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Utilization of habitat edges and linear features during movement in free-ranging domestic pet cats in Norway

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Abstract

Free-ranging domestic pet cats (*Felis catus*) pose a significant challenge to wildlife conservation and management worldwide, and a deeper understanding of their ranging characteristics is needed. Scientists often employ GPS technology in order to study movement, but tradeoffs between temporal resolution and battery life in GPS systems tend to obscure behavior at finer scales than home ranges. The aim of this study was to investigate how free ranging pet cats select linear landscape features and habitat edges as they move through their environment, and also demonstrate how citizen scientists and affordable off-the-shelf technology can be used to circumvent the tradeoff between temporal GPS resolution and battery life in order to quickly produce data with high spatial and temporal resolution. I studied pet cats living in suburban and rural landscapes in southern Norway. Cat owners were responsible for fitting and maintaining a rechargeable GPS collar to track their pet, with a fix-rate of 10 seconds for seven days. A total of 85887 position fixes from 103 pet cats were examined.

The GPS trajectories were analyzed using high-resolution map data and path selection functions to determine whether selection towards edges and linear features occurred. Even though there was a substantial variation in roaming tendencies between individuals, the analysis revealed that pet cats favor edges and ecotones between structurally dissimilar habitats over heterogenous habitat as they move through the landscape. Male cats used edges more than female cats, and senior cats (>9 years) used edges more than adults (2-9 years). In addition, cats with high owner-estimated predation rates favored edges more than low-prey individuals.

The participating owners were largely able to manage a tracking protocol for their pet on their own for the individual monitoring durations (seven days), indicating that citizen science is a promising framework to study small-scale movement and behavior of domestic cats, that can also be adapted and expanded upon in future similar studies.

The cat is the most abundant pet globally, and human activity continues to provide for this species while simultaneously fragmenting the landscape into linear features and edge habitats that it can potentially use to harm wildlife. The findings of the present study can help shape future conservation and management efforts to combat this, such as monitoring programs and buffer zones that restrict cat ownership near protected areas.

Sammendrag

Huskatter (*Felis catus*) som får bevege seg fritt utendørs er en utfordring for vern og naturforvaltning verden over, og en grundigere forståelse av deres atferd og bevegelsesmønstre er derfor nødvendig. Forskere benytter ofte GPS-teknologi til å studere dyr sine bevegelser, men kompromisser mellom batteriets levetid og antall registrerte posisjoner per tidsenhet gjør at fin-skala atferd ofte er vanskelig å avdekke. Formålet med denne studien var å undersøke hvordan huskatter selekterer lineære landskapselementer og kantsoner når de beveger seg utendørs, og også demonstrere hvordan folkeforskning («citizen science») kombinert med rimelig GPS-teknologi kan benyttes til å omgå utfordringen med batterilevetid for å produsere data med høy romlig og temporal oppløsning. Jeg studerte huskatter i forsteder og landlige omgivelser på Østlandet i Norge. Katteeiere var i løpet av syv dager ansvarlige for å håndtere og feste en oppladbar GPS-enhet til katten sin som registrerte dens posisjon hvert tiende sekund. Totalt ble 85887 posisjoner fra 103 katter analysert.

GPS-sporene ble analysert ved hjelp av høyoppløst kartdata (AR5) og sti-seleksjonsmodeller («path selection models») for å bestemme om det foregikk seleksjon for kanter og lineære elementer. Selv om det var betydelig variasjon i bevegelsesmønstre mellom individer avdekket analysen at huskatter foretrekker slike kanter og randsoner over heterogent habitat når de beveger seg gjennom landskapet. Hannkatter brukte kanter mer enn hunnkatter, og seniorkatter (>9 år gamle) brukte kanter mer enn voksne katter (2-9 år). I tillegg foretrakk katter med høy predasjonsrate kanter mer enn katter med lav predasjonsrate.

Katteeierne som deltok i prosjektet klarte for det aller meste å på egenhånd spore katten i syv dager etter gitte instruksjoner, noe som indikerer at folkeforskning kan være et lovende rammeverk for å studere små-skala bevegelser og annen atferd hos huskatten, som også kan utvides og tilpasses fremtidige studier.

Katten er verdens mest tallrike kjæledyr, og menneskelig aktivitet fortsetter å tilrettelegge for denne arten samtidig som landskapet i økende grad fragmenteres i lineære elementer og randsoner som den kan benytte til å gjøre økologisk skade. Funnene i denne studien kan bidra til å forme og tilrettelegge for fremtidige forvaltningsvedtak som sikter på å begrense dette, for eksempel overvåkningsprogrammer eller soner med katteforbud rundt reservater og liknende.

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Introduction

Invasive species are one of the biggest causes of irreversible global biodiversity loss, with introduced mammalian predators arguably being the most damaging group (Bellard, Genovesi and Jeschke, 2016). Through mechanisms of predation, competition, and transmission of disease, invasive predators have potentially caused 58% of modern bird, mammal and reptile extinctions, and continue to threaten almost 600 species globally (Doherty *et al.*, 2016). Such predators include rats (*Rattus spp.)* (Capizzi, Bertolino and Mortelliti, 2014; Harper and Bunbury, 2015), the red fox (*Vulpes vulpes)* (Burbidge and Manly, 2002; Johnson, Isaac and Fisher, 2006) and mustelids (Mustelidae*)* (Macdonald and Harrington, 2010; Parkes and Murphy, 2010). However, the domestic cat (*Felis catus*) has likely contributed almost half of these extinctions (Doherty *et al.*, 2016) and have been deemed "*the most ubiquitous and environmentally damaging invasive predator on Earth*" (Loss and Marra, 2017)

Modern domestic cats (hereafter "cats") descended from the wildcat (*Felis sylvestris*) and have possibly been a part of human society for as much as 12 000 years (Ottoni *et al.*, 2017). As human societies became more stationary and transitioned to agricultural production, free-roaming cats could hunt smaller vermin associated with homes, granaries and urban areas in exchange for access to shelter and more abundant food sources (Driscoll *et al.*, 2007).

Although the usefulness of cats as pest control agents has diminished over the centuries, this historically symbiotic arrangement continues to characterize the relationship between humans and cats today. Cats are the world's most numerous pet, and are typically viewed by the public as independent and autonomous individuals that require little in the way of monitoring and training compared to other household animals (Hall, 2016). Many owners regard their pets as "outdoor cats" meaning that they spend some or most of their day unsupervised outside (Crowley, Cecchetti and McDonald, 2019).

The management implications of owned free-ranging cats have received increasingly larger amounts of attention. As humans provide access to food, shelter and health benefits such as vaccinations, pet cat populations may exceed the carrying capacity of the environment and increase the predation impact due to being less limited by factors such as prey availability and disease (Kays and DeWan, 2004; Baker *et al.*, 2005). During a 5 month survey period, Woods, McDonald and Harris (2003) estimated that pet cats in Britain killed 52–63 million mammals, 25–29 million birds and 4– 6 million reptiles and amphibians. Pet owners also abandon their cats and contribute to growing feral populations that have an even larger predation impact than owned individuals (Loss, Will and Marra, 2013). Cats can compete with native predators (George, 1974; Crooks, 2002; Glen and Dickman, 2008), induce sub-lethal effects in prey species through fear of predation (Beckerman, Boots and Gaston, 2007), and are also able to carry and transmit multiple diseases that affect wildlife, humans, pets and livestock (Gerhold and Jessup, 2013; Hollings *et al.*, 2013),

The management of free-roaming pet cats is also a highly controversial topic socially. Surveys indicate that many cat owners are generally unaware of the ecological issues surrounding free-roaming cats, and are also reluctant to impose restrictions on their pets' ranging behavior in order to protect wildlife (Grayson, Calver and Styles, 2002; Hall, 2016; Crowley, Cecchetti and McDonald, 2019). However, as emphasized by Gramza and colleagues (2016), public knowledge and understanding of cat-related risks can induce changes in the attitude of cat owners, emphasizing the value of communication programs that promote risk-aversive ownership behavior.

Knowledge of a species' movement patterns at various scales, and the factors affecting this behavior, is essential to understand and conceptualize risks in conservation and management (Allen and Singh, 2016). Movement is a fundamental characteristic of life that both shapes and is shaped by the surrounding environment at all ecological scales (Nathan *et al.*, 2008). Knowing why and where animals move contributes to a mechanistic understanding of key ecological concepts such as resource use and home ranges, which can be used to develop effective, appropriate and employable management strategies (Cagnacci *et al.*, 2010).

Even for species with habitats of small spatial extent, direct visual observation of movement in a natural setting is largely restrictive and strenuous by nature, and scientists therefore employ telemetry technology in order to track the movement of animals from afar (de la Rosa, 2019). Recent rapid technological advancements have brought the advent of global positioning system (GPS) technology for use in animal tracking, which has many benefits over conventional tracking technology, such as VHF and Argos (Hebblewhite and Haydon, 2010). GPS can regardless of environmental conditions produce enormous amounts of continuous, accurate and unbiased high-resolution spatial and temporal data from free-roaming animals in their natural habitat, without the need for interference or disturbance from the operator (Soutullo *et al.*, 2007; Frair *et al.*, 2010; Urbano *et al.*, 2010). GPS loggers are becoming cheaper, smaller and lighter (Wilmers *et al.*, 2015), eliminating disadvantages of low sample sizes due to unit cost (Hebblewhite and Haydon, 2010) and also expanding the range of potential target species to include birds (Bridge *et al.*, 2011), reptiles (Price-Rees and Shine, 2011; Cochrane, Brown and Moen, 2019), and small mammals (McMahon *et al.*, 2017), including cats (e.g. Roetman, Tindle and Litchfield, 2018).

The majority of existing scientific literature concerning the movement and behavior of cats has primarily focused on feral cats, as these are believed to pose a greater environmental threat than pet cats (Loss, Will and Marra, 2013; Crowley, Cecchetti and McDonald, 2019). However, in many societies the proportion of feral cats is low compared to those owned by private individuals, and researchers have begun to express concerns regarding the ecological impacts from large concentrations of free-ranging pet cats (Kays and DeWan, 2004; Hall *et al.*, 2016; Loss and Marra, 2017). This necessitates the need to better understand how pet cats behave when roaming, separately to what is already known about feral individuals (Calver *et al.*, 2011; Kays *et al.*, 2020).

A relatively underexplored aspect of the movement of cats and other predator species is their association with linear features and edges (Červinka *et al.*, 2011; Bischof *et al.*, 2019). Urban and agricultural expansion fragments the landscape and creates linear configurations of habitat that have diverse, multidimensional effects on its wildlife (Lidicker, 1999; Benítez-López, Alkemade and Verweij, 2010; Graham, Maron and Mcalpine, 2012). Edges and ecotones that isolate habitat patches are often strongly preferred by mesopredators over habitat interiors (Crooks, 2002; Červinka *et al.*, 2011), and preferential use of linear features generated by roads, rivers, agricultural fields, fences and similar has previously been inferred for other medium and large carnivores, such as wolves (Dickie *et al.*, 2020), red foxes (Graham, Maron and Mcalpine, 2012; Bischof *et al.*, 2019), racoons (Barding and Nelson, 2008), quolls and Tasmanian devils (Andersen *et al.*, 2017) and feral cats (Graham, Maron and Mcalpine, 2012). Edges along isolated habitat patches in suburban-agricultural matrices can provide these predators better foraging opportunities (Lambertucci *et al.*, 2009; Šálek *et al.*, 2010), and linear features such as roads, fences, and similar can serve as a more efficient way for species to travel through the landscape to hunt (Larivihre, 2013; Zeller *et al.*, 2016; Dickie *et al.*, 2017) and/or mark their scent (Krofel, Hočevar and Allen, 2017).

A better understanding of how pet cats respond to structurally complex habitat with linear features is needed in order to plan and employ measures that mitigate for the negative effect on wildlife (Doherty, Bengsen and Davis, 2014). Cats might benefit from urban habitat fragmentation when some native carnivores do not (Crooks, 2002), and have also been shown to use edges and trails to range near ecologically sensitive areas (Morgan *et al.*, 2009; Woolley and Hartley, 2019). Disproportionally high use of edges and other linear features can shape conservation efforts (Bengsen, Butler and Masters, 2012), for example by providing hotspots for camera monitoring (Elizondo and Loss, 2016; Woolley and Hartley, 2019) or directing the placement of access roads into nature reserves and similar (Metsers, Seddon and Van Heezik, 2010).

To my knowledge, no existing study of pet cat habitat selection has examined linear feature use directly, but selection for edges and corridors in cats has been previously inferred. Warner (1985) found that free ranging, semi-owned cats (Crowley, Cecchetti and McDonald, 2019) on farmsteads in Illinois highly favored edges, roadsides, field interfaces and other linear configurations of cover, while Kays and DeWan (2004) observed that owned cats around a suburban nature preserve in the eastern U.S. rarely entered dense forest and instead stayed near the edges or in smaller forest fragments. Similarly, cats were more likely to be detected by camera traps at the edge of a nature reserve in New Zealand than further inside (Woolley and Hartley, 2019), and the cats living on a suburban-wetland periphery in New Zealand (Morgan *et al.*, 2009) were most frequently observed on the edge of the wetland or on walking tracks associated with it.

A feral cat population in an agricultural area of northern Italy preferred belts of forest on the edges of drain channels, meadows and cultivated fields over open terrain (Genovesi, Besa and Toso, 1995), and feral cats in New Zealand were attracted to vegetation buffers of long grass surrounding an open habitat containing potential prey (Alterio, Moiler and Ratz, 1998). Similarly, McGregor *et al.* (2014) describes feral cats exhibiting selection for edges in habitats that support high abundance of small animals. Gehring and Swihart (2003) used scent stations to show that cat presence was associated with fencerows, drainage ditches and railroad rights-of-way.

Tracking smaller animals with telemetry technology presents challenges inherently imposed by a tradeoff between battery life, unit (battery) weight and temporal resolution (Brown *et al.*, 2012). In order to infer accurate conclusions about behavior at small scales such as linear feature use, the positional data must be sampled with a temporal resolution that is large enough to actually capture changes in the animals' behavior (Mills, Patterson and Murray, 2006; Johnson and Ganskopp, 2008; Swain, Wark and Bishop-Hurley, 2008; Latham *et al.*, 2015). Since such sampling rates are highly demanding for the battery life of the units, researchers must often sacrifice accuracy for longevity when limited by weight (Brown *et al.*, 2012).

However, studying the movement patterns of pet cats introduces an interesting opportunity to use owners as citizen scientists to circumvent the issue of high fix-rates vs longevity. Technological advances in accessibility and increased portability of internet and location-aware devices has led to a tremendous increase in the number of successful citizen science projects worldwide (Bonney *et al.*, 2014). By putting the pet owners in charge of daily battery maintenance of a rechargeable, easy to use GPS unit, high intensity fix rates for long durations become possible. Transferring some of the responsibility to the pet owners also reduces workload for the researchers and potentially allows for a larger sample size, which has been a constraint in similar studies (Hall *et al.*, 2016). As an additional benefit, citizen science can also help inform and engage the public on issues in management and conservation (McKinley *et al.*, 2017), a subject in which free-ranging pet cats are a controversial topic (Gramza *et al.*, 2016)

In Norway there are an estimated 770 000 pet cats in around 400 000 households, with the majority of these cats having the opportunity to walk outside freely (Braastad, 2019). No study to my knowledge has examined the movement patterns of pet cats in Scandinavia. With the help of pet owner citizen scientists, free-ranging pet cats can be tracked with a very large temporal resolution, and this methodology has the potential to unveil truly small-scale activity patterns that would normally not be attainable using conventional means (Palacios and Mech, 2011).

This study examines very high-resolution (10 second) GPS data from pet cats roaming in rural-suburban matrix landscapes, gathered by citizen scientist owners. The tracking data is analyzed with conditional logistic regression using a step-level null model in order to investigate how cat movements associate with roads and ecotones between patches of habitat compared to entire patch interiors.

I expect that **1)** citizen scientist pet owners will largely be able to autonomously manage a tracking protocol for their pet and provide consistent data (Aceves-Bueno *et al.*, 2017; Roetman, Tindle and Litchfield, 2018). From the resulting tracking data, I predict that **2)** pet cats will show a marked preference for edges and linear features over habitat interiors similar to several other small carnivores (Šálek *et al.*, 2010; Červinka *et al.*, 2011). Lastly, if cats use edges primarily for hunting, I expect that **3)** cats with high owner-reported predation rates will show a larger selection for edges than those with lower reported predation rates, and that there will be no marked difference in edge selection between sexes or age groups (Hernandez *et al.*, 2013).

Materials and methods

Study area

The study was carried out in the so-called “Oslo region” in southern Norway, contained within a rectangle drawn by the coordinates 59.07 - 60.28 N, 10.05 - 11.27 E (Figure 1). Participants mostly lived in proximity to the Oslofjord, in the counties of Viken, Oslo, and Vestfold and Telemark at elevations 0–178 m.a.s.l (Kartverket, 2020). The landscape surrounding the urban centers is highly influenced by forestry and agriculture, creating a fragmented mosaic of fields and pastures (17.5%), forests (59.1%), developed areas (18.2%) and transportation networks (2.8%) (NIBIO, 2020b).

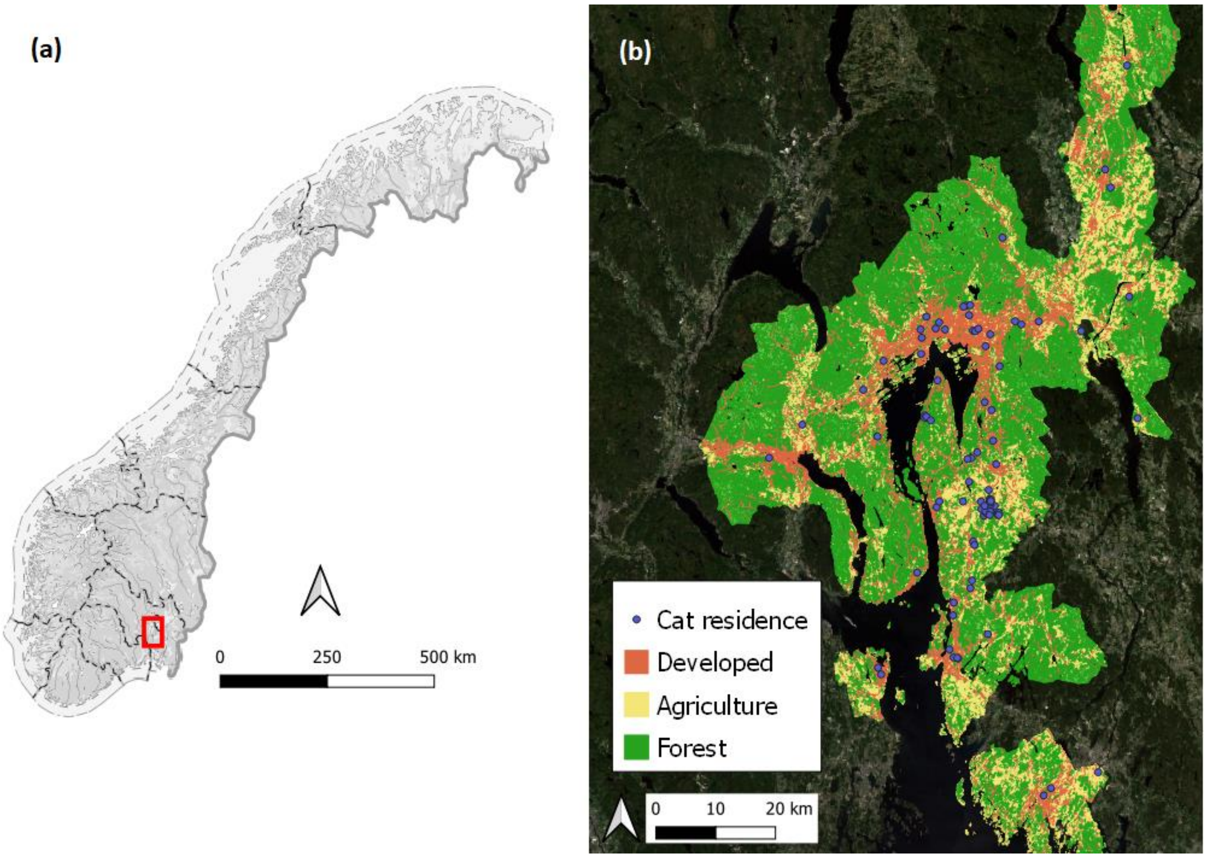


Figure 1: Map of the study area in southern Norway **(a)** and aerial photo of the study area overlaid with AR5 resource map data (NIBIO, 2020a) together with the location of the participating pet owners **(b)**.

The study area is situated in the boreonemoral vegetation zone (Lillethun and Moen, 1998), and has a warm humid continental climate (Kottek *et al.*, 2006) with maximum and minimum temperatures of 34.1 °C and -20.6 °C respectively (NKS, 2020). The average temperature in the area during the study period was 14.5 °C. The dominating tree species are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birch (*Betula* spp), rowan (*Sorbus aucuparia*) and *Salix* spp (NIBIO, 2020c). Common prey species for cats include small rodents and birds, such as the field vole (*Microtus agrestis*), brown rat (*Rattus norvegicus*), house sparrow (*Passer domesticus*) and dunnock (*Prunella modularis*) (Artsdatabanken, 2020).

Participant recruitment

Cat owners were invited to voluntarily take part in the project through publications on social media. Owners that were interested in participating were asked to fill out an initial survey that was used to exclude cats that did not spend much time outside or lived too far away to be convenient for the study. A second survey was then issued to the remaining participants recording their cats age and sex, geographic area of the home (rural, suburban/urban), how often the cat brings home prey/food items, and if the cat is used to having a collar.

Data collection

Each participant was sent a parcel containing a simple cat collar, a GPS unit with USB charger, and a set of instructions detailing how and when to use it. The GPS-units were beforehand set to obtain a fix every 10 seconds, which according to the associated software would provide the unit with around 15 hours of battery life. The participants were instructed to use the GPS unit to record the movements of their cat every day for one week from the first time they let their cat outside with the GPS. Due to constraints regarding the number of available GPS units, data collection from participating cat owners ran parallel to the recruitment of new participants from August 2019 to October 2019.

Participants were instructed to only turn on and attach the GPS unit when the cat was about to go outside, and otherwise remove, turn off, and charge the GPS unit when the cat was inside. Owners with cat flaps (i.e. any contraption that allows the cat to freely move in and out of the house) were instructed to attach the GPS at times they knew their cat usually spent the most time outside. When each owner finished recording a week of positional data, they were asked to mail the equipment back to Norwegian University of Life Sciences (NMBU), where data extraction and analysis took place.

GPS unit description

The study used i-gotU GT-120 GPS units (Mobile Action Technology, Inc., Taiwan), a commercially available consumer-targeted GPS logger (Figure 2). The units have a built-in patch antenna and feature a SiRF III chipset with 20 channels and a receiver sensitivity of -159 dBm while tracking (Morris and Conner, 2017). Each unit measures 2.4 x 2.7 x 1.3 cm and weighs 26 g including a silicone protection cover (4 g), well within the recommended instrument weight for domestic cats (Coughlin and Van Heezik, 2014). The units are not able to transfer data remotely, meaning they must be retrieved in order to download the data. Use of the units in this study does not imply endorsement.

Figure 2: i-gotU GT-120 attached to a simple cat collar

Even though it is not purposed for wildlife tracking, the i-gotU GT-120 has been used in many cat movement studies due to its light weight, availability, and ease of use (e.g. Coughlin and Van Heezik, 2014; Hervías *et al.*, 2014; Thomas, Baker and Fellowes, 2014; Hanmer, Thomas and Fellowes, 2017; Kays *et al.*, 2020). Both Morris and Conner (2017) and Allan and colleagues (2013) report average location errors of <10m in the majority of fixes, making the data accurate enough for fine-scaled analysis of animal movement (Frair *et al.*, 2010). Similar results are reported by Forin-Wiart *et al.* (2015) on a low-cost pet GPS with the same chipset.

The collars used in this study did not have counterweights, as initial tests (F. Sarfi, unpublished data) showed no noticeable difference in location error between units placed on the front or the back of the cat’s neck. They were also omitted for simplicity and to maximize the number of participants. Frair and colleagues (2010) do, however, state that while GPS orientation alone tend to have a negligible effect on data quality in open areas, it can interact with canopy cover to greatly reduce fix rates and location precision. Similarly, Coughlin and Van Heezik (2014) argue that this kind of collar-setup is likely to at least induce some degree of additional error.

Data extraction and processing

Coordinates and timepoints were extracted from the GPS units using the associated software (@trip PC, Mobile Action Technology, Inc.). The data was exported to Google Earth (Google Inc.) and examined visually for obvious outliers and user-error, such as the GPS unit being active while inside a moving vehicle. These points were removed from the datasets.

Using R (R Core Team, 2019), an algorithm was developed to identify and remove spatio-temporal clusters of points from the dataset, as these were assumed to indicate sections where the cat was more or less stationary as opposed to moving. First, the full relocation data from was broken into segments with time gaps equal or larger than 30 minutes. Within each segment, net squared displacement (NSD) was calculated for all positions. Clusters of relocations within these segments were labeled if they contained at least 15 consecutive relocations, and if each point lay within 10m of the previous point. As some clusters may be due to a cat simply moving slowly, stationary clusters were identified by fitting a simple linear regression to each cluster that estimated the effect of time (in seconds) on NSD (in m^2). Clusters with absolute regression coefficients of less than 100 m^2/sec were flagged as "stationary" and removed from the data. Individual movement trajectories ("tracks") were defined from the remaining, cluster-processed data by breaking it into segments that were equal to or more than 40 seconds apart in time, and then removing the segments that contained less than 30 points each.

Edge habitats and path selection

In order to determine how an animal selects habitat, resources and other landscape elements, resource selection functions (RSFs) are typically used. RSFs are statistical models that contrast "used" resource units to "available" units in order to determine the relative probability of an animal choosing a given resource (Boyce *et al.*, 2002). As technological advances have sufficiently improved the temporal grain of location data to determine the actual physical paths an animal takes, a subgroup of RSFs called step- and path selection functions (SSF, PSF) have been developed to capitalize on this (Thurfjell, Ciuti and Boyce, 2014). In this framework, "available" resource units are sampled using the animals own location data and contrasted with the "used" resource units in a conditional logistic regression (Zeller *et al.*, 2016). The "available" resource units in path selection analysis (i.e. the null model) are determined by rotating and/or moving each used track around a certain perimeter of its original placement. This makes it possible to determine whether the placement of the path is random or if it tends to coincide with specific habitat variable(s).

In order to determine "used" and "available" resource units, location data must also be linked to resource data. A simplified land-cover map was created using high resolution land-covers ("AR5", 5m) obtained from the Norwegian map catalogue Geonorge (NIBIO, 2020a). QGIS 3.12.0 (QGIS Development Team, 2020) was used to reclassify structurally similar landscape features into four categories: Open areas, forested areas, housing and roads (Figure 3).

For each point in a track, 20 random points representing the null model were generated using R (R Core Team, 2019) by randomly shifting and rotating the original track around its barycenter with the "NMs.randomShiftRotation"-function in the R package "adehabitatLT" (Calenge, 2006) (Figure 3). "Used" and "available" points were buffered by 10m, and the "over"-function in the R package "sp" (Pebesma and Bivand, 2005) was then used to sample presence/absence of the land-cover classes within each buffer. This presence-absence data was then used to create and assign each point new habitat types that indicated whether it was near an edge or not (Figure 4).

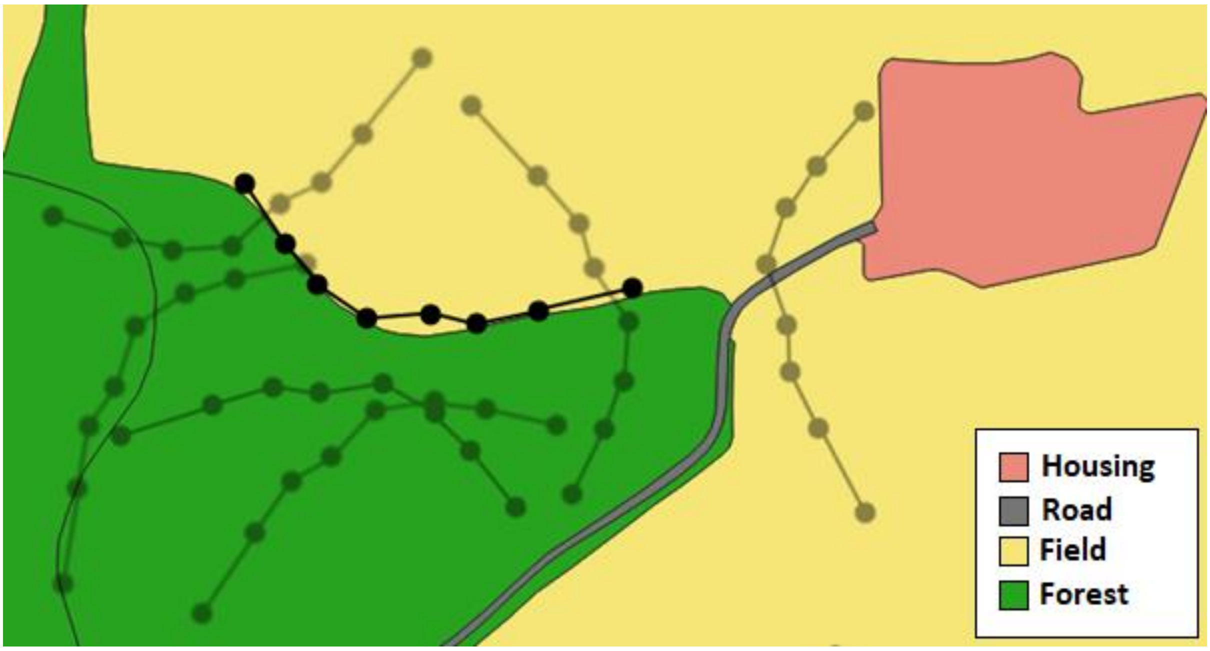
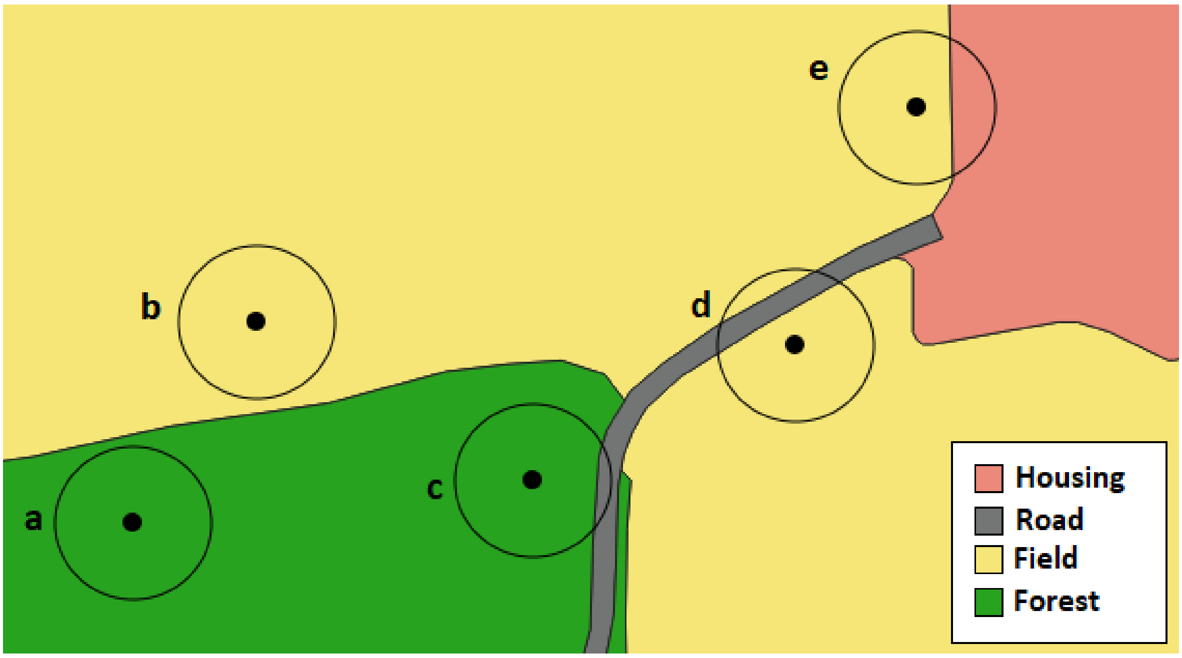


Figure 3: Conceptual illustration of a used path (black) along a rural habitat edge and six corresponding simulated "available" paths (transparent). In the actual models, 20 simulated paths were used.



Buffer	Forest	Field	Road	Housing	Edgetype	Edge
a	X	-	-	-	None	None
b	-	X	-	-	None	None
c	X	-	X	-	Road	Yes
d	-	X	X	-	Road	Yes
e	-	X	-	X	Other	Yes

Figure 4: Conceptual illustration of how "used" and "available" points were assigned edge habitat variables based on the presence/absence of different landscape elements within their buffer. In practice, all points are a part of a longer track akin to figure 3. For a full overview of edge assignment criteria, see Appendix.

Statistical analysis

Using R (R Core Team, 2019), each "used" point was paired with the corresponding 20 simulated "available" points in a stratum and then analyzed with conditional logistic regression models using the "survival" package (Therneau, 2020). The models estimate how the explanatory variables affects the tendency for a point to have the label "used" as opposed to "available". Because tracks from individual cats have high autocorrelation, cat ID was used as a clustering variable (Fortin *et al.*, 2005). I ran two different models:

Use ~ Edgetype + strata(Strata), cluster = ID, method = 'efron' (eq.1)

Use ~ Edge(Sex + Agegroup + Prey) + strata(Strata), cluster = ID, method = 'efron'* (eq.2)

In order to determine if cats prefer different kinds of edges over non-edges, the first model (eq. 1) examined selection for road-based edges and edges between habitats (e.g. forest-field interfaces). The second model (eq. 2) looked at edge presence as a binary “yes/no” variable to see if cat selection for any kind of edge is affected by sex, age, and owner-estimated predation rate.

Conditional logistic regression requires the use of a baseline reference level in order to calculate and display relative selection (Table 1). In the first model, the reference level for “Edgetype” is “none”, meaning that points near road-based edges and edges between habitats are contrasted to all points that are away from any kind of edge. In the second model, “Edgetype” was collapsed into a single binary category “Edge”, with “$Edge_{yes}$” contrasted to the reference level “$Edge_{none}$”. However, since the second model also examines interactions, there must also be a reference level for each one of these factors in order to show their relative effects on edge selection. The reference level for the interactions in the second model was set to “male, adult, low-prey” cats, which is the largest group in the dataset. The effects of the interactions are then presented in the model as the increase or decrease in selection for “$Edge_{yes}$” when changing one factor level in a category compared to the reference level.

The need for a reference level limits the number of explanatory variables the model can contain, because statistical power is gradually lost with each new variable that is added. For example, the reference level “male, adult, low-prey” contains fewer cats than a category

Table 1: Explanatory variables and their reference levels that were included in the two models.

	Variable	Factor levels	Explanation
Model 1	Edgetype	Road Other None*	Point is on/near an edge created by a road Point is on/near an edge that is not a road Point is away from any kind of edge
Model 2	Edge	Yes None*	Point is on/near any kind of edge Point is away from any kind of edge
	Sex	Male Female*	Male cat Female cat
	Agegroup	Young Adult* Old	<2 years old 2-9 years old >9 years old
	Prey	High Low*	Cat brings prey home daily or weekly Cat brings prey home monthly or rarer

(* = reference level)

representing “male, adult” cats. AIC criteria was therefore used to balance complexity with parsimony. The first model was as simple as possible, and therefore no AIC criteria was necessary. In the second model, AIC determined that all three explanatory variables should be included. Adding more explanatory variables such as residence or cat weight is desirable, but not practical with the current sample size.

Results

Owner recruitment and data collection

In total, 88 owners provided GPS data for the study (Figure 5). 307 cat owners showed initial interest in the project, but 131 owners were turned down due to the distance of their residence from the preferred study area. An additional 66 owners did not respond to a follow-up, resulting in a total of 110 owners that were given GPS units to participate in the study.

Out of the 110 owners that were given units, 22 did not register positional data at all. 11 of these participants simply returned their GPS units without responding to further inquiries, so it is difficult to determine the reason why data was not collected. The most common explanation given by the remaining participants that did not register data was that the cat did not accept the collar. Two GPS units were lost during tracking, and two owners were unable to finish due to reported illness. There were two cases of missing positional data that could definitively be attributed to either user error or possible GPS unit fault, as the owners in these cases were under the impression that data had been recorded.

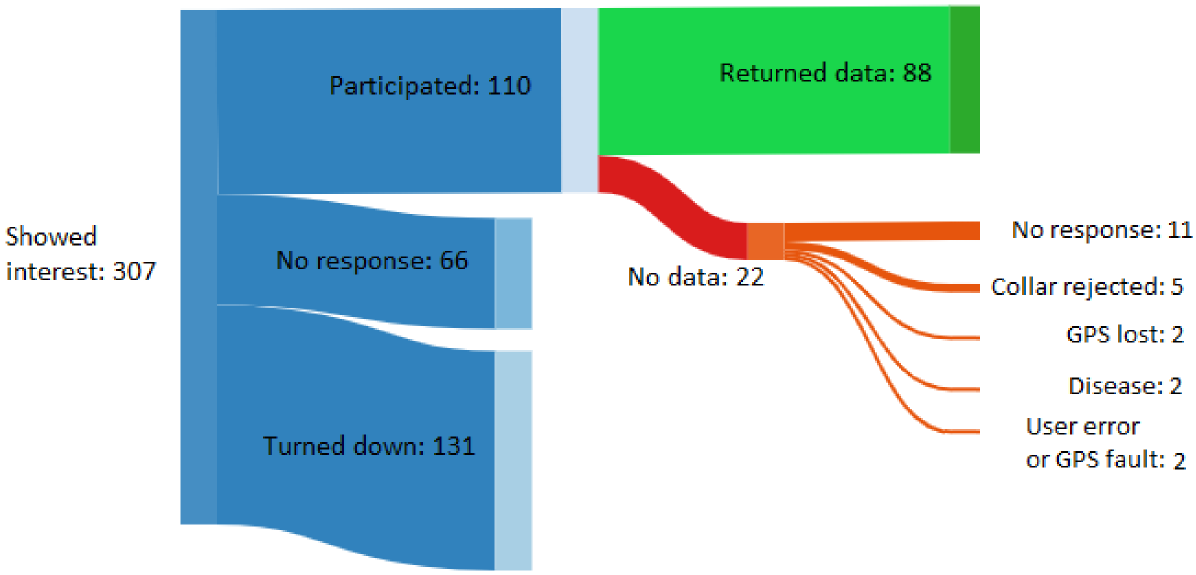


Figure 5: Sankey diagram describing the recruitment- and data collection process

Consequently, 88 owners returned GPS data from a total of 110 cats. 18 owners tracked two cats simultaneously, and two owners tracked three cats each. However, the total amount of cats in each household was not recorded, so it is likely that several owners had two or more cats even if only one was tracked in the study.

The tracking duration for each cat was calculated by counting unique dates in their data-timestamps (Figure 6). There was considerable variation in how long the owners tracked their cats, and only 72 out of 110 cats were tracked for the full seven or eight days. Eight days is regarded as about equivalent to seven days, since some cats might not have returned to their residences until past midnight on the seventh day. Twenty-four cats were tracked for less than seven days, and 14 cats for more than eight. Notably, one cat was tracked for 16 days.

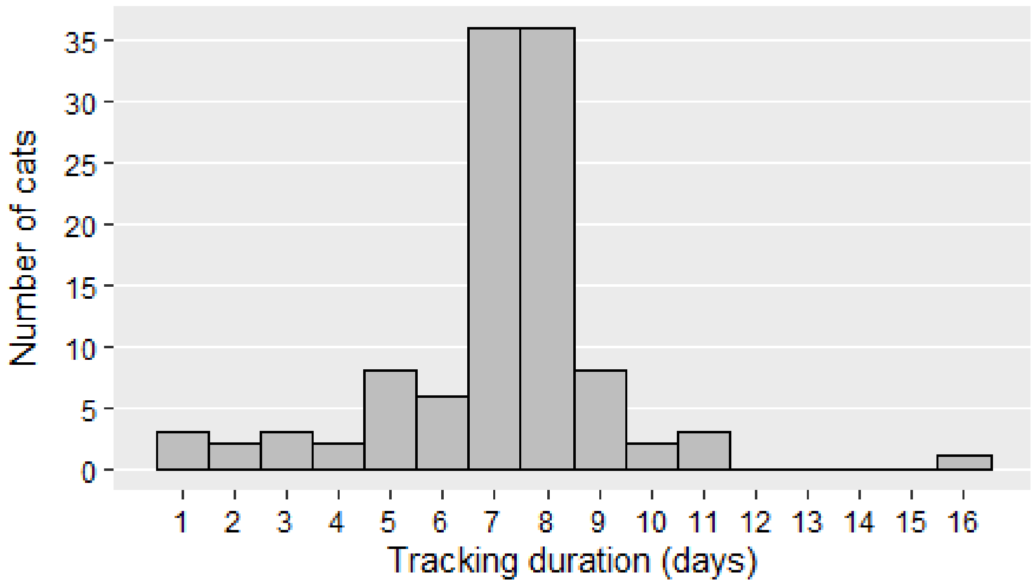


Figure 6: Histogram of tracking durations for all participating cats (n = 110)

Preliminary visual examinations of the unprocessed tracking data revealed that cats showed substantial variations in their movement. Movement behavior ranged from easily distinguishable, far-roaming “breadcrumb”-like trails to single clusters centered on the cat owner’s residence or garden (Figure 7)

Figure 7: Unprocessed tracking data showing two extremes of movement behavior in a similar environment; **(a)** far-roaming and **(b)** highly sedentary. Both cats were tracked for seven days each. Note the distinct use of habitat edges and linear features in cat (a).

Data processing

During the data extraction process, seven cats did not return any sequential position fixes that were long enough to be used in the analysis (see Methods), meaning that the final number of cats that provided track data for the edge habitat analysis was 103 (Table 2). Out of these 103 cats, 57 were male and 46 were female. The majority were adults, with only 15 individuals below two years old and 16 above nine years old. Based on predation estimates from their owners, 25 cats were deemed “high-prey” and the remaining 78 “low-prey”.

In total, 85887 track position fixes were used in the analysis (Table 2). Reflecting the variation in tracking duration, there was also large variations in how many fixes the algorithm returned for each cat. The five most contributing cats returned over 3000 positions each and made up 22.4% of the total dataset, while the bottom five contributed fewer than 40 fixes each, representing 2.21%. However, as indicated by visual examination of the unprocessed tracks, substantial variations still occurred even when accounting for the variation in tracking duration (Figure 8) .

Table 2: Variation in total fixes and mean fixes returned per hour spent tracking, for the entire sample and the different categories. N = number of cats.

Category	N	Total fixes	Mean	SD	Mean fixes/Hour	SD
All	**103**	**85887**	**834**	**913**	**11.36**	**10.08**
Sex						
Male	57	55233	969	1085	11.74	10.78
Female	46	30654	666	613	10.90	9.259
Age						
Young	15	18804	1254	1401	16.31	14.62
Adult	72	53107	738	689	10.31	7.869
Old	16	13976	874	1172	11.45	13.06
Prey						
Low	78	63693	817	908	11.39	10.62
High	25	22194	888	948	11.27	8.403

Table 3: Contingency table illustrating the sample size of all categories that the participating cats were placed in based on survey results.

	Male			Female		
	Low prey	High prey	**Sum**	Low prey	High prey	**Sum**
Young	6	0	**6**	4	5	**9**
Adult	33	10	**43**	20	9	**29**
Old	7	1	**8**	8	0	**8**
Sum:	**46**	**11**	**57**	**32**	**14**	**46**

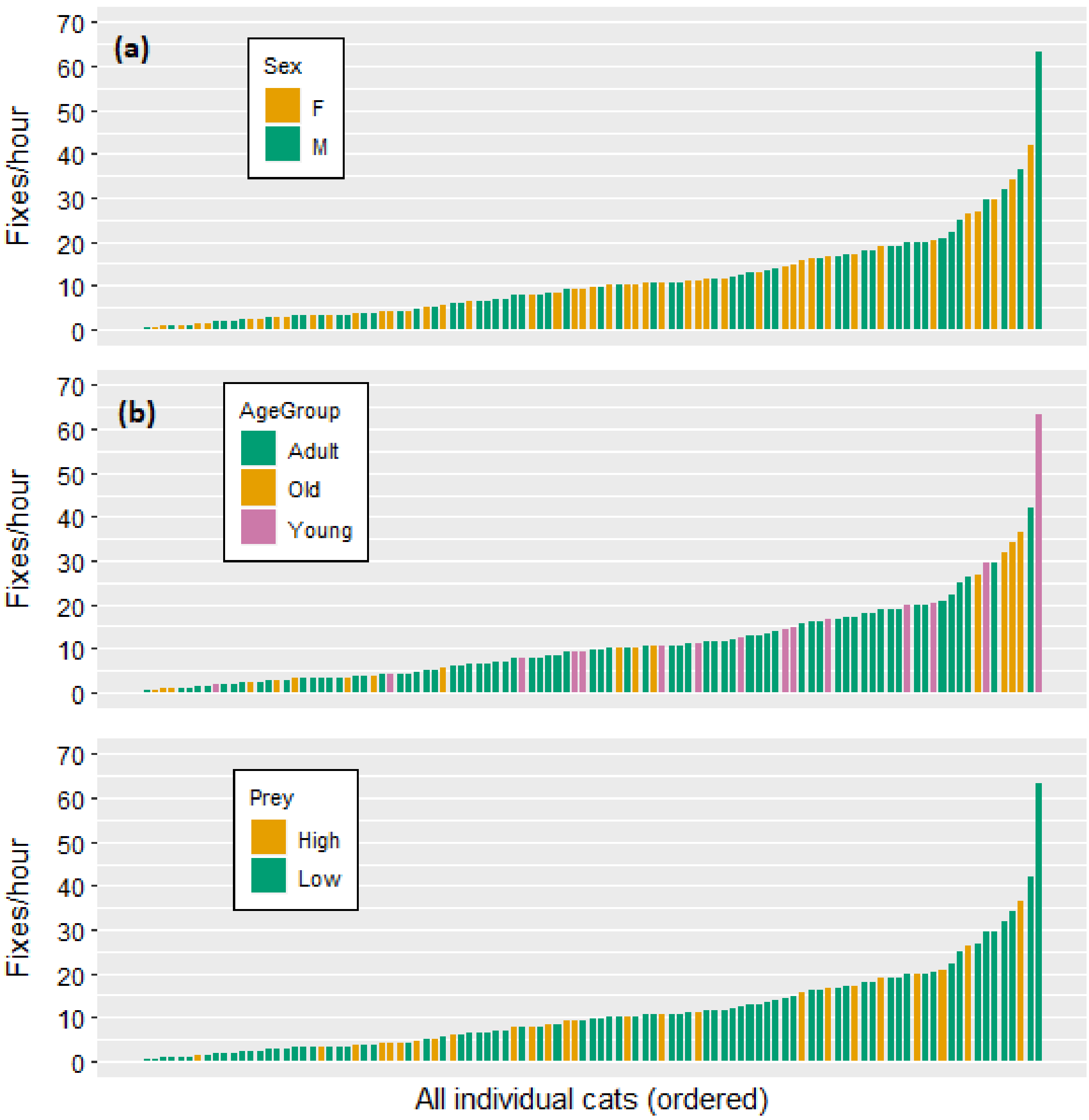


Figure 8: Visual representation of the variation between individual cats in the number of fixes returned per hour spent tracking, divided into **a)** sex, **b)** categorical age and **c)** owner-estimated predation rate.

Edge selection

The parameter estimates from the first model revealed that segments of movement extracted from cat GPS data were more likely to be associated with edges rather than habitat interiors (Figure 9a). Cat tracks were more than twice as likely to be along a road, and more than 1.6 times as likely to be along an ecotone between two kinds of habitat, than in a homogenous habitat interior such as a field, forest or housing area (Table 4, model 1). The preference for the two edge types over no edges was statistically significant, but the higher preference for roads-based edges relative to habitat edges was only a trend ($p = 0.0642$).

Effect of sex, categorical age and predation propensity on edge selection

Sex, categorical age and predation propensity all had significant effects on the tendency of a track to be found along any kind of edge (Figure 9b). Male, adult, low-prey cats were as the reference level 1.4 times as likely to choose an edge over a non-edge. While the effect of young cats was statistically insignificant, senior cats increased this odds ratio to 2.7 compared to adults. Similarly, high-prey cats increased the odds ratio to 2.3 compared to low-prey individuals. Female cats tended to not select for edges compared to male cats, reducing the odds ratio to 1 (Table 4, model 2)

Table 4: Clogit-estimates for the model parameters with associated standard errors, lower- and upper confidence intervals, odds ratio and p-values. The estimate-reference for both models is "$Edgetype_{none}$", and the reference level for the factors in model 2 is "male, adult, low prey".

Parameter	Estimate	± SE	LCI	UCI	Odds ratio	p-value
Model 1						
$Edgetype_{other}$	0.486	0.0580	0.373	0.600	1.626	0.000142
$Edgetype_{road}$	0.742	0.120	0.507	0.977	2.101	1.33e-06
Model 2						
Sex_{male} $Agegroup_{adult}$ $Prey_{low}$	0.343	0.106	0.135	0.551	1.410	2.87e-05
$Agegroup_{old}$	1.00	0.350	0.315	1.69	2.718	0.0350
$Agegroup_{young}$	0.471	0.306	-0.130	1.07	1.602	0.657
$Prey_{high}$	0.845	0.0972	0.655	1.04	2.328	0.00679
Sex_{female}	0.0241	0.206	-0.379	0.427	1.024	0.0471

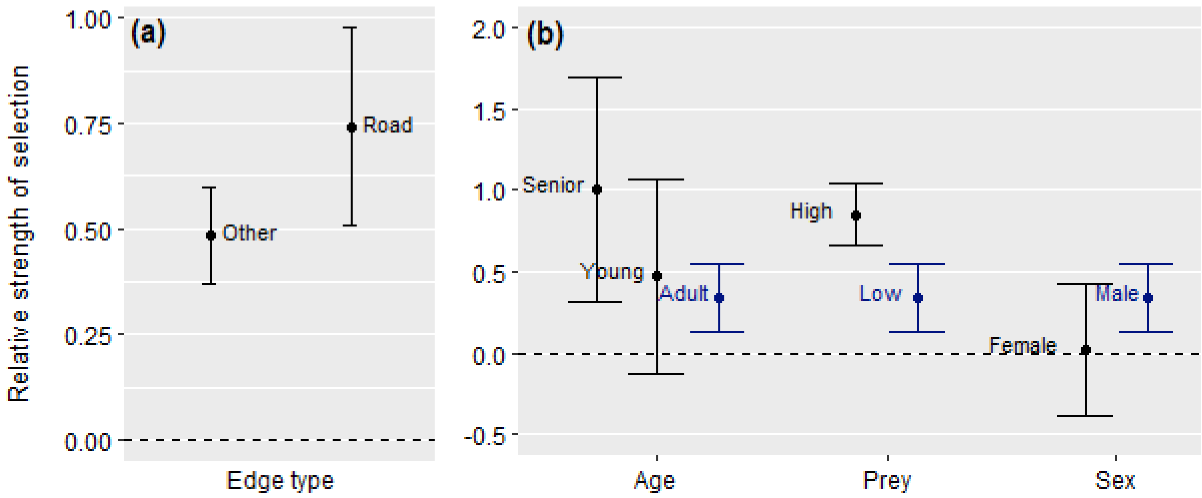


Figure 9: Coefficients from the conditional logistic regression models assessing **(a)** the propensity to use road-based edges and habitat edges over non-edges (model 1), and **(b)** how the propensity to select any kind of edge over non-edges is affected by changes in age group, predation tendency or sex in relation to the reference level (blue), (model 2). Mean coefficient estimates are shown as dots, and vertical bars indicate the 95% confidence interval of the estimate.

Discussion

Data collection through citizen scientists

Using a citizen science approach to gather very high-resolution location data with simple, inexpensive GPS loggers, this study succeeded in uncovering fine-scale habitat usage in roaming pet cats. It also showed that citizen scientist methodology is a practical and useful approach to answer questions that require high-resolution data over longer durations of time to capture this kind of behavior. Participants in this study were shown to be capable of using GPS technology to track their cat on their own. This was expected, as the study employed consumer-targeted GPS units that were simple to operate. There were no reported cases where a participant conveyed that they did not understand how to charge, attach or operate the GPS units, and only two cases of missing data indicated possible user error. However, 11 owners returned their GPS unit without data and did not correspond further, which could be because they did not understand how to manage the GPS and were reluctant to ask for further help. Missing data could also be attributed to faults in the GPS units, but these were tested afterwards and showed no apparent deficiencies.

Only 72 out of 110 cats were tracked for the full instructed tracking duration, which is lower than what was expected considering the level of detail in the instructions each participant received. Citizen scientists have made many notable contributions that help answer difficult-to-study questions in fields such as conservation science and natural resource management

(McKinley *et al.*, 2017), but citizen science methodology is not without downsides. Issues surrounding data fragmentation, inaccuracy, and incompleteness caused by non-adherence to study protocols and lack of objectivity amongst participants is always something that must be considered (Conrad and Hilchey, 2011). In general, this project likely required more effort from the participants than an "average" citizen science project, where data often is submitted more sporadically in an opportunistic fashion (Ries and Oberhauser, 2015). Owners had to make sure the GPS unit was switched on and attached to their pet when it was heading outside, as well as to detach, turn off, and charge the unit when it came back inside. This could potentially lead to several pitfalls, such as participants forgetting to charge their unit or letting the cat outside without the unit attached.

More accessible and dedicated channels for communication between participants and researchers during and after project completion could likely help reduce unexplained variations in tracking duration. Owners were not issued a post-completion survey or similar in which they could report their tracking experience, which could have provided valuable information and possibly revealed a dissonance between perceived tracking effort and actual tracking duration. However, individual variations in cat roaming behavior means that not all cats might roam outside every day. Future studies should consider a more rigid framework of owner reporting in order to include these kinds of variations in the analysis.

Selection for edges and its determinants

I found that cat movement showed a clear association with "edge"-type habitats over homogenous terrain such as open, forested or housing areas. Both edges associated with roads and edges between habitats such as ecotones were significantly preferred. This indicates that pet cats actively choose to use these edges and linear features as they navigate and relocate within their home range.

I found that pet cats whose owners report higher rates of prey predation were more likely to associate themselves with edges along roads and between habitats than cats with lower predation rates. This result is in line with previous studies that attribute linear feature or edge use to hunting behavior amongst cats and other small- and medium predators (e.g. Červinka *et al.*, 2011; Dickie *et al.*, 2020).

Between 50-80% of pet cats actively hunt (Trouwborst, McCormack and Martínez Camacho, 2020), and the propensity to catch prey is not significantly influenced by the amount of food they are provided (Baratt, 1998). A comparatively large amount of "edge"-type habitat in fragmented urban-agricultural matrixes consists of native-woodland patches dissected by housing, roads and agricultural fields (Di Giulio, Holderegger and Tobias, 2009). Abundances of prey species such as birds (Vickery, Carter and Fuller, 2002) and small mammals (Michel, Burel and Butet, 2006) respond positively to forest edge effects due to increased shrub and herb cover from better light-conditions along the edge (Panzacchi *et al.*, 2010). Edge habitat also offers cats concealment when hunting. Fitzgerald and Turner (2000) cited in Hansen (2010) describe two main foraging tactics of cats, namely a prey-seeking "mobile" mode, and a more ambush-based "sit-and-wait" tactic. Both modes are either way highly dependent on stealth and the element of surprise, and mixtures of shrub-based ground cover can provide cats with opportunities to stalk and observe the prey they hunt.

Even though my results indicate that high-predation cats use edges more than low-predation cats, the use of owner-reported estimations of predation makes the rigidity of this inference uncertain. Tschanz and colleagues (2011) found that cat owners tend to highly overestimate the amount of prey their cat brings home if they are not actively recording it on a day-to-day basis, indicating that surveys alone might not be adequate to estimate predation. In addition, other studies reveal that cats show individual variations in tendency to bring prey home, and many typically only bring a fraction of actual hunted prey back to their residences (Thomas, Fellowes and Baker, 2012; Hernandez *et al.*, 2013; Krauze-Gryz, Gryz and Żmihorski, 2019). This adds another layer of uncertainty to the suggestion that owner-reported predation rate can be used as an accurate proxy of predation behavior.

Edges and linear features can also grant physical shelter from the elements and potential predators. Both feral and pets cats actively avoid open habitats with sparse cover such as fields, pasture, beaches and cropland, and are known to seek out shade during sunny weather or dry spots during rain (Warner, 1985; Genovesi, Besa and Toso, 1995; Molsher *et al.*, 2005; Harper, 2007; Metsers, Seddon and Van Heezik, 2010; Horn *et al.*, 2011; Doherty, Bengsen and Davis, 2014). The cats in this study were only tracked for a week each, which means that local weather conditions could have played a significant role in determining if they used edges while roaming, or whether they even moved away from their gardens at all. No study that I am aware of has directly examined if small carnivores prefer to move through sheltered areas in harsh weather conditions, but observations from the abovementioned studies would suggest that it is likely. Thus, including a weather variable in future movement models or tracking for much longer durations would be beneficial.

The results of this study also suggest that there are differences in both sex and age of cats when it comes to edge use. This finding challenges the interpretation that edge use in pet cats is driven or at least largely influenced by predation. In a study of pet cat predation using collar-mounted video cameras (which is arguably the most accurate way to examine any such behavior), Hernandez and colleagues (2013) found that neither cat age nor sex influenced their hunting behavior. The most likely explanation for the apparent differences between ages and sexes found in this study is that the sample size was not large enough to accurately represent all cats. Out of 103 cats, only 15 and 16 individuals were labeled as “young” and “old” respectively, and 25 were labeled “high-prey” compared to the remaining 78 “low-prey” individuals. Considering the large variation in roaming behavior between individual cats, it is possible that the sample size does not capture the variation properly. Issues with sample size due to considerable variation in cat behavior is a recurring problem in cat studies (Hall, 2016).

Female cats used edges significantly less than males; I detected no preference for edges over non-edges by females. One possible explanation for this is that male pet cats have been found to have substantially larger home ranges than females (Hall *et al.*, 2016; Kays *et al.*, 2020), and employ these linear features in order to traverse the landscape more efficiently (Zeller *et al.*, 2016; Dickie *et al.*, 2017). A similar explanation is that male cats use linear features during movement in order to mark their territory. Krofel and colleagues (2017) found that another felid, the Eurasian lynx (*Lynx lynx*), scent marked at higher rates along anthropogenic linear features than in their natural habitat. In addition, male lynx were found to use human trails more often and scent marked more frequently than females. In the domestic cat, males are known to be more territorial and scent mark more than females (Feldman, 1994), which could mean that they employ roads and other edges to increase the probability of a conspecific receiving their chemical message.

Older cats were found to use edges significantly more than adults. Providing an explanation for this result based on this study alone is difficult, and no previous studies to my knowledge has examined the relationship between edge use and age. It is possible that senior cats are more lethargic and have developed a clear pattern of habituation and preference for their environment (Kays *et al.*, 2020). As many linear features provide shelter and often represent a more energy-efficient way to traveling, older cats could potentially prefer these over younger, curious individuals that have less prior knowledge of their environment and instead choose to explore their surroundings.

Limitations

This study found that there was a large variation in ranging characteristics between different cats. The algorithm that was used to extract segments of continuous movement from the tracking data failed to return any data for some cats, and about 30% of all participating cats returned less than 10 fixes per tracked hour. In contrast, some cats returned more than 30 fixes per tracked hour. This result likely reflects previous findings of how pet cats show large variations in home range size between individuals, with the majority rarely leaving their gardens (Hall *et al.*, 2016; Kays *et al.*, 2020). Indeed, visualizations of the unprocessed tracking data in this study showed that many cats rarely ventured more than 50m away from their home. In such cases, the algorithm would identify a large portion of their fixes as a single, stationary cluster and remove it from the dataset used in the analysis.

Similarly, it is likely that GPS position error in this study leads to an underestimation of edge habitat use of suburban cats and cats that roam in close proximity to their house. Sequential locations from these cats tended to be more cluttered and abstruse with larger spatio-temporal gaps and jumps, than cats that ranged farther away from housing. This is likely due to the detrimental effect that bushes, sheds, cars, housing and similar features have on GPS signal strength (Adams *et al.*, 2013). Presumably, a large proportion of the tracking data from these animals were also filtered out because it was either deemed as stationary clusters by the algorithm, or because the resulting tracks simply did not meet the requirement of at least 30 sequential fixes with less than 40 seconds between each fix.

Another point that also must be considered is the GPS resolution and element of scale (Zeller *et al.*, 2016). Linear features in suburban home, garden and park matrices are inherently shorter than those along stretches of fields and forests. For example, even if a roaming suburban cat traveled through linear configurations of trees in a large garden or briefly followed a small access road on its way towards the local park, it is possible that not even a 10 second fix rate would be a large enough resolution to capture this kind of edge use properly. Similarly, it is likely that cats with modest home ranges do use linear features on a smaller, local scale (for example bushes on the edges of their gardens or along the road to the neighboring house), but this would require a much higher spatio-temporal resolution to examine properly.

In summary, due to GPS inaccuracy and how segments of movement are extracted, this study likely biases edge use in cats with large home ranges that roam away from suburban or urban housing areas. This could again lead to a false inference that edge use is positively correlated with home range size or rural residences (which are again positively correlated with each other, Hall *et al.*, 2016).

Conclusions and implications for management

This study represents one of the first investigations of small-scale movement behavior of pet cats. The results presented here contribute to a growing pool of knowledge and evidence suggesting that researchers and environmental mangers alike need to consider the impacts that free-roaming pet cats have on their environment.

Understanding patterns of how cats use their environment is vital when trying to develop and implement mitigation strategies. I found that roaming pet cats have a clear preference for edges and linear features in their environment and will likely follow these instead of penetrating into homogenous habitat interiors. Previous studies of pet cat roaming- and predation behavior have emphasized a particular concern for cats that roam in or near nature reserves or other areas of high ecological significance (e.g. Wierzbowska *et al.*, 2012; Woolley and Hartley, 2019). Researchers have proposed buffer zone concepts to protect ecologically sensitive areas, using home-range estimates to determine “cat-exclusion” zones that ban or constrain cat ownership (e.g. Lilith, Calver and Garkaklis, 2008; Metsers, Seddon and Van Heezik, 2010). However, this study and other previous studies would suggest that it is difficult to determine an all-encompassing rule that can be applied to all cats in all places, because individual cats display such substantial variations in roaming behavior that are also influenced by a number of factors (Calver *et al.*, 2011; Hall *et al.*, 2016).

Since cat roaming behavior varies to such a degree, an optimal option for management, though likely costly and time-consuming, would be to instead gather area-specific data for each case in question, and from there also identify “high-risk” individuals that show a larger propensity to hunt and/or move near the ecological sensitive area(s) in question (Kauhala, Talvitie and Vuorisalo, 2015). Incidentally, the cat that had most fixes of all participants in this study lived right next to two separate nature reserves with high importance for migratory and overwintering bird species.

Lastly, the results of this study also suggest that future field surveys, camera trapping and similar kinds of control efforts that are employed in conjunction with pet cat research or management projects should focus on linear features and ecotones rather than habitat interiors if the goal is to capture as many cats as possible. If a reserve or some other kind of protected area is surrounded by dense forest or open, exposed habitat such as fields, cats are probably more likely to use a road or an edge in order to access it.

GPS technology has only relatively recently reached a level where tracking smaller animals such as cats becomes viable, and there are still issues centered around obtaining high-resolution data from units over longer time periods due to battery constraints. Although technological advances likely will help overcome these challenges in the future (Bouten and Baaij, 2013), the present study shows a proof-of-concept solution to this problem that can be employed straight away, using rechargeable GPS units and citizen scientists. Future studies of similar nature should consider using a similar approach if the goal is to describe behavior that requires this kind of high-resolution location data.

Appendix

Table 5: Complete reference for edge-variable assignment to each GPS-fix based on presence/absence of landscape elements within a 10m buffer.

Presence/Absence				Edge type	Edge
Open	Forest	Housing	Road		
-	-	-	-	NA	NA
X	-	-	-	None	None
-	X	-	-	None	None
X	X	-	-	Other	Yes
-	-	-	X	None	None
X	-	-	X	Road	Yes
-	X	-	X	Road	Yes
X	X	-	X	Other	Yes
-	-	X	-	None	None
X	-	X	-	Other	Yes
-	X	X	-	Other	Yes
X	X	X	-	Other	Yes
-	-	X	X	None	None
X	-	X	X	Other	Yes
-	X	X	X	Other	Yes
X	X	X	X	Other	Yes

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