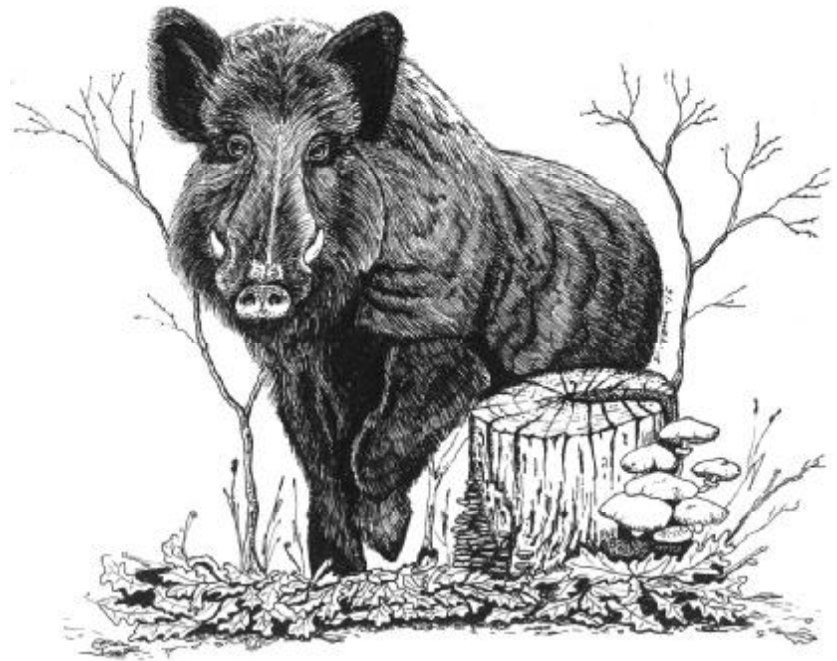


Eurasian Wild Boar *Sus scrofa* (Linnaeus, 1758)

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Names

Genus: *Sus* Linnaeus, 1758

New proposed species: *Sus scrofa* Linnaeus, 1758; *Sus nigripes* Blanford, 1875; *Sus ussuricus* Heude, 1888; *Sus moupinensis* Milne-Edwards, 1871; *Sus chiodontus* Heude, 1888; *Sus leucomystax* Temminck, 1842; *Sus riukiuanus* Kuroda, 1924; *Sus taevanus* Swinhoe, 1863; *Sus davidi* Groves, 1981; *Sus cristatus* Wagner, 1839; *Sus vittatus* Boie, 1828 (Groves & Grubb 2011; see also Chapter 1 in this book).

Subspecies within *Sus scrofa*: *S. s. algirus* Loche, 1867; *S. s. attila* Thomas, 1912; *S. s. baeticus* Thomas, 1912; *S. s. lybicus* Gray, 1868; *S. s. meridionalis* Forsyth Major, 1882

Names in other languages: **Albanian:** Derri i eger; **Arabic:** الخنزير; **Bulgarian:** Diva svinja; **Chinese:** 公猪; **Croatian:** Divlja svinja; **Czech:** Prase divoké; **Danish:** Vildsvin; **Dutch:** Wild zwijn; **Estonian:** Metssiga; **Finnish:** Villisika; **French:** Sanglier, Sanglier d'Eurasie; **German:** Wildschwein, Schwarzwild; **Hindi:** सूअर; **Hungarian:** Vaddisznó; **Italian:** Cinghiale; **Japanese:** イノシシ; **Lithuanian:** Sernas; **Norwegian:** Villsvin; **Polish:** Dzik; **Portuguese:** Javali; **Romansh:** Portg selvadi; **Russian:** кабан; **Slovak:** Diviak lesný; **Spanish:** Jabalí; **Swedish:** Vildsvin; **Turkish:** Yaban Domuzu

Other names: Eurasian wild pig, wild pig, wild hog

We point out that most of the information presented in this chapter pertains to *Sus scrofa sensu stricto* and the data related to some of the new proposed species regard only a few studies. This is due to the limited information available for some of the new proposed Asian wild boar species.

Taxonomy

Given its huge range many regional forms, species and subspecies have been described for wild boar. In the two major works of Groves (2007) and Groves and Grubb (1993), 16 distinct populations or subspecies of *Sus scrofa* have been recognized on the basis of craniometric characteristics. More recently, Groves and Grubb (2011) elevated the majority of them to 11 species (see also Chapter 1 in this book for more details) as follows: *S. scrofa*, *S. nigripes*, *S. ussuricus*, *S. moupinensis*, *S. chirodontus*, *S. leucomystax*, *S. riukiuanus*, *S. taevanus*, *S. davidi*, *S. cristatus*, and *S. vittatus*. We follow this classification in this chapter, acknowledging that they deserve the status of species. We recognize, however, that this new classification needs to be tested using comprehensive sampling along with genetic, genomic, comparative chromosome painting, the latest morphometrics approaches and reproductive analyses to better understand the complexity of wild boar taxonomy and level of hybridization through its large range. This validation is important because the new classification could have an impact on defining priorities for conservation of wild boar species.

Genetic studies have shed some light on the diversity of wild boar. The mitochondrial DNA control region (mtDNA CR), a maternally inherited marker, indicates that at least 13 mtDNA clades or lineages are distributed in wild boar from across Asia (Larson et al. 2005, 2010), while two lineages are found in those from Europe (Giuffra et al. 2000; Kusza et al. 2014). Additional clades containing both domestic pigs and wild boar have also been identified (Larson et al. 2005, 2010). However, the taxonomic status of the samples used in those studies was not clear, hindering correlations between taxonomy and genetic profiles. Despite this, in Table 21.1 we attempt to put the geographical distribution of proposed new species of wild boar shown in Figure 21.1 (Groves & Grubb 2011) in the context of the overall geographical distribution of mtDNA CR clades identified in wild boar studies (Larson et al. 2005, 2010). This preliminary comparison shows that the overall geographical distribution of some of the mtDNA CR clades (e.g. W5, W6, W7, W8; Table 21.1) falls within the range for some of the proposed new wild boar species (e.g. *S. leucomystax*, *S. riukiuanus*, *S. taevanus*, and *S. chirodontus*, respectively). This may be the basis for a test as to whether those genetic profiles are species-specific. In contrast, other clades (e.g. W11 and W12) appear to show a broader distribution that falls within that from 2–3 species (e.g. *S. cristatus*, *S. moupinensis*, and possibly *S. vittatus*; Table 21.1). In Europe, clades E1 and E2 are found in wild *S. scrofa*, with the former haplogroup also found in domestic pigs (Giuffra et al. 2000; Scandura et al. 2008; Kusza et al. 2014).

Biparental DNA markers have provided further insight into the genetic differentiation within wild boar. Microsatellite DNA studies indicate that there are at least six genetically divergent populations among wild boar from East Asia (Choi et al. 2014). Comparison of the geographical origins of these populations with that for the proposed new species (Groves & Grubb 2011) show that at least three of the genetic populations (South Korea, Yunnan, China and Vietnam) may fall within a single species (*S. moupinensis*) while the rest of the populations from the south of the Russian Far East, Japan and Indonesia fall within

Table 21.1 Comparison of the approximate distribution of mitochondrial DNA clades across the range of the proposed new species of wild boar.

Taxon	mtDNA clades*
<i>S. chirodontus</i>	W8, GC
<i>S. cristatus</i>	W11, W12, MC1, MC3
<i>S. davidi</i>	?
<i>S. leucomystax</i>	W5, GC
<i>S. moupinensis</i>	W1, W2, W3, W4, W9, W10, W11, W12, W13, MC1, MC2, MC3, MC4, GC
<i>S. nigripes</i>	?
<i>S. riukiuanus</i>	W6
<i>S. scrofa</i>	E1, E2 (Also known as D2, D4)
<i>S. taevanus</i>	W7
<i>S. ussuricus</i>	?W4, GC
<i>S. vittatus</i>	?W11, MC2

*This corresponds to a group of mtDNA CR haplotypes that have been defined previously by phylogenetic studies in the geographical regions (Larson et al. 2005, 2010) where the new proposed species are distributed. W, wild boar; D, see Greger's publications; MC, mixed clades.

the geographical distribution of *S. ussuricus*, *S. leucomystax*, and *S. vittatus*, respectively. In Europe, where *S. scrofa sensu stricto* is distributed, wild boar populations appear to show a low level of genetic divergence and are mostly divided into genetically differentiated subpopulations (Vernesi et al. 2003; Ferreira et al. 2009; Nikolov et al. 2009; Scandura et al. 2011a,b; Veličković et al. 2016).

Genome-wide SNP analyses of wild boar show no apparent differentiation between wild boar from Portugal and Spain, with both forming a single genetic population separate from domestic pigs (Herrero-Medrano et al. 2013). Genome-wide single nucleotide polymorphism (SNP) analyses have also shown that the genetic structure of wild boar from north-west Europe has been influenced by historical reintroductions and by genetic introgression from domestic pigs (Goedbloed et al. 2013). A genome sequencing study has shown the Korean wild boar as a separate genetic population from the domestic pigs including Korean native breeds (Choi et al. 2015).

Genov (1999, 2004) proposed that there are four groups of subspecies (Western, Indian, Eastern and Sundaic groups), but kept them as a single taxon based on morphological analyses similarly carried out by the study of Groves and Grubb (2011). Genov's classification was based on the following morphological characteristics:

- Concavity of cranium profile:** this concavity near the suture connecting the nasal and frontal bones is visible only in male individuals. The Bonferroni test shows that this concavity exists mainly for *Sus s. scrofa* and *Sus s. attila*, which corroborates the reliability that this character can be used in taxonomy.
- Shape of the lacrimal bone:** this is one of the basic characters used to classify the nominal species and nominal subspecies of wild boar. The shape is usually divided into two forms, rectangular (1) and square (4) (Figure 21.2). Two

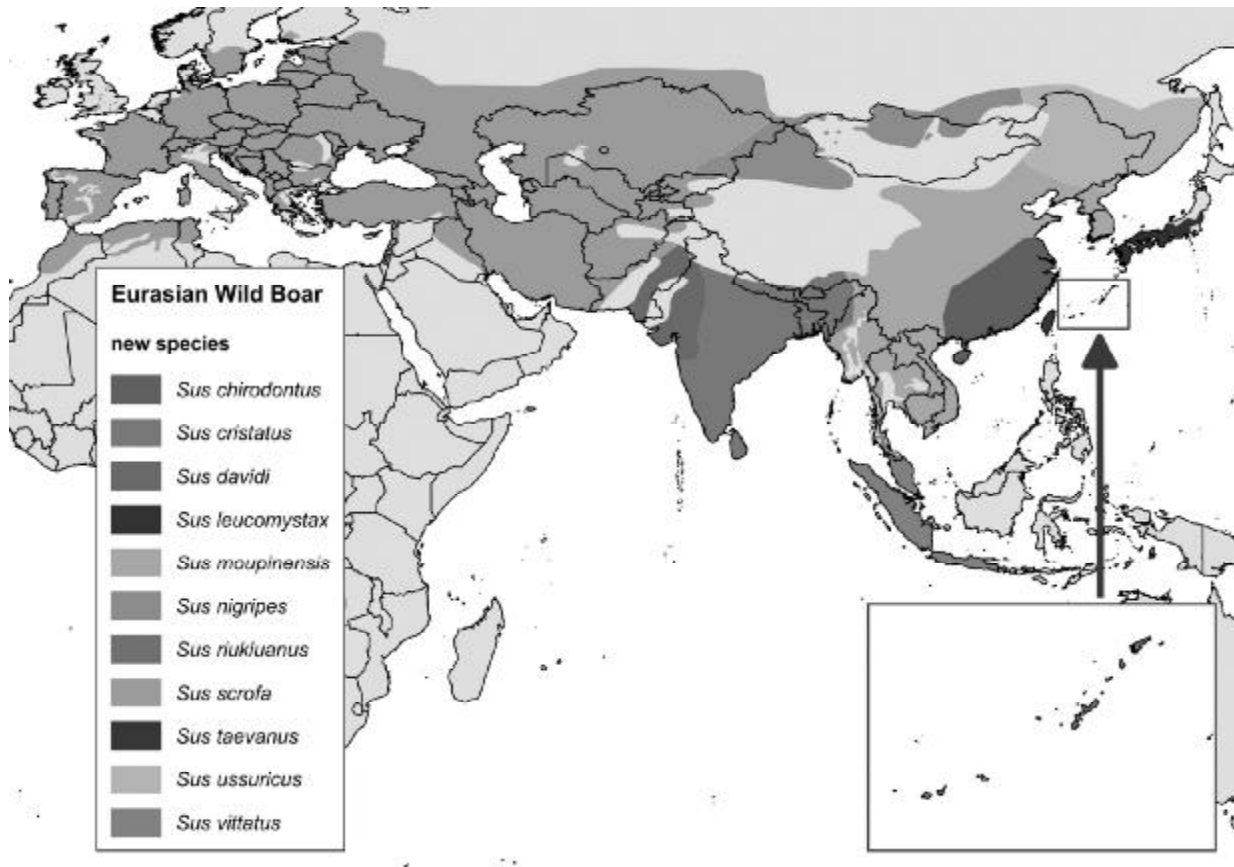


Figure 21.1 Approximate geographical distribution of 11 new proposed wild boar species. Occurrence is yet to be well assessed and for this reason there are some gaps in the map. Phylogenetic studies in the geographical regions (Larson et al. 2005, 2010) where the new proposed species are distributed shows that the overall geographical distribution of some of the mtDNA CR clades falls within the range of some proposed new wild boar species (e.g. *S. leucomystax*, *S. riukuanus*, *S. taevanus*, and *S. chirodontus*; see also Table 21.1). This could be the basis for a test to clarify if those genetic profiles are species-specific. However, this new classification needs to be tested using comprehensive sampling from genetic, comparative chromosome painting and morphometrics approaches to better understand the complexity of wild boar taxonomy and level of hybridization through its large range. This validation is important because the new classification could have an impact on defining priorities for conservation of the new proposed wild boar species. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

new shapes have been identified: pistol (2) and trapezium (3) (Figure 21.2). The most common shapes for the male specimens of European and North African populations are 1 and 3 (Figure 21.2). The other two shapes (pistol and trapezium) appear to be intermediate; they have been reported in specimens from the Volga Delta, Turkmenistan, Nepal, and the Ussuri River valley, the transitional boundary between the European and Asian nominal subspecies. It should be mentioned that the south Asian nominal subspecies show shapes 3 and 4 for that bone (Figure 21.2).

- (c) **Shape of the rear margin of the palatum durum:** the polymorphism of this character is higher for the male specimens. It can be seen more clearly for the species/subspecies, where all four shapes occur such as in *S. s. attila*, *cristatus*, *lybicus*, *nigripes* and *scrofa*. Among the female specimens, this character is only present in *S. scrofa sensu stricto*.

This indicates the geographical variation of this character and it can be used in taxonomy.

Shape	1	2	3	4
A				
B				

Figure 21.2 Shape of the lacrimal bone (a) and the rear end of the palatum durum (b) in different species/subspecies of wild boar through its range. The shapes are divided into four forms: (1) rectangular; (2) pistol; (3) trapezium; (4) square (from Genov 1999, 2004).

Subspecies and Distribution

The wild boar and its domesticated forms, the feral pig, hybrids (wild boar × feral pigs), are among the most widely distributed mammals in the world and pigs are one of the few domesticated species which are neither extinct nor near extinction in their wild form.

Pre-historical and Historical Introduction

The current distribution range of wild boar and feral pigs is indeed the result of the many introductions carried out intentionally by humans over the years throughout the world. In fact, this species, native to Eurasia, is currently present on all continents, including many oceanic islands, except Antarctica (Lever 1994; Long 2003; see also Table 21.2). The introductions of this species started early in human history, mostly as a consequence of the relevant domestication process. For example, during the fifth millennium BC domestic pigs, apparently from the Middle East, were introduced to France, where wild boar had occurred

naturally since the Pleistocene (Long 2003). However, in those times the species was also introduced in Corsica, where no native ungulates were present (see Pascal et al. 2006). The situation is similar to other Mediterranean islands, as the feral pigs were apparently introduced in Sardinia and Cyprus, i.e. since the seventh to sixth millennia BC (Sarà 1998; Boitani et al. 2003) and even earlier in Sicily and Crete (Sarà 1998). On the other side of its range, the species was also introduced early in human history, for example the occurrence of pigs in New Guinea introduced from Asia may date back to 10,000 years ago (Long 2003). Many other introductions were carried out more recently. For

Table 21.2 Worldwide distribution of wild boar (*Sus scrofa*) and feral pigs by country (main sources: www.cabi.org/isc/datasheet/119688; Long 2003; Oliver & Leus 2008; Mayer & Brisbin 2008; Chapter 28 in this book, modified and updated).

Occurrence	Origin	Notes	References
Europe		Populations in Corsica, Sardinia and Sicily are of old feral origin	Long 2003
Albania	Native		Oliver & Leus 2008
Andorra	Native		Oliver & Leus 2008
Austria	Native		Oliver & Leus 2008
Belarus	Native		Oliver & Leus 2008
Belgium	Native		Oliver & Leus 2008
Bosnia-Herzegovina	Native		Oliver & Leus 2008
Bulgaria	Native		Oliver & Leus 2008
Croatia	Native		Oliver & Leus 2008
Cyprus	Introduced	Introduced in 1994 for hunting and eradicated in 2004	Hadjisterkotis & Heise-Pavlov 2006
Czech Republic	Native		Oliver & Leus 2008
Denmark	Native	Recovering from German population in the south. The rest of population seems to originate from farm escapes	Jordt et al. 2016
Estonia	Native		Oliver & Leus 2008
Finland	Native		Oliver & Leus 2008; Erkinaro et al. 1982
France	Native	Corsica introduced several centuries ago	Long 2003; Pascal et al. 2006; Oliver & Leus 2008
Germany	Native		Oliver & Leus 2008
UK (Wales, Scotland, England, Northern Ireland)	Native	Originally native; exterminated centuries ago and recently re-established from farm escapes. Genetic studies indicate a mixture of wild boar and domestic pig ancestry	Goulding 2012; Frantz et al. 2012
Greece	Native	Introduced in Crete in the 7th–6th millennia BC	Sarà 1998
Hungary	Native		Oliver & Leus 2008
Ireland		Native centuries ago then eradicated. Recently introduced from farm escapes	McDevitt et al. 2013; Oliver & Leus 2008
Italy	Native	Sardinia and Sicily introduced in the 7th–6th millennia BC	Boitani et al. 2003
Latvia	Native	Wild boar invaded the area within the Baltic partially in the last century due to feeding practices	Oliver & Leus 2008; Keuling, personal communication
Liechtenstein	Native		Oliver & Leus 2008
Lithuania	Native		Oliver & Leus 2008
Luxembourg	Native		Oliver & Leus 2008
Macedonia	Native		Oliver & Leus 2008
Moldova	Native		Oliver & Leus 2008
Monaco	Native		Oliver & Leus 2008

(cont.)

Table 21.2 (cont.)

Occurrence	Origin	Notes	References
Montenegro	Native		Oliver & Leus 2008
Netherlands	Native	Probably spreading also from Germany	Oliver & Leus 2008; http://waarneming.nl/soort/maps/432?from=2015-08-16&to=2016-08-16
Norway	Introduced	Recently spreading from Swedish population in a small area in the south-east of Oslo. Considered alien species by Gederaas et al. 2012	Rosvold & Andersen 2008; E. Lund, personal communication
Poland	Native		Oliver & Leus 2008
Portugal	Native		Oliver & Leus 2008
Romania	Native		Oliver & Leus 2008
Russian Federation	Native		Oliver & Leus 2008
San Marino	Native		Oliver & Leus 2008
Serbia	Native		Oliver & Leus 2008
Slovakia	Native		Oliver & Leus 2008
Slovenia	Native		Oliver & Leus 2008
Spain	Native		Oliver & Leus 2008
Sweden	Native	Originally native; exterminated in sixteenth century and reintroduced accidentally from farms in recent decades	Truvé 2004
Switzerland	Native		Oliver & Leus 2008
Ukraine	Native		Oliver & Leus 2008
Asia			
Afghanistan	Native		Oliver & Leus 2008
Armenia	Native		Oliver & Leus 2008
Azerbaijan	Native		Oliver & Leus 2008
Bangladesh	Native		Oliver & Leus 2008
Bhutan	Native		Oliver & Leus 2008
Borneo		Introduction failed	Long 2003
Cambodia	Native		Oliver & Leus 2008
China	Native		Oliver & Leus 2008
Christmas Island (Indian Ocean)	Introduced		SPREP 2000
Georgia (Republic of)	Native		Oliver & Leus 2008
India	Native		Oliver & Leus 2008
Indonesia		Introduced to Indonesia, pigs are present on many islands	Oliver 1984; Long 2003
Irian Jaya	Native		Oliver & Leus 2008
Java	Native		Oliver & Leus 2008
Nusa Tenggara	Native		Oliver & Leus 2008
Iran	Native		Oliver & Leus 2008
Iraq	Native		Oliver & Leus 2008
Israel	Native		Oliver & Leus 2008
Japan	Native		Oliver & Leus 2008
Jordan	Native		Oliver & Leus 2008
Kazakhstan	Native		Oliver & Leus 2008
Korea DPR	Native		Oliver & Leus 2008
Korea (Republic of)	Native		Oliver & Leus 2008
Kyrgyzstan	Native		Oliver & Leus 2008

(cont.)

Occurrence	Origin	Notes	References
Laos	Native		Oliver & Leus 2008
Lebanon	Native		Oliver & Leus 2008
Malaysia Peninsular	Native		Ickes et al. 2005
Mongolia	Native		Oliver & Leus 2008
Myanmar	Native		Oliver & Leus 2008
Nepal	Native		Oliver & Leus 2008
Pakistan	Native		Oliver & Leus 2008
Palestine	Native		Oliver & Leus 2008
Sri Lanka	Native		Oliver & Leus 2008
Sumatra	Native		Oliver & Leus 2008
Syria	Native		Oliver & Leus 2008
Taiwan	Native		Oliver & Leus 2008
Tajikistan	Native		Oliver & Leus 2008
Thailand	Native		Oliver & Leus 2008
Turkey	Native		Oliver & Leus 2008
Turkmenistan	Native		Oliver & Leus 2008
Uzbekistan	Native		Oliver & Leus 2008
Vietnam	Native		Oliver & Leus 2008
Africa		Domestic pigs were released by the Forestry Department in the south-west parts of Cape Province (South Africa) in the 1920s. Further introductions of wild boar have been conducted in Gabon	Oliver & Leus 2008; Long 2003
Algeria	Native		Oliver & Leus 2008
Egypt	Native	Eradicated c.1902	Oliver et al. 1993; Oliver & Leus 2008
Gabon	Introduced	Localized	Blom et al. 1990; Long 2003
Libya	Native	Eradicated	Oliver et al. 1993; Oliver & Leus 2008
Madagascar	Introduced	Present in the 1970s	Long 2003
Mauritius	Introduced	First record c.1512	Carter & Bright 2002; Long 2003
Morocco	Native		Oliver & Leus 2008
Seychelles	Introduced	About 400 feral pigs were present on Bird Island in 1972–1973. Now eradicated	Long 2003
South Africa	Introduced	First introduction in the 1920s	Long 2003
Sudan	Introduced	Unreliable record?	Kingdon 1997
Tunisia	Native		Oliver & Leus 2008
Zimbabwe	Introduced	Free-ranging pigs in the 1980s	Smithers 1983
North America		Wild pig populations have had a long history in North America dating back to the European period of colonization. Two forms of <i>S. scrofa</i> , domestic swine and Eurasian wild boar, were introduced in different periods into the continent. The estimated population ranges between 4 and 11 million individuals	Mayer & Brisbin 2008; Chapter 28 this book
Canada		The presence of the species in Canada during the 1980s originates from the first stock presumably of pure wild boar that was imported from Europe. These animals were hybridized with domestic swine to increase reproduction	Chapter 28 this book
Alberta	Introduced	First introduction in the 1980s	Brook & van Beest 2014
British Columbia	Introduced	First records 2013–2014	Bostelaar 2014; BCMFLNRO 2014
Manitoba	Introduced	First records in the 1980s	Dokken 1999; Brook & van Beest 2014
Ontario	Introduced	First records 2013–2014	Bostelaar 2014; BCMFLNRO 2014
Quebec	Introduced	First records 2013–2014	Bostelaar 2014; BCMFLNRO 2014

(cont.)

Table 21.2 (cont.)

Occurrence	Origin	Notes	References
Saskatchewan	Introduced	First records in the 1980s	Brook & van Beest 2014
USA		In the last 15 years a mix of feral pigs and wild boar have been reported as being present (in some cases only temporarily) in 48 of 50 States with the exception of Rhode Island and Wyoming. They are currently reported to be established in 35 States	Mayer & Brisbin 2009; NFSMS 2015; Chapter 28 this book
Alabama	Introduced (established population)		Gaston 2008; Mayer 2014
Alaska	Introduced	Between 1984 and 1987 wild boars have been introduced on Marmot Island. Status to confirm	Franzmann 1988
Arizona	Introduced (established population)		NatureServe 2013
Arkansas	Introduced (established population)		Mayer 2014
California	Introduced (established population)	Eradicated on Santa Rosa Island	Schauss et al. 1990; Sweitzer et al. 2000; Barrett & Birmingham 2005; Mayer 2014
Colorado	Introduced (established population)		Chapter 28 this book
Florida	Introduced (established population)		Barrett & Birmingham 2005; NatureServe 2013; Mayer 2014
Georgia	Introduced (established population)		Barrett & Birmingham 2005; NatureServe 2013; Mayer 2014
Hawaii	Introduced (established population)	c.1000 AD, further introductions in 1778–1803	Long 2003; Barrett & Birmingham 2005
Illinois	Introduced (established population)		McCann et al. 2003
Indiana	Introduced (established population)		Chapter 28 this book
Kansas	Introduced (established population)		Gipson et al. 2006
Kentucky	Introduced (established population)		NatureServe 2013
Louisiana	Introduced (established population)		Barrett & Birmingham 2005; Mayer 2014
Michigan	Introduced (established population)		Rusz 2007
Mississippi	Introduced (established population)		NatureServe 2013; Mayer 2014
Missouri	Introduced (established population)		Chapter 28 this book
Nebraska	Introduced		Gipson et al. 2006
Nevada	Introduced (established population)		Chapter 28 this book
New Hampshire	Introduced (established population)		Chapter 28 this book
New Jersey	Introduced (established population)		Chapter 28 this book
New Mexico	Introduced (established population)		NatureServe 2013
New York	Introduced	Eradicated in 2016	Chapter 28 this book
North Dakota	Introduced (established population)	Spreading from Manitoba in 1999	Dokken 1999
North Carolina	Introduced (established population)		Barrett & Birmingham 2005; NatureServe 2013

(cont.)

Occurrence	Origin	Notes	References
Ohio	Introduced (established population)		Chapter 28 this book
Oklahoma	Introduced (established population)		Mayer 2014
Oregon	Introduced (established population)		Chapter 28 this book
Pennsylvania	Introduced (established population)		Chapter 28 this book
South Carolina	Introduced (established population)		Dewey & Hruby 2002; Mayer 2014
Tennessee	Introduced (established population)		Barrett & Birmingham 2005; NatureServe 2013
Texas	Introduced (established population)		Barrett & Birmingham 2005; NatureServe 2013; Mayer 2014
Utah	Introduced (established population)		Chapter 28 this book
Vermont	Introduced (established population)		Chapter 28 this book
Virginia	Introduced (established population)		NatureServe 2013
Washington	Introduced (established population)		Chapter 28 this book
West Virginia	Introduced (established population)		NatureServe 2013
Wisconsin	Introduced (established population)		Chapter 28 this book
Central America and Caribbean		Pigs were carried by the early European colonists to the New World. Thus Columbus introduced them to the West Indies in 1493	Long 2003
Antigua and Barbuda	Introduced		Oliver & Leus 2008
Bahamas	Introduced		Kairo et al. 2003
Cuba	Introduced	First introduction in 1493	Long 2003; Oliver & Leus 2008
Curacao	Introduced		Kairo et al. 2003
Dominica	Introduced		Kairo et al. 2003
Dominican Republic	Introduced		Oliver & Leus 2008
Haiti	Introduced		Oliver & Leus 2008
Jamaica	Introduced		Kairo et al. 2003
Mexico	Introduced	A mixture of domestic pigs and Eurasian wild boar have been introduced since colonial times	Long 2003; Copado et al. 2004; Villarreal et al. 2010
Montserrat	Introduced		Varnham 2006
Puerto Rico	Introduced	First introduction in the 1970s	Kairo et al. 2003; Barrett & Birmingham 2005
Saint Lucia	Introduced		Organisation of Eastern Caribbean States 2012
United States Virgin Islands	Introduced		Kairo et al. 2003; Barrett & Birmingham 2005
South America		A mixture of wild boar and domestic pigs have been introduced from the fifteenth century to recent decades in several countries of South America. This invasion covers about 12% of the Continental area	Long 2003; Chapter 29 this book
Argentina	Introduced	First introduction in 1906	Navas 1987; Novillo & Ojeda 2008; Ballari et al. 2015

(cont.)

Table 21.2 (cont.)

Occurrence	Origin	Notes	References
Brazil	Introduced		Long 2003; Salvador & Fernandez 2013
Chile	Introduced	First records in the 1950s. Further introductions in 2002–2009	Jaksic et al. 2002; Aravena et al. 2015; Skewes & Jaksic 2015
Colombia	Introduced		Oliver & Leus 2008
Costa Rica	Introduced	Cocos Island	Long 2003
Ecuador (Galapagos)	Introduced	First introduction between 1832 and 1890	Long 2003
Paraguay	Introduced	Spreading in the north and west from Brazil populations	Chapter 29 this book
Uruguay	Introduced	First introduction in the 1920s	Herrero & Fernández de Luco 2003; García et al. 2011
Oceania		By 1000 AD they had been introduced throughout much of Oceania, including the Hawaiian Islands	Long 2003
American Samoa	Introduced		SPREP 2000
Australia	Introduced	First introduction in 1788. Feral pig distribution covers 45% of Australia and occurs in all States with an estimated population of about 24 million of individuals. Range expansion and increasing densities in many areas in recent decades	West 2008; Chapter 30 this book; Chapter 21 this book
Cook Islands	Introduced	First introduction around 1800	SPREP 2000; Long 2003
Fiji	Introduced	First introduction c.1300 BC	SPREP 2000; Long 2003
French Polynesia	Introduced		SPREP 2000
Guam	Introduced	First introduction of domestic pigs between 1672 and 1685	SPREP 2000; Long 2003
Kiribati	Introduced		SPREP 2000
Lord Howe Is.	Introduced	Eradicated	Parkes et al. 2002
Marshall Islands	Introduced	Record not confirmed	SPREP 2000
Federates States of Micronesia	Introduced		SPREP 2000
Nauru	Introduced	Record not confirmed	SPREP 2000
New Caledonia	Introduced	First record in 1774	Long 2003
New Zealand	Introduced	First record in 1773; further introductions in 1807, 1840, 1842–1843	Long 2003; Chapter 30 this book
Niue	Introduced	Record not confirmed	SPREP 2000
Northern Mariana Islands	Introduced		SPREP 2000
Palau	Introduced		SPREP 2000
Papua New Guinea	Introduced	First introduction between 4000 and 10,000 years ago. Intermediate types between the wild boar <i>S. vittatus</i> and the Sulawesi warty pig <i>S. celebensis</i> exist	Oliver 1984; SPREP 2000; Long 2003
Pitcairn Island	Introduced	Record not confirmed	SPREP 2000
Samoa	Introduced		SPREP 2000
Solomon Islands	Introduced		SPREP 2000
Tasmania	Introduced	First introduction in 1770	Long 2003
Tokelau	Introduced		SPREP 2000
Tonga	Introduced		SPREP 2000
Tuvalu	Introduced		SPREP 2000
Vanuatu	Introduced		SPREP 2000
Wallis and Futuna Islands	Introduced		SPREP 2000



Figure 21.3 *Sus scrofa* in Slovakia (photo by M. Melletti). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

example, feral pigs have been introduced to the New World in the West Indies since 1493 by Columbus, and since then several other introduction events led to the establishment of the species in a number of countries in North and South America. The species was brought also to Oceania, reaching Tasmania in the 1770s (Long 2003), although it is unclear whether all early attempts to introduce this species succeeded. In Africa wild boar were introduced too, but not until more recent times, e.g. in the 1920s in South Africa (Long 2003). Additionally, the species has been introduced in over 200 oceanic islands, as reported in detail by Long (2003); see also Table 21.2). Some of these island introductions started in very early times, for example to Melanesia some 3500 years ago.

Present Distribution in Native Range

The distribution of the new proposed species is as follows: *S. scrofa* (western Europe; Figure 21.3); *S. nigripes* (north-west China and Kyrgyzstan); *S. davidi* (east Iran, Pakistan, and north-west India); *S. cristatus* (southern Himalayas, central India, and Indochina; Figure 21.4); *S. ussuricus* (east Russia and Manchurian region); *S. leucomystax* (main islands of Japan); *S. riukiuanus* (Ryukyu islands, south Japan); *S. taevanus* (Taiwan); *S. moupinensis* (South Korea, China, south Vietnam, and west Sichuan); *S. chirodontus* (south-central China); *S. vittatus* (Malay Peninsula; Figure 21.5). The main subspecies distribution is as follows: *S. scrofa meridionalis* (Corsica and Sardinia); *S. s. baeticus* (south Spain and south Portugal; Figure 21.6); *S. s. algerius* (North Africa); *S. s. lybicus* (south-east Europe and Middle East); *S. s. attila* (from Hungary maybe until east Turkey, western Iran, Iraq, and Syria); *S. s. sibiricus* (Mongolia and Transbaikalia) and *coreanus* (Korean Peninsula). Furthermore, *coreanus* could be treated as a subspecies of

Sus moupinensis following the new proposed classification in this book. For more details on worldwide distribution of wild boar by country see Table 21.2.

The species is regionally extinct in Egypt and Libya. In Ireland wild boar was officially recorded as present but subsequently locally eradicated in April 2009 (McDevitt et al. 2013). Since then, the species has been removed from many locations in the south-east of Ireland but still occurs in this country (McDevitt et al. 2013). In Denmark the wild boar is spreading from Germany and from farm escapes (Jordt et al. 2016), and in Norway it is recovering through influx from the Swedish population (Rosvold & Andersen 2008). The presence of this species in Sweden and the United Kingdom is mainly due to farm escapes (Goulding 2003; Truvé 2004; Oliver & Leus 2008; Thurfjell et al. 2009). In Sweden an annual growth rate of 28 per cent has been recorded from 2012 based on hunting harvest (H. Thurfjell, personal communication). In the United Kingdom, wild boar observations are increasing in several counties of England. In addition, the presence of the species has been recorded even in Wales and Scotland (for more details see Table 21.2). In Finland the presence of wild boar is due to a colonization that started in the last 100 years from Latvia, Estonia, and Soviet Karelia (Erkinaro et al. 1982). In Cyprus wild boar was illegally released in 1994 but attempts to eradicate this species failed. In 2004 it became extinct due to lack of food, high hunting pressure, and perhaps inbreeding (Hadjisterkotis & Heise-Pavlov 2006). In some countries, such as in Italy, since the 1950s restocking for hunting purposes with eastern subspecies, most probably *S. s. attila*, may have locally caused hybridization with wild boar that have produced, in some cases, mixed forms and reduced the genetic integrity of local populations (Scandura et al. 2008). See also Figure 21.7 and Table 21.2 for more details on distribution.



Figure 21.4 *Sus cristatus* in Kaziranga, Assam (photo by R. Wirth). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)



Figure 21.5 *Sus vittatus* in Taman Safari, Bogor, Indonesia (photo by R. Wirth). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)



Figure 21.6 *Sus scrofa baeticus* in Doñana N. P., Spain (photo by M. Melletti). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

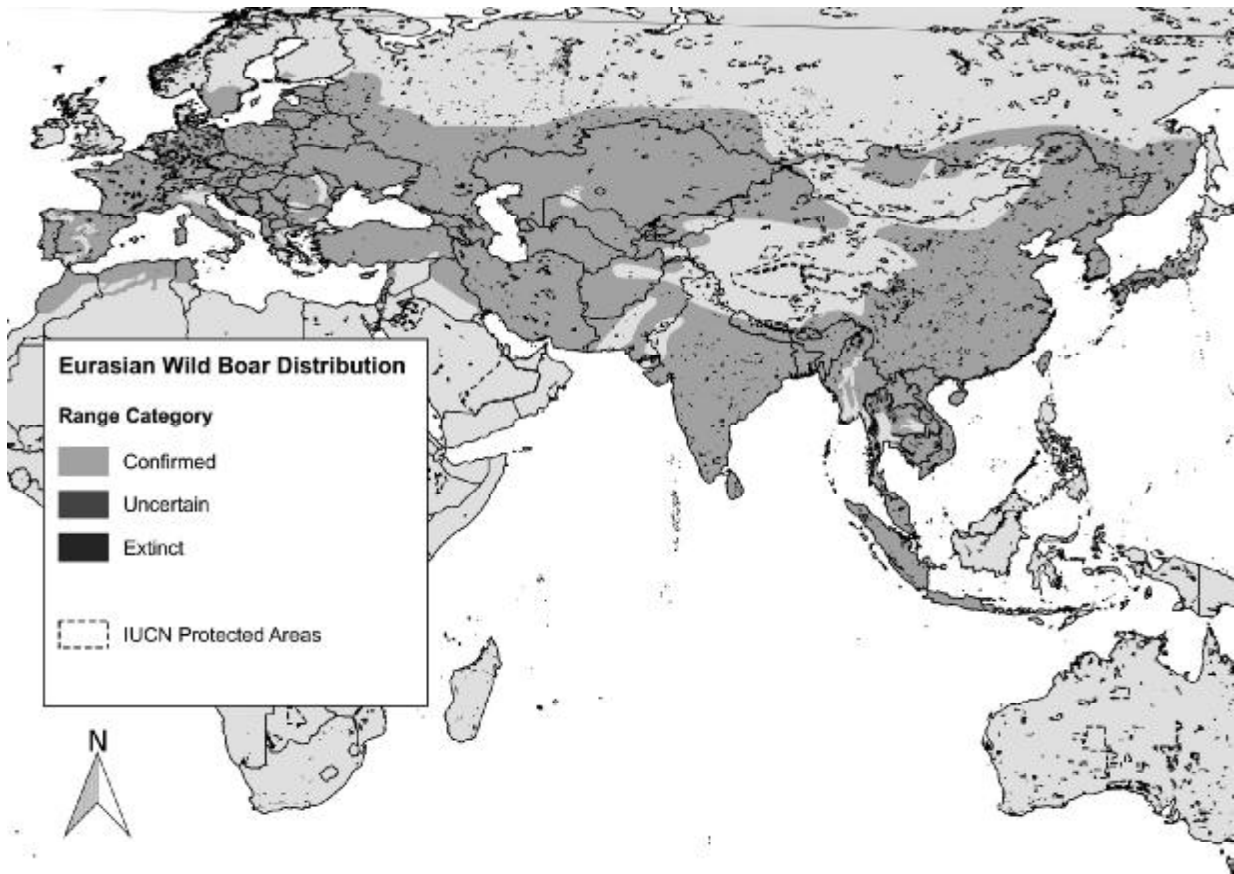


Figure 21.7 Eurasian wild boar distribution (source: IUCN 2008, *Red List of Threatened Species*). (A simplified black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

Distribution Outside its Native Range

During the course of the last centuries a mix of wild boar and feral pigs has been introduced in several regions around the world. Moreover, most wild boar used for introductions outside the native range have a Eurasian origin. In the USA introductions have been both accidental (e.g. escaped domestic swine) and intentional (e.g. Eurasian wild boar released as game species; Mayer & Brisbin 2008, 2009). Despite a prolonged presence on the continent, the wild pigs in North America have undergone a recent dramatic expansion in both their distribution and numbers (see Chapter 28 for more details). The species has been recorded in 48 of 50 States with the exception of Rhode Island and Wyoming. They are currently reported to be established in 35 States (Sweitzer et al. 2000; McCann et al. 2003; Gaston 2008; see also Chapter 28 in this book and Table 21.2 for more details). Recently, feral pigs have been eradicated in New York State (J. Mayer, personal communication).

The introduction of the species in **Canada** during the 1980s originated from the first stock, presumably of pure wild boar, that was imported from Europe. These animals were hybridized with domestic swine to increase reproduction. In the 2000s, established populations with significant numbers of wild boar were reported in Alberta, Manitoba, and Saskatchewan (Brook & van Beest

2014). Between 2013 and 2014 there were reports of sightings in eastern Ontario, western Quebec, and southern British Columbia (Bostelaar 2014; BCMFLNRO 2014; see also Table 21.2).

In **South America** the species is present in Ecuador (Galápagos), Colombia, and also in Argentina, from where it is spreading in its wild form into Chile and Brazil (where wild boar coming from the south and feral pigs from the north hybridize in the *Araucaria* forests of Florianópolis; Salvador & Fernandez 2013; Aravena et al. 2015; Ballari et al. 2015; Skewes & Jaksic 2015). It has also been introduced into Uruguay from Argentinean wild boar (García et al. 2011). The status in Paraguay is not well known, but a recent invasion of wild boar from south Brazil is affecting the north and west of the country (Salvador de Oliveira 2012; see also Chapter 29 in this book).

In addition to North and South America, wild boar and feral pigs have been introduced in Antigua and Barbuda, Cuba, Dominican Republic, Fiji, Haiti, Jamaica, New Zealand, Papua New Guinea, Africa, Central and South America, Oceania, and Indonesia (several islands). Australia has an estimated maximum population of feral pigs of 24 million, nearly the same as the human population (c.23 million; www.business.qld.gov.au/industry/agriculture/species/declared-pests/animals/feral-pig).

For a detailed worldwide distribution by country of wild boar and feral pigs see Table 21.2 and Table 21.3.

Table 21.3 Main morphological differences and worldwide occurrence of *Sus scrofa* species/subspecies.

Wild boar species/ subspecies	Skull length (cm)	Coat colour	Body mass (kg)	Occurrence
<i>S. scrofa</i>	30–45	Brown to grey	50–>200	Albania, Armenia?, Austria, Azerbaijan? Belgium, Czech Republic, Denmark, Estonia, Finland, France, Georgia?, Germany, Kazakhstan? Poland, Slovenia, W. Slovakia, Ireland, Italy, Latvia, Lithuania, Luxembourg, the Netherlands, Norway, Western Russia, N. Spain, Sweden, Switzerland, Turkmenistan? Uzbekistan?
<i>S. s. meridionalis</i>	30–33	Olive–fawn	40–60	Corsica and Sardinia (provisional subspecies as these two populations have probably an old feral origin)
<i>S. s. baeticus</i>	30–33	Dull olive–fawn	40–80	S. Spain and S. Portugal
<i>S. s. algirus</i>	29–35	Black–dark brown	42–95	Morocco, Algeria and Tunisia
<i>S. s. lybicus</i>	29–38	Pale brown	100–>200	Serbia, Croatia, Bosnia and Herzegovina, Montenegro, Kosovo, Bulgaria, Greece, Turkey, Syria, Jordan, Israel, and Palestine
<i>S. s. attila</i>	40–47	Pale yellow–grey	100–>200	Hungary, E. Slovakia, Ukraine, Belarus, Romania, Moldova, S. Russia, E. Turkey, W. Iran, Iraq, and Syria
<i>S. nigripes</i>	38–43	Pale brown	100–>200	NW China and Kyrgyzstan
<i>S. davidi</i>	31–38	Light brown	74–158	E. Iran, Pakistan, NW India
<i>S. cristatus</i>	34–42	Black–brown	80–170	S. Himalayas, C. India, Indochina
<i>S. ussuricus</i>	40–51	Black to yellowish–grey	100–>300	E. Russia, Manchurian region
<i>S. s. coreanus</i>	–	Black	–	Korean Peninsula
<i>S. leucomystax</i>	33–36	Yellow–brown	–	Japan's islands (Honshu, Shikoku, Kyushu, Nakadori, Hiburijima, Tojima, Kushima)
<i>S. riukiuanus</i>	~26–27	–	–	Japan's islands (Iriomote, Ishigaki, Okinawa, Tokunoshima, Amamioshima, Kakerome)
<i>S. taivanus</i>	32–33	Black	–	Taiwan
<i>S. moupinensis</i>	35–43	Yellowish	90–180	China, S. Vietnam, W. Sincuan
<i>S. vittatus</i>	29–36	Brown	75–160	Malay Peninsula(S of Kra, islands of Terutai, Langkawi), Sumatra, Java, Bali, Riau Archipelago, and most surrounding islands
<i>S. chirodontus</i>	34–43	–	–	South-Central China

Source: Groves & Grubb 1993; Genov 1999, 2004; Groves 2007; Wilson & Mittermeier 2011; see also Chapter 1 in this book). For some species/subspecies the occurrence needs to be better assessed and the distribution by country is still approximate..

Descriptive Notes

Body measurements: *Shoulder height:* 55–110 cm. *Head and body length:* 90–200 cm. *Tail length:* 15–40 cm. *Body mass:* 44–320 kg (Wilson & Mittermeier 2011). Wild boar represents the most widespread wild pig and, within its huge range, significant regional differences in colour and size exist. For example, the smallest individuals occur near the tropics and in the islands with the larger animals found towards the north and north-east of its range. In general, the coat colour varies from brown to almost black with older individuals tending to be grey. The species is dimorphic, in particular in size, with females being about 60 per cent of the body mass of males. The head is long with no tufts and beard. The muzzle is short with no facial warts. The face, cheeks, and throat may be greyish. Legs are relatively long, in particular in some northern and eastern subspecies. Offspring are born with longitudinal brown stripes that vanish within four months of age and at one year young are similar to adults. In old males lower canines grow to about 25 cm and curve with age. During mastication the lower canines become

sharp by rubbing against the upper canines. The longest tusk ever measured was 41.5 cm recorded in the Antalya region in Turkey in 2012 (Nicolaysen 2015). For more details on morphological characteristics of species and subspecies see Table 21.3.

Longevity in the wild rarely reaches 10–12 years of age (Massei & Genov 2004). In captive conditions, wild boar can live much longer, reaching 25 years (www.waza.org/en/zoo/visit-the-zoo/pigs-and-peccaris/sus-scrofa).

Habitat

The wild boar is generally adapted to dense woodland, scrubland, and understorey habitats. Its primary senses, olfaction and hearing, and body shape characterize them as a species living in dense vegetation. Thus its main habitats are forests, scrublands, and river valleys with abundant reeds. Wild boar has adapted very well to agricultural areas, which provide shelter and food for at least two months during the vegetation period (growing season in moderate climates). The most important factors shaping wild boar distribution and density in the environment are

shelter, food, and water (Fernández-Llario et al. 2003; Keuling et al. 2008a). Depth and duration of snow cover limit its northern extent and the availability of water limits its density and extent in the hot dry climates of the south of its native distribution range (Abaigar et al. 1994; Massei et al. 1997b). Within the introduced ranges, water is the limiting factor, such as in the hot and dry regions in central Australia and South America.

The wild boar is flexible and adaptive in its habitat preferences (Keuling et al. 2008a; Segura et al. 2014), as long as there is sufficient food, water, and shelter provided. Its wide ecological plasticity (Segura et al. 2014) and high reproductive rate (Frauendorf et al. 2016) explain the broad distribution and wide range of occupied habitats. Wild boar can adjust habitat utilization patterns in response to variation in natural predation risk, human hunting disturbance, and seasonal changes in food and shelter availability. The influence of natural predators on wild boar habitat use is poorly studied, but it seems that the presence of wolves (*Canis lupus*), the main natural predator of wild boar, is not perceived by wild boar as a significant risk factor (Kuijper et al. 2014). Human hunting, which is usually seasonal and often varies across the landscape, can have a larger impact on habitat utilization compared to natural predators (Keuling et al. 2008b). For example, a preference for refuge areas was observed during the hunting season in wild boar occupying ranges across hunting and protected land (Tolon et al. 2009). Females, particularly with piglets, tend to seek safe habitats away from disturbance, while males are more risk-tolerant and can remain hidden close to hunting activities (Saïd et al. 2012). Habitat utilization patterns vary seasonally due to weather conditions (elevation, shadow, moisture, temperature, rain protection), food availability (elevation, using fields and grassland, acorn mast), water availability, or changing shelter (resting in fields during vegetation period) (Singer et al. 1981; D'Andrea et al. 1995; Spitz & Janeau 1995; Santos et al. 2004; Keuling et al. 2009; Schiaffini & Vila 2012).

Wild boar is currently found across a wide range of habitats, yet some habitats are favoured. Forests are preferred over bush land (Caley 1997), and mixed and broadleaved forests are preferred over homogeneous coniferous forests (Tsachalidis & Hadjisterkotis 2009; Carpio et al. 2014). In temperate and colder climates within its native range, wild boar prefer mixed deciduous forest containing masting trees, mainly oak or beech, and dense vegetation. In newly settled areas outside the native range, wild boar and feral pigs show similar habitat preferences in terms of habitat structure and composition; when oaks are missing they may be substituted by other masting tree species such as *Nothofagus* sp. or *Araucaria* sp. (Caley 1997; Salvador de Oliveira 2012). During resting, dense vegetation with trees, preferably spruce or other coniferous species when available, and some open places nearby are the main habitats (Cargnelutti et al. 1995; Spitz & Janeau 1995; Keuling & Stier 2009). Only during the growing season of crops do wild boar rest outside forests (Keuling et al. 2009). Food search and feeding are the main factors driving habitat usage also in more open habitats (Spitz & Janeau 1995). This may change with spatial and temporal variation in food availability (Santos et al. 2004). The use of different crops is strictly dependent on their availability in

the place where and when diet has been studied. Even grassland close to sheltering structures is intensively rooted (Gallo Orsi et al. 1995; Keuling et al. 2009; Thurfjell et al. 2009; Daim et al. 2013; Daim 2015), especially when vegetation is short and livestock fertilizes the soil (Bueno et al. 2009; Daim 2015). Thus, movements also occur often along edges and hedges (Thurfjell et al. 2009). Food availability mainly shapes the occurrence and density of wild boar populations (Acevedo et al. 2006; Bobek et al. 2016). Consequently, populations reach their highest densities in areas dominated by mixed deciduous forests combined with agricultural areas (Saito et al. 2012; Bosch et al. 2014) in temperate climates, where most of the studies were conducted. Actually, it reaches really high densities in oil palm plantations of up to 47 pigs/km² (Ickes 2001). Thus, in the tropics, dynamics may be different, at least for some of the new established species (in that case it would be *S. vittatus*). Additionally, wild boar become more and more adapted to urban areas due to population spread and urban sprawl (Cahill et al. 2012; Podgórski et al. 2013). In hot dry climates, like the Mediterranean, wild boar use shady, cool and moist vegetation with milder climatic conditions (Baber & Coblentz 1986; Abaigar et al. 1994; Maillard 1996; Caley 1997; Dexter 1998; Fernández-Llario 2004; Santos et al. 2004; Schiaffini & Vila 2012).

Movements and Home Range

The search for food is the main driver for wild boar movement (Morelle et al. 2015). Movements as well as home range size are influenced by resource availability, predator avoidance (Brandt et al. 1998; Keuling et al. 2008a, 2008b, 2009; Podgórski et al. 2013; Morelle et al. 2015), and interactions with conspecifics and weather conditions (Morelle et al. 2015). When energetic demands increase or resource availability decreases (lactation, winter time), movements, and often also home range sizes, increase (Singer et al. 1981; Massei et al. 1997a; Morelle et al. 2015) until the point when the costs of movement exceed the benefits of additional resources, i.e. when resources are very limited (harsh winter conditions, dry season) (Caley 1997; Massei et al. 1997a, 1997b).

Wild boar perform daily movements with different movement types (Spitz & Janeau 1990; Janeau et al. 1995) due to their needs (feeding, dispersal, fleeing, searching). Usually wild boar do not move faster than 1 km/h for feeding and other general behaviours with a mean speed of 0.25 km/h. Trotting to 'travel' from one spot to another is not faster than 6–10 km/h. Wild boar may run at quite high speed for a short while with fast but short steps (Briedermann 2009; Morelle et al. 2015). When fleeing they may reach 10–40 km/h, which is not a very fast speed compared to other animals of similar size (Morelle et al. 2015). Daily distance travelled by wild boar is usually shorter than 10 km (Russo et al. 1997; Keuling & Stier 2009). Longer distances were observed in a fragmented environment of urban areas and during intensive hunts (Scillitani et al. 2010; Podgórski et al. 2013).

Natal dispersal is a major source of long-distance movements in the wild boar populations, although the number of young wild boar emigrating far from maternal range is rather low. The vast majority of young wild boar (70–80 per cent) remain within the natal range or in its close proximity, not emigrating further

than 5 km away (Truvé et al. 2004; Keuling et al. 2010; Prévot & Licoppe 2013; Podgórski et al. 2014a). Longer movements (5–30 km) are observed less frequently and are undertaken by males rather than females. Natal dispersal is the most intense during the second year of age (Podgórski et al. 2014a). Some individuals in the population (< 10 per cent) may perform linear movements of 50–250 km. Such long distances can be covered within just a couple of months by young animals but also by adult males and adult females with offspring (Andrzejewski & Jezierski 1978; Truvé & Lemel 2003; Jerina et al. 2014). During the rutting season the mobility of males increases. In this period, males roam widely in search of receptive females and may temporarily leave their home ranges. The movements of pregnant females decrease around parturition (Morelle et al. 2015). However, some weeks later, wild boar mothers enlarge their home ranges and move more to meet the nutritional demands for lactation (Keuling et al. 2008b, 2009; Morelle et al. 2015). Wild boar exhibit remarkable intraspecific variation in home range size (Keuling et al. 2008a) and considerable plasticity in spatial behaviour across a wide range of geographic locations and habitats (Spitz 1992, France; Boitani et al. 1994, Italy; Massei et al. 1997a, Italy; Podgórski et al. 2013, Poland). Annual home range sizes range from 100 ha up to about 7000 ha (Maillard & Fournier 1995; Keuling et al. 2008a; Podgórski et al. 2013) with a mean home range size of about 800 ha. The mean range span (largest diameter) is about 4–5 km, but may reach more than 15 km during one year (Keuling et al. 2008a). There is large individual variation in movements and home range sizes, resulting in differences in space use between and even within groups (Boitani et al. 1992; Morelle et al. 2015). Also in its non-native ranges the size of home ranges is similar to those in its native range (Kurz & Marchinton 1972; Singer et al. 1981; Baber & Coblentz 1986; Caley 1997). Some studies reported larger home ranges in male wild boar (Italy: Morini et al. 1995) or feral pigs (California, USA: Baber & Coblentz 1986; Australia: Saunders & Kay 1991), whereas no sex-related differences were found in other Italian wild boar populations (Boitani et al. 1994; Massei et al. 1997a, 1997b) and North American populations of feral pigs (Wood & Brenneman 1980; Singer et al. 1981). It seems that the annual home ranges of males are slightly larger than those of females (Caley 1997; Massei et al. 1997a). This difference results mainly from the extensive movements of males during the rutting season. The smallest home ranges are found in urban areas (Dinter 1991; Podgórski et al. 2013) and under extremely rich (e.g. supplementary feeding; Prévot 2010; Ježek et al. 2013, 2014a) or very poor environmental conditions (e.g. dry season; Caley 1997; Massei et al. 1997a, 1997b). Median home range sizes are found in lowland regions. In areas dominated by agriculture, wild boar inhabit home ranges just slightly smaller than in forest-dominated areas (Herbst & Keuling 2014), while biggest home ranges occur in mountainous areas or poor habitats (Singer et al. 1981; D'Andrea et al. 1995; Keuling et al. 2008a), mainly due to seasonal shifts. Wild boar shift their seasonal home ranges due to different habitat availabilities and requirements (food, shelter, water, weather protection, see also 'Habitat' section; D'Andrea et al. 1995; Keuling et al. 2008a, 2008b, 2009). Thus, seasonal home ranges are about half the size of annual

home ranges, but may reach even the same large size during the hunting season. Hunting disturbance may induce escape movements, resulting in greater distances travelled and larger ranges (Maillard & Fournier 1995; Sodeikat & Pohlmeier 2003; Keuling et al. 2008b; Scillitani et al. 2010). However, it is mainly heavily hunted or frequently disturbed (especially with high-intensity drive hunts) animals that enlarge their home range for some days to several weeks (during intense hunting seasons) to avoid hunting pressure, while others reduce the size or shift the location of their home range (compare 'Habitat' section) (Maillard & Fournier 1995; Baubet et al. 1998; Calenge et al. 2002; Sodeikat & Pohlmeier 2003; Keuling et al. 2008b; Tolon et al. 2009, 2012; Scillitani et al. 2010; Saïd et al. 2012; Thurfjell et al. 2013). Also, a greater dispersion of the daily resting sites during the hunting season may be induced by hunting with dogs (Maillard & Fournier 1995; Scillitani et al. 2010; Saïd et al. 2012). Low-intensity single hunts or slow beating drive hunts have a smaller impact on wild boar ranging behaviour (Keuling et al. 2008b; Thurfjell et al. 2013). A comparison of effects due to different hunting methods in Switzerland and France (Tolon et al. 2009) showed that during drive hunts wild boar moved more than when stalked by a single hunter. In contrast, a study in northern Germany (Keuling et al. 2008b) found no significant differences between hunting methods. In central Italy family groups reacted to drive hunts if directly chased by dogs and beaters, but moved to areas far from their native range only when frequently disturbed, both in terms of the frequency of drive hunts and the loss of group members (Scillitani et al. 2010).

Activity Patterns

Scarce data from natural and undisturbed populations indicate that wild boar activity is diurnal (Kurz & Marchinton 1972) or evenly spread throughout day and night (Podgórski et al. 2013). In human-dominated landscapes the wild boar has become largely nocturnal (Janeau & Spitz 1984; Boitani et al. 1994; Lemel et al. 2003; Keuling et al. 2008b; Quy et al. 2014). Hunting and human disturbance are the main drivers for the shift to nocturnal activity, but other seasonally variable factors can influence activity patterns as well. Ohashi et al. (2013) observed a higher proportion of nocturnal activity during the hunting season. In an undisturbed population in Białowieża Forest, the level of diurnal activity followed the natural cycle of day length, with the nocturnal one dominating in winter and the diurnal in summer (Podgórski et al. 2013). Under a moderate hunting pressure the distribution of activity is less influenced by hunting activities but mainly by daytime length and nutritional needs (Keuling et al. 2008b). Ohashi et al. (2013) found higher nocturnal activity during the hunting season and in the direct surroundings of settlements. In the urban environment, wild boar was almost exclusively nocturnal, independent of the seasonal changes in day length, in order to minimize interference with humans (Podgórski et al. 2013).

As with many aspects of wild boar biology, duration of activity may also be very flexible (McIlroy 1989). Within 24 hours, 30–80 per cent of time is used for activity (time exclusive of resting and sleeping). Within activity time, 45–97 per cent is used to search for food (Briedermann 1971a; Cousse & Janeau 1992;

Massei et al. 1997a; Lemel et al. 2000; Cahill et al. 2003; Kuijper et al. 2014). The activity cycles are flexible and may be mono-, bi- or polyphasic (Briedermann 1971a; Meynhardt 1989; Cousse & Janeau 1992; Boitani et al. 1994; Keuling et al. 2008b). Males have shorter activity times than females, probably due to differences in their own nutritional needs and the energetic demands of growing piglets (Massei et al. 1997a). Under harsh conditions like frost or drought, activity is reduced (Massei et al. 1997a; Keuling et al. 2008b; Ohashi et al. 2013).

In the nocturnal or crepuscular activity rhythm, the start of activity is strongly correlated with sunset, but may begin earlier in summer (Mauget 1980; Keuling et al. 2008b). The activity declines around sunrise but may continue throughout daylight when days are short (Lemel et al. 2000; Keuling et al. 2008b). The duration of activity is similar across seasons (Lemel et al. 2000; Keuling et al. 2008b) except for autumn (Podgórski et al. 2013), when wild boar may show increased foraging activity to accumulate fat reserves before winter. In Europe, a higher diurnal activity occurs in early summer (May–July) as females with piglets become polyphasic (Janeau & Spitz 1984; Russo et al. 1997; Keuling et al. 2008b). The highest activity occurs in the first half of the activity phase. With the start of activity wild boar move from resting sites to feeding places; after feeding, slower movements or even short resting phases occur. In many studies a period with less activity in the middle of the night was observed and interpreted as a biphasic cycle (Briedermann 1971a; Caley 1997; Saebel 2007; Keuling et al. 2008b). In the second half of the night a higher activity is observed, which is caused by comfort behaviour and a last feeding phase before moving back to the resting site (Saebel 2007; Keuling et al. 2008b, 2009).

Feeding Ecology

Wild boar are omnivorous and generally opportunistic in their food habits, and their diet varies greatly depending on the geographical region, season, and food availability. The total capacity of an adult wild boar's stomach is approximately 5–8 litres. Typically these animals eat between 3 and 5 per cent of their total body mass daily (Baskin & Dennell 2003).

Plant matter predominates in the annual cycle, constituting up to 96 per cent of the diet (Haber 1969; Danilkin 2002; Briedermann 2009; Barrios-García & Ballari 2012; Ballari & Barrios-García 2014). Plant food in the wild boar diet includes seeds, fruits, leaves, stems, shoots, bulbs, tubers, and roots of 173 species and genera of wild plants and 42 species of cultivated plants (Schley & Roper 2003). The fraction of seeds consists mainly of acorns (*Quercus* spp.), beechnuts (*Fagus sylvatica*), and sweet chestnuts (*Castanea sativa*), which appear to be most important for wild boar because of their high energetic value (Grodziński & Sawicka-Kapusta 1970; Groot Bruinderink et al. 1994; Fournier-Chambrillon et al. 1995). The above studies are mainly based in areas of cooler temperatures. However, although animal matter reaches higher proportions in warmer climates, plant matter also dominates the food (Barrios-García & Ballari 2012; Ballari & Barrios-García 2014). Very little is known about the feeding ecology in tropic climates.

While mast is a pulsed resource, the availability of this food category determines the amount and type of other plant food

in the wild boar diet (Durio et al. 1995; Herrero et al. 2005; Briedermann 2009). Agricultural crops are heavily used all year round by wild boar when they are available, particularly during the summer and autumn when their nutritional value is at its peak. A variety of agricultural food items include cereals (e.g. maize *Zea mays*, rye *Secale* spp., wheat *Triticum* spp., sorghum *Sorghum tuberosum*, barley *Hordeum* spp., oats *Avena* spp., rice *Oryza* spp.), vegetables (e.g. potatoes *Solanum tuberosum*, beets *Beta* spp.), legumes, fruits and others (Genov 1981a; Herrero et al. 2006; Ballari & Barrios-García 2014). Maize is one of the crop species preferred by wild boar (Herrero et al. 2006; Schley et al. 2008), but the consumption of maize does not necessarily imply crop damage, because it is commonly used as a bait by hunters and even to deter crop damage (Schley & Roper 2003; Cellina 2008). In areas where agricultural crops are absent and there is no supplemental feeding, ground flora, browse and roots constitute important dietary components (Abáigar 1993; Asahi 1995; Baubet et al. 2004; Koderá et al. 2013; Merta et al. 2014). Wild boar have innate immunity to some poisonous plants, including genera *Aconitum*, *Anemone*, *Calla*, *Caltha*, *Ferula*, and *Pteridium* (Baskin & Danell 2003).

Animal material is consumed by wild boar all year round and includes 47 species and genera. Invertebrate prey includes mainly earthworms, insects as well as snails and slugs; vertebrates include mainly small mammals (rodents, shrews), fish, amphibians, reptiles, and birds (generally eggs, larval or juvenile forms and adults; Danilkin 2002; Schley & Roper 2003; Keuling 2007). In the forest of western Poland, pest insects, i.e. leaf-feeding insects during outbreaking years, constitute 88.3 per cent of the stomach contents of wild boar (Haber 1969). Animal matter can be obtained by wild boar by scavenging or predation (Herrero et al. 2006; Gimenez-Anaya et al. 2008; Barrios-García & Ballari 2012). Large mammals are taken as carrion, although small hares, rabbits or newborn deer fawns are also taken directly as a prey (Schley & Roper 2003). Wild boar eat bird eggs and chicks nesting on the ground, e.g. *Galliformes* birds (Storch 1994; Merta et al. 2009; Oja et al. 2015). The consumption of animal food varies greatly between seasons. In the case of small mammals it is highest in autumn and winter, whereas earthworms were mainly consumed in spring and summer (Baubet et al. 2003; Schley & Roper 2003). A lack of animal matter (especially earthworms) in the nutrition may have negative effects on growth rates and condition (Rose & Williams 1983). The use of carrion can increase during autumn and winter due to the greater availability of carcasses (Briedermann 2009). Typically, wild boar consume animal matter frequently (11.3–90.5 per cent; Schley & Roper 2003; Baubet et al. 2004; Herrero et al. 2006; Gimenez-Anaya et al. 2008; Koderá et al. 2013), but at low total volume (0.2–5.6 per cent; Schley & Roper 2003; Herrero et al. 2005; Cellina 2008; Koderá et al. 2013); however, due to the rapid digestion of soft animal tissues, the proportion of this category may be underestimated (Keuling 2007).

Fungi can be found in the diet year-round but are generally reported in low frequency and volume (Genov 1981a; Groot Bruinderink et al. 1994; Baubet et al. 2004). This food category is also underestimated in stomach contents because of its

high passage rate through the digestive tract (Schley & Roper 2003). The diet of wild boar often contains other uncommon food items including biological materials such as algae, as well as garbage or inorganic material like plastic, rubber and stones (Ballari & Barrios-García 2014). In some cases, these materials are incidentally ingested during rooting or surface foraging. Beyer et al. (1994) estimated that 2.3 per cent of wild boar diet consisted of soil.

The data from published literature allowed grouping of the results of the analyses of wild boar diet according to four habitat types, i.e. forest–farmland, large mixed lowland forests, wetlands, and mountains (Figure 21.8). In terms of quality, five categories of fodder were distinguished. These included agricultural crops, soft and hard mast, as well as animal food, all of which contain high levels of metabolic energy (15.2–15.8 kJ/g dry weight). It also included roots, ground flora, and browse, whose nutritional value amounts to 14.3 kJ/g dry weight and

7.1 kJ/g dry weight, respectively (van Wieren 2000; Hodgkinson et al. 2008; Śliwiński et al. 2010).

The multi-annual and seasonal variability of the diet of wild boar was studied in the forest–farmland habitat of Luxembourg (Cellina 2008; Figure 21.9). For three subsequent years, the proportion of natural food (ground flora, browse, roots, and animals) was highest in the spring. In the summer season, agricultural crops predominate (50–65 per cent). Hunter-provided supplemental food was important to wild boar in the autumn and winter. During a heavy mast year (2004), the importance of the category of supplemental food dropped while the proportion of oak and beech seeds increased to 58.6 per cent (Figure 21.9).

Annual diet. According to Genov (1981a), Dardaillon (1987), Herrero et al. (2006) and Gimenez-Anaya et al. (2008), agricultural crops predominated in the year-round diet of the wild boar living in Polish and Spanish forest–farmland habitat (79 per cent) and in the wetlands situated on the western coast of

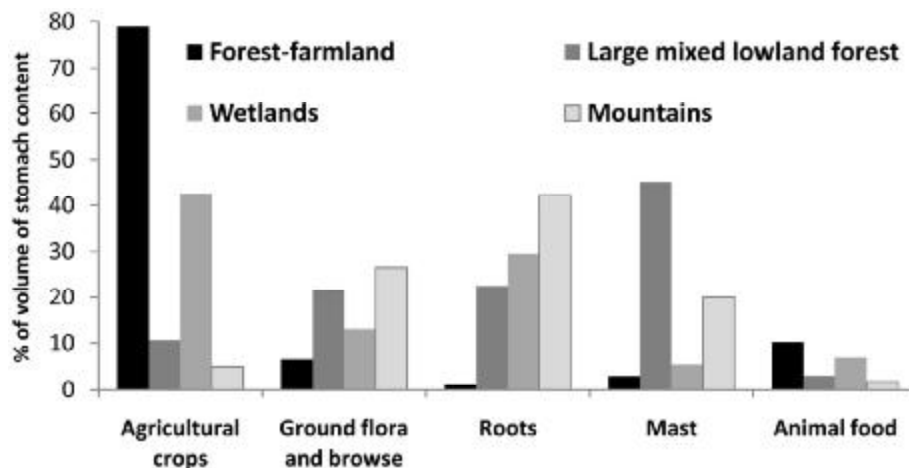


Figure 21.8 The proportions of particular food categories in the year-round diet of wild boar in different types of habitat (1) forest–farmland (Genov 1981b; Herrero et al. 2006); (2) large mixed lowland forests (Abáigar 1993; Groot Bruinderink et al. 1994; Fournier-Chambrillon et al. 1995); (3) wetlands (Dardaillon 1987; Gimenez-Anaya et al. 2008) and (4) mountain areas (Baubet et al. 2004; Koderá et al. 2013).

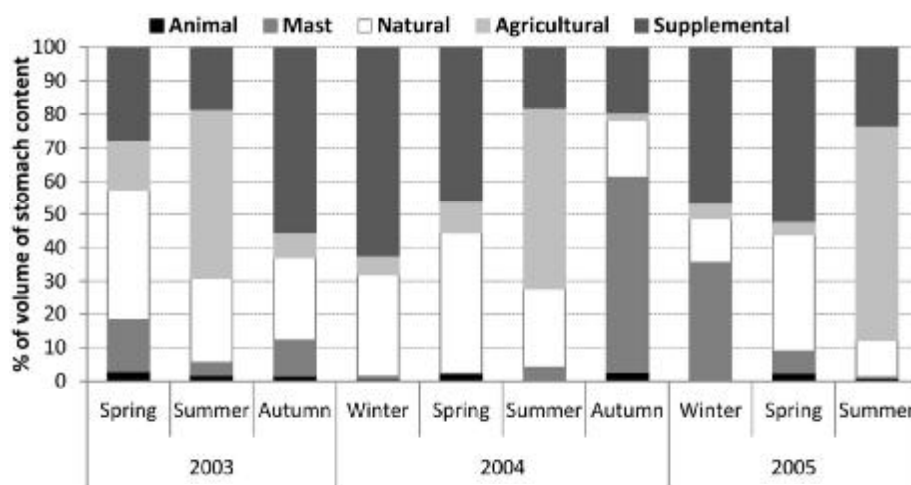


Figure 21.9 The proportions of food components (per cent of volume) in the diet of 1200 wild boar bagged from the spring of 2003 to the summer of 2005 in forest–farmland habitat in Luxembourg (from Cellina 2008).

the Mediterranean Sea (43 per cent). Ground flora and browse appeared in significant proportions in the diet noted in lowland mixed forests in Spain, the Netherlands, and in France (Abáigar 1993; Groot Bruinderink et al. 1994; Fournier-Chambrillon et al. 1995), whereas roots were an essential part of the diet in wild boar living in wetlands of the Mediterranean, in the mountains of Japan, and in the French Alps (Baubet et al. 2004; Kodera et al. 2013; Figure 21.8). The high proportion of mast (45 per cent) in the diet of animals inhabiting Spanish, Dutch, and French forests was due to the heavy mast year at the time of study (Abáigar 1993; Groot Bruinderink et al. 1994; Fournier-Chambrillon et al. 1995) and this category was also essential in the diet of wild boar inhabiting mountains in France and Japan (Baubet et al. 2004; Kodera et al. 2013). The study in the latter country is related to the proposed new species *Sus leucomystax*. Animal food was an important dietary component only in wild boar living in a Polish and Spanish forest–farmland habitats (Genov 1981a; Herrero et al. 2006) and wetlands in France (Dardaillon 1987) and Spain (Gimenez-Anaya et al. 2008) (Figure 21.8).

The autumn–winter diet of wild boar in various environments is presented in Table 21.4. Agricultural crops predominated in the diet of wild boar living in forest–farmland habitat in Spain (Herrero et al. 2006), Luxembourg (Cellina 2008) and Poland (Genov 1981a; Wlazelko et al. 2009; Merta et al. 2014). In Polish and Dutch mixed lowland forest (Groot Bruinderink et al. 1994; Miśkiewicz 2013; Merta et al. 2014) and in mountain areas this category was of no significant importance. Ground flora, browse, and animal food are important components of wild boar fodder in the Polish and Dutch mixed lowland forest. In mountain areas situated in Italy, Japan, Spain, Greece, in the French Alps and the Carpathians, root and mast predominate (Gunczak 1980; Durio et al. 1995; Baubet et al. 2004; Tschalidis et al. 2004; Herrero et al. 2005; Kodera et al. 2013), while in Mediterranean wetland habitats, roots and animal food are important components (Table 21.4).

Concluding remarks. The nutrient composition of food consumed by wild boar affects their body weight and fat reserves which, in turn, determines the age of puberty, rate of reproduction, mortality and population dispersion (Briedermann 2009; Merta et al. 2014). Knowledge of the diet of wild boar can be useful in population management, but the research has to take into account the geographical, seasonal, and annual differences associated with changes in the quantity and quality of potential food resources. The quality of research of the diet of wild boar could also be improved by performing long-term studies and increasing

the number of samples and reporting the proportions of food categories measured in dry mass based on stomach contents.

Reproduction and Growth

Being a multiparous species, wild boar reproduction rates differ from many other ungulates (Gaillard et al. 1989). *Sus scrofa* shows traits of the slow–fast pace of life continuum strategy. Typically it combines sexual size dimorphism (Focardi et al. 2008) and a low natural adult mortality rate in temperate climates (Keuling et al. 2013). At the same time, *Sus scrofa* has by far the highest reproductive potential and fecundity of all ungulate species worldwide in relation to its body mass (Gaillard et al. 1993; Boitani et al. 1995a; Focardi et al. 2008; Servanty et al. 2009; Fonseca et al. 2011) and therefore can reach high population densities within a very short time period (Geisser & Reyer 2005). The slow–fast pace of life continuum strategy is dependent on environmental conditions and has caused an enormous increase of wild boar in the whole of Europe during the last decades (Keuling et al. 2013; Lombardini et al. 2014; Massei et al. 2015; Vetter et al. 2015).

Male wild boar may reach puberty within the first year (Ahlers 2013). It is uncertain if this may lead to an early paternity, as mating was assumed to be mainly dominated by adult male boars interacting with various female routs (Briedermann 1986, 2009). However, there is evidence of multiple paternity in several cases (Delgado et al. 2008; Delgado-Acevedo et al. 2010; Müller et al. 2015). Female wild boar also reach puberty within 12 months and a pregnancy within the first year is feasible if a certain threshold body mass (about 30 kg) is reached (e.g. Gethöffer et al. 2007; Servanty et al. 2009). In Europe, high percentages of female piglets do start reproduction within their first year, as they live under optimal environmental conditions (Appelius 1995; Gethöffer et al. 2007; Lustig et al. 2015). Time of mating is clearly seasonal, depending mainly on photoperiodicity (Claus & Weiler 1985). In Europe, there is a peak of farrowing from March to April (Moretti 1995; Gethöffer et al. 2007; Fonseca et al. 2011), including within-year variations of several weeks depending on climate and nutritional factors (Fonseca et al. 2001; Fernández-Llario & Mateos-Quesada 2005; Gethöffer et al. 2007; Cutini et al. 2013; Canu et al. 2015). Under good environmental and climatic conditions, farrowing has been observed all year long with a peak in late winter–springtime (Monaco et al. 2003). Litter sizes differ depending on age and weight of wild boar females (Nahlik & Sandor 2003; Gethöffer et al. 2007; Lustig et al. 2015) as well as due to external conditions

Table 21.4 The proportions (%) of particular food categories in the autumn–winter wild boar diet estimated in various types of habitat.

Habitat type/food category	Agricultural crops	Ground flora and browse	Roots	Mast	Animal food	Others
Forest–farmland ^(1–5)	63.7	10.4	3.4	15.4	4.1	3.0
Large mixed lowland forests ^(4, 6, 7)	3.1	40.8	12.3	35.2	6.9	1.7
Wetlands ^(8, 9)	41.8	11.1	29.7	3.7	6.1	7.6
Mountains ^(10–15)	1.0	23.7	25.7	42.4	2.8	4.4

¹Herrero et al. 2006; ²Cellina 2008; ³Wlazelko et al. 2009; ⁴Merta et al. 2014; ⁵Genov 1981b; ⁶Groot Bruinderink et al. 1994; ⁷Miśkiewicz 2013; ⁸Gimenez-Anaya et al. 2008; ⁹Dardaillon 1987; ¹⁰Baubet et al. 2004; ¹¹Durio et al. 1995; ¹²Kodera et al. 2013; ¹³Herrero et al. 2005; ¹⁴Gunczak 1980; ¹⁵Tschalidis et al. 2004.

Table 21.5 Litter size in wild boar populations from several European countries.

Location	Adult litter size	Overall litter size	Reference
Spain	–	3.69	Fernández-Llario et al. 1999
	–	3.05	Fernández-Llario & Carranza 2000
	–	3.75	Fernández-Llario & Mateos-Quesada 2005
	–	4	Herrero et al. 2008
Portugal	–	4.17	Fonseca et al. 2004
Italy	5.03	4.95	Boitani et al. 1995b
	–	2.3–4.4	Massei et al. 1996
	–	4.2	Focardi et al. 2008
France	–	4.6	Mauget 1982
	–	5.5	Servanty et al. 2007
Switzerland	5.7	4.9	Moretti 1995
Hungary	–	6.7	Nahlik & Sandor 2003
Germany	6.5	5.3	Stubbe & Stubbe 1977
	6.2–6.8	–	Briedermann 1971b
	6.5–7.6	–	Gethöffer et al. 2007
	–	6.6	Frauendorf et al. 2016
Luxembourg	–	5.3	Cellina 2008
Poland	6.3	–	Fruzinski 1995

such as food availability (Gethöffer et al. 2007; Frauendorf et al. 2016), climate, and latitude (Fernández-Llario & Carranza 2000; Fernández-Llario & Mateos-Quesada 2005; Bywater et al. 2010; Rosell et al. 2012).

About after 115 days of gestation (Henry 1968), piglets of approximately 670–1090 g are farrowed (Briedermann 2009). Female piglets are usually smaller and lighter than their male siblings (Briedermann 2009). Within the first three to four months, piglets are striped and change into a unicoloured light brown later on. At that time, suckling has stopped and the animals gained an average of 12.8 kg carcass weight (Briedermann 1970). Sex ratio in litters seems to be influenced by female body weight and mast conditions, e.g. heavier wild boar sows produce more male offspring whereas in excellent mast crop conditions, female offspring predominated (Servanty et al. 2007; Frauendorf et al., unpublished). For litter sizes in several European countries see Table 21.5.

Behaviour

Social Organization

The Eurasian wild boar lives in matrilineal societies. The basic social unit is a family group centred around one to several adult females and their offspring from the current and previous years (Dardaillon 1988; Nakatani & Ono 1995; Rosell et al. 2004). Most members of the groups are genetically related to each other at the level of first- or second-order relatives (Kaminski et al.

2005; Poteaux et al. 2009; Podgórski et al. 2014a). High levels of relatedness within the groups indicate that multiple litters of related females are associated to form multigenerational social units. When natural group structure is disrupted (e.g. due to hunting) social units may be composed of unrelated individuals (Iacolina et al. 2009). Group size ranges between 2 and 70 individuals (Gabor et al. 1999; Rosell et al. 2004; Poteaux et al. 2009; Podgórski et al. 2014a; A. Monaco, personal observation), but the size of stable and coherent social groups usually falls within a range of 5–10 individuals: seven in north-eastern France (Poteaux et al. 2009), four in northern Spain (Rosell et al. 2004), six in Texas, USA (Gabor et al. 1999), and seven in north-eastern Poland (Podgórski et al. 2014a). Stable family groups are typically composed of 1–2 adult (≥ 2 years of age) females, few sub-adults (1–2 years) and several juveniles (≤ 1 year) of both sexes. Adult males are solitary and rarely found within the groups outside of the breeding season. During the rut, which takes place in the late autumn and early winter, males temporarily join female groups for mating (Graves 1984; Dardaillon 1988).

The wild boar is not territorial. Home ranges of neighbouring groups partly overlap and individuals from different groups interact regularly (Boitani et al. 1994; Podgórski et al. 2014b). Groups may temporarily merge to form larger units and single individuals may occasionally shift between groups. In a well-studied population of wild boar in France, social groups were relatively stable across 3 years of the study with a few fission–fusion events (Poteaux et al. 2009). Stable groupings were also observed in an undisturbed population of the Białowieża Primeval Forest, Poland, where strong associations among related group members resulted in distinct social, spatial, and genetic population structuring (Podgórski et al. 2014a, 2014b). Social organization of feral pig populations is more dynamic, with frequent inter-group associations and group rearrangements, high turnover within the groups, and low population structuring (Texas, USA: Gabor et al. 1999; Australia: Spencer et al. 2005). However, the social structure of these populations may be altered by intensive management.

Social dynamics observed in wild boar populations is largely a consequence of the species' life history. Male offspring leave maternal groups early in their life, usually around one year of age, and become solitary boars (Hirotani & Nakatani 1987; Dardaillon 1988), while female offspring show stronger fidelity to maternal groups and most of them (70–80 per cent) remain within or in close proximity of the natal range, frequently associating with their mothers (Hirotani & Nakatani 1987; Dardaillon 1988; Kaminski et al. 2005; Podgórski et al. 2014a). Young females maintain strong social bonds with their mothers throughout the nursing and post-weaning period until the next farrowing (February–April), when pregnant females separate temporarily from the groups to give birth. In this period, groups composed solely of yearling females are frequently observed (Hirotani & Nakatani 1987; Dardaillon 1988). After parturition, most of the yearling females reunite with the maternal group, but some of them may separate permanently and establish new, kin-based, social units (Kaminski et al. 2005). Despite seasonal fluctuations of group cohesion, adult females maintain stable, long-lasting relationships and rarely shift between groups for

longer periods of time (Gabor et al. 1999; Poteaux et al. 2009). Conversely, adult males engage in dynamic and short-lived relationships (Podgórski et al. 2014b), involving interactions with mating competitors (associations with other males) or assessment of females reproductive status and mating (with females).

Mating and Breeding

The breeding activity of wild boar is seasonal and regulated by photoperiodicity. The mating season peaks in November–December when most of the reproductively active females come into oestrus (Mauget 1982) and males show increased testes size, testosterone levels, and semen quality (Schopper et al. 1984; Mauget & Boissin 1987; Kozdrowski & Dubiel 2004). In this period, boars roam widely and regularly make excursions outside their home ranges in search of receptive females (Spencer et al. 2005). Roving males may visit several female groups and associate with them for short periods of time. Boars actively compete for access to oestrous sows. The opponents assess each other's quality through parallel walks with manes erected, shoulder pushing, and wrestling in a stand-up position. If neither gives up, the contest may escalate into a potentially fatal combat involving thrusting with bared tusks (Graves 1984; Barrette 1986). The winner gains access to receptive females within the group. During the courtship, boars approach and nudge the females, utter a series of grunts, and champ while salivating. In response to pheromones in the boars' saliva, receptive sows get into mating posture and accept being mounted by the boar (East & Dehnhardt 2013). Because oestrus among females within a group is often synchronized (Delcroix et al. 1990; Canu et al. 2015) males can copulate with several females consecutively. However, females can mate with more than one boar within 2–3 days of being in oestrus, e.g. when a dominant boar takes over a group shortly after females have been mated, and thus litters of multiple paternity may occur (Spencer et al. 2005; Delgado et al. 2008; Poteaux et al. 2009).

A few days before parturition, the pregnant sow separates from the group and commences building the farrowing nest. Nests are usually located in dense cover and are constructed by rooting a shallow depression in the ground or piling up rooted soil and vegetation with a central hollow on top of the pile. In cold environments large, well-insulated nests can be built from the available material such as branches, twigs, or reeds (Kurz & Marchinton 1972). Farrowing lasts for a few hours, with a 15-min interval between each piglet. Newborn piglets remain in the nest for a couple of days after parturition and then join the maternal group. Piglets are weaned at around 4 months of age, but already at 4 weeks they start rooting and processing solid food (Špinka 2009). Due to the synchronized oestrus of sows within a group, multiple litters of similar age may be present in a group at the same time and females may participate in cooperative nursing and guarding of the young. There are observations of females taking shifts in babysitting of the group's offspring, while other females are away foraging (Graves 1984).

Comfort Behaviours

Wild boar lack sweat glands and thus need to regulate body temperature behaviourally to avoid overheating (Huynh et al. 2005). One way of cooling down in hot weather is wallowing,

i.e. rolling in a depression filled with water or mud to moisturize the body surface (Fernández-Llario 2005). Such mud holes are utilized in all seasons but particularly frequently in summer (Bracke 2011, O. Keuling, T. Podgórski, personal observations). Wallowing also serves intraspecific communication and hygienic purposes, as it is often followed by rubbing against the trees, when mud plastered to the skin is removed along with the ectoparasites. Wild boar spend long periods of inactivity in bedding spots. Such resting sites may just be a depression of the forest floor with loosened litter. They are often located at the base of a tree or by fallen logs. In winter, animals rest close to each other, choose sites better protected from adverse conditions (e.g. under dense canopy), and may add available material (e.g. brush, leaves) as bedding. When human disturbance is high (e.g. hunting, urban areas) day beds are better sheltered and often found in dense vegetation.

Communication

Wild boar have a particularly well-developed sense of smell, which is used in foraging, communication, navigation, and predator avoidance. Pigs use olfactory cues to locate and distinguish food items at close distance (Suselbeek et al. 2014) and to assess predation risk (Kuijper et al. 2014). Scent signals play an important role in social communication. They help in individual recognition and advertising sexual status. Young piglets can use olfactory cues to locate familiar individuals and rejoin native groups early in life (Kittawornrat & Zimmerman 2011). Adult males produce pheromones (e.g. androsterone present in saliva and urine) which trigger the mating behaviour of the females and may advance their puberty (Brooks & Cole 1970; Kirkwood et al. 1983). Chemical marking is often performed while wallowing and tree-rubbing. Scent marks also seem to act as landmarks, helping to navigate within the home range (Bracke 2011). Wild boar also have good auditory capacities and a rich repertoire of vocal signals used in social communication. There are around 20 types of calls, such as grunts, squeals, and trumpets, which may vary in amplitude, frequency, and modulation depending on the context (Garcia et al. 2016). This diversity reflects many functions of the vocalizations, which have yet to be fully explored. Grunts are produced when foraging, in signalling danger, or serve as contact calls (Meynhardt 1980). Squeals are often emitted during agonistic interactions, when pigs are threatened or attacked. In domestic pigs, nursing sows emit regular grunts to announce a milking episode and call the piglets to the udder (Špinka 2009) and the piglets produce emergency calls of varying volume and pitch when distressed or in need (Weary & Fraser 1995). Vision is poorly developed in wild boar and its role in communication is limited. Visual signals, usually displayed by competing or threatened animals, include ears and body positioning, erection of the dorsal mane, tail movement, bristle rising, and back arching (Graves 1984; Barrette 1986).

Attacks on Humans

The overall expansion and increase in number of wild boar have also resulted in more encounters with or even attacks on humans, in particular within urban and suburban areas

(Licoppe et al. 2013) where this problem is often exacerbated because of direct feeding by local people (Cahill et al. 2012). Wild boar are rarely dangerous to humans and usually try to flee from people. Nevertheless, even though very rare, attacks on humans have been reported since prehistoric times (e.g. Mesolithic paintings at the Rock Shelters of Bhimbetka, Madhya Pradesh, India) and can cause severe injuries or even fatalities, typically due to blood loss (Mayer 2013). Unlike as is reported for attacks by some large predators, the goal of wild boar attacks is defensive rather than predatory. Wounded animals are the typical cause of an attack under hunting circumstances (Mayer 2013; Šprem et al. 2014). Conversely, the most common cause for attacks by healthy animals is the animal being threatened. Most of these attacks are done by large solitary males or sows defending their piglets (Mayer 2013).

Parasites and Diseases

Wild boar are carriers of at least 45 different parasitic (external and internal) and infectious (bacterial and viral) diseases that pose a threat to livestock, wildlife, or human health. The most important are reviewed extensively in the published literature (Meng et al. 2009; Ruiz-Fons 2017) and Chapter 35. The role of wild boar as disease carriers has become of increasing concern in industrialized countries where its population densities are increasing (Wu et al. 2011; Boadella et al. 2012). They are particularly perceived as a threat by the pig industry due to their reservoir role for many pathogens such as Aujeszky's disease, brucellosis, and classical swine fever that have been eradicated from domestic pigs but persist in wild boar populations. African swine fever is equally affecting wild boar and threatening domestic pig production in Eastern Europe (Sanchez-Vizcaino et al. 2013) and is still endemic on Sardinia. Other porcine viral diseases such influenza, circovirus type 2, and parvovirus can be found at high prevalence, even in natural isolated unmanaged populations of wild boar (Cano-Manuel et al. 2014).

An association between density and prevalence of pathogens has been described for many diseases (Boadella et al. 2012; Meier et al. 2015). Therefore, any wild boar population management programme should encompass a disease surveillance component. This is particularly relevant for activities that can affect population density, aggregation, or competition for food (such as estate fencing, supplementary feeding) or those that can induce population stress (Meier et al. 2015). A large number of wild swine diseases can affect humans (Meng et al. 2009). However, those are mainly responsible for localized disease outbreaks and are limited to persons professionally linked with forestry or hunting activities, and only a few viruses and bacteria are more prone to be able to infect human hosts (Ruiz-Fons 2017).

Status in the Wild

Eurasian wild boar is both a highly adaptable and highly resistant species to a variety of destructive processes and may withstand conditions of habitat degradation and high hunting pressure which have eradicated other forms of wildlife (Oliver & Leus 2008).

Wild boar is the most widespread pig in the world and many populations are abundant in several regions. For example, in Europe, wild boar numbers have increased in recent decades,

probably due to a combination of factors, such as the depopulation of rural areas, changes in agricultural practices, reintroduction for hunting purposes, lack of predators, reduced hunting pressure in some regions, and climatic changes (Genov 1981b; Erkinaro et al. 1982; Saez-Royuela & Telleria 1986; Apollonio et al. 2010; Massei et al. 2015; Vetter et al. 2015).

There are not many data available on wild boar population trends and harvest in its huge range. In a study conducted in 18 European countries in 2012 and 2013, Massei et al. (2015) analysed wild boar hunting bags and the result shows that some countries such as Spain, Poland, France, Italy, and Germany harvest between 200,000 and 640,000 wild boar per year. These trends in hunting bags follow the population growth in all countries throughout the last three decades, although growth rates are different among countries. The mean annual population growth rate index averaged across all countries showed a regular pattern, with peaks followed by troughs at 3–4 year intervals. In four of the 30 years considered for the analysis, the mean wild boar population growth index across Europe was lower than 1 showing a population decrease (with 1 = stable population), while in all other years the growth rate index varied between 1.00 and 1.46, indicating a stable or increased population (Massei et al. 2015).

Globally this species is not threatened and is classified as Least Concern in the IUCN Red List except for some subspecies (Oliver & Leus 2008). Some of these, such as the *riukiuanus* (proposed as new species in this book) in Japan, have been greatly reduced at local level due to habitat destruction, control measures for crop damage, and hunting pressure. Although *riukiuanus* is recognized threatened in its restricted range by the scientific community and protected by the Japanese government, it is still hunted. This subspecies is the only one included in the Red List of IUCN as Vulnerable. In this context, priority should be given to the establishment of national or regional breeding programmes for each of the rarest species, in particular *riukiuanus*. In some areas another threat is interbreeding with domestic and feral pigs, which reduces the genetic purity of some populations. For example, in Ishigaki Island (Japan) the local *riukiuanus* population have interbred with domestic pigs for a long time and it is unlikely that the remaining population can be considered genetically pure (Obara 1982). Another example of a threat to the genetic purity of native wild pigs is reported by Genov et al. (1991) in eastern Bulgaria, where the traditional practice of rearing domestic pigs in semi-wild conditions has led to their hybridizing with the wild boar populations. As a result, it seems that pure wild boar in Bulgaria now occur only in the Rila-Pirin-Rhodopes Mountains in the south of this country, where domestic pigs are not reared in the wild (P. Genov, personal communication). Other threats, for example, are the contagious diseases that can strongly reduce some populations in small areas, as happened in Sri Lanka in 1989 due to swine fever (Wilson & Mittermeier 2011).

Besides the threatened *riukiuanus*, other less well-known forms, such as the populations of Sri Lanka and Taiwan, should also deserve priority conservation actions as we know little about their taxonomic relationship, distribution, and conservation status. In addition, studies on the ecology and biology of populations in extreme habitats should also be implemented. Finally,

our knowledge on the genetic relationships in regions such as the Malayan Peninsular and Sumatra or Java should be improved where wild boar occur in sympatry with *Sus barbatus* and *Sus verrucosus*, respectively (Oliver et al. 1993; Oliver & Leus 2008).

Pigs also play an important role as a food resource in some tribal societies, for example on the Andaman Islands. In other areas such as the Nicobar Islands, Papua, Macronesia, and Micronesia, complex human–pig cultures have evolved with domesticated *Sus scrofa* and *Sus celebensis* having an important cultural role (Wilson & Mittermeier 2011).

Population Growth and Climate Change

Wild boar populations all over Europe have grown considerably during the last decades (Massei et al. 2015). A recent study investigating factors causing this population growth in 64 regions from 12 European countries showed that climate change is one major driver (Vetter et al. 2015). Wild boar are highly susceptible to cold winter conditions and average winter temperature is known to affect juvenile mortality (Geisser & Reyer 2005), a major determinant of population dynamics in the wild boar (Vetter et al. 2015). However, cold winter conditions, which were consistently followed by population declines (Vetter et al. 2015), have become increasingly rare (Figure 21.10a).

Although the positive effect of mild winter temperatures was weaker in generally warmer regions compared to colder ones, it was detected over a large climatic range and thus is not restricted to cold areas only (Vetter et al. 2015). This is most likely because of phenotypic differences between wild boar populations, as a result of local adaptation or phenotypic plasticity, causing population-specific temperature thresholds for population growth. Wild boar populations in warmer areas consist on average of smaller individuals and start to grow only at higher absolute average winter temperatures compared to those in colder regions (Vetter et al. 2015). These local differences can explain why an increase in mean winter temperatures has led to almost concurrent increases in wild boar population sizes all over Europe (Figure 21.10A–C; Saez-Royuela & Telleria 1986; Massei et al. 2015; Vetter et al. 2015), despite differences in local climates.

Besides the direct effect of increasingly mild winter temperatures, climate change also affects wild boar populations indirectly by increased food availability (Vetter et al. 2015). Wild boar in Europe strongly rely on tree seeds in their diet (Jędrzejewska et al. 1997; Schley & Roper 2003; Bieber & Ruf 2005; Briedermann 2009). As described above, the availability of this food source varies greatly between years, but climate change causes years of low abundance to decrease in frequency (Övergaard et al. 2007; Vetter et al. 2015). It is only in these years, however, that cold winter temperatures affect wild boar population growth negatively, whereas this is not the case in years of high food availability (Vetter et al. 2015). In such years, beechnuts or acorns are available in vast amounts from autumn until spring of the following year (Schley & Roper 2003; Bieber & Ruf 2005; Briedermann 2009). This likely enables adults to accumulate high amounts of body energy reserves for reproduction in the following year and juveniles to cope even with high thermoregulatory costs in a severe winter.

Consequently, the positive effect of climate change on wild boar population growth in Europe was twofold: first, cold winters

became increasingly rare and, second, the remaining severe winters were less effective at reducing wild boar populations because of the increasing frequency of years with high food availability.

Population Trend in Europe

Because wild boar population estimates on a large scale require a large effort and results are generally poor in terms of accuracy (Engeman et al. 2013), only a few countries attempt to apply some kind of census technique, whereas others do not undertake any form of census at all. Commonly, estimates of population size rely on hunting bags. The accuracy of hunting bags could vary significantly between countries; in some cases, data are available only for a part of the country or unavailable at all. Moreover, the accuracy of harvest records is often difficult to assess, for instance because reports provided by hunters underestimate the true number of harvested wild boar and no data are available on poaching. Table 21.6 shows the last general picture available (Massei et al. 2015) for what concerns bags for most European countries.

Using hunting bag statistics as a proxy of population size and assuming that potential biases of accuracy of hunting bags are constant within each country over time, trends of wild boar populations in Europe during the last three decades have been recently quantified (Massei et al. 2015; Vetter et al. 2015). Trends showed a continuous general increase of wild boar numbers since 1982, partially confirming the trends highlighted between the 1960s and the 1980s from a previous review (Saez-Royuela & Telleria 1986). In spite of the increase of hunting bags (more than 150 per cent from 1992 to 2012) and over 3 million wild boar annually harvested in Europe, hunting seems to be insufficient to limit population growth. A country-specific combination of factors can account for this growing trend, including changing hunting intensities, deliberate releases, supplementary feeding, landscape changes (i.e. reforestation), as well as climate change causing milder winters and increased natural food availability (Massei et al. 2015; Vetter et al. 2015). Additionally, the hunting seems not to harvest all the needed population growths (Keuling et al. 2013), mainly as hunters do not want to reduce wild boar densities (Keuling et al. 2016).

Despite the importance of wild boar in terms of economic interests, there is a lack of general data on human–wild boar conflicts (i.e. damage to crops, vehicle collisions; see Chapter 32 for more details) and no continental figures are available on this topic. However, data coming from different countries support the finding that wild boar numbers have grown. Indeed, both crop damage and road traffic accidents caused by wild boar are growing (Schley et al. 2008; Liberg et al. 2010; Maillard et al. 2010; Morelle et al. 2013), causing an increase in human–wild boar conflicts throughout Europe (Glikman & Frank 2011; Frank et al. 2015). Simultaneously, there is also growing evidence for the impacts of wild boar overabundance on ecosystems (Massei & Genov 2004; Bueno et al. 2011; Barrios-Garcia & Ballari 2012).

Genetics

Recent studies focused on the genetic diversity and philogeography of wild boar in Europe. These analyses rarely resulted in homogeneous populations, but usually showed genetic

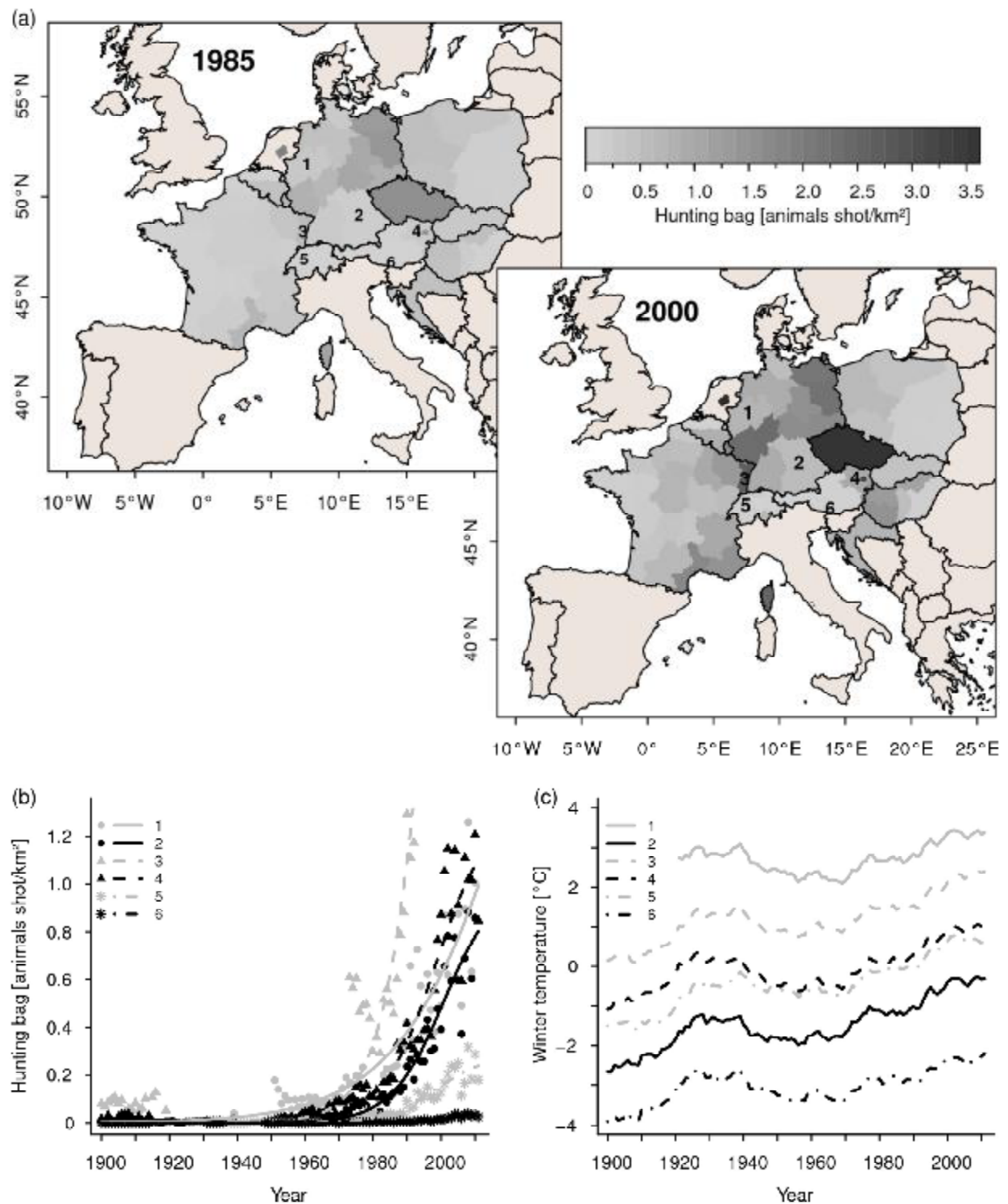


Figure 21.10 Increase of European wild boar populations and mean winter temperatures. (a) Wild boar densities in various regions 1985 and 2000, respectively. For six exemplary regions time courses of wild boar hunting bags (b) as well as corresponding changes in long-term mean winter temperatures (30-year means, 1973–2002) (c) are shown: 1 = North-Rhine Westphalia (DE), 2 = Bavaria (DE), 3 = Alsace (FR), 4 = Lower Austria (AT), 5 = Espace Mittelland (CH), 6 = Carinthia (AT). Figure modified from figure 1 in Vetter et al. (2015) licensed under CC BY 4.0 (<http://creativecommons.org/licenses/by/4.0/>). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

Table 21.6 Annual hunting bag of wild boar in 17 European countries (modified from Massei et al. 2015).

Country	Hunting bag*
Austria	37,743
Belgium	24,182
Czech Rep.	145,565
Croatia	20,608
France	560,811
Germany	518,086
Hungary	129,685
Italy	185,518
Latvia	25,568
Luxembourg	4,968
Poland	223,000
Portugal	22,753
Serbia	5,386
Slovenia	9,324
Spain	216,370
Sweden	69,075
Switzerland	7,027

*Mean value 2010–2013.

differentiation into subpopulations (Ferreira et al. 2006, 2009; Scandura et al. 2008; Nikolov et al. 2009; Scandura et al. 2011a; Veličković et al. 2012, 2015; Kusza et al. 2014). A continental picture seems to highlight the existence of three well-differentiated gene pools, each related to one of the three southern European peninsulas (Balkans, Italy, and Iberia), and a central-eastern European pool with an admixed origin as a result of an extensive gene flow from all three peninsular gene pools (Alexandri et al. 2012; Vilaça et al. 2014; Veličković et al. 2015). The three peninsulas therefore seem to have played a crucial role as refuge areas during glaciations and in the subsequent postglacial recolonization of Europe. Some subpopulations in peninsulas, such as the one in the Preserve of Castelporziano (central Italy), are well known for their distinctive genetic assembly (Scandura et al. 2008; Vilaça et al. 2014) and a low level of diversity and heterozygosity compared to other subpopulations (Veličković et al. 2016). Their peripheral location within peninsulas supports the hypothesis that they may have been relict and isolated during glacial periods (Veličković et al. 2015).

Studies almost unanimously support the hypothesis that patterns of genetic diversity and the structure of wild boar populations in Europe have been shaped by quaternary glacial/interglacial cycles more than by human actions in the last centuries (Scandura et al. 2008; Vilaça et al. 2014; Veličković et al. 2015). Indeed, despite the indisputable role of hybridization or translocations on a local scale, no evidence of extensive gene flow between wild boar and domestic pig breeds (Scandura et al. 2008, 2011b) or between geographically distant subpopulations of wild boar has been evidenced (Veličković et al. 2016).

Status in Captivity

Of all wild pig species, *S. scrofa* is by far the one most widely kept and bred in captivity, although the relative abundance of this species has resulted in a decreased interest in its propagation. Many zoos, particularly in Western Europe, therefore relinquished their stocks of these animals, mostly to wild boar breeding farms. Such farms increased in number to meet growing demands in the meat markets in many countries where, for example, a variety of different products are made from wild boar meat. In addition, increasingly restrictive quarantine and other veterinary regulations concerning international movements of live suids made it extremely difficult to establish new breeding programmes in zoos (AZA 2008).

The wild boar in Europe is not threatened and is not considered a candidate for any particular in-situ conservation action plan. Most countries manage and regulate their populations for hunting purposes. At the present time the TAG (Taxon Advisory Group) has recommended that this species is phased out of collections in North America unless compelling reasons are presented to maintain a population for institutions that are committed to a zoogeographic theme. Until 2008, the North America population counted a very small captive population with just 28 males, 38 females and one juvenile in 34 Institutions (AZA 2008).

Currently there are no ex-situ conservation programmes for any *Sus scrofa* species/subspecies (AZA 2008), although *riukiuanus* should deserve particular attention due to its limited range and threats (see above). The IUCN Red List has proposed a conservation action plan aimed at promoting the development of a coordinated breeding programme for *S. riukiuanus*, both nationally and internationally (Oliver & Leus 2008). However, zoological institutions should use caution to keep together some threatened species/subspecies coming from restricted areas, in particular from Asia. This should reduce hybridization between them and, given the recent development in wild boar taxonomy, it is important to treat them as separate taxonomy units.

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