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Juggling a "junk-food" diet: responses of an urban bird to fluctuating anthropogenic-food availability

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Abstract
Within highly urban systems, anthropogenic activity often fluctuates cyclically, e.g. between weekdays and weekends. Thus, urban species may regularly experience significant changes in human activity and anthropogenic food abundance over very short time scales. Knowledge of how urban birds cope with such fluctuations may improve our understanding of how some species exploit and thrive in urbanised habitats. In this study, we explore the consequences of highly fluctuating anthropogenic food for Red-winged Starlings *Onychognathus morio* at the University of Cape Town campus, South Africa. Here, high numbers of students (and therefore anthropogenic food resources) are present during weekdays in term time (high human presence "HHP" days). However, students are largely absent and food outlets closed during weekends and vacation periods ("LHP" days). Using focal observations and morning and evening weights of habituated colour-ringed starlings during the non-breeding season, we investigated how diet, behaviour and daily mass gain differed between HHP and LHP days. We hypothesised that anthropogenic food supply is beneficial to this city-dwelling species. We predicted that on HHP days starlings would consume overall more food and a greater proportion of anthropogenic food items, resulting in less time spent foraging and greater daily mass gain compared to LHP days. We found that on HHP days, starlings consumed more anthropogenic food, however overall food intake, and time budgets were similar to LHP days. Additionally, there was an indication that mass gain was greater on HHP days. Thus, starlings appear to cope with potential food shortage on LHP days by including more natural items in their diet.

Keywords Red-winged Starling · *Onychognathus mori* · Food abundance · Foraging · Anthropogenic food · Fluctuating human activity · Cape Town · Africa

Introduction

Animals living in urban environments face multiple novel challenges, including the replacement and fragmentation of natural vegetation by anthropogenic structures, elevated human disturbance (Lowry et al. 2012; Sol et al. 2013), pollution (including light (Kempenaers et al. 2010), noise (Slabbekoorn 2013) and chemical pollution (Tsipoura et al. 2011)), introduced pathogens and disease (Bradley and Altizer 2007; Brearley et al. 2013), collision with vehicles or predation by domestic animals (Sorace 2002; Ibáñez-Álamo et al. 2015; Loss et al. 2013). However, despite these challenges, some species successfully colonise and thrive in urban environments (Kark et al. 2007). This is especially true for species that can exploit anthropogenic resources, such as processed food and artificial nest sites that are often available in urban settings (Chace and Walsh 2006; Møller 2009; Evans et al. 2011).

Anthropogenic food is a major driver facilitating the colonization of cities by animals (Shochat 2004; Marzluff 2001; Anderies et al. 2007) and is an important feature along migration routes (Ciach and Kruszyk 2010) and wintering grounds (Ciach and Fröhlich 2017) of migratory birds. Food in cities is often relatively more abundant, more predictable in time and space, and less likely to undergo seasonal fluctuations compared to natural resources (Schoech and Bowman 2003; Shochat 2004; Anderies et al. 2007). This abundance and predictability of anthropogenic food can allow animals living in human proximity to devote less time and effort into foraging (Liker and Bókony 2009; Sol et al. 2011), become more resident (Evans et al. 2009) and maintain smaller territories. For example, Alpine Choughs (*Pyrrhocorax graculus*) with access

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to a ski resort town had smaller home ranges, than birds living in more natural areas. They were also able to exploit the available anthropogenic food during heavy snowfalls, whereas birds disconnected from the ski resorts had to move to lower altitudes to find food (Rolando et al. 2003). Likewise, Steller's Jays (*Cyanocitta steller*) inhabiting areas associated with campgrounds, spent less time foraging, than birds in more natural areas (Goldenberg et al. 2016). Supplementary feeding experiments on birds in natural areas have also confirmed that access to extra food allows individuals to invest less time searching for food, providing more time to invest into other behaviours such as self-maintenance and vigilance (Tieleman and Williams 2002; Cucco and Malacarne 1997).

However, although food may be more predictably available in cities than in natural environments over seasonal and annual timescales, the same may not be true over timescales of days and weeks. In urban centres, human activity follows pronounced short-term cycles that could greatly affect the availability of anthropogenic food resources to urban animals. For example, central business districts of large cities support substantially larger numbers of humans during weekday working hours than they do during the weekends. One aspect of urban ecology that has received little attention is how urban wildlife cope with the high fluctuations in anthropogenic food abundance that can occur over these short timeframes in many urbanized settings.

Educational institutions represent another prime example where the abundance of anthropogenic food resources exhibits high temporal fluctuation, including over very short temporal scales. For example, the relative abundance of anthropogenic food at a university is likely to fluctuate according to the academic calendar (du Plessis 2005) and the weekly cycle of week days and week-ends. Here we explore how an urban-exploiting bird species, the Red-winged Starling (*Onychognathus morio*, hereafter "starling"), copes with extreme fluctuations of anthropogenic food resources on the Upper Campus of the University of Cape Town (UCT), Western Cape, South Africa. The temporal fluctuations of human activity provide a 'natural' experiment to study the impact of highly variable anthropogenic food quantity on the diet composition, activity budget and body mass of this city-dwelling bird species.

Using focal watches of 59 colour-ringed individuals we investigate the effects of high human presence (as a proxy for associated anthropogenic food abundance) on Red-winged Starlings' diet composition (% diet composed of anthropogenic or natural foods), amount of food consumed and behavioural time budgets. Furthermore, using 16 habituated individuals trained to sit on a top-pan balance in the morning and evening for a small food reward (following Ridley and Raihani 2006), we investigate the effects of high human presence on the daily mass gain of Red-winged Starlings. We hypothesised that heavy human presence (hereafter "HHP days") on campus during weekdays in term time could benefit the resident starlings by providing a high abundance of easy-to-access anthropogenic food. If so, starlings might be food limited on low human presence days (hereafter "LHP days") such as weekends and vacation days when anthropogenic food should be less available. We predicted that, if resident starlings are indeed "anthropogenic-food dependent", they would incorporate a greater proportion of anthropogenic food items into their diet on HHP days and in doing so spend less time foraging and more time on other behaviours (e.g. self-maintenance) than on LHP days. We further expected a higher daily body mass gain due to greater anthropogenic food consumption or higher foraging efficiency on easily-obtainable anthropogenic food during HHP days compared to LHP days.

However, if starlings have sufficient behavioural flexibility to avoid potential resource bottlenecks posed by the fluctuations in student numbers on campus and therefore fluctuations in availability of associated anthropogenic food; then we would still expect to see a significant change in diet composition (i.e. proportion of natural versus anthropogenic food items), but minimal change in time-activity budgets or daily body mass gain.

Methods

Study site and species

We worked on the main campus of the University of Cape Town (UCT hereafter; 33°57′31.5"S 18°27′36.4″E). The campus is located on the eastern slopes of Devil's Peak, a mountainous area in the Western Cape, South Africa overlooking the residential areas of the city of Cape Town. The study site is located at the periphery of the city, making it unlikely that starlings find other anthropogenic food (e.g. shopping malls or restaurants) on weekends and during the academic vacation.

Red-winged Starlings are common, medium-sized (~130 g) omnivorous birds distributed from Eastern Africa in Ethiopia to the Cape in Southern Africa (Craig 2005). Their natural diet consists mainly of fruits, seeds, nectar and arthropods (Hockey et al. 2005). The resident population at UCT are often seen scavenging anthropogenic food around students, kiosks and in rubbish bins (du Plessis 2005).

During the non-breeding season, between April and August 2017 (the austral winter), 124 starlings (63 females and 61 males) were captured at UCT's upper campus using spring-traps baited with cheese and raisins. Each bird was uniquely marked with three coloured plastic rings and one engraved metal SAFRING (South African Bird Ringing Unit) for individual identification.

Observations of colour-ringed starlings were conducted from April to September 2017 and were undertaken on days with low human presence on campus ("LHP days"); including weekends and the academic vacation when students are largely absent and many campus food-stalls are closed (1st vacation: 29 April – 07 May 2017; mid-year vacation: 15 July – 13 August 2017), and on days with heavy human presence on campus ("HHP days"); including week days of the semester term (1st quarter: 13 March - 28 April 2017; 2nd quarter: 08 May – 14 July 2017; 3rd quarter: 14 August 2017–22 September 2017), when students were present on campus in large numbers and most food-stalls were open. Daily admissions records from the Chancellor Oppenheimer Library (the main library located in the centre of Upper Campus) support the assumption of a difference in student activity on campus between weekdays ($\bar{x}$ = 2892 students, CI [2175; 3610 students) and weekends ($\bar{x}$ = 1489 students, CI [962; 2017 students) (two-sample t-test, $t = -2.8776$, $df = 45$, $P = 0.006$) (data from Catto 2018), and this data was used as a proxy for anthropogenic food abundance on campus.

Behavioural observations: Time-activity budgets

Focal observations (focals) (Altmann 1974) were used to investigate the effect of differences in anthropogenic food supply between HHP and LHP days on the diet composition and behaviour of starlings. Behavioural data were collected between 10 h00-17 h30 by carrying out repeated observations of colour-ringed individuals, at distances of 2–3 m (campus starlings were already pre-habituated to close presence of humans; see supplementary material Fig. S1 for images). Focals involved continuously recording the behaviour of a single starling for a period of c. 15 min. All focals were conducted by a single observer (MS) using a smartphone with Cybertracker software (The CyberTracker Team 1997) to record the data. We allocated all focals into one of four time-of-day categories 10 = 10 h00-11 h59, 12 = 12 h00-13 h59, 14 = 14 h00-15 h59 and 16 = 16 h00-17 h59.

We defined six main categories of activities: foraging, bill-cleaning, perching, calling, flying and preening. "Foraging" was defined as: visually searching, hopping on the ground, table, bench, in a rubbish bin or in bushes/trees, probing, gleaning, hawking, handling or ingesting a food item. "Perching" was defined as sitting silent and immobile on the ground, in a tree or manmade structure. "Preening" also included scratching, shaking and stretching ("comfort" behaviours). If a starling flew out of sight of the observer during a focal, the time was logged as 'out of sight', once the bird was relocated the focal would resume. The percentage of time spent on each behaviour type within a focal was then calculated as total time (to the nearest second) engaging in that behaviour divided by the total time the bird was observed during the focal (i.e. total focal length – time the bird was out of sight).

Diet composition analysis

Food types were recorded as part of the diet only if they were consumed (i.e. excluding handled and discarded food items). We classified whether the food item was natural (e.g. insect or fruit taken from a bush or tree) or anthropogenic (e.g. baked goods, maize-based snakes, fruits obtained from student discards or waste-bins, Table 1). For each food item we also recorded the number of beakfuls consumed in order to better estimate the quantity of food consumed by the starlings. We used "beakfuls" as a standardised "bite size" measure, allowing us to estimate the intake of different types of food items that themselves are different sizes: starlings tend to break these up into "beakful" sized pieces for consuming them. The percentage of anthropogenic food consumed on HHP and LHP days was calculated using only focals where a food item was consumed i.e. excluding focals where individuals foraged but nothing was consumed ($n = 101$; HHP = 44; LHP = 57). The amount of food consumed on HHP and LHP days was calculated using the number of beakfuls consumed throughout the duration of the focal, while the starling was observed ($n = 155$; HHP = 67; LHP = 88).

Daily mass gain

Body mass change between the morning and evening on HHP and LHP observation days was obtained by training colour-ringed starlings to stand on a portable top-pan scale in return for a small food reward (a raisin), following Ridley and Raihani (2006). For these measurements, we used a portable scale (Ohaus, New Jersey) which could weigh up to a maximum of 500 g with a resolution of 0.1 g, equipped with a small cardboard box measuring 14.7 cm × 7.5 cm × 7.5 cm taped to

Table 1 The variety of anthropogenic food and natural food items consumed by non-breeding red-winged starlings at the university of Cape Town, expressed as percentages

Anthropogenic food items	%	Natural food items	%
Unknown anthropogenic	23.5	Unknown natural	51.9
Apple	28.1	Natural berry	22.5
Bread	18.7	Flower	13.2
Muffin	15.5	Leaf	8.9
Crisps	5.2	Insects	3.1
Pop-corn	5.2	Natural nuts	0.3
Hot chips	1.7		
Bones	1.4		
Meat	0.3		
Banana	0.2		
Grape	0.1		

Consumed food items were obtained from 155 20-min focal observations and the percentages of food items consumed were calculated using the average number of beakfuls consumed for each food item the top of the scale to encourage the birds to jump onto the scale for the food reward. On location of a marked habituated individual, a crumbled raisin (0.3–0.5 g) was placed on the scale on the box, and the scale placed on the ground (and zeroed). When a starling hopped onto the scale its mass was recorded by the observer (MS). Mass measurements were taken twice daily, an early reading taken between 09 h00-11 h30 (w_1) and a late reading between 16 h30-18 h00 (w_2). The order in which individuals were weighed was kept the same in the morning and the evening on that day to ensure a similar time period between the two records for each bird, (~8–10 h apart). The daily proportional mass change was calculated as follows:

$$\text{Percentage mass change} = ((w2–w1)/w1)*100$$

Statistical analyses

All analyses were performed using generalized linear mixed models (GLMMs) and linear mixed models (LMMs) using the packages 'lme4' (Bates et al. 2014) and 'MASS' (Venables and Ripley 2002) within the R statistical environment (R Development Core Team 2018). All models were fitted with the day status (HHP or LHP) as an explanatory variable and a unique bird identity (based on colour ring combination) was fitted as a random term to account for repeated measurements taken from the same individual. The hour during which focals were taken was fitted as an additional categorical explanatory variable in four levels for all analyses based on focal observations. Additional factors were fitted to some models as described below.

For the diet composition analysis, focals where nothing was consumed were excluded. A GLMM was fitted with binomial error distribution with the number of beakfuls of anthropogenic versus natural food items consumed fitted with the *cbind* syntax as response variable (supplementary material Table S1, analysis 1). To account for overdispersion in the model we also included an observation level random effect (OLRE, Harrison 2014). To compare the amount of food consumed between HHP and LHP days a glmmPQL with a quasi-Poisson error distribution was fitted with the number of beakfuls consumed during the focal as the response variable and with focal duration added as an offset term to account for the varying length of focal observations (supplementary material Table S1, analysis 2).

To explore whether and how behaviour differed between HHP and LHP days, time-activity budgets were calculated as percentages of the total time of each focal observation. The % time spent on behaviours perching, foraging, preening, flying, bill cleaning and calling were then reduced into uncorrelated parameters through a correspondence analysis (R-package 'ca' (Nenadic and Greenacre 2007)). Only scores along dimension 1 (CA1) and dimension 2 (CA2) were considered for further analysis because they accounted for most of the variation (60.1%, supplementary material Table S2). CA1 and CA2 were set as response variables in separate linear mixed models, with hour category as a fixed term and weighted by the duration of the focal to account for the varying length of focal observations (supplementary material Table S1, analysis 3).

Finally, an LMM was fitted to explore how body mass gain differed between HHP and LHP days. For this analysis we fitted proportion body mass gained as response variable and days status (HHP or LHP) as an explanatory variable. Additionally, to check that the order in which we weighed birds did not influence the result we included the order in which individuals were weighed as an additional fixed effect (supplementary material Table S1, analysis 4).

All results are presented as means [$\bar{x}$] and 95% confidence intervals [lower CI, upper CI]. Results were taken as statistically significant if $p < 0.05$.

Results

A total of 155 focal observations (27.7 h) were collected from 58 individual starlings (30 females and 28 males); 67 focals were conducted on HHP days and 88 on LHP days. Focals had an average length of 10.7 min: CI [4.8 min, 12.0 min] and lengths did not differ significantly between HHP and LHP days, (HHP: $\bar{x}$ = 10.8 min, CI [9.4 min, 12.2 min]; LHP: $\bar{x}$ = 10.6 min, CI [9.3 min, 12.0 min]; $F_{1, 150} = 0.79$, $P = 0.37$, $n = 155$).

Diet composition

Starlings foraged successfully (consumed at least one food item) in 101 of 155 focals (44 HHP and 57 LHP). These focals were used for the analysis of percentage anthropogenic food consumed on HHP versus LHP days. Overall starlings consumed a wide range of anthropogenic and natural food items. Apple (28%), bread (19%), muffin (16%) and crisps (10%) made up the greatest proportions of known anthropogenic food items consumed (Table 1). The majority of natural food consumed (52%) could not be identified because the observer's view was obstructed when starlings foraged in grass and in trees. However, there was no access to anthropogenic food in trees on campus. On grassy lawns, we checked whether any anthropogenic food was present in the environment during the observation and can therefore be confident that natural food was consumed on these occasions. Of the remainder, natural berries and nectar made up the greatest proportions of the natural food part of the starling's diet. Starling diet comprised a higher percentage of anthropogenic food on HHP ($\bar{x}$ = 80.6%, CI [68.9%; 92.3%] than LHP days ($\bar{x}$ = 34.48%, CI [22.7%; 46.3%]), a difference that was highly significant ($\chi^2 = 72.86$, df = 1, $P < 0.001$; Fig. 1a).

Food consumption: Beakfuls consumed during focal

All 155 focals collected were used to analyse the difference in the amount of beakfuls consumed on HHP days (67 focals) versus LHP days (88 focals). The number of beakfuls consumed did not differ significantly between HHP days ($\bar{x}$ = 9.0 beakfuls, CI [5.5; 12.6]) and LHP days ($\bar{x}$ = 9.6 beakfuls, CI [6.5; 12.6]) ($\chi^2 = 0.37$, df = 1, $P = 0.542$; Fig. 1b).

Time budgets: Foraging effort

The main starling behaviours recorded were perching (41.1%), foraging (37.0%), preening (6.1%), calling (5.3%), flying (3.6%) and bill cleaning (1.6%). Correspondence analysis separated the six behaviours into two groups along CA1; low CA1 values are associated with perching, preening, calling and flying, whereas high CA1 values are associated with foraging and bill cleaning; with foraging carrying the highest eigen value (Fig. 2). Along CA2, calling was separated from all other behaviours, and carried the highest eigen value. Collectively, these two dimensions explained 60.1% of the variance in behaviours (36.8% for CA1 and 23.8% for CA2).

There was no significant difference in % of time spent engaging in these key behaviours between HHP days and LHP days (CA1: $\chi^2 = 0.23$, df = 1, $P = 0.63$; CA2: $\chi^2 = 0.02$, df = 1, $P = 0.88$). Starlings foraged similarly on HHP days ($\bar{x}$ = 39.61%, CI [31.26%; 47.97%]) and on LHP days ($\bar{x}$ = 34.20%, CI [27.78%; 40.57%]) ($\chi^2 = 0.07$, df = 1, $P = 0.80$).

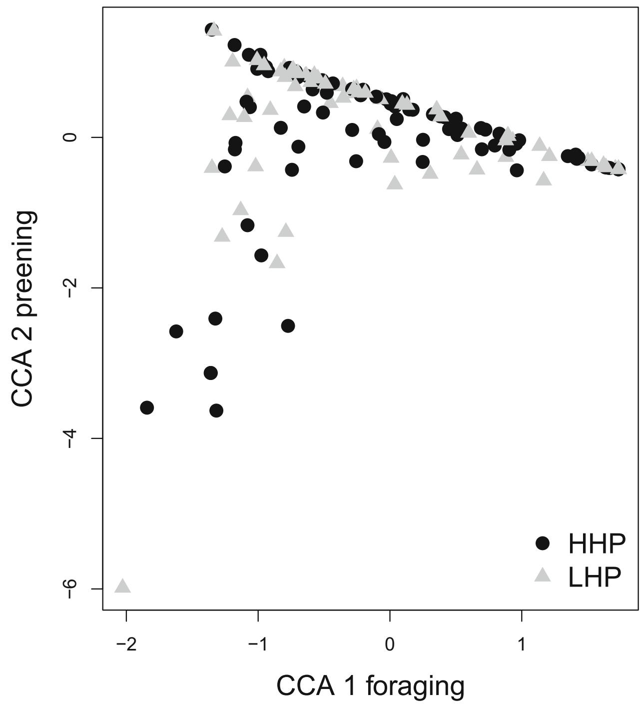

Fig. 2 Correspondence analysis of 28.34 h of observations ($n = 158$ focals) used to generate behavioural scores CCA1 and CCA2 for Red-winged Starlings during the non-breeding season. CCA1 represents the foraging dimension and CCA2 the calling dimension. The behavioural parameters used in the analysis are perching, foraging, preening, calling, flying and bill cleaning. The black dots represent the behavioural proxies for HHP days and the grey triangles represent behavioural proxies for LHP days

Percentage mass gain

Percentage body mass change on HHP days ranged from a reduction of −7.0% to an increase of 11.4% and on LHP days of −4.7% to 12.9%. Starlings tended to gain a greater proportion of their body mass on HHP days ($\bar{x}$ = 3.6%, CI [2.5%; 4.6%]) compared to LHP days ($\bar{x}$ = 2.5%, CI [0.4%; 4.6%]) but this difference was marginally significant ($\chi^2 = 3.68$, df = 1, $P = 0.06$, Fig. 3).

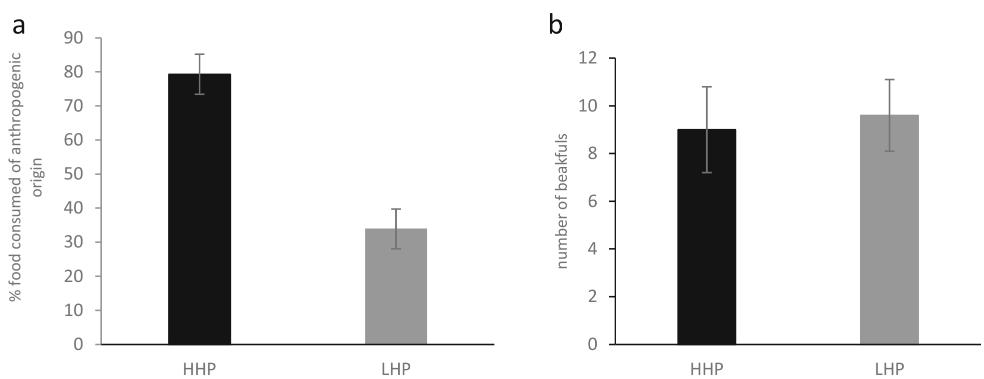

Fig. 1 **a** The % anthropogenic food consumed on HHP and LHP days during the non-breeding season of Red-winged Starlings resident to the University of Cape Town, Upper Campus. Percentages were obtained from 101 focals where food was consumed (44 HHP days and 57 WE days). Standard error bars are included. **b** Amount of food consumed by Red-winged Starlings on HHP and LHP days during the non-breeding season expressed as the number of beakfuls consumed throughout the duration of the focal, while the starling was in sight. Standard error bars are included

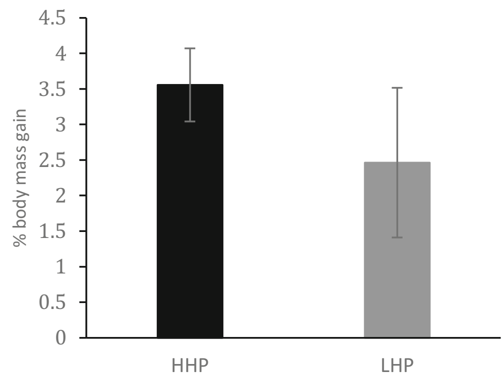

Fig. 3 The average percentage of daily body mass gained on HHP days and LHP days with standard error bars shown

Discussion

Urban Red-winged Starlings at our study site seem to have the behavioural flexibility to cope with dramatic fluctuations in anthropogenic food availability over short time scales, at least during the non-breeding period. As predicted, starlings' diet composition differed significantly between HHP days (when student numbers on campus were high) and LHP days (when student numbers were low). On HHP days, starling diet mostly (>80%) comprised food of anthropogenic origin, whereas on LHP days the birds switched to eating predominantly natural food items, with only 35% being anthropogenic food. Despite this, starlings devoted similar amounts of time to foraging on HHP and LHP days, consumed similar amounts of food and had overall similar time budgets. There appeared to be some consequence of foraging more on anthropogenic food on HHP days on mass gain, with birds tending to gain more mass on HHP days compared to LHP days, albeit marginally non-significantly. Our findings support the idea that urban-living Red-winged Starlings are not dependent on anthropogenic food, at least not during the non-breeding season when energy requirements are lower than during breeding. They are successfully able to switch rapidly from predominantly anthropogenic to predominantly natural food sources, depending on food availability that undergoes strong short-term variation. Similar food switching was demonstrated by Black-tailed Gulls, *Larus crassirostris* in response to extremely short-term temporal heterogeneity in availability of different food types (Yoda et al. 2012). Gulls used natural food resources (found in paddy fields) around noon and anthropogenic food sources (found at private houses, fisheries, meat processing plants and markets) during the afternoon, reflecting the time windows of greatest food availability at each type of feeding ground.

The ability to gain required nutrients in urban habitats and to take advantage of new foraging opportunities is considered one major component in the successful colonization of urban environments (Sol et al. 2013). In this study we focused on behavioural flexibility and which type of food was consumed, and not on their exact nutritional composition. However the majority of the anthropogenic food items we observed (bread, muffin, and crisps) are generally considered to be carbohydrate rich foods, in keeping with the suggestion that carbohydrates are the most common macronutrient available in human food waste (Coogan et al. 2018), and some species may even shift their dietary preference towards high carbohydrate food resources in urban environments (Coogan et al. 2017). The quality of food items consumed could influence short-term physiological responses as well as long-term evolutionary adaptations: an issue which has still received little attention (but see review in Coogan et al. 2018), however we were unable to assess these effects within the scope of this study.

Food consumption

Our study is among the first to show that the ability to deal with fluctuations in anthropogenic food abundance over short time scales via flexibility in diet composition might be a key trait of successful urban birds. Contrary to the idea that anthropogenic food may provide a stable alternative food source for species to sustain themselves during periods of natural food shortage (Lowry et al. 2012); starlings in our study coped with anthropogenic food scarcity on LHP days by switching to naturally-occurring food sources. This was visible in similar amounts of food consumption between HHP and LHP days, but different food origin (anthropogenic vs natural). The ability to flexibly switch between food types according to their abundance might be critical for meeting daily energy requirements in an environment where some food sources exhibit high temporal fluctuations. Our results also emphasise the importance of remnants of natural food sources in urban environments as they can act as a buffer against anthropogenic food shortages.

Foraging effort

Surprisingly, the higher consumption of anthropogenic food on HHP days did not translate into lower foraging effort as we expected. In fact, starling time budgets remained similar between HHP and LHP days. As stated above, this may suggest that starlings at the University of Cape Town are not severely food limited on LHP days and have sufficient behavioural flexibility to easily switch between anthropogenic and natural food. However, an alternative explanation might be alterations in predation risk during periods of fluctuating human presence. Urban habitats are often thought to release prey from the pressures of predators (Shochat et al. 2006) however, the density and/or activity of some generalist and opportunistic predators may increase (Rodewald et al. 2011) in response to abundant prey populations and decreased persecution by humans (Seress and Liker 2015; Chace and Walsh 2006, Rutz 2008). The most abundant diurnal predators of adult starlings in our system are raptors, principally Black

Sparrowhawks *Accipter melanolecus* (Suri et al. 2017) and Peregrine Falcons *Falco peregrines* (Jenkins 2000). Both species might be more reluctant to depredate starlings when they are in close proximity to humans. Starlings showed a slight and non-significant tendency to forage more on HHP days possibly in keeping with the idea that elevated human activity can act as a refuge against natural predators (Møller 2012).

Mass gain

Despite similar amounts of food being consumed between HHP and LHP days, starlings experienced greater daily body mass gain on HHP than on LHP days, albeit this difference was statistically marginally non-significant. This tendency towards greater mass gain on HHP days could be due to the greater intake of anthropogenic foods that may contain more calories and may be rich in carbohydrates (Coogan et al. 2018). Other studies investigating the diet of birds feeding on anthropogenic refuse have reported that anthropogenic foods have higher calorific and fat content compared to natural dietary items (Ottoni et al. 2009; Auman et al. 2008; Toledo et al. 2016). Alternatively, this result could also indicate dependence on anthropogenic-food after all, with starlings being resource-limited on LHP days, but unable to compensate by increasing the amount of food they consumed (perhaps due to predation risk as outlined above). However, we suggest that if starlings were under pressure either from having to forage under severe weather conditions (i.e. heat waves or heavy rain) or during the breeding season (i.e., having to provision chicks); then the effect size and the significance of the difference in mass gain between HHP and LHP days could be more pronounced, and could be supporting the anthropogenic-food dependence hypothesis.

Conclusion

The urban environment clearly provides an additional resource that urban birds can exploit to sustain themselves. The ability to tolerate human presence and to incorporate novel food resources may be important to prevent overnight-starvation and allow starlings to satisfy their daily metabolic demands, but flexibility in diet composition may also be important if birds are to deal with highly fluctuating anthropogenic food availability over short time scales. The time spent foraging by Red-winged Starlings at the UCT was seemingly not dependent on human presence and their associated foods on campus, as they did not respond with increasing foraging effort on days of anthropogenic food shortage. Future research should be aimed at the physiological effects of a predominantly anthropogenic diet as anthropogenic food might be of lower quality (e.g., Andersson et al. 2015; Toledo et al. 2016) or different nutrient composition (Machovsky-Capuska et al. 2015; Peneaux et al. 2017; Coogan et al. 2017) and a high consumption could be costly in terms of bird health (Shochat et al. 2010; Lowry et al. 2012). Exploring how other urban bird species cope with these short-term food fluctuations would improve our understanding of whether the strategy seen here is generalized to other species and may help to understand whether these behaviours are integral to allow species to exploit urban habitats.

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