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THE EUROPEAN WILDCAT *FELIS SILVESTRIS* – A BRIEF REVIEW OF STATUS AND RESEARCH IN GERMANY

The European wildcat is a Palaearctic species with an initially wide distribution from the Iberian Peninsula to the Caucasus and Scotland (Piechocki 1990; Hemmer 1993; Heptner/Sludskij 1980). After the eradication of carnivores was enforced (e.g. von Hoberg 1687), especially in the 18th and 19th century, it was nearly extirpated at the beginning of the 20th century. Therefore, its distribution is discontinuous (Mitchell-Jones 1999; Aulagnier et al. 2009). It is generally assumed that relict populations have survived in the northeast and east of France, the south of Belgium, Luxembourg, the west and southwest of Germany and areas of the Harz Mountains, and in Eastern Europe, mainly in the Carpathian Mountains (Hemmer 1993, 1100). Within Germany wildcats survived in the Eifel, Hunsrück, Harz Mountains (de Leuw 1976) and probably Thuringia, the Taunus, Black Forest, Palatinate Forest and some areas in Hesse (Petzsch 1968; Röben 1974). Due to near extirpation, the wildcat is protected in Germany since 1934 in the Reichsjagdgesetz (Görner 2012). This – and a reduced hunting activities during and after World War II – was probably the main reason for the survival of the species in Germany (Röben 1974). Since 1992 it is also strongly protected in Europe under the European Habitat Directive where it is listed in appendices II and IV. These measures led to increasing population size and dispersal in recent years (i.e. Görner 2012; Krug et al. 2012; Sodeikat/Köglsperger 2012; Streif et al. 2012), but also a greater effort was made in detecting the species than before. Most dispersal occurred by natural population growth, but there was also a reintroduction programme in Bavaria where 580 wildcats were released from 1984 to 2008 (Worel 2009; Heinrich 1992). The current distribution range in Germany is quite substantial and increased over the decades (**fig. 1**). The national report in relation to the Habitat Directive (BFN 2013) gives a minimum of 914 and maximum of 934 individuals in Germany.
The domestic cat is considered to be the result of the domestication of the African wildcat (*Felis silvestris lybica*) about 9000 years ago in the villages of the Fertile Crescent in the Near East (Driscoll et al. 2007; 2009). Hard evidence from the early period of domestication (9500-4000 years ago) is lacking. It is only from approx. 4000 years ago that domestic cats are represented in ancient Egyptian art. However, there is evidence from an early agricultural village in China from about 5560-5280 years BP (Hu et al. 2013). A cat buried next to a human grave on Cyprus dating about 9500 years ago is considered to be the first evidence that humans kept cats as pets (Vigne et al. 2004). It is assumed that African wildcats followed humans because of the rich source of mice attached to their cereal storages. As an important pest control the cat obtained a special status in Egypt; by about 2900 years ago, it was the symbol of a god (Driscoll et al. 2009). Later the domestic cat was widely distributed by the Romans who also treasured it for keeping mice at bay about 2000 years ago (Clutton-Brock 1987; Daniels et al. 1998; Driscoll et al. 2009). The Romans also introduced them (probably in small numbers) to Central Europe but even more so during the Carolingian period about 1100 years ago (Knapp et al. 2002). Hamilton (1869), however, assumed that Egyptian cats were already introduced into Europe about 300-400 years BC. Cats were treasured because of their pest control qualities but in medieval times the tide turned and the image was ambivalent; in high medieval times the cat was seen as a symbol of the devil (see Plos 2015 for more information).

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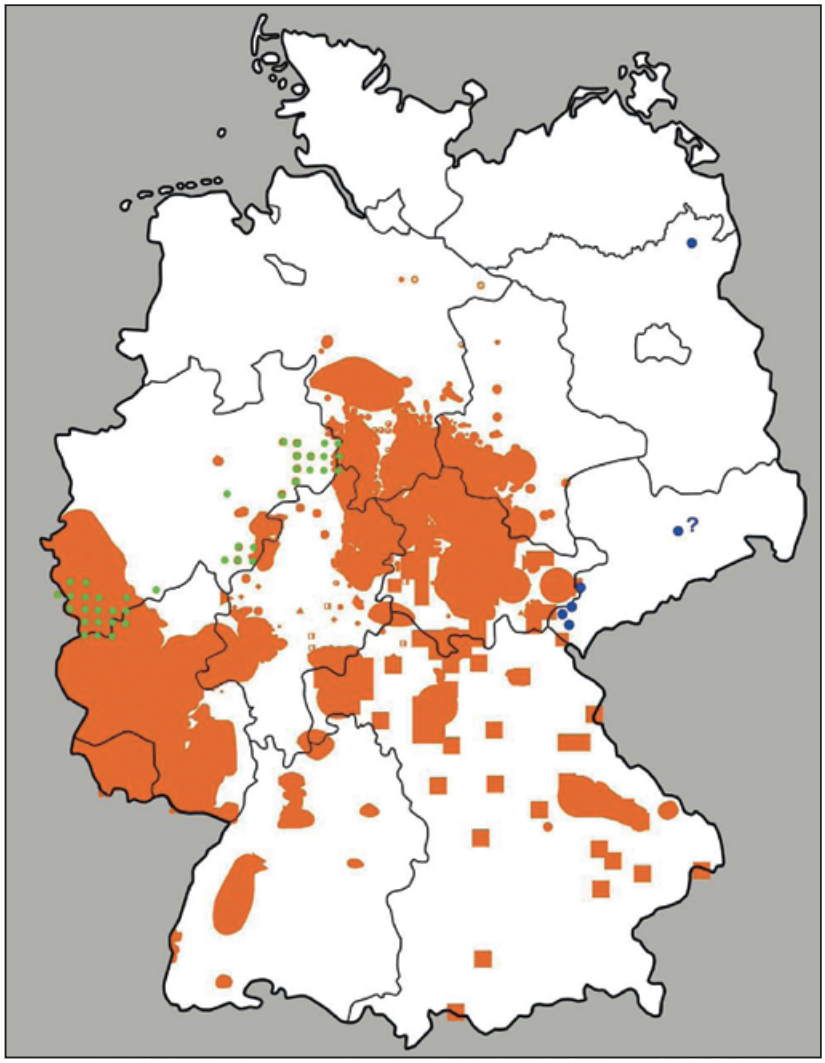

Fig. 1 Map indicating the distribution of wildcats in Germany derived from 28 maps published between 1957 and 2009 scaled to the same size (adapted after Stefen/Görner 2009; Stefen 2012). Included are maps from: Haltenorth 1957; Röben 1974; Jost 1978; Vogt 1985; Pflüger 1987; Piechocki 1987; 1989; 1990; Büttner/Worel 1990; Herrmann 1991; Piechocki/Möller 1991; Hossfeld et al. 1993; Raimer 1994; Stubbe/Stubbe 1994; Kock/Altmann 1999; Görner 2000; Raimer 2001; Knapp et al. 2002; Mölich/Klaus 2003; BUND 2004; Denk/Jung 2004; Frobel/Thein 2006; NABU 2007; Munlv NRW 2007; Pott-Dörfer/Dörfer 2007; Simon/Raimer 2007; Götz/Roth 2007; Stefen et al. 2009, and information according to Hucht-Ciorga (2011; in green), Stefen (2011; in blue) and new material in the Senckenberg Naturhistorische Sammlungen Dresden (2015; in black).

HISTORY, SYSTEMATICS AND TAXONOMY OF WILDCATS

The family Felidae probably originates from a predecessor that lived about 10-15 million years ago (Johnsen/O'Brien 1997). The first felid-like carnivores are known from the Oligocene about 35 million years ago, the genera of today arose during the Miocene. The most recent lineages within the family, the domestic cat lineage and the leopard lineages only separated about 6.2 to 6 million years ago (Johnson/O'Brien 1997; Johnson et al. 2006). Based on mtDNA the domestic cat lineages including *F. catus, F. silvestris, F. lybica, F. bieti* (these species are also sometimes summarized as subspecies of *F. silvestris* [Driscoll et al. 2009]), *F. margarita* and the older but associated *F. nigripes* and *F. chaus* started to separate 6.2 (Johnson et al. 2006) or 6 million years ago (Johnson/O'Brien 1997).

According to pelage colouring, size and robustness, three groups of wildcats are distinguished: the *silvestris*-group (European wildcats), the *lybica*-group (African wildcats) and the *ornata*-group (Indian wildcats; Haltenorth 1953; Weigel 1972; Kitchener 1991). The differentiation of wildcats probably occurred during the Pleistocene (Hemmer 1984), *lybica* and *silvestris* separated approximately 20 000 years ago during the cool periods of the Late Pleistocene (Hemmer 1984; 1993; Randi/Ragni 1991). The distribution of Late Pleistocene and Early Holocene finds of wildcats in Europe have been summarized by Sommer/Benecke (2006).

characteristic	wildcats	domestic cats
cranial volume	32.5-50 cm³ if between 32 and 35 cm³, the cranial index has to be calculated and used	2-35 cm³
cranial index (total skull length: cranial volume)	< 2.75	> 2.75
intestine length (measured from end of stomach lying flat or hanging)	120-170 cm, males 110-150 cm, females	165-254 cm, males 155-220 cm, females
intestine index (intestine length: head-body length)	2.04-3.17	3.20-4.84
skull: glabella, nasal bones	no depression at the suture between nasal bones and frontal	a slight depression at the suture between nasal bones and frontal, and nasals extending further into frontal
mandible: angular process (but variable and changing during ontogeny!)	angular process usually extending further caudally; mandible stands if placed on coronoid, condyle and angular processes	angular process usually not extending as far caudally as coronoid and condyle; mandible paced on coronoid, condyle and angular processes is instable and falls
neck pelage pattern	3-5 clearly separated stripes	stripes usually not as cleary separated
basic underlying fur colour	brownish, ochreous	greyish, greater variability in shades of grey
basic pelage pattern	indistinct, vague stripes	tabby, stripes more distinct and usually stronger in colour

Tab. 1 Distinctive characteristics to distinguish between wildcats and domestic cats (in wildcat colouring) in accordance to Schauenberg (1969; 1977), Piechocki (1990), Piechocki/Möller (1983).

DIFFERENTIATION FROM DOMESTIC CATS – MORPHOLOGY AND MOLECULAR DATA

In the following paragraphs the European wildcat is solely referred to as wildcat. One of the long debated issues that is of importance in species conservation is the differentiation of the cat forms and particularly the separation of domestic cat and wildcat. Both species are close enough that they can hybridize. There are many papers dealing with the characteristics of wildcats and their differentiation from domestic cats, mainly based on morphology or molecular data (i. e. Schauenberg 1969; 1971; 1977; Piechocki 1990; Daniels et al. 1998; Beaumont et al. 2001; Reig et al. 2001; Kitchener et al. 2005; Müller 2005; Devillard et al. 2014). Several studies deal with the skull morphology of wildcats (e. g. Sládek et al. 1971; 1972; Kratochvíl/Kratochvíl 1970; Kratochvíl 1973; French et al. 1988; Yamaguchi et al. 2004; Krüger et al. 2009), some also describe the craniometric variability between and within different populations (Krüger et al. 2009; Stefen/Heidecke 2011; Stefen 2012a). Other studies deal with the outer phenotype, the pelage pattern and colouring (Eckstein 1919; Vogt 1985; Müller 2011a; 2011b; Ragni/Possenti 1996; Reher/Stefen submitted). Wildcats and domestic cats can be distinguished morphologically on the basis of a few characteristics (**tab. 1; figs 2-5**) but hybrids cannot really be detected.

In outer morphology the most striking and distinctive characteristic of the wildcat is the blunt, relatively thick tail (due to long and dense hairs) with marked, separated dark (black) bands and a black tip. Also on the back of the head and neck there are well distinguished stripes (often not as well developed in domestic cats), continuing on the forehead, two separated stripes above the shoulder, and a black dorsal stripe end-

Fig. 2 Old illustration of a wildcat by Blasius 1857 indicating some characteristic features: blunt, thick tail with distinctive black bands and black tip, black eel back, two stripes above the shoulders, distinct stripes on head and neck. Only the stripes at the back are too distinct for a typical German wildcat. – (After Blasius 1857).

ing at the base of the tail. The overall base colour is brownish or ochreous and the hairs, particularly the guard hairs, are very long and fine (often described as silky). But there is a substantial overlap in hair length to domestic cats. The overall pelage pattern of wildcats are faint stripes, and usually there is a white spot on the throat. Anatomically the most distinctive characters between wildcats and domestic cats are cranial volume, cranial index, intestine length and intestine index (see **tab. 1**). There are other differences listed, which are, however, not as distinctive as those given characteristics. Krüger et al. (2009) consider the length of the lower canines, width between the frontal-parietal suture at the smallest position of the orbita, length of lower p4, length between lower p2 and m1, coronoid height, rostrum width at canines as distinctive.
In recent decades molecular analyses are used to differentiate between domestic and wildcats; a regularly used technique is genotyping using several genetic markers (usually more than ten microsatellite loci – loci in the nuclear genome) (i. e. Daniels et al. 2001; Lecis et al. 2006; Oliveira et al. 2007; Hertwig et al. 2009; Eckert et al. 2010; Driscoll et al. 2011; Hartmann et al. 2013; Steyer et al. 2013). This method needs a large sample size and a good database of well defined species as reference sample as it works with probabilities of group membership and has been criticised (Gehle 2012; Gehle/Herzog 2012). Nussberger et al. (2013, 2014) developed another method using single nucleotide polymorphism (SNP) markers to differentiate both cat forms and to detect introgression, thus hybridization, and is now widely accepted.

REPRODUCTION, DEVELOPMENT OF JUVENILES, AGE AND DEATH RATES

The wildcat is a (mainly) monoestric species with the main runt in winter, November to early March with the main period in February and March (see Stefen/Görner 2009). After a gestation period of 66 days on average about 2-4 young are born (Hemmer 1993). Some juveniles have also been recorded in other seasons so it is assumed that a second or even third period of runt is possible (Piechocki/Möller 1983). Weaning usually occurs by the end of the fourth month »when survival rate of cubs was 20 %« (Götz et al. 2009). The main mortality cause is predation by mustelids (Götz/Roth 2007). Probably free ranging dogs might also be listed here. The role of the increasing number of raccoons (*Procyon lotor*), known to take eggs, nestlings

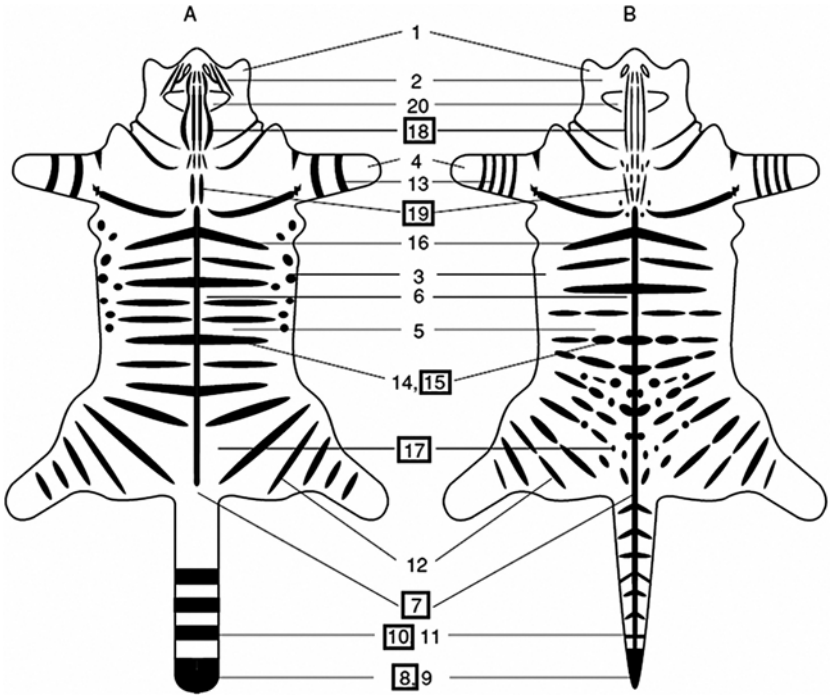

Fig. 3 Comparison of pelage characteristics illustrated for Scottish wildcats (**A**) and putative domestic cats (**B**): **1** white on chin. – **2** stripes on cheek. – **3** dark spots on ventral side. – **4** white on paw. – **5** white on flank. – **6** white on back. – ***7*** extent of dorsal line. – ***8*** shape of tail tip. – **9** colour of tail tip. – ***10*** distinctness of tail bands. – **11** alignment of tail bands. – **12** stripes on hind leg. – **13** bands encircling foreleg. – **14** tabby coat patterns. – ***15*** broken stripes on flanks & hindquarters. – **16** stripes on body. – ***17*** spots on flanks & hindquarters. – ***18*** stripes on nape. – ***19*** stripes on shoulder. – **20** colour of the back of the ears. – Properties best suited for discrimination of **A** and **B** are in italics and in black boxes. – (After Kitchener et al. 2005).

and disturb breeding birds, on wildcats raising pups is unknown. Reaching adulthood, the wildcat does not have real enemies, though it might be killed by lynx (Raimer 2006), considered its foremost enemy for a long time (Haltenorth 1957), or potentially by large birds of prey (Schauenberg 1970).

The life expectancy has been stated to reach 16 years (Piechocki/Möller 1983), but Piechocki/Stiefel (1988) assumed that a life expectancy of 12-15 years in nature is too high. Büttner (1994) noted that the life expectancy has to be corrected to 6 years only. Recently, however, a 12-year-old female was detected in Thuringia (Krüger et al. 2015).

Fig. 4 Wildcat in the Senckenberg Naturhistorische Sammlungen Dresden (no data and no collection number) displaying some typical pelage characteristics and the thick banded tail. – (Photo C. Stefen).

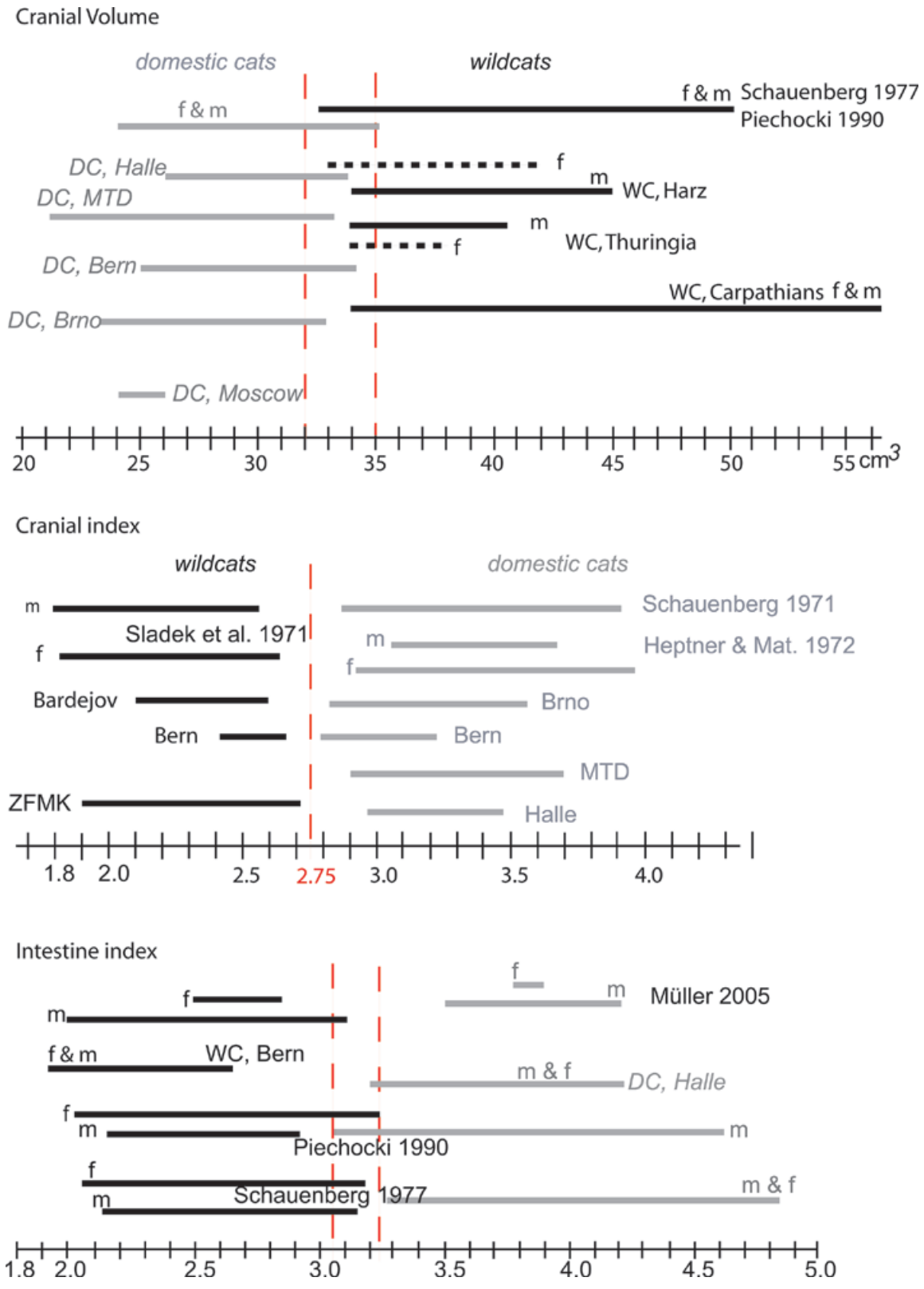

Fig. 5 Data of cranial volume, cranial index and intestine index for wildcats (WC) and domestic cats (DC) according from literature (REFS) or from own measurements in different collections: Bardejov – Museum Bardejov, Slovakia, SMB; Bern – Naturhistorisches Museum der Burgergemeinde Bern, Switzerland, NMBE; Brno – Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic; Halle – Zoological Institute of the Universtity Halle-Wittenberg, now part of the central repository of natural history collections, Germany; MTD – Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Germany; and ZFMK – Zoologisches Forschungsmuseum Alexander König, Bonn, Germany; f – females; m – males.

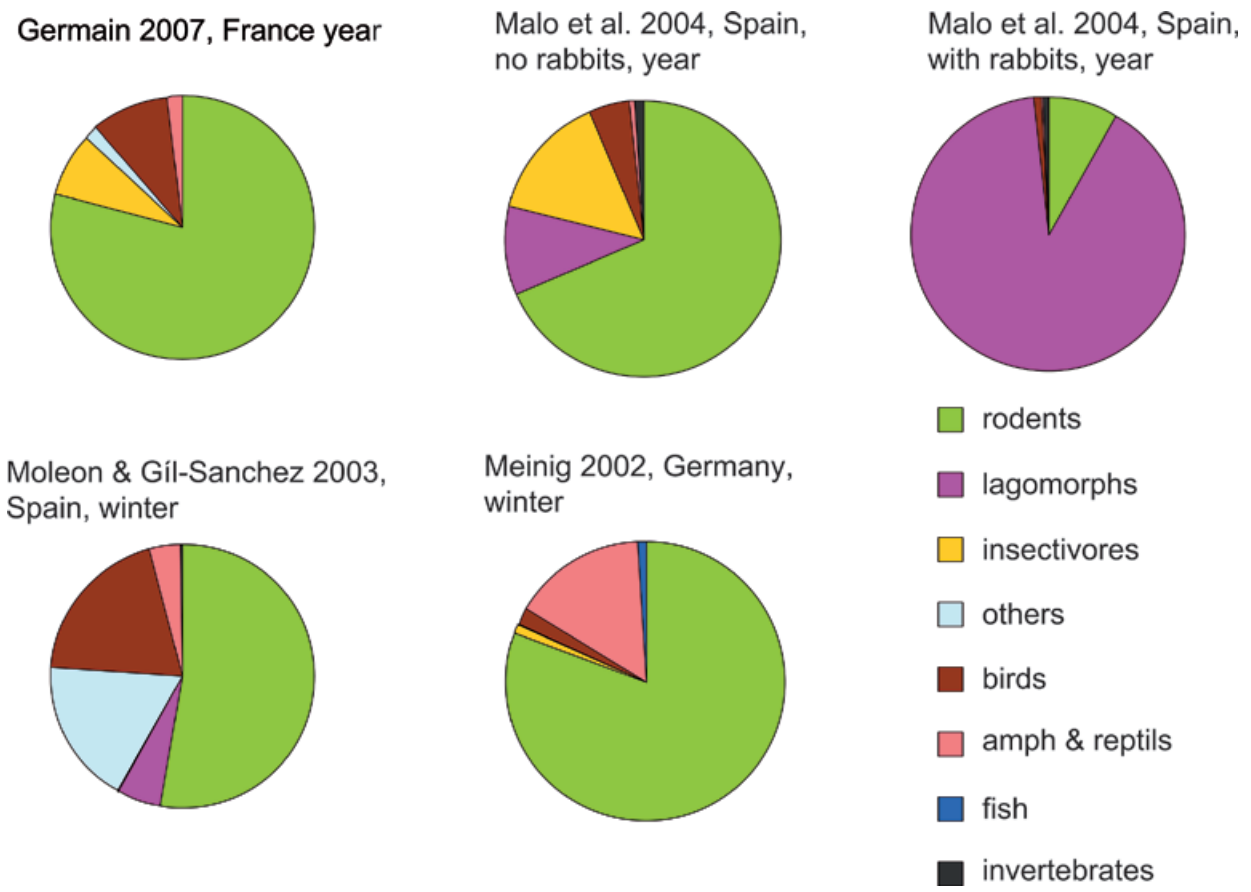

Fig. 6 Proportions of food sources consumed by wildcats from some studies (REFS) indicating the variability in intake of taxonomic groups. Given is the study, the country and season of the study. Malo et al. (2004) compared two regions, one with rabbits and one without. Amph – amphibia.

DIET

Cats eat mice and this is true for wildcats as well. But of course, the diet of both cat forms is much more diverse (fig. 6) as it has been shown in different studies. The main prey animals of wildcats in Central Europe are common voles (*Microtus arvalis*) but also other small mammals, like shrews, Muridae, Arvicolidae, Cricetidae, Lagomorpha, birds, amphibians and reptiles, fish, invertebrates, many insects and arthropods, plant matter, and even artiodactyls as carrion (i. e. summarized by Haltenorth 1957; Sládek 1973a; Stefen 2012b). The wildcat's diet depends on regional occurrence but »depends more on the factor of availability than that of abundance of prey« (Sládek 1973b, 143). The diet changes over the year (i. e. Sládek 1973b), and can vary between regions. In Spain, rabbits or hares are preferred (Malo et al. 2004; Moleón / Gil-Sánchez 2003). Therefore, wildcats have been termed facultative specialists but might even behave as a generalist species (Malo et al. 2004). Hansen (2014) documented a wildcat killing a hare in Germany and for example Heidemann (1973), Splitter (1978) or von Borkenhagen (1979) documented lagomorphs as food of domestic cats. According to historic literature the common hamster was also part of the wildcat's diet and a change in prey species with the decreased availability of some prey species for the wildcat has been hypothesized (Stefen 2012b). In general it can be assumed that the overall abundance of small mammals in fields decreased over the last century due to the use of rodenticides.

Tab. 2 Habitat requisites needed or used by wildcats mentioned in the analysed literature (from 100 publications with reference to the habitat, Stefen/Görner 2009).

	requisite mentioned	number of mentions
1	rocks, cracks	31
2	hollows in trees	28
3	dens of badger or fox	23
4	coppice, undergrowth	20
5	roots of fallen trees	13
6	depression in the ground	9
7	empty sheds, hunting stands	8
8	empty nests of birds of prey	3
9	tree studs	4
10	strong vertical branches, crotches	1
	old bunkers in the Eifel (Western Germany)	5
11	heaps of brushwood, or cut wood	11
12	low branches	5
13	hay racks	2
14	young plantations	1

ECOLOGY AND HABITAT

To briefly summarize the ecology and habitat preferences of wildcats is difficult and for more details see Stefen/Görner (2009). Overall, the wildcat can be considered a species with few important basic requirements, primarely cover, food and dry spots without drafts for raising their young. In addition, modern wildcats have been shown to use different kinds of habitats utilising varied requirements (tab. 2).

The older descriptions of preferred habitats like continuous old growth woodlands in mainly the rugged or rocky areas of low mountain ranges probably result from the fact that such areas were not easily accessible to humans and thus were ideal refuge areas for wildcats. Woodlands and forests are dynamic structures in time due to natural processes and human activity. In the middle of the 18th century, Central European forests were strongly overused by humans: traditional use as wood pasture, the collection of forest litter and firewood but also the need of wood for rafting of timber, metallurgical processes, heating, building etc. increased the demand of wood. Hunting and the collection of wild berries also occurred in woods and forests. The natural rejuvenation of beech and silver fir was impossible. At the end of the 18th century, at least in Thuringia/D did not have continuous closed woodlands any more (Witticke 2015). The wildcat had to adapt to this modified habitat. The main prey species changed to *Microtus arvalis*, which lives in open grasslands and agricultural areas, but not in woods or forests. The wildcats increased use of open areas is shown by telemetric studies (i. e. Jerosch/Götz 2011) and the most typical habitat today is a mosaic landscape (Lozano et al. 2003) of wood and open grasslands, the edges or contact zones between the habitats are apparently important as well as water courses and the accompanying vegetation (Heinrich 1992).

As the observed use of anthropogenic structures indicates, wildcats can tolerate human activities (Vogt 1985) and their records increase close to and in villages, particularly in very cold winters (Piechocki 1990). This trend is also observed in Russia (Heptner/Sludkii 1980), Scotland (Scott et al. 1993) and France (Artois 1985).

HOME RANGES

As a rule, the home ranges of wildcats range from 1000 to 2000 ha (summarised in Stefen/Görner 2009). The home ranges of males are usually larger than those of females and overlap those of several females (i. e. Hötzel et al. 2007; Krug et al. 2012). The size of the home ranges varies with the season, and with females decreases when young are being reared. The ranges of two individuals of the same sex usually do not overlap (Hupe et al. 2004), but there are exceptions for females (Götz/Roth 2007; Hötzel et al. 2007) as well as for males (Wittmer 2001, 366; Mölich/Klaus 2003, 127; Götz/Roth 2007).

ENDANGERMENT AND PROTECTION

Most authors agree that the destruction or fragmentation of the wildcat habitat and the hybridization with domestic cats are the two main factors endangering wildcats (i. e. Stahl/Artois 1991; Hubbard et al. 1992; Daniels/Corbett 2003; Lozano et al. 2007). Fragmentation of habitats is often used very figuratively in conservation. It is assumed that wildcats cannot cross structures that are considered as barriers by humans. These are mainly roads or railway lines, which can only be crossed in dangerous circumstances, thus most cats are killed by traffic (Klaus et al. 2012). The wildlife protection fences at these structures reduce traffic casualties but turn them into insurmountable barriers. Therefore, green bridges, over-/underpasses or valley bridges are important for wildcats.

FUTURE PERSPECTIVE

In recent years wildcats have been detected in more and more regions, particularly with the use of lure sticks to collect hairs and the subsequent genetic analysis (Hupe/Simon 2007; Steyer et al. 2013). The increasing population and dispersal is also indicated by the increasing number of wildcats casualties in traffic.
The (increasing?) hybridization with domestic cats (which is debated as indicated above) has to be reduced if the protection of the »genetic« status of the wildcat is to be given priority. The older practice of killing domestic cats outside of human settlements is hardly implemented anymore. Assuming that not all domestic cats are sterilized, it might be hypothesized that the hybridization potential could increase. On the other hand, wildcat populations also increase, which might make it easier to find adequate partners and the hybridization potential remains the same or even decreases. But increasing numbers of free ranging or feral domestic cats might have another negative impact on wildcats: As their prey preferences are very similar (i. e. Biró et al. 2005; Germain et al. 2009; Stefen 2012b), more domestic cats may limit the food resources of wildcats, particularly in periods with extreme weather reducing small mammal abundance. In this context the still common practice of using rodenticides in years with an estimated vole (*Microtus arvalis*) gradation (year of mass repodution) has to be questioned.
Another possible new endangerment of wildcats might be climate change. Within the wildcats the European wildcat has adapted to cooler climates and thus might be more susceptible to an increasingly warmer climate in Central Europe, but up to now no change in size could be attributed to climate change (Stefen 2015). However, climate change might also induce a change in the distribution of parasites and pathogens, or have impact on a species physiology and immunology.

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SUMMARY / ZUSAMMENFASSUNG

The European Wildcat *Felis silvestris* – A Brief Review of Status and Research in Germany

The European wildcat is a Palaearctic species which probably evolved in the cooler periods of the Late Pleistocene. It is morphologically very similar and phylogenetically close to but not the direct ancestor of the domestic cat. Like other carnivores it has been strongly hunted prosecuted particularly in the 17th to 19th century and nearly extirpated in the early 20th century. In Germany it was first protected in 1934 and has been under special protection under the European Habitats Directive ever since then. This interesting history is reflected in a substantial amount of literature in zoology, hunting and ecology. This article presents a brief review on the most important aspects of their morphology, differentiation from domestic cats, ecology including diet, reproduction and habitat, as well as endangerment, population status and protection.

Die Europäische Wildkatze *Felis silvestris* – ein kurzer Rückblick auf Stand und Forschung in Deutschland

Die Europäische Wildkatze ist eine paläarktische Art, die sich wahrscheinlich in den kühleren Perioden des Spätpleistozäns entwickelt hat. Sie ist morphologisch sehr ähnlich und phylogenetisch nahe, aber nicht der direkte Vorfahre der Europäischen Wildkatze. Wie andere Fleischfresser wurde sie im 17.-19. Jahrhundert stark gejagt und im frühen 20. Jahrhundert fast ausgerottet. In Deutschland wurde sie erstmals 1934 geschützt und steht unter dem besonderen Schutz der Europäischen Habitatrichtlinie. Diese interessante Geschichte spiegelt sich in einer beträchtlichen Menge an Literatur in Zoologie, Jagd und Ökologie wider. Dieser Artikel gibt einen kurzen Überblick über die wichtigsten Aspekte ihrer Morphologie, Unterscheidung von Hauskatzen, Ökologie einschließlich Ernährung, Fortpflanzung und Lebensraum sowie Gefährdung, Populationsstatus und Schutz.