Fawn bedsite selection by a large ungulate living in a peri-urban area

Kimberly Conteddu[1*], Katie Wilson[2], Bawan Amin[1,3], Srivats Chari[4], Amy Haigh[1], Laura L. Griffin[1,5], Matthew Quinn[6], Andrew Ryan[1], Adam F. Smith[7,8,9], Simone Ciuti[1]

1. Laboratory of wildlife Ecology and Behaviour, School of Biology and Environmental Science, University College Dublin, Ireland

2. United Nations Environmental Programme World Conservation Monitoring Centre, Cambridge, UK

3. Faculty of Social and Behavioural Sciences, Utrecht University, Utrecht, Netherlands

4. Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland

5. University of British Columbia, Department of Forest Resources Management, 2424 Main Mall, Vancouver, V6T 1Z4, Canada

6. Insect Neuro Laboratory, Durham University, Durham, UK

7. Department of Wildlife Ecology and Management, Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, Germany

8. The Frankfurt Zoological Society, Frankfurt, Germany

9. Department of National Park Monitoring and Animal Management, Bavarian Forest National Park, Grafenau, Germany

*kimberly.conteddu@ucdconnect.ie

Abstract

Human-wildlife conflict in expanding peri-urban and urban areas is of increasing concern, as a result of growing human populations along with the associated anthropogenic footprint on wildlife habitats. Empirical data from wildlife research carried out within human dominated landscapes are key to understanding the effects of human pressures on wildlife ecology and behaviour, exploring wildlife behavioural flexibility (or phenotypic plasticity), and informing wildlife management decisions. Here, we explored how female fallow deer (*Dama dama*) responded to human and dog presence during the birthing period in the largest walled urban park in Europe. We collected data on 477 bedsites utilised by 283 neonate fawns across three consecutive fawning seasons, gathered fine-scale data on humans and dogs space use, and built Resource Selection Functions at multiple spatial scales. We found that, when choosing bedsites to give birth and leave fawns unattended, fallow deer mothers significantly avoided hotspots of park visitors on foot (and their dogs) along the hiking trail routes. Bedsites were also unlikely to be in close proximity of paved roads used by vehicle traffic. Additionally, fallow deer mothers were found to select for dense understory vegetation for bedsites, providing low visibility to conceal their offspring. Our results provide detailed insights into bedsite spatial and habitat selection by a large herbivore in response to human activities, and we provide clear indications to wildlife managers to preserve established fawning sites and alleviate human-wildlife conflict during a critical period of the deer annual biological cycle.

Keywords: human-wildlife conflict, deer, urban wildlife, Resource Selection Functions, bedsite selection.

Introduction

We are currently in the Anthropocene, defined by extensive human impact on our planet's ecology and geology (Morelli et al., 2020). It is estimated that more than 50% of the human population will be concentrated in cities by 2030 (Lowry et al., 2013, Shochat et al., 2006), with these cities presently expanding at an unprecedented rate worldwide (Wolff et al., 2018). This process leads to increased synurbanisation, i.e. wildlife increasingly living in and adapting to urban environments, with a concurrent increase in encounters between humans and wildlife (Barber et al., 2010, Gallo et al., 2019, Huijbers et al., 2013, Tucker et al., 2018). Several concerns have been raised about the potential for artificial selection processes to occur as a result of human-wildlife interactions (i.e., certain morphological and/or behavioural traits favoured over others) within urban settings (Griffin et al., 2022, Lowry et al., 2013).

Empirical research has repeatedly shown that human presence can affect wildlife behaviour significantly (Gander and Ingold, 1997, Hebblewhite et al., 2005, Recarte et al., 1998, Shen-Jin et al., 2007, Whittington et al., 2004). Wildlife species may increase flight response in locations with high human presence (Recarte et al., 1998), as well as increase selection of safer habitats and reduced movement (Gander and Ingold, 1997, Hebblewhite et al., 2005, Recarte et al., 1998, Shen-Jin et al., 2007, Whittington et al., 2004). Within urban settings, however, wildlife species need to adapt their anti-predator strategies (e.g., reduced flight distance) as fleeing any time that they encounter humans would be energetically expensive. This highlights how behavioural flexibility (or phenotypic plasticity) may be an important characteristic for succeeding in urban environments (Lowry et al., 2013).

Dog owners within urban areas need to walk their dogs and make any possible use of

green areas and urban parks, potentially leading to high encounter rate between dogs and

wildlife inhabiting urban areas. Dog presence has been shown to alter wildlife behaviour, though

responses vary depending on the wildlife species (Manor and Saltz, 2004, Martinetto and

Cugnasse, 2001, Miller et al., 2001). Both domestic and feral dog presence increases alert and

escape distances in many ungulate species, and has been associated with a reduction in

offspring:female ratios (Manor and Saltz, 2004, Martinetto and Cugnasse, 2001, Miller et al.,

2001). These decreases in offspring production could be caused by associated increases in

vigilance in mothers, decreased breeding behaviour, or a combination of both (St. Clair and

Forrest, 2009). Due to the importance of successful breeding seasons in keeping wild animal

populations healthy, changes in breeding behaviours during this sensitive period can lead to

indirect effects, with potential long-term consequences for the composition (i.e., age ratios) of

wild populations and natural selection processes (Lowry et al., 2013). As humans and their dogs

are both likely to come into more regular contact with wild animals within increasingly human

dominated environments, studies assessing the consequences of human and dog presence on

wildlife are increasingly important.

Ungulates exhibit various strategies to increase offspring survival during their first

weeks of life; this constitutes a continuum ranging from "hider" to "follower" species (Walther,

1961a). As a "hider" species, fallow deer (*Dama dama*) mothers hide their offspring in dense

vegetation, where they remain separated for several hours at a time (Chapman and Chapman,

1997). Selection of these "bedsites" after parturition plays a major role in increasing offspring

survival (Gerlach and Vaughan, 1991, Tull et al., 2001, Van Moorter et al., 2009, Monestier et al.,

2015). During this vulnerable time for offspring, fallow deer mothers decrease their home-range

sizes and select for denser vegetation to increase concealment and decrease predators' ability to

detect fawns (Ciuti et al., 2006). However, research to date has focused almost exclusively on

rural areas, with little understanding of bedsite selection in peri-urban landscapes (Smith and

Lecount, 1979, Long et al., 1998, Piccolo et al., 2010). This highlights the need for an empirical

quantification of the impact of people and their dogs on deer behaviour during fawning to

manage wildlife populations within urban settings.

Here, we gathered data on 477 bedsites used by 283 individual fallow deer fawns

across 3 consecutive fawning seasons in the largest walled urban park in Europe, Phoenix Park,

located at the heart of Dublin, Ireland. This is the largest dataset ever compiled on bedsite

selection in a large ungulate in an urban parkland. We explored bedsite selection by fallow deer

mothers that have adapted to live in a peri-urban area under high human pressure. Phoenix Park

is an ideal model for this study as boasts a substantial herd of wild fallow deer, it receives 10

million annual visitors, typically on foot with many walking their dogs, and large amounts of

vehicular traffic (which includes commuters to and from Dublin city centre) at the edge of a

capital city. Also, because of the walled nature of the park and the peri-urban environment, it is

extremely hard for the deer to leave and find suitable habitat outside the park.

We made 3 main predictions related to our hypothesis that fallow deer mothers would

select for the most suitable bedsite features while attempting to minimise human disturbance,

where possible, in such a restricted space: (i) mothers would select bedsites characterized by

denser vegetation and lower visibility, when compared to random available sites, to reduce fawn

detectability by terrestrial predators (including humans); (ii) bedsites would be located outside

and at greater distances from hotspots of human and dog presence along hiking trails; and (iii)

mothers would avoid roads with vehicle traffic when selecting fawns' bedsites. Our study site,

Phoenix park, is dominated by park visitors during the day; as a consequence, fallow deer

mothers are expected to find the best balance between selecting suitable vegetation and an

appropriate distance from humans for their fawns' bedsites, giving us the opportunity to describe

deer plasticity and adaptation to extreme conditions in terms of human presence. To better

disentangle such behavioural response, we analysed our data looking at two spatial scales: large

scale (study-site-level), to depict general avoidance of human presence hotspots; and a small

scale (bedsite-level), to understand specific decisions made by mothers when selecting for

bedsite characteristics and visibility. Our work has important management implications because

our analytical approach allows to estimate threshold distances (distance to roads and hiking

trails) and vegetation characteristics (vegetation density and related visibility) that may be used

by park managers to create buffer zones and strictly protected core areas for wild deer during

this important stage of their annual biological cycle.

Materials and methods

Study site

The study was conducted in Phoenix Park, a 709ha urban park located in Dublin,

Ireland (53°22'N, -6°21'W, Fig. 1), which receives an estimated 10 million visitors annually (Office

of Public Works, OPW, official data). The vegetation is mainly grassland (56%) and woodland

(31%), with 7% of the park covered by roads and buildings (OPW, 2020). The Park management

(OPW) maintains a fallow deer population of around 600 individuals (end of summer population

estimate, which includes newborn fawns, OPW official data), and this number is kept constant

by yearly culls. The only natural predator in the park is the red fox, which seldomly predates

newborn fawns. Over the years, however, we have made several direct observations of

unleashed dogs chasing fawns, in many cases resulting in the injury or death of fawns.

Data collection

Fawn captures and bedsite characteristics

Fawns have routinely been captured in June (from June 5th to June 28th) and ear-tagged

with unique numbered plastic tags (Allflex medium; Mullinahone Co-op, Ireland) since the early

1970s as part of the monitoring and management of the fallow deer herd (Hayden et al., 1992,

Amin et al., 2021). We split the geographical area typically used by females as fawning sites

(displayed in both Fig 1 and Fig. 2a) into seven sectors. These were patrolled routinely, visiting 2-

3 sectors daily, with each sector visited at least once every 2-3 days. Approximately 10-15 trained

team members supervised by a certified wildlife biologist captured fawns using circular fishing

nets (1–1.5m of diameter) manoeuvred by long handles (1.5m long). The capture team usually

worked between 9:00 to 16:00 hrs daily, 7 days a week for more than three consecutive weeks,

with the goal of tagging most of the newborn fawns within this population (~85%).

The capture team collected data on fawns and their associated bedsites following a

well-defined protocol; see Amin et al. (2021) for a full description of the information collected on

fawns. For this study, we used the following data: fawn identity (ear tag code) and sex; fawn

weight (i.e. an objective proxy for age *sensu* Amin et al. (2021), determined by placing the fawn

into a 100-litre bag, which was weighed using a digital scale – resolution: 0.01 kg, Dario

Markenartikelvertrieb); GPS coordinates of the bedsite (using a Garmin etrex 30 hand-held unit);

and bedsite visibility (see below for full description). Fawns were routinely recaptured to monitor

body growth (Griffin et al., 2023), allowing us to collect bedsite characteristics in older fawns.

Our final database consisted of fawn capture data collected in 2018 (n = 102 individual fawns),

2019 (n = 81), and 2020 (n = 100). Note that we also had data on 4 additional bedsites outside

the capture sectors which we excluded due to the lack of random available points. Because of

recaptures, we gathered data on a total of 477 bedsites (n = 163 in 2018, n = 152 in 2019, and n

= 162 in 2020, Fig. 3). Note that the bedsite location of recaptured fawns could be different from

the one of the first capture, either because the mother moved the fawn, the fawn – once old

enough to move independently (1-2 weeks old) – decided to relocate elsewhere, or because of

our disturbance. Nevertheless, we were interested in capturing the behavioural process behind

the selection of bedsites in an area heavily used and disturbed by humans, and therefore keen

to learn from multiple recaptures of the same individual, with the *a priori* assumption that when

a bedsite was disturbed, the next one would be selected to minimise human disturbance.

Concurrent research in the same park (Faull et al. 2024) has showed that bedsite selection is

dictated by the mother when the fawns are neonates (first few days of life). Older (heavier)

fawns, however, tend to be more mobile and may have a role in selecting the exact place where

to settle down when moving from one bedsite to another (Faull et al. 2024).

We assessed the average visibility of the fawn bedsite – ranging from 0 (no visibility)

to 1 (full visibility) (*sensu* Bongi et al., 2008) – as follows: from a distance of 10m along the four

cardinal directions we recorded the proportion of visually unobstructed triangles on a cardboard

shape the size of a standing fawn (height: 45cm, width: 36cm), with the bedsite set as the

centroid. We observed the cardboard shape from an eye height of 70cm, which approximately

corresponds to the eye height of a red fox or a medium-sized dog. The study protocol and all

research procedures were approved by the UCD Animal Research Ethics Committee for the

duration of 5 years (2018-2023), under the permit AREC-E-18-28.

Presence-available study design

We used a presence-availability design to depict bedsite selection using Resource

Selection Functions (RSFs) (Thurfjell et al., 2014, Ciuti et al., 2018). RSFs allowed us to estimate

the relative probability of selection by comparing environmental features of used sites (a.k.a.

presence data from sites where fawns were found and captured) to those of sites selected at

random, defining environmental characteristics available in the study site. Random available

points were selected in R 3.6.3 (R Core Team, 2020) within the capture areas with the rule that

they each had to be at least 20m apart to avoid overlap (and therefore dependency) of visibility

measurements taken at each bedsite. Random points were visited during the fawning season,

and, for each location, we recorded the visibility following the same protocol adopted for the

true fawn bedsites (Fig. 3).

Spatially-explicit data collection on park visitors and their dogs during the fawning season

We collected data on park visitors and their dogs during the fawning season of 2019

(7th-28th of June, Fig. 2b) to build a spatially-explicit model of human abundance. Hiking trails

were the same in 2018, 2019, 2020, and our goal was not to estimate the variation in human

abundance across years, but rather understand which hiking trails were commonly used by park

visitors. We walked at a constant pace (5km/hr) along all hiking trails following a strict systematic

stratification, to survey each trail equally as a function of time of the day and day of the week.

We used a GPS handheld unit to record the position of human and dog presence on paths or

trails. If people or dogs were outside the path or trail (see Fig. 2b) – which occurred seldomly –

their GPS location was estimated by combining data from the GPS hand-held unit (Garmin etrex

30), a rangefinder (Hawke Endurance), and a compass. For each observation, we counted the

number of visitors and dogs.

Data Analysis

All analyses were carried out in R 3.6.3 (R Core Team, 2020). Using the human and dog

presence observations, we created probability maps of park visitors and dogs in the fawning area. We

first overlaid a grid of 50x50m cells on the fawning area and added the observation counts to each

cell, once for humans and once for dogs, and separately for weekdays and the weekend, resulting in

four observation maps. Since the observations of dogs were considerably lower than the observations

of humans, dog presence was converted into a binomial value (presence-absence). We then fitted

two spatial Generalized Additive Models (GAMs; Wood, 2017) for humans and dogs as a function of

the fawning area location (east coordinate, north coordinate) and day of the week (categorical, 2

levels: Mon-Fri weekday, and Sat-Sun weekend), specified in R as follows: (i) Human abundance

model: *gam*(human abundance ~ s(east coordinate, north coordinate, k=29) + day of the week, family

= Poisson (quasi-Poisson corrected)); (ii) Dog presence model: *gam*(dog presence ~ s(east coordinate,

north coordinate, k=29) + day of the week, family = binomial). We used a quasi-Poisson-corrected

Poisson error distribution for the human abundance model to account for a mild overdispersion (Zuur

et al., 2009). For both models, the spline knots were manually set to 29 to avoid overfitting the data

following the indications from the *gam.check* function (Wood, 2017). Both models were used to

predict human abundance (number of visitors) and dog presence at the 50x50m resolution using the

predict function in *mgcv* (Wood, 2017).

For each used and available point we assigned land cover type (Ordinance Survey

Ireland, official data – 10m resolution) using the o*ver* function from the *sp* package (i.e.

categorical variable with two levels: forest, and open habitat – corresponding to grassland), as

well as predicted (either weekday or weekend) human abundance and dog presence, and

distance to the nearest paved road (where vehicular traffic was allowed, in meters) using the

function *gDistance* from the *sp* package (Pebesma and Bivand, 2005, Bivand et al., 2013). We

created buffers of 250m and 2500m around all bedsites to assign the random available points at

the two spatial scales (bedsite-level and study-site-level). The small size diameter was chosen

since it was the smallest buffer that allowed for all bedsites to be compared with enough

available points at this resolution (used:available ratio 1:6). The large scale corresponded to the

distance between the two most distant vertices of the polygon defining the fawning area,

therefore in this instance availability was defined at the population level (Manly et al. 2007).

Buffer zones were created using the *gBuffer* function from the *sp* package in R. Our sampling

design did not match presence data with available points in the close proximity only, which

should have been analysed using a conditional logistic regression able to stratify on matching

pairs where each stratum would have its own intercept (*sensu* Thurfjell et al. 2014). We were

interested instead in building multiple scale resource selection functions, meaning that given a

spatial scale – e.g. 250m – the environmental characteristics of used points were compared to

those of the random available points occurring within the 250 meters of all used points. This

allowed us to understand the decisions taken by mothers when selecting for fawn bedsites at

different spatial scales: when looking at 250m scale, for instance, we were investigating the

selection of environmental characteristics on a small scale, but unable to understand the effect

of larger scale patterns (e.g. the avoidance of human hotspots at a greater distance than 250

meters) that could be depicted instead by the large scale analysis.

We screened all variables described above, to include in the RSF, for collinearity

(Dormann et al., 2013), and found that the spatially-explicit predictions of number of park visitors

were highly collinear with dog presence (see Supporting information). We therefore retained the

number of park visitors since it was continuous data and able to give a better picture of different

levels of disturbances when compared to the binomial probability of dog presence.

Resource Selection Functions, built assuming an exponential form, require normally

distributed continuous predictors (Thurfjell et al., 2014). Therefore, we transformed both human

abundance and road distance data to meet model assumptions. We succeeded with the

transformation of human abundance data using a box-cox transformation, a family of power

transformations which selects the best mathematical function for the data transformation to

achieve data normality (i.e., achieved using a log-likelihood procedure to find lambda and

transform the non-normally distributed variable, see Supporting information) using the *MASS*

package (Venables and Ripley, 2002). We were not able to improve the extremely skewed

distribution of road distance; this variable was therefore converted into a two-level categorical

predictor (close vs far) using a threshold point of 50m. The threshold point was selected by

running a sensitivity analysis with preliminary resource selection functions fitted with different

threshold values, and the best model was the one with the lowest Akaike Information Criterion,

AIC (see Supporting information).

To estimate the coefficients for the small and large scale RSFs, we fitted Generalized

Mixed-effect Models (GLMM, *glmer* function from package *lme4* - Bates et al., 2015) with a

binomial distribution of errors (response variable: used points, 1s; and random available points,

0s) and fawn identity as random intercept. The *a priori* model structure – fitted for both spatial

scales - is reported in Table 1. We scaled numerical predictors to improve model convergence

and included quadratic terms to account for non-linear effects. We defined our model structure

a priori by considering the predictors that we hypothesized to be ecologically relevant in driving

habitat selection in this population living in a peri-urban area. We therefore intentionally did not

attempt to simplify the model structure, but rather opted for interpreting the full model structure

(Dorman et al. 2018). The inclusion of quadratic effects was motivated by the fact that we did

not expect bedsite visibility, distance to roads, nor human abundance to have a straight linear

effect but rather a plateau effect (e.g. flat after a certain value of the predictor variable) or fully

quadratic effect. Note that sex, weight of the fawn (proxy for age), and year of study were

included in the model as confounding predictors to specify the dependency structure of the data

(see Table 1 for full details) but no ecological inference will be made because their significant

levels would simply predict that e.g. more used locations have been collected in a year compared

to the next one. Sex and year could have been included as random intercepts in the GLMM but

this was avoided due to reduced degrees of freedom.

Parameters estimated by the GLMM were extracted and plugged into the RSF taking

the exponential form (Thurfjell et al., 2014, Fechter et al., 2019, Brivio et al., 2019). RSF

scenarios estimating relative probabilities of selection (Thurfjell et al., 2014) were built by

varying the predictor of interest (e.g., visibility) while keeping all the other variables to median

values (for numerical variables) or to a fixed level (for categorical variables: Year = 2018, Sex = f,

Land cover type = open).

Results

We depicted human abundance and dog presence probability maps (50x50m resolution)

of the fawning area in Phoenix Park as predicted by the Generalized Additive Models in Fig. 4 (see

Supporting Information for full details). In terms of bedsite use, the n = 477 bedsites were

characterised by a mean visibility of 0.06 (min-max: 0-1); 21% of them were at a distance lower

than 50m from roads (average distance from roads 119m; min-max: 4-338m); mean human

abundance predicted at bedsites was 1.22 people per 50x50m pixels(min-max: 0.0009-5.81), and

70% of the besites were found in forest habitat.

We reported the parameter estimates of the two GLMMs (small and large scale,

respectively) in Table 2. Year, sex, and weight were included in the model to specify the

dependency structure of the data, but no inference was made because not included as

interaction terms *a priori*. Areas with higher human abundance were avoided at the large spatial

scale (Table 2), with bedsites clustered and located outside human hotspots (Fig. 4), whereas

human abundance was not significant at the small spatial scale, where both used and available

points were far from the areas with higher human abundance. We found bedsite visibility to be

a key driver of selection at both spatial scales, with bedsites characterised by significantly lower

visibility (denser vegetation) than random available points (Table 2). Bedsites were more likely to

be located at distance greater than 50m from roads with vehicle traffic. Finally, bedsite locations

were more likely to be selected within forest habitat than open areas (Table 2). We depicted the

key scenarios which described bedsite visibility and avoidance of human hotspots and roads in

Fig. 5 and Fig. 6. In Fig.5, we showed the highly significant avoidance of human hotspots at the

large spatial scale, with bedsites more likely to be located in an area with less than 5 people/ha

and at a distance greater than 50m from paved roads. In Fig. 6, we can see for both spatial scales

how bedsites were selected in areas with horizontal visibility close to zero and – again – at

distance from paved roads greater than 50 meters.

Discussion

We found that, when selecting bedsites, fallow deer mothers significantly avoided

hotspots of humans on foot (which was also associated with dog presence) along the hiking trail

network. Bedsites were located away from paved roads used by vehicular traffic (rarely being

located within 50m from a road), mostly within forest habitat, and in dense understory

vegetation with low horizontal visibility (nearly zero, from a distance of 10m). For the first time,

through the combination of bedsite data and observations of human abundance and dog

presence, we described bedsite selection at a high spatial resolution, gathering empirical

evidence on the features of bedsites selected by mothers to successfully give birth and protect

their fawns during their first weeks of life in a peri-urban setting. This data can be used by urban

wildlife managers to identify and protect fawning sites and alleviate human-wildlife conflict

during this critical period of the deer annual biological cycle. This is fundamental for maintaining

high welfare standards for urban wildlife through the implementation of good management

practices and improve human-wildlife coexistence.

Despite both humans on foot and vehicular traffic being highly predictable in the park

– cars never leave paved roads and humans on foot rarely leave walking trails – our study showed

higher disturbance from humans on foot compared to roads used by vehicular traffic. The first

50m from the nearest paved road was avoided, but bedsites were located at a much higher

distance from human hotspots. This may be because vehicles on the road follow a strictly

predictable course (vehicles are not allowed off road) compared to people walking/running in

the park who could leave the trails (even if they rarely do so) and are often in the company of

unleashed dogs. Several studies have shown that wildlife disturbance is highly dependent on the

type of human activity (Stankowich, 2008, Naylor et al., 2009, Ciuti et al., 2012). For example,

Ciuti et al. (2012) showed that large herbivore behaviour is impacted more by humans on foot

than bicycles and horses on trails and roads. Further studies on ungulates have shown human

avoidance and behavioural changes when close to locations with high human disturbance levels

(Shen-Jin et al., 2007, Whittington et al., 2004, Manor and Saltz, 2004). Mountain Gazelles

(*Gazella gazelle*), for example, not only actively avoid humans, but they have also been shown to

alter their flight distance when close to hotspots of human presence (Manor and Saltz, 2004).

Similar results were found in a study by Shen-Jin et al. (2007); fallow deer were observed to

increase vigilance rates when close to locations with higher human density, whereas they

increased resting time when further away from humans. Our study adds new empirical evidence

on the effects of human presence and activity on ungulate behaviour by reporting novel effects

on bedsite selection in a peri-urban setting.

Vehicular disturbance has also been widely documented to impact wildlife behaviour.

Noise disturbance created by busy roads, for example, creates a phenomenon called "noise

masking". Noise masking impacts communication between individuals in a wide range of taxa.

Many studies have shown severe effects on reproductive success, density and community

structure as well as anti-predator and foraging behaviour (Barber et al., 2010, Pelletier, 2014,

Papouchis et al., 2001, Bonnot et al., 2013). Most ungulates avoid being close to roads, especially

when high-traffic levels are present (Pelletier, 2014, Papouchis et al., 2001). For example, a study

by Bonnot et al. (2013) showed that roe deer avoid roads even if it compromises their access to

important feeding sites. Similar avoidance behaviour has been shown in our study, although we

found that, at this limited spatial scale, fallow deer mothers had to balance a trade-off between

finding suitable bedsites and keeping a safe distance from roads, which resulted in avoidance of

roads being limited to 50m.

338   Concealment and safety from predators are the top priorities for ungulate mothers

when selecting a bedsite to hide their newborns (Barbknecht et al., 2011). This anti-predator

strategy manifests in this study through the selection for low visibility habitats for fawns'

bedsites. Bongi et al. (2008) showed that lactating roe deer females select for habitats with

reduced visibility. Likewise, Ciuti et al. (2006) revealed a preference for dense vegetation and low

visibility by fallow deer mothers to hide their fawns from predators. We found that this anti-

predator behaviour remains intact even within urban areas. Our study demonstrates consistency

in the selection for low visibility when choosing fawns' bedsites at both spatial scales after

accounting for the presence of humans on foot (and their dogs) and vehicles on roads. Our

findings can therefore inform management decisions when it comes to reducing human pressure

on fawning sites within these urban and peri-urban areas. During the fawning season, for

instance, hiking trails closer than ~200m to established fawning sites should be temporarily

closed to minimise disturbance, and policies regarding keeping dogs on a leash should be

enforced. Understory vegetation within forest habitats as well as grasslands should not be cut

(which may be a practice in several urban parks to improve human access): in Phoenix Park, for

instance, hiking trails are the only linear features where the grassland is managed, therefore

promoting use by park visitors, and making it less likely that they will walk in the high grass closer

to fawning areas. Knowing the impact that humans are having on wildlife populations living in

urban areas is fundamental to avoid detrimental effects on wildlife welfare and health. The

impacts that we have on wildlife can be minimised by understanding the issues present and

creating management plans to mitigate them. In this case, wildlife managers working within

urban parks and green spaces can incorporate our findings into management plans in order to

promote human-deer coexistence during the birthing season.

Funding

This publication has emanated from research conducted with the financial support of Science

Foundation Ireland under Grant number 18/CRT/6049. For the purpose of Open Access, the

author has applied a CC BY public copyright licence to any Author Accepted Manuscript version

arising from this submission.

Availability of data and materials

The datasets generated and/or analysed during the current study as well as the R markdown

script/HTML showing the statistical analysis of this study are available in the '*Fawn bedsite*

selection by a large ungulate living in a peri-urban area' repository,

https://doi.org/10.5281/zenodo.10886373.

References

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.
BARBER, J. R., CROOKS, K. R. & FRISTRUP, K. M. 2010. The costs of chronic noise exposure for
terrestrial organisms. *Trends Ecol Evol,* 25**,** 180-9.
BARBKNECHT, A. E., FAIRBANKS, W. S., ROGERSON, J. D., MAICHAK, E. J., SCURLOCK, B. M. &
MEADOWS, L. L. 2011. Elk parturition site selection at local and landscape scales. *The*
Journal of Wildlife Management, 75**,** 646-654.
BATES, D., MÄCHLER, M., BOLKER, B. & WALKER, S. 2015. Fitting Linear Mixed-Effects Models
Using lme4. *Journal of Statistical Software,* 67**,** 1 - 48.
BIVAND, R. S., PEBESMA, E. & GOMEZ-RUBIO, V. 2013. *Applied spatial data analysis with R,* NY,
USA, Springer.
BONGI, P., CIUTI, S., GRIGNOLIO, S., DEL FRATE, M., SIMI, S., GANDELLI, D. & APOLLONIO, M.
2008. Anti-predator behaviour, space use and habitat selection in female roe deer during
the fawning season in a wolf area. *Journal of Zoology,* 276**,** 242-251.
BONNOT, N., MORELLET, N., VERHEYDEN, H., CARGNELUTTI, B., LOURTET, B., KLEIN, F. &
HEWISON, A. J. M. 2013. Habitat use under predation risk: hunting, roads and human
dwellings influence the spatial behaviour of roe deer. *European Journal of Wildlife*
Research, 59**,** 185-193.
BRIVIO, F., ZURMÜHL, M., GRIGNOLIO, S., VON HARDENBERG, J., APOLLONIO, M. & CIUTI, S.
2019. Forecasting the response to global warming in a heat-sensitive species. *Sci Rep,* 9**,**
3048.
CHAPMAN, D. & CHAPMAN, N. 1997. *Fallow deer: Their history, distribution, and biology,*
Machynlleth, Coch-y-Bonddu Books.
CIUTI, S., BONGI, 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., NORTHRUP, J., MUHLY, T., SIMI, S., MUSIANI, M., PITT, J. & BOYCE, M. 2012. Effects of
Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of
Fear. *PloS one,* 7**,** e50611.
CIUTI, S., TRIPKE, H., ANTKOWIAK, P., GONZALEZ, R. S., DORMANN, C. F. & HEURICH, M. 2018. An
efficient method to exploit LiDAR data in animal ecology. *Methods in Ecology and*
Evolution, 9**,** 893-904.
DORMANN, C. F., ELITH, J., BACHER, S., BUCHMANN, C., CARL, G., CARRÉ, G., MARQUÉZ, J. R. G.,
GRUBER, B., LAFOURCADE, B., LEITÃO, P. J., MÜNKEMÜLLER, T., MCCLEAN, C., OSBORNE,
P. E., REINEKING, B., SCHRÖDER, B., SKIDMORE, A. K., ZURELL, D. & LAUTENBACH, S. 2013.
Collinearity: a review of methods to deal with it and a simulation study evaluating their
performance. *Ecography,* 36**,** 27-46.
DORMANN, C.F., CALABRESE, J.M., GUILLERA-ARROITA, G., MATECHOU, E., BAHN, V., BARTOŃ,
K., BEALE, C.M., CIUTI, S., ELITH, J., GERSTNER, K., GUELAT, J., KEIL, P., LAHOZ-MONFORT,
J.J., POLLOCK, L.J., REINEKING, B., ROBERTS, D.R., SCHRÖDER, B., THUILLER, W., WARTON,

D.I., WINTLE, B.A., WOOD, S.N., WÜEST, R.O. AND HARTIG, F. 2018. Model averaging in ecology: a review of Bayesian, information-theoretic, and tactical approaches for predictive inference. Ecol Monogr, 88: 485-504.

FAULL, J., CONTEDDU, K., GRIFFIN, L.L, AMIN, B., SMITH, A.F., HAIGH, A., CIUTI, S. 2024. Do human–wildlife interactions predict offspring hiding strategies in peri-urban fallow deer? Royal Society Open Science 11: 231470..

FECHTER, D., CIUTI, S., KELLE, D., PRATJE, P., DORMANN, C. F. & STORCH, I. 2019. Spatial behavior in rehabilitated orangutans in Sumatra: Where do they go? *PLOS ONE,* 14**,** e0215284.

GALLO, T., FIDINO, M., LEHRER, E. W. & MAGLE, S. 2019. Urbanization alters predator-avoidance behaviours. *J Anim Ecol,* 88**,** 793-803.

GANDER, H. & INGOLD, P. 1997. REACTIONS OF MALE ALPINE CHAMOIS Rupicapra r. rupicapra TO HIKERS, JOGGERS AND MOUNTAINBIKERS. *Biological conservation,* 79**,** 107-109.

GERLACH, T. P. & VAUGHAN, M. R. 1991. Mule Deer Fawn Bed Site Selection on the Pinon Canyon Maneuver Site, Colorado. *The Southwestern Naturalist,* 36**,** 255-258.

GRIFFIN, L. L., HAIGH, A., AMIN, B., FAULL, J., CORCORAN, F., BAKER-HORNE, C. & CIUTI, S. 2023. Does artificial feeding impact neonate growth rates in a large free-ranging mammal? *Royal Society Open Science,* 10**,** 221386.

GRIFFIN, L. L., HAIGH, A., AMIN, B., FAULL, J., NORMAN, A. & CIUTI, S. 2022. Artificial selection in human-wildlife feeding interactions. *Journal of Animal Ecology,* 91**,** 1892-1905.

HAYDEN, T. J., MOORE, N. P. & KELLY, P. F. 1992. The fallow deer of Phoenix Park: An evolving management plan. In Proc. 2nd Deer Park Symp.: management, welfare and conservation of park deer

HEBBLEWHITE, M., WHITE, C. A., NIETVEL, C. G., MCKENZIE, J., HURD, T., FRYXELL, J. M., BAYLEY, S. E. & PAQUET, P. C. 2005. Human Activity Mediates a Trophic Cascade Caused by Wolves. *Ecology,* 86**,** 2135-2144.

HUIJBERS, C. M., SCHLACHER, T. A., SCHOEMAN, D. S., WESTON, M. A. & CONNOLLY, R. M. 2013. Urbanisation alters processing of marine carrion on sandy beaches. *Landscape and Urban Planning,* 119**,** 1-8.

LONG, R. A., O'CONNELL, A. F. J. & D.J., H. 1998. Mortality and survival of white-tailed deer *Odocoileus virginianus* fawns on a north Atlantic coastal island. *Wildlife Biology,* 4**,** 237-247.

LOWRY, H., LILL, A. & WONG, B. B. 2013. Behavioural responses of wildlife to urban environments. *Biol Rev Camb Philos Soc,* 88**,** 537-49.

MANLY, B. F., MCDONALD, L., THOMAS, D. L., MCDONALD, T. L. & ERICKSON, W. P. 2007. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*, Springer Netherlands.

MANOR, R. & SALTZ, D. 2004. The impact of free-roaming dogs on gazelle kid/female ratio in a fragmented area. *Biological Conservation,* 119**,** 231-236.

MARTINETTO, K. & CUGNASSE, J. M. 2001. Reaction distance in Mediterranean mouflon (Ovis gmelini musimon x Ovis sp.) in the presence of hikers with a dog on the Caroux plateau (Hérault, France). *Revue d Ecologie,* 56**,** 231-242.

MILLER, S. G., KNIGHT, R. L. & MILLER, C. K. 2001. Wildlife Responses to Pedestrians and Dogs. *Wildlife Society Bulletin (1973-2006),* 29**,** 124-132.

MONESTIER, C., MORELLET, N., GAILLARD, J.-M., CARGNELUTTI, B., VANPÉ, C. & HEWISON, A. J.
M. 2015. Is a proactive mum a good mum? A mother's coping style influences early fawn
survival in roe deer. *Behavioral Ecology,* 26**,** 1395-1403.
MORELLI, F., TRYJANOWSKI, P., MØLLER, A. P., KATTI, M. & REIF, J. 2020. Editorial: Partitioning
the Effects of Urbanization on Biodiversity: Beyond Wildlife Behavioural Responses to a
Multilevel Assessment of Community Changes in Taxonomic, Functional and Phylogenetic
Diversity. *Frontiers in Ecology and Evolution,* 8.
NAYLOR, L., WISDOM, M. & ANTHONY, R. 2009. Behavioral Responses of North American Elk to
Recreational Activity. *Journal of Wildlife Management,* 73.
OPW. 2020. *Phoenix Park* [Online]. http://phoenixpark.ie. Available: http://phoenixpark.ie
[Accessed 18 November 2020].
PAPOUCHIS, C. M., SINGER, F. J. & SLOAN, W. B. 2001. Responses of desert bighorn sheep to
increased human recreation. *Journal of Wildlife Management,* 65**,** 573-582.
PEBESMA, E. J. & BIVAND, R. S. 2005. Classes and methods for spatial data in R. *R News,* 5**,** 9-13.
PELLETIER, F. 2014. Effects of tourist activities on ungulate behaviour in a mountain protected
area. *Journal of Mountain Ecology,* 8.
PICCOLO, B. P., VAN DEELEN, T. R., HOLLIS-ETTER, K., ETTER, D. R., WARNER, R. E. & ANCHOR, C.
2010. Behavior and survival of white-tailed deer neonates in two suburban forest
preserves. *Canadian Journal of Zoology,* 88**,** 487-495.
R CORE TEAM, R. C. 2020. R: a language and environment for statistical computing. Vienna,
Austria: R Foundation for Statistical Computing.
RECARTE, J. M., VINCENT, J. P., A.J.M., H., VINCENT, J. P. & A.J.M., H. 1998. Flight responses of
park fallow deer to the human observer. *Behavioural processes,* 44**,** 65-72.
SHEN-JIN, L., LIN, Y., YU-QING, L., YAN, Y., GUO-HONG, C. & WAN-HONG, W. 2007. The Effect of
Visitor Density on the Behaviour of the Captive Fallow Deer (Dama dama). *Research*
Journal of Animal Sciences, 1**,** 81084.
SHOCHAT, E., WARREN, P. S., FAETH, S. H., MCINTYRE, N. E. & HOPE, D. 2006. From patterns to
emerging processes in mechanistic urban ecology. *Trends Ecol Evol,* 21**,** 186-91.
SMITH, R. H. & LECOUNT, A. 1979. Some Factors Affecting Survival of Desert Mule Deer Fawns.
The Journal of Wildlife Management, 43**,** 657-665.
ST. CLAIR, C. & FORREST, A. 2009. Impacts of vehicle traffic on the distribution and behaviour of
rutting elk, Cervus elaphus. *Behaviour,* 146**,** 393-413.
STANKOWICH, T. 2008. Ungulate flight responses to human disturbance: A review and meta-
analysis. *Biological Conservation,* 141**,** 2159-2173.
THURFJELL, H., CIUTI, S. & BOYCE, M. S. 2014. Applications of step-selection functions in ecology
and conservation. *Movement Ecology,* 2**,** 4.
TUCKER, M. A., BÖHNING-GAESE, K., FAGAN, W. F., FRYXELL, J. M., VAN MOORTER, B., ALBERTS,
S. C., ALI, A. H., ALLEN, A. M., ATTIAS, N. & T., A. 2018. Moving in the Anthropocene: Global
reductions in terrestrial mammalian movements. *Science,* 359**,** 466–469.
TULL, J. C., KRAUSMAN, P. R. & STEIDL, R. J. 2001. Bed-Site Selection by Desert Mule Deer in
Southern Arizona. *The Southwestern Naturalist,* 46**,** 354-357.
VAN MOORTER, B., GAILLARD, J.-M., MCLOUGHLIN, P. D., DELORME, D., KLEIN, F. & BOYCE, M. S.
2009. Maternal and Individual Effects in Selection of Bed Sites and Their Consequences
for Fawn Survival at Different Spatial Scales. *Oecologia,* 159**,** 669-678.

VENABLES, W. N. & RIPLEY, B. D. 2002. Modern applied statistics with S. Fourth Edition. Springer,
New York.
WALTHER, F. 1961a. Entwicklungszüge im Kampf und Paarungsverhalten der Horntiere.
Jaharbuch G. V. Opel, Freigehege für Tierforshung, 3**,** 90-115.
WHITTINGTON, J., ST. CLAIR, C. C. & MERCER, G. 2004. Path Tortuosity and the Permeability of
Roads and Trails to
Wolf Movement. *Ecology and Society,* 9.
WOLFF, M., HAASE, D. & HAASE, A. 2018. Compact or spread? A quantitative spatial model of
urban areas in Europe since 1990. *PLoS One,* 13**,** e0192326.
WOOD, S. N. 2017. *Generalized Additive Models,* Boca Raton, Chapman and Hall/CRC.
ZUUR, A. F., IENO, E. N., WALKER, N., SAVELIEV, A. A. & M., S. G. 2009. *Mixed Effects Models and*
Extensions in Ecology with R, New York, Springer.

Table 1: Structure of the GLMM models (binomial distribution of errors) fitted to estimate the parameters for the Resource Selection Functions at two spatial scales (250 and 2500m, respectively) and explaining fawn bedsite selection in the fallow deer population of Phoenix Park, Dublin, Ireland.

Variable type	Variable name	*A priori* rationale for including the variable in the model
Response variable	Used, available (1,0)	Response variable.
Explanatory (inclusive of quadratic term)	Bedsite visibility (ranging from 0 to 1)	Bedsites were expected to be characterised by lower visibility. Relationship was expected to be non-linear *a priori*.
Explanatory variable	Road distance (lower or equal to 50m, greater than 50m)	Bedsites were expected to be less likely located close to roads.
Explanatory variable (inclusive of quadratic term)	Human abundance (predicted number of people per 50x50m pixel)	Bedsites were expected to be selected in areas with reduced probability of encountering humans and their dogs (being dogs presence highly correlated with human abundance). Relationship was expected to be non-linear *a priori*.
Explanatory variable	Land cover type (2 levels: forest, open)	Bedsites were expected to be selected in habitats with greater cover, i.e. forest.
Confounding variable	Year (3 levels: 2018, 2019, 2020)	To specify to the model the dependency structure of the data, with data collected either in 2018, 2019, or 2020. Note that this was not included as random effect due to low degrees of freedom. This variable is included in the model as a confounding but should not be interpreted ecologically.
Confounding variable (inclusive of quadratic term)	Fawn weight (in kg)	To account for age of the fawn (older fawns = heavier) and specify to the model the dependency structure of the data. This variable is included in the model as a confounding but should not be interpreted ecologically because not included as interaction term.
Confounding variable	Sex of fawn (male, female)	To account for sex of the and specify to the model the dependency structure of the data Note that this was not included as random effect due to low degrees of freedom. This variable is included in the model as a confounding but should not be interpreted ecologically.
Random effect	Ear-Tag (identification code of the fawn)	To account for repeated observations of multiple besites belonging to the same fawn.

Table 2: Parameters estimated by the GLMMs fitted at two spatial scales (small: 250m; large: 2500m) explaining the relative probability of bedsite selection by fallow deer in the Phoenix Park, Dublin. Significance abbreviations: *** p<0.001, ** p<0.01, * p<0.05, · p<0.1, ns p>0.1, with p < 0.05 corresponding to 95% CI not overlapping zero.

Scale	Variables	Estimate	Std. Error	Z value	Pr(>|z|)	Significance
250m	(Intercept)	-3.39045	0.16137	-21.011	<2e-16	***
	Visibility	-2.30137	0.21582	-10.663	<2e-16	***
	Visibility^2	1.29053	0.25683	5.025	5.04e-07	***
	Road distance [>50]	0.30066	0.12802	2.349	0.0188	*
	Human abundance	-0.05440	0.05392	-1.009	0.3130	ns
	Human abundance^2	-0.01307	0.05243	-0.249	0.8031	ns
	Year2019	-0.97618	0.12207	-7.997	1.28e-15	***
	Year2020	-1.33774	0.12380	-10.805	<2e-16	***
	Sex (male)	0.02158	0.10011	0.216	0.8293	ns
	Weight	0.08826	0.31559	0.280	0.7797	ns
	Weight^2	-0.11144	0.31421	-0.355	0.7228	ns
	Land cover type (open)	0.19751	0.11180	1.767	0.0773	.
2500m	(Intercept)	-5.77268	0.16877	-34.204	<2e-16	***
	Visibility	-2.37996	0.22760	-10.457	<2e-16	***
	Visibility^2	1.29965	0.28195	4.610	4.04e-06	***
	Road distance [>50]	0.26029	0.12131	2.146	0.0319	*
	Human abundance	-0.11213	0.06320	-1.774	0.0760	.
	Human abundance^2	-0.32845	0.07786	-4.219	2.46e-05	***
	Year2019	-0.70036	0.11676	-5.998	1.99e-09	***
	Year2020	-0.98314	0.11871	-8.282	<2e-16	***
	Sex (male)	0.03313	0.09717	0.341	0.7331	ns
	Weight	0.08524	0.31048	0.275	0.7837	ns
	Weight^2	-0.09228	0.30750	-0.300	0.7641	ns
	Land cover type (open)	-0.22119	0.10763	-2.055	0.0399	*

Figure Legends

Fig. 1: Map of the Dublin metropolitan area, with the study site location, Phoenix Park, clearly
        visible as the largest green space in the top left of the map. The highlighted polygon (in
        green) in the western side of Phoenix Park represents the fallow deer fawning area, with
        the 7 sectors clearly defined.

Fig. 2: Map of the Phoenix Park, Dublin (a) including land cover types (open, forest), roads (black
        linear features. Within the fawning area, (b) hiking trails (grey lines) were systematically
        walked during the fawning season to locate park visitors and their dogs (blue triangles).
        The fallow deer fawning area, which has been patrolled by the team during ear-tagging
        procedures, is indicated by the pink polygon in both plots.

Fig. 3: Locations of fallow deer fawn bedsites (blue circle) and random available points (purple
        triangle) across the 3 years of the study (2018-2020) within the traditional fawning area
        (pink area) of the Phoenix Park, Dublin.

Fig. 4: Predicted maps depicting human abundance (a: greater abundance indicated by lighter
        colours, see legend indicating predicted human abundance) and dog presence (b: greater
        probability indicated by lighter colours, see legend indicating predicted human presence)
        in the fawning area of Phoenix Park. Both maps include bedsite locations (triangle) and
        random available points (circle). X-axis (corresponding to longitude) and Y-axis
        (corresponding to latitude) are expressed in meters. Note how the location of the fawn
        bedsites are outside the hotspots of people and dog occurrence.

Fig. 5: Predicted effect of the number of people per hectare (x-axis, 100x100m) on the relative
        probability of bedsite selection (y-axis, RSF score [w(x)]) when the distance to the closest
        road is between 0 and 50 meters from the road (light blue line) or greater than 50 meters
        from the road (dark blue line). Note the stronger selection for bedsites far from roads,
        particularly when the number of people per hectare is lower. Also note avoidance of
        humans was remarkable at the large spatial scale (2500m), and weaker at the small spatial
        scale (250m), where both bedsites and random available points are both far from human
        hotspots.

Fig. 6: Predicted effect of the bedside visibility (x-axis, ranging from 0% to 100% of a standing
        fawn visible from 10 meters and eye height of 70cm) on the relative probability of bedsite
        selection (y-axis, RSF score [w(x)]) when the distance to the closest road is between 0 and
        50 meters from the road (light blue line) or greater than 50 meters from the road (dark
        blue line). Note the stronger selection for bedsites with low visibility and more distant
        from roads when compared to random available points at both spatial scale.

a.

2 km
6000 ft

Land Cover Type

Open

Forest

b.

1 km
3000 ft

Trails
People and dog observations