Chapter 3. Heads up! Social vigilance behaviour in urban American crows

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Introduction

Groups of American crows (*Corvus brachyrhynchos*) can be found in most North American cities and are an example of an urbanized species able to exploit human-altered environments (Marzluff et al., 2001; Withey & Marzluff, 2009). Behavioural adaptations have allowed them to use anthropogenic resources and deal with the challenges of urban living (Isaksson, 2018; Lowry et al., 2013). Adaptive social foraging behaviours could further help mitigate the risks of foraging in urban areas, and potentially increase their foraging efficiency. These adaptations are beneficial to the success of crows but could have broader ecological implications, namely contributing to the decrease in North American avifauna through increased competition or predation (Latta & Latta, 2015; Rosenberg et al., 2019). Studying the behaviour of American crows in urban environments is therefore crucial for several reasons. Understanding how crows can alter their individual and social behaviours to better forage in urban landscapes can contribute to our understanding of urban adaptation of wildlife. By examining how crows respond to urban challenges such as increased ambient noise, impermeable surfaces, and increased frequency of disturbances, we can better comprehend how animals perceive their environment. Lastly, by studying changes in their social behaviours, we can better discern the contribution of social adaptation to the success of urbanized social species.

American crows are capable of a variety of social behaviours (Johnson, 1994; Latta & Latta, 2015; Maccarone, 1987). Of particular interest is sentinel behaviour, a coordinated social behaviour where an individual is constantly vigilant to monitor threats while others forage (Bednekoff, 2015). Sentinels often adopt prominent, exposed positions to maximize their field of view, making them more likely to detect approaching predators. This behaviour can be observed in a variety of social animals, including birds, mammals, and fish (Bednekoff, 2015). Initially perceived as an altruistic act benefiting the group at the expense of the sentinel, sentinel behaviour is now recognized as a more selfish behaviour, with the sentinel reaping the primary benefits through increased safety (Bednekoff, 1997, 2001; Blumstein, 1999; Clutton-Brock et al., 1999). The selfish state-dependent model for sentinel decision-making proposes that an individual with sufficient energetic reserves will choose to be sentinel if the alternative is foraging without a sentinel, a considerably more dangerous option (Bednekoff, 1997). Other group members then benefit from the increased protection and early warning provided by the sentinel, leading to higher overall foraging success and potentially greater biomass intake (Hollén et al., 2008).

American crows in urban centres might rely on sentinel behaviour for feeding due to increased human presence and frequent disturbances. Increased ambient noise levels in cities can interfere with acoustic communication, reducing the effectiveness of sentinel signalling (Kern & Radford, 2016). The presence of urban predators such as the red-tailed hawk (*Buteo jamaicensis*) could increase the risk of predation (Morrison et al., 2016), increasing the need for the added vigilance of a sentinel (Ridley et al., 2010). The increased availability and predictability of anthropogenic food sources that are usually concentrated (e.g. trash cans, litter) and highly caloric, can lead to changes in foraging strategy (Lowry et al., 2013), a reduction in resource competition (Łopucki et al., 2021), and high energetic levels in urban individuals (Auman et al., 2008).

Research on striped field mice (*Apodemus agrarius*) has shown that urban individuals are less likely to avoid contact, more tolerant of conspecifics, and exhibit a lower tendency to monopolize resources compared to rural individuals (Łopucki et al., 2021). These behavioural changes suggest a shift towards more social behaviours in response to the increased abundance of food in urban environments. The effects of urbanization can also be more subtle. A study on black-capped chickadees (*Poecile atricapillus*) found no direct effect of urbanization on their social behaviours, instead exhibiting decreased effects of seasonality, remaining more consistent in their group foraging behaviour throughout the year (Jones et al., 2019). This suggests that urban environments could have more stable food resources, leading to less behavioural plasticity in response to seasonal changes (Jones et al., 2019).

The multitude of ways urbanization can affect social behaviours reinforces the need for further research on urbanized social species. Despite the growing interest in urban wildlife ecology, studies on the adaptation of social behaviours to urban living are limited. Sentinel behaviour is a complex social adaptation that can have far-reaching effects on group dynamics and foraging efficiency. By examining the effects of sentinel presence and generalized environment, we seek to gain insights into how adaptive social behaviours contribute to the success of this species in urban environments. With these findings, we could be able to determine how other social species capable of sentinel behaviour could respond to urbanization.

In this study, we aimed to determine the effects of sentinel presence and the environment on the social foraging behaviour of urban American crows. We hypothesized that sentinel behaviour and the generalized environment would affect the alert and foraging behaviour of crows. We predicted in urban green spaces where the longer lines of sight and decreased ambient noise would increase the sentinel’s effectiveness, and crows would show decreased individual vigilance and increased reliance on the sentinel’s vigilance, leading to more efficient foraging compared to crows in commercial areas.. In contrast, we predicted that crows foraging in commercial areas where the environment is highly variable and frequently disturbed, crows would have increased reliance on individual vigilance, with longer bouts of alert behaviour, and shorter bouts of foraging behaviour, resulting in decreased foraging efficiency.

Methods

Site Selection

To find areas in which crows aggregate, we launched a community science initiative in the greater St. Catharines and Niagara region called Crowkemon Go (www.crowkemon.weebly.com) in spring 2022. Community members were invited to report the location of crow sightings to identify areas with a high likelihood of crow occurrences. In total, the community recorded 221 crow sightings using Crowkemon Go between January and May 2022. From April-May 2022, we visited potential observation sites and baited them with whole peanuts to attract crows and reinforce an association with food at these locations. We limited data collection to the summer months (June-September 2022). One site was sampled repeatedly (Fairview Park, 43°10'57.4"N 79°14'44.9"W; Figure 1). We also visited areas with many crow sightings for opportunistic sampling, as the presence of crows was not guaranteed at other potential recurrent sampling locations (Figure 1).

Field observations

Data collection was performed during the 2-3 hours following sunrise (approx. 6-9 AM). No sampling was performed when it was raining or during adverse weather (e.g., thunderstorms or heatwave). Upon arriving at the recurrent sampling location, a Nikon D5300 camera with a 70-300mm Nikkor lens was set up on a tripod at a minimum of 15m away from a concrete pad (predetermined bait location). If crows were already foraging in the area, we would begin recording immediately and not bait the site because approaching could cause them to abandon the site. If the crows were not foraging (e.g. perched nearby), an observer approached and visibly dropped 30g of Cheez-Its. If crows were on-site, recording would start immediately, whereas if

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Figure 1: Map of observations from Crowkemon Go and sampling locations.

The black dots represent observations collected from Crowkemon Go, and the circular icons are sampling locations. The single recurrent site used is in green. Opportunistic sampling sites are in yellow. The focal area was limited to the St. Catharines & Niagara region. This map was created using Google My Maps.

the crows were absent, a crow-caller would be used for 20 minutes (one 5 seconds call per minute, 5 mins on, 5 mins off for 20 minutes or until crows appeared) to attract them. We began recording when crows arrived and recorded up to a maximum of 20 minutes. The recording was stopped if the crows vacated the area for longer than 5 minutes and we remained in the area for 10 minutes post-departure in case the crows returned. If the crows returned within 5 minutes, we would resume the recording. For opportunistic sampling, we looked for crows using Crowkemon Go as a guide. If we found crows that were already foraging, we would set up in the same manner as for recurrent sampling and did not bait the site. Conversely, if the crows were not already foraging, we would bait the site as we did for recurrent sampling.

The presence of a sentinel, whether heard or seen, was announced verbally by the observer during the recording. For each location, we classified the type of environment using St. Catharines municipal zoning maps, later generalized as either “commercial” or “green” (Table S1**)**. Disturbance frequency was calculated by dividing the number of disturbances by the duration of the recording. We identified disturbances as anything passing within 5m of the crows’ foraging area, including vehicles, pedestrians, and domestic and wild animals. The group size was binned into two categories: small (4) and large (4).

Video Analysis

For video analyses, we used the Behavioral Observation Research Interactive Software (BORIS v.8.9.4) (Friard & Gamba, 2016). We recorded each individual in frame separately, and we classified and individual’s behaviours as either “foraging” or “alert”. “Alert” behaviour was defined as an upright posture where the individual is scanning their surroundings, and “foraging” was when the individual was looking downward, either pecking at or looking for food on the ground (Table S2). We recorded the duration of bouts of each behaviour longer than 0.01 seconds. Movement behaviour was noted, but, since not all bouts of movement were filmed in their entirety, “moving” behaviour was excluded from these analyses. We then calculated the proportion of time spent performing each behaviour. An individual could have two observations if sentinel presence changed, as bouts were recorded separately for whether a sentinel was present or not.

We also recorded the number of pecks (handling food with their beaks to eat it) to quantify foraging effort. The peck rate (per minute) was calculated for every individual by dividing the total number of pecks at food performed by the total duration of “foraging” behaviour. The peck rate of individuals who spent no time foraging could not be calculated and were therefore excluded from peck rate analysis.

Statistical Analysis

All statistical analyses were performed in the R environment (v.4.2.2; R Core Team, 2022). We first ran separate chi-squared tests to determine if the generalized environment, the group size, or the disturbance frequency affected the likelihood of sentinel presence. To determine the effects of generalized environment and sentinel presence on the proportion of time allocated to each behaviour (alert or foraging), we used the “lm()” function to fit separate linear models using behaviour type, sentinel presence, and generalized environment as predictors.

To determine the effects of generalized environment and the presence of a sentinel on the duration of bouts of all behaviours, we used the “rlmer()” function from the “robustlmm” package (Koller, 2016) to fit a robust linear mixed model to the log-transformed duration of bouts with behaviour type, sentinel presence, generalized environment, group size, and bait presence as fixed factors, the disturbance frequency (number of disturbances per min.) as a fixed effect and the individual ID as a random effect. We included in these models the interaction between sentinel presence and generalized environment. We then fitted post-hoc robust linear mixed models on each behaviour to determine the effects of sentinel presence and generalized environment on each behaviour.

To determine the effects of sentinel presence and generalized environment on peck rate, we used the “rlmer” function from the “robustlmm” package (Koller, 2016) to fit a robust linear mixed model to the peck rate of foragers using sentinel presence, generalized environment, group size, and bait presence as fixed factors, the disturbance frequency (per min) as a fixed effect, and the individual ID as a random effect. We included in this model the interaction between sentinel presence and generalized environment, as well as the interaction between generalized environment and disturbance frequency.

Finally, we counted the number of transitions from each behaviour to determine the effects of sentinel presence and generalized environment on the frequency of each transition type. Using the “glmer” function from the “lme4” package (Bates et al., 2015), we fitted a generalized linear mixed model using a Poisson distribution to the number of occurrences of each transition. Sentinel presence, generalized environment, and bait presence were fixed factors, the disturbance frequency (per min) was used as a fixed effect, and the total number of transitions performed between all behaviours by the individual was used as a random effect in the model. Post hoc estimated marginal means tests were performed as appropriate using the “emmeans” function from the “emmeans” package (Lenth, 2023), and false discrovery rate (FDR) correction was applied to the p-values.

Results

Sentinel presence changed in 8 videos, and therefore, we made 19 observations with a sentinel present and 14 observations without a sentinel for a total of 33 observations. The generalized environment (χ2 = 0.122, df = 1, p = 0.727; Figure S1), group size (χ2 = 0.248, df = 1, p = 0.618; Figure S2), and the disturbance frequency (χ2 = 2.033, df = 2, p = 0.362; Figure S2) did not significantly affect if a sentinel was present or not.

Proportion of time allocated to each behaviour

Crows allocated similar proportions of time to foraging and vigilance ( = 0.026, SE = 0.023, t = 1.160, p = 0.248; Figure 2, Table 1), and neither the presence of a sentinel ( = -0.034, SE = 0.023, t = -1.431, p = 0.154; Figure 2, Table 1) or the generalized environment ( = 0.034, SE = 0.023, t = 1.463, p = 0.146; Figure 2, Table 1) had an effect on the proportion of time allocated to either alert or foraging behaviour.

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Figure 2: Proportion of time allocated to each behaviour by foragers in commercial and green areas

Table 1: Effects of sentinel presence and generalized environment on the proportion of time allocated to each behaviour.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Predictors | Estimates | Std. Error | Statistic | p-value |
| Intercept | 0.3658 | 0.0240 | 15.2636 | <0.001 |
| Behaviour | 0.0263 | 0.0226 | 1.1600 | 0.248 |
| Sentinel Presence | -0.0335 | 0.0234 | -1.4314 | 0.154 |
| Generalized Environment | 0.0336 | 0.0230 | 1.4625 | 0.146 |
| Observations | 154 |  |  |  |
| R2/R2 adjusted | 0.037/0.018 |  |  |  |

Duration of bouts of all behaviours

In total, 3897 bouts were recorded, of which 2110 bouts were of “alert” behaviour, and 1787 bouts were of “foraging” behaviour. The average duration of bouts was 1.75 seconds. Bouts of alertness and foraging differed significantly ( = -0.256, SE = 0.051, t = -5.002, p = <0.001; Figure 3, Table 2), with bouts of alertness significantly (1.64 seconds) shorter than bouts of foraging (1.88 seconds). Sentinel presence significantly increased the duration of bouts of all behaviours ( = 0.197, SE = 0.072, t = 2.741, p = 0.006; Figure 3, Table 2). In green areas, bouts of all behaviours were significantly longer than in commercial areas ( = 0.353, SE = 0.087, t = 4.048, p = <0.001; Figure 3, Table 2). Disturbance frequency had a significant effect on the duration of all bouts ( = -0.088, SE = 0.030, t = -2.975, p = 0.003; Figure S3, Table 2), with bout duration decreasing as disturbance frequency increased. We found a significant interaction between generalized environment and sentinel presence ( = -0.252, SE = 0.088, t = -2.863, p = 0.004; Figure 3, Table 2), and between behaviour type and generalized environment ( = -0.202, SE = 0.054, t = -3.769, p = <0.001; Figure 3, Table 2).

Duration of bouts of “foraging” behaviour

Sentinel presence had no significant effect on the duration of bouts of foraging behaviour ( = 0.092, SE = 0.072, t = 1.280, p = 0.201; Figure 3, Table 2). Generalized environment had a significant effect on the duration of bouts of foraging behaviour, with longer bouts in green areas ( = 0.383, SE = 0.078, t = 4.919, p = <0.001; Figure 3, Table 2). Larger groups had significantly longer bouts of foraging behaviour ( = -0.152, SE = 0.068, t = -2.221,

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Figure 3: Mean bout duration of foragers in commercial and green areas. The error bars represent the standard error.

Table 2: Results of the linear mixed models fit to the mean bout duration.

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p = 0.026; Figure 4, Table 2). Bouts of foraging behaviour were significantly shorter in the presence of bait ( = -0.139, SE = 0.070, t = -1.989, p = 0.047; Figure S4, Table 2). The duration of bouts of foraging significantly decreased as disturbance frequency increased ( = -0.108, SE = 0.030, t = -3.566, p = <0.001; Figure S5, Table 2). We found a significant interaction between generalized environment and sentinel presence ( = -0.227, SE = 0.091, t = -2.485, p = 0.013; Figure 3, Table 2). Post hoc tests showed significant differences in the duration of bouts of foraging behaviour. In the absence of a sentinel, foragers in green areas had significantly longer bouts of foraging behaviour than in commercial areas ( = -0.383, SE = 0.078, z-ratio = -4.919, p < 0.001; Table S3). In the presence of a sentinel, foragers in green areas also had significantly longer bouts of foraging behaviour than in commercial areas ( = -0.156, SE = 0.067, z-ratio = -2.337, p = 0.029; Table S3). In green areas, foragers in the presence of a sentinel had marginally shorter bouts of foraging behaviour than in the absence of a sentinel ( = 0.135, SE = 0.068, z-ratio = 1.977, p = 0.058; Table S3).

Duration of bouts of “alert” behaviour

Sentinel behaviour, generalized environment, group size, bait presence and disturbance frequency had no significant effect on the duration of bouts of alert behaviour (p > 0.05; Table 2). We found a significant interaction between sentinel behaviour and generalized environment ( = -0.274, SE = 0.135, t = -2.024, p = 0.043; Figure 3, Table 2,). Post hoc pairwise t-tests revealed no significant differences in the duration of bouts of alert behaviour.

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Figure 4: Mean foraging bout duration of crows in small and large groups. Error bars represent the standard error.

Foraging rate

Neither the presence of a sentinel, the generalized environment, nor group size had a significant effect on the peck rate of foragers (p > 0.233; Figure S6, Table 3). Foragers increased their peck rate in the presence of bait ( = 13.990, t = 2.231, p = 0.020; Figure S7, Table 3). Peck rate increased significantly with disturbance frequency ( = 5.290, t = 2.312, p = 0.021; Figure 5, Table 3). We found a significant interaction between generalized environment and disturbance frequency ( = 16.150, t = 3.046, p = 0.002; Figure 5, Table 3).

Transition analysis

The number of transitions from foraging to alert behaviour was significantly higher in green areas (IRR = 0.421, SE = 0.157, z = -1.355, p = 0.020; Figure 6, Table 4), and when disturbances were more frequent (IRR = 0.728, SE = 0.109, z = -2.130, p = 0.033; Figure 7, Table 4). We found a significant interaction between generalized environment and sentinel presence (IRR = 5.021, SE = 2.457, z = 3.298, p = 0.001; Figure 6, Table 4). The number of transitions from foraging to pecking was significantly higher in the presence of bait (IRR = 1.710, SE = 0.384, z = 2.386, p = 0.017; Figure S8, Table 4). Sentinel presence, generalized environment, disturbance frequency, or the interaction between sentinel presence and generalized environment did not affect the number of transitions from foraging to pecking (p-value > 0.385; Table 4). The number of transitions from pecking to alert behaviour was also significantly higher in the presence of bait (IRR = 2.204, SE = 0.538, z = 3.238, p = 0.001; Figure S8, Table 4).

Table 3: Result of the linear mixed model fit to peck rate.

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Figure 5: Peck rate in relation to disturbance frequency.

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Figure 6: Number of transitions performed by foragers in commercial and green areas. Error bars represent the standard error. Three outliers (Nb.>100) omitted from figure.

Table 4: Results of generalized linear mixed model fit to the number of transitions performed by foragers

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Figure 7: The number of transitions from foraging to alert behaviour decreases as disturbance frequency increases. The grey shadow represents the standard error of the curve.

Sentinel presence, generalized environment, disturbance frequency, or the interaction between sentinel presence and generalized environment did not affect the number of transitions from pecking to alert behaviour (p-value > 0.235; Table 4). The number of transitions from alert to foraging behaviour were not significantly affected by any factors; however, bait presence had a marginally significant effect (IRR = 1.513, SE = 0.351, z = 1.789, p = 0.074; Figure S8, Table 4).

Post hoc testing on the number of transitions from foraging to alert behaviour showed that in green areas, individuals performed more transitions from foraging to alert in the presence of a sentinel ( = -1.124, SE = 0.346, z-ratio = -3.250, p = 0.007; Table S4). Foragers in the presence of a sentinel had a marginally significant increase in the number of transitions from foraging to alert in green areas compared to foragers in commercial areas ( = -0.749, SE = 0.364, z-ratio = -2.062, p = 0.079; Table S4). However, foragers in the absence of a sentinel performed marginally more transitions from foraging to alert behaviour in commercial areas than in green areas ( = 0.864, SE = 0.372, z-ratio = 2.321, p = 0.061; Table S4).

Discussion

We investigated if the presence of a sentinel and the type of environment affected the behaviour of foraging American crows. We hypothesized that in the presence of a sentinel the individual vigilance of crow foragers would decrease and that this effect would be stronger in green areas where reduced ambient noise and longer lines of sight would make a sentinel more effective. We found that sentinel presence alone had no significant effects on the behaviour of foragers apart from the duration of all behaviours were significantly higher in the presence of a sentinel. We did observe a significant interaction between sentinel presence and generalized environment on the duration of bouts of foraging and alert behaviour. This suggests that the benefits of sentinel coverage are affected by the type of foraging environment, and that foragers will rely more on sentinels when their coverage is most effective. Moreover, neither the environment, disturbance frequency, nor group size significantly affected the likelihood of a sentinel being present. This result partially supports the hypothesis that crows could decide to perform sentinel behaviour based more on selfish needs rather than on the benefits imparted to the foragers. We found that the generalized environment had a significant effect on forager behaviour, with foragers in green areas having longer bouts of foraging behaviour and more transitions from the vulnerable foraging or pecking behaviors to the alert state. This suggests that crows need to spend more time being vulnerable to search for food items. The increased vulnerability, and therefore risk, could be traded off for increased likelihood of finding higher quality food items. Overall, our results do not fully support our initial hypotheses and suggest that sentinel behaviour and forager behaviour in crows could be influenced by complex interactions between individual factors and forager’s perception of the safety in their environment. Additional factors, such as group composition, could likewise affect foraging behaviour, with the presence of juveniles potentially increasing the vigilance of adults (Santema & Clutton-Brock, 2013).

The effects of sentinel presence on forager behaviour

Our results contrast with previous studies that found that the presence of a sentinel led to a decrease in alert behaviour (Hollén et al., 2008; Ridley et al., 2014). For example, pied babblers, *Turdoides bicolor*, increased the proportion of time spent foraging after the start of a sentinel bout and had increased biomass intake (Hollén et al., 2008). In our case, American crows did not appear to alter their alert or foraging behaviour in response to sentinel presence alone. Instead, sentinel coverage appears to be most effective in green areas, as we saw a decrease in the duration of bouts of alert behaviour, and an increase in the duration of bouts of foraging behaviour. The significant interaction between sentinel presence and generalized environment shows that the comparatively busier and noisier commercial areas can potentially make sentinel-forager communication more difficult. This could result in decreased reliance on sentinel coverage, and greater individual vigilance in foragers. In the absence of a sentinel, foragers in green areas appear to have comparatively longer bouts of alert and foraging behaviour though these differences were not significant. This increase could potentially be the result of increased reliance on some form of coordination of vigilance between foragers, with longer but fewer bouts of alert behaviour. Whether crows have ground-level coordination of vigilance, and how they could be switching between reliance on the sentinel and reliance on ground-level vigilance, is an interesting topic for future research.

Foragers in commercial areas and in the absence of a sentinel do not appear to rely on other group-members, as the duration of their bouts of alert and foraging behaviour are similar, and short. Foraging crows could be devoting as little time as possible to each behaviour to decrease the duration time spent on the ground where the risk is greatest. In the presence of a sentinel, foragers in commercial areas appear to have slightly longer bouts of alert and foraging behaviour than in the absence of a sentinel, although this comparison was not significant in our post-hoc tests. Though potentially impaired by ambient noise, sentinels in commercial areas could inform the foragers of more dangerous disturbances (e.g. raptors, humans), potentially resulting in the longer bouts of foraging behaviour. As for the increased duration of alert behaviour, foragers in the absence of a sentinel could elect to immediately take flight when disturbed, while foragers in the presence of a sentinel could have longer to decide whether to stay or flee.

The benefits of sentinel behaviour can be more subtle or indirect than intitially thought, such as providing a greater sense of security that allows foragers to focus more on foraging without actively reducing their vigilance (Hollén et al., 2008). The proportion of time allocated to alert behaviour might also be used to scan for foraging patches and other foragers, explaining the absence of effects of sentinel presence on the proportion of time spent being alert. Foragers could also benefit from sentinel presence by increasing the distance between foragers, permitting the group to forage over a greater surface area while compensating for the increased predation risk from foraging further apart (Hollén et al., 2008). Sentinel behaviour could therefore compensate for riskier group-foraging strategies, not only individual changes in behaviour. This suggests the relationship between sentinels and foragers could be more complex, reinforcing the importance of considering individual differences and motivations when studying social behaviours. The presence of juveniles in the foraging group could also affect how group-members forage and is an important aspect to consider in future studies.

Effects of foraging in commercial vs green areas.

We found that the generalized environment had significant effects on forager behaviour, particularly in terms of the duration of bouts of foraging behaviour and the number of transitions from the vulnerable to the alert state. In green areas, crows exhibited longer bouts of foraging behaviour, suggesting that they spent more time searching for food to forage on. Vegetation might obscure food items, making them harder to spot and, in the case of prey, harder to catch. Likewise, an increase in the number of transitions from the vulnerable state to the alert state was observed in green areas, suggesting that crows were more vigilant to potential threats possibly indiciating a higher perceived predation risk in green areas compared to commercial areas.

Green areas, such as parks, offer longer lines of sight and less ambient noise which makes the sentinel more effective (Hollén et al., 2011) but could also benefit urban raptors. Urban red-tailed hawk (*Buteo jamaicensis*) populations make large green areas the cores of their home ranges (Morrison et al., 2016). Foraging in green areas could therefore be risky, explaining an individual’s need to maintain vigilance. Though not formally quantified, we did observe foraging crows abandon sites when disturbed by raptors but only temporarily flee when disturbed by vehicles. This suggests that the type of disturbances in each environment could change how risky an environment is to forage on.

We observed shorter bouts of foraging behaviour but a higher peck rate in commercial areas. The increased duration of foraging bouts in green areas could suggest that crows need to spend more time actively searching for and consuming food. In green areas, food can be more dispersed, require more time to locate, and could be obscured by vegetation. Comparatively, food scraps and litter in commercial areas are considerably easier to forage when on impermeable surfaces. Moreover, anthropogenic foods have a greater caloric content than non-anthropogenic foods, making them more satiating than other food sources and easier to find when on impermeable surfaces, likely playing a role in the shift in their foraging preferences for anthropogenic foods (Marzluff et al., 2001; Marzluff & Neatherlin, 2006).

The absence of effect of generalized environment on the likelihood of a sentinel being present in our videos is not necessarily unexpected. Bedneckoff's state-dependent model states that individuals make decisions based on their own energetic needs and the benefits they receive (Bednekoff, 1997). An individual with sufficient energetic reserves could decide to perform sentinel behaviour as a safer option if the alternative is foraging without a sentinel. In urban areas, the presence of high-calorie food patches could facilitate the replenishment of energetic reserves. As a result, individuals might be more likely to engage in sentinel behaviour and increase their sentinel efforts, either by increasing frequency and/or duration of behaviour bouts. In our case, all individuals are urban, and can move between environments within the urban area. If travel time or time between foraging events is short, individuals could then be able to immediately sentinel upon arriving at a foraging site. Unfortunately, we were unable to track crow movements within a city to test this hypothesis, but it would be an interesting avenue for future research.

Disturbances

Higher disturbance frequency led to a decrease in the duration of bouts of all behaviours, particularly foraging. American crows could be decreasing the duration of bouts of foraging behaviour to minimize their exposure to perceived threats. Areas with higher disturbance frequencies typically had a greater frequency of vehicular disturbances, which American crows could be more tolerant of (Mukherjee et al., 2013). Peck rate was significantly correlated with disturbance frequency, and we found a significant interaction between disturbance frequency and generalized environment on peck rate. In response to increasing disturbance frequency, foragers in green areas increased their peck rate more than foragers in commercial areas, further supporting the hypothesis that the type of disturbance as well as the frequency affects the foraging behaviour of urban crows. Higher disturbance frequency was also associated with a significant decrease in the number of transitions from foraging to alert behaviour. Crows could then be foraging as quickly as possible while maintaining minimal vigilance and flying away as soon as a threat is detected.

Baited sites

The presence of bait, which can be considered a proxy for human-generated litter in the environment, increased the peck rate and decreased the duration of foraging bouts. This suggests that foraging on bait or litter could be quicker and decrease time being vulnerable when compared to foraging on natural food patches. The latter could take more time to forage on since grass and other vegetation can obscure food items, making them harder to identify and catch. This observation could explain why a shift in preference for anthropogenic foods is observed in American crows and potentially other urbanized species (Marzluff et al., 2001; Marzluff & Neatherlin, 2006). Future research could further elucidate the effects of foraging on different types of litter and anthropogenic foods, and how urbanized species adapt their foraging behaviours to best capitalize on these resources.

Group Size

As group size increased, the duration of bouts of foraging behaviour increased but was not associated with a decrease in the duration of bouts of alert behaviour. The proportion of time allocated to either behaviour was also unchanged by the size of the group. This finding is surprising, as previous studies suggest that larger group sizes should decrease individual vigilance while increasing foraging efficiency (Beauchamp, 2008, 2013; Lima, 1995; Ward & Low, 1997), yet the effect of group size was only observed in the duration of bouts of foraging behaviour. Bouts of alert behaviour could have a minimal duration to effectively monitor the surrounding environment for sources of threat. Alternatively, foraging crows could be maintaining vigilance due to increased competition for resources in larger groups. Instead of only looking out for sources of threat, foragers could be looking at the behaviour of other group members in case they found a better patch to forage on.

Future directions and improvements

Our study has several limitations that should be acknowledged. Our sample size could have limited the ability to detect significant effects. As such, caution should be exercised when interpreting the results, and further studies with larger sample sizes are required to make conclusive statements. Future studies should make use of long-term video recorders in areas where crows forage across a wider breadth of urbanization. Additionally, the study focused on the population of crows in St. Catharines Ontario, which could limit the generalizability of our results to other populations or environments. Factors such as local food availability, the number and area of green spaces, and predator presence can vary widely between cities, and these factors can affect the behaviour of foraging crows. Therefore, the findings of our study could differ from those of a similar study performed in a different city.

Our study investigated the effects of sentinel behaviour and the generalized environment on the behaviour of foraging American crows in urban environments. Contrary to expectations, sentinel presence did not have a significant effect on forager behaviour. This suggests that sentinel decision-making could be more influenced by individual needs rather than group benefits, aligning with Bednekoff's state-dependent model. The generalized environment, however, had a significant impact on forager behaviour. Crows in green areas exhibited longer bouts of foraging behaviour and more transitions from the vulnerable to the alert state compared to those in commercial areas. This indicates that environmental factors such as resource distribution and predation risk could play a crucial role in shaping forager behaviour. Disturbance frequency, bait presence, and group size also influenced forager behaviour. Higher disturbance frequency led to shorter bouts of behaviour but increased peck rate, indicating a trade-off between vigilance and foraging efficiency. Bait presence increased peck rate and decreased foraging time, suggesting that small, concentrated patches of food are easier and quicker to forage on, though we have only used one type of bait. Further research could delve into how crows forage on different types of human litter and how they use their problem-solving capabilities to defeat packaging.

These findings have several implications for understanding crow behaviour. They suggest that crows can adapt their behaviour based on environmental conditions and individual needs. The lack of significant effects of sentinel behaviour points towards the complexity of social behaviour in crows and the importance of considering individual variation in decision-making. Overall, the study provides valuable insights into the factors influencing crow behaviour in urban environments and highlights the need for further research to fully understand these complex behaviours.

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Supplemental Material

Table S1: Explanation of generalized environment.

|  |  |
| --- | --- |
| Generalized Environment | Zones included |
| Commercial Area | Arterial Commercial, Business Commercial Employment, Community Commercial, Major Commercial |
| Green Area | Major Green Space, Minor Green Space |

Each zone type was identified using the St. Catharines and Niagara zoning maps for each sampling location.

Table S2: Ethogram of behaviours analyzed during foraging events.

|  |  |  |  |
| --- | --- | --- | --- |
| Behaviour | Code | Definition | Illustration |
| Foraging | Head Down | Focal individual is stationary and has its head downwards or in a non-upright position, either pecking or handling food, looking for food. | A black silhouette of a bird  Description automatically generated |
| Moving | Moving | Focal individual is moving, either by flying, hopping (leaping), or walking. | A black background with white spots  Description automatically generated |
| Alert | Head Up | The focal individual is stationary and has its head and body in an upright position. Individuals can have a mobile (scanning) or immobile head but must not be looking downwards. Individuals can be handling food. | A black bird with a black background  Description automatically generated |

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A graph of different colored bars

Description automatically generated

Figure S1: Sentinel presence in commercial and green areas.

A graph of a number of crowns

Description automatically generated

Figure S2: Frequency plots of observations in the presence and absence of a sentinel.

A graph of a number of orange and blue lines

Description automatically generated

Figure S3: Decreasing bout duration of all behaviours in response to increasing disturbance frequency.

Table S3: Results of post hoc tests on foraging bout duration.

A screenshot of a computer

Description automatically generated

A graph of a number of objects

Description automatically generated with medium confidence

Figure S4: Mean bout duration in the presence and absence of bait. The dots represent the mean value, and the error bars represent the standard error.

A graph of a number of orange and blue dots

Description automatically generated

Figure S5: Foraging bout duration decreasing with increasing disturbance frequency.

A graph of numbers and letters

Description automatically generated

Figure S6: Mean peck rate of foragers in commercial and green areas. Error bars represent the standard error.

A graph of a number of objects

Description automatically generated with medium confidence

Figure S7: Mean forager peck rate in the presence and absence of bait. The dots represent the mean value, and the error bars represent the standard error.

A graph with text and numbers

Description automatically generated with medium confidence

Figure S8: Number of transitions performed by foragers in the presence and absence of bait. The dots represent the mean value, and the error bars represent the standard error.

Table S4: Result of post hoc test performed on the number of transitions from foraging to alert behaviour.

A screenshot of a computer

Description automatically generated