



**Fluctuating human activity and associated anthropogenic food availability
affect behaviour and parental care of Red-winged Starlings**

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Abstract

Increased food availability associated with urbanisation is widely recognised as one of the key factors influencing avian demography. Temporal fluctuations in food availability, tied to variation in human presence, are of particular interest as they occur frequently in urban environments, but their impacts on the survival and reproduction of birds have not been particularly well-studied. In this study, I explored whether breeding Red-winged Starlings at a university campus in Cape Town, South Africa alter their behaviour and parental care of nestlings in response to fluctuating numbers of people and associated food over a relatively short timescale. I used data from nest watches and behavioural observations collected during both incubation and nestling periods to test whether differences in food availability due to day status (week days with thousands of students present versus weekends with substantially fewer students) affected a number of behaviours related to parental care. I found that, with less available food on weekends, parent birds appeared to trade off feeding their offspring for maintaining their own energetic requirements, meaning that nestlings received less food on weekends. I also found that parents preferentially fed their nestlings natural food on week days, despite an increased availability of anthropogenic food. This suggests that, with increased food availability, birds in this system may use anthropogenic food to supplement their own diets, allowing them to prioritise the feeding of natural food to their chicks. These results provide evidence that fluctuating food resources impact the behaviour and parental care of starlings, but it is still unclear what effect they have on the individual health of adult birds and their developing young. To further enhance our understanding of some of the ecological implications of urbanisation, future research should prioritise understanding the potential health impacts such a variable urban diet may have on the birds exploiting it.

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PLAGIARISM DECLARATION

I understand that plagiarism is wrong. Plagiarism is using another's work and pretending it is one's own. I have used the journal *Conservation Biology* as the convention for citation and referencing. Each significant contribution to, and quotation in, this project from the work, or works of other people, has been attributed, cited and referenced.

This project is my own work. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as their own.

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Introduction

Over the last half a century, a process of rapid urbanisation has occurred globally. Today, over half the world's population lives in urban areas, although this varies substantially across countries (United Nations 2014). Continued urbanisation and human population growth are projected to add 2.5 billion people to the urban population by 2050, with the vast majority of this concentrated in developing countries in Africa and Asia (United Nations 2014). This rapid urban growth presents cities with huge challenges in providing adequate basic services for their citizens (Cohen 2006). It also represents one of the most extreme forms of land-use change, leading to a complete restructuring of habitat and species composition (Shochat et al. 2006). Urban landscapes vary dramatically, ranging from heavily built-up environments in city centres to suburban areas with relatively high proportions of green space in the form of parks and gardens (Chamberlain et al. 2009). Urbanisation is therefore a topic of major concern in conservation biology, and urban ecology has become a large, multidisciplinary field in which researchers attempt to understand the many complex processes at work (Shochat et al. 2006).

Habitat alteration from urbanisation is a long-term change that dramatically modifies large parcels of land as they are devegetated, paved, and built up (Marzluff and Ewing 2001). Identifying how this impacts animal and plant diversity is important for conservation and management so we can understand ecological implications and mitigate subsequent threats to biodiversity. Urbanisation promotes biotic homogenisation because of the uniform nature of cities, and marked differences between cities and natural habitats with regards to food resources, weather conditions, predator communities, and pollution (McKinney 2006). This massive disturbance therefore not only destroys habitat of native species, but creates new habitat and niches for a relatively small suite of species that can behaviourally adjust to urban and suburban conditions (McKinney 2006; Evans et al. 2009). The result is that the ecological community composition of urban environments differs dramatically from the surrounding local natural environments (Parsons et al. 2003; Taylor et al. 2013).

In recent decades, research has indicated that urbanisation is indeed a strong evolutionary driver, creating a unique setting in which ecological patterns and processes are often disrupted by human activities (Shochat et al. 2006). These selective forces require rapid behavioural adaptation, and each species has a unique way of adjusting to the complex biotic and abiotic factors present in urban areas. To further understand the mechanisms allowing colonisation of urban areas by plant and animal species, attempts have been made to create theoretical

generalisations about characteristics or traits possessed by urban adapters, thus taking a more comparative approach to identifying how urban-adapted species differ from those more sensitive to urbanisation (McKinney 2006; Shanahan et al. 2014).

Adapting to unique ecological niches requires changes in the behaviour of animals settling in urban areas (Luniak 2004). When comparing species that fare well in urban environments with those who fare poorly (urban avoiders), it appears that no single characteristic can discriminate between the two, but rather a combination of several behavioural changes allows some species to thrive in urban areas (Crocì et al. 2008). Luniak (1996) describes some of the most common characteristics of well-adapted urban populations as follows: animals able to live at higher population densities with decreased individual (pair/family) territory size; lower levels of migratory behaviour and prolonged breeding seasons mediated by rich food resources and a milder urban microclimate; changes in nesting behaviour, including the use of human-built structures for nesting; changes in feeding behaviour; and tameness towards people. In general, having a wide dietary spectrum and having the ability to use a wide range of habitats is beneficial, and subsequent adjustments demonstrate ecological, behavioural, and demographic plasticity within species (Luniak 2004).

The community response of birds to urban living has been particularly well-studied. In general, the response of avian species richness or diversity to urbanisation appears to be non-linear, with the highest levels of richness at intermediate levels of urbanisation, and with few species dominating the urban environment in high individual numbers (Parsons et al. 2003; Blewett and Marzluff 2005; Taylor et al. 2013). Reviews by Marzluff (2001), and Chace and Walsh (2006) found that bird species which are successful in urban areas include a high proportion of a few feeding guilds. In European and North American cities these include omnivorous and insectivorous ground foragers, as well as granivorous birds, and aerial sweepers. Each of these guilds responds to distinct aspects of the anthropogenic environment such as bird feeding stations, and highly productive gardens and lawns (McKinney 2006). Tree and cavity nesters are also common among urban adapters (Chace and Walsh 2006). These trends occur over large geographic regions so that bird communities living in distinctly different habitats are the most similar in urbanised sites, and the least similar in surrounding natural areas (Meffert and Dziock 2013).

Availability of anthropogenic food is one of the major ways in which urban and natural areas differ, and appears to be of crucial importance when investigating urbanisation and its impacts

on various species (Martin 1987; Chamberlain et al. 2009). Urban centres offer rich resources of anthropogenic food – through refuse (Auman et al. 2008) and deliberate bird feeding by people (Jones and Reynolds 2008) – and these resources are attractive and important to many bird species (Luniak 2004). The provisioning of food to birds is an extremely popular activity globally, with documented benefits experienced by over-wintering birds, including increased survival and improved body condition (Jones 2011). In the United States of America and the United Kingdom, 18% and 39% of households, respectively, state that they frequently feed birds, representing a large food resource (U.S. Fish and Wildlife Service 2001; Fuller et al. 2012).

Increased food availability therefore undoubtedly has a fundamental influence on urban animals and is recognised as one of the key factors influencing avian demography. Research has recently expanded to cover this issue, allowing a greater understanding of how the urban environment and an urban diet impact the survival and reproduction of birds living therein (reviewed in Robb et al. 2008a). Several studies have compared productivity of urban and non-urban birds, with emergent patterns suggesting that anthropogenic food can have positive impacts, such as increased adult over-winter survival (Greig et al. 2017), earlier lay dates and increased egg and clutch sizes (Robb et al. 2008a). However, it can also have negative impacts on productivity, and has been found to reduce breeding success of birds in subsequent seasons (Plummer et al. 2013).

A review and meta-analysis by Chamberlain et al. (2009) found that in 16 of 19 comparisons, laying dates were advanced in urban areas, which could be attributed to the abundance of food enhancing adult body condition. Despite this, mean nestling body mass was lower in urban environments in 10 of 11 studies (Chamberlain et al. 2009). A study conducted in England over three seasons showed that supplementary feeding with peanut cake significantly advanced laying dates in both Blue Tit (*Cyanistes caeruleus*) and Great Tit (*Parus major*) populations (Harrison et al. 2010). Notably, however, supplementation also significantly reduced brood size. These findings mirror observed patterns in urban Blue and Great Tit reproduction (Jones and Reynolds 2008; Robb et al. 2008b), and confirm that supplementary feeding, a common activity in the UK, may not always enhance birds' breeding productivity (Harrison et al. 2010).

In some cases, the urban environment contains a relatively large quantity of natural food available for breeding birds; however, the quality of this food may influence breeding success. A Swedish study found that Great Tit provisioning frequencies were almost twice as high in

urban sites than rural sites, likely due to the greater abundance of caterpillar prey these birds rely on during the breeding season (Isaksson and Andersson 2007). However, when compared to rural caterpillars, urban caterpillars had significantly lower carotenoid concentrations (Isaksson and Andersson 2007) which are important dietary components which can influence the health of chicks (Goodwin 1984). Similarly, a study comparing the reproductive success of House Wrens (*Troglodytes aedon*) in suburban and rural habitats found that even though parental feeding rates during the early nesting period were higher at suburban sites, nestlings weighed less and were smaller in size than at rural sites (Newhouse et al. 2008). The authors suggest that this pattern may be due to reduced average quality of food provisioned by parents in urban areas.

In other cases, natural food items are scarcer in urban areas. Pollock et al. (2017) found that the availability of caterpillars was significantly reduced at an urban site close to the city centre of Glasgow, Scotland. Urban Blue Tit parents consequently provisioned fewer caterpillars to their offspring than rural conspecifics, negatively impacting fledging success. Additionally, a study by Ibáñez-Álamo and Soler (2010) showed that Common Blackbird (*Turdus merula*) nests in urban areas displayed significantly higher starvation rates than those in woodland areas. This suggests that, for some urban bird populations, appropriate nestling food items are in poor supply, and anthropogenic alternatives cannot act as substitutes for the low abundance of natural items. While many studies of this kind exist, in general, this area of research within urban ecology is relatively restricted to developed countries within the northern hemisphere, and more investigations are needed in developing regions with the highest projected growth in human population and urbanisation, such as Southeast Asia and Africa (Chamberlain et al. 2009).

Fluctuations in food availability may also occur in urban areas. It is well known that fluctuations in food availability, regardless of food type or habitat, can influence several avian demographic parameters. For instance, clutch sizes of both Tengmalm's Owl (*Aegolius funereus*) and Eurasian Kestrels (*Falco tinnunculus*) in western Finland varied predictably in three-year cycles, aligning with the fluctuating abundance of voles, their main prey source (Korpimäki and Hakkarainen 1991; Korpimäki and Wiehn 1998). In both cases, clutch size was smaller in low vole years. This illustrates that annual fluctuations in natural food can impact reproductive outputs.

While considerable research exists examining how birds cope with fluctuating disturbance levels associated with periods of high and low human activity (Burger and Gochfield 1983; Bautista et al. 2004), there is a lack of research regarding fluctuations in food availability on a shorter timescale, particularly with regards to anthropogenic food in the urban environment. On a longer temporal scale, food availability in an urban environment may fluctuate less than in a natural environment. For example, fluctuations may be smaller across the seasons or between years, as anthropogenic food may not be subject to the same seasonal processes as natural food items, and because supplementary feeding is such a common activity (Fuller et al. 2012). However, many anthropogenic activities are based on a weekly cycle, meaning fluctuations in food availability take place over a shorter temporal scale with a high degree of spatial predictability, and may result in more scheduled behaviour for some species (e.g. Deygout et al. 2010). For example, within leisure areas, food supply may be greater during the weekend than within the week. The impact of these fluctuations on bird behaviour are not yet understood and therefore require investigation.

In this study, I explored whether urbanisation, and specifically the associated variation in anthropogenic food availability, has an impact on birds' behaviour and breeding investment. I took advantage of a unique situation in which the abundance of anthropogenic food fluctuates strongly over short periods of time. The main campus of the University of Cape Town (UCT), South Africa was used to explore this issue, as anthropogenic food is abundant during the week when thousands of students are present but presumably declines dramatically on weekends and during holidays. I explore the influence of these extreme fluctuations on the Red-winged Starling (Sturnidae: *Onychognathus morio*) – an urban adapter species which has successfully colonised cities throughout Africa. I monitored individually colour-ringed birds on UCT's main campus (the Upper Campus) over a period of 8 weeks during the breeding season through systematic nest watches and focal observations of behaviour.

I aimed to determine whether adults alter their behaviour in response to the fluctuating numbers of people (and associated food) on campus. I hypothesised that adults would exploit anthropogenic food more on week days than weekends. If so, I then hypothesised that this would influence parental care behaviour between week days and weekends because of changes in food availability. I predicted that on week days parents would spend less time foraging and would consequently invest more time in parental behaviours such as incubating or brooding, and in self-maintenance behaviour due to increased food availability. I also predicted that

parents would provision more food, and specifically more anthropogenic food, to incubating females (provisioning by the male parent) and to chicks (provisioning by both parents) on week days. I expected parental decision-making (i.e. whether breeding individuals chose to eat or provision any given food item) to differ between day status, predicting that with greater availability of anthropogenic food on week days, a higher proportion of anthropogenic food would be provisioned than on weekends.

Because of the different pressures on parents during incubation, early, mid and late nestling periods, I expected that the above impacts of day status may differ between different nesting stages and depending on the age of chicks. I predicted that with increasing chick age, females would spend less time brooding and more time foraging, and parents would provision a greater proportion of anthropogenic as opposed to natural food as chicks might become more resilient to this diet as they age.

Materials and Methods

Ethical statement

Capture and handling of both adult and juvenile starlings was approved by the Science Faculty Animal Ethics Committee at the University of Cape Town (Clearance Number 2016/V15/AA).

Study system

This study took place on the main campus of the University of Cape Town (UCT), Western Cape, South Africa (33°57'27.5"S, 18°27'40.31"E). The university is located on the slope of Table Mountain and experiences a Mediterranean climate with winter rainfall and warm, dry summers (Rebelo et al. 2006). Over 25 000 students are enrolled at UCT annually, and on weekdays during the academic term, most of these students attend classes on upper campus. This abundance of people corresponds with an abundance of anthropogenic food provided by cafeteria stalls and brought by students from off campus. Cafeteria stalls are closed during weekends and the number of students visiting campus is dramatically reduced.

The Red-winged Starling (*Onychognathus morio*) is a common, omnivorous bird with a native range from Ethiopia to the Cape in South Africa. They are medium sized birds weighing between 115 and 155g, and their natural diet consists of fruit, nectar, seeds, and arthropods (Craig 2005). They are described as a gregarious bird, but resident pairs appear together throughout the year. During the breeding season, these pairs breed in territories which they

aggressively defend against other starling pairs, as well as other animals, including humans (Martin 1955). Their laying dates are between September and March and they are frequently double-brooded with the second clutch laid three to four weeks after the first brood leaves the nest (Craig 2005). Although they are primarily a cliff-nesting species, Red-winged Starlings often make use of suitable ledges and recesses on man-made structures and have been documented breeding on buildings at UCT since the 1940s (Martin 1955).

This population takes advantage of anthropogenic food on UCT's upper campus and starlings are often seen scavenging food dropped by students, retrieving it from rubbish bins, and in some cases even snatching food from the hands of unsuspecting people (du Plessis 2005). The most common food items starlings obtain are carbohydrate-based items such as bread and french fries, which are abundant on the campus. It has been suggested that food availability is tied to the student calendar, and breeding pairs appear to have adjusted their nesting attempts somewhat so that a first breeding effort is made in October, peaking in November, and most nestlings have fledged by the time undergraduates leave for vacation in December (du Plessis 2005). A second breeding effort then occurs in February, coinciding with the start of the first term of the year, and the return of students to campus (du Plessis 2005).

Prior to the start of this study, ~130 adult starlings were captured on UCT's upper campus between April and August 2017 using spring traps baited with raisins or processed cheese. Each starling was individually marked with three colour rings, and one metal SAFRING band, stamped with a unique alphanumeric sequence. Field work was conducted between 20 October and 4 December 2017, aiming to cover the peak breeding season of first broods in this starling population. This time period also overlapped with an academic term (20 October to 14 November), an exam period (15 to 30 November), and vacation (1 December onwards, Fig. 1).

Week days vs weekends

In addition to the annual seasonality in anthropogenic food availability, there is variability on a much shorter timescale with more human food available on week days with students present on campus than on weekends with fewer students present. Data were collected every Friday, Saturday, Sunday, and Monday to facilitate direct comparisons between week days and weekends. Daily admissions records from the Chancellor Oppenheimer Library (the main library located in the centre of Upper Campus) throughout the field work period were used to

validate the assumption that Fridays and Mondays had substantially more students present than Saturdays and Sundays (Fig. 1).

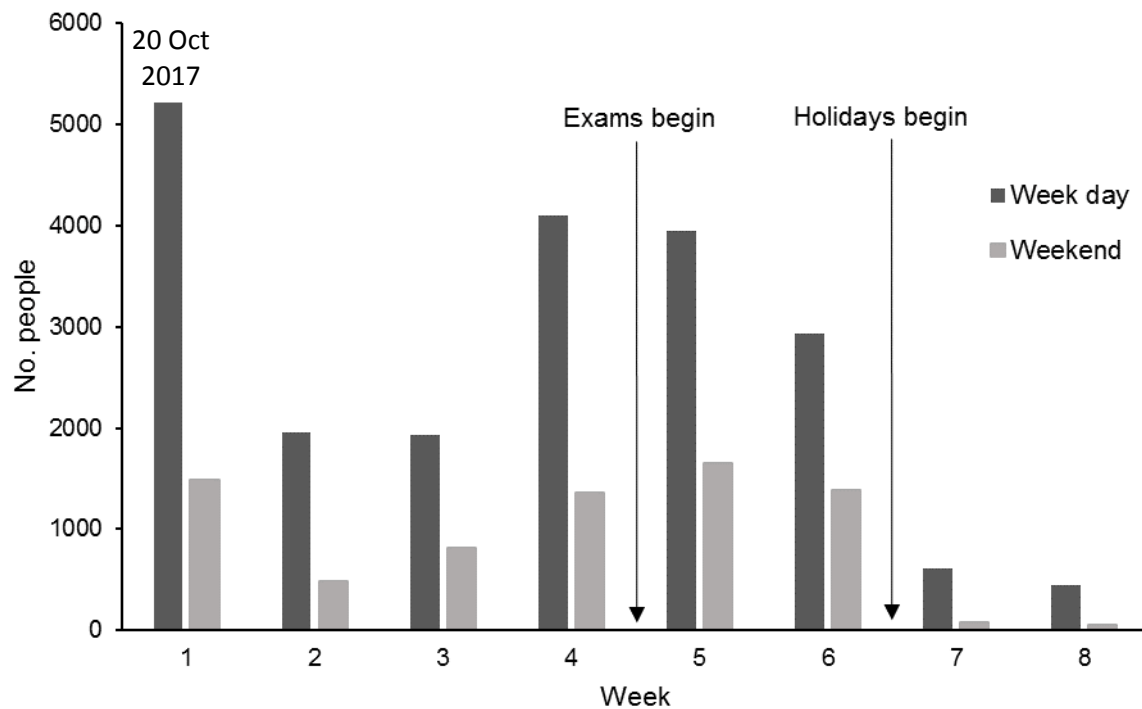


Figure 1: Mean number of people that entered the Chancellor Oppenheimer Library on Friday and Monday (week days) and Saturday and Sunday (weekends) during each week of the study period.

Monitored nests and pairs

Nests chosen for data collection were found through observations of nest building activity by the starlings as reported by students via a dedicated WhatsApp group (set up as part of the broader Red-winged Starling Research Project on campus, with a membership ~45 students from across Faculties) and by searching systematically on campus. They were selected if at least one adult in the breeding pair was individually colour ringed, enabling easy identification of individuals from a distance using binoculars by comparing their colour rings with the broader project's database. A total of sixteen active nests were monitored during the study. Of these, ten were identified during the incubation period, and data for nine of them were collected during both incubation and nestling periods. Six nests were only identified during the nestling period. For one nest, neither parent was colour ringed, but in this case only nest watches were performed. Focal observations were not performed on this pair as they could not be individually identified once they moved away from the nest.

Each day of data collection was divided into three time blocks to account for the potential effect time of day might have on peak bird activity. Within each of these blocks, two hour-long observations were undertaken in which one nest (1-hr nest watch conducted by a volunteer – see below) and the associated starling pair (2 x 20 min focal observations conducted by myself) were monitored in parallel. Observations were conducted at the following intervals: morning blocks, 08:30–09:30, 10:00–11:00; early afternoon blocks, 12:00–13:00, 13:30–14:30; late afternoon blocks, 15:30–16:30, and 17:00–18:00. Data were collected from all sixteen nests in every time block on both a week day and a weekend day at least once.

Nest watches

Six one-hour-long nest watches were performed by volunteers on different monitored nests every day of data collection. These nest watches were used to obtain the following data: 1) incubation bout lengths (females only were observed incubating); 2) male food provisioning rates to the incubating female; 3) parental food provisioning rates to chicks; 4) the proportion of provisioned food that was of anthropogenic origin (See Table 1 for details of measured variables). Trained volunteers recorded all activity at the nest for the full hour using CyberTracker software (<http://www.cybertracker.org/>): a customisable data collection app loaded onto a smartphone. These data enabled the variables listed above to be compared between week days and weekends.

Behavioural observations

In parallel with the nest watches, I performed behavioural focal observations on the starling pair associated with each watched nest. Focals were performed for 20 minutes on each member of the starling pair, and involved continuously following an individual at a distance of two to three meters (possible due to the habituation of the birds to the heavy human presence on campus) and recording behaviours exhibited using CyberTracker software. When a starling flew out of sight, the duration of absence was recorded, and subsequently removed from all analyses. Therefore, only the amount of time spent engaging in known behaviours was analysed. The behavioural category ‘on nest’ was used for females incubating eggs or brooding chicks, and only if the female actually sat down in the nest. Otherwise, the category ‘visit nest’ was used for both males and females bringing food, removing faecal sacs, or examining the nest.

Birds were recorded as ‘foraging’ when visually hopping, searching for, and handling food items. Items were recorded as ‘swallowed’ if this action was seen, or ‘loaded’ if the bird held the item in its beak and flew towards the nest. I used ‘beakful’ as a unit to quantify the food amount rather than ‘item’ as some items were larger than others (i.e. contained more beakfuls). I recorded the number of beakfuls loaded (held in the beak – usually as a precursor to being fed to the partner or a chick) or swallowed, and whether the item was of anthropogenic (e.g. bread, noodle, apple) or natural (e.g. insect, berry, seed) origin. Data were used to investigate whether foraging effort and efficiency, food ‘capture’ (acquisition) rates, as well as the proportion of anthropogenic food foraged differed between week days and weekends. I also used these data to investigate decision-making by the adults, examining whether day status impacted the probability of certain captured food items being taken to the nest as opposed to eaten by the foraging adult.

Nestling mass

To determine whether increased human activity and associated increases in the availability of anthropogenic food may impact chick condition, 17 nestlings from nine nests were weighed at approximately day 15 after hatching (exact hatch dates for all nine nests had to be estimated due to the cryptic nature of some of the nests). This age was chosen for weighing because Red-winged Starling nestlings are fully feathered by 15 days, but the risk of forced fledging is low as the nestling period is 22–28 days (Craig 2005). Nestling mass was explored in relation to the number of week days experienced by chicks prior to weighing (i.e. during the preceding 15 days). For example, chicks may have experienced fewer week days due to hatching on a Saturday morning.

Statistical analyses

Data collected during the incubation and nestling periods were analysed separately. All analyses were performed using the statistical software R (v.3.3.2, R Core Team 2016). Generalised linear mixed models (GLMMs) were implemented using the package *lme4* (Bates et al. 2015), with post-hoc tests using the package *lsmeans* (Lenth 2016) providing p-values for each pairwise contrast for factor variables with more than two levels. Models with binomial and Poisson error structures were tested for overdispersion and, if necessary, corrected by including a unique identification term for each observation as a random factor (Elston et al. 2001). For models with Gaussian error structures, the assumption of normality of residuals was

checked by visually inspecting residual plots. Global models included all biologically meaningful terms and their relevant interactions. Sex of parent was only included in the analyses of focal observation data as nest watch data were analysed per nest, rather than per parent.

I modelled all behavioural data from both nest watches and focal observations in independent GLMMs with either a Poisson error structure for count data or a binomial error structure for data with two vector response variables. For models with Poisson error structures, appropriate offsets were used to control for varying durations of observations (see Tables 1 and 2 for details). In all models, I included a random term of Nest ID to account for repeat sampling of the same nests. To account for discrepancy in the absolute number of humans present on campus due to exam and holiday periods, Week ID was fitted as an additional random term in all models. Global models for each analysis are presented in Tables 1 (incubation period) and 2 (nestling period). Non-statistically significant interaction terms were removed from the global models. Model effects plots were generated using the package *effects* (Fox 2003). In the results section I reported χ^2 and p-values which were based on ANOVA Tables of Deviance using Type II Wald χ^2 tests to test the overall significance of categorical variables. Additionally, I report effect sizes as means \pm standard error as well as post-hoc contrasts in the Appendix.

Table 1: GLMMs performed on data collected during the incubation period. Variables included in the global models are displayed. Models (a)–(c) were performed on nest watch data, and models (d)–(h) were performed on focal observation data. For model (c), ‘Time of day’ was not included as a fixed term as the model would not converge, even when including an optimiser. DS = Day status (i.e. week days vs weekends); TOD = Time of day (morning, early afternoon, or late afternoon); Sex = Sex of adult.

Incubation Period				
Analysis	Type of model	Response variable	Explanatory variables	Offset
(a) Incubation bout lengths	Binomial GLMM	Time female spent on vs off nest	DS; TOD; DS*TOD	n/a
(b) Provisioning rate	Poisson GLMM	No. items provisioned during nest watch	DS; TOD; DS*TOD	log(Nest watch length)
(c) Anthropogenic vs natural food provisioning	Binomial GLMM	No. anthropogenic vs natural food items provisioned per nest watch	DS	n/a
(d) Foraging effort	Binomial GLMM	Time spent foraging vs not foraging	DS; TOD; DS*TOD; Sex	n/a

(e) Foraging efficiency	Poisson GLMM	No. beakfuls of food captured	DS; TOD; DS*TOD; Sex	log(Foraging mins)
(f) Food capture rate	Poisson GLMM	No. beakfuls of food captured	DS; TOD; DS*TOD; Sex	log(Focal mins)
(g) Anthropogenic food capture	Binomial GLMM	No. captured food items of anthropogenic vs natural origin	DS; TOD; DS*TOD; Sex	n/a
(h) Captured food provisioned vs eaten	Binomial GLMM	No. captured food items taken to nest vs swallowed by adult	DS; TOD; DS*TOD	n/a

Table 2: GLMMs performed on data collected during the nestling period. Variables included in the global models are displayed. Models (a)–(c) were performed on nest watch data, and models (d)–(j) were performed on focal observation data. DS = Day status; TOD = Time of day; NestlingAge = Week one, two or three of chicks’ lives; Sex = Sex of adult.

Nestling period				
Analysis	Type of model	Response variable	Explanatory variables	Offset
(a) Brooding bout lengths	Binomial GLMM	Time female spent on vs off nest	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge	n/a
(b) Provisioning rate	Poisson GLMM	No. items provisioned during nest watch	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge	log(Nest watch length)
(c) Anthropogenic vs natural food provisioning	Binomial GLMM	No. anthropogenic vs natural food items provisioned per nest watch	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge	n/a
(d) Foraging effort	Binomial GLMM	Time spent foraging vs not foraging	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge; Sex	n/a
(e) Foraging efficiency	Poisson GLMM	No. beakfuls of food captured	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge; Sex	log(Foraging mins)
(f) Food capture rate	Poisson GLMM	No. beakfuls of food captured	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge; Sex	log(Focal mins)
(g) Anthropogenic food capture	Binomial GLMM	No. captured food items of anthropogenic vs natural origin	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge; Sex	n/a
(h) Captured food provisioned vs eaten	Binomial GLMM	No. captured food items taken to nest vs swallowed by adult	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge; Sex	n/a
(i) Anthropogenic food provisioned vs eaten	Binomial GLMM	No. captured anthropogenic food items taken to nest vs swallowed by adult	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge; Sex	n/a
(j) Natural food provisioned vs eaten	Binomial GLMM	No. captured natural food items taken to nest vs swallowed by adult	DS; TOD; DS*TOD; NestlingAge; DS*NestlingAge; Sex	n/a

Correspondence analyses

Two correspondence analyses (CAs) were performed using the R package *ca* (Nenadic and Greenacre 2007) to allow investigation of starlings' time-activity budgets by incorporating several different behaviours into two dimensions, accounting for collinearity in the data. For focal data captured during the incubation period, the percentage of time spent foraging, on nest, flying, hopping, bill cleaning, perching, and preening were reduced using a single CA. This resulted in two uncorrelated axes (Dim 1 hereafter called 'incubation vs others', 57.82% of variance; and Dim 2 hereafter called 'incubation period forage vs preening', 15.47% of variance). For nestling period data, the same variables were investigated with the addition of the percentage of time spent visiting the nest. This CA again resulted in two uncorrelated dimensions (Dim 1 hereafter 'brooding vs others', 52.98% of variance; and Dim 2 hereafter called 'nestling period forage vs preening', 14.19% of variance). On both 'incubation vs others' and 'brooding vs others', negative values indicate more time spent on the nest (incubating eggs or brooding chicks) than other behaviours. For both 'incubation period forage vs preening' and 'nestling period forage vs preening', negative values indicate more time spent preening while positive values indicate more time spent foraging. For full CA results, see Appendix Figures A1 and A2, and Tables A1–A4.

Eigenvalues associated with the uncorrelated axes from both CAs were extracted and used as response variables in subsequent linear mixed models (LMMs with Gaussian error structure and an identity link-function, using *lme4*) to explore the effects of day status, time of day, and sex on starling behaviour, as well as age of chick for the nestling period only. To determine significance of explanatory variables, p values were calculated using the Satterthwaite approximation for degrees of freedom, available in the R package *lmerTest* (Kuznetsova et al. 2017).

Nestling mass LMM

Lastly, an LMM with Gaussian error distribution and an identity link-function was used to test whether variation in nestling mass at day 15 post hatching could be explained by the number of week days experienced by chicks over the prior nestling period. Brood size was added into the model to check for any patterns associated with adults provisioning multiple chicks, and Nest ID was incorporated as a random term.

Results

Incubation period

During the incubation period I obtained behavioural data from 45.6 hours of focal observations from nine males and nine females. On average, I obtained 15.5 ± 0.84 mins of focal data per individual (excluding the time birds were out of sight). A total of 89 nest watches were performed on 10 nests with an average of 59.93 ± 0.07 mins of nest watch data obtained per nest.

For almost all the variables I tested from incubation period data, there were no differences between week days and weekends (Table 3). Thus, I found no differences between incubation bout length, provisioning rates of the male to the incubating female (i.e. the number of items provisioned per nest watch), foraging effort in terms of the amount of time spent foraging vs other behaviours, foraging efficiency (the number of items captured per minute foraging), food capture rates (the number of items captured per focal minute), and the amount of food captured that was anthropogenic. The only variable that did differ according to day status was the proportion of captured food that males provided to the female (rather than consuming themselves) (Table 3, model (h)), which was 14 times larger on weekends than on week days (Table A5, Fig. 2a).

Time of day and the sex of adults explained a significant amount of variation in some of the tested variables. Provisioning rates of males to incubating females were related to time of day (Table 3, model (b)), with five times as many items delivered in the morning and early afternoon than late afternoon (Table A5, Fig. A3). Post-hoc tests showed that both late afternoon–morning (estimate = -0.10, $p = 0.03$) and early afternoon–late afternoon (estimate = 1.69, $p = 0.02$) pairwise comparisons were statistically significant (Table A6).

Table 3: Results from GLMMs performed on incubation period data. All interaction terms were non-significant and were thus removed. Models (a)–(c) correspond with nest watch data (hence sex was not included in the models, because in (a) only females incubate, and (b) only males provisioned to the incubating female); (d)–(h) with focal observation data (sex included in (d)–(g) as observations were conducted on both males and females, but not (h) as only males provisioned to incubating females). All models included Nest ID and Week ID as random terms. Significant p-values indicated in bold.

Analysis			
Explanatory variable	χ^2	df	p-value
(a) Incubation bout lengths			
Day status	0.32	1	0.57

Time of day	5.12	2	0.08
(b) Provisioning rate			
Day status	0.62	1	0.43
Time of day	7.48	2	0.02
(c) Anthropogenic vs natural food provisioning			
Day status	1.97	1	0.16
(d) Foraging effort			
Day status	1.92	1	0.16
Time of day	0.97	2	0.62
Sex	7.87	1	<0.01
(e) Foraging efficiency			
Day status	0.42	1	0.52
Time of day	2.81	2	0.24
Sex	2.43	1	0.12
(f) Food capture rate			
Day status	0.07	1	0.79
Time of day	1.24	2	0.54
Sex	1.11	1	0.29
(g) Anthropogenic food capture			
Day status	0.32	1	0.57
Time of day	3.01	2	0.22
Sex	11.86	1	<0.001
(h) Captured food provisioned			
Day status	12.32	1	<0.001
Time of day	9.37	2	0.01

During the incubation period, males spent significantly more time foraging than females (Table 3, model (d); Fig. A4), and captured almost exclusively anthropogenic food (mean proportion food captured that was anthropogenic in origin \pm s.e. = 0.99 ± 0.02) while females showed the opposite pattern, capturing almost no anthropogenic food, only natural food (0.0006 ± 0.01) (Table A5). Males also provisioned a significantly larger proportion of captured items in the late afternoon compared with both the morning and early afternoon (Table A6, Fig. 2b).

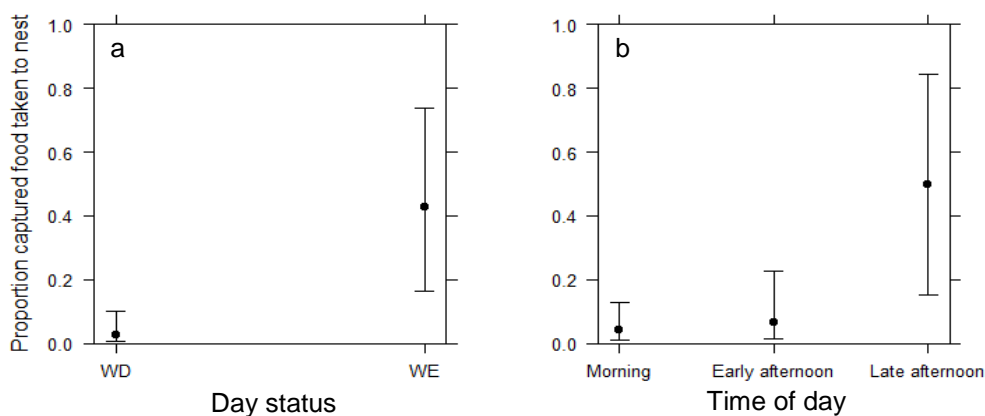


Figure 2: Captured food provisioned during incubation period. Mean proportion of food captured by the male that was provisioned to the female as opposed to eaten (a) on week days

(WD) and weekends (WE), and (b) in the morning, early afternoon, and late afternoon. Upper and lower 95% confidence intervals are displayed.

Nestling period

During the nestling period I obtained behavioural data from 35.9 hours of focal observations from 15 males and 15 females. On average, I obtained 12.2 ± 0.63 mins of focal data per individual (excluding the time birds were out of sight). A total of 91 nest watches were performed on 15 nests with an average of 59.9 ± 0.07 mins of nest watch data obtained per nest.

Similar to the incubation period, I found no differences in many of the variables in relation to day status. Thus, there were no differences between week days and weekends in brooding bout lengths, provisioning rates of both parents to chicks, the amount of provisioned food anthropogenic in origin, foraging efficiency (the number of items captured per minute foraging), food capture rate (the number of items captured per focal minute), and the amount of captured anthropogenic food that was provisioned as opposed to eaten.

However, day status did have an effect on a number of the tested variables, often as part of an interaction with either nestling age or time of day (Table 4). Provisioning rates were affected to an extent – birds provisioned their chicks with a greater amount of anthropogenic food on week days than weekends (Table A7), as would be expected, but this difference was non-significant overall (Table 4, model (c)). The interaction between day status and nestling age had a significant effect on foraging effort (Table 4, model (d)), where the proportion of time spent foraging increased with increasing chick age on week days, whereas on weekends, time spent foraging was the same when chicks were in weeks one and two of their lives, but decreased in week three (Fig. 3). The interaction between day status and nestling age was also related to anthropogenic food capture where more anthropogenic food was captured in the second week of chicks’ lives than the first or third on both week days and weekends (Fig. 4b).

Table 4: Results from GLMMs performed on nestling period data. Only significant interaction terms were retained in models. Models (a)–(c) correspond with nest watch data (sex was not included in these models as data were collected per nest watch as opposed to per individual); (d)–(j) with focal observation data. All models included Nest ID and Week ID as random terms. Significant p-values indicated in bold.

Analysis			
Explanatory variable	χ^2	df	p-value
(a) Brooding bout lengths			
Day status	0.64	1	0.42

Time of day	1.42	2	0.49
Nestling age	14.6	2	<0.001
(b) Provisioning rate			
Day status	0.89	1	0.34
Time of day	16.84	2	<0.001
Nestling age	8.46	2	0.01
(c) Anthropogenic vs natural food provisioning			
Day status	3.66	1	0.06
Time of day	9.5	2	<0.01
Nestling age	1.77	2	0.41
(d) Foraging effort			
Day status	2.69	1	0.1
Time of day	0.27	2	0.87
Sex	9.51	1	<0.01
Nestling age	1.54	2	0.46
Day status*Nestling age	7.62	2	0.02
(e) Foraging efficiency			
Day status	0.39	1	0.53
Time of day	11.35	2	<0.01
Sex	5.22	1	0.02
Nestling age	16.41	2	<0.001
(f) Food capture rate			
Day status	0.46	1	0.5
Time of day	0.73	2	0.69
Sex	3.59	1	0.06
Nestling age	1.57	2	0.46
(g) Anthropogenic food capture			
Day status	4.95	1	0.03
Time of day	15.14	2	<0.001
Sex	15.43	1	<0.001
Nestling age	18.55	2	<0.001
Day status*Nestling age	6.65	2	0.04
(h) Captured food provisioned vs eaten			
Day status	2.62	1	0.1
Time of day	15.21	2	<0.001
Sex	0.01	1	0.95
Nestling age	2.94	2	0.23
Day status*Time of day	17.74	2	<0.001
(i) Anthropogenic food provisioned vs eaten			
Day status	0.74	1	0.39
Time of day	4.55	2	0.1
Sex	0.19	1	0.66
Nestling age	2.36	2	0.31
(j) Natural food provisioned vs eaten			
Day status	7.22	1	<0.01
Time of day	1.3	2	0.52
Sex	0.05	1	0.82
Nestling age	6.97	2	0.03

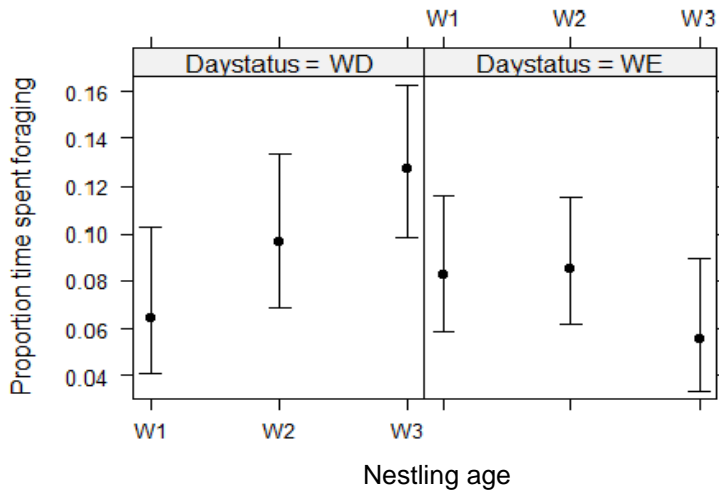


Figure 3: Foraging effort during the nestling period. Mean proportion of time spent foraging as opposed to other activities as a function of the interaction between day status (week day, WD; weekend, WE) and three nestling age classes (week one, W1; week two, W2; week three, W3). Upper and lower 95% confidence intervals are displayed.

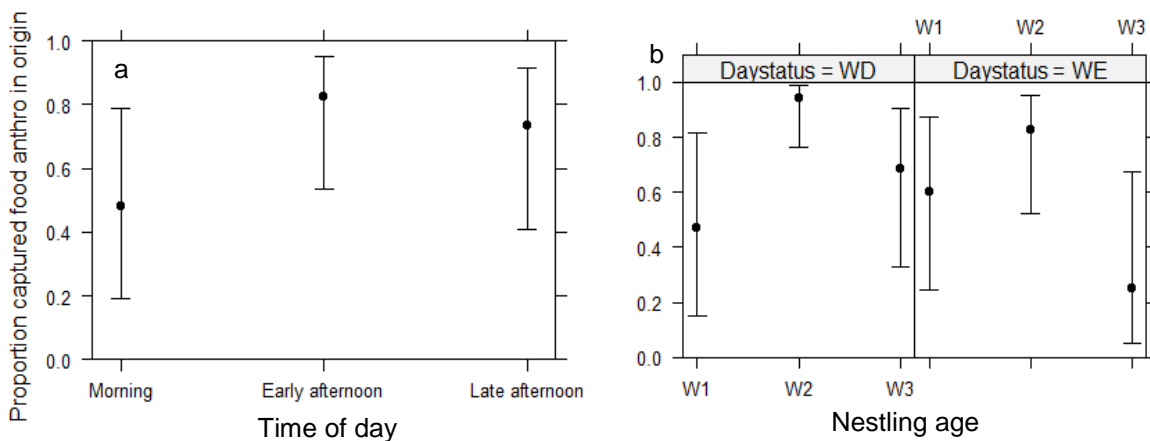


Figure 4: Anthropogenic food capture during the nestling period. Mean proportion of food captured that was anthropogenic vs natural in origin (a) in the morning, early afternoon, and late afternoon, and (b) as a function of the interaction between day status (week day, WD; weekend, WE) and three nestling age classes (week one, W1; week two, W2; week three, W3). Upper and lower 95% confidence intervals are displayed.

The interaction between day status and time of day explained a significant amount of variation in one analysis involving decision-making by parents (Table 4, model (h)). Parents provisioned a much smaller proportion of all captured food to the nest on weekends in the late afternoon when compared with all other combinations of day status and time of day (Fig. 5). None of the explanatory variables investigated explained a significant amount of variation in the proportion of captured anthropogenic food that was provisioned rather than eaten; however, both day status and nestling age significantly affected the proportion of captured natural food that was

taken to the nest instead of consumed by parents (Table 4, model (j)). On week days, parents provisioned nearly three times the amount of the natural food they captured than on weekends (Table A7, Fig. 6a), and chicks in week three of their lives received a smaller proportion of the natural food their parents captured than those in weeks one and two (Table A7, Fig. 6b).

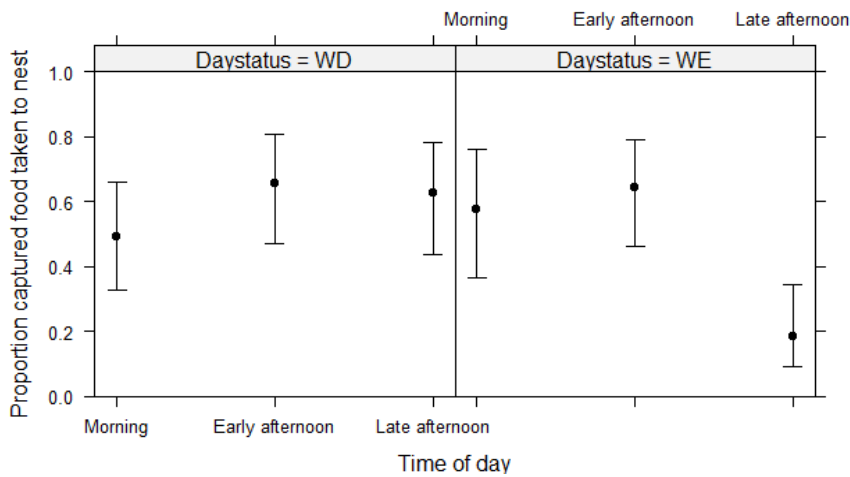


Figure 5: Captured food provisioned to chicks during nestling period. Mean proportion of food captured by parents that was taken to the nest as opposed to eaten as a function of the interaction between day status (week day, WD; weekend, WE) and time of day (morning, early afternoon, and late afternoon). Upper and lower 95% confidence intervals are displayed.

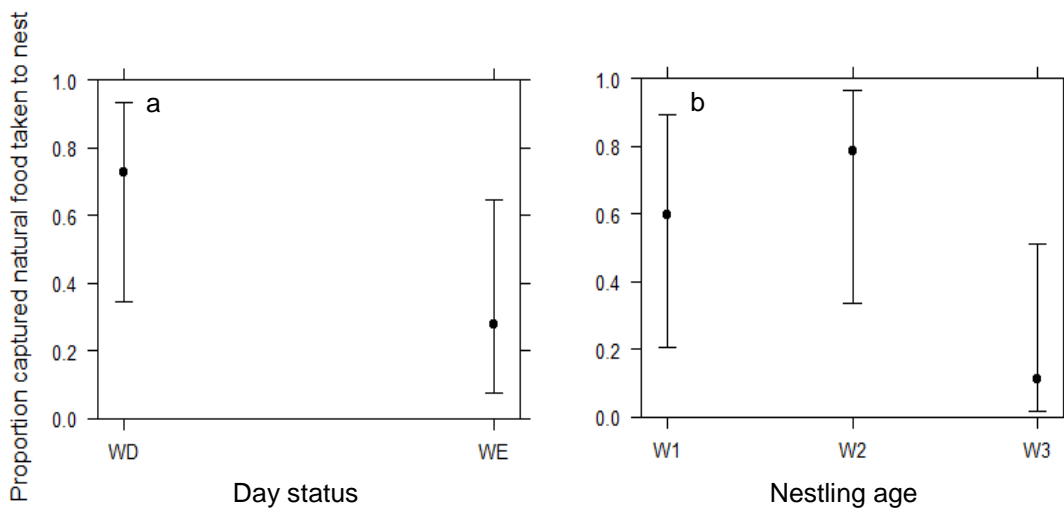


Figure 6: Natural food provisioned to chicks during nestling period. Mean proportion natural food captured that was taken to the nest instead of eaten (a) on week days (WD) and weekends (WE), and (b) when chicks were in one of three age classes (week one, W1; week two, W2; week three, W3). Upper and lower 95% confidence intervals are displayed.

The age of nestlings explained a significant amount of variation in a number of the variables tested, as did time of day and sex of adult (Table 4). The proportion of time females spent

brooding chicks during the nestling period was significantly related to the age class of chicks (i.e. week 1, week 2, or week 3 of age; Table 4, model (a)). Brooding bouts decreased with increasing age of nestlings, with females spending only 6% of their time brooding chicks in the third week of their lives (Table A7, Fig. A5). Post-hoc tests showed that this differed significantly from time spent brooding chicks in weeks one (estimate = 1.98, $p < 0.001$) and two (1.18, $p = 0.04$; Table A8). Provisioning rates of parents to chicks were also related to age class, where significantly fewer items were provisioned per nest watch during week one than week two (estimate = -0.31, $p = 0.01$; Table A8, Fig. A6a). Time of day was also strongly related to provisioning rates (Table 4, model (b)). Post-hoc tests showed this effect was attributable to a significantly larger number of items being provisioned in the morning (estimate = -0.45, $p < 0.001$) and early afternoon (estimate = 0.42, $p < 0.001$) compared with late afternoon (Table A8, Fig. A6b).

A smaller proportion of anthropogenic food was captured by parents in the morning than in both early (estimate = 1.61, $p < 0.001$) and late afternoon (estimate = 1.07, $p = 0.01$; Table A8, Fig. 4a). Birds thus provisioned a significantly lower proportion of anthropogenic food in the morning (mean \pm s.e. = 0.31 ± 0.07) compared with early afternoon (0.50 ± 0.08) and late afternoon (0.49 ± 0.09 , Table A7, Fig. A7). Foraging effort differed between sexes with males spending a significantly greater proportion of their time foraging; however, females were more efficient than males, capturing a greater number of beakfuls per minute spent foraging. Females also captured a greater proportion of anthropogenic food, on average, than males (estimate = 1.18, $p < 0.001$; Table A8), an opposite pattern to that observed during the incubation period where females captured almost no anthropogenic food at all (Fig. A8). Foraging efficiency was significantly related to both age of chicks and time of day (Table 4, model (e)). This was due to parents capturing significantly fewer beakfuls per minute foraging in the third week of chicks' lives than in the earlier two, and significantly fewer in the early afternoon than late afternoon (Table A8, Fig. A9).

Analyses of time budgets

In the correspondence analysis (CA) performed on data collected during the incubation period, Dimension 1, ('incubation vs others') separated the behaviour 'on nest' from all other behaviours, and Dimension 2 ('incubation period forage vs preening') strongly separated the behaviours 'preening' and 'forage' (Table A2, Fig. A1). The two LMMs performed on eigenvalues associated with 'incubation vs others' and 'incubation period forage vs preening',

respectively, indicated that there were no differences in overall behavioural time budgets between week days and weekends (Table 5). There were, however, significant sex-specific differences in behaviour related to ‘incubation vs others’ where females exhibited, on average, lower values than males, and so spent more time on the nest, in relation to other behaviours, than males (Table 5, Fig. 7b). Although non-significant overall, a clear pattern emerged with regards to time of day where smaller values associated with ‘incubation vs others’ were present in the early afternoon than both morning and late afternoon (Fig. 7c). The variation in eigenvalues associated with ‘incubation period forage vs preening’ was not explained by any of the variables investigated (Table 5).

Similar patterns were observed in the CA performed on nestling period data for both dimensions. Again, time budgets did not differ between week days and weekends (Table 6, Fig. 8a), and there were no differences related to time of day (Table 6, Fig. 8c). Females had lower values associated with ‘brooding vs others’ (i.e. on nest) than males (Table 6, Fig. 8b). Additionally, age of nestlings explained a significant amount of variation in ‘brooding vs others’ (Table 6). As nestling age increased, the values on ‘brooding vs others’ were more positive, indicating that less time was allocated to brooding chicks and more time allocated to other behaviours as chicks aged (Fig. 8d). The variation in ‘nestling period forage vs preening’ was, again, not explained by any of the variables investigated (Table 6).

Table 5: Results from LMMs performed on eigenvalues associated with ‘incubation vs others’ and ‘incubation period forage vs preening’ extracted from the CA performed on birds’ activity budgets during the incubation period. Significant p-values indicated in bold.

Explanatory variable	χ^2	df	p-value
incubation vs others			
Day status	0.39	1	0.53
Time of day	5.63	1	0.06
Sex	1930.94	2	<0.001
incubation period forage vs preening			
Day status	1.07	1	0.30
Time of day	1.75	1	0.42
Sex	0.99	2	0.32

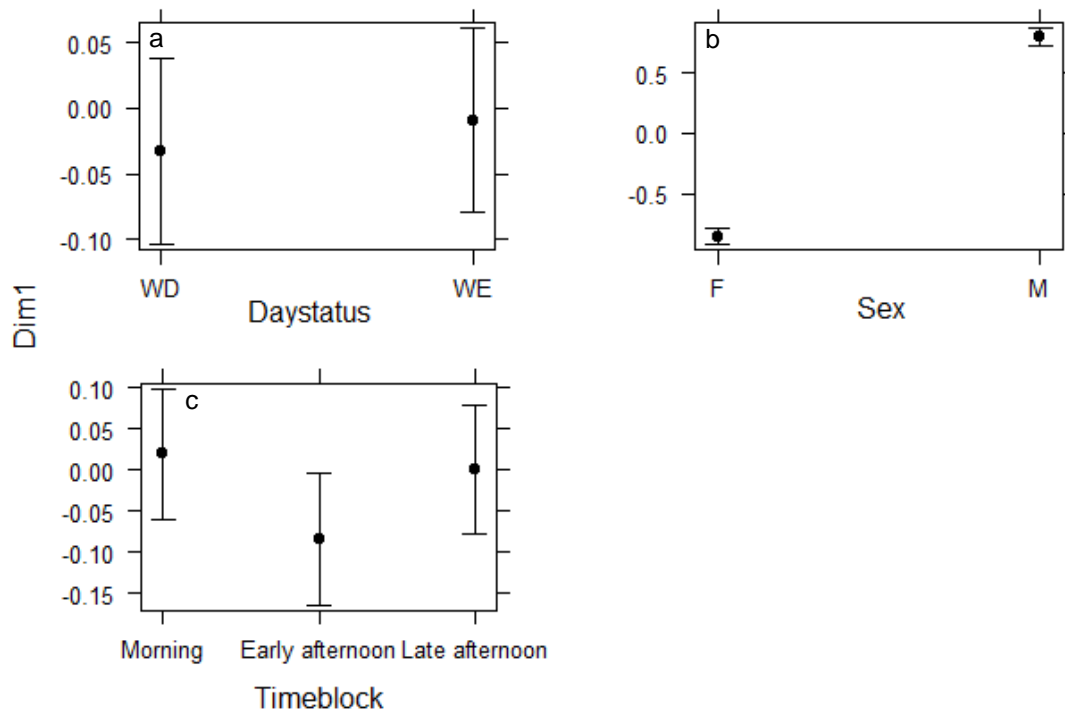


Figure 7: Mean eigenvalues associated with Dimension 1 (‘incubation vs others’) of the incubation period CA according to (a) week days (WD) and weekends (WE), (b) sex, and (c) time of day. Upper and lower 95% confidence intervals are displayed.

Table 6: Results from LMMs performed on eigenvalues associated with ‘brooding vs others’ and ‘nestling period forage vs preening’ extracted from the CA performed on birds’ activity budgets during the nestling period. Significant p-values indicated in bold.

Explanatory variable	χ^2	df	p-value
brooding vs others			
Day status	2.49	1	0.11
Time of day	0.38	1	0.83
Sex	132.59	2	<0.001
Nestling age	17.46	2	<0.001
nestling period forage vs preening			
Day status	0.49	1	0.48
Time of day	0.79	1	0.67
Sex	0.01	2	0.95
Nestling age	0.74	2	0.69

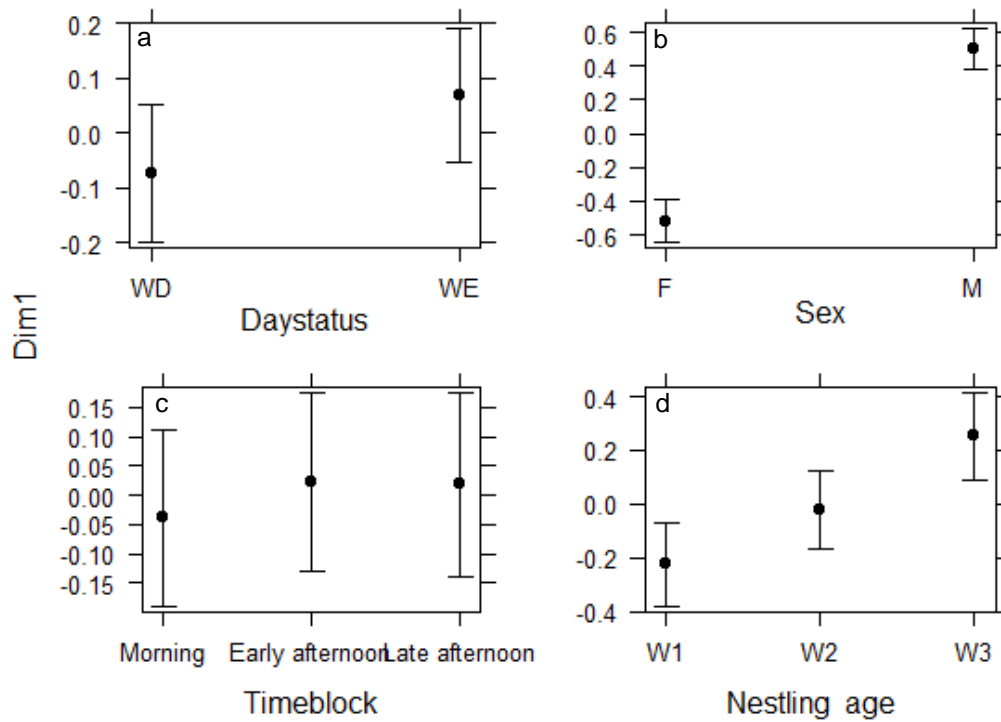


Figure 8: Mean eigenvalues associated with Dimension 1 (‘brooding vs others’) of the nestling period CA according to (a) week days (WD) and weekends (WE), (b) sex, (c) time of day, and (d) nestling age classes (week one, W1; week two, W2; week three, W3). Upper and lower 95% confidence intervals are displayed.

Nestling mass

There was no indication that nestling mass was influenced by the number of week days experienced by nestlings prior to measurement of mass at ~day 15 of age ($p = 0.35$) nor by the brood size ($p = 0.56$) (Fig. 9).

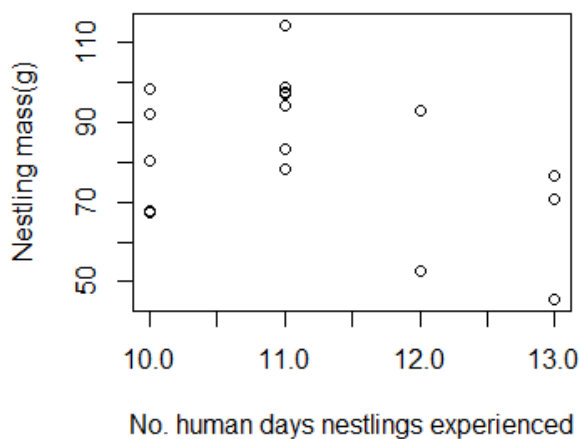


Figure 9: Individual nestling mass at approximately day 15 post hatching plotted against the number of week days experienced by each nestling prior.

Discussion

This study is one of the first studies to explore how an urban population of birds adjusts behaviourally to highly fluctuating anthropogenic food supplies. I studied selected birds from a single population whereas most work in avian urban ecology has drawn comparisons between urban and rural populations within species (reviewed in Chamberlain et al. 2009). This approach largely eliminates several confounding factors such as location and individual bird identity, but teasing apart the impacts of a constantly and rapidly fluctuating food resource is a complex task. Several of my results showed that day status (days on which anthropogenic food was highly available, or otherwise scarce) did impact the behaviour and parental care of Red-winged Starlings; however, other variables, notably time of day, sex of focal birds and the age of their nestlings, also influenced the observed behavioural patterns – in many cases to a larger extent than day status.

During the incubation period, and contrary to what was predicted, I did not detect any evidence of an effect of day status on the amount of time birds spent foraging, or the amount of time females spent incubating eggs. This indicated that, despite increased food availability on week days, females did not appear to specifically exploit this resource. I expected that females would allocate less time to foraging on week days, freeing up more time for parental care in the form of increased length or frequency of incubation bouts. Red-winged Starling females in more natural settings usually incubate eggs throughout the night and do not leave the nest unattended for more than 45 minutes at a time during the day (Rowan 1955), a pattern which was also observed in this study. During the nestling period, brooding bouts were also unaffected by day status, indicating that these forms of parental care seem not to be influenced by changes in food availability of the magnitude that occurred during my study.

During the nestling period, several results indicated a relative food shortage on weekends, specifically in anthropogenic food; this impacted parental decision-making. On weekends, parents provisioned a smaller proportion of all captured food to nestlings than on week days, especially in the late afternoon. Additionally, nestlings received less anthropogenic food on weekends. This suggests that parents might have been less able to fulfil their energetic requirements on weekends and therefore needed to prioritise themselves instead of provisioning their chicks. Evolutionary theory of parent-offspring conflict suggests that if parents are unable to replenish the resources they invest in their offspring on a daily basis, the costs of this depletion will increase disproportionately with time (Trivers 1974). Therefore, following this scenario of limited food resources on weekends, parents might trade parental

investment for self-maintenance. Birds in this study experienced fluctuations in food availability over short timescales which might actually benefit them since this trade-off is relaxed on week days and thus does not need to occur over extended periods of time (seldom more than two days consecutively).

Day status also had a significant effect on the amount of natural food captured and fed to nestlings. Thus, contrary to my predictions, parents showed a preference to feed their nestlings natural food on week days despite the increased availability of anthropogenic food. Other studies have also shown that parents prefer to feed nestlings natural food when it is available (Cowie and Hinsley 1988; Mennechez and Clergeau 2001). There is also empirical evidence that nutritional deficits in early nestling development can have severe negative consequences for long-term health (Metcalf and Monaghan 2001). Thus, diet may contribute to a shorter lifespan for birds raised in urban areas and exposed to anthropogenic food as nestlings (Salmón et al. 2016; Ibáñez-Álamo et al. 2018). Therefore, on week days, parent starlings in my study system may use anthropogenic food to supplement their own diets in order to prioritise the feeding of natural food to young chicks. This was additionally supported by the fact that older chicks received a smaller proportion of natural food captured by their parents than those in the first two weeks of their lives. This pattern has also been observed in other studies, possibly because older chicks are more resilient to a diet high in anthropogenic food than those in early nestling developmental stages (Cowie and Hinsley 1988).

Multiple studies comparing urban and rural bird populations have demonstrated that nestlings reared in urban environments receive insufficient food loads and have smaller masses at fledging than conspecifics raised in more natural areas (e.g., Mennechez and Clergeau 2006; Newhouse et al. 2008; Meillère et al. 2015). In this study, provisioning rates did not differ between week days and weekends, and parents preferentially fed their nestlings natural food. Nestlings who experienced the greatest number of week days did appear to have smaller masses than those who experienced the least, but this correlation was not significant, although this may have been due to a lack of power in the analysis.

Even if no correlation exists, however, this does not mean that nestlings in this population experience no negative impacts due to the anthropogenic food that they receive. Nutritional deficits in early development stages have been shown to negatively influence health traits independent of body mass such as fatty acid profiles (Toledo et al. 2016), carotenoid-based colouration (Sumasgutner et al. 2018), or plasma cholesterol levels (Gavett and Wakely 1986) which all reflect a differential diet between urban and rural populations. Longer term effects

such as impacts on fecundity and survival can also be influenced by dietary differences (reviewed in Metcalfe and Monaghan 2001). For example, an urban diet was linked to lower breeding success in Blue Tits (Pollock et al. 2017) and to telomere shortening in Great Tits raised in an urban environment, an indication of cellular senescence (Salmón et al. 2016). The same study showed selective disappearance of individuals with shorter telomeres (Salmon et al. 2017). In this urban population, a wider spectrum of parameters related to nestling health must be considered in relation to anthropogenic food variability to more thoroughly tease apart the impact this diet might have on individual health.

In addition to the effect of day status, I also found significant sex-specific differences in the behaviour of breeding Red-winged Starlings. For example, males spent significantly more time foraging than females during both incubation and nestling periods, while females prioritised incubating eggs or brooding chicks. In species with bi-parental care, behavioural plasticity is often observed where individuals adjust their investment in reproduction to partially compensate for their partner (Harrison et al. 2009). This may be the case in this population, where males increase their foraging effort to compensate for females who allocate more time to incubating eggs and brooding chicks.

Interestingly, during the nestling period, females were much more efficient than males when they did spend time foraging, capturing a greater number of beakfuls per minute. However, provisioning rates to chicks did not differ between males and females, suggesting that males and females were capturing a similar number of items – females were just doing it more quickly. It is unclear exactly as to why this pattern emerged as, presumably, parents would capture a food item whenever encountering one. If so, perhaps females were just luckier than males during their foraging trips. Alternatively, a possible anecdotal explanation for this trend is something I observed several times during the study: when finding a large food resource, males would often provision some of it to chicks in the nest with a brooding female, after which she would follow him back to the resource, thereby eliminating foraging effort and maximising her efficiency. This maximisation occurred several times throughout the study and may have been enough to result in the significant difference between males' and females' foraging efficiency.

There were also nestling age-mediated impacts on parental behaviour. Similar to what has been observed in other bird species, provisioning rates to nestlings differed depending on their age. Chicks in week one of their lives were provisioned significantly less than those in weeks two and three, corresponding with the S-shaped growth curve exhibited by passerines (Ricklefs

1968). Newly-hatched chicks require less food than those in the second weeks of their lives where growth rates increase, but growth rates then begin to decrease mid-development and eventually level off (Ricklefs 1968). Chicks in week three require more food than week one chicks due to their larger size. Other studies have also demonstrated increased feeding rates to older chicks, and that as provisioning rates increase, time spent brooding decreases, a pattern observed in this study as well (Newhouse et al. 2008).

Time of day effects, which were also observed in this study, indicate that fluctuating availability of anthropogenic food influences temporal patterns of provisioning of this resource on a within-day scale as well as according to day status (between-day scale). Parents provisioned a significantly larger number of items to nestlings in the early afternoon than late afternoon, coinciding with a potentially greater abundance of food at lunch time. During the incubation period, males provisioned more of their captured food to females in the late afternoon, but fewer items overall when compared with the morning and early afternoon. This indicates a lower abundance of food in general in the late afternoon, as foraging effort was no different during this time period. It may also indicate that males prioritised feeding females over themselves in the late afternoon, contradicting the pattern observed in the nestling period where parents provisioned less of their captured food to nestlings. This could be because males' required levels of energy reserves had been fulfilled by this point (Bonter et al. 2013). There were several gaps in data from birds foraging out of sight, which may be preventing the teasing apart of the mechanism behind these results.

Indeed, one of the main limitations of this study was an inability to monitor starlings' behaviour when they were out of sight. During the nestling period I observed that parents would fly away from the nest and disappear for much longer periods of time than during the incubation period, usually returning with large arthropods such as stick insects or mantises, as well as natural berries which they would provision to their chicks. While these deliveries were captured in nest watch data, I was unable to obtain any information regarding foraging effort and efficiency, or decision-making by parents while they were out of sight. While this is unavoidable in studies concerning highly mobile animals, this lack of data may have influenced my results. For example, conclusions made about decision-making by adults were limited in these cases, as I could not determine how many items parents were capturing out of sight, and what proportion of these were being delivered to chicks.

While this behaviour may have limited some of the conclusions I could make, it may also be common among birds. A previous study found that the mean traveling distance of adult Blue

Tits was twice as great in a resource-poor habitat than a resource-rich one, indicating that adults compensate for decreased local food abundance by increasing their foraging range to ensure their chicks receive adequate food (Tremblay et al. 2005). My study suggests a similar pattern of behaviour demonstrated by the increased time and energy adults invested to access the natural prey items they preferred feeding their chicks.

Another area of interest which could be incorporated in future studies, and would enhance our understanding of this system, would be to examine body condition of adults throughout the breeding period by measuring daily mass gain as well as other health indicators. This could provide information about how parents use these fluctuating anthropogenic food resources, how it affects their body condition, and whether this influences parental investment. For example, a study performed on Sooty shearwaters (*Puffinus griseus*) found that adult body mass plays a central role in foraging decisions, affecting whether parents decide to feed close to or far from the colonies, and allocate more energy to feeding chicks or to storing their own body reserves (Weimerskirch 1998).

Similarly, a study examining provisioning behaviour in the Antarctic petrel (*Thalassoica antarctica*) found that parents in good body condition provisioned larger meals to chicks, and provisioned more food to small than large chicks than parents in poor body condition (Tveraa et al. 1998). Results from this study suggest that adult body condition determines, to a certain extent, whether parents can adjust the amount of food they provision to their chicks based on their chicks' and their own needs. If this pattern holds true in this population of starlings, it could contribute to understanding variables such as chick body mass and fledging success. By gathering information at what is effectively the source, we may be able to grasp more strongly some of the mechanisms at work in this system.

Additionally, this study only focused on the first brood of one breeding season of this population of starlings. There could therefore be seasonal variation in the parameters investigated, as well as differences between first, second, and subsequent broods within a season. Growth rates of nestlings, for example, have been shown to vary markedly within populations due to seasonal effects (Ricklefs 1968). Current and future predicted climate change may also impact several of the variables of interest such as birds' activity budgets and decision-making. Warmer and drier conditions are predicted for the Western Cape of South Africa, within which Cape Town is located. These effects are already apparent in many areas (Tyson et al. 2002). During the study period, behaviours associated with heat stress such as panting and wing-drooping were observed. If parents must allocate increasing energetic

resources to these behaviours, their investment in parental care may suffer. Indeed, previous studies have shown that birds make trade-offs between provisioning behaviour and their own thermoregulatory needs in extremely hot environments (Luck 2001; Cunningham et al. 2013; Wiley and Ridley 2016). Therefore, a long-term study in this system would be useful to investigate all these potential impacts.

The results from this study provided some support for my hypotheses that Red-winged Starling adults exploit anthropogenic food resources on week days, and that this influenced parental care behaviour. Importantly, however, they also showed that, when possible, starlings preferentially feed their nestlings natural food – a finding similar to that seen in studies of other urban passerines (Cowie and Hinsley 1988; Mennechez and Clergeau 2001). In spite of this, parent birds in this population clearly do make use of anthropogenic food resources to fulfil their own energy requirements as well as some of their chicks', and the effect of this diet on both parents and offspring is as yet unknown. Further research should focus on the relative nutritional value of anthropogenic and natural food in this system, and its subsequent effects on the health of these urban adapters. This would aid in establishing whether these birds are experiencing negative impacts, or whether they truly thrive in the urban environment.

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Appendix

Table A1: The percentage of variance explained by each dimension in the CA performed on birds' activity budgets during the incubation period.

Dimension	% variance explained
Dim1 (incubation vs others)	57.82
Dim2 (incubation period forage vs preening)	15.47
Dim3	12.85
Dim4	9.29
Dim5	3.40
Dim6	1.17

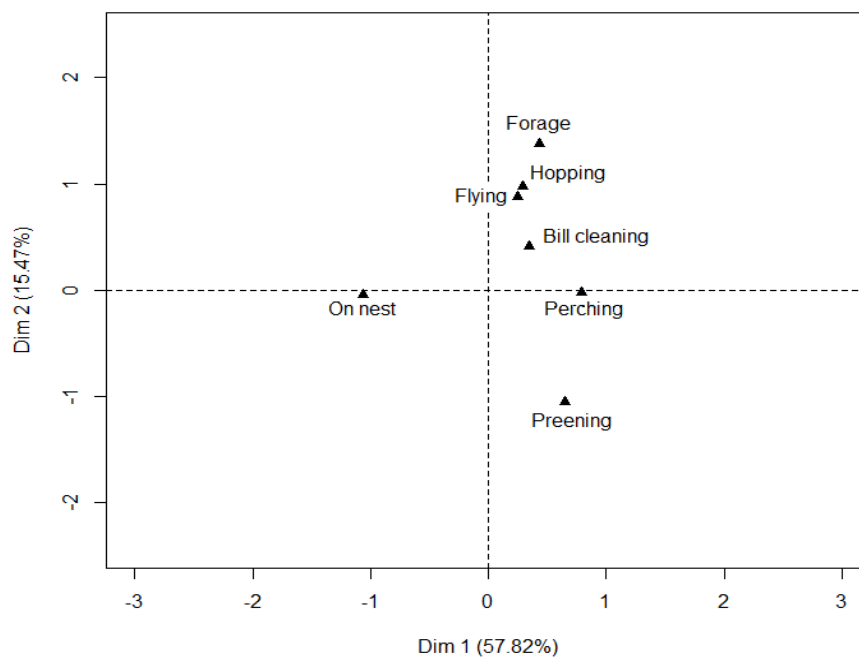


Figure A1: CA ordination diagram with predominant starling behaviours exhibited during the incubation period. For direction and strength of featured behaviours, see Table A2.

Table A2: The direction and strength of each parameter featured in 'incubation vs others' and 'incubation period forage vs preening' from the CA performed on birds' activity budgets during the incubation period.

Parameters	incubation vs others	incubation period forage vs preening
Perching	0.7839	-0.0206
Forage	0.4365	1.3782
Bill cleaning	0.3405	0.4124

Flying	0.2481	0.8786
Hopping	0.2867	0.9737
On nest	-1.0593	-0.0498
Preening	0.6461	-1.0536

Table A3: The percentage of variance explained by each dimension in the CA performed on birds' activity budgets during the nestling period.

Dimension	% variance explained
Dim1 (brooding vs others)	52.98
Dim2 (nestling period forage vs preening)	14.19
Dim3	13.01
Dim4	8.47
Dim5	7.05
Dim6	2.80
Dim7	1.50

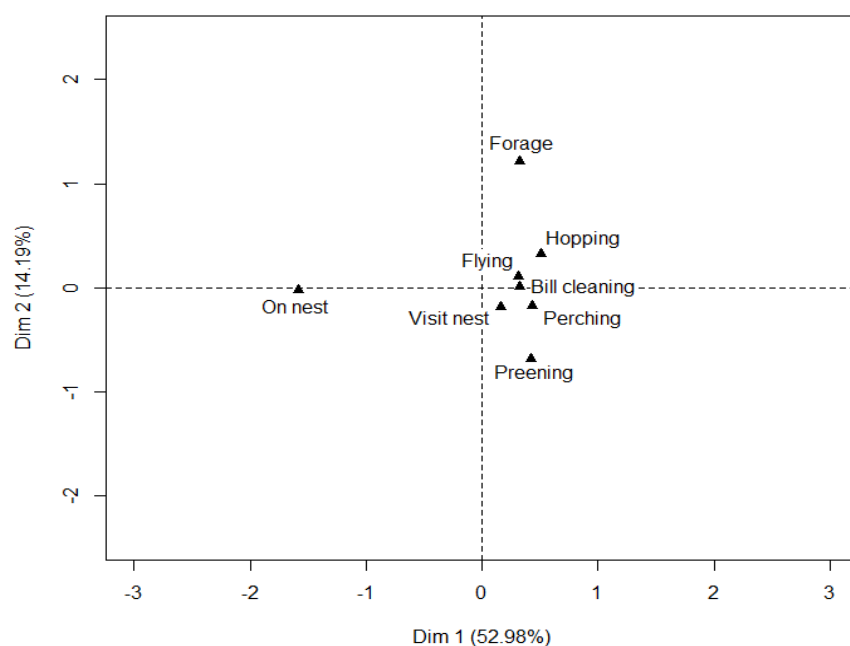


Figure A2: CA ordination diagram with predominant starling behaviours exhibited during the nestling period. For direction and strength of featured behaviours, see Table A4.

Table A4: The direction and strength of each parameter featured in 'brooding vs others' and 'nestling period forage vs preening' from the CA performed on birds' activity budgets during the nestling period.

Parameters	brooding vs others	nestling period forage vs preening
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Forage	0.3198	1.2109
Bill cleaning	0.3083	0.1105
Flying	0.3267	0.0070
Hopping	0.5075	0.3206
On nest	-1.5813	-0.0224
Preening	0.4230	-0.6885
Visit nest	0.1613	-0.1880
Perching	0.4339	-0.1776

Table A5: Estimated least square means and standard errors obtained from GLMMs performed on data collected during the incubation period.

Response variable	Day status				Time of day						Sex			
	Week day		Weekend		Morning		Early afternoon		Late afternoon		Female		Male	
	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error
Time female spent on vs off nest	0.69	0.02	0.7	0.02	0.68	0.02	0.74	0.02	0.66	0.02				
No. items provisioned during nest watch	0.24	0.08	0.32	0.1	0.46	0.14	0.51	0.14	0.09	0.05				
No. anthropogenic vs natural food items provisioned per nest watch	0.74	0.26	0.13	0.15										
Time spent foraging vs not foraging	0.03	0.01	0.02	0.01	0.03	0.01	0.02	0.01	0.03	0.01	0.02	0.01	0.03	0.01
No. beakfuls food captured per min foraging	4.64	0.76	4.01	0.64	4.56	0.84	5.3	1.1	3.32	0.66	5.16	0.89	3.6	0.55
No. beakfuls food captured per focal min	0.01	0.01	0.02	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.01
No. captured food items of anthropogenic vs natural origin	0.12	1.5	0.69	2.23	0.0004	0.01	0.93	0.66	0.97	0.32	0.0006	0.01	0.99	0.02
No. captured food items taken to nest vs swallowed by adult	0.03	0.02	0.42	0.16	0.04	0.02	0.06	0.04	0.49	0.22				

Table A6: Summary of post-hoc tests for all linear contrasts of GLMMs performed on data collected during the incubation period.

Response variable	Day status			Time of day						Sex of adult					
	Weekday-Weekend			Early afternoon-Late afternoon			Early afternoon-Morning			Late afternoon-Morning			Female-Male		
	Estimate	Std. error	p-value	Estimate	Std. error	p-value	Estimate	Std. error	p-value	Estimate	Std. error	p-value	Estimate	Std. error	p-value
Time female spent on vs off nest	-0.08	0.13	0.57	0.36	0.16	0.07	0.26	0.17	0.26	-0.10	0.16	0.82			
No. items provisioned during nest watch	-0.28	0.35	0.43	1.69	0.63	0.02	0.11	0.37	0.96	-1.59	0.63	0.03			
No. anthropogenic vs natural food items provisioned per nest watch	2.94	2.10	0.16												
Time spent foraging vs not foraging	0.32	0.23	0.16	-0.22	0.30	0.73	-0.27	0.28	0.61	-0.05	0.27	0.98	-0.63	0.22	<0.01
No. beakfuls food captured per min foraging	0.14	0.22	0.52	0.47	0.29	0.23	0.15	0.27	0.84	-0.32	0.27	0.47	0.36	0.23	0.12
No. beakfuls food captured per focal min	-0.13	0.50	0.79	0.11	0.62	0.98	-0.53	0.61	0.66	-0.64	0.61	0.55	-0.52	0.50	0.29
No. captured food items of anthropogenic vs natural origin	-2.79	4.91	0.57	-0.93	5.71	0.99	10.34	10.37	0.58	11.28	7.08	0.25	-13.65	3.96	<0.001
No. captured food items taken to nest vs swallowed by adult	-3.24	0.92	<0.001	-2.64	1.03	0.03	0.47	0.75	0.80	3.11	1.03	0.01			

Table A7: Estimated least square means and standard errors obtained from GLMMs performed on data collected during the nestling period. For means pertaining to significant interaction terms see Table A5.

Response variable	Day status		Time of day						Sex				Age of nestling							
	Week day		Weekend		Morning		Early afternoon		Late afternoon		Female		Male		Week 1		Week 2		Week 3	
	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error	Mean	Std. error
Time female spent on vs off nest	0.16	0.04	0.13	0.04	0.11	0.04	0.15	0.05	0.18	0.06					0.3	0.08	0.16	0.05	0.06	0.02
No. items provisioned during nest watch	5.63	0.47	6.12	0.5	6.87	0.61	6.7	0.59	4.39	0.46					4.89	0.49	6.68	0.58	6.18	0.63
No. anthropogenic vs natural food items provisioned per nest watch	0.49	0.08	0.37	0.07	0.31	0.07	0.5	0.08	0.49	0.09					0.4	0.09	0.48	0.08	0.41	0.09
Time spent foraging vs not foraging	0.09	0.01	0.07	0.01	0.08	0.01	0.08	0.01	0.08	0.01	0.07	0.01	0.1	0.01	0.07	0.01	0.09	0.01	0.08	0.01
No. beakfuls food captured per min foraging	2.87	0.47	2.68	0.46	2.75	0.48	2.28	0.39	3.41	0.59	3.08	0.51	2.5	0.4	3.4	0.6	3.22	0.56	1.96	0.37
No. beakfuls food captured per focal min	0.12	0.02	0.1	0.02	0.1	0.02	0.13	0.03	0.1	0.02	0.09	0.02	0.14	0.02	0.09	0.02	0.13	0.03	0.12	0.03
No. captured food items of anthropogenic vs natural origin	0.76	0.12	0.58	0.17	0.46	0.18	0.81	0.11	0.71	0.14	0.79	0.12	0.53	0.17	0.54	0.18	0.9	0.06	0.46	0.19
No. captured food items taken to nest vs swallowed by adult	0.59	0.07	0.44	0.08	0.53	0.08	0.64	0.07	0.38	0.08	0.52	0.08	0.52	0.08	0.45	0.09	0.6	0.08	0.5	0.09
No. captured anthropogenic food items taken to nest vs swallowed by adult	0.65	0.17	0.72	0.16	0.66	0.18	0.78	0.13	0.62	0.18	0.7	0.16	0.67	0.16	0.58	0.21	0.68	0.16	0.79	0.14
No. captured natural food items taken to nest vs swallowed by adult	0.7	0.17	0.26	0.15	0.44	0.21	0.31	0.24	0.68	0.23	0.45	0.21	0.5	0.19	0.6	0.21	0.79	0.17	0.11	0.11

Table A8: Summary of post-hoc tests for all linear contrasts of GLMMs performed on data collected during the nestling period.

Nestling	Day status			Time of day						Sex of adult			Age of nestling											
	Weekday-Weekend			Early afternoon-Late afternoon			Early afternoon-Morning			Late afternoon-Morning			Female-Male			Week 1-Week2			Week 1-Week 3			Week 2-Week 3		
Response variable	Est.	Std. error	p-value	Est.	Std. error	p-value	Est.	Std. error	p-value	Est.	Std. error	p-value	Est.	Std. error	p-value	Est.	Std. error	p-value	Est.	Std. error	p-value	Est.	Std. error	p-value
Time female spent on vs off nest	0.30	0.38	0.42	-0.18	0.45	0.92	0.36	0.45	0.69	0.54	0.47	0.47				0.80	0.44	0.16	1.98	0.52	<0.001	1.18	0.50	0.04
No. items provisioned during nest watch	-0.08	0.09	0.34	0.42	0.12	<0.001	-0.02	0.10	0.96	-0.45	0.12	<0.001				-0.31	0.11	0.01	-0.24	0.13	0.16	0.08	0.11	0.77
No. anthropogenic vs natural food items provisioned per nest watch	0.47	0.25	0.06	0.02	0.31	0.99	0.80	0.28	0.01	0.78	0.32	0.04				-0.34	0.31	0.51	-0.05	0.38	0.99	0.29	0.30	0.60
Time spent foraging vs not foraging	0.26	0.16	0.11	0.18	0.19	0.92	-0.02	0.20	0.99	-0.10	0.20	0.88	-0.47	0.15	<0.01	-0.23	0.20	0.50	-0.16	0.22	0.75	0.07	0.20	0.93
No. beakfuls food captured per min foraging	0.07	0.11	0.53	-0.40	0.12	<0.01	-0.19	0.13	0.30	0.22	0.13	0.22	0.21	0.09	0.02	0.05	0.15	0.94	0.55	0.16	<0.01	0.50	0.14	<0.001
No. beakfuls food captured per focal min	0.17	0.24	0.50	0.19	0.30	0.80	0.24	0.30	0.70	0.05	0.31	0.99	-0.46	0.24	0.06	-0.37	0.30	0.44	-0.28	0.32	0.66	0.09	0.30	0.95
No. captured food items of anthropogenic vs natural origin	0.85	0.37	0.02	0.54	0.40	0.36	1.61	0.43	<0.001	1.07	0.38	0.01	1.18	0.30	<0.001	-2.03	0.56	<0.001	0.30	0.62	0.88	2.33	0.54	<0.001
No. captured food items taken to nest vs swallowed by adult	0.57	0.26	0.03	1.10	0.28	<0.001	0.49	0.27	0.16	-0.61	0.30	0.10	-0.01	0.20	0.95	-0.61	0.37	0.22	-0.24	0.39	0.82	0.38	0.36	0.54
No. captured anthropogenic food items taken to nest vs swallowed by adult	-0.35	0.40	0.39	0.75	0.43	0.19	0.59	0.38	0.27	-0.16	0.52	0.95	0.12	0.28	0.66	-0.40	0.66	0.82	-0.96	0.66	0.31	-0.56	0.54	0.55
No. captured natural food items taken to nest vs swallowed by adult	1.94	0.72	<0.01	-1.55	1.53	0.57	-0.59	1.12	0.86	0.96	0.89	0.52	-0.16	0.71	0.82	-0.92	1.08	0.67	2.45	1.11	0.07	3.38	1.34	0.03

Table A9: Estimated least square means and standard errors for significant interaction terms obtained from GLMMs performed on data collected during the nestling period.

Response variable	Day status*Age of nestling											
	Week day*Week 1		Weekend*Week 1		Week day*Week 2		Weekend*Week 2		Week day*Week 3		Weekend*Week 3	
	Mean	Std error	Mean	Std error	Mean	Std error	Mean	Std error	Mean	Std error	Mean	Std error
Time spent foraging vs not foraging	0.06	0.02	0.08	0.01	0.1	0.02	0.08	0.01	0.13	0.02	0.06	0.01
No. captured food items of anthropogenic vs natural origin	0.47	0.2	0.6	0.19	0.94	0.04	0.83	0.11	0.69	0.16	0.26	0.18
Response variable	Day status*Time of day											
	Week day*Morning		Weekend*Morning		Week day*Early afternoon		Weekend*Early afternoon		Week day*Late afternoon		Weekend*Late afternoon	
	Mean	Std error	Mean	Std error	Mean	Std error	Mean	Std error	Mean	Std error	Mean	Std error
No. captured food items taken to nest vs swallowed by adult	0.49	0.09	0.57	0.11	0.65	0.09	0.64	0.09	0.62	0.09	0.18	0.06

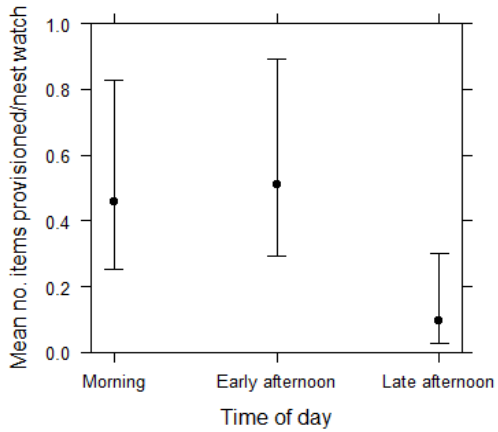


Figure A3: Provisioning rate of male to incubating female. Mean number of items provisioned by male to female per nest watch in the morning, early afternoon, and late afternoon during the incubation period. Upper and lower 95% confidence intervals are displayed.

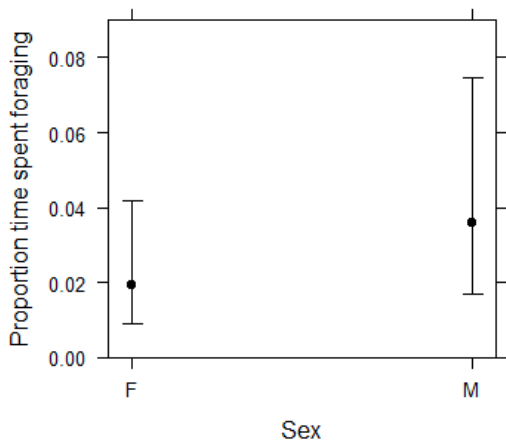


Figure A4: Foraging effort during incubation period. Mean proportion of time female and male birds spent foraging as opposed to other activities during the incubation period. Upper and lower 95% confidence intervals are displayed.

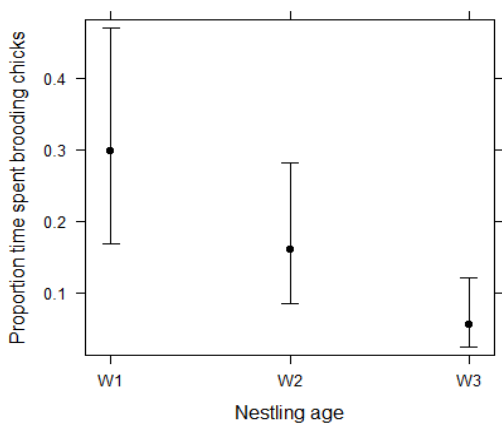


Figure A5: Brooding bouts during nestling period. Mean proportion of time females spent brooding chicks of three different age classes (week one, W1; week two, W2; week three, W3). Upper and lower 95% confidence intervals are displayed.

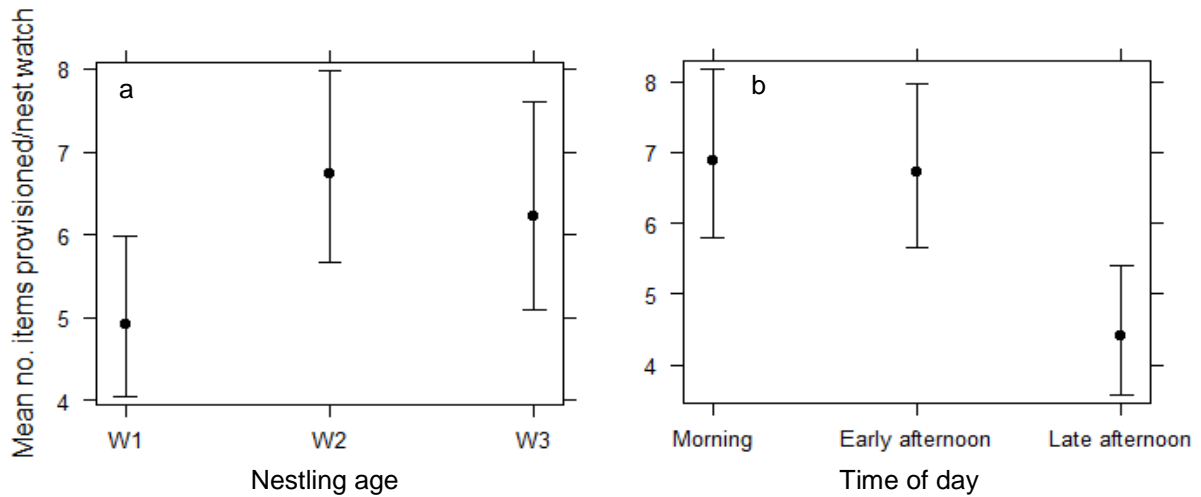


Figure A6: Provisioning rate of both parents to chicks during nestling period. Mean number of items provisioned per nest watch by parents to chicks of (a) three different age classes (week one, W1; week two, W2; week three, W3), and (b) in the morning, early afternoon, and late afternoon. Upper and lower 95% confidence intervals are displayed.

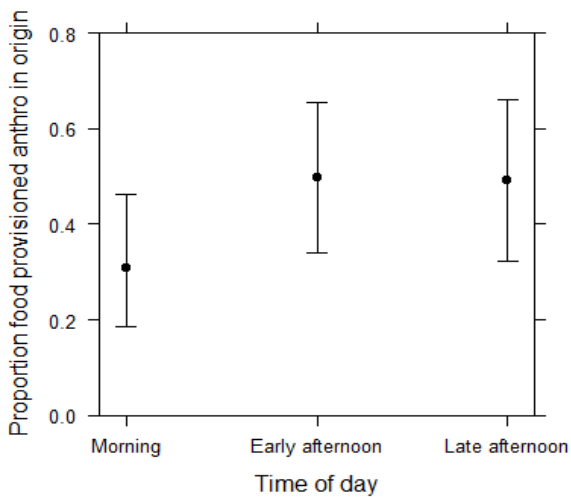


Figure A7: Anthropogenic vs natural food provisioning of both parents to chicks during nestling period. Mean proportion of food provisioned to chicks that was anthropogenic in origin in the morning, early afternoon, and late afternoon. Upper and lower 95% confidence intervals are displayed.

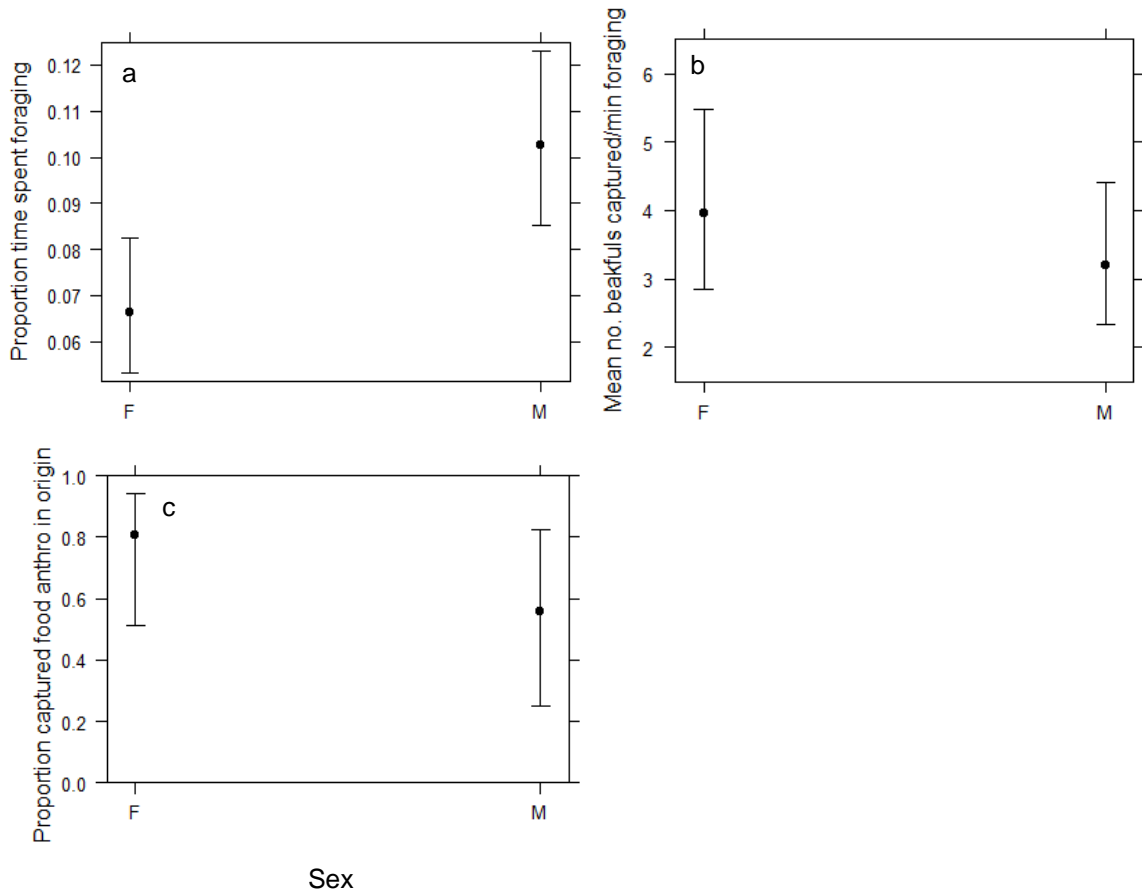


Figure A8: Sex-specific differences during the nestling period in (a) proportion of time spent foraging, (b) beakfuls captured per foraging minute, and (c) proportion of captured food anthropogenic in origin. Upper and lower 95% confidence intervals are displayed.

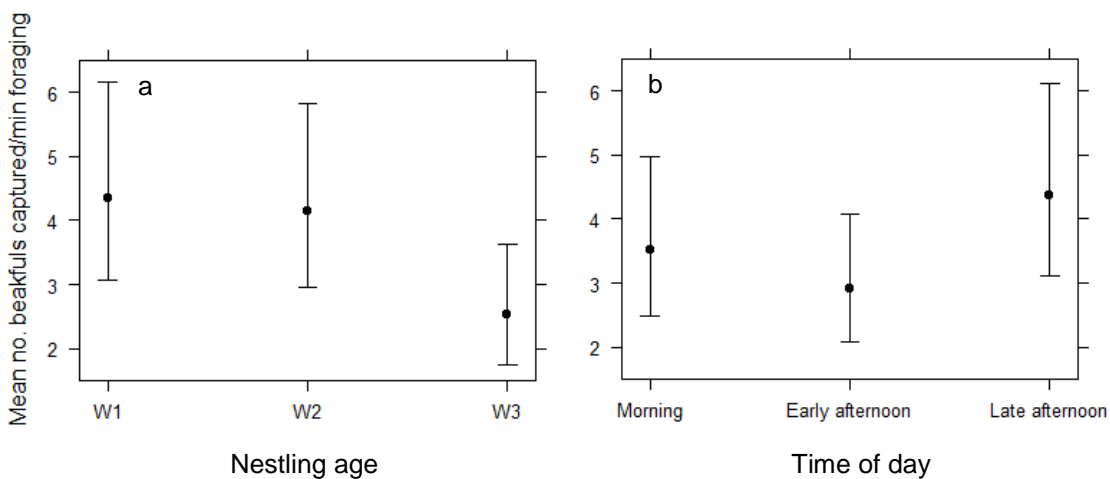


Figure A9: Foraging efficiency of parents during the nestling period. Mean number of beakfuls of food captured per minute spent foraging (a) when chicks were in one of three age classes (week one, W1; week two, W2; week three, W3), and (b) in the morning, early afternoon, and late afternoon. Upper and lower 95% confidence intervals are displayed.