availability of habitats in the study area (bars). We investigated the effect of urbanization on birds' space use by assigning an urbanization index score based on the

proportion of the different habitat features, building size, height and use using Principal Component Analysis (D). We then explored the distribution of the exploited sites (except the roosting sites) across the urbanization index (dark grey bars) in comparison to the classification of the study area (light grey bars) (E). In B and D, roads (in white) are only given as visual landmarks

other habitat type as our response variable. We included the date, the hour of the day, the weekday and the month as predictive variables and tested for any interactions between these terms and the roosting site of each bird (Botanic Garden or Clifton Gardens). We controlled individual effects by adding individual as a random effect term in the model. We tested the value of each term independently and selected the best model according to AIC. To avoid sampling bias, we performed 100 iterations, sampling randomly 300 visits at buildings and 300 visits to other habitat types and selected the most common winning model (based on AIC) as our final selected model.

We then described the timing of visits to buildings. We created a time series with one-hour resolution from 06:00 to 20:00, only including timestamps for which GPS locations were recorded. For each time stamp, we reported the number of visits per bird. Time was reported in AEDT (UTC + 11) throughout the study period. We used General Additive Models (GAM) in R (R Core Team 2019) using the mgcv package (Wood et al. 2016) with a zero inflated

Poisson distribution to fit the seasonality of visits considering daily, weekly, and monthly patterns. For each of these variables we set the number of knots, which controls the “wiggleness” of the model, according to the number of values each parameter can take. For modelling daily and monthly variations, we used cubic spline functions allowing a maximum of 16 and 6 knots respectively (because GPS were recording data for 15 h/day and 6 month/year). For weekly variations, we used cyclic cubic splines (allowing for cyclic variations) setting a maximum of 7 knots.

To avoid overfitting, we computed a penalty for each smooth term according to the number of knots by setting the select argument to “true” (Wood et al. 2016). We tested the significance of interactions between hours and weekdays and hours and months by adding tensor product smooths. To account for site variations between the two roosts, we allowed different seasonal patterns at each site. Because our recording encompassed daylight-saving time change, we considered its potential impact in hourly variations by computing separate smooth terms, before and after time change.

We controlled for individual variation and year effect by adding these as random effects (slopes and intercepts) and for accounting for temporal autocorrelation and sampling variations by adding the timestamp as smooth term using p-splines and a maximum of 24 knots.

We assigned an urbanization index to each visited site, performing a Principal Component Analysis. We included the proportion of each habitat within a radius of 30 m around each identified site, using the function “*prcomp*” in R environment (R Core Team 2019). We used the first component described by this analysis as an index of urbanization, negative values indicating greener areas and positive values more urbanized areas (Fig. 3D). We then tested with a Wilcoxon rank sum test the differences in urbanization index score for sites around the Botanic Gardens vs. Clifton Gardens. To document human provisioning, we identified in which habitat it occurred via classification of the pictures. We discretized the temporal patterns in recreational feeding of birds by creating a time series of the number of bird feeding event to resolution of one-hour. For consistency between GPS and citizen science data, time was reported in AEDT (UTC + 11) throughout the year. We used GAM with a zero inflated Poisson distribution to model the seasonality of the behavior taking into account monthly, weekly, and daily patterns using cyclic cubic splines with a maximum of 12, 7, and 12 knots respectively.

Citizen science data can be biased toward specific populations in the different studied sites. We therefore controlled variations in human provisioning patterns at the two different sites (Botanic Garden and Clifton Gardens). by allowing these monthly, weekly and daily patterns to vary according to site. We considered daylight saving time by estimating separate smoothed terms for hourly patterns for each period (Standard time and Daylight Savings Time). We tested for the interaction between daily and weekly patterns and between daily and monthly patterns using a tensor product smooth. We controlled temporal autocorrelation by adding the timestamp as smooth term using p-splines and a maximum of 24 knots (for the 24 months of data).

To test for synchrony between birds’ foraging patterns and human provisioning, we predicted bird visits to buildings and recreational feeding from October 2017 to March 2018 around Clifton Gardens and the Botanic Garden using our GAM models. Based on the model computed with GPS data, we predicted what could have been the foraging patterns of the birds in another year using the same predictive variables (month, day of the week and hour of the day, function predict). We then used a partial mantel test, using the package ‘vegan’ (Oksanen et al. 2014) with 1 000 permutations (sufficient to reach stability in the model output) to compare the variations of these two variables through time (hour and month).

Results

Recursively exploited sites

We identified 4695 ARS from bird GPS data, indicating stationary behaviors for all birds. Of these ARS, 93.4% (± 6.3) were located within 45 m of at least three other ARS, indicating 188 re-visited sites. Among these re-visited sites, the roosting site itself contained on average 53.2% (± 27.3) of the total ARS identified for each bird (min - max tree coverage: 46 – 75%) with a low urbanization index (min: -3.1, max: 0.9). As a reference, cells with such environmental characteristics (minimum of 46% tree coverage and urbanization index value below 0.9) represented 19.53% of the grid cell within the area.

Birds recursively exploited 181 other sites. Among these sites, 62.4% were covered mostly by trees, 26.0% mostly by buildings, 5.5% mostly by grass, and 5.5% mostly by other urban features. As a comparison, the study area (area within a radius of 4 km around both roosting sites) was covered by 30.2% of trees, 31.9% buildings, 7.6% grass, 25.2% urban features, and 4.6% low vegetation (excluding the surface covered by the sea, Fig. 3). We identified 486 visits to buildings, 84.4% of which occurred in residential areas (sites covered by more than 50% of residential buildings). All visits to non-residential buildings occurred within the Botanic Garden area where visits to non-residential areas represented 30.6% of all visits to buildings. Most recursively visited sites occurred in areas with low urbanization index scores (score below 0: 47.9%) or areas with median scores (score between 0 and 3: 48.4%). Only 3.7% of revisited sites occurred in areas with an urbanization index above 3, despite this category representing 13.5% of the cells in the study area (Fig. 3).

Timing of bird visits to different sites, identified with GPS data

Within our sampling schedule (from 5:00 to 21:00), ARS located at roosting sites and trees were predominantly used during the morning and around midday, with no specific weekly patterns. Buildings were visited by the tracked birds from 8:00 to 18:00 (GAM: edf=8.48, reference df=14, $\chi^2=60.87$, $p<0.001$), and significantly later than visits to other habitat types (Fig. 4a. Logistic regression: estimate=0.13, s.e. = 0.03, $z=4.6$, $p<0.001$). Visits to buildings were more frequent during weekdays, particularly Tuesdays and Thursdays (Fig. 4b. Logistic regression: estimate = -0.17, s.e. = 0.05, $z = -3.4$, $p<0.001$; GAM: edf=1.66, Ref.df=5, $\chi^2=4.89$, $p=0.04$).

Across the study area, roosting sites were used most intensively during November, which coincided with nesting

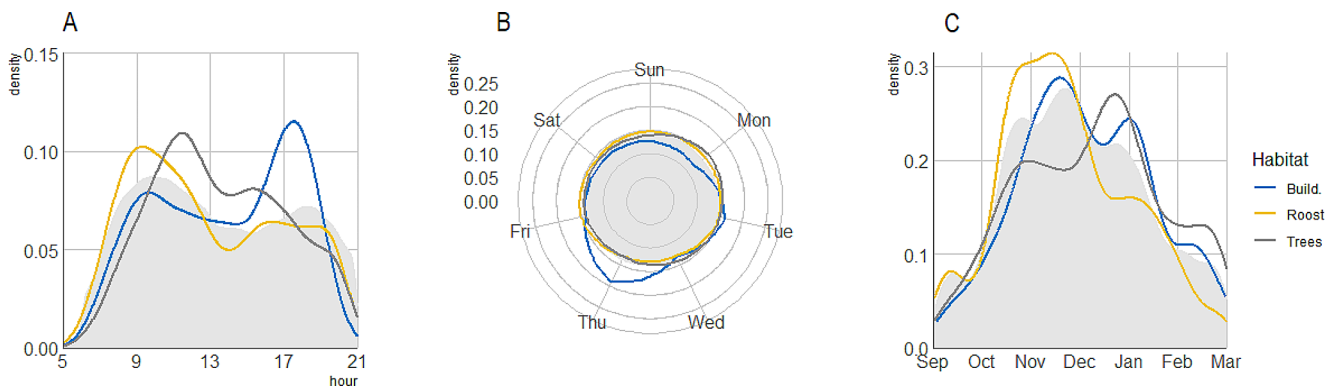


Fig. 4 Density plots showing the timing of the visits to the different ARS ($N=4695$), classified according to the dominant habitat type (i.e., roost, buildings, and trees) considering (A) hour of the day, (B) day of the week, and (C) month. Note that GPS recording depended upon

solar input. Locations were recorded from 5:00 to 21:00 and data from March to September were not included in the study due to too few recordings. The density of GPS location through time is represented by the light grey area

and chick rearing. Buildings were visited with a specific monthly pattern varying according to the birds' ranging area (Fig. 4C; Logistic regression: BG: estimate = 1.3, s.e = 0.23, $z = 5.70$, $p < 0.001$, CG: estimate = 0.25, s.e = 0.07, $z = 3.33$, $p < 0.001$). Buildings around the Botanic Garden were visited around 18:00 from September to December and throughout daytime in January. Buildings located around the Clifton Gardens were more specifically visited around 18:00 during October–December and February and less frequently visited in January (Fig. 5; GAM tensor (hour, month, by site): BG: edf = 3.36, Ref.df = 89, $\chi^2 = 12.86$, $p < 0.001$, CG: edf = 11.80, Ref.df = 89, $\chi^2 = 55.06$, $p < 0.001$).

The timing of visits to buildings did not vary through the day despite daylight saving schemes (GAM without vs. with daylight savings: difference in degrees of freedom = -10.0, difference in AIC = 10.88). Buildings' visitation rate also depended on time autocorrelation and sampling variation (edf = 10.16, reference df = 23, $\chi^2 = 56.01$, $p < 0.001$) and varied according to individuals (GAM random intercept: edf = 5.05, Ref.df = 6, $\chi^2 = 28.25$, $p < 0.001$, random slope: edf = 0.22, Ref.df = 6, $\chi^2 = 0.44$, $p = 0.744$).

Recreational bird feeding, identified with citizen science data

Across the study area, 120 people participating in the Big City Birds Project actively fed and reported individually wing-tagged SCC (56 around the Botanic Garden and 65 around Clifton Gardens, citizen science data) throughout all months of the year. Most people fed birds from residential areas with 74% of reports (versus to 1.9% in grass and 0.3% in trees), which could be separated, to balconies (51.8%), windowsills (20.0%), or inside buildings (3.2%). Reports were mostly located in areas with an urbanization score comprised between 1.6 and 2.9 (1st – 3rd quartile). Participants around Clifton Gardens reported feeding birds

in significantly greener areas according to our urbanization score than around the Botanic Garden (CG median = 1.7, BG median = 2.7, Wilcoxon test: $W = 547,865$, $p < 0.001$).

Feeding occurred with a monthly and daily pattern, which varied according to the location (GAM; tensor (hour, month, by site): BG edf = 38.58, reference df = 120, $\chi^2 = 146.4$, $p < 0.001$; CG edf = 27.20, reference df = 120, $\chi^2 = 191.7$, $p < 0.001$, see Fig. 5). Most reports occurred at 18:00 throughout the year with a peak from September to March. A second peak of feeding occurred in the morning at 8:00 around the Botanic Garden but not Clifton Gardens. Most reports occurred from 9:00 to 18:00 (AEDT) during Australian Eastern Standard Time (UTC + 10) and from 8:00 to 18:00 (AEDT) during Australian Eastern Daylight Time (UTC + 11, GAM hour by time zone: AEST: edf = 8.57, reference df = 10.0, $\chi^2 = 123.3$, $p < 0.001$; AEDT: edf = 8.81, reference df = 10.0, $\chi^2 = 151.5$, $p < 0.001$). Note that, for consistency, we modelled time in AEDT all year round, considering civil clock people therefore reported feeding birds from 8:00 to 17:00 during AEST and from 8:00 to 18:00 during AEDT. The number of reports collected also varied daily (GAM: edf = 8.58, reference df = 8.92, $\chi^2 = 293.0$, $p < 0.001$).

Synchrony between time patterns identified in human provisioning and bird visits to buildings

The time patterns of visits of the GPS tagged birds to buildings (GAM model for birds) was correlated with the time patterns of human provisioning (GAM model for human provisioning) at both sites, although the effect was stronger at Clifton Gardens. Clifton Gardens: Mantel statistic $r = 0.42$, $p < 0.001$; Botanic Garden: Mantel statistic $r = 0.11$, $p < 0.001$ (significance test based on 1000 permutations).

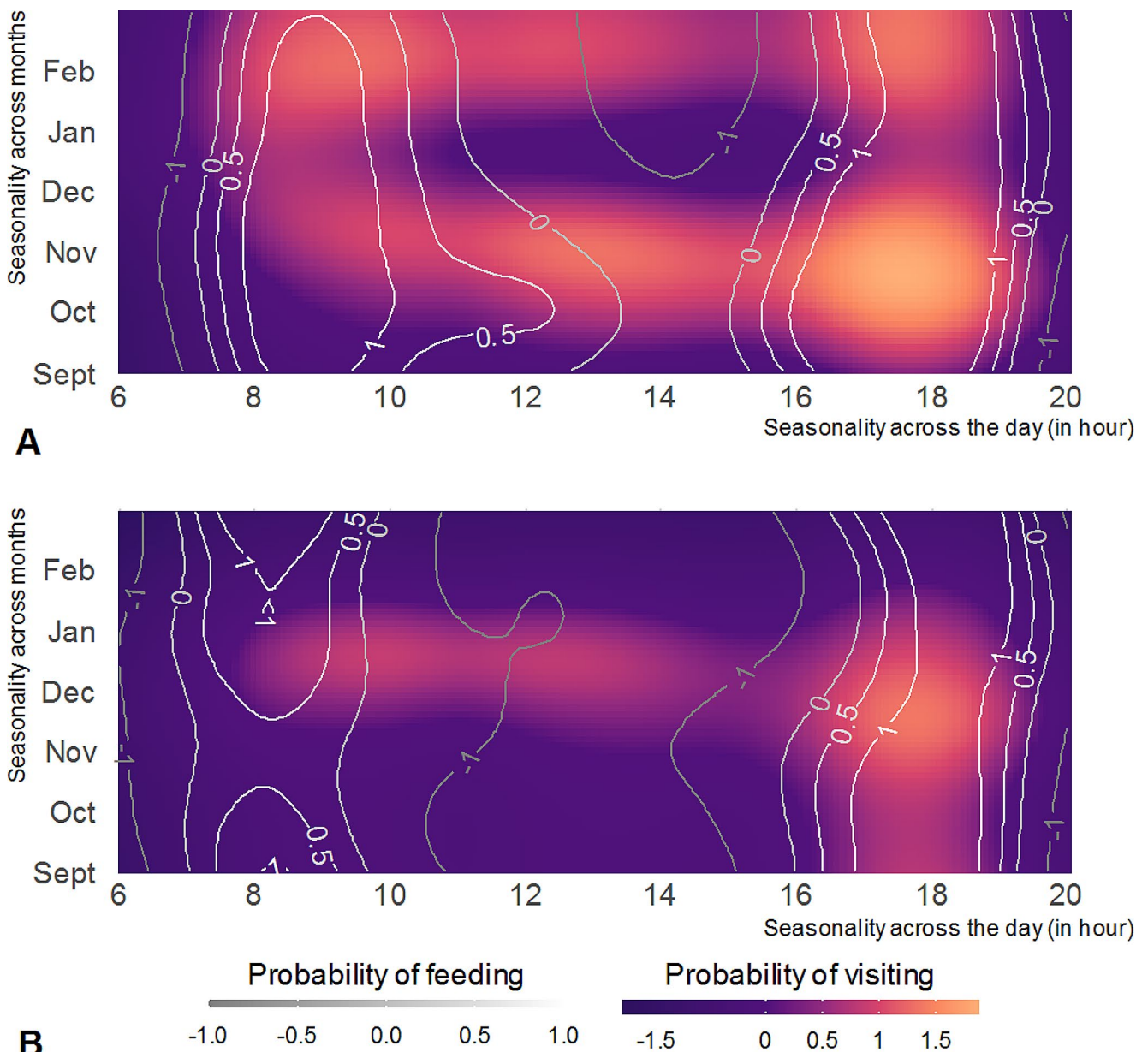


Fig. 5 Timing of bird visits to ARS classified as buildings ($N=486$, color scheme) and the timing of recreational feeding patterns ($N=1657$, contour plot) throughout the day and month (data presented are GAM outputs). Birds fitted with GPS at Clifton Gardens (**A**) and Botanic Garden (**B**) visited buildings with distinctive time patterns over the day and throughout the month. We compare this pattern to the recreational feeding patterns that were also following variations throughout the day and the month. The likelihood of bird visits was

predicted by the following General Additive Model: probability of visiting $\sim$ (Hour: Month, by Site) + Weekday + Hour + Date + Individual) and people fed bird according to the following model: probability of feeding $\sim$ (Hour: Month, by Site) + (Hour, daylight saving) + Date. We focused our analysis from September to February (included), a time period during which GPS sampling was high (we control for data sampling in both model by including date as a smoothed factor). Note that we scaled predictions for the two models to allow comparisons

Discussion

Our study shows that large parrots living in the city center of Sydney megalopolis can tolerate an urbanized landscape, exploiting greener areas with a high proportion of trees, low vegetation, or grass (according to our urbanization index), and visiting urban features with specific time patterns

correlated with human recreational feeding routines. Their urban adaptation may be a reason as to why their populations have increased over the past decades, with similar or higher abundance in suburban and urban areas than in the surrounding natural habitat (Burgin and Saunders 2007; Davis et al. 2012). Yet, our study also suggests that there are limits to this tolerance, with our GPS birds avoiding areas

where the urbanization index was high (above 3). This suggests that highly urbanized areas with tall and large buildings, mostly covered by infrastructure and few vegetation, may not be suitable for SCC.

Our data support the general claim that retaining green spaces (areas with a high proportion of grass, trees, low vegetation) in cities is essential to sustainable urban planning (Campos-Silva and Piratelli 2021), and key to allow species to exploit the urban environment. SCC did successfully exploit areas of medium urban density when foraging, however roosting sites and the most intensively exploited areas were greener, covered by at least 43% of trees and located in less urbanized areas such as parks or patches of remnant vegetation. Habitat composition is one of the main factors influencing bird diversity in urban landscapes, with patches of remnant vegetation hosting more biodiverse birds communities (Aronson et al. 2014; Callaghan et al. 2018; Kuras et al. 2020). When wildlife can tolerate urban features, or benefit from them, this frequently relies on adjacent patches of more natural vegetation as a refuge or for reproduction (Davis et al. 2013; Gallo and Fidino 2018; Grafius et al. 2017).

Provisioning of wildlife, for example via bird feeders, is a globally popular activity attracting wildlife in urban spaces (Reynolds et al. 2017). In Sydney central district, our data shows that at least 2.5 people reported feeding SCC per km², with most feeding occurring directly at people's balconies or windowsills; note that this is an underestimate as our data is not comprehensive. Such sites were exploited at even higher rates than grass patches, foraging sites that form an important part of the natural repertoire of this species (Polley and Lill 2021). In urban areas, parks are predominantly lawn monocultures, with low plant and animal biodiversity (Aronson et al. 2017), and ground foraging may be vulnerable to attack from domestic dogs and harassment from children. Balconies and windowsills may thus appear as a more attractive foraging space. Furthermore, the nutritional reward of seeds and nuts may eclipse that of grass leaves, shoots, seeds, and roots (Støstad et al. 2017). Further research into the nutritional benefits of urban foraging resources is warranted, particularly in the context of cognitive and behavioral traits. For wildlife that can solicit or take advantage of provisioning, such behavioral adaptations can have large consequences for the structuring of urban bird assemblages (Callaghan et al. 2019; Fuller et al. 2008; Galbraith et al. 2017).

Our analysis of citizen science reports of such feeding of SCC further revealed that human provisioning was cyclic, with most feeding reported either at 8:00 or between 17:00–18:00. While our data collection could not ascertain the causation of this patterning, the close match to the most common work hours strongly suggests that this was driven

by human activities. The visits of the GPS tagged birds to buildings mirrored the peak of this feeding activity. Indeed, the timing of the 486 identified visits was restricted in time, with a more distinct pattern than visits to trees or the roost; they occurred later in the day and were overall correlated with human provisioning. Other recent work also suggests that SCC can take advantage of periodic human activities, such as exploiting household bins, only available to SCC once a week when on the curb for collection (Klump et al. 2021, 2022).

Episodic memory (what-when-where) has been shown in food-caching species, such as corvids, that are able to integrate spatial-temporal information to return to a cache before food items perish (Grodzinski and Clayton 2010). Here, the process may be comparable and allow these birds to adaptively exploit specific sites in more urbanized areas. Interestingly, birds living in the most urbanized area (around Botanic Garden) and, visiting residential and commercial/business buildings, expressed a different daily rhythm which did not correlate as strongly to the feeding patterns recorded through the app. Indeed, people feeding SCC from their office window would happen during business hours and therefore encourage birds to visit buildings during daytime. Unfortunately, visits to such areas were rare and did not allow us to model the periodic patterns of such visits. In addition, the Botanic Garden is also one of the most visited areas of Sydney (Hale and Macdonald 2005) and even if feeding SCC is discouraged in the park, it is still often undertaken by visitors. Combined, these may break the clear diel rhythm of bird feeding observed in more residential areas. This could suggest more individual-specific foraging strategies, with more continuous sampling of multiple sites throughout the day. Unfortunately, our sample size did not allow us to explore individual variation in more detail.

In summary, our study suggests that SCC take advantage of the urban environment by relying on green spaces including trees as roosting and main foraging areas, while using more urbanized areas at specific times when human-derived food is available. Surprisingly, urban foraging was more frequent than grass foraging, which would be expected to be a major foraging behavior for this species (Polley and Lill 2021), even despite the short-lived nature of handfeeding. This is perhaps due to the relatively high nutritional value of provisioned food, or alternatively the risk of disturbance, e.g., from dogs. However, it further implies a role for sophisticated time and place learning, with birds matching activity to human patterns. While our study focusses on eight birds, their time patterns converge with human activity, with only little individual variations. This result is therefore likely generalizable to the local population. Our results highlight the unique opportunity that studies

on urban wildlife have for understanding urban biodiversity maintenance and cognitive ecology. Human activities expose many species to dynamics of attraction and/or repulsion, and cognition may allow species to maximize potential benefits from urban living (Fehlmann et al. 2017; Goumas et al., 2020; Lee and Thornton 2021). Overall, expanding our knowledge on the challenges faced by wildlife and their adaptation mechanisms across taxa is key if we are to make urban areas become as suitable as possible for wildlife and globally threatened bird taxa such as parrots (Aronson et al. 2014; de Matos Fragata et al. 2022; Old et al. 2014).

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Author contributions GF, LMA, and KS conceived the study. LMA and JM equipped the birds and collected data. GF processed the bird and citizen science data, and performed the analysis. GF wrote the manuscript with the support of KS. All authors commented previous versions of the manuscript, and read and approved the final manuscript.

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Declarations

Ethical approval GF, LMA, and KS conceived the study. LMA and JM equipped the birds and collected data. GF processed the bird and citizen science data and performed the analysis. GF wrote the manuscript with the support of KS. All authors commented on previous versions of the manuscript and read and approved the final manuscript. All procedures were approved by the ACEC (ACEC Project No. 19/2017), and were conducted under a NSW Scientific License to JM (SL100107).

Competing interests The authors declare no competing interests.

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