Spatial ecology and prey choice of tagged feral cats on the island of Schiermonnikoog

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Abstract: Feral cats (*Felus catus*) inhabiting the Dutch island of Schiermonnikoog are a potential threat for local prey species populations. To get more insight into the spatial ecology of this invasive predator, ten feral cats were equipped with GPS tags and followed from May till July 2014. Spatio-temporal analyses show an average 3-month home range of 81 ha for Kernel 95% and 158 ha for MCP 95%. Nocturnal home ranges were larger than diurnal home ranges but no differences were found between sexes or age classes. Habitat use showed that the cats had a small preference for short salt marsh vegetation during the night. Also, the cats showed a higher nightly displacement, while the daily migration and cumulative daily displacement varied greatly per cat. Scat analyses revealed that hares contributed the most to the diet in terms of relative prey volume, but the common vole (*Microtus arvalis*) was the most numerous prey item. The preference for short salt marsh vegetation during the night could indicate hunting for nocturnal species foraging there, such as hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*). While voles were the main prey, frequent bird remains in the scats still suggest a potential threat for bird populations.

Keywords: *Felis catus*, feral, Schiermonnikoog, trapping, GPS, home range, activity pattern, habitat use, prey.

Introduction

Cats (*Felis catus*) were domesticated about 4000 years ago and are now one of the most widespread invasive terrestrial carnivores (Long 2003). Several studies indicate that this introduced species has caused vast declines and even extinctions of multiple animal species (e.g. Fitzgerald & Turner 1988, Dickman et al. 1993, Courchamp et al. 2003). Particularly animal species that evolved without the presence of mammalian ground predators are vulnerable for the effects of an introduced predator (Fitzgerald & Turner 2000, Bradshaw et al. 2012). Most striking examples of the devastating effects of cats come from islands. Medina et al. (2011) reviewed 229 cases and showed that global insular feral cat populations “contributed to a minimum of 14% of all bird, mammal and reptile extinctions and the decline of at least 8% of critically endangered bird, mammal and reptile species.”

Several studies have investigated feral cats at the Dutch Waddensea islands (Niewold 1986, Langeveld 1987, Jansman & Müskens 2001, Hofman & Postma 2006, op de Hoek 2012, Maris 2013). A feral cat is defined by

Natoli (1985) and Liberg et al. (2000) as a domestic cat that occupies areas for food and/or shelter and is unwanted or unowned. On these Waddensea islands, ground breeding birds are potentially extra vulnerable for the effects of feral cats as natural mammalian ground predators such as red fox (*Vulpes vulpes*) or mustelids (Mustelidae spp.) used to be absent or uncommon. To better understand the impact of feral cats on their environment, it is important to consider their behaviour in space and time, as well as their diet. This type of information is often lacking but crucial for management decisions, such as whether or not interventions are necessary to control feral cat populations.

Home range is an important spatial characteristic that gives insight into the space use of an animal. Originally, Burt (1943: 351) defined the concept of home range as "that area traversed by an individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range." At present, various methods and metrics exist to estimate the home-range of an animal, and these different types of information should best be combined to give proper insight into the space use of animals (Powell & Mitchell 2012).

In general, habitat use is driven by the presence of prey (Recio & Seddon 2013) and daily activity patterns are often synchronised with the active period of the main prey (Langeveld 1987). So, in areas with many diurnal prey species, cats are expected to adapt their main activity period to the day. Locomotive behaviour, e.g. cumulative displacement distance or daily migration, is often used to understand the spatial behaviour of free ranging animals (Langham 1992, Schai-braun 2012)

Diets are often used to understand secretive free-ranging mammals (e.g. Worton 1989, Laver & Kelly 2008). Langeveld (1987) indicated that the diet of the feral cats on the Dutch Waddensea Island of Schiermonnikoog consisted of 60% brown hares (*Lepus europaeus*) and/or rabbits (*Oryctolagus cuniculus*) and 30% birds. Op de Hoek (2012) and Maris (2013) analysed the ingested prey in 2011 and 2012 respectively and suggested that the feral cats switched to common vole (*Microtus arvalis*) as staple food (main prey) (~60%), which was first spotted in 2003 (de Jong 2003). They also estimated that almost 25% of Schiermonnikoogs' population of small breeding-birds (table 1) was eaten annually by the feral cats. Schiermonnikoog is particularly interesting, because introduced prey species occurring in high densities (here the common vole), are often the main food source for feral cats. This could result in a growth of the feral cat population and thus indirectly increase the impact on native species (e.g. birds) (Medina et al. 2011).

Feral cats have been subject of several telemetry studies to get insight in their spatial behaviour (e.g. Lammertsma et al. 2011, Recio et al. 2011, Bridges et al. 2015, McGregor et al. 2015; and Langeveld (1987) for Schiermonnikoog). However, for a better understanding of the ecology of feral cats, improved spatio-temporal analyses such as home ranges, daily activity patterns, habitat use and locomotive behaviour are needed. The aim of this study was to get more insight into the spatial ecology of the feral cat population on Schiermonnikoog. We specifically addressed: 1. home ranges and their seasonal variability; 2. daily timing of activity, daily variation in space use and daily variation in displacement and migration; and 3. ingested prey and its relation to presence of prey.

This research was assessed by the Dutch Animal Ethical Experiment committee (DEC) of the University of Groningen and approved by the Netherlands Food and Consumer Product Safety Authority (project 6796A) for the Experiments on Animals Act. It was approved for the Flora and Fauna act under project number FF/75A/2013/047 and for the Nature Conservancy Act under reference number 01094376.

Table 1. input for prey volume calculation.

Species		Weight used (g)	Size class
Pheasant	*Phasianus colchicus*	975	Large
Mallard	*Anas platyrhynchos*	970	Large
Shellduck	*Tadorna tadorna*	900	Large
Curlew	*Numenius arquata*	770	Large
Oystercatcher	*Haematopus ostralegus*	540	Medium
Redshank	*Tringa totanus*	110	Medium
Skylark	*Alauda arvensis*	38	Small
Meadow pipit	*Anthus pratensis*	19	Small
Common whitethroat	*Sylvia communis*	16	Small
Hare	*Lepus europaeus*	3000	
Rabbit	*Oryctolagus cuniculus*	1200	
Lagomorpha sp	*Leporidae*	1200	
Brown rat	*Rattus norvegicus*	200	
Common vole	*Microtus arvalis*	25	
Wood mouse	*Apodemus sylvaticus*	22	
Greater white-toothed shrew	*Crocidura russula*	10	

Methods

Study area and species

This study was performed at the Dutch Waddensea island of Schiermonnikoog. The natural area of Schiermonnikoog (figure 1) (53°30'N, 6°10'E) can be subdivided in five main categories; salt marshes, dune valleys, former beach plain, beaches with young dunes, and polders (Pranger & Tolman 2012). The population of feral cats (hereafter referred to as cats) originates from abandoned or escaped house cats. The population size in the natural area was estimated at 34 cats in 1984 (Langeveld 1987) and 50 in 2011 (op de Hoek 2012). Nowadays there are no competing mammalian ground predators. Also, cats are no longer hunted at Schiermonnikoog since the establishment of a National Park on the island in 1994 (Berendse 2011). Potential prey species occurring on the island are hares, rabbits, common vole (hereafter referred to as vole), mice (Muridae, Arvicolinae) species, shrew (Soricidae) species, and several species of birds. The occurring mammals have no Dutch Red list status, while 37 bird species occur that are enlisted (FREE Nature 2011) and are potentially threatened by the cat population.

Data collection and analysis

All statistical analyses were performed using IBM SPSS Statistics 22.0 (IBM Corporation 2013). All spatial analyses were executed using Geospatial Modelling Environment (GME) 0.7.3.0 (Beyer 2012), ArcGIS 10.2.1 (ESRI 2014), R 3.2.1 (R Core Team 2015), Python 2.7.5 (Python Software Foundation 2013) and the LatLon 1.0.2 python package (Del Raye 2014). Full descriptions of the methods are given in the MSc Thesis report of van der Ende (2015).

Cat trapping and tagging
Twenty-eight live traps (Drahtexpress 2013) were used to catch cats in April 2014. Caught cats were intramuscularly injected with Ketamine (0.1 ml/4kg) and Medetomidine (0.1 ml/2kg), and Atipamezole 0.1ml/4kg was used as antagonist before release. Sex, age, bodyweight and size measures were recorded. All

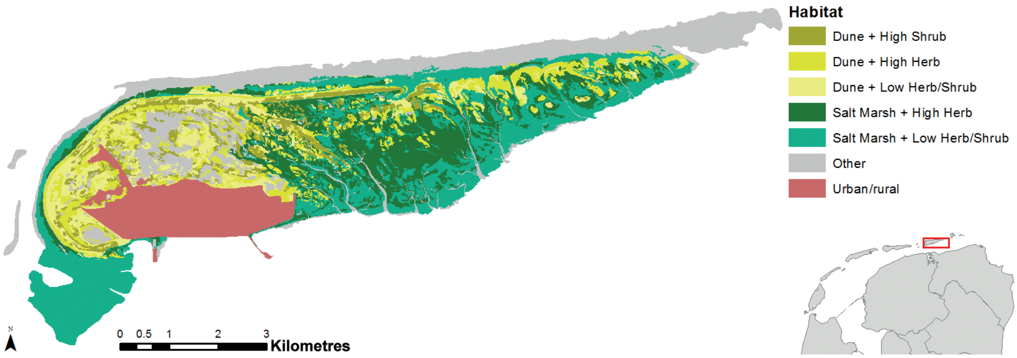

Figure 1. Different habitat types on Schiermonnikoog (Rijkswaterstaat 2011; CBS, n.d.).

caught cats weighed more than 2.3 kg (tag <5% bodyweight) (Wilson et al. 1996, Gannon & Sikes 2007). The GPS tag (Collar 1C-light, 115 gr) was equipped with a GPS receiver (U-Blox LEA-4S), an UHF (868/916 MHz bands) transmitter, and a tri-axial-accelerometer (e-obs digital telemetry 2010). Data collection started on 4 May 2014 and covered three months (over the breeding season) with a temporal resolution of 15 minutes. In November and December 2014 we executed new catching sessions to retrieve tags.

Home ranges

To calculate the home range (HR) a fixed Kernel was chosen with a plug-in bandwidth selection method (Jones et al. 1996) and the Gaussian type Kernel shape. 95% Contour isopleth polygons were created, the 5% which was discarded avoided Burt's (1943) 'occasional sallies' being incorporated in the HR. HRs were calculated for different daily and seasonal intervals: diurnal HR (~65 fixes), nocturnal HR (~30 fixes), daily HR (max. 96 fixes), weekly HR (max. 672 fixes), monthly HR (max. 2880 fixes) and 3-monthly HR (max. 8640 fixes). Minimum Convex Polygon (MCP) 100% & 95% HR estimators (Mohr 1947, Hayne 1949) were also applied to compare the trend of the Kernel HR estimator. To test for differences between mean nocturnal and mean diurnal HR, we used a Wilcoxon signed-rank test. We used Mann-Whitney U tests to test for differences in 3-month HR sizes between sex and age-classes.

Daily activity pattern, space use & locomotive behaviour

To calculate daily activity patterns, the displacement between the fixes (15 minutes) was calculated. Each day was divided in three periods: 1. early morning (sunrise till two hours after sunrise); 2. day (two hours after sunrise till sunset); 3. night (sunset till sunrise). To test if the period had an effect on the average displacement per 15 minutes a Linear Mixed Model (LMM) analysis was used. Cat ID was used as subject variable, mean displacement as dependent variable and period, age, sex and all two-way interactions between these variables as fixed factors. Variables and interactions were excluded until the lowest Hurvich and Tsai's Criterion (AICC) was reached.

Habitat is defined by Hall et al. (1997, p.175) "as the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism". Using Pranger & Tolman (2012), we distinguished the following habitats at Schiermonnikoog (figure 1): 1. Salt Marsh + High Herb; 2. Salt Marsh + Low Herb/Shrub; 3. Dune + High Shrub; 4. Dune + High Herb; 5. Dune + Low Herb/Shrub; 6. Other. These habitats were assigned to the GPS fixes. We used chi-square tests to assess if habitat use per cat differed between the three periods. If

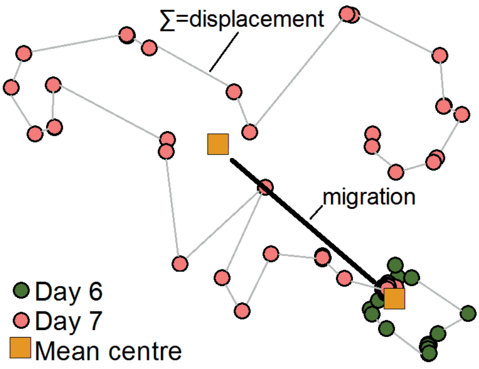

Figure 2. Example of daily migration and displacement.

the mean displacement per 15 minutes for a period (see paragraph above) did not significantly differ from another, both periods were merged. A random sample (*n*=600) from each period per cat was extracted to make the data quasi-independent.

The distances between the consecutive mean centres per day were regarded as daily migration distances (figure 2). It was compared in a scatterplot with the average cumulative daily displacement (distance between fixes) per cat to identify different movement patterns and recognise clustering in age classes or sexes.

Diet and prey presence

Fresh scats were collected haphazardly (i.e. found by chance without systematic approach) from March 2014 till December 2014. The aggregation of the outer locations formed the 'scat area'. Scats were analysed following op de Hoek (2012), Maris (2013) and Husson (1962), matching bone, hair and feathers to mammal and bird species. We dried the scats and searched for prey remains in the laboratory. We attempted to separate hares from rabbits by identifying the hairs based on the patterns of the cuticular scales (Teerink 1991). When it was impossible to distinguish, the sample was identified as 'Leporidae species'. The results were expressed in 'relative frequency of occurrence' and were compared with previous years.

Using a more conservative method for assessing independence of samples than previous studies (op de Hoek 2012, Maris 2013), scats with Leporidae remains were only selected for analyses if they were found >30 days apart or >6 km apart. It was assumed that the scats which then remained represented one prey item. The 'relative frequency of occurrence' was recalculated into estimated volume of prey. Estimates for body-weights of the prey were obtained from results of a small mammal trapping session (see next paragraph), or were obtained from information acquired from the Dutch Mammal Society (n.d.) or The Wildlife Trusts (n.d.). Bird remains in the scats could be subdivided in size class (small; medium; large) but not in species, so one body mass had to be decided per size class. Therefore, the average weight of the small (<100 g), medium (100-600 g) and large (>600 g) ground breeding bird species present in the area was used as estimated prey size (table 1). The results were expressed as relative 'volume of prey ingested'.

From 15 July until 1 August 2014, prey density parameters were estimated on Schiermonnikoog. The hare and rabbit density estimations using pellet counts, proved to be unreliable because of an inappropriate sampling design and the results were discarded. Instead, we used the estimate of van Wieren et al. (2006) as a reliable estimate for our research, with a hare density of 71.5 hares/km^2 between 1996 and 2003. Rabbits were discarded from prey presence analysis. The density of small mammals (mice, shrews and voles) was estimated following the trapping method of Koelman (2007) and Gurnell & Flowerdew (2006), by placing 55 life traps (Longworth) on 20 different line transects, with each transect randomly placed in the scat area.

The ground breeding bird density was calculated based on the results from Klemann & Kleefstra (2012). Only the bird territories occurring in the scat area were used. Greylag goose (*Anser anser*), Egyptian goose (*Alopochen aegyptiaca*), and gull species (*Larus*

Table 2. Overview of caught cats and data collected by the tags.

			Weight (kg)					
Cat no.	Sex	Age	1st catch	2nd catch	GPS started	GPS stopped	# Total fixes	Remark
0	M	Ad	4.6	6.2	04 May 2014	-	-	Tag damaged
1	F	Ad	3.3	3.3	04 May 2014	24 Aug 2014	10,848	
2	M	Sub	2.6	-	04 May 2014	16 Sep 2014	13,056	
3	M	Sub	2.6	-	04 May2014	16 Sep 2014	13,056	
4	F	Sub	2.6	2.7	04 May2014	16 Sep 2014	13,056	
5	F	Sub	2.4	-	04 May 2014	16 Sep 2014	13,056	
6	M	Sub	3.0	-	04 May 2014	31 Jul 2014	8,544	
7	F	Ad	3.6	3.9	04 May 2014	16 Sep 2014	13,056	Mating observed with cat 9
8	F	Ad	2.8	3.4	04 May 2014	16 Sep 2014	13,056	Pregnant / Kittens found
9	M	Ad	4.1	-	04 May 2014	16 Sep 2014	13,056	
Total							110,784	

spp.) were assumed to be unavailable for the cats because of their body size combined with their aggressive behaviour towards predators, and therefore left out of the analysis. Species occurring in very low frequency (<5 territories) were also left out. Species used in the calculation are shown in table 1.

For all prey species groups (hares, birds and small mammals) a rough abundance estimation was made for the scat area by multiplying the density with the area size. The abundance was then multiplied with the weight per species and expressed as the relative 'volume of prey present' in the scat area. This result was compared with the 'volume of prey ingested'.

Data preparation

To increase the spatial accuracy of the observations the data were prepared and processed using Microsoft Excel 2010 and Python 2.7.5 (Python Software Foundation 2013). We used the following external Python site packages: LatLon 1.0.2 (Del Raye 2014), Fiona 1.5.1 (Gillies 2014a), Shapely 1.5.7 (Gillies 2014b) and ArcPy 10.2.1 (ESRI 2014). The most accurate fix from a burst was used (one unsuccessful fix was recalculated using linear interpolation). Based on field measurements, the fixes with a given accuracy above 40 m were excluded (2.4% of the data), and spikes were smoothed. One tag collected exceptionally inaccurate data and was discarded from analyses.

Results

During the April sessions, ten cats (table 2) were caught during 680 trapping hours (total trapping time of all traps together). One tag did not function at all, another was no longer located after 31 July 2014, and a third tag was drained on 24 August 2014. All remaining tags were turned off on 16 September 2014. After the study period, final trapping sessions were performed in November and December to retrieve tags from cats. During these sessions, 24 catches were successful during 1550 trapping hours. Sixteen different individuals were caught, of which five with tags.

All tagged animals had gained on average 0.52 kg bodyweight (range: 0.1-1.6 kg) (table 2), except for cat 1 which remained constant. The nine functioning tags collected 110,784 fixes in total. After data preparation 108,512 suitable fixes remained of which we used 76,896 fixes to cover the study period (May, June & July).

In total, 2505 HR sizes were calculated on

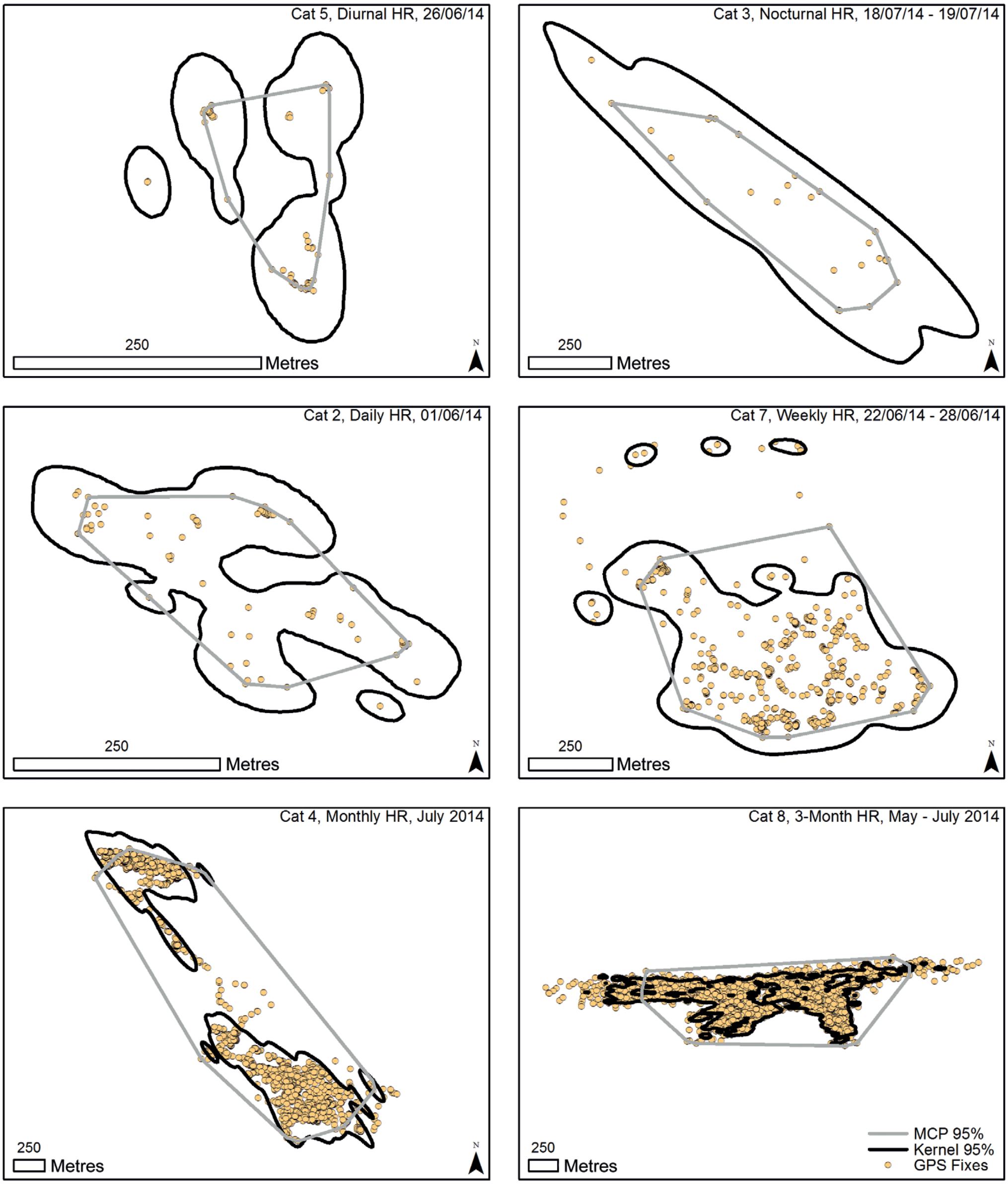

Figure 3. Examples of MCP 95% and Kernel 95% HR estimations for different time periods.

the nine cats, subdivided over the six different HR timings: 782, 783, 790, 114, 27, and 9, for diurnal HR, nocturnal HR, daily HR, weekly HR, monthly HR and 3-monthly HR, respectively. Examples in figure 3 show the difference of Kernel 95% and MCP 95% HR methods. The Kernel density estimator did not discard 5% of the data when the sample sizes were small for the diurnal, nocturnal and daily timings. This resulted in relatively large HRs. With larger sample sizes (weekly, monthly and 3-monthly) and a discarded 5% of the data, HRs appeared more stable and realistic.

Cat 9 had the largest diurnal HR (22 ha Ker-

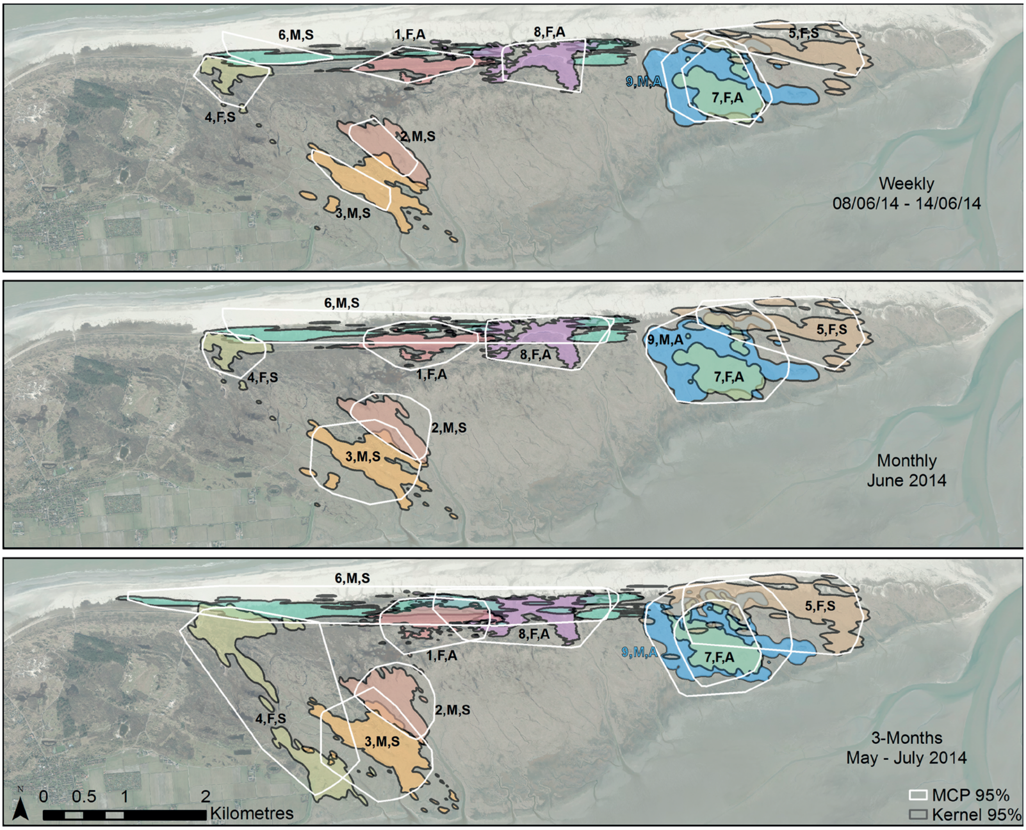

Figure 4. Different temporal Kernel 95% and MCP 95% home ranges of cats (n=9) on Schiermonnikoog. 1-9 = cat ID, A-S = adult - subadult, M-F = male-female.

nel 95%). The HR of cat 7 (female) and 9 (male) showed the highest overlap compared to other cats (they fully overlapped for three months (figure 4)), and these cats were observed to mate in May. Cat 2 and 3 (both males) hardly overlapped while living close to each other. The HR expansion of cat 4 showed that she made some sallies in southern direction. In three months' time she showed expansion of her HR in SSE direction, close to cat 3, but with negligible overlap. Finally, the largest Kernel 95% 3-monthly HR was from male cat 6 (6.8 km2) with a very elongated HR, overlapping at least three other HRs.

In table 3 the average HR sizes are presented for each individual cat. For all three HR methods the males appeared to have larger HR than females, but this was not statistically significant (Mann–Whitney U: range 7.0-10.0, $n1$=5, $n2$=4, two-tailed P-values: range 0.462-1.000). Subadults appeared to have smaller HR sizes than adults, except for monthly or 3-month HR where the subadults had similar or bigger HR sizes, but none of these differences were statistically significant (Mann–Whitney U: range 4.0-7.0, $n1$=5, $n2$=4, two-tailed P-values: range 0.142-0.462). The largest Kernel 95% 3-monthly HR was from the large adult male cat 9 (140 ha), followed by female cat 5 (110 ha). The smallest was from female cat 1 (37 ha), followed by subadult male cat 2 (48 ha). For the MCP 95% method the female cat 4 had the largest HR (289 ha), more than two times the size of her Kernel 95% HR (111 ha). Male cat 2 had the smallest MCP 95% HR

Table 3. Average HR size (ha) for different cats, sexes, ages and periods, using Kernel 95%, MCP 95% and MCP 100% density estimator methods. *M*=average; *n*=sample size; sd=Standard Deviation.

		Diurnal			Nocturnal			Day			Week			Month			3-Month		
	Sex, age	*M*	*n*	sd	*M*	*n*	sd	*M*	*n*	sd	*M*	*n*	sd	*M*	*n*	sd	*M*	*n*	sd
Kernel 95%	Male	9	4	9	22	4	19	19	4	17	52	4	34	75	4	36	90	4	39
	Female	6	5	5	17	5	10	12	5	4	36	5	13	55	5	21	74	5	29
	Adult	12	4	8	21	4	18	20	4	16	48	4	37	64	4	42	76	4	42
	Subadult	4	5	3	18	5	11	11	5	5	40	5	11	64	5	18	85	5	25
	Overall	7	9	7	20	9	14	15	9	11	43	9	24	64	9	29	81	9	33
MCP 95%	Male	7	4	7	11	4	9	19	4	16	66	4	40	120	4	60	161	4	81
	Female	5	5	4	9	5	5	12	5	3	59	5	23	95	5	34	155	5	89
	Adult	9	4	7	11	4	9	19	4	16	65	4	40	96	4	50	124	4	60
	Subadult	3	5	2	9	5	5	11	5	4	60	5	23	114	5	46	185	5	90
	Overall	6	9	5	10	9	7	15	9	11	62	9	29	106	9	46	158	9	80
MCP 100%	Male	8	4	9	12	4	10	23	4	19	80	4	41	149	4	56	203	4	73
	Female	6	5	4	10	5	5	16	5	4	74	5	26	133	5	54	208	5	104
	Adult	11	4	8	12	4	10	23	4	18	78	4	42	119	4	49	160	4	56
	Subadult	3	5	2	10	5	6	15	5	5	76	5	25	157	5	52	243	5	92
	Overall	7	9	6	11	9	7	19	9	13	77	9	31	140	9	52	206	9	86

(62 ha). It is also remarkable that the Kernel 95% method showed a larger size for nocturnal HR (~30 fixes) than for the daily HR (~96 fixes). The difference between nocturnal and diurnal HR was very close to significance (with 90% confidence) for all three methods (Z=-1.955, P=0.051). The spread (sd) for nearly all HR estimations is remarkably high.

A total of 23,283, 6,108 and 44,618 suitable displacement measurements were used to calculate an activity pattern for night, early morning and day, respectively. Figure 5 depicts how the average displacement of all cats changed during the daily cycle. The cats appeared to displace more during the night (44.57 m, sd=66.17) than during the day (22.29 m, sd=39.68) and there was hardly any displacement during the early morning (13.41 m, sd=32.24). The result of the LMM analysis showed that the average displacement per 15 minutes differed significantly between the three daily periods (LMM; $F(2,10)$=29.167, P<0.001), but not between sex or age classes. Pairwise comparison showed that night displacement differed significantly from day (LMM; ±24.71 m, se=4.45, 10, P<0.001) and early morning displacement (LMM; ±32.55 m, se=4.45, 10, P<0.001), but day and early morning did not (LMM; ±7.84 m, se=4.45, 10, P=0.108). Thus, day and early morning data were merged for further analyses of habitat use.

All day and night fixes were used for the representation in figure 6. A total of 600 GPS fixes per period (day or night) were randomly selected to calculate the habitat use per cat for statistical analysis with a chi-square test. Habitat class 'Other' accounted for less than 2% of the data and was discarded. The habitat use results showed no clear overall pattern. Cat 1 and 4 mainly used dune habitat, cat 2 and 3 mainly used salt marsh and for cats 5-9 the use of dunes or salt marsh was similar. The results of the chi-square tests showed that for eight cats the habitat use significantly differed between day and night (χ^2; 28.6- 111.3, df 4-5, *P<0.001 – 0.003).* Cats 3-7 and cat 9 showed an increase of 'Salt Marsh & Low Herb/Shrub' use during the night by 24%, 1%, 6%, 14% 2% and 17%, respectively (figure 6). Cat 3 appeared to specialise on this habitat during the night. A decrease of 'Saltmarsh & High Herb' usage during the night was observed for cats 2-7 and with -10%, -23%, -2%, -2%, -1%, -6% and -3%

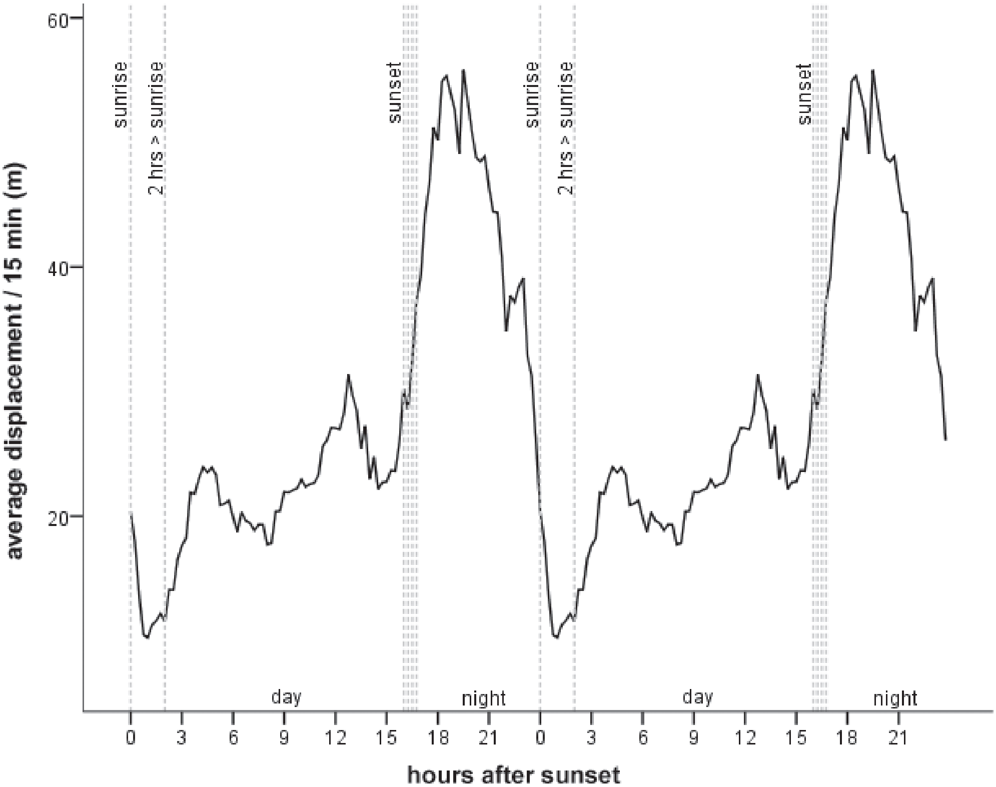

Figure 5. Average displacement per 15 minutes for all cats during the circadian cycle from May-July. The areas between dashed lines indicate the three periods, night, day and early morning. The sunrise in the study period was between 05:03 and 05:51 and the sunset between 21:12 and 22:10 (CET +02:00).

respectively. For the dune habitats no obvious day-night pattern was observed.

The difference in migration (distances between the consecutive mean centres per day, figure 2) and displacement (sum of distance between fixes) patterns between the cats are visualised in figure 7. Two obvious patterns of cat 6 and cat 9 emerge. Cat 6 migrated each day over relatively large distances, but during the day it hardly displaced compared to other cats. Cat 9 showed a similar daily migration distance as cat 6, but also displaced a lot during the day; on average, it covered more than four kilometres during the day. There is a large variation between cats and no clear patterns or clustering (adult/subadult or male/female) could be recognised.

A total of 160 scats were analysed for prey remains (table 4 and figure 8). The vole was the main prey species found (189 individuals, 52.6%). No large diet shifts could be identified when compared to previous years. A small decrease in voles and Leporidae and an increase in small birds could be identified for the ‘relative frequency’ measured in 2014. The result from the differentiation of the Leporidae species showed 5% rabbit remains in the scats. After the correction of the Leporidae species eaten (assumed that several scats contained one prey) the numbers dropped from 9 to 4 for hares and from 18 to 5 for rabbits. It was found that the ‘relative frequency corrected’ of hares became 1.2% and for rabbits 1.5% (figure 8). When the relative ‘volume of

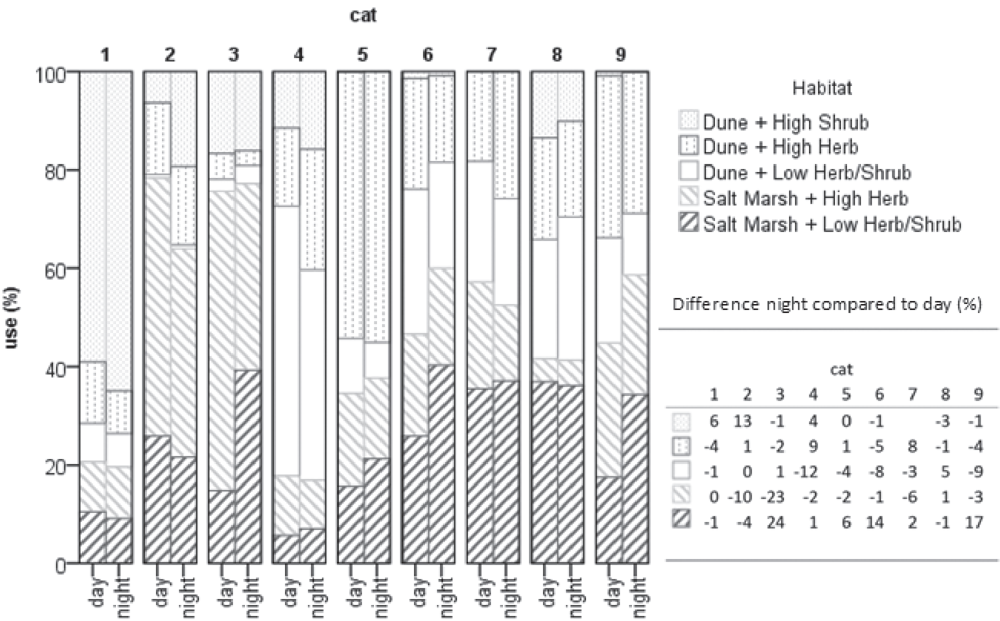

Figure 6. Habitat use per cat per daily period.

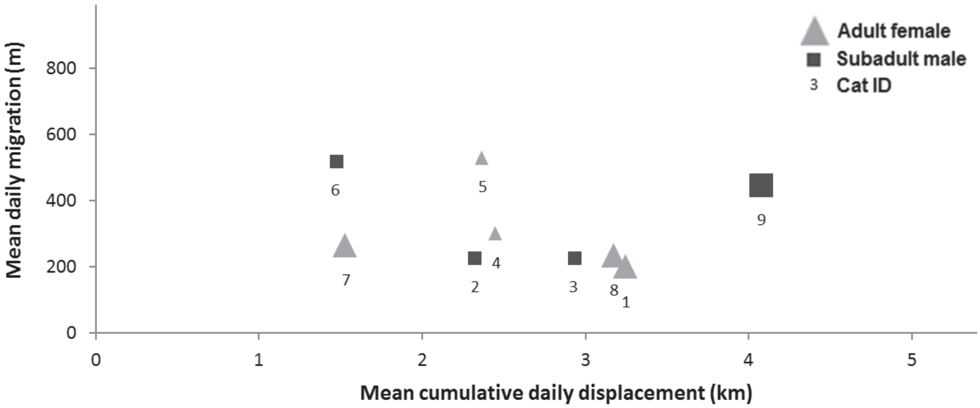

Figure 7. Migration vs displacement behaviour, indicating variances between cats. Square = male, triangle = female, small icon = subadult, large icon = adult.

prey ingested' was compared with the 'relative frequency corrected' (figure 8) the nine hares and rabbits took up more than 50% of the total volume ingested by the cats.

During the small mammal trapping session 104 animals were caught in total. The captures consisted of 81 unique individuals: 36 wood mouse (*Apodemus sylvaticus*), 33 greater white-toothed shrew (*Crocidura russula*) and 12 voles. After calculation, this resulted in a 'relative volume of prey present' value of 5.1% for voles and 19% for mice and shrews (figure 8). Wood mouse was the most caught small mammal (36), but represented only 5% of the total 'relative frequency' of prey ingested (table 4). The calculation of the present volume of birds in the area resulted in a value of 15%. Hares came out high with a value of 61%. If the relative 'volume

Table 4. Results from scat analysis, compared with previous years. For 2014 the Leporidae total is the sum of Leporidae sp., hare and rabbit.

	year	Number of scats	Vole	Mice	Shrew	Rat	*Leporidae* Unknown	Hare	Rabbit	*Leporidae total*	S-birds	M-birds	L-birds	Insect	Total
Frequency of occurence	2011	180	241	13	26	10	-	-	-	61	27	21	8	3	410
	2012	120	151	1	9	0	-	-	-	45	15	11	5	1	238
	2014	160	189	18	33	15	11	9	18	38	45	21	0	0	359
Relative frequency %	2011	180	58.8	3.2	6.3	2.4	-	-	-	14.9	6.6	5.1	2.0	0.7	100
	2012	120	63.7	0.4	3.8	0.0	-	-	-	19.0	6.3	4.6	2.1	0.0	100
	2014	160	52.6	5.0	9.2	4.2	3.1	2.5	5.0	*10.6*	12.5	5.8	0.0	0.0	100

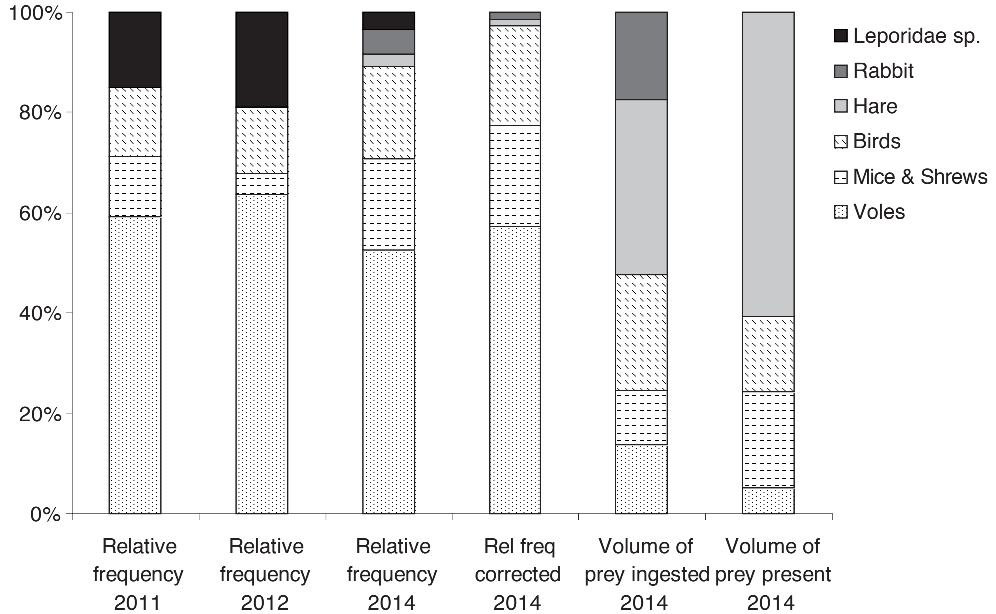

Figure 8. Relative frequency of different prey groups found in scats for three years and corrected relative frequency, volume of prey ingested and volume of prey present in research area.

of prey present' was compared to the 'volume of prey ingested' it could be seen that cats ingest (relatively) more voles and birds than present, and (relatively) less mice, shrews and hares. Because no rabbit and rat data were available it must be noted that those potential prey species were not included in this comparison.

Discussion

Trapping

The trapping sessions were very successful, with one cat per 67 trapping hours. Langeveld (1987) caught one cat per 2184 trapping hours at Schiermonnikoog. Several factors could explain this substantial difference. Firstly, Langeveld applied many techniques to catch the cats and several types of bait, but the use of sardines in oil and a fish scent were not mentioned. Secondly, Langeveld did not apply prebaiting, whereas we used a four month prebaiting period. A final reason could be a larger cat population, which increased from about 34 in 1986 to about 50 in 2010 (Langeveld 1987, op de Hoek 2012). Indeed, our results indicate that cats successfully reproduce in the research area, because the majority of the cats caught in November/December were young cats, most likely born in the same year.

The cats' bodyweight ranged between 2.4–4.6 kg. Hence, we found no indication that feral cats are heavier than regular house cats (~4.5 kg; Leray et al. 2006). On average the re-caught cats gained weight by 0.52 kg, i.e. in the (early) summer season. This was relatively high compared to weight changes observed in other studies, such as Bengsen et al. (2012), who found a 14% bodyweight reduction during a Mediterranean winter on Kangaroo island (South-Australia), or Bridges et al. (2015), who found a 0.01 kg bodyweight gain (range between -0.81 and 0.94 kg), also during a Mediterranean winter on San Clemente Island (California, USA). Our observed weight gain is probably best explained by the higher availability of prey on Schiermonnikoog in summer compared to winter.

Home ranges

We found that the average HR size of males was not significantly larger than HR size of females, which is in line with other GPS studies on feral cats. Bridges et al. (2015) found an average Kernel 95% HR size of 168 ha for males and 132 ha for females (not significantly different). Bengsen et al. (2012) mentioned much larger average HRs for males (838 ha) than females (516 ha) using the MCP 100% HR, but differences were also not statistically significant. Thomas et al. (2014) showed a daily average MCP 95% HR of 1.94 ha, which is much smaller compared to our research (15 ha), but also here no significant difference between male and female was found. Similar to our research, they also found that the nocturnal HR (2.74 ha) was larger than the diurnal HR (1.84 ha). This was also found by Metsers et al. (2010) for two of their study sites on domestic cats. This shows that the cats on Schiermonnikoog appear to use the more usual nocturnal lifestyle. A nocturnal lifestyle may indicate that preferred prey on Schiermonnikoog are mostly nocturnal, such as rabbit, hares and small rodents, and not day-active species, such as birds. However, feral cats are known to be very flexible with their daily activity pattern and can even change to a diurnal lifestyle (Fitzgerald & Turner 2000).

Daily activity pattern, habitat use & locomotive behaviour

The daily activity patterns show a larger displacement distance during the night, again suggesting more nightly activity and a nocturnal lifestyle. Our results are much in line with those of Langham (1992) who found that cats moved significantly further between dusk and dawn. We found a very low average displacement distance right after sunrise, with low activity between 0.5 and two hours after sunrise (figure 5), suggesting a period of rest. A reason could be the energy conservation of both prey and cats during this relatively cold time of day (Campbell & Reece 2005). Kestler & Wilson (2014) found a similar pattern using acceleration data from a subset of the cats in our study. The cats spent more time on the inactive behaviour laying down during dawn and less during dusk.

Habitat use varied largely between individual cats. This can firstly be explained by the fact that cats are generalists that can easily adapt to many environmental factors (Liberg et al. 2000, Turner 2014). According

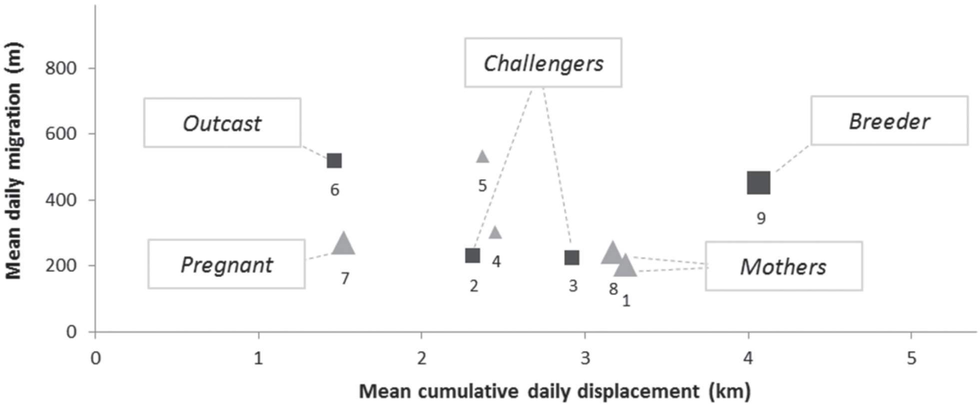

Figure 9. Scatterplot showing the relation between mean daily migration and mean cumulative daily displacement, and identifying different categories of behaviour. Square = male, triangle = female, small icon = subadult, large icon = adult.

to Liberg et al. (2000), a cat may increase its HR if it cannot find enough resources (e.g. food). These authors found a strong correlation between cat density and home range size (r^2= 0.9). As an example they mentioned that cats may live around garbage disposal bins or fish dumps when densities are high (>100 cats/km^2) but also when densities are much lower (<5 cats/km^2) and food is scarce. Six cats showed a slight preference for 'Salt Marsh & Low Herb/Shrub' which could suggest that they hunt on nocturnal prey in that habitat. It is known that rabbits and hare prefer to forage on short vegetation (Drees et al. 2007, Kuijper & Bakker 2008), and are also night-active. So, it is well possible that cats go out at night to prey on rabbits and hares in this habitat.

Natal dispersal happens mainly with young males, and much less with young females as they are longer accepted by the mother than young males (Liberg 1980). Young males migrate large distances away from the natal area and are called 'outcasts'. They will settle at a location where no harassment of 'breeders' (big dominant, settled, males) will occur. Once settled they fall in the category 'challengers' (mostly 2-3 years old) and will increasingly challenge 'breeders' (Liberg 1980, Kerby & Macdonald 1988). According to Liberg et al. (2000), the success of mating is strongly correlated with the dominance, age and weight of the males, indicating that outcasts and challengers have to gain weight and age before they can outcompete a breeder. In this study two breeders (cat 0 and cat 9) and three young males were caught (cat 2, 3, 6), and the latter were expected to be outcasts or challengers. We tried to identify these two categories from the migration vs displacement behaviour (figure 9). Cat 2 and 3 are not searching for a new area to settle (low daily migration) and could be called challengers. Cat 6 does migrate long distances presumably in search of a new area to settle. He does not displace much, probably to prevent confrontations with a breeder (cat 0), which is roaming that area as well (personal observation). Cat 9 is a breeder, a dominant heavy adult male (4.1 kg) that roams the area, displacing large distances in search of females. Similar cases were found in the study of Langham (1992). Cat 8 was known to have kittens during the time of study so she stayed relatively close to her litter (low daily migration). Nevertheless she had to catch food for her youngsters, so she showed a large displacement. Cat 1 is presumed to have kittens, supported by the fact that she comes out on the same location in the scatter plot (figure 9). Cat 7 was observed mating with cat 9 in May 2014, and was assumed to be pregnant during the largest time of study. It is known that female cats become less active as parturition nears and thus the average displacement was expected to be lower during the gestation phase (9 weeks) (Hart & Hart 2014). Indeed, cat 7 showed a relatively low average displacement during this study.

Diet and prey presence

Our scat analyses show that the diet of the cats remained relatively stable over the last three years of study (~70% small rodents; ~15% Leporidae spp.; ~15% birds) (op de Hoek 2012, Maris 2013). However, a new insight from our Leporidae hair analysis is that cats on Schiermonnikoog do eat hares and rabbits, although it turned out to be ambiguous to properly translate frequency of scats found with Leporidae hairs to individuals eaten. We applied a conservative method in our study that could have resulted in an underestimation of individuals eaten. The calculation from frequency of prey to volume of prey is very rough and needs more fine-tuning e.g. by inclusion of age of the prey eaten, given that cubs and juveniles are much lighter than adults.

For the estimation of prey presence some assumptions were made that need to be taken into consideration. Firstly, for the small mammal density estimation it was assumed that all present species on a transect would have the same chance to be caught. However, it is known that species like voles are trap-shy which can lead to an underestimation of their density (Gurnell & Flowerdew 2006). Secondly, it was assumed that all present prey items would be equally available for the cats. However, prey availability is not the same as prey presence. For example, in dense thorny shrub thickets prey presence may be high but physically out of reach for cats. Thirdly, it was assumed that the availability of prey does not fluctuate during the season. However, it is known that chicks of birds only become available when hatched, and densities of mice are the highest in autumn and lowest in early spring (Gurnell & Flowerdew 2006). Finally, it was assumed that the numbers of birds in 2014 were similar as in 2012 (Klemann & Kleefstra 2012) while this may not have been the case. Yet, despite these assumptions, we still believe that our study is valuable as it gives insights in prey selection and nutritional choices of feral cats.

Conclusions

This study gives new insights in the spatial ecology and behaviour of feral cats in a natural part of the Dutch Waddensea island of Schiermonnikoog. The cats showed a nocturnal lifestyle during the study period: they are more active during the night and their nocturnal HR is generally bigger. Males do not have a larger HR than females. Each cat had an individual specific habitat use and no indication of a preferred habitat was recognised. The diurnal and nocturnal habitat use does differ significantly, and we found a small preference for the short salt marsh vegetation during the night. This could suggest that cats hunt on prey (e.g. Leporidae) foraging in that habitat during the night. Although the methods used to relate two spatial behaviour variables and to identify different behavioural categories (breeders vs challengers) was exploratory, they proved to work relatively well and may be a useful tool to implement for future animal tracking studies. The scat analyses showed no large shifts in diet compared to previous years: voles remained the main source of prey. Nevertheless, sufficient bird remains were found in the scats (23% of the total volume of prey ingested) indicating that feral cats are still a potential threat for the bird population. The recalculation of frequency of prey into volume of prey showed that Leporidae species are a bigger part of the diet as initially thought. Our findings shed more light on the behaviour of freely roaming cats in a Dutch Waddensea ecosystem.

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Samenvatting

Ruimtelijke ecologie en prooikeuze van gezenderde verwilderde katten op Schiermonnikoog

De verwilderde katten (*Felis catus*) populatie die leeft op Schiermonnikoog, kan een potentiële bedreiging vormen voor de lokale populaties van verschillende prooisoorten. Om meer inzicht te verkrijgen in de ruimtelijke ecologie van deze invasieve predator zijn tien verwilderde katten voorzien van een GPS-halsbandzender en gevolgd van mei tot juli 2014. Er werden ruimtelijke en temporele analyses gedaan. Ten eerste werden de home ranges berekend alsmede de verplaatsing overdag (diurnus) en in de nacht (nocturnus). Daarnaast is het habitatgebruik inzichtelijk gemaakt en is het verplaatsingsgedrag vergeleken tussen de katten. Als laatste is een dieetstudie uitgevoerd. De resultaten laten ten eerste zien dat de gemiddelde home range van de katten 81 ha (Kernel 95%) and 158 ha (MCP 95%) bedraagt. Er was echter geen verschil tussen de geslachten of leeftijdsgroepen, maar de nachtelijke home ranges waren wel groter dan de home ranges overdag. Het habitatgebruik liet zien dat de katten een lichte voorkeur hebben voor korte kweldervegetatie tijdens de nacht. De katten lieten tevens een grotere nachtelijke verplaatsing zien, en de dagelijkse migratie en cumulatieve verplaatsing varieerde sterk tussen de katten. Tot slot waren hazen (*Lepus europaeus*) het sterkst vertegenwoordigd in het totale geschatte prooigewicht, maar de veldmuis (*Microtus arvalis*) was het meest frequent. Concluderend kan gesteld worden dat katers niet zwaarder en groter waren dan poezen. De lichte voorkeur voor korte kweldervegetatie gedurende de nacht kan betekenen dat katten jagen op prooien die daar graag ’s nachts foerageren, zoals hazen en konijnen (*Oryctolagus cuniculus*). De vogelresten in de uitwerpselen van de katten laten een potentiële bedreiging voor de vogelpopulatie zien, maar er is geen indicatie gevonden dat katten actief naar vogels zoeken vanuit de ruimtelijke analyses.

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