


RESEARCH ARTICLE

Artificial selection in human-wildlife feeding interactions

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Abstract

1. The artificial selection of traits in wildlife populations through hunting and fishing has been well documented. However, despite their rising popularity, the role that artificial selection may play in non-extractive wildlife activities, for example, recreational feeding activities, remains unknown.
2. If only a subset of a population takes advantage of human-wildlife feeding interactions, and if this results in different fitness advantages for these individuals, then artificial selection may be at work. We have tested this hypothesis using a wild fallow deer population living at the edge of a capital city as our model population.
3. In contrast to previous assumptions on the randomness of human-wildlife feeding interactions, we found that a limited non-random portion of an entire population is continuously engaging with people. We found that the willingness to beg for food from humans exists on a continuum of inter-individual repeatable behaviour; which ranges from risk-taking individuals repeatedly seeking and obtaining food, to shyer individuals avoiding human contact and not receiving food at all, despite all individuals having received equal exposure to human presence from birth and coexisting in the same herds together. Bolder individuals obtain significantly more food directly from humans, resulting in early interception of food offerings and preventing other individuals from obtaining supplemental feeding.
4. Those females that beg consistently also produce significantly heavier fawns (300–500g heavier), which may provide their offspring with a survival advantage. This indicates that these interactions result in disparity in diet and nutrition across the population, impacting associated physiology and reproduction, and may result in artificial selection of the begging behavioural trait.
5. This is the first time that this consistent variation in behaviour and its potential link to artificial selection has been identified in a wildlife population and reveals new potential effects of human-wildlife feeding interactions in other species across both terrestrial and aquatic habitats.

KEYWORDS

among-individual differences, artificial feeding, birthweight, cervids, fitness, human-wildlife interactions, welfare

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1 | INTRODUCTION

Artificial selection (i.e. selection driven by human activities) shapes wild populations through the removal or promotion of certain morphological and behavioural traits (Ciuti et al., 2012; Coltman, 2008; Festa-Bianchet, 2003). Traditional artificial selection studies focus on the impacts associated with harvesting activities, such as hunting and fishing. These activities, when performed passively (as opposed to under selective or 'active' conditions, whereby harvesters are instructed by managers to target a specific trait), typically target larger body sizes, resulting in selection for the survival of smaller individuals across both terrestrial (Stenseth & Dunlop, 2009) and aquatic environments (Fenberg & Roy, 2008). The selective removal of 'desirable' morphological traits from individual populations through these processes is well-documented (Darimont et al., 2009). For example, hunting has led to a documented reduction in the tusk size of African elephants *Loxodonta africana* (Chiyo et al., 2015), horn size in sable antelope *Hippotragus niger* (Crosmarty et al., 2013), and antler size in moose *Alces alces* (Schmidt et al., 2007) and deer (Allendorf & Hard, 2009).

In recent years, the selection of behavioural traits by these harvest activities has also been documented. Variability in consistent inter-individual behavioural differences (i.e. 'personality' or 'temperament') is believed to be important for the functional ecology and dynamics of wildlife populations (Wolf & Weissing, 2012). Hunting and fishing studies have been shown to extract different personality types from a population, for example hunting often targets bolder personality types (Ciuti et al., 2012), as does passive gear in fishing (i.e. traps and angling) (Arlinghaus et al., 2017), whereas active gear (i.e. trawls) often captures shy individuals (Diaz Pauli & Sih, 2017), in both cases promoting the presence of the other behavioural type within the population. This is further supported by evidence from studies focusing on random capture methods, which indicate sampling bias regarding behavioural traits (Biro & Dingemanse, 2009), with additional studies indicating that active-bold individuals are more likely to be captured than their inactive-shy counterparts (Wilson et al., 1993).

As human populations and urban environments expand (Finn et al., 2008) putting humans into increased contact with wildlife (Madden, 2008), focus on artificial selection is shifting to alternative human activities beyond traditional harvesting (Lowry et al., 2013). For example, urbanisation selects for bolder individuals that will risk attempting establishment in an urban environment (Lowry et al., 2013), while road development may select against bold individuals that are more likely to attempt crossings (Oxley & Fenton, 1976). However, little attention has been paid to one of the most popular human-wildlife activities; the self-motivated, unregulated provision of food for wildlife by humans (Christiansen et al., 2016; Lowry et al., 2013), particularly within human-dominated landscapes such as urban gardens and parks.

There are documented cases of people recreationally feeding wild mammals (Burns & Howard, 2003; Orams et al., 1996) and birds (Conover, 1999; Jones, 2011), and this is now often reported on

social media—signifying that recreational feeding is an increasingly popular activity. However, the dynamics and impacts of these interactions on the wildlife species involved require further research (Hammerschlag et al., 2012; Orams, 2002). Potential impacts have often been extrapolated from studies on provisioning (e.g. artificial feeding stations) or refuse sites. Feeding at these sites has been shown to impact population density (Gilchrist & Otali, 2002), inter-individual competition (Mudge & Ferns, 1982), and behaviour (Burgin & Hardiman, 2015). Additionally, studies on urban species that utilise human-subsidised resources (i.e. refuse and food left out) flag concerns regarding malnutrition and shifts in reproductive behaviours (Lowry et al., 2013). However, little attention has been paid to whether behavioural variation plays a role in the utilisation of these resources or whether willingness to access these sites acts as an intra-population selective force. Additionally, these studies take place in environments where the animals involved experience limited human exposure or contact, therefore the risk involved is limited (especially as they may be more active in these areas at night), whereas recreational feeding interactions require that an animal engage directly with a human to obtain a food item (for example, directly from the hand) which involves a higher level of risk-taking. Therefore, relying upon these feeding station/refuse site studies to understand recreational feeding activities, especially in the context of artificial selection, could be misleading.

Where studies have actually focused on recreational feeding interactions themselves (e.g. in tourism activities), willingness to engage has typically been associated with conditioning (Finn et al., 2008) rather than considering whether this behaviour could be indicative of variation in behavioural traits. Researchers argue that animals' engagement in interactions increases with exposure (Laroche et al., 2007), which would imply that engagement is a random process based on circumstantial learning. For example, some behavioural variation has been documented between wild dolphins that receive food from people, with some approaching more often than others, leading to suggestions that these individuals have experienced 'more conditioning' (Smith et al., 2008). The randomness of this process would imply that artificial selection of traits in these populations, whether morphological or behavioural, is not at work. However, these studies can only focus on the individuals that are easily observable while accepting food from humans. To determine whether recreational feeding activities are, therefore, actually resulting in artificial selection, we must test whether a significant proportion, if not an entire population, of animals that have experienced equal exposure to interactions behave differently. Additionally, if this is the case, we must uncover whether this particular behavioural trait is promoted, for example through reproductive advantages, indicating that it is artificially selected for.

Here, for the first time, we explore willingness to engage in direct feeding interactions across an entire wild fallow deer *Dama dama* population living at the edge of a metropolis, in which all individuals have equal opportunity to interact with humans (Griffin, Haigh, Conteddu, et al., 2022). If artificial selection is at work, we predict that only a subset of individuals repeatedly engage in these

interactions, with others existing along a spectrum of decreasing levels of engagement, which would indicate that it is not a random process. Providing only a subset of the population with additional food could potentially result in weight gain (Clout et al., 2002) and, therefore, increased weight of those individuals' offspring, which would provide them with survival advantages (Amin et al., 2022; Clutton-Brock et al., 1987). Notably, individual behavioural differences are documented as having a degree of heritability, potentially through a combination of genetic and/or environmental factors (Poissant et al., 2013; Réale et al., 2009), so there is the potential that this behaviour could become more prevalent with time. This would mark human-wildlife feeding interactions as a driver of artificial selection in wild populations. Specifically, our goals are to

1. explore individual differences in willingness to interact (or 'beg') by testing whether only a subset of individuals repeatedly approach and engage with humans to obtain food, checking whether this is repeatable within the individual (i.e. indicative of a behavioural trait associated with inter-individual variability), and categorising our population accordingly;
2. investigate differences in levels of supplemental food intake as a function of begging behaviour (i.e. direct link between begging behaviour and food intake) and assess variance in food acceptance among individuals displaying different levels of interactions with humans (i.e. animals that beg more consistently may have a greater variance among them than those that beg less because only certain individuals within their category may actually obtain food from humans);
3. Determine whether there is a reproductive advantage for those individuals receiving supplementary food from humans by testing whether the offspring of females that beg consistently are heavier at birth, which is associated with survival advantages (sensu Albon et al., 1983; Clutton-Brock et al., 1982; Amin et al., 2022), than the offspring of those that either beg less or do not beg at all.

2 | MATERIALS AND METHODS

2.1 | Study area and population

The study was conducted in Phoenix Park, a 707 ha urban park located in Dublin, Ireland, which receives an estimated 10 million visitors annually. There is a resident fallow deer population of approximately 600 free-ranging individuals (late summer 2018–2019 estimates inclusive of newborn fawns). This is a wild population in a natural area surrounded by a wall and the environs of a capital city, with no chance for the deer to emigrate and no natural predators (with the only exception being red foxes who occasionally prey upon neonate fawns). Since the 1980's, University College Dublin wildlife biologists have been capturing and ear-tagging newborn fawns in June, resulting in >80% of the entire population being identifiable with ear-tags (ID). Deer are culled annually by professional stalkers over the winter period as part of the population management led by the Office of Public Works.

According to park rangers, it was not historically possible to approach most deer closer than 50 meters, with males being slightly easier to approach compared to females (sensu Ciuti et al., 2004), without causing herd displacement. However, between 5 and 10 years ago, tourists began entering this tolerated distance to feed the deer; a phenomenon boosted by the increased popularity of social media. Due to the Park's limited size and the high level of human presence and vehicular traffic, all the deer experience continuous human exposure from birth.

2.2 | Data collection

All behavioural observations for this study were carried out at a greater distance than that entered by tourists, were non-invasive and conducted under research permit UCD AREC-E-18-28. Observers remained passive and did not interact with either the deer or the public, preventing the need for further ethical approval. Observations ran from the start of May to the end of July in 2018 and 2019. This period was selected as nutrition intake is of key importance; males are regrowing antlers (Dryden, 2016) and females are nursing offspring (Ciuti et al., 2006). Collections were performed from dawn to dusk using a stratified sampling design based on time of the day, day of the week and area of the park. The area used by deer in the Park was divided into eight sectors (four in the eastern side of the Park where the males reside, and four in the western side where the females reside), excluding two small areas (St Mary's hospital and OSI campus, less than 3 hectares in total) that are accessible to deer but not open for public access. We then surveyed these sectors following an a priori strict schedule of which sector to enter daily.

We recorded herd size, IDs present (accurate sex and age available from capture data after birth), location, and time upon finding the herd. A unique 'herd code' was also assigned to each herd as it was observed. If no herd was present in the scheduled sector, then we entered the next sector in the ordered system and continued through the order until locating a herd. If multiple herds were present in a sector (with a herd defined as a group of 2+ individuals within a visual estimate of approximately 50m of each other and within view of each other), then we selected one at random by flipping a coin. We continued data collection on the same herd until the end of the allotted time period for that day, or until the herd split or merged with another group. If the herd split or merged with another group, then we ended the observation and selected a new herd at random for observation. The deer often form large herds, with female herds (mean \pm SD 105 \pm 78 deer) usually being larger than male ones (41 \pm 33 deer).

When humans approached to interact with the herd, we documented the number of people interacting, time and duration of the interaction, location and IDs of the deer begging. Begging was defined as a deer directly approaching a group of people with the ears erect and eyes focused, remaining in alert and waiting for a food offering. If and when the humans offered food items we recorded

the time, the IDs of the deer present begging for it, the type of food (e.g. carrot, bread, biscuit, etc.) and exact number of items accepted by each ID, the way it was accepted (from the ground after being thrown or directly from the hand, see Supporting Information, S1), and interaction duration.

To test whether females begging for food have a reproductive advantage, that is, increased body mass of fawns at birth, we collected body weight (kg) of neonate deer over 3 consecutive fawning seasons (2018–2020) and linked the identity of fawns to that of the mothers via direct behavioural observations. The collection protocols for fawn capture and weight measurement are outlined in Amin et al. (2021), while recalibration to true birth weight and mother-fawn pairings are outlined in the Supporting Information (S2). All collections were performed with full ethical approval under research permit UCD AREC-E-18-28.

2.3 | Data analysis—Modelling begging behaviour (Goal 1)

Data analyses were performed in R 4.0.5 (R Core Team, 2021). Our dataset was composed of 25,291 rows, with each row corresponding to an observation of an identified individual, the code for the herd that they were present in, whether or not they engaged with an interaction (binomial; 1 = a line for each time they engaged in a separate feeding interaction over the course of that herd observation, 0 = they were documented as being present in the herd but never approached any available feeding interactions), information on the interaction (i.e. how many people were involved), what, if any, food items they accepted if they did beg, and all additional data outlined above including spatial and temporal information (see Supporting Information, S3, for a sample of the dataset—note that ‘carrots’ are included here as sample food columns, but our original database has additional columns for multiple food types which have been removed for simplification).

We fit a generalised linear mixed-effects model (GLMM) with binomial distribution of errors following a priori structure using *glmer* function in *lme4* (Bates et al., 2015), with begging as response variable and deer ID and herd ID (observation number) as crossed random intercepts. Our model a priori structure was built using predictors of interest that we selected prior to the beginning of the data collection. We included deer age, sex, herd size, the total number of people that attempted to interact with the herd during the observation session, the time of the week (categorical: weekday or weekend), the time of the day, the amount of time the observer spent monitoring the herd (duration, i.e. sampling effort), the month of observation (categorical: May, June, July) and year of study (categorical: 2018, 2019) as explanatory variables in our model. All numerical predictors were scaled to improve model convergence, and were included as both single and quadratic terms in the model to allow for non-linear patterns.

We also included three two-way interactions in the model: sex and age, sex of the individual and total amount of people that

attempted to interact with the herd, and sex and herd size, all of which were included in both their linear and quadratic forms (resulting in six interactions in total). For details on variable selection rationale and a priori expectations, see S4.

We explored model simplification of our a priori model structure by later re-running the model after excluding insignificant interactions. However, as no changes to our results occurred, we opted to pursue a modelling strategy using the full a priori model without removing any insignificant predictor or interaction, therefore producing the model with the more accurate confidence intervals and coverage as recommended by Dormann et al. (2018). All predictors included in the model structure were not collinear ($|r_p| < 0.7$) (Dormann et al., 2013).

Despite our sampling design allowing us to monitor the entire population in a systematic fashion, we were aware of a number of underrepresented individuals, that is, individuals monitored for just a few hours, such as newborn fawns that did not join herds until mid-July or deer that died early in collection. We were interested in the random intercepts estimated by the GLMM for individual ID (sometimes known as conditional modes, or best linear unbiased predictors, BLUPs; Robinson, 1991), expected to span from the deer that showed the lowest begging rate to the one that showed the highest rate after taking all model predictors into account. However, we did not want these estimates to be affected by noise introduced by underrepresented deer. After data screening, we arbitrarily removed any deer ID observed for less than 3 observation sessions (equivalent to 18 hr over the 2-year monitoring period). We then fitted the GLMM with the full sample size (database 25,291 rows) and the one with censored underrepresented individuals, for example mostly neonate fawns (database 23,490 rows), extracted the random intercepts for individual deer from both and tested for the repeatability of such estimates between the two models. Using the *rpt* function in the *RPTR* package (Stoffel et al., 2017), we found a remarkably high repeatability in random effect estimates ($R = 0.993$, $SE = 0.001$, $CI = [0.992, 0.994]$). In the light of this preliminary analysis, we decided to remove under-sampled individuals with no impact on the overall random effect output.

Final model predictions for fixed effects were plotted using *library effects* (Fox & Weisberg, 2018), which provided marginal 95% confidence intervals. The *r.squaredGLMM* function from the *MuMIn* package (Barton, 2019) was used to compute the conditional and the marginal R^2 . Temporal autocorrelation was screened using the partial autocorrelation *pACF* function (Box et al., 2015), whereas spatial autocorrelation was visually inspected by producing a variogram (Zuur et al., 2009).

2.4 | Data analysis—Begging behavioural categories within the population (Goal 1)

Begging behaviours displayed by individuals are ecologically significant in the context of artificial selection if they are repeatable over time. To test this, we ran a repeatability test on the same

mixed-effect model structure described above using the *rptBinary* function in the *rptR* package (Stoffel et al., 2017).

After testing for repeatability, we extracted the 95% confidence intervals for each random intercept value for deer ID and then summarised them into behavioural categories. These behavioural categories were identified depending on how the random effects and related confidence intervals were distributed around the median random effect (zero, i.e., the median begging behaviour of the population). Ultimately, these behaviours exist on a continuum, but for clarification we subdivided these into three categories; those whose random effect's 95% CIs remained greater than zero, overlapped zero or was less than zero. This approach considers and categorises the BLUPs (random intercept) while connecting them with the associated error (confidence intervals; sensu Hadfield et al., 2010, Houslay & Wilson, 2017). We then calculated the percentage of individuals of the population falling into each of these categories.

2.5 | Data analysis—Food acceptance within begging behavioural categories (Goal 2)

To quantify the different food intake of deer depending on their begging behaviour, we calculated the rate of food acceptance by dividing the number of food items by the total amount of time the individual was observed for and rescaling this to an hour. We ran a non-parametric Kruskal-Wallis one-way analysis of variance, which we selected due to the non-normality of the data, to test for significant variation in acceptance rates among begging categories using the *kruskal.test()* function in the *stats* package (R Core Team, 2018). We then performed a Kruskal-Wallis multiple comparison test to investigate differences between categories using the *kruskalmc()* function in the *pgirmess* package (Giraudoux et al., 2018). We opted to utilise begging categories as opposed to the random effect outputs (BLUPs/random intercept) as differences in confidence intervals were incorporated into an individual's assignment to each category, allowing us to moderate for error (sensu Hadfield et al., 2010, Houslay & Wilson, 2017).

We also predicted that different begging categories would have a different variance in their acceptance rate within their category, that is, deer that avoid engaging in a lot of interactions with humans are more likely to have a reduced variance in acceptance rate (close to zero), whereas consistent beggars may have a greater variance because only certain individuals within their category may actually obtain food. We therefore tested for the homogeneity of variance in acceptance rates across begging categories by fitting a non-parametric Fligner-Killeen test using the *fligner.test()* function in the *stats* package (R Core Team, 2018).

When deer beg for food, they can obtain a food item in two different ways: they can take it directly from the humans' hands, or they can collect it from the ground when dropped or thrown by humans. Collecting food thrown on the ground does not require these animals to get too close to humans, whereas deer getting food directly from

people's hands are expected to be those animals particularly capable of coping with close-distance human-deer interactions. We therefore repeated the same process described above (Kruskal-Wallis one-way analysis of variance test followed by Kruskal-Wallis multiple comparison test and Fligner-Killeen homogeneity of variance test), this time analysing interactions involving food hand-delivered as opposed to thrown food items.

2.6 | Data analysis—Fawn birth weight analysis (Goal 3)

We extracted all females from our population for which we had both a begging category assignment for their ID and a confirmed fawn pairing at least once over 3 years of data, 2018–2020. We then analysed the link between mother begging category and fawn weight, (which, as previously mentioned, was recalibrated to weight at birth, see Supporting Information, S2). We fit a priori linear mixed effect model using the *lmer* function in the *lme4* package (Bates et al., 2015), with the recalibrated fawn birth weight as the response variable and mother begging category, sex of the fawn and year of birth as the predictors. We also included mother ID as a random effect as some mothers appeared across multiple years in our dataset. Here, we used begging category (derived from the BLUPs and their associated uncertainty—see above) but there is no full consensus on this practice (see Dingemans et al., 2020; Hadfield et al., 2010; Houslay & Wilson, 2017). We, therefore, re-ran the same linear mixed effect model with mother begging behaviour (BLUPs) instead of begging category.

To ensure that any effects found linking mothers' begging behaviour to fawns' weight at birth were indeed due to the differences in diet caused by variation in engagement in feeding interactions, as opposed to natural variation in resource intake among mothers caused by different space use and habitat selection, we produced a map to visually compare the home range of consistent begging females with females from other begging categories. We also assessed herd composition and calculated the mean percentages that each begging behavioural category represent within all female herds. This check aimed to confirm whether all behavioural categories were exposed to the same conditions and, therefore, variances in results were not due to a subset being consistently isolated.

3 | RESULTS

3.1 | Sample sizes

We collected data across 92 days (45 in 2018; 47 in 2019). Total time spent in observation was just under 612 hr (314.3 hr in 2018; 291.4 hr in 2019). The resulting dataset was composed of data on 458 ear-tagged individuals and 503 different herd combinations (259 female herds, which included subadult males remaining with mother groups

and the occasional buck, and 244 male herds). In total, we observed 87% of our entire population (434 out of 502 tagged individuals) in 2018, and 85% of our entire population (384 out of 453 tagged individuals) in 2019, after excluding newborn fawns that did not join the herd permanently before sampling ended. For the fawn birth weight analysis, our dataset was composed of 94 mothers and 134 fawns, with 5 mothers delivering offspring all 3 years, 30 twice and 59 only once.

3.2 | Modelling begging behaviour in fallow deer (Goal 1)

The GLMM explained 88.5% of variation, including that explained by inter-individual variability, whereas 62.1% of the variance was explained by fixed effects alone (Table 1). After taking the year of the study into account, the following single predictors were all flagged as significant by the model (Table 1): herd size, sex of the deer, time of the week, number of people present to interact with, time of the day, and age of the animal. In terms of the interactions included in the model, only that between age and sex was flagged as significant (Table 1). The model did not have residual spatial or temporal autocorrelation (Supporting Information, S5). We also calculated the odds ratios for this model (available in Supporting Information, S6).

Begging decreased with increasing deer herd size (Figure 1a). There was an optimum number of people present for maximum begging behaviour; begging increased with the number of people present and peaked at ~40–50 people, before it then decreased (Figure 1b). In terms of temporal analysis, begging behaviour increased on the weekends (Figure 1c) and peaked between 13:00–14:00 daily (Figure 1d). Males were, in general, more likely to beg for food than females, with begging increasing in females (Table 1) continuously with age but dropping off in senescent males after they reach approximately 8–9 years old (Figure 1e).

3.3 | Begging behavioural categories within the population (Goal 1)

We found that begging behaviour was significantly repeatable among individuals ($R = 0.371$, $SE = 0.025$, $CI = [0.296, 0.389]$, $p < 0.001$ over 100 bootstraps; Supporting Information, S7). Based on the random effect estimates and related 95% confidence intervals, we classified each deer as a consistent beggar, occasional beggar or rare beggar (Figure 2a), with all categories being well distributed among the two sexes (Figure 2b). By simply looking at the number of times individuals were observed during the study and how many times they were seen begging, we found that consistent beggars begged for food approximately 3 out of 10 times that they were observed (mean \pm SD: $29 \pm 20\%$ of times observed begging at least once during an entire observation session), whereas occasional beggars and rare beggars each only begged 3–4 out of 100 times that they were observed ($3 \pm 6\%$, and $4 \pm 5\%$ respectively).

TABLE 1 Parameters estimated by the GLMM explaining the likelihood of deer to beg for food in the Phoenix Park population, Dublin. The model was fitted on 23,490 observations carried out on 503 different herds ('obs') and 458 unique deer ('ID'); both 'obs' and 'ID' were fitted as crossed random intercepts, with the variance of 'obs' being 2.23 ($SD = 1.49$) and the variance of 'ID' being 5.36 ($SD = 2.32$)

Fixed effects	Estimate	Standard error	Z value	Pr(> z)
Intercept	-6.85845	0.33369	-20.55	<0.001
Herd size	-1.77399	0.50712	-3.50	<0.001
Herd size ²	1.11612	0.49824	2.24	0.0251
Sex [female]	0			
Sex [male]	1.45744	0.34324	4.25	<0.001
Month [May]	0			
Month [June]	-0.44285	0.24618	-1.80	0.0720
Month [July]	0.02018	0.24901	0.08	0.9354
Year [2018]	0			
Year [2019]	0.34128	0.20237	1.69	0.0917
Time of the week [Weekdays]	0			
Time of the week [Weekend]	0.49155	0.21224	2.32	0.0206
Monitoring time	-0.03588	0.30970	-0.12	0.9078
Monitoring time ²	0.25956	0.28909	0.90	0.3693
People present	6.07857	0.45728	13.29	<0.001
People present ²	-3.58509	0.39164	-9.15	<0.001
Average time of day	3.91266	1.35286	2.89	0.0038
Average time of day ²	-3.78090	1.31860	-2.87	0.0041
Age	1.59402	0.55892	2.85	0.0043
Age ²	0.24444	0.50815	0.48	0.6305
Sex [male]: Age	3.68469	0.90932	4.05	<0.001
Sex[male]: Age ²	-4.57017	1.02529	-4.46	<0.001
Sex [male]: People present	0.08524	0.47516	0.18	0.8576
Sex [male]: People present ²	-0.04942	0.38710	-0.13	0.8984
Sex [male]: Herd size	0.31321	0.54406	0.58	0.5648
Sex [male]: Herd size ²	-0.29170	0.52204	-0.56	0.5763

In total, consistent beggars represent ~24% of the observed population, while occasional beggars represent ~68% of the population and rare represent ~8% (Figure 3). All three categories were present across the sexually mature (4–8 yo) and older (9+ yo) population, though subadult individuals (0–3 yo) were only composed of consistent and occasional beggars (Supporting Information, S8). Notably, these begging categories only summarise the ear-tagged deer observed in each season (87% in 2018, 85% in 2019), meaning that 13% of individuals in 2018 and 15% of individuals in 2019 (≤ 70 individuals per year) known

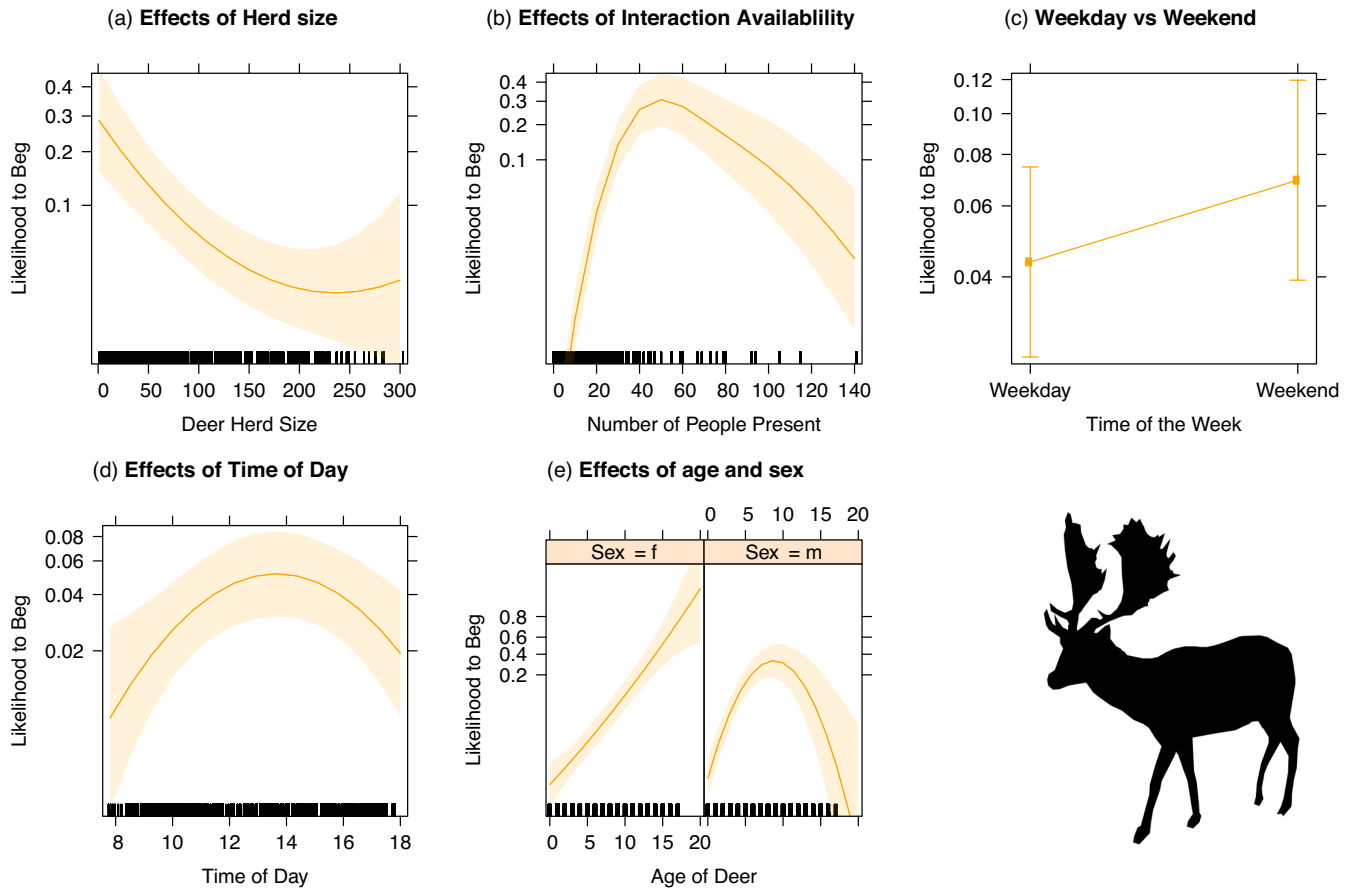


FIGURE 1 Plots depicting the effect of deer herd size (a), number of people present (b), time of the week (c), time of the day (d), and age interacted with sex (e) on the likelihood of a fallow deer to beg (y-axes) in the Phoenix Park, Dublin, as predicted by a generalised linear mixed-effect model GLMM. Predicted effects are shown as lines surrounded by marginal 95% confidence intervals.

to be alive were never observed. These individuals likely selected to remain in sites that were excluded from our sampling area as they are permanently closed to the public and were, therefore, categorised as 'avoiders', that is, individuals that not only avoided direct human interaction, but avoided areas where humans were present altogether.

3.4 | Food acceptance within begging behavioural categories (Goal 2)

Food items delivered by humans were mainly carrots ($n = 4319$, 45.3% of the total items delivered), plants collected within the Park itself ($n = 1461$, 15.3%), bread ($n = 1168$, 12.3%), apples ($n = 1016$, 10.7%), and biscuits/chocolate/crisps ($n = 587$, 6.2%), and other miscellaneous food and non-food (i.e., plastic bag, piece of papers) items ($n = 978$, 10.3%). We found that there was significant variation in food acceptance among begging categories in both females ($n = 238$; Kruskal–Wallis test: chi-squared = 112.34, $df = 2$, $p < 0.001$, Figure 4a) and males ($n = 220$; chi-squared = 95.75, $df = 2$, $p < 0.001$, Figure 4b). Consistent beggars accepted more food than both occasional and rare beggars (Kruskal–Wallis multiple comparison test $p < 0.05$ in both cases); however, occasional and rare beggars did not differ significantly from each other ($p > 0.05$). The median acceptance rate for female consistent beggars was 0.14 food items/

hr (min = 0, max = 1.76), for female occasional beggars was 0 items/hr (min = 0, max = 0.31), and 0 items/hr (min = 0, max = 0.32) for female rare beggars. Male consistent beggars had a median acceptance rate of 0.7 items/hr (min = 0, max = 2.21), 0 items/hr (min = 0, max = 0.58) for male occasional beggars, and 0 items/hr (min = 0, max = 0.17) for male rare beggars. We found different variances in food acceptance among begging categories in both sexes (Fligner–Killeen test: females: chi-squared = 141.77, $df = 2$, $p < 0.001$; males: chi-squared = 103.97, $df = 2$, $p < 0.001$), with a higher level of variance in the consistent beggars when compared to the other categories (Figure 4).

We also found significant variation in food acceptance among begging categories irrespective of mode of acceptance of food (food directly from the human's hand or mouth: $n = 458$; Kruskal–Wallis test: chi-squared = 186.14, $df = 2$, $p < 0.001$, Figure 5a; food items thrown on the ground: chi-squared = 167.61, $df = 2$, $p < 0.001$, Figure 5b). In both cases, consistent beggars accepted more food than occasional or rare beggars (Kruskal–Wallis multiple comparison test: $p < 0.05$ in all cases, Figure 5), whereas occasional and rare beggars did not differ ($p > 0.05$ in all cases). However, we did find higher levels of variation in acceptance directly from the human (Fligner–Killeen test: chi-squared = 321.35, $df = 2$, $p < 0.001$) than acceptance from the ground (chi-squared = 128.51, $df = 2$, $p < 0.001$). Consistent beggars did generally display a higher rate of acceptance of food from the hand/mouth

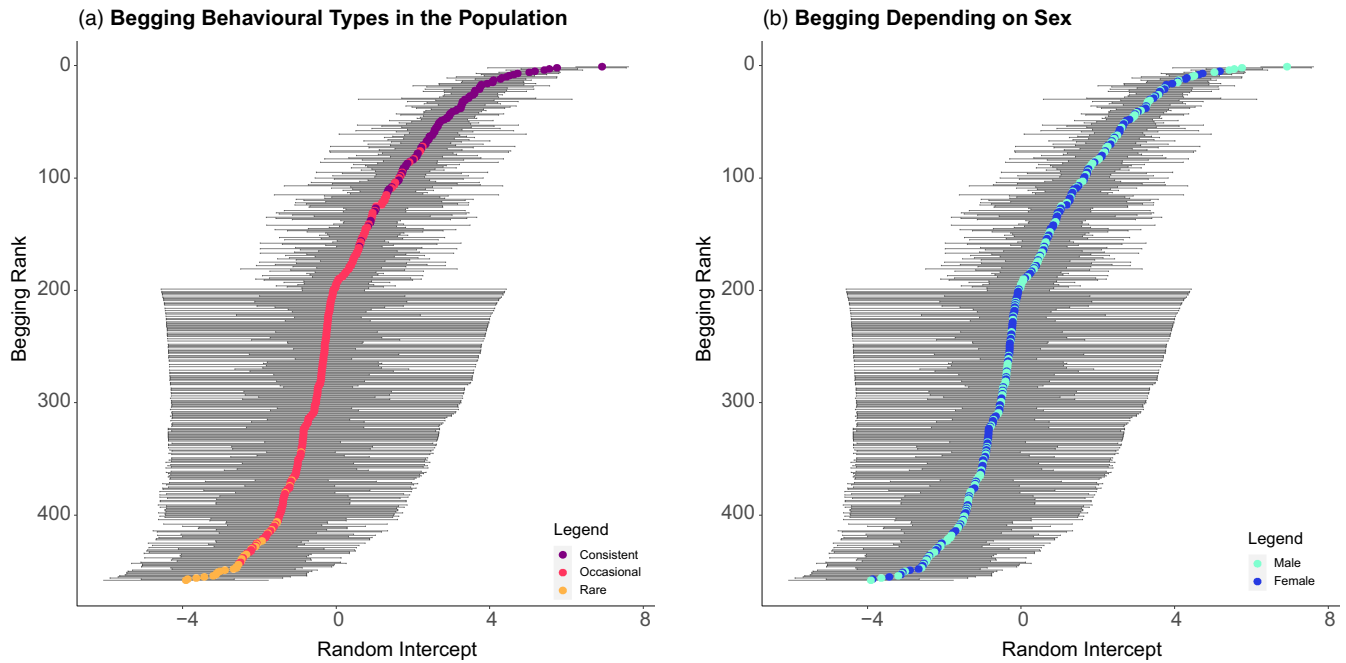


FIGURE 2 Breakdown of the deer population of Phoenix Park, into (a) three behavioural categories, consistent, occasional, and rare beggars, based on GLMM random intercept estimates and the overlap of the 95% confidence intervals on zero, that is, the median begging behaviour recorded for the population. The right plot (b) shows the distribution of the two sexes across the three begging categories.

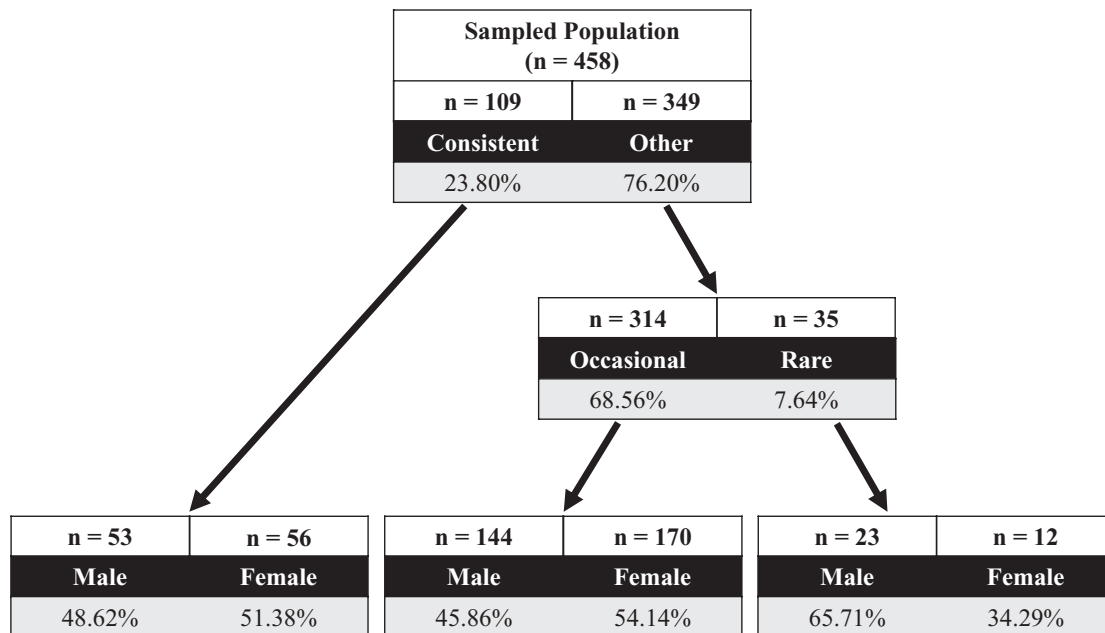


FIGURE 3 Flow chart outlining the percentages of each behavioural category present in the deer population of Phoenix Park.

(min = 0, median = 0.27, max = 1.90 food items/hour), than occasional beggars (min = 0, median = 0, max = 0.50) and rare beggars (min = 0, median = 0, max = 0.11). Similarly, we also found higher rates of acceptance from the ground in consistent beggars (min = 0, median = 0.09, max = 0.46) than in occasional beggars (min = 0, median = 0, max = 0.36) or rare beggars (min = 0, median = 0, max = 0.25), though the rates were considerably less variable among begging categories here than in acceptance from the hand/mouth (Figure 5).

3.5 | Effect of mother begging behaviour on fawn birth weight (Goal 3)

In our final database, the 134 fawns were paired with 47 consistent beggars, 85 occasional beggars and 2 rare beggars as mothers (note that some mothers appeared repeatedly in the database as specified in the 'sample sizes' section above). Due to the low number of rare beggar mothers in this dataset, combined with

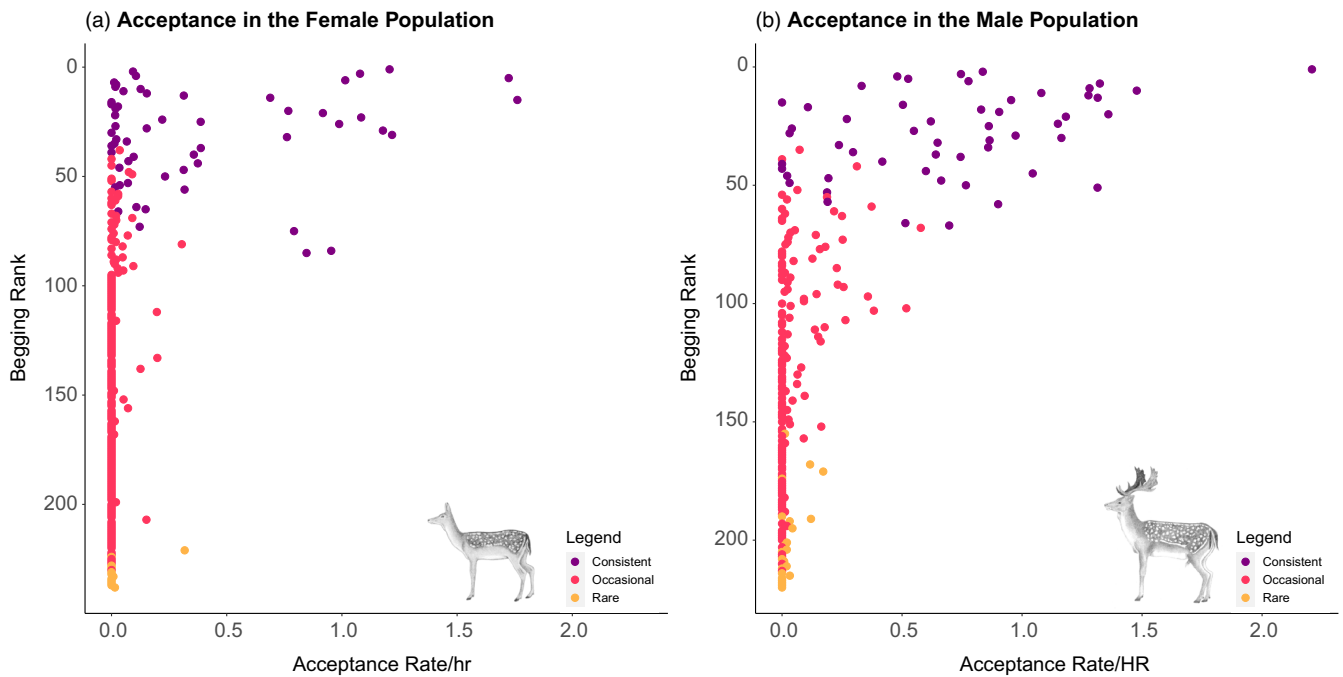


FIGURE 4 Deer acceptance rate per hour of food provided by humans (a: Female deer, b: Male deer; each point corresponding to an individual deer) in Phoenix Park, in relation to begging tendency (y-axis, GLMM random effect estimate) and begging category (consistent, occasional, and rare beggar).

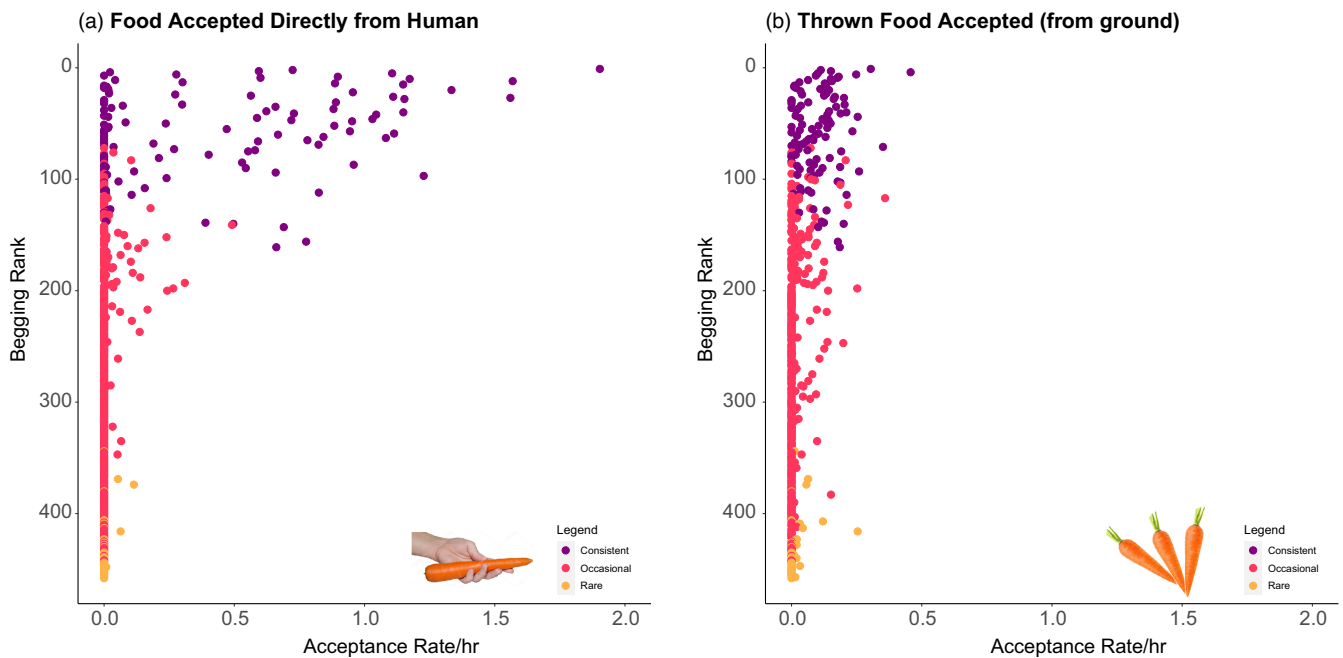


FIGURE 5 Deer acceptance rate per hour of food provided by humans with the hand (a) or thrown to the ground (b) in Phoenix Park, in relation to begging tendency (y-axis, GLMM random effect estimate) and begging category (consistent, occasional, and rare beggar). Males and females are cumulated, each point corresponding to an individual deer.

the results from our analyses on food acceptance showing little variation in food intake between occasional and rare beggars, we opted to group these in the analysis for comparison with consistent beggars. The mixed-effect model explained 32.6% of variation in birth weight, with 18.0% being explained by the fixed effects alone (Table 2). Both begging category of the mother and sex of

the fawn (i.e. heavier males) were flagged as being significant (Table 2). Consistent beggars produced significant heavier fawns at birth than occasional and rare beggars (Figure 6), with our results indicating that mothers who beg consistently are delivering fawns that are up 300–500g more than those mothers who display reduced begging behaviour.

TABLE 2 Parameters estimated by the LMER explaining the variability of birth weight in fawns as a function of mother begging category, sex of fawn and year of birth. The model was fitted on 134 different fawns across 94 different mothers, with the ID of the mother being set as a random effect (variance = 0.077, *SD* = 0.28)

Fixed effects	Estimate	Standard error	T value	Pr(> t)
Intercept	4.53324	0.14418	31.44	<0.001
Category [consistent]	0			
Category [occasional and rare]	-0.32290	0.12680	-2.55	0.0013
Sex [female]	0			
Sex [male]	0.52288	0.11382	4.59	<0.001
Year [2018]	0			
Year [2019]	-0.10440	0.14828	-0.70	0.4828
Year [2020]	0.01516	0.13111	0.12	0.9082

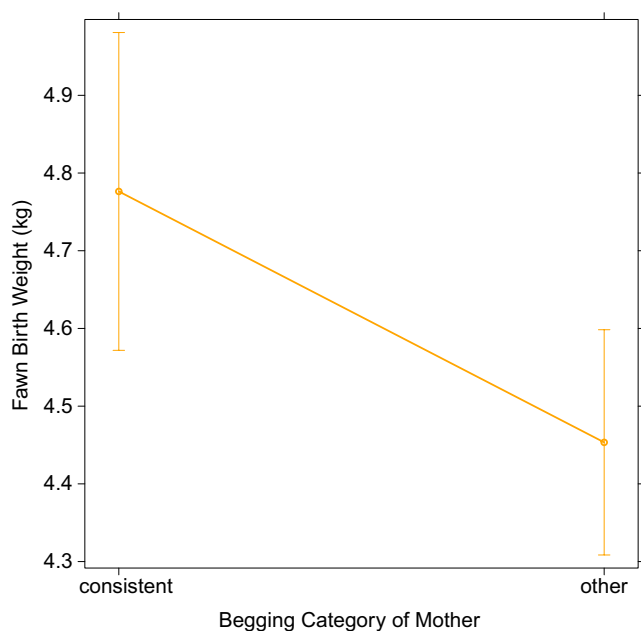


FIGURE 6 The effect of the begging behavioural category of the mother on the birth weight (in kg) of the associated fawn. Predicted effect is depicted along the marginal 95% CI.

Our replicated analysis, using BLUPs instead of the begging category for mothers, showed similar patterns, and is shown as Supporting Information (S9). In terms of assessing other factors outside of begging behaviour that may have an effect (such as differences in resource availability per category), we found that not only do female occasional and rare beggars share the same home range, and therefore resource availability, as female consistent beggars (Supporting Information, S10), but they are also consistently observed in the same groups and therefore have equal opportunity to interact. Female herds are commonly composed of multiple behavioural categories, with consistent beggars representing less than 1/3 of the herd members (mean \pm *SD*: 28.97% \pm 15.93%), occasional beggars representing the vast majority (62.18% \pm 16.57%) and rare representing a minority (8.85% \pm 8.64%).

4 | DISCUSSION

As outlined in the first goal of our study, we wished to determine whether engagement by wild animals with humans was random or whether only certain individuals would tolerate these close contact, 'high-risk' interactions. This aimed to identify this behaviour, for the first time, in a free-ranging population (i.e. not comparable to pen-based behaviour) interacting with humans directly, as opposed to the indirect interactions associated with site or feeding station-based studies. We have now identified that likelihood to interact or 'beg' from humans exists on a continuum of repeatable behaviour across a deer population of individuals that, notably, have all experienced the same levels of human exposure. It is well known that behaviours in animals exist on a continuum (Wilson et al., 1994), but this had yet to be explored in relation to wildlife begging for food from humans. We were able to classify the population that was observable in areas with open access to the public (~86%) into three categories, which we argue may also exist in other wildlife populations in close contact with humans; those that consistently beg, occasionally beg and rarely beg. The remaining subset of the population (~14%, avoiders) selected to limit themselves to smaller areas that are closed to the public. This reflects what is widely accepted in random capture studies, that is, that we are less likely to trap, or in this case observe, the shy-inactive individuals present in any population due to their careful avoidance of humans (Biro & Dingemanse, 2009; Leclerc et al., 2017, 2019; Wilson et al., 1994). Notably, the proportions of different begging behaviours seen within this deer population are reflected in similar proportions in other populations relating to different foraging techniques, such as in the classical examples of producers and scroungers in pigeons and zebra finches (David et al., 2011; Giraldeau & Lefebvre, 1986). Our data report current levels, however, it is possible that 5–10 years ago, when humans started feeding deer in the park, the percentage of individuals interacting was lower than the one recorded during this study period, leading to the possibility that the current observations may already be the result of artificial selection. Long-term research will be able to disentangle the variation in the proportion of consistently begging individuals over time.

The repeatable variation in behaviour between individuals/categories is only of consequence if it results in differences in dietary

intake (reasoning for Goal 2), as this may establish it as a driver of new evolutionary forces reminiscent of resource competition studies (Wolf & Weissing, 2012). We have established that the consistent, occasional and rare beggars had access to a variety of high concentrate food items, including bread, biscuits and fruit, among others, which were mostly accessed by consistent beggars. In particular, these consistent beggars obtain the majority of food offered directly by humans, which enables early interception of food offerings as they compete with other members of the herd. The high level of variation in food item intake present within this category is further evidence of inter-individual competition at work, with the boldest and most aggressive individuals potentially receiving the most food items. Notably, it is possible that these bolder individuals may also naturally invest more time in foraging activities (Kurvers et al., 2010), meaning that human provision of food could be further exacerbating variations in nutrition intake.

This dietary variation raises questions regarding differences in nutrition intake, the associated physiological impacts, and how these are likely to result in artificial selection. For example, in deer, supplementary feeding may result in increased body weight and size (Volpelli et al., 2003), which is also linked to increased antler size (Dryden, 2016), both of which play an important role in mating success (Jennings et al., 2004). In our own study (Goal 3), we have shown that the supplementary feeding provided to those females that consistently beg produce heavier offspring. Notably, studies from this system have shown that heavier fawns are afforded a greater survival advantage (Amin et al., 2022), similar to what has been suggested in other studies regarding different species survival (Cabrera et al., 2012; Clutton-Brock et al., 1987; Maniscalco, 2014). Therefore, human-mediated artificial selection may favour begging individuals, and attention must extend to other targeted populations in terrestrial (e.g. birds in gardens) and marine ecosystems (e.g., dolphins and seals in harbours and tourist hotspots; Jones & Reynolds, 2008; Orams et al., 1996), as clearly these activities, which are perceived by many in the public as benign (Hockett & Hall, 2007), are actually having unseen effects.

As these repeatable behavioural traits are noted as having a degree of heritability (Dingemanse et al., 2012; Dochtermann et al., 2015) they may be lost if selected against, especially in enclosed populations with no inflow of genetics, such as wildlife populations embedded within human dominated landscapes and urban areas. The artificial selection potentially driven by these interactions may also contribute to other driving forces; for example, the growing popularity of hand feeding in a variety of bird species has continued to gain traction through videos posted on social media (Moller, 2008). With studies already showing genetic divergence between birds in urban and rural areas (Charmanier et al., 2017), potentially stimulated by urban environments favouring bold behavioural types (Lowry et al., 2013). The reproductive promotion of bold individuals that accept food shown in our study may further drive this evolutionary force in these avian species. In terms of marine wildlife, hand feeding has become increasingly popular as a recreational activity (Semeniuk et al., 2007), and the

possibility that these activities could be contributing to the forces acting upon these often at-risk populations requires consideration. As previously mentioned, the feeding of terrestrial mammals by humans has also been documented (Burns & Howard, 2003), yet, no empirical studies regarding variation in begging behaviours have been performed for these species. Now that we have gathered empirical evidence that this may be occurring, it is of fundamental importance that the associated impacts caused by this activity be evaluated.

Our study has also uncovered key information, which contributes to our understanding of how these interactions may function in other wildlife species. Details regarding the roles of different predictors are of key importance to ecologists and wildlife managers as we begin to unravel the dynamics of these complex interactions. We have uncovered interesting findings regarding the age and sex of the targeted animal, the congregation size of both humans and the targeted wildlife group, and temporal aspects, which enable us to better understand what drives these complex interactions, as expanded upon below.

Overall, males beg proportionally more than females; males are larger than females (McElligott et al., 2001), requiring a greater nutritional intake for size maintenance (Demment & Van Soest, 1985). Males also tolerate human presence more than their female counterparts and generally tend to exploit richer feeding areas, even when characterised by higher human presence, in order to invest in body size (Ciuti et al., 2004). In our study's case, it is likely that males invest more in these feeding interactions than females during the spring and summer months as a larger body size is advantageous during the rut (McElligott et al., 2001) and that this would continue afterwards to compensate for the loss of condition typically associated with the rut (Clutton-Brock et al., 1982) during the harsher winter months. However, in terms of age, our results showed that older individuals beg more overall among females, whereas males show a decrease in begging behaviour later in life. It is likely that females, who typically live longer than males (McElligott et al., 2002), become more adept at spotting and intercepting food offerings with age. Conversely, older males are likely impeded by the physiological decline associated with cervids after years of exposure to the rut (Clutton-Brock et al., 1982; McElligott et al., 2002; Yoccoz et al., 2002), preventing them from competing against prime males efficiently and, therefore, resulting in reductions in their begging behaviour.

Understanding how herd size may influence interactions is particularly important as popular targets for feeding interactions, such as ruminants and birds, tend to form herds or flocks. We found that individuals in larger herd sizes are less likely to beg, as larger herd sizes may prevent individuals from spotting or reaching all interactions, also favoured by reduced levels of vigilance and scanning in larger herds (Childress & Lung, 2003). Conversely, it is also important to understand how human congregation may influence an animal's likelihood or willingness to interact. Our findings show that begging increases with the number of interactions available up to ~40–50 people before it plateaus and then decreases. Animals may become more stressed beyond this cut-off point, which likely bears

important consequences for cortisol levels and associated health impacts (Roth, 1985).

As for the temporal aspects, we found that begging behaviours peak circa 13:00–14:00 in the day and over the weekend (compared to on weekdays). Wildlife in human-dominated landscapes typically show peaks in activity at dawn and/or at dusk (Ensing et al., 2014; Grinder & Krausman, 2001; Ossi et al., 2020) avoiding periods of intensive human activity. However, animals seeking feeding interactions show a high level of begging activity during the times which coincide with the most outdoor activity by humans globally (Glass et al., 1992; Walls et al., 2018), potentially altering the typical circadian patterns of targeted wildlife.

Our study has begun to unravel the complex dynamics and impacts of these popular human-wildlife interactions. For the first time, we have found definitive evidence that engagement with humans in these interactions is not random, but instead is a repeatable trait driven at the individual level. This results in dietary differences, which may be driving artificial selection by providing reproductive advantages for the individuals involved. Additionally, we have uncovered key drivers of these interactions which may prove to be invaluable, for example, for park officials who wish to design targeted management campaigns to reduce human-wildlife contact. Ultimately, our study opens the field for further research into the role of human-wildlife feeding interactions in artificial selection within wild populations, which must now be explored in other species across different ecological contexts and varying levels of human presence and pressure.

AUTHOR CONTRIBUTIONS

Laura L. Griffin and Simone Ciuti conceived the study. Laura L. Griffin, Amy Haigh, Jordan Faull and Alison Norman collected the data. Laura L. Griffin and Simone Ciuti analysed the data. Bawan Amin and Simone Ciuti contributed the fawn birth weight data. Bawan Amin and Laura L. Griffin completed the fawn weight analysis. Laura L. Griffin wrote the manuscript, revised by Amy Haigh, Bawan Amin, and Simone Ciuti.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data is available on Dryad Digital Repository [10.5061/dryad.4tmgp4fcx](https://doi.org/10.5061/dryad.4tmgp4fcx) (Griffin, Haigh, Amin, et al., 2022).

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REFERENCES

- Albon, S. D., Guinness, F. E., & Clutton-Brock, T. H. (1983). The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). *Journal of Zoology*, 200, 295–298.
- Allendorf, F. W., & Hard, J. J. (2009). Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 9987–9994.
- Amin, B., Jennings, D. J., Smith, A. F., Quinn, M., Chari, S., Haigh, A., Matas, D., Koren, L., & Ciuti, S. (2021). In utero accumulated steroids predict neonate anti-predator response in a wild mammal. *Functional Ecology*, 35, 1255–1267.
- Amin, B., Verbeek, L., Haigh, A., Griffin, L., & Ciuti, S. 2022. Risk-taking neonates do not pay a survival cost in a free-ranging large mammal (pre-print).
- Arlinghaus, R., Laskowski, K. L., Alós, J., Klefoth, T., Monk, C. T., Nakayama, S., & Schröder, A. (2017). Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries*, 18, 360–373.
- Barton, K. 2019. Mumin: Multi-model inference. R package version 1.43.15. <https://Cran.R-project.org/package=Mumin>
- Bates, D., Machler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Biro, P. A., & Dingemanse, N. J. (2009). Sampling bias resulting from animal personality. *Trends in Ecology and Evolution*, 24, 66–67.
- Box, G. E. P., Jenkins, G. M., Reinsel, G. C., & Ljung, G. M. (2015). *Time series analysis: Forecasting and control*. John Wiley & Sons.
- Burgin, S., & Hardiman, N. (2015). Effects of non-consumptive wildlife-oriented tourism on marine species and prospects for their sustainable management. *Journal of Environmental Management*, 151, 210–220.
- Burns, G. L., & Howard, P. (2003). When wildlife tourism goes wrong: A case study of stakeholder and management issues regarding dingoes on Fraser Island, Australia. *Tourism Management*, 24, 699–712.
- Cabrera, R. A., Lin, X., Campbell, J. M., Moeser, A. J., & Odle, J. (2012). Influence of birth order, birth weight, colostrum and serum immunoglobulin G on neonatal piglet survival. *Journal of Animal Science and Biotechnology*, 3, 1–10.
- Charmantier, A., Demeurier, V., Lambrechts, M., Perret, S., & Grégoire, A. (2017). Urbanization is associated with divergence in pace-of-life in great tits. *Frontiers in Ecology and Evolution*, 5, 53.
- Childress, M. J., & Lung, M. A. (2003). Predation risk, gender and the group size effect: Does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour*, 66, 389–398.
- Chiyo, P. I., Obanda, V., & Korir, D. K. (2015). Illegal tusk harvest and the decline of tusk size in the African elephant. *Ecology and Evolution*, 5, 5216–5229.
- Christiansen, F., Mchugh, K. A., Bejder, L., Siegal, E. M., Lusseau, D., McCabe, E. B., Lovewell, G., & Wells, R. S. (2016). Food provisioning increases the risk of injury in a long-lived marine top predator. *Royal Society Open Science*, 3, 1–12.
- Ciuti, S., Bongí, P., Vassale, S., & Apollonio, M. (2006). Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. *Journal of Zoology*, 268, 97–107.

- Ciuti, S., Davini, S., Luccarini, S., & Apollonio, M. (2004). Could the predation risk hypothesis explain large-scale spatial sexual segregation in fallow deer (*Dama dama*)? *Behavioral Ecology and Sociobiology*, *56*, 552–564.
- Ciuti, S., Muhly, T. B., Paton, D. G., Mcdevitt, A. D., Musiani, M., & Boyce, M. S. (2012). Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B-Biological Sciences*, *279*, 4407–4416.
- Clout, M. N., Elliott, G. P., & Robertson, B. C. (2002). Effects of supplementary feeding on the offspring sex ratio of kakapo: A dilemma for the conservation of a polygynous parrot. *Biological Conservation*, *107*, 13–18.
- Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red deer: Behavior and ecology of two sexes*. University of Chicago Press.
- Clutton-Brock, T. H., Major, M., Albon, S. D., & Guinness, F. E. (1987). Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *The Journal of Animal Ecology*, *56*, 53–67.
- Coltman, D. W. (2008). Molecular ecological approaches to studying the evolutionary impact of selective harvesting in wildlife. *Molecular Ecology*, *17*, 221–235.
- Conover, M. (1999). Can waterfowl be taught to avoid food handouts through conditioned food aversions? *Wildlife Society Bulletin*, *27*, 160–166.
- Crosmary, W. G., Loveridge, A. J., Ndaimani, H., Lebel, S., Booth, V., Cote, S. D., & Fritz, H. (2013). Trophy hunting in Africa: Long-term trends in antelope horn size. *Animal Conservation*, *16*, 648–660.
- Darimont, C. T., Carlson, S. M., Kinnison, M. T., Paquet, P. C., Reimchen, T. E., & Wilmsers, C. C. (2009). Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 952–954.
- David, M., Cézilly, F., & Giraldeau, L.-A. (2011). Personality affects zebra finch feeding success in a producer–scrounger game. *Animal Behaviour*, *82*, 61–67.
- Demment, M. W., & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, *125*, 641–672.
- Diaz Pauli, B., & Sih, A. (2017). Behavioural responses to human-induced change: Why fishing should not be ignored. *Evolutionary Applications*, *10*, 231–240.
- Dingemanse, N. J., Barber, I., Wright, J., & Brommer, J. E. (2012). Quantitative genetics of behavioural reaction norms: Genetic correlations between personality and behavioural plasticity vary across stickleback populations. *Journal of Evolutionary Biology*, *25*, 485–496.
- Dingemanse, N. J., Moiron, M., Araya-Ajoy, Y. G., Mouchet, A., & Abbey-Lee, R. N. (2020). Individual variation in age-dependent reproduction: Fast explorers live fast but senesce young? *Journal of Animal Ecology*, *89*, 601–613.
- Dochtermann, N. A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic variation to personality variation: Heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142201.
- Dormann, C. F., Calabrese, J. M., Guillera-Arroita, G., Matechou, E., Bahn, V., Bartoń, K., Beale, C. M., Ciuti, S., Elith, J., & Gerstner, K. (2018). Model averaging in ecology: A review of Bayesian, information-theoretic, and tactical approaches for predictive inference. *Ecological Monographs*, *88*, 485–504.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., & Leitao, P. J. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46.
- Dryden, G. M. (2016). Nutrition of antler growth in deer. *Animal Production Science*, *56*, 962–970.
- Ensing, E. P., Ciuti, S., De Wijs, F. A. L. M., Lentferink, D. H., Ten Hoedt, A., Boyce, M. S., & Hut, R. A. (2014). Gps based daily activity patterns in European red deer and north American elk (*Cervus elaphus*): Indication for a weak circadian clock in ungulates. *PLoS ONE*, *9*, e106997.
- Fenberg, P. B., & Roy, K. (2008). Ecological and evolutionary consequences of size-selective harvesting: How much do we know? *Molecular Ecology*, *17*, 209–220.
- Festa-Bianchet, M. (2003). Exploitative wildlife management as a selective pressure for the life-history evolution of large mammals. In *Animal Behavior and Wildlife Conservation* (pp. 191–207). Island Press.
- Finn, H., Donaldson, R., & Calver, M. (2008). Feeding flipper: A case study of a humandolphin interaction. *Pacific Conservation Biology*, *14*, 215–225.
- Fox, J., & Weisberg, S. (2018). Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. *Journal of Statistical Software*, *87*, 1–27.
- Gilchrist, J. S., & Otali, E. (2002). The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. *Canadian Journal of Zoology*, *80*, 1795–1802.
- Giraldeau, L.-A., & Lefebvre, L. (1986). Exchangeable producer and scrounger roles in a captive flock of feral pigeons: A case for the skill pool effect. *Animal Behaviour*, *34*, 797–803.
- Giraudoux, P., Antonietti, J.-P., Beale, C., Pleydell, D., & Treglia, M. 2018. Pgirmess: Spatial analysis and data mining for field ecologists. R package version, 1, 678.
- Glass, R. J., Walton, G., & Echelberger, H. E. 1992. Estimates of recreational stream use in the White River drainage, Vermont. *Res. Pap. Ne-658. Radnor, pa: Us. Department of Agriculture, Forest Service, northeastern Forest Experiment Station. 10 p., 658.*
- Griffin, L. L., Haigh, A., Amin, B., Faull, J., Norman, A., & Ciuti, S. (2022). Data from: Artificial selection in human-wildlife feeding interactions. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.4ttmpg4fcx>
- Griffin, L. L., Haigh, A., Conteddu, K., Andaloc, M., McDonnell, P., & Ciuti, S. (2022). Reducing risky interactions: Identifying barriers to the successful management of human–wildlife conflict in an urban parkland. *People and Nature*, 1–13. <https://doi.org/10.1002/pan3.10338>
- Grinder, M. I., & Krausman, P. R. (2001). Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *The Journal of Wildlife Management*, *65*, 887–898.
- Hadfield, J. D., Wilson, A. J., Garant, D., Sheldon, B. C., & Kruuk, L. E. B. (2010). The misuse of Blup in ecology and evolution. *The American Naturalist*, *175*, 116–125.
- Hammerschlag, N., Gallagher, A. J., Wester, J., Luo, J. G., & Ault, J. S. (2012). Don't bite the hand that feeds: Assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Functional Ecology*, *26*, 567–576.
- Hockett, K. S., & Hall, T. E. (2007). The effect of moral and fear appeals on park visitors' beliefs about feeding wildlife. *Journal of Interpretation Research*, *12*, 5–27.
- Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of Blup in behavioural ecology. *Behavioral Ecology*, *28*, 948–952.
- Jennings, D. J., Gammell, M. P., Carlin, C. O. M., & Hayden, T. J. (2004). Effect of body weight, antler length, resource value and experience on fight duration and intensity in fallow deer. *Animal Behaviour*, *68*, 213–221.
- Jones, D. (2011). An appetite for connection: Why we need to understand the effect and value of feeding wild birds. *Emu*, *111*, I–VII.
- Jones, D. N., & Reynolds, S. J. (2008). Feeding birds in our towns and cities: A global research opportunity. *Journal of Avian Biology*, *39*, 265–271.
- Kurvers, R. H. J. M., Prins, H. H. T., Van Wieren, S. E., Van Oers, K., Nolet, B. A., & Ydenberg, R. C. (2010). The effect of personality on social foraging: Shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 601–608.

- Laroche, R. K., Kock, A. A., Dill, L. M., & Oosthuizen, W. H. (2007). Effects of provisioning ecotourism activity on the behaviour of white sharks *Carcharodon carcharias*. *Marine Ecology Progress Series*, 338, 199–209.
- Leclerc, M., Zedrosser, A., & Pelletier, F. (2017). Harvesting as a potential selective pressure on behavioural traits. *Journal of Applied Ecology*, 54, 1941–1945.
- Leclerc, M., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2019). Hunters select for behavioral traits in a large carnivore. *Scientific Reports*, 9, 1–8.
- Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, 88, 537–549.
- Madden, F. M. (2008). The growing conflict between humans and wildlife: Law and policy as contributing and mitigating factors. *Journal of International Wildlife Law & Policy*, 11, 189–206.
- Maniscalco, J. M. (2014). The effects of birth weight and maternal care on survival of juvenile Steller Sea lions (*Eumetopias jubatus*). *PLoS ONE*, 9, e96328.
- McElligott, A. G., Altwegg, R., & Hayden, T. J. (2002). Age-specific survival and reproductive probabilities: Evidence for senescence in male fallow deer (*Dama dama*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269, 1129–1137.
- McElligott, A. G., Gammell, M. P., Harty, H. C., Paini, D. R., Murphy, D. T., Walsh, J. T., & Hayden, T. J. (2001). Sexual size dimorphism in fallow deer (*Dama dama*): Do larger, heavier males gain greater mating success? *Behavioral Ecology and Sociobiology*, 49, 266–272.
- Moller, A. P. (2008). Flight distance of urban birds, predation, and selection for urban life. *Behavioral Ecology and Sociobiology*, 63, 63–75.
- Mudge, G. P., & Ferns, P. N. (1982). The feeding ecology of five species of gulls (Ayes: Larini) in the inner Bristol Channel. *Journal of Zoology*, 197, 497–510.
- Orams, M. B. (2002). Feeding wildlife as a tourism attraction: A review of issues and impacts. *Tourism Management*, 23, 281–293.
- Orams, M. B., Hill, G. J. E., & Baglioni, A. J. (1996). "Pushy" behavior in a wild dolphin feeding program at Tangalooma, Australia. *Marine Mammal Science*, 12, 107–117.
- Ossi, F., Ranc, N., Moorcroft, P., Bonanni, P., & Cagnacci, F. (2020). Ecological and behavioral drivers of supplemental feeding use by roe deer *Capreolus capreolus* in a peri-urban context. *Animals*, 10, 2088.
- Oxley, D. J., & Fenton, M. B. (1976). The harm our roads do to nature and wildlife. *Canadian Geographic Journal*, 92, 40–45.
- Poissant, J., Réale, D., Martin, J. G. A., Festa-Bianchet, M., & Coltman, D. W. (2013). A quantitative trait locus analysis of personality in wild bighorn sheep. *Ecology and Evolution*, 3, 474–481.
- R Core Team. (2018). *R: A language and environment for statistical computing [online]*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, 22, 1599–1607.
- Robinson, G. K. (1991). That Blup is a good thing: The estimation of random effects. *Statistical Science*, 6, 15–32.
- Roth, J. A. (1985). *Cortisol as mediator of stress-associated immunosuppression in cattle*. *Animal stress*. Springer.
- Schmidt, J. I., Hoef, J. M. V., & Bowyer, R. T. (2007). Antler size of Alaskan moose *Alces alces gigas*: Effects of population density, hunter harvest and use of guides. *Wildlife Biology*, 13, 53–65.
- Semeniuk, C. A. D., Speers-Roesch, B., & Rothley, K. D. (2007). Using fatty-acid profile analysis as an ecologic indicator in the management of tourist impacts on marine wildlife: A case of stingray-feeding in the Caribbean. *Environmental Management*, 40, 665–677.
- Smith, H., Samuels, A., & Bradley, S. (2008). Reducing risky interactions between tourists and free-ranging dolphins (*Tursiops* sp.) in an artificial feeding program at monkey Mia, Western Australia. *Tourism Management*, 29, 994–1001.
- Stenseth, N. C., & Dunlop, E. S. (2009). Unnatural selection. *Nature*, 457, 803–804.
- Stoffel, M. A., Nakagawa, S., Schielzeth, H., & Goslee, S. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8, 1639–1644.
- Volpelli, L. A., Valusso, R., Morgante, M., Pittia, P., & Piasentier, E. (2003). Meat quality in male fallow deer (*Dama dama*): Effects of age and supplementary feeding. *Meat Science*, 65, 555–562.
- Walls, M., Wichman, C., & Ankney, K. (2018). *Nature-based recreation: Understanding campsite reservations in National Parks*. Resources for the Future.
- Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, 9, 442–446.
- Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*) - an ecological study of a psychological trait. *Journal of Comparative Psychology*, 107, 250–260.
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27, 452–461.
- Yoccoz, N. G., Mysterud, A., Langvatn, R., & Stenseth, N. C. (2002). Age- and density-dependent reproductive effort in male red deer. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269, 1523–1528.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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