MASTERARBEIT | MASTER'S THESIS

Titel | Title

Exploring crow behavior in crow-visitor interactions at Zoo Vienna
Potential signs of behavioral optimization

verfasst von | submitted by

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angestrebter akademischer Grad | in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien | Vienna, 2025

Studienkennzahl lt. Studienblatt | Degree programme code as it appears on the student record sheet:	UA 066 878
Studienrichtung lt. Studienblatt | Degree programme as it appears on the student record sheet:	Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie
Betreut von | Supervisor:	Ass.-Prof. Barbara Klump PhD

Abstract

The local crow population at Zoo Vienna (Tiergarten Schönbrunn), comprising the closely related species *Corvus corone* (carrion crow), *Corvus cornix* (hooded crow), and their hybrid offspring, frequently interact with zoo visitors, primarily through scrounging behavior. These crows often acquire food by displaying social and playful behaviors that encourage visitors to share willingly or by covertly seizing opportunities to steal from unsuspecting individuals. While many behavioral and cognitive components involved in such interactions have been extensively studied in isolation, there remains a gap in understanding their interplay in a holistic and ecologically relevant context, such as the dynamic crow-visitor interactions at Zoo Vienna. To address this, an observational study was conducted at four points of interest, selected for their proximity to anthropogenic food sources. The study aimed to identify the factors facilitating these interactions, assess their profitability, explore preferences for specific hosts, and analyze associated behavioral patterns. Additionally, it sought to infer cognitive processes underlying these behaviors. Visitors targeted by the crows were categorized based on various characteristics, such as age and worn accessories, while interactions were classified by initiation type and profitability for the initial corvid participants and any conspecifics that joined. Results revealed significant correlations between visitor characteristics, conspecific densities, and specific man-made objects (e.g., strollers) with the likelihood and type of crow approaches. Moreover, targeting conspecifics with prior scrounging success was shown to be a profitable strategy. The findings suggest that crows selectively target visitors with particular traits, likely associating these with a higher probability of scrounging success.

Kurzfassung

Die lokale Krähen-Population in Tiergarten Schönbrunn, bestehend aus den zwei nahe verwandten Arten *Corvus corone* (Rabenkrähe), *Corvus cornix* (Nebelkrähe) und ihren hybriden Nachkommen, interagiert häufig mit Zoobesuchern, meistens im Kontext von Betteln und Stehlen. Die Krähen versuchen Nahrung zu erlangen, indem sie entweder soziales oder spielerisches Verhalten aufweisen, um Besucher dazu zu bringen die Nahrung freiwillig zu teilen oder indem sie sich heimlich annähern, um von ahnungslosen Wirten zu stehlen. Während viele der verhaltensbiologischen und kognitiven Bestandteile, die zu diesen Interaktionen beitragen umfangreich in Isolation voneinander erforscht wurden, finden wir immer noch eine Lücke in unserem Wissen über das Zusammenspiel dieser Bestandsteile in einem mehr holistischen Ansatz, besonders nicht in einem ökologisch so relevanten Kontext wie die dynamisch stattfindenden Interaktionen zwischen Krähen und Besuchern im Tiergarten Schönbrunn. Eine Beobachtungsstudie wurde an 4 Standorten, die auf Grund ihrer Nähe zu anthropogenen Nahrungsquellen gewählt wurden, durchgeführt. Das Ziel war, die Faktoren zu identifizieren, welche diese intraspezifischen Interaktionen fördern und ihre Profitabilität, Präferenz für individuelle Wirte und assoziierten Verhaltensmuster bestimmen, und möglicherweise aus den Funden auf die zu Grunde liegenden kognitiven Prozesse zu schliessen. Die anvisierten Besucher wurden basierend auf einer Auswahl von Eigenschaften wie Alter und getragene Accessoires kategorisiert, während die Interaktionen nach Art und Weise wie sie initiiert wurden und nach ihrer Profitabilität für die anfänglich teilnehmenden Krähen und ihren hinzukommenden Artgenossen unterschieden wurden. Die Ergebnisse zeigen signifikante Korrelationen zwischen Besuchereigenschaften, Artgenossendichten, bestimmten Objekten menschlichen Ursprungs wie Kinderwägen, und der Wahrscheinlichkeit, dass ein Besucher von einer Krähe anvisiert wird und wie sie sich annähert. Es konnte auch gezeigt werden, dass es sich für eine Krähe lohnt, einen Artgenossen für eine Annäherung anzuzielen, der zuvor erfolgreich gebettelt oder gestohlen hat. Es wurde geschlussfolgert, dass Krähen Besucher mit bestimmten Eigenschaften häufiger anzielen, weil sie diese wahrscheinlich mit erfolgreichem Betteln oder Stehlen assoziieren.

Acknowledgements

I wish to extend my heartfelt gratitude to Barbara Klump for her excellent guidance and support as my supervisor throughout the research for this thesis. My thanks also go to Christian Blum for his invaluable assistance with data preparation and statistical modeling, as well as to Guillam McIvor and Thomas Bugnyar for their insightful advice and thoughtful feedback.

I am deeply grateful to the Vienna Zoo administration, particularly the curator of research, Regina Kramer, for granting me unrestricted access during data collection. I also want to express my appreciation to the zoo staff for their kindness and cooperation throughout the study.

Lastly, I am profoundly thankful to Roger Mundry for providing invaluable custom scripts for statistical analysis.

I dedicate this thesis to Peter Skolaude - a loving father and husband - whose untimely passing during the planning phase of this study left a deep void. Although he was not a scientist, I like to believe he would have found the results of this work fascinating and would have been proud of my work.

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1. Introduction

Wild bird populations, particularly a variety of corvid species, have become a central element of the zoo visitor experience worldwide - whether appreciated or not. Visitors purchasing meals from refreshment kiosks or using designated resting areas with benches and picnic tables frequently encounter scrounging crows (Kövér et al., 2019; Benmazouz et al., 2021). This in turn makes the zoo an excellent setting to examine various cognitive processes underlying interspecific scrounging in the local corvid population. This study focuses on Zoo Vienna (Tiergarten Schönbrunn), known for its local crow populations comprising two species, *Corvus corone* (carrion crow) and *Corvus cornix* (hooded crow), as well as their hybrid offspring, to investigate the cognitive mechanisms behind these crow-visitor interactions. Despite the zoo's location in a densely urbanized environment, it offers ample greenery and small, artificially created ecosystems within its enclosures and exhibits. Most importantly, it attracts a steady stream of visitors seeking opportunities to reconnect with nature within the confines of a large city landscape. Many of these visitors carry food and are willing to share it (Cox and Gaston, 2016; Howell et al., 2019). Kövér et al. (2019) found that crow density and activity levels in zoos peak in the afternoon, likely due to accumulated food waste from visitors and scheduled feeding events for zoo animals. Particularly relevant feeding events in Zoo Vienna's daily schedule include those for Humboldt penguins at 11:00, Northern rockhopper penguins at 11:30, and anteaters, capybaras, vicuñas, rheas, seriemas at 14:30, and South American sea lions at 15:30, as their enclosures are near sampling locations.

The corvid species at Zoo Vienna thrive amidst the ecological homogenization of the Anthropocene (Benmazouz et al., 2021), characterized by uniform patches of nature across anthropogenic landscapes inhospitable to most wildlife. Corvids excel in urban environments due to their ecological generalism and physiology, which allow them to digest anthropogenic food sources with minimal health risk (Townsend, Staab, and Barker, 2019), as well as their advanced cognitive capabilities supporting behavioral flexibility (Yosef, Reuven, et al., 2019), problem-solving (Heinrich, 1995), and social complexity (Skandrani et al., 2017). Together, these traits enable innovative foraging strategies, granting access to previously inaccessible resources (Kark et al., 2007). As flexible and cognitively adaptive generalists (Emery and Clayton, 2004; Kabadayi and Osvath, 2017), crows benefit significantly from both anthropogenic food sources and the diverse environments (Withey and Marzluff, 2009) provided by the zoo (Kark et al., 2007; Benmazouz et al., 2021) - far more so than many other bird species.

The forested areas within and surrounding the zoo boundaries serve as excellent nesting and roosting grounds. Studies show that individual corvids have adapted their foraging patterns to anthropogenic food sources and urban environments (Boarman et al., 1995; Harju et al., 2018).

Constant anthropogenic influence also tends to keep predator populations low (Anderies, Katti, and Shochat, 2007), providing particular benefits to crows during breeding seasons (Vuorisalo et al., 2003). In some urban settings, crows even face less anthropogenic disturbance compared to rural areas, due to reduced persecution in cities (Wilkins et al., 2019). This trend may reflect shifting attitudes among urban populations and evolving local management policies (Jokimäki et al., 2017). However, this pattern is not universal. In many urban areas worldwide, invasive corvid species are considered pests that damage infrastructure, scatter waste, spread diseases, disrupt ecosystems, and outcompete native bird species (Benmazouz et al., 2021).

A paradoxical aspect of corvid success in urban areas is their well-documented neophobia (Heinrich, Marzluff, and Adams, 1995; Miller et al., 2022), which coexists with their innovative and adaptable nature. Corvids tend to exhibit higher neophobia compared to other avian species. A study relevant to Zoo Vienna (Greggor et al., 2016) revealed only minimal adaptation in general novel object aversion among urban-reared crows compared to their rural counterparts. This is likely the result of the rapid pace of modern urbanization, which is far too quick for meaningful genetic changes to occur at the population level. Urban birds may approach novel objects more quickly, but this behavior is likely heavily influenced by their ability to quickly categorize novel objects based on prior experiences with similar ones, reacting with less fear only on a case-by-case basis. Another factor assisting crows in overcoming their risk aversion is their ability to keenly observe conspecific individuals (Ward and Zahavi, 1973; Morand-Ferron and Quinn, 2011), gaining information socially and implementing innovative foraging strategies observed to be effective for others. In this way, a few novelty-seeking individuals can sustain a flow of innovation in a large social structure vital for survival in anthropogenic environments (Chiarati et al., 2012; Miller, Schwab, and Bugnyar, 2016). However, it is expected that most individual crows will be observed to still struggle to overcome intrinsic fear responses, particularly during periods of high anthropogenic disturbance, even when doing so would be highly beneficial (Miller et al., 2022).

Another cognitive skill aiding wild crows in urban environments is their remarkable social recognition (Kondo, Izawa, and Watanabe, 2012), which appears to extend to other species, including humans (Marzluff et al., 2010). Crows have demonstrated the ability to recognize human faces and react to individuals who have wronged them in the past with harsh vocalizations and mobbing behavior. This ability was tested by Marzluff and colleagues on Corvus brachyrhynchos (American crow) using a unique mask worn during trapping, banding, and releasing near Seattle, USA. Despite subsequent wearers of the mask differing in age, stature, and gender, the crows consistently reacted aggressively towards it, even two years after the stressful event. Later work (Marzluff et al., 2012) identified neurological circuits underlying their ability to recognize human faces, suggesting crows use interconnected visual stimuli to recall and identify individuals, regardless of species. They may have even evolved neural structures functionally analogous to facial recognition regions in mammalian brains.

The mechanisms that allow crows to recognize individuals may work differently, however, as Brecht et al. (2017) found that crows are unaffected by the face inversion effect, which describes humans' difficulty processing inverted faces compared to other inverted images. This discrepancy suggests humans may uniquely specialize in facial processing, which is not the case for crows. Faces convey critical social information to humans (Jack and Schyns, 2015), offering cues about identity, emotion, and attention. Humans may have been evolutionarily selected to process facial information holistically and quickly, unlike less socially relevant stimuli (Richler, Cheung, and Gauthier, 2011). This specialized holistic processing is disproportionately disrupted by visual distortion, hence the face inversion effect.

While crows can distinguish human faces based on characteristics such as gender (Bogale, Aoyama, and Sugita, 2011) and facial expressions (Bogale, Aoyama, and Sugita, 2018), they appear to rely on perceptual similarities, particularly in color, for discrimination, as observed in other bird species (Brown and Dooling, 1992; Brown and Dooling, 1993; Troje et al., 1999). Crows use visual stimuli to differentiate between known conspecifics, though they likely depend on different identifiers than humans (Kondo, Izawa, and Watanabe, 2012). Evolutionarily, it is logical that crows have not developed specialized facial processing, despite their advanced social cognition. They communicate almost all social information through plumage, body language (Leopold and Rhodes, 2010), and vocalizations (Chamberlain and Cornwell, 1971; Yorzinski et al., 2006). Without the mimetic muscles necessary for diverse facial expressions (Burrows et al., 2016), crows likely depend on alternative visual cues. While the exact stimuli used for individual recognition remain unclear, these studies demonstrate their ability to differentiate between individuals of other species.

In interactions with human visitors, crows are likely capable of forming positive associations with certain superficial facial characteristics (Clucas et al., 2013) and food availability. They may also categorize humans by clothing, accessories, body morphology, age, or objects carried (Sun et al., 2024). Objects often used for food storage, such as bags, backpacks, and strollers, are likely to attract scrounging crows. If a stressful event involving a mask can leave a lasting negative association (Marzluff et al., 2010), it follows that for example, particularly prolific bird feeders, who visit regularly and always carry food in large bags and backpacks, could also create a lasting positive association with such objects within the local crow population.

Surveys of urban bird-feeders (Davies et al., 2012; Cox and Gaston, 2016) provide insights into the visitor characteristics crows may use to identify profitable scrounging targets. These surveys suggest that a willingness to engage with wild birds increases with age but does not significantly differ by gender or social status. Older individuals may prioritize relaxing experiences over more stimulating activities due to age-related physical and social limitations. Restricted mobility and flexibility can also limit their access to natural spaces, further reducing opportunities to connect with nature beyond urban environments. Another motivation for bird-feeding is the desire to aid wildlife during times or in places where natural food sources are limited. Although this motivation may not apply to Zoo Vienna - where food is plentiful year-round - the emotional need to act as a guardian figure may still lead visitors to feed crows particularly during harsher weather conditions in late fall and winter. In these cases, crows may enhance their success by drawing attention to themselves through direct approaches and specific behaviors, such as begging calls, which could trigger empathetic responses encouraging visitors to feed them more (Marzluff and Angell, 2005). Visitors inclined to feed birds may also bring their own food, often stored in bags or packs, further contributing to the formation of positive associations with these objects (Sun et al., 2024).

The interactions between visitors and crows at Zoo Vienna can be classified as a specialized form of social foraging (Giraldeau and Dubois, 2008), which involves interdependent foraging decisions within a group, as well as behavioral diversity among foraging individuals. A key aspect of social foraging is the interplay between producers - individuals who gain access to new resources - and scroungers - those who exploit resources discovered by producers without expending equivalent effort (Barta, Liker, and Mónus, 2004). Energy investment by producers may be physical, such as hunting prey, or cognitive, such as applying innovative or socially learned behaviors (Arbilly et al., 2014; Aplin and Morand-Ferron, 2017) in novel situations (Emery and Clayton, 2004). In the context of the crow-visitor interactions at Zoo Vienna two different types of producers can be identified: human visitors providing food act as interspecific producers, while crows can assume the roles of intraspecific producers by either stimulating these hosts to share willingly or by being the first to steal food, making it more accessible to their conspecifics. Despite the advantages of scrounging, a population can achieve a dynamic equilibrium between producers and scroungers, as the benefits of scrounging decrease when it becomes too prevalent. Since scrounging is a flexible behavioral strategy rather than a genetically fixed one (Ha and Ha, 2003), scroungers can shift to becoming producers if their profitability diminishes below that of producers. This threshold depends on various environmental factors, including food patch quality, predation risk, and resource availability (Barta and Giraldeau, 2000; King, Isaac, and Cowlishaw, 2009).

Miller et al. (2014) found that free-range crows at Zoo Vienna exhibit remarkable social tolerance toward conspecifics, preferring to forage alongside them rather than adopting more exploitative behaviors. Zoo Vienna, with its network of diverse ecological patches rich in both natural and anthropogenic food resources, fosters foraging groups composed primarily of producers (Barta and Giraldeau, 2000). Additionally, high social tolerance among conspecifics can promote social learning (Massen, Ritter, and Bugnyar, 2015) and accelerate the spread of novel behavioral patterns within the population (Schnöll, 2014).

Despite many visitors willingly sharing food, events of kleptoparasitism - the stealing of food from other individuals - occur frequently at Zoo Vienna, both intraspecifically and interspecifically. This exploitative foraging strategy is common among various corvid species. For example, members of a carrion crow population near a refuse dump in León, Spain (Baglione and Canestrari, 2009), have become so specialized in interspecific kleptoparasitism that it now serves as their preferred foraging strategy. Their favored hosts are starling species (*Sturnus vulgaris* and *Sturnus unicolor*) and rooks (*Corvus frugilegus*), and they spend significantly more time scanning their environment for potential targets to rob rather than foraging independently. Although such behavioral specialization at the population level may seem at odds with their behavioral plasticity, it actually highlights their remarkable flexibility. In this anthropogenic ecosystem, kleptoparasitism likely proved so effective that individuals innovated and refined their strategies over time, ultimately making it the primary means of acquiring food for much of the population (Flower, Child, and Ridley, 2013).

Another example of kleptoparasitism as a primary foraging strategy (Yosef, Zvuloni, and Yosef-Sukenik, 2012) is the cooperative kleptoparasitism observed among *Corvus splendens* (house crows) targeting *Pandion haliaetus* (the western osprey) - an almost exclusively piscivorous species - on islands and archipelagos in the Red Sea. This case, however, is less characterized by innovative strategies and novel behavior, resembling instead the predator mobbing behavior innate to most corvids (Yorzinski and Vehrencamp, 2009). Since house crows are invasive to these islands, they likely first identified the osprey as a predator and employed mobbing behavior defensively. Secondarily, they may have recognized that this behavior often resulted in ospreys dropping energy-rich food while posing minimal risk. This scenario suggests that while advanced cognitive mechanisms such as social learning or insightful learning (Emery and Clayton, 2004; Seed, Emery, and Clayton, 2009) can aid corvid populations in rapidly adopting novel strategies, these mechanisms may not always be necessary. Associative learning, which can also involve forming connections between innate behavioral responses and favorable outcomes (Lu, Gudowska, and Rutkowska, 2023), might similarly lead to widespread behavioral adaptations within populations in certain circumstances (Alem et al., 2016).

Local specialization in interspecific kleptoparasitism has been widely documented among corvid populations globally, yet comparable adaptations to intraspecific kleptoparasitism at the population level appear much rarer, if at all. Intraspecific kleptoparasitism certainly plays a significant role at the individual level; for example, caching species such as *Corvus corax* (common raven) adjust their caching behavior to evade conspecific observers, potentially exhibiting deception and mental state attribution in the process (Bugnyar and Kotrschal, 2002; Bugnyar and Heinrich, 2005; Bugnyar, 2011; Bugnyar, Reber, and Buckner, 2016). A population specializing extensively in intraspecific kleptoparasitism would likely only remain sustainable if kleptoparasitic individuals were far less successful than those employing other primary strategies (Barnard and Sibly, 1981; Ha and Ha, 2003). Otherwise, the diminishing proportion of producers would fail to support the increasing number of scrounging conspecifics (Ranta et al., 1998). This dynamic suggests that sustained behavioral specialization on intraspecific kleptoparasitism may not be profitable for kleptoparasitic individuals long-term, potentially explaining its rarity in crows.

In bird species where intraspecific kleptoparasitism occurs frequently - such as *Larus dominicanus* (kelp gulls) - environmental or behavioral controls prevent populations from reaching unsustainable states (Steele and Hockey, 1995). Kleptoparasitic individuals are often young, inexperienced foragers who rely temporarily on this strategy until learning more effective foraging methods, or natural resource abundance may allow producers to overproduce, compensating for losses to scroungers without affecting their overall food intake. An intriguing phenomenon connecting intraspecific competition with interspecific kleptoparasitism is observed in *Mareca strepera* (gadwalls), where lower-ranking individuals use interspecific kleptoparasitism to avoid competition with dominant members during periods of reduced food availability (LeSchack and Hepp, 1995). Food abundance at Zoo Vienna is typically high, but it may be valuable to investigate whether elevated conspecific density leads to a similar rise in interspecific kleptoparasitism within the local crow population.

Kleptoparasitism has been studied extensively in corvids, as have other behavioral and cognitive components involved in crow-human interactions - such as facial recognition (Marzluff et al., 2010), neophobia (Miller et al., 2022), scrounging (Bugnyar and Kotrschal, 2002), social learning, and foraging (Skandrani et al., 2017). However, there remains a gap in understanding how these elements interplay holistically, particularly in the ecologically relevant context of crow-visitor dynamics in zoos. Observing these interactions could provide further insights into crow cognition (Seed, Emery, and Clayton, 2009). For crows to identify visitor patterns, recognize individuals in crowded environments, and potentially produce stimuli to manipulate humans - a species with a drastically different evolutionary history - would represent a notable cognitive achievement.

This study aims to provide insight into the ethological processes shaping human-crow interactions. By examining how wild crows choose human targets for scrounging, and identifying commonalities between interactions and individual characteristics, it may be possible to determine the cues crows use to assess risks, select preferred hosts, and the impacts of preferential targeting on the producer-scrounger dynamics within the population.

Additionally, signs of behavioral optimization - defined as maximizing benefits while minimizing costs - may emerge. In the context of scrounging from visitors, optimal behavior would yield high food rewards while minimizing risks. Given evidence of crows' abilities in recognizing humans (Marzluff et al., 2010) and categorical learning (Seed, Emery, and Clayton, 2009), consistent patterns of preferential targeting and correlations between crow behavior, visitor traits, and interaction profitability could indicate behavioral optimization. Furthermore, the dynamic between initiating and joining crows is very intriguing. Initiating crows could act as producers, reducing the risks and costs of identifying and approaching a host (Arbilly et al., 2014; Aplin and Morand-Ferron, 2017) for joining conspecifics. Joining individuals may benefit more by scrounging from successful initiators than approaching new visitors independently - a strategy with potential risks involved, even within the zoo's safe environment (Giraldeau and Dubois, 2008), as humans can be considered a large predator species.

Three hypotheses have been developed to refine these broad goals into a manageable scope for an observational study, based on current scientific understanding. First, it was hypothesized that crows show a preference for visitors exhibiting certain characteristics, such as age, gender, or accessories, when choosing a host. It was predicted that crows would approach visitors with preferred characteristics at proportionally higher rates (Seed, Emery, and Clayton, 2009; Marzluff et al., 2010). Second, the hypothesis that crows optimize their scrounging behavior would be supported if preferential targeting and approach behaviors align with the highest expected profitability (Howell, 1983). Finally, the third hypothesis posits that joining conspecifics target successful event initiators rather than initiating new events to maximize their benefits. This led to the prediction that higher rates of successful scrounging attempts would be observed for joiners compared to new initiators (Arbilly et al., 2014; Aplin and Morand-Ferron, 2017).

2. Methodology

2.1. Study Sites

This research was conducted as an observational study, divided into two phases due to the unavailability of two out of the four selected observational sites (see Figure 1; see Table 2 in the appendix for detailed descriptions and the exact coordinates of the observer's position) within Zoo Vienna over the course of the study. Despite their eventual unavailability, these sites provided valuable data during the first phase of the study.

A total of 32 workdays were selected between October 7, 2024, and December 10, 2024. Weekends were excluded to minimize potential large fluctuations in visitor densities in the data set. Observations were conducted between 11:00 and 16:00 on Mondays, Tuesdays, Thursdays, and Fridays. This time frame was chosen to align with mid to late fall, when the daily activity of both human visitors and crows started later and ended earlier compared to summer months.

Equal observation time was allocated to each location, with one hour per site during Phase 1 and two hours per site during Phase 2. An additional hour was reserved daily as buffer time for rotation between sites, setup, or handling unforeseen interruptions and delays. The rotation schedule was adjusted daily and weekly to ensure equal distribution of time across sites during different hours and weekdays.

Phase 1, which lasted for the first 16 observation days and concluded on November 11, 2024, included all four sites. Phase 2 focused on observation site 1 and observation site 4 during the second half of data collection. The observational sites were selected based on the presence of at least one distinct anthropogenic food source. However, sites 2 and 3 were excluded from Phase 2 due to the unavailability of their food sources. Specifically, observation site 2 featured a restaurant that closed for the remainder of the fall season, while the refreshment kiosk at observation site 3 was obstructed due to construction work.

The observer's position was maintained as consistently as possible throughout the study (see Table 2 in the appendix for coordinates). In cases of unavailability - such as high visitor density, cleaning staff presence, or construction work obstructing the designated position or field of view - the closest feasible position within range was selected instead.

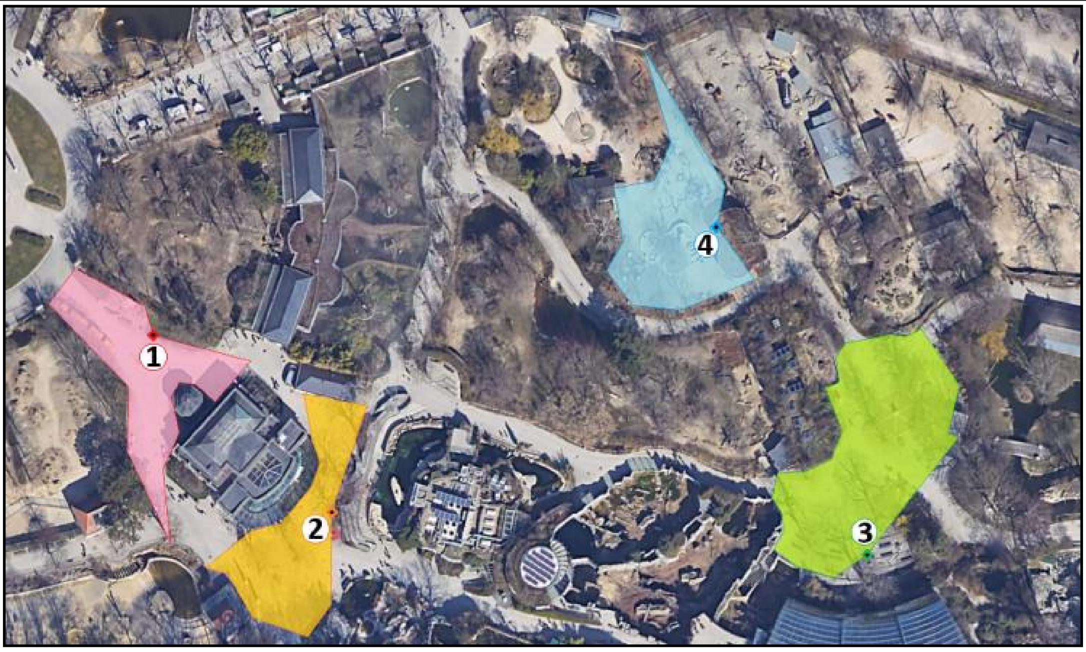

Figure 1. Satellite image of Zoo Vienna, illustrating the observational ranges for scan sampling and behavioral event sampling. Colored sections represent the distinct observational ranges for each location, while numbered spots indicate the precise placement of the observer during the sampling process.

2.2. Study Subjects

The study sampled two distinct groups. Sample Group 1 comprised the local free-range corvid population within Zoo Vienna, which included two crow species, *Corvus cornix* (hooded crow) and *Corvus corone* (carrion crow). These species frequently hybridize within Vienna and are not visually distinguishable, leading to their grouping together for sampling purposes. Sample Group 2 consisted of human visitors interacting with the corvid population.

2.3. Data Collection

Primary data for this study were collected using group scan sampling and behavioral event sampling.

Scan Sampling: Observations were conducted at 5-minute intervals to approximate the number of zoo visitors and crows within view, as well as to briefly describe the overall weather conditions (see Table 3 in the appendix for detailed descriptions of each recorded variable).

Behavioral Event Sampling:

Two criteria had to be met for an event to be recorded:

1. At least one individual from a sample group had to come within a proximity of less than 1 meter of an individual from a different sample group.
2. At least one of the individuals had to display intentional movement toward the other individual.

For human participants, intentional movement was accurately determined based on gaze direction. For corvid individuals, it was inferred from body movements and their approach trajectory. Two general types of approaching behaviors were defined in this study for crows: careful/stealthy approaches and social/open approaches. Careful approaches involved gaze avoidance (Davidson et al., 2014), lack of vocalization, and pauses or backward movements that slightly increased the distance before closing in on the target (Brown and Jones, 2016). Social approaches were characterized by direct movement within a visitor's field of view, vocalizations, and wing twitching without dominance displays, interpreted as signs of excitement or friendly encouragement rather than aggression (Diamond and Bond, 2003). An event was deemed concluded when either participant exited a radius of approximately 3 meters. This radius also established the boundary for grouping additional interactions and participants as part of the same event, rather than initiating a new one. Simultaneous interactions occurring more than 3 meters apart were recorded as separate events.

Variables recorded for behavioral event sampling included the initiation type, group sizes of visitors and crows present at the start of the event, how the initiating crow profited, and various visitor characteristics such as age, gender, worn accessories, and mobility aids. Additional variables, such as the target of joining conspecific crows, type of profit, and the individual they profited from, were recorded only if a crow joined an event in progress (see Table 4 in the appendix for detailed descriptions of each variable). To avoid confusion, crows joining an ongoing interspecific interaction are henceforth referred to as "joiners" (Giraldeau and Dubois, 2008).

All primary data were manually entered into an `.xlsx` file in real time during both scan and behavioral event sampling. To facilitate the efficient recording of numerous variables, 2-letter-code shortcuts were used for manual entries. These shorthand codes were later converted into full labels for enhanced readability.

2.4. Analysis

2.4.1. Tools

Initial modifications to the data set, aimed at enhancing its suitability for statistical analysis, were performed directly within the `.xlsx` file using WPS Office. For detailed information on variable changes, refer to Table 5 in the appendix, and for descriptions of finalized variables used in the statistical models, see Table 6 in the appendix.
Subsequent data preparation, statistical analysis, and visualization were conducted using R (version 4.3.2).

2.4.2. Data Preparation

Three multinomial baseline-category logit models were developed to test the study's hypotheses. Some variables initially recorded were modified, removed, or merged prior to loading the data into R Studio. These adjustments were performed directly in the `.xlsx` file using WPS Office (refer to Table 5 in the appendix for details on variable changes; see Table 6 in the appendix for descriptions of finalized variables used in the statistical models).
Once the original data collection sheet was corrected and finalized, it was converted into a `.csv` file. The dataset was subsequently loaded into R using the `read_csv` function from the `readr` package, and all predictor variables were dummy coded with the `fe.re.tab` custom function from Roger Mundry's `diagnostic_fcns.r` script. Variables such as Date, Hour, Weather, and Location were coded into the modified data set as random effects using the same function, allowing them to be accounted for in the analysis without explicitly including them in the model functions (see Table 7 in the appendix for model functions).
Next, factor variables were adjusted by subtracting their arithmetic mean using the `mean` function from the `base` package. Numeric predictor variables were z-score-normalized to ensure their values followed a normal distribution with a mean of 0 and a standard deviation of 1. This normalization process was performed using functions from the `base` package, including `scale`, `as.vector`, `mean`, and `sd`.

2.4.3. Data Analysis

The full statistical models developed to test each hypothesis, along with their reduced versions containing only the most essential predictors and null models for comparison with the respective null hypotheses, were fitted using the `mblogit` function from the `mclogit` package. These models underwent multiple corrective cycles, during which dispersion was assessed with the `dispersion` function from the `mclogit` package, and collinearity was evaluated using the `multicollinearity` function from the `performance` package. When dispersion ratios deviated from 1 or variance inflation factors (VIFs) were high, variables were adjusted until all values fell within acceptable ranges without significant loss of information (see Table 7 in the appendix for comparisons of full models before and after corrective cycles, along with explanations for changes made to each model).

The full, reduced, and null models were compared using Chi-square tests conducted with the `anova` function from the `stats` package. Results were exported as data frames with the `as.data.frame` function from the `base` package to determine whether the full models provided better explanations of variance and were appropriate for hypothesis testing.

A power analysis was conducted by first creating intercept-only versions of each final model using the `mblogit` function from the `mclogit` package. Log-likelihoods for both the final and intercept-only models were calculated with the `logLik` function from the `stats` package, and McFadden R^2 values were determined by subtracting the ratio of the final model's log-likelihood to that of the intercept-only version from 1. Average effect sizes were calculated as the ratio of the McFadden R^2 values to 1 minus the McFadden R^2 values. These effect sizes were used in the `pwr.f2.test` function from the `pwr` package to compute the actual power of each model at a significance level of 0.05, which exceeded 0.99 for all final models.

Correction for multiple testing was implemented using a custom function that looped through each final model to extract p-values and variable names from their respective summaries, generated with the `summary` function from the `base` package. Two correction methods were applied: the Benjamini-Hochberg correction, to control for false discovery rates, and the Hochberg correction, a stricter method to control family-wise error rates. Both corrections were performed using the `p.adjust` function from the `stats` package. Employing two correction methods allowed for cross-validation of results and ensured that significant statistical trends remained robust under stricter conditions.

When multiple categories of a single variable exhibited significant effects on a response variable, Wald tests were performed to compare categories and assess whether their effects differed significantly in magnitude.

2.5. Ethical Considerations

As the study was purely observational, it did not require ethical approval. The observer was positioned on a bench, resembling a regular resting visitor, ensuring minimal intrusion. Event participants were anonymously and superficially categorized into broad groups without recording any personal information. No animals were handled or disturbed, and the study had no discernible impact on the visitor experience or any obstructive effect on the daily routines of zoo employees.

3. Results

The probability of crows initiating an event decreased significantly with the number of conspecifics nearby.

Both careful crow initiators (event-initiating crow approached carefully/stealthily) and social crow initiators (event-initiating crow approached visitor socially/openly) showed a sharp decline in initiation probabilities as the number of participating crows at the start of the event increased (see Figure 2).

Crows predominantly preferred approaching older visitors with developing or fully developed secondary sexual characteristics compared to the prepubescent reference group, both socially and carefully (see Figure 3).

However, no preference was observed regarding visitor sex.

Crows initiated interactions more carefully as visitor group sizes increased (see Figure 4).

Visitors with strollers were targeted preferentially, both socially and carefully (see Figure 5), whereas other man-made objects showed no significant effects.

Visitors were significantly more likely to feed larger groups of crows (see Figure 6) and during higher overall crow densities in the area.

Adult visitors fed crows much more than prepubescent individuals (see Figure 7).

Although crows had lower probabilities of receiving food during events initiated by themselves rather than visitors, success rates were still significantly higher for crows that engaged socially than crows that approached in an oblique and careful manner (see Figure 8).

However, crows approaching carefully were far more likely to steal food from visitors (see Figure 8).

Profitability for crows joining an event in progress was higher when an initial crow participant received food beforehand (see Figure 9).

Joining crows benefited significantly more from events initiated by an initial crow participant than initiating new events with other crows and visitors (see Figure 9).

For a list of estimates, z-values, and p-values of only predictor variables with statistically significant p-values, refer to Table 1 below.

For a comprehensive list of all estimates, z-values, and p-values of predictor variables, refer to Table 8 in the appendix.

Table 1. Estimates, Standard Errors, Z-values, and Hochberg Corrected P-values for Predictors with Statistically Significant P-values

Variable	Estimate (± Standard Error)	Z-value	Hochberg Corrected P-value
Social Crow Initiator: ***(a)***			
(Intercept)	0.613 ± 0.0944	6.49	1.77e-09*
Initial Crow Group Size ***(b)***	-0.505 ± 0.0948	-5.33	1.87e-06*
Pubescent Visitor ***(c)***	2.58 ± 0.379	6.82	1.95e-10*
Adult Male Visitor ***(c)***	3.02 ± 0.255	11.8	5.73e-31*
Adult Female Visitor ***(c)***	2.76 ± 0.246	11.2	9.60e-28*
Visitor has Stroller	0.717 ± 0.222	3.23	2.00e-02*
Careful Crow Initiator: ***(a)***			
Initial Visitor Group Size ***(b)***	0.364 ± 0.0957	3.81	2.37e-03*
Initial Crow Group Size ***(b)***	-0.680 ± 0.122	-5.58	4.80e-07*
Pubescent Visitor ***(c)***	1.77 ± 0.451	3.94	1.50e-03*
Adult Male Visitor ***(c)***	3.23 ± 0.279	11.6	1.37e-29*
Adult Female Visitor ***(c)***	3.12 ± 0.267	11.7	3.70e-30*
Visitor has Stroller	0.742 ± 0.233	3.19	2.16e-02*

Initial Crow Fed: ***(d)***			
(Intercept)	-2.02 ± 0.117	-17.3	2.01e-65*
Crow Density ***(b)***	0.257 ± 0.0829	3.10	4.31e-02*
Initial Crow Group Size ***(b)***	0.542 ± 0.0851	6.37	5.09e-09*
Adult Male Visitor ***(c)***	1.55 ± 0.295	5.25	3.72e-06*
Adult Female Visitor ***(c)***	1.71 ± 0.293	5.84	1.32e-07*
Social Crow Initiator ***(e)***	-0.965 ± 0.237	-4.08	1.05e-03*
Careful Crow Initiator ***(e)***	-2.89 ± 0.359	-8.05	2.29e-14*
Initial Crow Stole: ***(d)***			
(Intercept)	-3.14 ± 0.216	-14.5	2.48e-46*
Careful Crow Initiator	3.01 ± 0.652	4.62	9.22e-05*
Joiner Profited: ***(f)***			
(Intercept)	-6.45 ± 0.650	-9.92	5.48e-22*
Initial Crow Profited	4.77 ± 0.572	8.33	1.11e-15*
Joiner Joins Initiator ***(g)***	5.97 ± 0.662	9.01	3.17e-18*
Joiner Initiates New Event ***(g)***	3.88 ± 0.695	5.58	3.10e-07*

Unless explicitly stated otherwise, all variables were compared against their absence or a baseline condition.

***a*: *Social Crow Initiator* (event-initiating crow approached visitor socially/openly) and *Careful Crow Initiator* (event-initiating crow approached carefully/stealthily) compared against *Human Initiator* (event initiated by visitor).

***b*: Count data scaled to mean = 0 and standard deviation = 1 for better model convergence/comparability.

***c*: Visitors of *pubescent/adult* development stage compared against *prepubescent* stage.

***d*: *Initial Crow Fed* (initial crow participant profited by being fed) and *Initial Crow Stole* (initial crow participant profited by stealing) compared against *No Profit*.

***e*: A Wald test showed significant differences between the effect sizes for *Social Crow Initiator* and *Careful Crow Initiator* (Wald Statistic = 36.526, $p < 0.001$).

***f*: *Joiner Profited* (event-joining crow profited) compared against *No Joiner Profit*.

***g*: A Wald test showed significant differences between the effect sizes for *Joiner Joins Initiator* and *Joiner Initiates New Event* (Wald Statistic: 10.69624 , $p < 0.005$).

***Significant p-values:** Statistically significant at $\alpha = 0.05$.

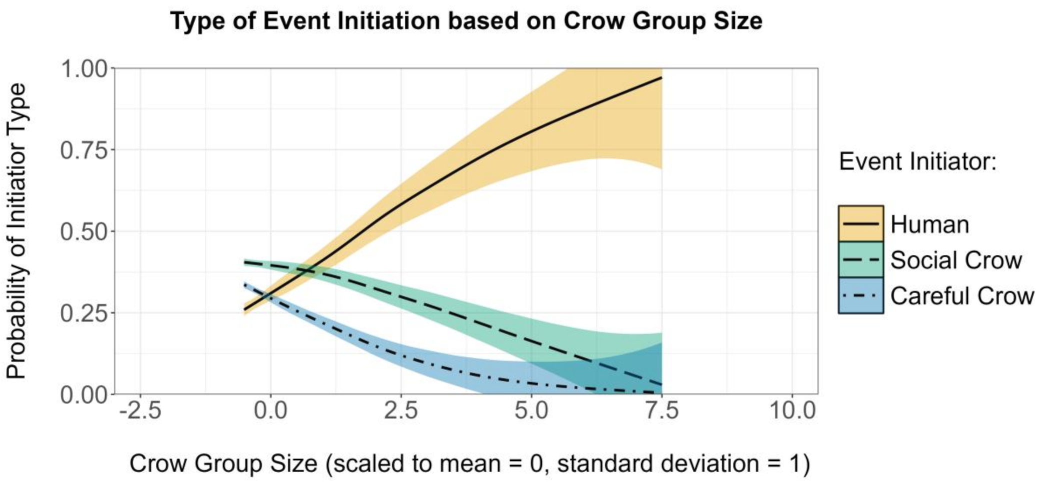

Figure 2. Probability of the initiator in an interspecific interaction between a crow and a zoo visitor being one of the following: a human zoo visitor, a socially engaging crow, or a carefully approaching crow; modeled based on the crow group size at the start of the interaction, scaled to a mean of 0 and a standard deviation of 1.

Note: The x-axis represents standardized group size (mean = 0, standard deviation = 1), so negative values reflect standardization rather than actual negative counts.

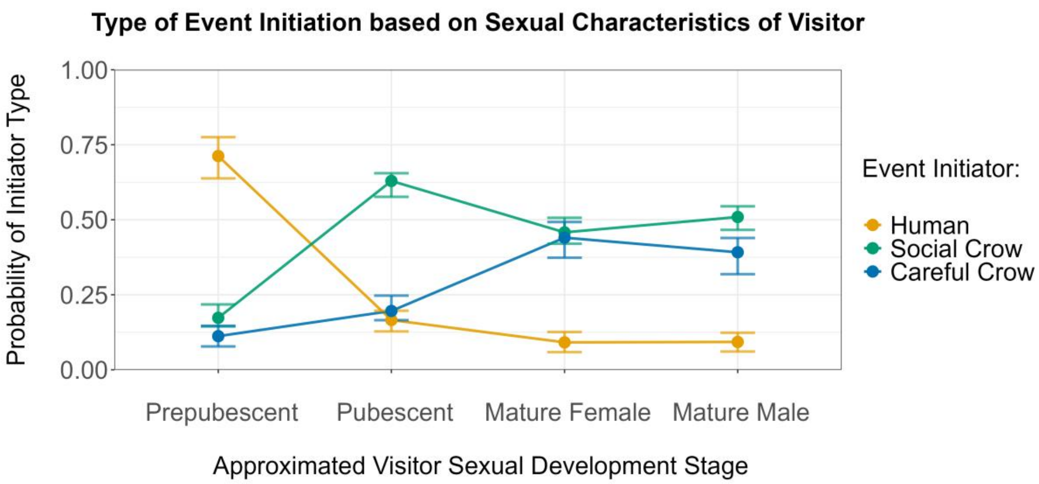

Figure 3. Probability of the initiator in an interspecific interaction between a crow and a zoo visitor being one of the following: a human zoo visitor, a socially engaging crow, or a carefully approaching crow; modeled based on the interacting visitor's approximated stage of sexual development.

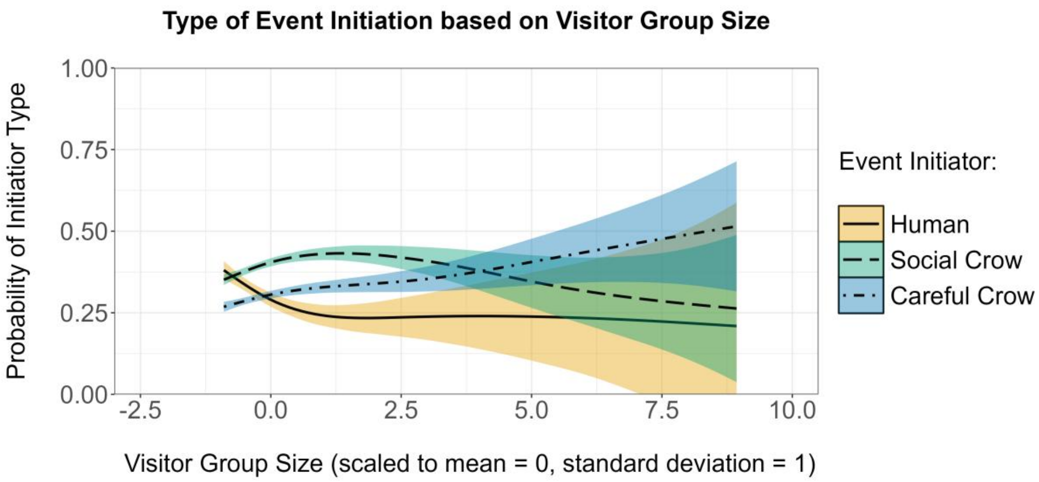

Figure 4. Probability of the initiator in an interspecific interaction between a crow and a zoo visitor being one of the following: a human zoo visitor, a socially engaging crow, or a carefully approaching crow; modeled based on the visitor group size at the start of the interaction, scaled to a mean of 0 and a standard deviation of 1.

Note: The x-axis represents standardized group size (mean = 0, standard deviation = 1), so negative values reflect standardization rather than actual negative counts.

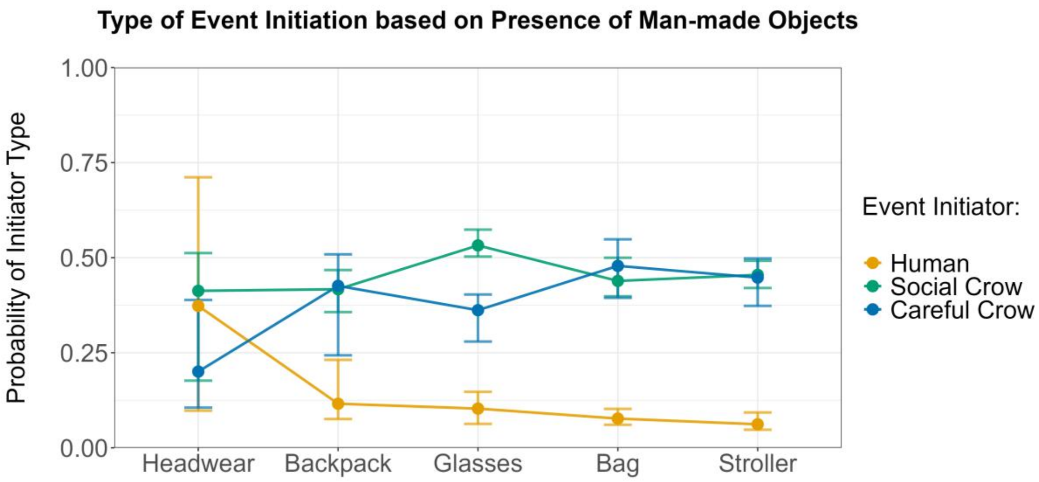

Figure 5. Probability of the initiator in an interspecific interaction between a crow and a zoo visitor being one of the following: a human zoo visitor, a socially engaging crow, or a carefully approaching crow; modeled based on the presence of specific man-made objects.

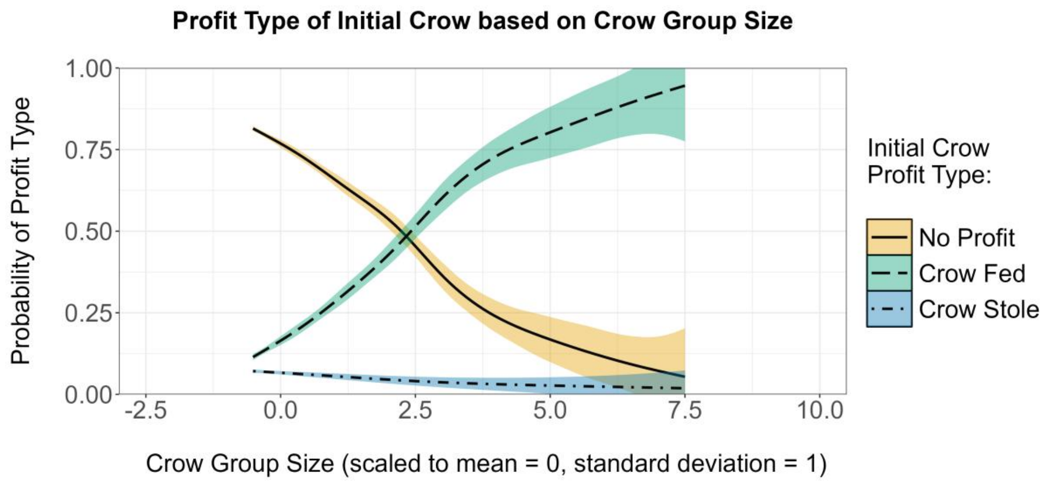

Figure 6. Probability of an initial crow participant in an interspecific interaction between a crow and a visitor receiving no food, being fed by the visitor, or stealing food from the visitor; modeled based on the crow group size at the start of the interaction, scaled to a mean of 0 and a standard deviation of 1.

Note: The x-axis represents standardized group size (mean = 0, standard deviation = 1), so negative values reflect standardization rather than actual negative counts.

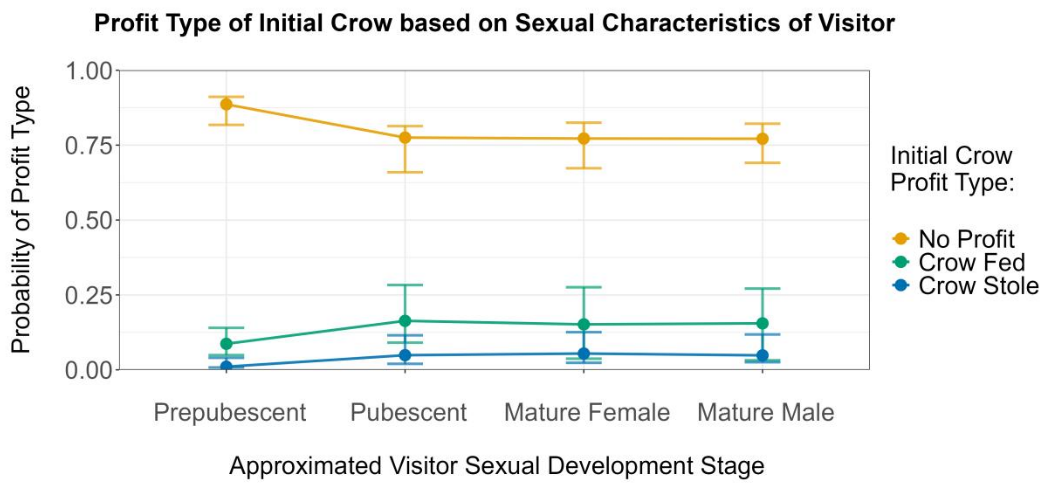

Figure 7. Probability of an initial crow participant in an interspecific interaction between a crow and a visitor receiving no food, being fed by the visitor, or stealing food from the visitor; modeled based on the interacting visitor's approximated stage of sexual development.

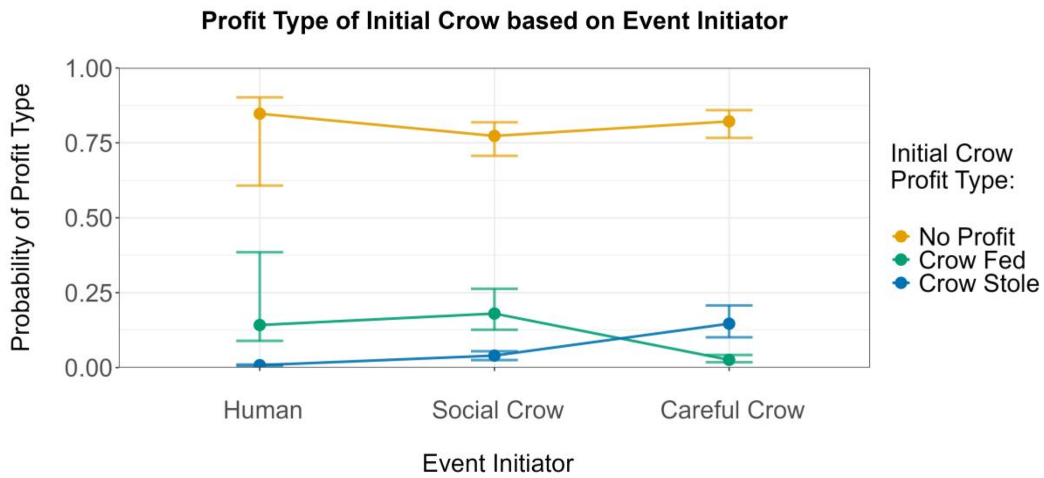

Figure 8. Probability of an initial crow participant in an interspecific interaction between a crow and a visitor receiving no food, being fed by the visitor, or stealing food from the visitor; modeled based on whether the event initiator was a human zoo visitor, a socially engaging crow, or a carefully approaching crow.

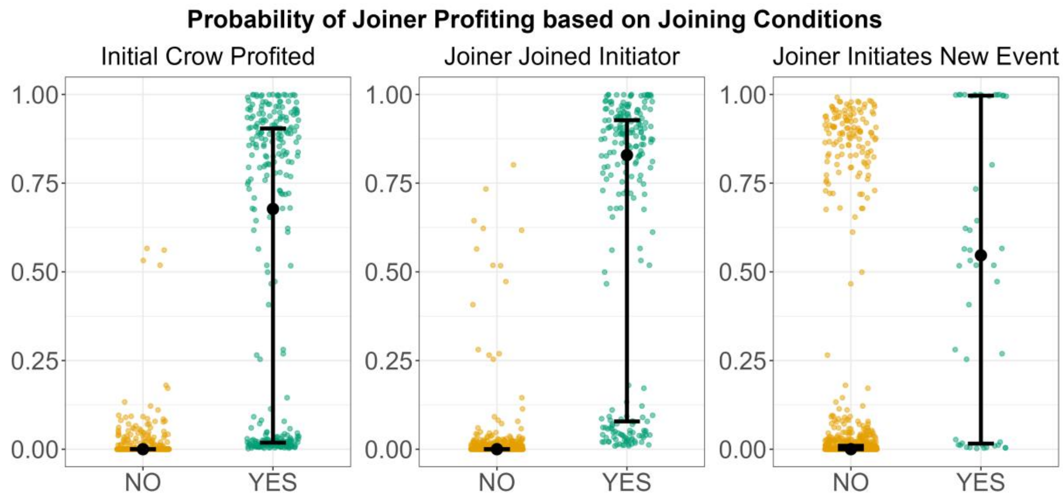

Figure 9. Probability of a joining crow participant in an interspecific interaction between a crow and a visitor receiving food; modeled based on specific joining conditions, including whether an initial crow participant received food first, whether the joining crow participant approached an event initiator, or whether the joining crow participant initiated a new event with a different visitor.

4. Discussion

4.1. Summary

The main objectives of this study were to provide evidence that crows preferentially target human hosts with characteristics they associate with higher success rates for scrounging and to determine whether their behavioral patterns during interspecific interactions reflect a trend toward maximizing profitability while minimizing risks and energetic costs. This behavioral optimization (Howell, 1983), in the context of interspecific scrounging, was hypothesized to extend to the scrounger-producer dynamic between conspecific crows (Bugnyar and Kotrschal, 2002; Flower, Child, and Ridley, 2013) and potentially influence the distribution of predominant foraging strategies at the population level.

The results of this study support most, though not all, predictions for these hypotheses. The crows exhibited preferential targeting of specific visitors and visitor groups for their approaches, validating the first hypothesis. The following visitor characteristics significantly influenced the likelihood of becoming a scrounging target: higher visitor age (see Figure 3), larger visitor group size (see Figure 4), and the use of strollers (see Figure 5). These traits suggest that crows predominantly targeted large family groups, characterized by a wide range of ages. This inference arises from the simultaneous presence of older individuals and strollers, which are exclusively associated with aiding very young children in mobility.

Contrary to predictions, crows did not adjust their approach behavior based on the characteristics of their targets. However, the outcomes of interactions were strongly dependent on the approach type (see Figure 8).

Careful approaches did not increase during periods of high overall visitor density, indicating that the local crow population is strongly habituated to human activity. However, crows were more hesitant when approaching larger visitor groups (see Figure 4). Visitors were most likely to feed crows when they initiated interactions themselves, but when crows approached first, visitors preferred to feed individuals that engaged socially rather than those displaying careful, oblique behavior (see Figure 8). Other key factors facilitating bird-feeding practices included overall crow density and the number of crows interacting with the visitor (see Figures 2 and 6). Older visitors were significantly more likely to engage with crows in a positive social manner (see Figure 7). Notably, the choice of a careful approach was identified as the strongest predictor of successful interspecific kleptoparasitism on human hosts (see Figure 8).

In the interspecific context, human visitors acted as producers in the scrounger-producer dynamic. However, the crows also interacted intraspecifically while scrounging from visitors. In these cases, the initial crow receiving food from a human served as the producer, while other crows joining later and profiting from the interaction acted as scroungers (Aplin and Morand-Ferron, 2017).

Joiners were most likely to secure food when they first approached a conspecific already interacting with a visitor, rather than attempting to secure food independently, as predicted (see Figure 9). This finding supports the hypothesis that joiners achieve greater success by targeting successful conspecifics rather than initiating new events with visitors. Additionally, joiners were more successful when the event-initiating crow had already profited from the interaction.

4.2. General Discussion

The most significant cue for a scrounging crow's host choice appears to be age (see Figure 3). While the presence of strollers increased the likelihood of a crow approaching (see Figure 5), adult visitors with fully developed secondary sexual characteristics were overwhelmingly preferred as approach targets over very young individuals typically occupying strollers. This aversion to targeting very young individuals - within the approximate age range of three years and below, determined by their dependency on strollers for mobility - is unlikely to stem from fear. Rates of careful approaches, indicative of a fear response, were found to be lowest for this age group. It can be inferred that crows, known for their ability to recognize and categorize human features (Marzluff et al., 2010; Marzluff et al., 2012), have learned through repeated exposure to human family units (Marzluff and Angell, 2005) to associate individuals in this age group with traits that make them less suitable scrounging targets. These traits include an inability to provide food independently and, except for those nearing the upper age limit of this group, a lack of mobility due to underdeveloped motor skills.

Interestingly, other objects potentially used for carrying food, such as bags and backpacks, did not significantly influence approach rates. This observation can be interpreted in several ways. Crows may recognize strollers as easier targets (Bugnyar and Kotrschal, 2002; Flower, Child, and Ridley, 2013), as strollers, unlike bags and backpacks, are not carried directly on the person and are typically more accessible from multiple directions. Bags - defined as smaller, portable storage carried by hand or across the shoulder with a single strap - and backpacks - defined as storage carried on the back using two straps - often remained on the person, even during resting or eating. In contrast, strollers were frequently placed farther away. For example, at the playground, parents often left strollers near tables or benches while joining their children in play areas on the opposite side. However, it is worth noting that kleptoparasitism events were only recorded if the host remained within the predefined 3-meter event radius, as this study focused exclusively on direct interspecific interactions.

Another possibility is that strollers act more as indicators of family units than as direct food sources (Marzluff and Angell, 2005). Local crows may have learned to associate family units with increased generosity, and strollers could serve as easily recognizable symbols of such groups. Due to their size and uniform appearance, strollers are more visible from greater distances compared to other potential identifiers. A potential contradiction to the association of family units with food lies in the finding that larger visitor group sizes did not significantly correlate with bird-feeding practices. This discrepancy could be explained by the presence of very young individuals counteracting the higher profitability of older individuals within the family unit, identified as primary providers (see Figure 7). This aligns with prior findings that older individuals are more likely to feed birds (Davies et al., 2012) and spend more money on food during zoo visits when accompanied by children (Knežević, Žučko, and Ljuština, 2016). It is therefore possible that crows formed a secondary association between family units and food due to the presence of multiple older individuals within them, even if approaching these groups over solitary older individuals was not more profitable in practice.

Another notable finding is that larger foraging groups of crows were less likely to initiate interspecific interactions with humans (see Figure 2). This result is somewhat counterintuitive, as vigilance behavior (Beauchamp, 2001) - which might discourage a crow from approaching humans - generally decreases with increasing group size (Ward and Low, 1997), and scrounging behavior in birds often increases with larger flock sizes (Aplin and Morand-Ferron, 2017). A study investigating interspecific interactions between park visitors, red squirrels, and corvids (Beliniak and Krauze-Gryz, 2024) found that the presence of conspecifics reduced the likelihood of corvids scrounging, possibly due to avoidance of intraspecific competition. However, differences in study design limit the direct applicability of this explanation here. Since this study focused exclusively on interactions between two species, an interaction could only occur if either a human or a crow initiated it, resulting in an inverse relationship between crow and human initiation rates. This complicates determining whether crows were less likely to engage with visitors when foraging in groups, or whether visitors were more motivated to interact with larger flocks than with solitary crows. Evidence supporting the latter interpretation includes the finding that crows approaching more openly and in larger groups increased their chances of being fed.

Despite the expectation that social facilitation (Federspiel et al., 2023) would play a primary role in interspecific engagement with visitors, close proximity to a large number of conspecifics may nonetheless incentivize individual crows to adopt alternative foraging strategies to minimize intraspecific competition (Giraldeau and Dubois, 2008). Like many avian populations, the Zoo Vienna crow population exhibits fission-fusion dynamics (Silk et al., 2014; Uhl et al., 2019), with numerous unfamiliar conspecifics entering and leaving the area. This dynamic may lead to foraging groups comprising conspecifics outside the approaching crow's kin group, social alliance, or circle of familiarity. Members of such groups are more likely to perceive one another as competitors rather than collaborators. Under these circumstances, and considering the high abundance of natural resources within Zoo Vienna, crows may favor safer, conventional foraging strategies (Beauchamp and Giraldeau, 1997; Bugnyar and Kotrschal, 2002).

The benefits of kleptoparasitism are often outweighed by the inherent risks associated with it (Flower, Child, and Ridley, 2013), such as high variance in success rates, significant energy investment in observing, following, and attacking hosts, and the potential for serious injuries from retaliating hosts. These risks are largely mitigated in crow-visitor interactions at Zoo Vienna, where visitors rarely pose physical danger, do not require attacking, and often share food willingly. Additionally, food sourced from predictable locations like restaurants and kiosks makes visitors reliable targets, reducing the time and energy spent on tracking. However, conspecifics in close proximity still pose challenges to crows initiating interactions, as they may compete for the same target or benefit from the scrounger's success without incurring the associated costs and risks (Beauchamp and Giraldeau, 1997).

Effect sizes of approach types did not vary significantly with visitor age, indicating that older individuals are generally more attractive targets regardless of how cautiously or hesitantly a crow may approach them. This suggests that the association between older visitors and food rewards is strong enough to encourage even hesitant crows to approach, despite the need to overcome an initial fear response. A study by Tätte, Møller, and Mänd (2020) on dynamic risk assessment found that crows adjust their behavior in response to perceived risks, even during a flight response. Similar cognitive processes are likely employed when approaching human visitors, especially since the study used a human observer as a simulated predator.

The correlation between higher visitor group size and increased approach rates - particularly careful approaches, but not open ones (see Figure 4) - suggests that large visitor groups, especially family units, are attractive but also perceived as riskier targets. Another interpretation is that careful approaches may not always indicate fear but could instead reflect the crow's perception of visitors' conspecifics as interspecific competitors, prompting a more covert attempt to secure food. This interpretation, however, implies a higher level of cognitive complexity to account for behaviors such as gaze avoidance. In this context, gaze avoidance might signify an attempt to outmaneuver a resource competitor rather than evasion of a predator's attention (Davidson et al., 2014; Bugnyar and Kotrschal, 2002; Clucas et al., 2013).

Higher crow group sizes at the onset of an interaction inhibited both careful and open approaches (see Figure 2). Crows did not show an increase in direct engagement with visitors during periods of high conspecific density, even though prior studies suggest that larger numbers of conspecifics within the sensory space often reduce inhibition in other bird species, such as zebra finches, when interacting with novel objects (Coleman and Mellgren, 1994).

High conspecific density is also commonly associated with reduced vigilance behavior (Bednekoff and Lima, 1998), a pattern that had been expected to extend to crows' interspecific engagements with visitors (Ward and Zahavi, 1973). Prior research (Freeman and Miller, 2018) showing that larger crow groups defend themselves more aggressively against predators through mobbing behavior when flock-to-predator ratios are favorable, suggested that the tendency for larger groups to engage interspecifically might even reflect broader behavioral trends beyond sociopositive interactions.

The lack of a significant effect of high overall visitor activity on careful approach rates highlights the habituation of the Zoo Vienna crow population to intense human presence. However, it remains crucial to emphasize that humans are still a predator species, and crows face risks from improperly assessing individual visitors. Although rare, observations included visitors throwing rocks, striking with sticks or umbrellas, or attempting to step on crows. Having vigilant conspecifics nearby to help deter such aggressors is essential for minimizing these risks, which makes the inhibitory effect of crow group size on approach rates particularly unexpected.

The lack of preference among crows for open approaches over careful ones could challenge the notion of behavioral optimization in this population, as visitors were significantly more likely to feed crows that approached them directly. Crows are adept at observing conspecifics and learning quickly in social contexts (Miller, Schwab, and Bugnyar, 2016; Federspiel et al., 2023). Individual crows with prior experience interacting with various visitor types should accelerate the categorical learning of safe approach targets for conspecifics. While the Zoo Vienna crows appear adept at identifying optimal hosts based on scrounging success likelihood, they may still need to refine their ability to manipulate host behavior to maximize benefits.

It is also unexpected that crows showed no preference for careful approaches during high visitor densities, as increased activity would typically be considered intimidating and discouraging. However, several possible explanations might account for this. The habituation to high human activity could have diminished the fear response in the local crow population to such an extent that more visitors are perceived as additional scrounging opportunities rather than potential threats (Clucas et al., 2013). If this were the case, one would expect higher overall approach rates during periods of high visitor density. However, as previously noted, this was not observed, likely due to visitors initiating the interactions instead.

Contradicting this level of habituation is the finding that larger visitor group sizes increased the likelihood of careful approaches, which could suggest an elevated fear response, at least under a straightforward interpretation. Alternatively, if careful approaches do not necessarily reflect fear but rather a perception of visitors as potential food competitors, crows may benefit from avoiding attention while approaching larger groups. Direct and social approaches, especially those involving playful or begging behaviors, may draw the attention of unwanted competitors (Bugnyar and Kotrschal, 2002). Corvids are known to interpret gaze direction as an attention cue (Schloegl, Kotrschal, and Bugnyar, 2007; Davidson, Clayton, and Thornton, 2015). Thus, a crow perceiving visitors as competitors might prefer a covert approach to exploit the host quickly before other scroungers intervene (von Bayern and Emery, 2009). This could explain their preference for careful approaches, even if they have learned that direct and social interspecific engagement is more likely to elicit bird-feeding. The potential loss of maximum biomass intake may be outweighed by a reduced risk of competition from other scroungers.

Careful approaches preceding kleptoparasitism events could also be interpreted conservatively as neophobic behavior (Brown and Jones, 2016) or, more compellingly, as goal-directed behavior. If viewed as neophobia, strongly fearful crows may avoid direct interaction with humans and only profit from food within the 3-meter event radius when left unattended. This form of indirect kleptoparasitism could be the only viable strategy for such neophobic individuals in crow-visitor interactions. Alternatively, careful approaches may reflect intentionality in approach type selection, suggesting some degree of goal-directed behavior. While studies have shown corvids are capable of planning and adjusting their actions flexibly (Boeckle and Clayton, 2017; Kabadayi and Osvath, 2017; Boeckle et al., 2020), including carrion crows (Corvus corone) (Rinnert and Nieder, 2021) and hooded crows (Corvus cornix) (Smirnova et al., 2024), caution is warranted when inferring complex cognitive processes solely from body movement patterns observed and interpreted by a single individual. However, high habituation levels and the absence of typical fear indicators within the observation data lend support to the interpretation of goal-directed behavior (Benmazouz et al., 2021).

Regardless of approach behavior, the preference for older visitors partially supports the hypothesis that crows have learned to optimize their host choices. Older visitors were significantly more likely to engage with crows positively and feed them, while very young visitors were particularly unlikely to share food (see Figure 7). This discrepancy may stem from younger individuals' underdeveloped prosocial tendencies and responsiveness to interspecific expressions of need (Brownell, Svetlova, and Nichols, 2009).

The higher success rates of crows in larger groups and during higher overall density suggest that Vienna Zoo visitors are generally inclined to feed wild birds when made aware of their presence (see Figure 6). The increased frequency of feeding events during higher local crow densities likely results from repeated exposure and more opportunities for visitors to engage with crows. This aligns with findings that establishing connections with wildlife is a key motivation for zoo visitors and bird feeders alike (Cox and Gaston, 2016; Knežević, Žučko, and Ljuština, 2016; Howell, McLeod, and Coleman, 2019). The tendency for direct approaches to increase crows' chances of success (see Figure 8) likely reflects their effectiveness in drawing visitors' attention. Additionally, the social aspects of open approaches - such as vocalizations and playful or pleading body language - may elicit empathetic responses, even if visitors do not interpret the interspecific communication cues entirely correctly.

Unexpectedly, the frequency of bird-feeding events did not correlate with higher visitor densities. It was assumed that increased visitor numbers would lead to more bird-feeding events, particularly since the number of directly approaching crows did not significantly decrease, and humans are known to exhibit susceptibility to social facilitation (Bond and Titus, 1983) and social contagion effects (Christakis and Fowler, 2013). However, this discrepancy may be explained by higher visitor density disrupting potentially profitable interactions for crows. Noise pollution, interruptions caused by other visitors, or dense oncoming foot traffic may startle crows or compel them to abandon interactions prematurely.

The most compelling discovery of this study, with significant implications for future behavioral patterns and foraging strategy dynamics within the local population, is that joiners exhibited higher success rates when joining ongoing interactions between a crow and a visitor, rather than initiating new interactions (see Figure 9). The costs of being a joiner are inherently lower (Flower, Child, and Ridley, 2013), as their primary risk only involves intraspecific conflict rather than retaliation from the human host - a large potential predator capable of inflicting fatal injuries. The higher success rates of joiners targeting initial crows that had already profited suggest that joiners were not disadvantaged by joining feeding events later. The same visitor groups most responsible for feeding initiating crows also fed joiners more frequently.

Initiators play a critical role in sustaining scrounging as a viable foraging strategy for the local population. However, the low costs and high effectiveness of joining behavior could reduce the number of initiators over time. The lower rates of scrounging observed in larger foraging groups could act as a counterbalance to the inherent advantages joiners enjoy (Beauchamp and Fernández-Juricic, 2005), and may contribute to maintaining a dynamic equilibrium, supporting the development of a behaviorally stable strategy within the population (Giraldeau & Dubois, 2008).

4.3. Limitations

The high behavioral flexibility of *Corvus* species means individual behavioral adaptations to unique environments cannot be entirely ruled out (Emery and Clayton, 2004; Miller et al., 2022). Consequently, significant findings from this population may not be universally applicable to each species. Furthermore, this study was conducted within a single season - Fall - which could further limit the scope of its conclusions.

A positive aspect of the study was the relatively high throughput during data collection, with a large sample size of 1,212 behavioral events. This allowed for the development of three statistical models without significantly compromising statistical power. General limitations inherent to observational studies conducted by a single observer - such as observer bias, data loss due to poor visibility, and simultaneous behavioral events - were anticipated and accounted for during the design phase.

Several additional limitations emerged later during data collection and analysis. Logistical constraints included the loss of observation site 2 due to the restaurant - the primary point of interest - closing for the remainder of the allocated observation time. Similarly, observation site 3 was rendered unusable due to construction work obstructing the field of vision and disturbing the study subjects.

During data analysis, nearly all variables required modifications to fit the statistical models. While this was achieved without introducing errors, some categories of data points had to be cut or merged due to insufficient sample sizes (see Table 5 in the appendix for details). Variables such as human gender and human approach type, which initially contained enough data points for all categories, were poorly designed and required modification or removal. For the human gender variable, the majority of data points for toddlers (0–3 years) and children (4–10 years) were categorized as unidentified/non-binary due to undeveloped secondary sexual characteristics. Classification based on current cultural identifiers of gender - such as style of hair, clothing, and choice of accessories - was avoided due to its unreliability as a predictor of gender identity, especially for individuals of such young age. This resulted in high collinearity between age and gender, negatively impacting statistical models. Merging data points into a new variable based solely on the presence of developing or fully developed secondary sexual characteristics mitigated this issue. Only four adult visitors were classified as potentially non-binary or transitioning due to incongruities between secondary and tertiary sexual characteristics. Removing these data points allowed for inclusion of the variable while retaining 1,208 data points overall.

The human approach type variable, designed to categorize visitor interactions with crows, was replaced with a binary outcome after observing an intriguing phenomenon during sampling: visitors often behaved contrary to their initial approach type. For example, a visitor might initiate an interaction calmly, offering food, only to later use threatening gestures to chase the crow away - or vice versa. Initially considered rare, by observation day 12, it became apparent that the initial approach type was an unreliable predictor of subsequent behavior. This rendered the initial categories of the variable largely uninformative. Although it was too late to revise the variable at that stage, future studies adopting a similar design could benefit from introducing a follow-up variable to capture instances of threatening or nonthreatening behaviors during an interaction. Alternatively, new categories, such as "nonthreatening approach + threatening interaction" and "threatening approach + nonthreatening interaction," could be added to more accurately represent these observed patterns.

Ambiguities also emerged in the interpretation of the response variables: careful approach and kleptoparasitism. Careful approaches were broadly defined, encompassing behaviors resembling fear responses as well as deliberate, covert movements around competitors. This was particularly evident in cases where careful approaches preceded kleptoparasitism. Regarding kleptoparasitism, requiring human proximity for event recording resulted in the exclusion of many interactions between crows and unattended objects. Expanding the definition of behavioral events to include objects such as strollers and backpacks as proxies for visitors could have mitigated this limitation.

While more a limitation of scope than study design, future research could benefit from investigating color composition as an important characteristic for host targeting. Plumage color is a crucial visual cue for recognizing conspecifics, which crows may substitute with human clothing, hair, eye, and skin color when identifying and targeting individual visitors as hosts. Intrinsic color preferences could also influence host selection (Brown and Dooling, 1992; Brown and Dooling, 1993; Troje et al., 1999; Chantoufi et al., 2025).

Another inherent limitation of the study design may explain why visitors did not exhibit social facilitation (Bond and Titus, 1983) or social contagion effects (Christakis and Fowler, 2013), which might otherwise have led to a significant increase in bird-feeding rates during periods of high visitor activity. Events only partially visible for most of their duration - lacking key information such as the individual initiating the interaction, visitor characteristics, or outcomes - were excluded from the data set. During peak activity, dense visitor groups often obstructed visual access to points of interest, leaving crows carrying fast food as the only indicator of an event. This limitation likely disproportionately affected bird-feeding events compared to approach events, as the latter typically occurred at the periphery of visitor activity where visibility was better. Feeding events often followed unsuccessful approaches, with crows moving further into dense crowds where they were no longer visible to the observer.

5. Conclusion

This observational study sought to identify key factors shaping and facilitating interactions between Vienna Zoo visitors and wild crows and to explore how the components of these interactions influence one another. It was hypothesized that scrounging crows would use visitor characteristics as cues for host selection, adjust their behavior during interactions to optimize profitability, and benefit more from joining successful scroungers than from attempting to scrounge alone.

The results largely support the main hypotheses, though not all additional predictions were confirmed. Crows demonstrated preferential targeting of visitor groups and individuals belonging to specific predefined categories (see Figures 3 and 4), suggesting that preexisting associations between visitor characteristics and food availability - likely formed through experience - play a key role in determining host selection. Visitors were also more likely to feed crows that approached them directly and socially (see Figure 8), supporting the idea that learning to produce stimuli capable of eliciting empathetic responses from humans is a valuable skill in an anthropogenic environment. Joiners increased their own success rates by targeting conspecifics that had already profited from interspecific interactions, confirming that it was more advantageous to act as a joiner than to initiate a new interaction (see Figure 9). This dynamic could have long-term implications for the foraging strategies of the local population if no intraspecific competition avoidance mechanisms mitigate the profitability of joiners.

Contradictions between predictions and statistical outcomes were particularly intriguing, as they revealed unexpected correlations that provide further insight. For instance, lower approach rates among larger foraging groups of crows, independent of visitor density, suggest that the avoidance of intraspecific competitors exerts a stronger influence on interspecific scrounging behaviors than social facilitation - despite the latter being a key factor in the dynamics of social foraging groups in previous studies (Dally, Clayton, and Emery, 2008). Furthermore, the findings suggest that scrounging in this population may function less as an alternative foraging strategy to circumvent high intraspecific competition and more as an effective means of food acquisition during periods of relatively low intraspecific competition.

Visitors, on average, appear comfortable around the crows and may even find interactions with them enriching, as evidenced by high bird-feeding rates among older age groups, particularly in response to direct and social approaches. As such, it may not be advisable for zoo administrators to implement policies restricting these interspecific interactions (Cox and Gaston, 2016; Davies et al., 2012). Should the local crow population ever be shown to interfere with zoo staff, damage property, or pose risks to zoo animals, preventive measures should aim to address harmful behaviors without hindering the crows' engagement with visitors (Jokimäki et al., 2017).

This study might offer a small contribution to our understanding of visitor-crow interactions and the factors facilitating interspecific scrounging behavior. The findings raise numerous follow-up questions and open avenues for future research, not only within ethology but also in human psychology. Although the primary focus was on crows, owing to the study's background in corvid cognition (Emery & Clayton, 2004; Seed et al., 2009) and its limited scope, future research could delve deeper into visitor behavior - particularly the discrepancies between initial approach types and subsequent actions during interactions.

Further investigation could explore the interplay between social facilitation and intraspecific avoidance, examining how these factors interact to establish a dynamic equilibrium within the population. It would also be intriguing to study the mechanisms supporting the coexistence of initiators and joiners, as well as the dynamics of intraspecific scrounging from interspecific scroungers within populations where kleptoparasitism is prevalent. This would be particularly insightful in contexts where scrounging from other successful scroungers not only proves profitable but also allows joiners to face reduced risks compared to initiators.

Finally, one of the most compelling unanswered questions for cognitive biologists concerns the extent to which intentionality, goal-directed behavior, or flexible planning influences kleptoparasitism at both individual and population levels. The significant correlation between the careful approach type and acts of kleptoparasitism suggests a potential cognitive component that warrants deeper exploration.

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7. Appendix

Table 2. Description of Observational Sites

Site	Location	Observer Position (Coordinates)	Food Source	Food Type
1	Between the cheetah enclosure, monkey house, and antelope enclosure	48°10'55"N 16°18'13"E	Refreshment kiosk	Hot dogs, fries, langos
2	Between the monkey house, sea lion enclosure, “Jumbo Grill Garden” restaurant, and penguin enclosure	48°10'53"N 16°18'15"E	Restaurant, ice cream kiosk	Burgers, fries, ice cream
3	Between the polar bear enclosure, rainforest house, and pelican enclosure	48°10'53"N 16°18'21"E	Refreshment kiosk, ice cream kiosk	Sausages, ice cream
4	Between the playground and petting zoo	48°10'55"N 16°18'20"E	Refreshment kiosk	Sausages, popcorn, ham sandwiches

Table 3. List of Variables Initially Recorded During Scan Sampling

Name	Type	Categories	Description
Date	Quantitative, Random Effect	-	Date of recorded data point
Time	Quantitative, Random Effect	-	Time of day (in hours and minutes)
Location	Categorical, Random Effect	Site 1, Site 2, Site 3, Site 4	Observation site
Weather	Categorical, Random Effect	Sunny, Cloudy, Windy, Foggy, Rainy, Snowy, Hail	Short description of weather conditions on site
Visitor density	Quantitative, Predictor	-	Count of all visitors within view
Crow number	Quantitative, Predictor	-	Count of all crows within view

Table 4. List of Variables Initially Recorded During Behavioral Event Sampling

Name	Type	Categories	Description
Initiator species	Categorical, Response	Crow, Human	The species the initiator of the interspecific interaction belongs to.
Initiation type	Categorical, Response, Predictor	Careful (Crow), Social (Crow), Threatening (Human), Nonthreatening (Human)	How the event initiator approached the other individual, subdivided based on initiator species: - **Careful initiation:** Gaze avoidance, no vocalization, slow and hesitant movement. - **Social initiation:** Within visitor's field of view, vocalizations, wing twitching without dominance display. - **Threatening initiation:** Running, chasing off, shouting, rapid hand and arm movements. - **Nonthreatening initiation:** Walking slowly, soft speaking, offering food.
Visitor group size	Quantitative, Predictor	-	Number of visitors within the 3m event radius.
Crow group size	Quantitative, Predictor	-	Number of crows within the 3m event radius.

Visitor age	Categorical, Predictor	Toddler (0–3 years), Child (4–10 years), Adolescent (11–19 years), Adult (20–59 years), Elderly (60+ years)	Approximate age of the initial human event participant.
Visitor gender	Categorical, Predictor	Unknown, Woman, Man	Only recorded if secondary sexual characteristics were at least partially developed; in case of prepubescent individuals or those showing incongruities between sexual characteristics and gender expression, the gender was recorded as unknown.
Accessories	Categorical, Predictor	Backpack, Bag, Glasses, Headwear, Umbrella, Walking Stick	Accessories worn on the person.
Wheeled mobility aids	Categorical, Predictor	Wheelchair, Stroller	Wheeled mobility aids designed to assist disabled or very young individuals.
Initiator crow profit type	Categorical, Response	No profit, Profited by being fed, Profited by stealing food	How the initial corvid participant profited from the interaction; only recorded if the corvid participant received food in some form.

Conspecific crow approach target	Categorical, Predictor	Initial Crow, Initial Human, New Crow, New Human	Which participant of the interaction later joining crows approached first; only recorded if crows entered the event radius that were not present before.
Conspecific crow provider	Categorical, Predictor	Initial Crow, Initial Human, New Crow, New Human	Which participant later joining crows profited from; only recorded if crows entered the event radius that were not present before and received food in some form.
Conspecific crow profit type	Categorical, Response	Profited by being fed, Profited by stealing food	How later joining crows profited from the interaction; only recorded if crows entered the event radius that were not present before and received food in some form.

Table 5. List of Initial Variables Modified for Data Analysis			
Initial Variable	**New Variable**	**Type of Modification**	**Reason for Modification**
Time	Hour	Removed minutes from data points (initial format: h:m). Changed from quantitative variable to categorical variable with 5 levels: 11:00–12:00, 12:00–13:00, 13:00–14:00, 14:00–15:00, 15:00–16:00.	Reduction of model complexity.
Weather	Weather	Removed 2 categories: snowy, hail.	Not enough data points for these categories.
Initiator species	Initiator crow, Initiator human	Split into 2 variables with binary outcomes (no/yes).	Added more flexibility to model design.
Initiation type	Initiator crow approach type	Merged two categories: threatening (human) and nonthreatening (human) into "no approach".	Reduced complexity of response variable. Events where humans approached crows first were merged; crow initiation types were kept distinct to test hypotheses.

Visitor age	Visitor sexual development stage	Merged with visitor gender into 4 categories: prepubescent, pubescent, adult female, adult male.	Addressed high collinearity between age and gender. Merging alleviated problems; sex was kept distinct only for fully developed individuals due to fewer data points for earlier stages.
Visitor gender	Visitor sexual development stage	Merged with visitor age into 4 categories: prepubescent, pubescent, adult female, adult male.	Same as above: resolved collinearity between age and gender while keeping distinct categories for adults with sufficient data.
Accessories	Initial human has backpack, Initial human has bag, Initial human has glasses, Initial human has headwear	Removed 2 categories: umbrella and walking stick. Remaining categories split into 4 distinct variables with binary outcomes (no/yes).	Avoided treating combinations of accessories as separate factor levels with few data points; simplified to ensure sufficient data for each variable.
Wheeled mobility aids	Initial human has stroller	Removed 1 category: wheelchair. Remaining category converted into binary outcomes (no/yes).	Not enough data points for wheelchair users.

Initiator crow profit type	Initiator crow profit type, Initial crow profit	Created a simplified binary variable (no/yes) alongside the original variable.	Original variable used as response in one model, simplified binary variable used as predictor in another.
Conspecific crow approach target	Joiner joins, Joiner initiates	Merged initial crow and initial human into one category; merged new crow and new human into another category; split these into binary variables (no/yes).	Insufficient data points for 2 categories per species; merged into single categories for each species and split into distinct binary variables.
Conspecific crow provider	-	Removed entirely.	Insufficient data points, even after merging categories. Redundant with conspecific crow profit variable.
Conspecific crow profit type	Conspecific crow profit	Merged 2 categories: profited by being fed and profited by stealing food. Converted to binary variable (no/yes).	Insufficient data for 2 categories, but deemed important as response variable; data points sufficient after merging.

Table 6. Description of Variables Used for Statistical Models Analyzed in R			
Variable Name in Coding	**Variable Name in Text**	**Categories**	**Description**
INITIATOR CROW APPROACH TYPE	Initiator crow approach type	NO APPROACH, OPEN APPROACH, STEALTHY APPROACH	How the event-initiating crow approached the visitor. The category **NO APPROACH** was used for cases when the visitor approached the crows instead.
z.VISITOR DENSITY	Visitor density (scaled to mean = 0, sd = 1)	-	Count of all visitors within view. Scaled to a mean of 0 and standard deviation of 1 to improve model convergence and interpretation.
z.CROW NUMBER	Crow density (scaled to mean = 0, sd = 1)	-	Count of all crows within view. Scaled to a mean of 0 and standard deviation of 1 to improve model convergence and interpretation.

z.INITIAL HUMAN GROUP SIZE	Visitor group size (scaled to mean = 0, sd = 1)	-	Visitor group size participating at the start of an event. A visitor group was defined as all visitors within less than 3m of the event initiator. Scaled to mean = 0 and sd = 1.
z.INITIAL CROW GROUP SIZE	Crow group size (scaled to mean = 0, sd = 1)	-	Crow group size at the start of an event. A crow group was defined as all crows within less than 3m of the event initiator. Scaled to mean = 0 and sd = 1.
HUMAN SEX DIFFERENTIATION	Approximated visitor sexual development stage	PREPUBESCENT, PUBESCENT, MATURE FEMALE, MATURE MALE	Approximation of visitor age range and sex, based on the development stage of secondary sexual characteristics.
INITIAL HUMAN HAS BACKPACK	Visitor has a backpack	NO, YES	Approached or approaching visitor wears a backpack or is in very close proximity to one (<1m).

INITIAL HUMAN HAS BAG	Visitor has a bag	NO, YES	Approached or approaching visitor wears a bag or is in very close proximity to one (<1m). A bag was defined as any portable storage carried by hand or worn using a single strap.
INITIAL HUMAN HAS GLASSES	Visitor wears glasses	NO, YES	Approached or approaching visitor wears either sunglasses or prescription glasses.
INITIAL HUMAN HAS HEADWEAR	Visitor wears headwear	NO, YES	Approached or approaching visitor wears headwear. Headwear was defined as any article of clothing or gear covering a majority of the visitor's scalp.

INITIAL HUMAN HAS STROLLER	Visitor has a stroller	NO, YES	Approached or approaching visitor uses or pushes a stroller or is in very close proximity to one (<1m). Strollers were defined as wheeled mobility aids for very young children.
INITIATOR CROW PROFIT TYPE	Initiator crow profit type	NO PROFIT, INITIATOR FED, INITIATOR STOLE	How the first crow that approached or was approached during an event profited from the event. Applies to all members if multiple crows were involved simultaneously.
INITIAL CROW PROFIT	Initiator crow profited	NO, YES	Whether the first crow that approached or was approached during an event acquired food. Simplified version of INITIATOR CROW PROFIT TYPE.

JOINER JOINS	Joiner joined event in progress	NO, YES	A crow joining later during an event in progress participates in the event.
JOINER INITIATES	Joiner initiates new event	NO, YES	A crow joining later during an event in progress initiates a new event by targeting a different visitor.
CONSPECIFIC CROW PROFIT	Joiner profits	NO, YES	A crow joining later during an event in progress acquires food from it.

Table 7. Comparison of the Function Between Full Models and Final Versions, and Explanations for the Changes

Function of the Full Model	Function of the Final Model
INITIATOR CROW APPROACH TYPE~ z.VISITOR DENSITY+ z.CROW NUMBER+ z.INITIAL HUMAN GROUP SIZE+ z.INITIAL CROW GROUP SIZE+ HUMAN AGE GENDER.CHILD+ HUMAN AGE GENDER.ADOLESCENT FEMALE+ HUMAN AGE GENDER.ADOLESCENT MALE+ HUMAN AGE GENDER.ADULT FEMALE+ HUMAN AGE GENDER.ADULT MALE+ HUMAN AGE GENDER.ELDERLY FEMALE+ HUMAN AGE GENDER.ELDERLY MALE+ INITIAL HUMAN HAS BACKPACK.YES+ INITIAL HUMAN HAS BAG.YES+ INITIAL HUMAN HAS GLASSES.YES+ INITIAL HUMAN HAS HEADWEAR.YES+ INITIAL HUMAN HAS STROLLER.YES	INITIATOR CROW APPROACH TYPE~ z.VISITOR DENSITY+ z.CROW NUMBER+ z.INITIAL HUMAN GROUP SIZE+ z.INITIAL CROW GROUP SIZE+ HUMAN SEX DIFFERENTIATION.PUBESCENT+ HUMAN SEX DIFFERENTIATION.MATURE MALE+ HUMAN SEX DIFFERENTIATION.MATURE FEMALE+ INITIAL HUMAN HAS BACKPACK.YES+ INITIAL HUMAN HAS BAG.YES+ INITIAL HUMAN HAS GLASSES.YES+ INITIAL HUMAN HAS HEADWEAR.YES+ INITIAL HUMAN HAS STROLLER.YES

INITIATOR CROW PROFIT TYPE~ z.VISITOR DENSITY+ z.CROW NUMBER+ z.INITIAL HUMAN GROUP SIZE+ z.INITIAL CROW GROUP SIZE+ HUMAN AGE GENDER.CHILD+ HUMAN AGE GENDER.ADOLESCENT FEMALE+ HUMAN AGE GENDER.ADOLESCENT MALE+ HUMAN AGE GENDER.ADULT FEMALE+ HUMAN AGE GENDER.ADULT MALE+ HUMAN AGE GENDER.ELDERLY FEMALE+ HUMAN AGE GENDER.ELDERLY MALE+ INITIAL HUMAN HAS BACKPACK.YES+ INITIAL HUMAN HAS BAG.YES+ INITIAL HUMAN HAS GLASSES.YES+ INITIAL HUMAN HAS HEADWEAR.YES+ INITIAL HUMAN HAS STROLLER.YES+ INITIATOR CROW APPROACH TYPE.OPEN APPROACH+ INITIATOR CROW APPROACH TYPE.STEALTHY APPROACH	INITIATOR CROW PROFIT TYPE~ z.VISITOR DENSITY+ z.CROW NUMBER+ z.INITIAL HUMAN GROUP SIZE+ z.INITIAL CROW GROUP SIZE+ HUMAN SEX DIFFERENTIATION.PUBESCENT+ HUMAN SEX DIFFERENTIATION.MATURE MALE+ HUMAN SEX DIFFERENTIATION.MATURE FEMALE+ INITIAL HUMAN HAS BACKPACK.YES+ INITIAL HUMAN HAS BAG.YES+ INITIAL HUMAN HAS GLASSES.YES+ INITIAL HUMAN HAS HEADWEAR.YES+ INITIAL HUMAN HAS STROLLER.YES+ INITIATOR CROW APPROACH TYPE.OPEN APPROACH+ INITIATOR CROW APPROACH TYPE.STEALTHY APPROACH

CONSPECIFIC CROW PROFIT~ z.VISITOR DENSITY+ z.CROW NUMBER+ z.INITIAL HUMAN GROUP SIZE+ z.INITIAL CROW GROUP SIZE+ HUMAN AGE GENDER.CHILD+ HUMAN AGE GENDER.ADOLESCENT FEMALE+ HUMAN AGE GENDER.ADOLESCENT MALE+ HUMAN AGE GENDER.ADULT FEMALE+ HUMAN AGE GENDER.ADULT MALE+ HUMAN AGE GENDER.ELDERLY FEMALE+ HUMAN AGE GENDER.ELDERLY MALE+ INITIAL HUMAN HAS BACKPACK.YES+ INITIAL HUMAN HAS BAG.YES+ INITIAL HUMAN HAS GLASSES.YES+ INITIAL HUMAN HAS HEADWEAR.YES+ INITIAL HUMAN HAS STROLLER.YES+ INITIAL CROW PROFIT.YES+ JOINER JOINS.YES+ JOINER INITIATES.YES	CONSPECIFIC CROW PROFIT~ z.VISITOR DENSITY+ z.CROW NUMBER+ z.INITIAL HUMAN GROUP SIZE+ z.INITIAL CROW GROUP SIZE+ HUMAN SEX DIFFERENTIATION.PUBESCENT+ HUMAN SEX DIFFERENTIATION.MATURE MALE+ HUMAN SEX DIFFERENTIATION.MATURE FEMALE+ INITIAL HUMAN HAS BACKPACK.YES+ INITIAL HUMAN HAS BAG.YES+ INITIAL HUMAN HAS GLASSES.YES+ INITIAL HUMAN HAS HEADWEAR.YES+ INITIAL HUMAN HAS STROLLER.YES+ INITIAL CROW PROFIT.YES+ JOINER JOINS.YES+ JOINER INITIATES.YES
Change from Full to Final Version: The variable HUMAN AGE GENDER was replaced with HUMAN SEX DIFFERENTIATION. Reason for Change: This modification addressed high Variance Inflation Factor (VIF), which indicated collinearity between several age and gender categories and other variables in the model. Categories like ADOLESCENT FEMALE and ADOLESCENT MALE lacked sufficient data points when analyzed separately. By merging these and other similar categories into the variable HUMAN SEX DIFFERENTIATION, collinearity issues were alleviated, leading to a more stable and interpretable model.	

Table 8. Estimates, Standard Errors, Z-values, and Hochberg Corrected P-values for all Predictors in Models 1, 2, and 3

Variable	Estimate (± Standard Error)	Z-value	Hochberg Corrected P-value
Social Crow Initiator: ***(a)***			
(Intercept)	0.613 ± 0.0944	6.49	1.77e-09*
Visitor Density ***(b)***	0.180 ± 0.0973	1.85	7.11e-01
Crow Density ***(b)***	-0.00837 ± 0.0915	-0.0914	9.81e-01
Initial Visitor Group Size ***(b)***	0.237 ± 0.0927	2.56	1.38e-01
Initial Crow Group Size ***(b)***	-0.505 ± 0.0948	-5.33	1.87e-06*
Pubescent Visitor ***(c)***	2.58 ± 0.379	6.82	1.95e-10*
Adult Male Visitor ***(c)***	3.02 ± 0.255	11.8	5.73e-31*
Adult Female Visitor ***(c)***	2.76 ± 0.246	11.2	9.60e-28*
Visitor has Backpack	0.00619 ± 0.265	0.0233	9.81e-01
Visitor has Bag	0.305 ± 0.432	0.705	9.81e-01
Visitor has Glasses	0.205 ± 0.238	0.861	9.81e-01
Visitor has Headwear	0.0946 ± 0.187	0.506	9.81e-01
Visitor has Stroller	0.717 ± 0.222	3.23	2.00e-02*

Careful Crow Initiator: [(a)]			
(Intercept)	0.235 ± 0.103	2.28	2.70e-01
Visitor Density [(b)]	0.0545 ± 0.105	0.519	9.81e-01
Crow Density [(b)]	-0.274 ± 0.106	-2.58	1.38e-01
Initial Visitor Group Size [(b)]	0.364 ± 0.0957	3.81	2.37e-03*
Initial Crow Group Size [(b)]	-0.680 ± 0.122	-5.58	4.80e-07*
Pubescent Visitor [(c)]	1.77 ± 0.451	3.94	1.50e-03*
Adult Male Visitor [(c)]	3.23 ± 0.279	11.6	1.37e-29*
Adult Female Visitor [(c)]	3.12 ± 0.267	11.7	3.70e-30*
Visitor has Backpack	0.355 ± 0.276	1.29	9.81e-01
Visitor has Bag	0.642 ± 0.440	1.46	9.81e-01
Visitor has Glasses	-0.0575 ± 0.252	-0.228	9.81e-01
Visitor has Headwear	0.0154 ± 0.200	0.0771	9.81e-01
Visitor has Stroller	0.742 ± 0.233	3.19	2.16e-02*

Initial Crow Fed: *(d)*			
(Intercept)	-2.02 ± 0.117	-17.3	2.01e-65*
Visitor Density *(b)*	-0.195 ± 0.117	-1.68	8.83e-01
Crow Density *(b)*	0.257 ± 0.0829	3.10	4.31e-02*
Initial Visitor Group Size *(b)*	0.217 ± 0.0872	2.49	2.44e-01
Initial Crow Group Size *(b)*	0.542 ± 0.0851	6.37	5.09e-09*
Pubescent Visitor *(c)*	1.19 ± 0.416	2.85	9.14e-02
Adult Male Visitor *(c)*	1.55 ± 0.295	5.25	3.72e-06*
Adult Female Visitor *(c)*	1.71 ± 0.293	5.84	1.32e-07*
Visitor has Backpack	-0.0382 ± 0.258	-0.148	8.83e-01
Visitor has Bag	0.178 ± 0.336	0.530	8.83e-01
Visitor has Glasses	0.309 ± 0.208	1.48	8.83e-01
Visitor has Headwear	-0.319 ± 0.189	-1.69	8.83e-01
Visitor has Stroller	-0.310 ± 0.224	-1.38	8.83e-01
Social Crow Initiator	-0.965 ± 0.237	-4.08	1.05e-03*
Careful Crow Initiator	-2.89 ± 0.359	-8.05	2.29e-14*

Initial Crow Stole: *(d)*			
(Intercept)	-3.14 ± 0.216	-14.5	2.48e-46*
Visitor Density *(b)*	-0.0663 ± 0.132	-0.502	8.83e-01
Crow Density *(b)*	-0.313 ± 0.191	-1.64	8.83e-01
Initial Visitor Group Size *(b)*	-0.213 ± 0.152	-1.41	8.83e-01
Initial Crow Group Size *(b)*	0.310 ± 0.185	1.68	8.83e-01
Pubescent Visitor *(c)*	0.438 ± 0.592	0.740	8.83e-01
Adult Male Visitor *(c)*	-0.0942 ± 0.389	-0.242	8.83e-01
Adult Female Visitor *(c)*	-0.125 ± 0.377	-0.332	8.83e-01
Visitor has Backpack	0.658 ± 0.303	2.17	5.39e-01
Visitor has Bag	-0.851 ± 0.630	-1.35	8.83e-01
Visitor has Glasses	-0.309 ± 0.311	-0.991	8.83e-01
Visitor has Headwear	0.104 ± 0.265	0.392	8.83e-01
Visitor has Stroller	0.512 ± 0.273	1.88	8.83e-01
Social Crow Initiator *(e)*	1.74 ± 0.670	2.59	1.90e-01
Careful Crow Initiator *(e)*	3.01 ± 0.652	4.62	9.22e-05*

Joiner Profited: [f]			
(Intercept)	-6.45 ± 0.650	-9.92	5.48e-22*
Visitor Density [b]	-0.245 ± 0.312	-0.787	9.97e-01
Crow Density [b]	0.281 ± 0.230	1.22	9.97e-01
Initial Visitor Group Size [b]	0.110 ± 0.256	0.431	9.97e-01
Initial Crow Group Size [b]	0.204 ± 0.183	1.12	9.97e-01
Pubescent Visitor [c]	-0.476 ± 1.03	-0.462	9.97e-01
Adult Male Visitor [c]	-0.136 ± 0.650	-0.209	9.97e-01
Adult Female Visitor [c]	-0.510 ± 0.663	-0.770	9.97e-01
Visitor has Backpack	-1.11 ± 0.593	-1.87	7.31e-01
Visitor has Bag	-0.410 ± 0.848	-0.483	9.97e-01
Visitor has Glasses	-0.237 ± 0.458	-0.518	9.97e-01
Visitor has Headwear	0.00170 ± 0.454	0.00373	9.97e-01
Visitor has Stroller	-0.833 ± 0.506	-1.65	9.97e-01
Initial Crow Profited	4.77 ± 0.572	8.33	1.11e-15*
Joiner Joins Initiator [g]	5.97 ± 0.662	9.01	3.17e-18*
Joiner Initiates New Event [g]	3.88 ± 0.695	5.58	3.10e-07*

Unless explicitly stated otherwise, all variables were compared against their absence or a baseline condition.

***a*:** *Social Crow Initiator* (event-initiating crow approached visitor socially/openly) and *Careful Crow Initiator* (event-initiating crow approached carefully/stealthily) compared against *Human Initiator* (event initiated by visitor).

***b*:** Count data scaled to mean = 0 and standard deviation = 1 for better model convergence/comparability.

***c*:** Visitors of *pubescent/adult* development stage compared against *prepubescent* stage.

***d*:** *Initial Crow Fed* (initial crow participant profited by being fed) and *Initial Crow Stole* (initial crow participant profited by stealing) compared against *No Profit*.

***e*:** A Wald test showed significant differences between the effect sizes for *Social Crow Initiator* and *Careful Crow Initiator* (Wald Statistic = 36.526, $p < 0.001$).

***f*:** *Joiner Profited* (event-joining crow profited) compared against *No Joiner Profit*.

***g*:** A Wald test showed significant differences between the effect sizes for *Joiner Joins Initiator* and *Joiner Initiates New Event* (Wald Statistic: 10.69624 , $p < 0.005$).

***Significant p-values:** Statistically significant at $\alpha = 0.05$.