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Home-range size of the European wildcat (*Felis silvestris silvestris*): a report from two areas in Central Italy

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Abstract: Although the behavioural ecology of the European wildcat (*Felis silvestris silvestris*) has been studied in several European countries, its home-range size is still poorly known due to elusive behaviour of the species living in typically low population densities. In our study, 11 wildcats from two distinct areas, the Maremma Regional Park (Tuscany; 3 males and 1 female) and the Paradiso di Pianciano Estate (Umbria; 6 males and 1 female), both located in Central Italy, were studied by means of classical VHF radio-tracking. Home ranges were calculated by means of the Brownian bridge movement model (BBMM). Variables significantly affecting home-range size were: study area, gender and the interaction between gender * age. The potential effect of the reproductive season and the nocturnal period was not supported. The main findings indicate that: (1) home-range sizes in Tuscany were larger than those in Umbria; (2) home-range size was positively related to the age of individuals; (3) males exploited larger home ranges than females in all age-classes except for the sub-adult age-class; this latter pattern has never emerged from any previous wildcat radio-telemetry study. Population density, different management regimes in the areas considered and the local abundance of prey may explain differences in home-range sizes between the study areas. The estimated home ranges of wildcats in Umbria were slightly larger than those reported across Europe, while those calculated in the Tuscan study area were significantly greater.

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Introduction

The European wildcat (*Felis silvestris silvestris*) is a small felid (body weight: 3–5 kg) (Ragni 1981, Kery et al. 2011) which is widely distributed throughout Europe, from Sicily to Scotland and from Portugal to the Caucasus (Nowell and Jackson 1996). Although the species is currently classified as being of "Least Concern" by the IUCN (data access 17/07/2015), many wildcat populations are shrinking, especially in southern regions (Yamaguchi et al. 2015). The chief threats to the long-term conservation of the European wildcat are: habitat fragmentation (Ragni 1981, 2006, Say et al. 2012), human-induced mortality (Ragni 2006, Klar et al. 2009, Lozano and Malo 2012) and hybridisation with the domestic cat (*Felis silvestris catus*) (Randi et al. 2001, Ragni 2006, Oliveira et al. 2008a). Locally, the overgrazing of wild ungulates (*Sus scrofa* and *Cervus elaphus*) (Lozano et al. 2007) and the presence of humans (Piñeiro et al. 2012) may also impact negatively on wildcat populations.

Italy hosts at least three geographically distinct wildcat populations (Mattucci et al. 2013), with some territories (namely in the North-West Apennines) having been recently recolonised (Velli et al. 2015). The general trend of the population can be considered stable at the national level. However, wildcat studies (and ensuing conservation measures) have been relatively scarce in Italy, resulting in a general lack of knowledge of wildcat ecology and behaviour.

Assessment of the animal's spatial behaviour is a crucial initial step in order to undertake the action needed to conserve wildcat populations throughout their range (Birò et al. 2004, Sarmento et al. 2006, Monterroso et al. 2009). Species-specific home-range size is a key parameter in numerous frameworks, such as landscape genetics (e.g. calibration of uncertainty for spatial genetic analysis; Mattucci et al. 2013), population estimates (e.g. calibration of camera-trap spacing within study areas; Anile et al. 2014) and habitat modelling (e.g. as a response variable in modelling analysis; Germain et al. 2008, Klar et al. 2008, Monterroso et al. 2009).

To date, radio-telemetry studies on the home-range size of the European wildcat have been undertaken in several European countries, such as France (Germain et al. 2008), Scotland (Corbett 1979, Scott et al. 1992, Daniels et al. 2001), the Iberian Peninsula (Sarmento et al. 2006, Monterroso et al. 2009, Soto and Palomares 2013), Hungary (Birò et al. 2004) and Germany (Wittmer 2001). Notably, however, radio-telemetry studies are lacking in Italy. More importantly, owing to the elusive behaviour of the species and the typically low population densities (in addition to the cost and feasibility of radio-tracking), very few studies with a sample size of 10 or more animals have been conducted (Corbett 1979, Stahl et al. 1998). The home range of the wildcat has been seen to vary greatly among the areas studied. Males usually exploit larger areas than females, with low or null overlapping among males and different degrees of overlapping among females and between males and females (Corbett 1979, Stahl et al. 1998, Wittmer 2001, Birò et al. 2004, Germain et al. 2008). Moreover, home-range size can also be affected by the age of the animals, with juveniles and sub-adults of both sexes using smaller home ranges than adults (Corbett 1979, Daniels et al. 2001, Monterroso et al. 2009). Finally, wildcats typically display crepuscular/nocturnal peaks of activity (Corbett 1979, Daniels et al. 2001, Germain et al. 2008) and can travel long distances at night (Wittmer 2001). Indeed, most of the day they spend in well-characterised resting places (Corbett 1979, Jerosch et al. 2010). Diurnal home ranges can therefore be expected to be smaller than nocturnal ranges.

In the current study, we aimed to

1) contribute to filling the gap in the ecology (specifically, the home-range size) of the wildcat in Italy by analysing the spatial behaviour of wildcats in two distinct areas of Central Italy: the Maremma Regional Park (MRP) in Southern Tuscany and the Paradiso di Pianciano Estate (PPE), a private game reserve in Umbria. Specifically, we sought to estimate the home range of the wildcat both on a yearly basis and during the reproductive season, and to identify which variables (e.g. study area, gender and age) significantly affected the wildcat's home-range size.
2) On the basis of the above-mentioned behavioural traits (marked nocturnal activity and the use of daytime resting sites), we aimed to ascertain whether there was a difference between nocturnal and diurnal home-range sizes.

Materials and methods

Study areas

We assumed that the catch-ability of wildcats was equal in both our study areas (see also Results section, below). Thus, our observation that trap rates (#wildcats/trap-days) were higher in the PPE than in the MRP (4/1516 = 0.0026 vs. 11/3352 = 0.0033), as was the number of cats per trapping area (#wildcats/trapping area calculated as the minimum convex polygon: 4/7022 = 0.0005 vs. 11/3590 = 0.0031), prompted us to hypothesise that wildcat population density differed between the two study areas. In addition, the MRP hosts a relative recently established population, as a direct result of a reintroduction project carried out from the late 1980s to the mid-1990s (Ragni et al. 2007, Sforzi et al. 2010), whereas the PPE is located within a core area of species distribution in the Apennines. Finally, our study areas also differ in terms of management regimes, the MRP being a national park (tourism) while the PPE is a private game estate (hunting).

The MRP is located on the Tyrrhenian coast in southern Tuscany (Grosseto Province) (Figure 1) and covers an area of approximately 10,000 ha, ranging from 0 to 417 m. a.s.l. The typically Mediterranean local climate is characterised by a dry, warm spring-summer period and a rainy, mild autumn-winter period. Mediterranean oaks (*Quercus ilex* and *Quercus suber*) grow in most of the hilly areas, while the plain-coastal areas are characterised by pine woodland (*Pinus pinea* and *Pinus pinaster*), scrub, garigue and marshland. The PPE is a 7200 ha hilly-mountainous portion (400–1354 m a.s.l.) of the Umbrian Apennines (Figure 1) and is managed as a "private game estate". The climate is temperate-continental, with a wet, warm summer-autumn period and a wet, cold winter-spring period and annual snowfalls. Deciduous broad-leaf forest (*Ostrya carpinifolia*, *Quercus cerris*, *Fagus sylvatica*) covers 69% of the land area, while the remainder comprises secondary grassland (15%), olive-groves (6%), cropland (7%), sclerophyll woods and hedges (3%). The mammalian fauna of both areas includes: the wild boar (*Sus scrofa)*, roe deer (*Capreolus capreolus)*, red fox (*Vulpes vulpes)*, wildcat, badger (*Meles meles)*, stone marten (*Martes foina)*, brown hare (*Lepus europaeus*), crested porcupine (*Hystrix cristata*), red squirrel (*Sciurus vulgaris*), common dormouse (*Muscardinus avellanarius*), wood mouse (*Apodemus sylvaticus*) and black rat (*Rattus rattus*). The fallow deer (*Dama dama)*, pine marten (*Martes martes*), coypus (*Myocastor coypus*), house mouse (*Mus musculus*) and brown

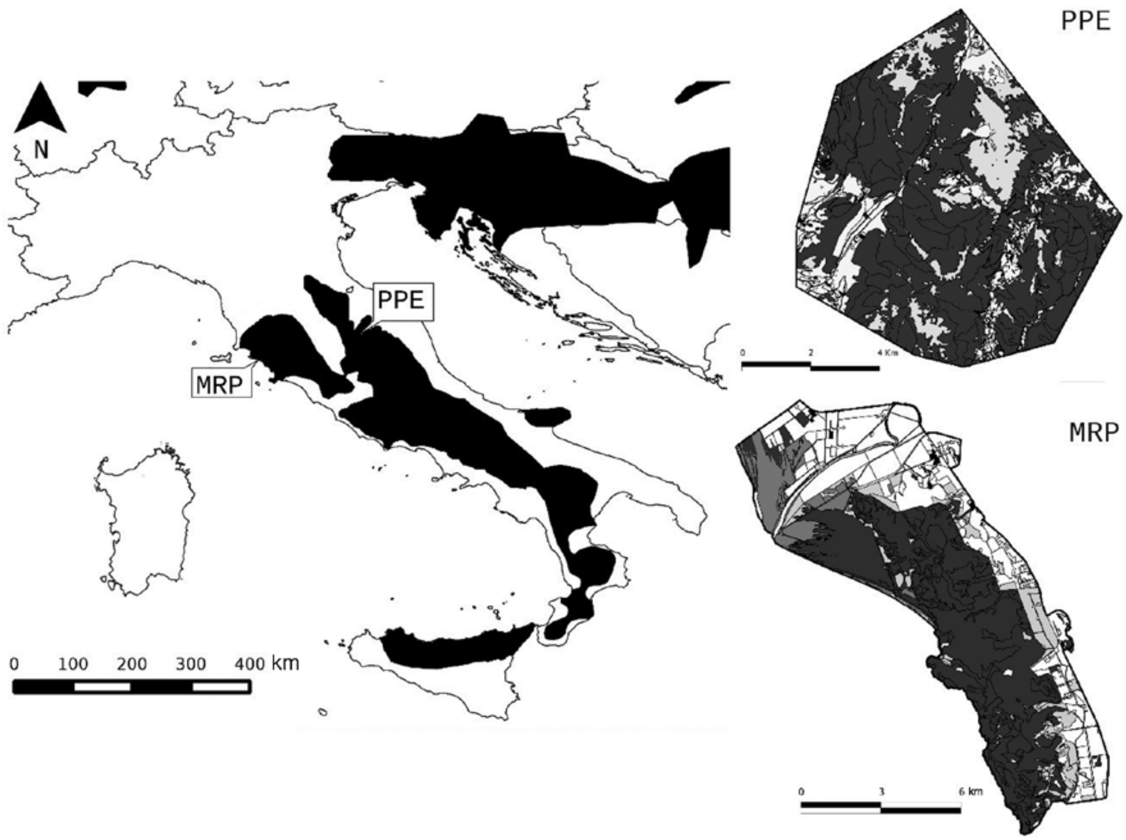

Figure 1: Map showing the location of the two study areas and wildcat distribution in Italy (modified from the IUCN red list). Black: settlements and roads; dark grey: woodland; mid grey: marsh vegetation; pale grey: grassland; white: cropland.

rat (*Rattus norvegicus*) are only present in the MPR, while the Apennine wolf *(Canis lupus italicus*), polecat (*Mustela putorius*), edible dormouse (*Glis glis*), garden dormouse (*Eliomys quercinus*), bank vole (*Clethrionomys glareolus*) and yellow necked mouse (A*podemus flavicollis*) are only present in the PPE.

Trapping and radio-tracking

Trapping sessions were undertaken from April to June 1995 and from February to November 1999 in the MRP and from June 2003 to June 2006 in the PPE. Traps were checked once a day, at sunrise, (see details in Bizzarri et al. 2010). Morphological identification and assignment to the European wildcat were performed on the basis of coat pattern markings (Ragni and Possenti 1996). Blood samples were taken for genetic identification (Mattucci et al. 2013). Trapped wildcats were anaesthetised in accordance with standard procedures (Bizzarri et al. 2010). For each wildcat, the following data were recorded: gender, weight and approximate age (juvenile = 0–12 months; subadult = 12–24 months; adult > 24 months), as estimated by visual inspection of body size and structure and the degree of emergence and integrity of teeth. Trapped animals were then fitted with VHF radio-transmitter loop collars (Televilt, SE. weight: 50 g; frequency: 150,000–151,999 MHz) and released once deemed to be fully alert. Individuals were tracked according to scheduled monitoring of four 6-h periods (00–06; 06–12; 12–18; 18–24) per month, in order to sample a whole 24-h period per month. Within each 6-h period monitored, fixes were recorded every 30 min, field conditions permitting (e.g. adverse weather, orography, speed of radio-tagged individuals, viable paths for operators, etc.). Further fixes were also collected opportunistically. Overall, across the study areas, a total of 8950 fixes were taken, 1233 of which (13.7%) were randomly recorded. Spatial triangulation was undertaken by means of the Best Biangulation method in LOAS 3.0.1 (Ecological Software Solution 2004). Sunrise and sunset times on each monitoring day in each study area were calculated by means of the equations reported by Teets (2003).

The home-range size (*hrs*) of each individual was estimated for each year, with each year being broken down into the reproductive season (mating = winter vs.

sexual rest = all other seasons together) and daylight phases (diurnal vs. nocturnal). Consequently, four home-range sizes per year were attributed to each individual (mating diurnal/mating nocturnal/sexual rest diurnal/sexual rest nocturnal), the year being split into four $individual_{seasons.periods}$. Thus, the response variable [*log*(*hrs*), see below] used in modelling represented the same ecological unit (i.e. only fixes collected during a given reproductive period and nocturnal/diurnal period constituted the input for the home-range estimation). Home-range size estimates were further associated with the number of fixes per $individual_{season.period}$ in order to account for this potentially confounding factor in data modelling. We also calculated yearly (over all seasons and periods) and seasonal (spring, summer, autumn, winter over all periods) within-year (over all periods) home-range sizes in order to provide a baseline reference for comparison with other studies.

Wildcat home-range size was calculated by means of the Brownian Bridge Movement Model (BBMM) provided in the R (version 3.0.2, R Development Core Team 2014) package "*BBMM*" (Nielson, R. M., Sawyer H. and McDonald T. L., unpublished). This approach jointly uses the locations and the time spent in an area to estimate the home-range size of an animal (Horne et al. 2007) and is particularly useful when dealing with locations recorded during short time-intervals, such as those considered in the present study (Horne et al. 2007, Kranstauber et al. 2012). Field trials (n = 42) were conducted in both study areas to quantify the location error associated with recorded fixes; this value was required in order to calculate the BBMM home-range appropriately. According to these trials, the mean error associated with locations was 97 ± 18 m; hence, the grid-cell size (required for BBMM calculation) was set at 200 m (approximately twice the location error).

Statistical analyses

We implemented a general additive mixed model (GAMM) fitted with restricted maximum likelihood estimation (REML, Zuur et al. 2009) and used the R package "*mgcv*" (Wood S., unpublished) to investigate the variation in $individual_{season.period}$ home-range size. Specifically, we built the "saturated model" (a model including all potential explanatory variables) which was fitted to the data as follows: (1) the variable "*individuals*" was used as a random effect; (2) *year* was used as a random effect with a hierarchical structure within individuals, as we had no biological hypothesis about its effect; (3) the number of fixes (*nfixes*) per $individual_{season.period}$, which might affect the home-range size estimation, was smoothed in order to allow a potential non-linear relationship between the home-range size and the number of fixes; (4) study area (*area*, MRP/PPE), gender (*gender*, male/female), reproductive season (*repro*, mating/sexual rest), age-classes (*age*, juvenile/sub-adult/adult) and light/dark period (*period*, diurnal/nocturnal) were used as fixed effects; (5) additionally, on the basis of biological reasoning and previous data exploration, the following interaction terms were included as fixed effects, and model fine tuning specifications were employed as follows: (i) gender * age, to take into account the differential effect of age on the spatial behaviour of each gender; (ii) *repro* * *gender*, to take into account the differential effect of the reproductive season on the spatial behaviour of each gender; (6) home-range size (*hrs*) was log-transformed; (7) a Gaussian family distribution and the identity link function were employed because the response variable is normal (Zuur et al. 2010).

We then selected for the more parsimonious (sensu "best") model among the set of candidate models using AICc. The starting model for AICc model selection was thus:

$$log(hrs_i) = \beta_0 + area_i + period_i + \mathrm{F}(nfixes_i) + gender_i * age_i + repro_i * gender_i + \mathrm{b}_i + \varepsilon_i$$

where β_0 is the intercept, b_i the random intercept, ε_i the residual for the ith $individual_{season.period}$ and f the smoothing function for the number of fixes and with $\varepsilon_i \sim \mathrm{N}(0, \sigma^2)$ and $\mathrm{b}_i \sim \mathrm{N}(0, \sigma^2)$. From this starting model, we selected the most parsimonious model by using the *dredge* function from the *R* package "*MuMIn*" (Barton 2013). All results are reported as mean ± standard error unless stated otherwise.

Results

Trapping and radio-tracking

Overall, 1516 trap-days (trapping rate = 1 wildcat/379 days) were performed in the MRP, and four wildcats (morphological identifications were confirmed by genetic identification) were caught: three males and one female. All were tracked for an average of 253 ± 56 days, with 134 ± 14 fixes over a period of 904 ± 318 days (Tables 1 and 2). In the PPE, 11 wildcats (9 males and 2 females) were captured over a total of 3352 trap-days (trapping rate = 1 wildcat/304 days). Owing to the immaturity and/or

Table 1: BBMM home-ranges (in km²) of wildcat in Italy according to each *time period*.

Id	Area	Sex	Year	Days	Nfixes	BMV	Repro	Period	Status
F1	MRP	F	1998	311.88	61	4.10	Mating	Diurnal	Adult
F1	MRP	F	1998	308.46	48	3.07	Mating	Nocturnal	Adult
F1	MRP	F	1998	169.90	166	16.90	Relax	Diurnal	Adult
F1	MRP	F	1998	163.74	97	28.01	Relax	Nocturnal	Adult
F1	MRP	F	1999	52.86	54	1.13	Mating	Diurnal	Adult
F1	MRP	F	1999	21.04	28	0.62	Mating	Nocturnal	Adult
F1	MRP	F	1999	33.42	40	0.21	Relax	Diurnal	Adult
F1	MRP	F	1999	13.94	22	0.81	Relax	Nocturnal	Adult
F2_G	PPE	F	2005	27.78	19	0.64	Mating	Diurnal	Juveniles
F2_G	PPE	F	2005	24.96	15	2.28	Mating	Nocturnal	Juveniles
F2_G	PPE	F	2005	266.39	132	1.49	Relax	Diurnal	Juveniles
F2_G	PPE	F	2005	159.12	92	0.05	Relax	Nocturnal	Juveniles
F2_G	PPE	F	2006	336.84	29	21.03	Mating	Diurnal	Sub-adult
F2_G	PPE	F	2006	49.34	17	7.66	Mating	Nocturnal	Sub-adult
F2_G	PPE	F	2006	273.05	407	12.18	Relax	Diurnal	Sub-adult
F2_G	PPE	F	2006	223.00	125	11.40	Relax	Nocturnal	Sub-adult
M1	MRP	M	1995	28.98	78	15.50	Mating	Diurnal	Sub-adult
M1	MRP	M	1995	21.33	57	11.61	Mating	Nocturnal	Sub-adult
M1	MRP	M	1995	139.89	654	0.40	Relax	Diurnal	Sub-adult
M1	MRP	M	1995	139.50	534	32.62	Relax	Nocturnal	Sub-adult
M1	MRP	M	1996	56.01	150	51.53	Mating	Diurnal	Adult
M1	MRP	M	1996	49.24	142	26.62	Mating	Nocturnal	Adult
M1	MRP	M	1996	190.550	552	22.09	Relax	Diurnal	Adult
M1	MRP	M	1996	182.35	434	0.43	Relax	Nocturnal	Adult
M1	MRP	M	1998	18.85	23	8.90	Mating	Diurnal	Adult
M1	MRP	M	1998	17.49	25	31.88	Mating	Nocturnal	Adult
M1	MRP	M	1998	23.08	3	524.71	Relax	Diurnal	Adult
M1	MRP	M	1999	29.97	49	11.83	Mating	Diurnal	Adult
M1	MRP	M	1999	9.25	9	21.16	Mating	Nocturnal	Adult
M1	MRP	M	1999	128.92	136	31.68	Relax	Diurnal	Adult
M1	MRP	M	1999	119.36	113	15.97	Relax	Nocturnal	Adult
M1_G	PPE	M	2003	91.96	45	12.89	Relax	Diurnal	Adult
M1_G	PPE	M	2003	64.95	47	12.15	Relax	Nocturnal	Adult
M2	MRP	M	1995	68.02	129	13.17	Relax	Diurnal	Adult
M2	MRP	M	1995	66.10	61	31.77	Relax	Nocturnal	Adult
M2	MRP	M	1996	48.14	249	61.30	Mating	Diurnal	Adult
M2	MRP	M	1996	47.98	173	35.51	Mating	Nocturnal	Adult
M2	MRP	M	1996	225.93	401	59.83	Relax	Diurnal	Adult
M2	MRP	M	1996	224.00	244	58.36	Relax	Nocturnal	Adult
M2_G	PPE	M	2003	16.92	16	11.31	Mating	Diurnal	Adult
M2_G	PPE	M	2003	15.26	16	1.13	Mating	Nocturnal	Adult
M2_G	PPE	M	2003	144.91	93	5.09	Relax	Diurnal	Adult
M2_G	PPE	M	2003	140.22	86	4.12	Relax	Nocturnal	Adult
M3	MRP	M	1998	148.86	155	11.46	Relax	Diurnal	Sub-adult
M3	MRP	M	1998	144.36	108	95.49	Relax	Nocturnal	Sub-adult
M3_G	PPE	M	2003	17.13	19	0.83	Mating	Diurnal	Adult
M3_G	PPE	M	2003	14.41	17	4.67	Mating	Nocturnal	Adult
M3_G	PPE	M	2003	48.18	28	1.75	Relax	Diurnal	Adult
M3_G	PPE	M	2003	30.48	10	12.81	Relax	Nocturnal	Adult
M3_G	PPE	M	2004	349.14	49	9.80	Mating	Diurnal	Adult
M3_G	PPE	M	2004	356.00	53	18.05	Mating	Nocturnal	Adult
M3_G	PPE	M	2004	273.31	314	6.36	Relax	Diurnal	Adult
M3_G	PPE	M	2004	267.83	186	0.19	Relax	Nocturnal	Adult
M3_G	PPE	M	2005	54.98	56	1.89	Mating	Diurnal	Adult
M3_G	PPE	M	2005	51.24	37	1.93	Mating	Nocturnal	Adult
M3_G	PPE	M	2005	262.16	205	3.92	Relax	Diurnal	Adult

Table 1 (continued)

Id	Area	Sex	Year	Days	Nfixes	BMV	Repro	Period	Status
M3_G	PPE	M	2005	246.92	98	20.43	Relax	Nocturnal	Adult
M4_G	PPE	M	2004	101.76	133	4.32	Relax	Diurnal	Adult
M4_G	PPE	M	2004	98.83	101	5.10	Relax	Nocturnal	Adult
M5_G	PPE	M	2004	18.35	11	455.22	Mating	Diurnal	Adult
M5_G	PPE	M	2004	28.90	15	0.44	Mating	Nocturnal	Adult
M5_G	PPE	M	2004	37.29	41	2.97	Relax	Diurnal	Adult
M5_G	PPE	M	2004	36.06	14	12.71	Relax	Nocturnal	Adult
M5_G	PPE	M	2005	358.69	81	4.58	Mating	Diurnal	Adult
M5_G	PPE	M	2005	353.72	55	8.85	Mating	Nocturnal	Adult
M5_G	PPE	M	2005	274.19	223	4.25	Relax	Diurnal	Adult
M5_G	PPE	M	2005	267.18	140	10.34	Relax	Nocturnal	Adult
M5_G	PPE	M	2006	50.95	27	2.27	Mating	Diurnal	Adult
M5_G	PPE	M	2006	49.40	19	12.11	Mating	Nocturnal	Adult
M5_G	PPE	M	2006	120.03	44	5.77	Relax	Diurnal	Adult
M5_G	PPE	M	2006	93.80	13	12.88	Relax	Nocturnal	Adult
M7_G	PPE	M	2005	26.78	17	12.13	Mating	Diurnal	Juveniles
M7_G	PPE	M	2005	24.87	11	1.90	Mating	Nocturnal	Juveniles
M7_G	PPE	M	2005	259.38	211	4.13	Relax	Diurnal	Juveniles
M7_G	PPE	M	2005	254.19	120	4.96	Relax	Nocturnal	Juveniles
M7_G	PPE	M	2006	51.00	25	6.02	Mating	Diurnal	Sub-adult
M7_G	PPE	M	2006	49.43	18	5.44	Mating	Nocturnal	Sub-adult
M7_G	PPE	M	2006	212.15	117	3.07	Relax	Diurnal	Sub-adult
M7_G	PPE	M	2006	197.00	32	3.23	Relax	Nocturnal	Sub-adult
M9_G	PPE	M	2005	27.79	19	0.76	Mating	Diurnal	Sub-adult
M9_G	PPE	M	2005	19.97	13	3.00	Mating	Nocturnal	Sub-adult
M9_G	PPE	M	2005	42.34	43	1.36	Relax	Diurnal	Sub-adult
M9_G	PPE	M	2005	37.96	26	0.86	Relax	Nocturnal	Sub-adult
M9_G	PPE	M	2006	349.97	30	740.62	Mating	Diurnal	Adult
M9_G	PPE	M	2006	49.38	21	3.44	Mating	Nocturnal	Adult
M9_G	PPE	M	2006	272.07	141	6.67	Relax	Diurnal	Adult
M9_G	PPE	M	2006	222.96	70	9.23	Relax	Nocturnal	Adult

For each cat it is reported year of monitoring (year), study area (area), age (age), days of monitoring (days) and number of fixes collected (nfixes).

the poor physical condition of some individuals, however, only seven individuals (6 males and 1 female) in the PPE were fitted with radio-collars. Wildcats in the PPE were tracked for an average of 128 ± 50 days, with 44.8 ± 4 fixes over a period of 1017 ± 236 days (Tables 1 and 2). Overall, from 11 wildcats we obtained 85 estimations for the time periods considered.

The home range of adult male wildcats was 22.74 ± 4.79 km^2 and 6.53 ± 0.66 km^2 in the MRP and PPE, respectively. The adult female wildcat (F1) in the MRP displayed a home range of 6.17 ± 4.71 km^2, whereas the sub-adult female wildcat (F2_G) in the PPE had a home range of 4.78 km^2. The home range of sub-adult male wildcats was 16.62 ± 1.66 km^2 and 6 ± 1.84 km^2 in the MRP and PPE, respectively. The home ranges of juveniles (both in the PPE) was 3.03 km^2 for a male (M7_G) and 1.66 km^2 for a female (F2_G) (Tables 1 and 2).

Model selection to determine home-range size

The model including study area, sex, age and interaction gender * age was best supported by the data (AICc < 2, Table 3 and Supplemental Table 1). Reproductive season (*repro*), period (*period*) and the smoothing function for the number of fixes f(*nfixes*) (d.f. = 1.164, F = 2.443, p = 0.115) were not significant, whereas study area (*area*), gender (*sex*) and the interaction term *sex * age* were significant (Table 3). The results indicate that home ranges of wildcats in the MRP were larger than those in the PPE ($\beta = 1.6203 \pm 0.45$, $t = 3.539$, $p < 0.001$) (Figure 2, Table 4). In addition, there was a significant interaction between *gender* and *age*, with males exploiting larger home ranges than females, with the notable exception of the sub-adult class in both populations (Figure 2, Table 4).

Table 2: BBMM home-ranges (in km²) of wildcat in Italy for each year and season.

Id	Area	Gender	Year	Nfixes	Yearly	Spring	Summer	Autumn	Winter	Age
F1	MRP	Female	1998	372	10.89	NA	10.13	18.89	6.97	Adult
F1	MRP	Female	1999	144	1.46	2.23	NA	NA	1.00	Adult
F2G	PPE	Female	2005	257	1.66	NA	2.59	0.95	0.49	Juveniles
F2G	PPE	Female	2006	578	4.78	2.58	1.92	18.00	3.09	Sub-adult
M1	MRP	Male	1995	1310	18.29	NA	13.89	21.79	12.13	Sub-adult
M1	MRP	Male	1996	1277	23.30	21.85	12.26	1.30	38.85	Adult
M1	MRP	Male	1998	54	18.48	NA	NA	NA	17.17	Adult
M1	MRP	Male	1999	306	22.32	22.08	23.08	NA	10.05	Adult
M2	MRP	Male	1995	190	10.11	NA	NA	10.11	NA	Adult
M2	MRP	Male	1996	1067	39.49	12.69	70.47	33.29	39.11	Adult
M2G	PPE	Male	2003	211	4.94	NA	6.34	1.94	1.2	Adult
M3	MRP	Male	1998	263	14.96	NA	7.02	19.68	NA	Sub-adult
M3G	PPE	Male	2003	74	10.38	NA	NA	1.70	4.51	Adult
M3G	PPE	Male	2004	601	7.12	7.58	5.86	6.86	13.51	Adult
M3G	PPE	Male	2005	396	7.01	6.44	5.83	11.90	4.79	Adult
M4G	PPE	Male	2004	234	3.89	NA	4.12	3.92	NA	Adult
M5G	PPE	Male	2004	81	4.84	NA	NA	5.52	2.38	Adult
M5G	PPE	Male	2005	49	6.50	6.36	5.65	4.02	5.91	Adult
M5G	PPE	Male	2006	103	8.31	13.70	0.35	NA	4.94	Adult
M7G	PPE	Male	2005	359	3.03	3.10	3.38	3.46	5.79	Juveniles
M7G	PPE	Male	2006	192	7.84	2.21	11.25	17.50	5.57	Sub-adult
M9G	PPE	Male	2005	101	4.16	NA	NA	5.43	2.35	Sub-adult
M9G	PPE	Male	2006	262	5.84	8.25	6.63	3.27	2.77	Adult

For each cat it is reported year of monitoring (year), study area (area), age (age) and number of fixes collected (nfixes).

Table 3: AICc model selection (top five models only and the null model) starting from the model $log(hrs_i) = \beta_0 + area_i + period_i + f(nfixes_i) + gender_i * age_i + repro_i * gender_i$.

Model notation	D.f.	LogLik	AICc	ΔAICc	AICw
$log(hrs) = \beta_0 + area + gender + age +$ gender * age	**12**	**−144.289**	**316.9**	**0.00**	**0.612**
$log(hrs) = \beta_0 + area + period + gender + age +$ gender * age	13	−144.253	319.6	2.72	0.157
$log(hrs) = \beta_0 + area + repro + gender + age +$ gender * age	13	−144.416	320.0	3.05	0.133
$log(hrs) = \beta_0 + area + period + repro + gender + age +$ gender * age	14	−144.387	322.8	5.86	0.033
$log(hrs) = \beta_0 + area + period + repro + gender + age + period * repro +$ gender * age	15	−143.450	323.9	6.94	0.019
$log(hrs) = \beta_0$ (*null model*)	6	−158.410	329.9	12.99	0.001

Random effects (*id* and *year* random effects) and $f(nfixes)$ were kept identical in all GAMM models for model selection. The best model ($\Delta AICc < 2$) is shown in bold.

Discussion

Our study was the first extensive research carried out in Italy on the home-range size of the European wildcat. Collated data came from two ecologically distinct areas in which a difference in population density can be reasonably hypothesised as suggested by higher trapping rates and number of wild cats trapped per area in PPE. Furthermore, the small wildcat population in the MRP was the result of reintroduction, whereas the PPE population fell well within the historical wildcat distribution. Nevertheless, our study areas are also characterised by different management regimes, the MRP being a national park for tourism, while the PPE is a private game estate for hunting.

Pattern of variation of home-range size in Italy

Our results suggest that light conditions (night/day) and the reproductive season (mating/sexual rest) did not influence home-range sizes. The majority of felid species usually exhibit clear nocturnal activity patterns (Di Bitetti et al. 2006, Lucherini et al. 2009, Harmsen et al. 2010,

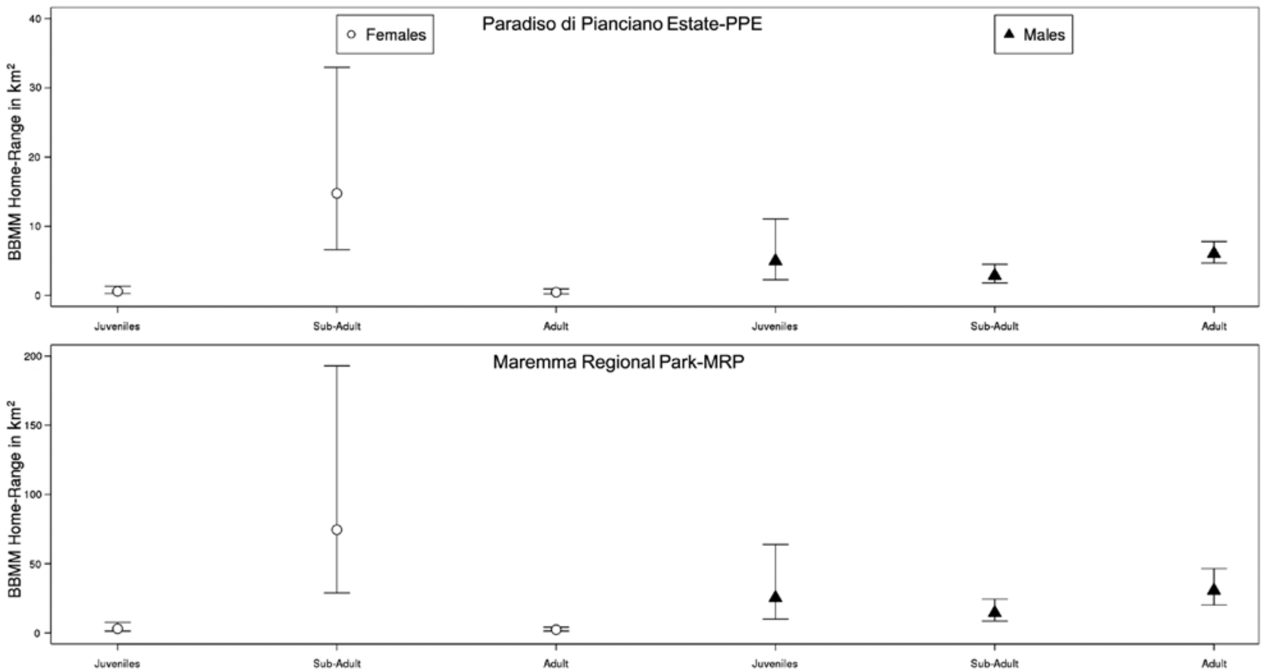

Figure 2: Wildcat home-range size predicted by gender, age-class and study site from the "best" GAMM model. *nfixes* was set at the median value (n = 55) recorded for the dataset and *y*-axis are on a different scale.

Table 4: Estimates and significance of the variables included in the GAMM model.

Variables	Estimate	Std. error	*t*-Value	Pr(>|z|)
β_0	**6.0229**	**0.7418**	**8.119**	**<6.09e–12**
***Area* (MRP)**	**1.6203**	**0.4579**	**3.539**	**0.000686**
***Gender* (male)**	**2.5789**	**0.6958**	**3.706**	**0.000395**
Age (juveniles)	0.2674	1.0754	0.249	0.804286
***Age* (sub-adult)**	**3.4699**	**1.1003**	**3.154**	**0.002302**
Gender (male) * *age* (juveniles)	–0.4613	1.3170	–0.350	0.727089
***Gender* (male) * *age* (sub-adult)**	**–4.2213**	**1.2177**	**–3.466**	**0.000867**

Significant variables are shown in bold.

Cheyne et al. 2013). Specifically, both Daniels et al. (2001) and Germain et al. (2008) found that wildcats were more active during the night.

Contrary to our expectations and despite the above mentioned difference in the activity rhythm between diurnal and nocturnal periods, we didn't find marked differences in home-range sizes between night/day periods. This finding might suggest that the spatial distribution of resting sites overlaps the entire home range over a given season.

The relative stability of the estimated home-range sizes between the reproductive period and the sexual rest period has been observed in other studies (Stahl et al. 1998, Daniels et al. 2001, Germain et al. 2008). However, it is worth noting that a decrease in home-range sizes during the spring period has been previously reported among female wildcats (Sarmento et al. 2006), though Corbett (1979) found contrasting results. This concurs with the annual birthing period (Ragni 1981, Sarmento et al. 2006), as female wildcats involved in parental activities reduce their movements. In the present study, however, this expected phenomenon was not encountered, probably owing to the low number and relative proportion of females in our sample.

The home ranges of wildcats in the MRP were larger than those in the PPE. Wildcats in the PPE are part of the Apennine mountain wildcat population (hence a "long-term" resident population), while MRP wildcats are the descendants of a nucleus reintroduced prior to initiation of the telemetry study. Accordingly, it may be argued that the potential difference in population density (as suggested by higher trapping rates and number of wild cats trapped in PPE) could markedly affect spatial behaviour, as previously reported among populations of both lynx (*Lynx lynx*) and bobcat (*Lynx rufus*) (Benson et al. 2006, Pesenti and Zimmermann 2013). Similarly, Soto and Palomares (2013) found very large wildcat home ranges (~24 km^2) within an area of low population density. However, various controlling or explanatory factors cannot be excluded; for example environmental variables such as vegetation and altitude or different habitat management regimes (e.g. potential disturbance due to hunting or tourism in our two areas) (Piñeiro et al. 2012) may also have determined the difference between home-range sizes within the two study areas.

Nevertheless, also a difference in prey densities between the study areas may have contribute in producing larger home-range in MRP; indeed it is a common finding that, when prey density is lower, home-range estimations are larger (Litvaitis et al. 1986, Avenant and Nel 1998, Herfindal et al. 2005).

Adult male wildcats displayed larger home ranges than adult females. This is in agreement with previous findings on wildcats (Daniels et al. 2001, Birò et al. 2004, Germain et al. 2008, Monterroso et al. 2009) and, more generally, on solitary and territorial carnivores. Indeed, adult males patrol large territories, which may overlap extensively with those of several females, and only slightly with those of other males (Daniels et al. 2001). This intersexual difference was also observed in juveniles, whose home-range sizes were similar to those of adults of the same sex. More surprisingly, in both populations, subadult females exhibited home-range sizes that were typical of males, albeit more variable. This pattern has never been reported before, and might be underpinned by the necessity to explore the surrounding habitat in order to find a "free" home-range for their first gestation and parturition. Further studies are required in order to understand whether this pattern should be regarded as a dispersal movement (i.e. emigration) or rather an active search for dens within the animal's own home-range.

Comparison with other studies in Europe

Wildcat home ranges have been shown to vary widely across Europe, ranging from 1.95 to 50.17 km^2 for males and 0.69–13.85 km^2 for females (Monterroso et al. 2009). However, as these figures are associated with different study methodologies, local features (prey abundance) and animal ages, direct comparison is very difficult. Assuming that home ranges in the PPE are the most representative of a "stable" wildcat population (i.e. long-term population), we can observe that our yearly home-range estimates for adult male wildcats (6.53 ± 0.66 km^2) were similar to those reported by Daniels et al. (2001) in Scotland for adult tabby wildcats (4.59 km^2), by Germain et al. (2008) (4.04 km^2) in France and by Birò et al. (2004) (6.88 km^2) in Hungary, though they were considerably smaller than that calculated by Monterroso et al. (2009) for a male wildcat (13.71 km^2) in southern Portugal.

Conversely, the mean yearly home range of male wildcats in the MRP (22.74 ± 4.78 km^2) was similar to that observed by Soto and Palomares (2013) (~24 km^2) and larger than that reported by Wittmer (2001) (16.62 km^2); indeed, our estimates were very similar to the largest home-range size reported by Wittmer (25.15 km^2).

The mean yearly home-range size of the adult female tracked in the MRP was 6.17 ± 4.71 km^2; this was larger than the values reported in most previous studies, including that of Daniels et al. (2001) (1.77 km^2), Sarmento et al. (2006) (2.89 km^2), Germain et al. (2008) (1.63 km^2) and Monterroso et al. (2009) (2.28 km^2). However, it closely matched the female home ranges observed by Birò et al. (2004) (6.24 km^2).

The annual home range of the other radio-tracked female (PPE), which was a yearling at the time of capture, increased (from 1.66 to 4.78 km^2) during the second year, when the sub-adult age-class was reached. Consequently, the sub-adult *age* effect (i.e. large home range in sub-adult females, see above), was noted within the same individual, which was monitored over the years.

Whether the variability of population density across study sites and countries is related to variability in home-range sizes on the pan-European scale remains to be investigated.

Conclusion and perspectives

The present study was the first to document the effect of population, sex and age on the home-range size of wildcats in Italy, which currently hosts four distinct populations of European wildcat (Mattucci et al. 2013), all of which are threatened with extinction. As Italian populations are among the least genetically admixed throughout their range (Randi et al. 2001, Pierpaoli et al. 2003, Lecis et al. 2006, Oliveira et al. 2008b; Mattucci et al. 2013, Anile et al. 2014), they constitute a true genotypic stronghold of wildcats in Europe. The present study fills a gap in our knowledge on a key aspect of the ecology of the wildcat in Italy. Nevertheless, further radio-telemetry research across different study areas in Italy is needed in order to describe the spatial behaviour of other Italian wildcat populations. Radio-tracking studies are difficult and expensive, hence collaboration between wildcat researchers and the authorities is necessary to effectively promote the long-term survival of this small feline in Italy.

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References

Anile, S., B. Ragni, E. Randi, F. Mattucci and F. Rovero. 2014. Wildcat population density on the Etna volcano, Italy: a comparison of density estimation methods. J. Zool. 293: 252–261.

Avenant, N.L. and J.A. Nel. 1998. Home-range use, activity, and density of caracal in relation to prey density. Afr. J. Ecol. 36: 347–359.

Barton, K. 2013. MuMIn: Multi-model inference. R package version 1.9.5. Available at: http://www.CRAN.R-project.org/.

Benson, J.F., M.J. Chamberlain and B.D. Leopold. 2006. Regulation of space use in a solitary felid: population density or prey availability? Anim. Behav. 71: 685–693.

Birò, Z., L. Szemethy and M. Heltai. 2004. Home range sizes of wildcats (*Felis silvestris*) and feral domestic cats (*Felis silvestris f. catus*) in a hilly region of Hungary. Mamm. Biol. 69: 302–310.

Bizzarri, L., M. Lacrimini and B. Ragni. 2010. Live capture and handling of the European wildcat in central Italy. Hystrix Ital. J. Mamm. 21: 73–82.

Cheyne, S.M., D.J. Stark, S.H. Limin and D.W. Macdonald. 2013. First estimates of population ecology and threats to Sunda clouded leopards *Neofelis diardi* in a peat-swamp forest, Indonesia. Endanger Species Res 22: 1–9.

Corbett, L.K. 1979. Feeding ecology and social organization of wildcats (*Felis silvestris*) and domestic cats (*Felis catus*) in Scotland. PhD Thesis. University of Aberdeen, Aberdeen, UK.

Daniels, M.J., M.A. Beaumont, P.J. Johnson, D. Balharry, D.W. Macdonald and E. Barratt. 2001. Ecology and genetics of wild-living cats in the north-east of Scotland and the implications for the conservation of the wildcat. J. Appl. Ecol. 38: 146–161.

Di Bitetti, M.S., A. Paviolo and C.D. De Angelo. 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. J. Zool. 270: 153–163.

Germain, E., S. Benhamou and M.L. Poulle. 2008. Spatio-temporal sharing between the European wildcat, the domestic cat and their hybrids. J. Zool. 276: 195–203.

Harmsen, B.J., R.J. Foster, S.C. Silver, L.E.T. Ostro and C.P. Doncaster. 2010. Jaguar and puma activity patterns in relation to their main prey. Mamm. Biol. 76: 320–324.

Herfindal, I., J.D. Linnell, J. Odden, E.B. Nilsen and R. Andersen. 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). J. Zool. 265: 63–71.

Horne, J.S., E.O. Garton, S.M. Krone and J.S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecol. 88: 2354–2363.

Jerosch, S., M. Gotz, N. Klar and R. Mechthild. 2010. Characteristics of diurnal resting sites of the endangered European wildcat (*Felis silvestris silvestris*): implications for its conservation. J. Nat. Conserv. 18: 45–54.

Kery, M., B. Gardner, T. Stoeckle, D. Weber and J.A. Royle. 2011. Use of spatial capture-recapture modelling and DNA data to estimate densities of elusive animals. Conserv. Biol. 25: 356–364.

Klar, N., F. Néstor, S. Kramer-Schadt, M. Herrmann, M. Trinzen, I. Buttner and C. Niemitz. 2008. Habitat selection models for European wildcat conservation. Biol. Conserv. 141: 308–319.

Klar, N., M. Herrmann and S. Kramer-Schadt. 2009. Effects and mitigation of road impacts on individual movement behaviour of wildcats. J. Wildl. Mgmt. 73: 631–638.

Kranstauber, B., R. Kays, S.D. LaPoint, M. Wikelski and K. Kamran Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. J. Anim. Ecol. 81: 738–746.

Lecis, R., M. Pierpaoli, Z. Birò, L. Szemethy, B. Ragni, F. Vercillo and E. Randi. 2006. Bayesian analyses of admixture in wild and domestic cats (*Felis silvestris*) using linked microsatellite loci. Mol. Ecol. 15: 119–131.

Litvaitis, J., J. Sherburne and J. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. J. Wildl. Mgmt. 50: 110–117.

LOAS™. 2004. Ecological Software Solutions LLC. Version 3.0.1.

Lozano, J. and A.F. Malo. 2012. Conservation of the European wildcat (*Felis silvestris*) in Mediterranean environments: a reassessment of current threats. In: (G.S. Williams, ed.) Mediterranean Ecosystem: dynamics, management and conservation. Nova Science Publishers, Hauppauge, NY. pp. 1–31.

Lozano, J., E. Virgos, S. Cabezas-Diaz and J.C. Mangas. 2007. Increase of large game species in mediterranean areas: is the European wildcat (*Felis silvestris*) facing a new threat? Biol. Conserv. 138: 321–329.

Lucherini, M., J.I. Reppucci, R.S. Walker, M.L. Villalba, A. Wursten, G. Gallardo, A. Iriarte, R. Villalobos and P. Perovic. 2009. Activity pattern segregation of carnivores in the high Andes. J. Mammal. 90: 1404–1409.

Mattucci, F., R. Oliveira, L. Bizzarri, F. Vercillo, S. Anile, B. Ragni, L. Lapini, A. Sforzi, P.C. Alves, L.A. Lyons and E. Randi. 2013. Genetic structure of wildcat (*Felis silvestris*) populations in Italy. Ecol. Evol. 3: 2443–2458.

Monterroso, P., J.C. Brito, P. Ferreras and P.C. Alves. 2009. Spatial ecology of the European wildcat in a Mediterranean ecosystem: dealing with small radio-tracking datasets in species conservation. J. Zool. 279: 27–35.

Nowell, K. and P. Jackson. 1996. Status survey and conservation action plan wild cats. IUCN Publication Services Unit, Cambridge. pp. 383.

Oliveira, R., R. Godinho, E. Randi, N. Ferrand and P.C. Alves. 2008a. Hybridization versus conservation: are domestic cats threatening the genetic integrity of wildcats (*Felis silvestris silvestris*) in Iberian peninsula? Philos. Trans. R. Soc. Biol. Sci. 363: 2953–2961.

Oliveira, R., R. Godinho, E. Randi, N. Ferrand and P.C. Alves. 2008b. Molecular analysis of hybridisation between wild and domestic cats (*Felis silvestris*) in Portugal: implications for conservation. Conserv. Genet. 9: 1–11.

Pesenti, E. and F. Zimmermann. 2013. Density estimations of the Eurasian lynx (*Lynx lynx*) in the Swiss alps. J. Mammal. 94: 73–81.

Pierpaoli, M., Z.S. Birò, M. Herrmann, K. Hupe, M. Fernandes, B. Ragni, L. Szemethy and E. Randi. 2003. Genetic distinction of wildcat (*Felis silvestris*) populations in Europe, and hybridization with domestic cats in Hungary. Mol. Ecol. 12: 2585–2598.

Piñeiro, A., I. Barja, G. Silván and J. Illera. 2012. Effects of tourist pressure and reproduction on physiological stress response in wildcats: management implications for species conservation. Wildl. Res. 39: 532–539.

Ragni, B. 1981. Gatto selvatico. *Felis silvestris* Schreber, 1777. In: (C. Pavan, ed.) Distribuzione e biologia di 22 specie di Mammiferi in Italia. CNR, Roma (in Italian). pp. 185.

Ragni, B. 2006. Il gatto selvatico. In: (M. Frassinet and F. Petretti, eds.) Salvati dall'Arca, Airplane, Bologna (in Italian). pp. 663.

Ragni, B. and M. Possenti. 1996. Variability of coat-colour and markings system in *Felis silvestris*. Ital. J. Zool. 63: 285–292.

Ragni, B., L. Bizzarri and A. Sforzi. 2007. Methods and problems for the reintroduction of the European wildcat: the case of the Maremma Regional Park. In: (Parco Nazionale della Majella, ed.) From the EU LIFE-projects to guidelines for the reintroduction of threatened species. Campo di Giove (in Italian). pp. 202.

Randi, E., M. Pierpaoli, M. Beaumont, B. Ragni and A. Sforzi. 2001. Genetic identification of wild and domestic cats (*Felis silvestris*) and their hybrids using bayesian clustering methods. Mol. Biol. Evol. 18: 1679–1693.

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org. Accessed April 16, 2014.

Sarmento, P., J. Cruz, P. Tarroso and C. Fonseca. 2006. Space and habitat selection by female European wildcats (*Felis silvestris silvestris*). Wildl. Biol. Pract. 2: 79–89.

Say, L., S. Devillard, F. Leger, D. Pontier and S. Ruette. 2012. Distribution and spatial genetic structure of European wildcat in France. Anim. Conserv. 5: 18–27.

Scott, R., N. Easterbee and D. Jefferies. 1992. A radio-tracking study of wildcats in Western Scotland. In: (Council of Europe, ed.) Proceedings of the Seminar on the biology and conservation of the wildcat (*Felis silvestris*). Nancy, France September 23–25, 1992.

Sforzi, A., L. Bizzarri, B. Ragni and D. Paoloni. 2010. Reconstruction of an European wildcat viable population in the Maremma Regional Park: a twenty years of experience. In: (E. Randi, B. Ragni, L. Bizzarri, N. Agostini and G. Tedaldi, eds.) Proceedings of the Felid Biology and Conservation in Italy Conference. Santa Sofia (FC) November 7–8, 2008. Ente Parco Nazionale Foreste Casentinesi (in Italian).

Soto, C.A. and F. Palomares. 2013. Surprising low abundance of European wildcats in a Mediterranean protected area of southwestern Spain. Mammalia 78: 57–65.

Stahl, P., M. Artois and M.F.A. Aubert. 1998. Organisation spatiale et déplacements des chats forestiers adultes (*Felis silvestris*, Schreber, 177) en Lorraine. Rev. Ecol (Terre Vie) 43: 113–132.

Teets, D.A. 2003. Predicting sunrise and sunset times. Coll. Math. J. 34: 317–321.

Velli, E., M.A. Bologna, S. Castelli, B. Ragni and E. Randi. 2015. Non-invasive monitoring of the European wildcat (*Felis silvestris silvestris* Schreber, 1777): comparative analysis of three different monitoring techniques and evaluation of their integration. Eur. J. Wildl. Res. 61: 657–668.

Wittmer, H.U. 2001. Home range size, movements, and habitat utilization of three male European wildcats (*Felis silvestris* Schreber, 1777) in Saarland and Rheinland-Pfalz (Germany). Mammal. Biol. 66: 365–370.

Yamaguchi, N., A. Kitchener, C. Driscoll and B. Nussberger. 2015. *Felis silvestris. The IUCN Red List of Threatened Species 2015*: e.T60354712A50652361.en. Available at: http://dx.doi.org/10.2305/IUCN.UK.20152.RLTS.T60354712A50652361.en Accessed November 28, 2015.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A Saveliev and G.M. Smith. 2009. Mixed effects models and extensions in Ecology with R. Springer, New York. pp. 574.

Zuur, A.F., E.N. Ieno and C.S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1: 3–14.

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