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REVIEW

A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges

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ABSTRACT

1. The wild boar *Sus scrofa* is an omnivore with one of the largest geographical ranges of all species. However, no synthesis exists on its diet, feeding behaviour and factors affecting food selection in its native and introduced ranges.
2. A literature review and a test of effect size revealed significant differences in wild boar diet composition in native and introduced ranges. Wild boar diet is dominated by plant material (~90%) in both ranges, but animal matter and fungi are consumed in greater proportions in the introduced range than in the native range. Food items frequently include agricultural crops (especially in the native range) and endangered animal species (especially in the introduced range). Energy requirements, food availability, and seasonal and geographical variations are major factors influencing food selection by wild boar. These factors may also interact with human activities (e.g. agricultural crops, supplementary feeding) to influence diet composition further.
3. Dietary studies should be more rigorous and consistent across ranges to allow better comparisons. A detailed study of diet in combination with seasonal patterns of habitat use could provide key information such as target species and susceptible habitats on which management efforts should focus.

INTRODUCTION

Wild boars *Sus scrofa* have highly plastic diets, and their ability to adapt to diverse foods has allowed them to establish populations in almost every location where they have been introduced (Genov 1981a, Rosell et al. 2001, Baubet et al. 2004, Irizar et al. 2004). Wild boars are opportunistic omnivores feeding on all types of organic matter and sometimes on inorganic materials like stones, mud and plastic (Schley & Roper 2003, Massei & Genov 2004, Herrero et al. 2005, Hafeez et al. 2011). The diet of the wild boar has been well studied in some parts of its native range (Genov 1981a, Asahi 1995, Fournier-Chambrillon et al. 1995, Sáenz de Buruaga 1995, Baubet et al. 2004, Herrero et al. 2004, 2005, 2006, Irizar et al. 2004, Cellina 2008) and its introduced range (Challies 1975, Rudge 1976, Everitt & Alaniz 1980, Wood & Roark 1980, Howe et al. 1981, Baber & Coblentz 1987, Thomson & Challies 1988, Chimera et al. 1995, Taylor & Hellgren 1997, Adkins & Harveson 2006, Desbiez 2007, Skewes et al. 2007, Cuevas et al. 2010, Cuevas et al. 2013), but there are no syntheses or comparisons between native and introduced ranges in terms of diet composition and feeding behaviour.

Depending on the habitat type, wild boars may carry out different trophic functions, acting as crop pests, frugivores, predators, destroyers of seed banks and plant dispersers (Genov 1981b, Geisser & Reyer 2004, Bueno et al. 2011, O'Connor & Kelly 2012). These functions are carried out through four main feeding behaviours: browsing and grazing (grasses, herbs, stems, leaves), foraging on the ground (fruits, fungi, animal matter), rooting (rhizomes, roots, invertebrates), and predation (vertebrates; Thomson & Challies 1988, Baubet et al. 2004, Wilcox & Van Vuren 2009, Bueno et al. 2011). Overall, wild boars seem to show

no particular foraging preference except for plant matter over animal matter (Schley & Roper 2003, Massei & Genov 2004, Herrero et al. 2005, Adkins & Harveson 2006, Keuling 2007, Wilcox & Van Vuren 2009). However, some authors emphasize their preference for a few items: stenophagy (Herrero et al. 2006). For example, Herrero et al. (2005) found that wild boars feed on a few abundant preferred items that are highly digestible and nutritious, such as acorns from the downy oak *Quercus humilis*.

Studies of the diet composition are important to determine target species, food categories (plant vs. animal matter) and seasonal variation, which may allow prediction of when and why certain plant or animal communities might be impacted (Wood & Roark 1980). Determining diet composition can aid in understanding how wild boars use different ecosystems and consequently in identifying their role in the food web (Baubet et al. 2004). The aim of this study is to compare the diet and feeding patterns of wild boars in their native and introduced ranges, with special emphasis on introduced ranges, because these environments are not adapted to support the species (Barrios-Garcia & Ballari 2012, Spatz & Mueller-Dombois 1972, Nogueira-Filho et al. 2009). By means of a literature review, we also assess how variation in food availability, habitat use and behavioural patterns is reflected in the diet. Understanding feeding habits in combination with seasonal patterns of space and habitat use may inform management plans.

METHODS

We conducted a literature search for articles using the keywords 'diet', 'feed*', 'wild boar' and '*Sus scrofa*' in the search engine ISI Web of Knowledge and also checked the references cited in all papers we found. We set the search for studies between 1970 and 2013 and included studies referring to wild boar, feral pigs and hybrids.

The literature search yielded 145 studies, of which 78 were relevant to wild boar diet (Appendix S1). Thirty-nine studies were conducted in the native range and 39 in the introduced range. The majority of the studies were focused on descriptive aspects of diet such as diet composition and feeding habits ($n = 45$, Fig. 1). Many studies were focused on impacts such as predation, damage to plant species, habitat degradation and crop damage ($n = 31$), or on processes or patterns such as rooting and seed dispersal ($n = 20$). Only 12 studies were on nutritional aspects of the diet, and six were on management aspects.

To determine the relative contribution of food items in the native and introduced ranges, we used the log-response ratio. We extracted data from 36 studies in which the dietary composition was listed in terms of frequency and percentage stomach volume of plant and animal matter as well as fungi (Appendix S2). The response ratio was calculated as $\ln(X_N/X_I)$, where X_N is the mean of the response variable in the native range, and X_I is the mean of the response in the introduced range of wild boar (Hedges et al. 1999, Osenberg et al. 1999). A response ratio of 0 (or if the confidence intervals overlaps 0) indicates that wild boar diet does not differ between the ranges. A positive response ratio indicates that the diet includes the item in a greater proportion in the native range, whereas a negative response ratio indicates a greater use of the food item in the introduced range.

RESULTS AND DISCUSSION

Importance of plant matter

Wild boar diet in both native and introduced ranges consists primarily of plant matter including bulbs, roots, aerial parts, fruits and seeds (Briedermann 1976, Wood & Roark 1980, Genov 1981a, Baber & Coblentz 1987, Schley & Roper 2003, Baubet et al. 2004, Keuling 2007, Giménez-Anaya et al. 2008). The response ratio indicates that the volume of plant matter consumed is slightly greater in the native range than in the introduced range (Fig. 2).

In the native range, the frequency and volume of plant matter are very high, 99% and 93%, respectively

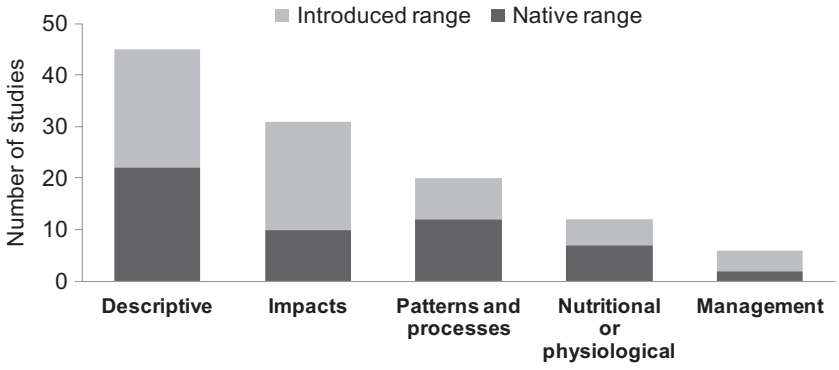

Fig. 1. Main objectives of wild boar studies used in this review (a single study could have more than one objective).

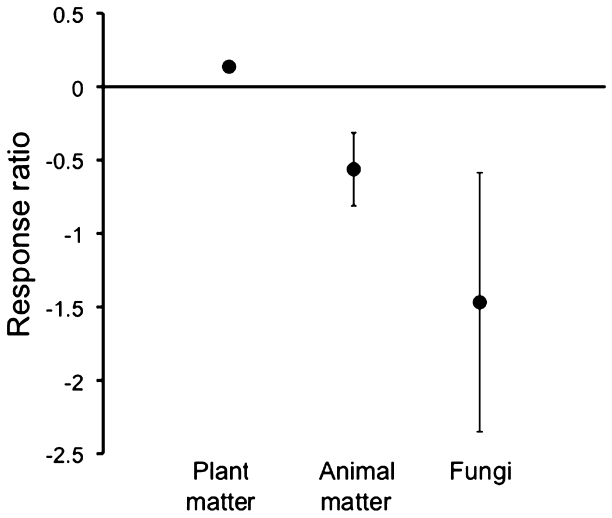

Fig. 2. Response ratios of food items in the diets of wild boars in their native and introduced ranges. A positive ratio indicates a greater use of a food item in the native range; a negative ratio indicates a greater use in the introduced range. Symbols represent means; bars show 95% confidence intervals.

(Appendix S2). Herrero et al. (2005) found that above-ground parts of plants comprise up to 71% of the volume, whereas below-ground parts comprise 24% of the volume. Authors disagree about the importance of below-ground plant parts. On the one hand, Eriksson and Petrov (1995) in the Ukraine found that the diet contains little leaf material and lots of roots (35%), whereas on the other hand, Genov (1981a) and Irizar et al. (2004) argue that roots and bulbs are of no importance as foods. The ratio of above-ground to below-ground plant material in the diet is determined by the season (see 'Factors affecting food selection' below). Wild boars eat fruits and seeds (Durio et al. 1995, Fournier-Chambrillon et al. 1995, Sáenz de Buruaga 1995, Irizar et al. 2004, Herrero et al. 2005), which provide a great source of energy during periods of food scarcity (Barrett 1978, Belden & Frankenberger 1990, Loggins et al. 2002). For example, in France, acorns of holly oak *Quercus ilex* were found in 90% of sampled stomachs (Fournier-Chambrillon et al. 1995).

Wild boars may act as seed dispersers (endozoochory and epizoochory) or simply as seed predators (Campos & Ojeda 1997, Heinken & Raudnitschka 2002, Schmidt et al. 2004, Sanguinetti & Kitzberger 2010, Dovrat et al. 2012). In the native range, Herrero et al. (2006) found that wild boars are not important seed dispersers because the seeds they consume are too large to avoid damage during digestion. Similarly, Dovrat et al. (2012) found that although wild boars can disperse seeds (mostly introduced plants), few of them survive, whereas Wiedemann et al. (2009) showed that maize seeds found in wild boar faeces retain their germination capacity only in extremely rare cases. In contrast, other authors show that seed dispersal by wild boars is important for both native and introduced plants (Heinken & Raudnitschka 2002, Schmidt et al. 2004, Matías et al. 2010, O'Connor & Kelly 2012).

In the introduced range, plant matter occurs in 99% of the samples, whereas the volume is slightly smaller than in the native range (87%, Fig. 2, Appendix S2). Some authors emphasize the importance of leaf intake. For example, Chimera et al. (1995) in New Zealand found that leaves of *Anisotome antipoda* were the largest single food item, and in the Galapagos Islands (Ecuador), forbs appeared to be highly preferred over grasses (Coblentz & Baber 1987). Similarly, in Texas, USA, Everitt and Alaniz (1980) found that forbs make up more of the diet (56%) than any other classes of food items. Fruits are also important in the introduced range; in Brazil, Desbiez (2007) found that fruit fibres make up approximately 60% of wild boar faecal samples. Fruits were also found to be important food items in the USA (Wood & Roark 1980) and in New Zealand (Thomson & Challies 1988). Roots comprise ~17% of volume, less than fruits, forbs and grasses (Wood & Roark 1980, Thomson & Challies 1988).

The role of wild boars as seed predators or dispersers in the introduced range is debated. In the Brazilian Pantanal, Desbiez (2007) showed that the weight of crushed seeds never exceeds the weight of intact seeds in the stomach, indicating that wild boars effectively transport and disperse native seeds. By contrast, Campos and Ojeda (1997) and Sanguinetti and Kitzberger (2010) found that wild boars eat and destroy seeds of the shrub *Prosopis flexuosa* and the tree *Araucaria araucana* in Argentina.

Importance of animal matter

Typically, wild boars consume animal matter frequently but at low total volume (Appendix S2, Howe et al. 1981, Hahn & Eisfeld 1998, Irizar et al. 2004, Herrero et al. 2006, Skewes et al. 2007, Giménez-Anaya et al. 2008). All authors highlight the low proportion of animal matter, but some emphasize its importance as an essential dietary component (Fournier-Chambrillon et al. 1995, Sáenz de Buruaga 1995). For example, Fournier-Chambrillon et al. (1995), Keuling (2007), and Wilcox and Van Vuren (2009) argue that though the proportion of animal food is low, the importance of this type of food should not be underestimated given its high digestibility. In the USA, animal matter rarely exceeds 2% of the diet but occurs in 94% of stomachs (Howe et al. 1981), suggesting that animal matter is required for the species. In their native range, Herrero et al. (2006) in Spain found that wild boars feed on a variety of terrestrial arthropods, which are energetically rewarding. In contrast, Genov (1981b) indicated that in Poland, animal

food is not important in the wild boar diet. The consumption of animal matter could be associated with a scarcity of protein in the environment or could augment the diet when other resources are scarce. For example, some authors have indicated that, because acorns are deficient in protein, wild boar may supplement an acorn diet with animal matter (Barrett 1978, Belden & Frankenberger 1990, Loggins et al. 2002). More research is needed to test this hypothesis.

The importance of animal matter in terms of volume varies (Fig. 2). In the native range, the volume of animal matter is generally low, ranging from 1 to 16%. By contrast, in the introduced range, values range from 2% to more than 33%, two times more than in the native range (Fig. 2, Appendix S2). Animal items in both ranges include mammals (Taylor & Hellgren 1997, Taylor & Uvalde 1999, Skewes et al. 2007, Wilcox & Van Vuren 2009), birds (Challies 1975, Rudge 1976, Herrero et al. 2004, Desbiez 2007, Skewes et al. 2007, Giménez-Anaya et al. 2008, Wilcox & Van Vuren 2009), amphibians and reptiles (Jolley et al. 2010), insects (Baber & Coblentz 1987, Thomson & Challies 1988, Eriksson & Petrov 1995, Taylor & Hellgren 1997, Herrero et al. 2004), earthworms (Challies 1975, Genov 1981a, Thomson & Challies 1988, Asahi 1995, Fournier-Chambrillon et al. 1995, Baubet et al. 2004), snails (Howe et al. 1981, Irizar et al. 2004, Herrero et al. 2005, 2006), and crustaceans (Giménez-Anaya et al. 2008). Furthermore, wild boars may select a few items in large numbers. For example, Wilcox and Van Vuren (2009) found in the USA that California voles *Microtus californicus* were the dominant prey species, totalling 109 individuals and occurring in more than one-third of all stomachs (104 samples). The prevalence of multiple vertebrates per stomach suggested that they are not eaten only occasionally (Wilcox & Van Vuren 2009). Although the bulk of animal matter is usually composed of birds and mammals, the presence of invertebrates (such as myriapods, insect larvae and snails), especially earthworms, is remarkable in the native and introduced range, and they are probably eaten because of their high protein content (Wood & Roark 1980, Genov 1981b, Thomson & Challies 1988, Fournier-Chambrillon et al. 1995, Massei et al. 1996, Baubet et al. 2004, Irizar et al. 2004).

Predator or scavenger?

Scavenging is a widespread phenomenon in vertebrate animal communities. In particular, facultative scavenging is common (DeVault et al. 2003, Selva et al. 2003). Wild boars can be predators that opportunistically consume carrion (facultative scavengers, Wilson & Wolkovich 2011), although the overall relative proportion of scavenged vs. preyed-upon vertebrate foods in wild boar diets is frequently unknown (Taylor & Hellgren 1997, Taylor & Uvalde 1999) because it is often impossible to know whether an animal was killed or ingested as carrion (Wood & Roark 1980).

In the introduced range, wild boars search for prey, and most vertebrates found in stomachs are taken alive (Wilcox & Van Vuren 2009). Prey include rodents, deer, birds, snakes and frogs (Schneider 1975, Taylor & Hellgren 1997, Rollins & Carroll 2001, Skewes et al. 2007, Wilcox & Van Vuren 2009, Jolley et al. 2010), as well as livestock (Pavlov et al. 1981, Pavlov & Hone 1982, Choquenot et al. 1997). This predatory behaviour seems to be more severe on islands where a variety of species is affected (Challies 1975, Coblentz & Baber 1987, Cruz & Cruz 1987). However, some researchers emphasize the importance of carrion, such as carcasses of cows, brushtail possums *Trichosurus vulpecula* and deer because it comprises a major portion of the animal matter in the diet (Rudge 1976, Everitt & Alaniz 1980, Thomson & Challies 1988, Desbiez 2007). Additionally, it is believed that carrion cannibalism is common (Coblentz & Baber 1987, Thomson & Challies 1988, Taylor & Hellgren 1997). In the native range, Selva (2004) found that the wild boar, usually acting in groups, is one of the most important scavengers in the forests of eastern Poland. Likewise, in Spain, wild boars eat carrion of the European roe deer *Capreolus capreous* and badger *Meles meles* (Sáenz de Buruaga 1995, Herrero et al. 2005), and are predators of ground-nesting birds (Nyenhuis 1991, Keuling 2007, Giménez-Anaya et al. 2008) and amphibians (Carretero & Rosell 1999).

Other food items

Wild boar diet often contains other uncommon food items at low frequency and volume (1–7% of volume, Appendix S2). These items include biological material such as algae, fungi and garbage, as well as inorganic material including plastic and stones.

In the native range, fungi are present in the diet occasionally and are generally reported in low frequency and volume (Genov 1981a, Groot Bruinderink et al. 1994, Sáenz de Buruaga 1995, Baubet et al. 2004). However, Fournier-Chambrillon et al. (1995) found a high frequency of fungi, and Hohmann and Huckschlag (2005) found a high proportion by weight of hart's truffle *Elaphomyces granulatus*. Inorganic items such as stones are regularly ingested by wild boar, but in low proportion and perhaps accidentally (Sáenz de Buruaga 1995).

In the introduced range, there are very few records of the consumption of fungi, but overall fungus consumption is significantly greater than in the native range (Fig. 2). In Chile, Skewes et al. (2007) found that fungi are common in stomachs (65%, mainly hypogeous forms). Similarly, Wood

and Roark (1980) in the USA found fungi during all seasons and at relatively high frequencies, and in New Zealand, there are records of the presence of toadstools (Challies 1975). In New Zealand, two species of seaweed have also been found in wild boar stomachs (Challies 1975, Chimera et al. 1995). Items such as garbage and stones are not common in wild boar diets in the introduced range (Henry & Conley 1972, Taylor & Hellgren 1997).

Effects of wild boars on conservation and endangered species

Wild boars frequently consume endangered or keystone species; however, because estimates of population abundance are unavailable for many species, the impact such predation might have is unknown (Baber & Coblentz 1987, Chimera et al. 1995). Ground-nesting birds are one of the groups most affected by predation and nest destruction (Challies 1975, Opermanis et al. 2001, Herrero et al. 2004, Skewes et al. 2007, Giménez-Anaya et al. 2008). In the native range, eggs and young of the purple gallinule *Porphyrio porphyrio* in Spain are part of the wild boar's diet (Herrero et al. 2004, Giménez-Anaya et al. 2008), whereas in the UK, Purger and Meszaros (2006) found that the wild boar could be the main cause of loss of nests of ferruginous ducks *Aythya nyroca*. In the introduced range, the yellow-eyed penguin *Megadyptes antipodes* and the Auckland Island prion *Pachyptila desolata* are two of the species most commonly consumed by the wild boar (Challies 1975). Skewes et al. (2007) in Chile emphasize the high frequency of endemic birds *Scelorchilus rubecula* and *Pteroptochos tarnii* in wild boar stomachs.

Predation on reptiles has been reported in the Galápagos (Ecuador), where the reproductive success of the green sea turtle *Chelonia myda* and the giant land tortoise *Geochelone elephantop* is severely reduced by the wild boar (MacFarland et al. 1974, Coblentz & Baber 1987), as well as in Australia, where predation by the wild boar is reducing the survival of the northern snake-necked turtle *Chelodina rugosa* (Fordham et al. 2006). Predation on amphibians has also been reported in the introduced range, where wild boars threaten eastern spadefoot toad *Scaphiopus holbrookii* populations (Jolley et al. 2010), and in the native range, where vulnerable *Salamandra salamandra* are eaten (Irizar et al. 2004). Overall, it is expected that as wild boar populations continue to grow and spread, threats to native wildlife will also increase (Massei & Genov 2004).

Supplemental feeding and agricultural damage

Wild boars are considered an agricultural pest in many countries because of their preference for crops and because their feeding behaviour can severely damage crops (Fournier-Chambrillon et al. 1995, Hahn & Eisfeld 1998, Herrero & Fernández de Luco 2003, Schley & Roper 2003, Chauhan et al. 2009). Agricultural products are important components of wild boar diet in western Europe (Schley & Roper 2003), where food selection varies depending on the occurrence of different crops or by positive selection of certain crops over others (Genov 1981a, Schley & Roper 2003, Schley et al. 2008).

In their native range, wild boars depend heavily on agricultural products and are well adapted to crop changes (Schley & Roper 2003, Herrero et al. 2006). For example, Herrero et al. (2006) reported that agricultural crops comprise almost 90% of the volume of the stomach contents of wild boars. Agricultural plants in the Mediterranean are consumed year-round, but primarily during summer and autumn when their nutritional value is highest (Genov 1981a, Herrero et al. 2006, Cellina 2008, Giménez-Anaya et al. 2008) or when the availability of natural foods becomes unpredictable (Fournier-Chambrillon et al. 1995). Furthermore, cultivated crops such as maize *Zea mays* (in winter), oats *Avena sativa* (autumn and winter), rye *Secale cereale* (winter), wheat *Triticum* spp. (winter), sugar beet *Beta vulgaris* (autumn and winter), rice *Oryza* spp., barley *Hordeum vulgare*, alfalfa *Medicago sativa*, sorghum *Sorghum* spp. and potatoes *Solanum tuberosum* (spring) are used by wild boars (Genov 1981a, Herrero et al. 2006, Madsen et al. 2010).

In the introduced range, wild boars cause crop damage, but it is reported less often than in the native range. In the USA, wild boars consume large quantities of crops (wheat, sorghum, barley, oilseeds, sugar cane *Saccharum* spp., oats and maize) and tree seedlings (Lipscomb 1989, Mayer et al. 2000), causing serious damage (Seward et al. 2004). Furthermore, wild boars cause economic losses by preying on livestock such as newborn lambs *Ovis aries* and goats *Capra hircus* (Moulk 1954, Rowley 1970, Pavlov et al. 1981, Beach 1993) as well as game birds such as bobwhite quail *Colinus virginianus*, woodcock *Scolopax rusticola*, capercaillie *Tetrao urogallus* and hazel grouse *Bonasa bonasia* (Nyenhuis 1991, Tolleson et al. 1995, Saniga 2002, Schley & Roper 2003).

Supplemental feeding consists of providing additional food for wild animals for different purposes: dissuasive feeding, baiting, massive feeding and vaccination among others (Cellina 2008). There is speculation about the role of supplemental food in the wild boar diet; it can attract wild boars to hunting grounds or prevent crop damage, but it may also help maintain wild boar populations when natural resources are scarce. Indeed, some authors working in the native range found that supplemental food comprises more of the diet than some natural resources. For example, Baubet et al. (2004) in the French Alps found that maize

(8%) is more important than humus (6%), forest fruits (7%), animal matter (1%) and fungi (1%). Hahn and Eisfeld (1998) found that supplemental food (mainly maize) plays a key role throughout the year, and Cellina (2008) reported that supplemental food constituted up to 55% of the stomach contents. Similarly, Fournier-Chambrillon et al. (1995) found that maize can account for one-third of the annual diet and is eaten constantly throughout the year except in winter. In contrast, in the introduced range, there are no accurate records of the importance of supplemental food in wild boar diets.

Factors affecting food selection

Several factors determine what food resources wild boars use, and these can be grouped into four categories relating to: food availability, energy requirements, seasonal variations and geographical variations.

Several authors agree that wild boar diet is determined by food availability and energetic requirements (Diong 1982, Fournier-Chambrillon et al. 1995, Massei et al. 1996, Schley & Roper 2003, Geisser & Reyer 2004, Keuling 2007, Cellina 2008, Schley et al. 2008, Cuevas et al. 2013). For example, Massei et al. (1996), in a Mediterranean coastal area, found strong dependence on energy-rich food throughout the range, irrespective of the habitat and latitude. Moreover, they found that wild boar diet depends on the availability of food items which are not necessarily related to seasons, and they suggested that season could not be used to predict wild boar diet. In Europe, when supplementary food or crops are available, wild boars may modify their behaviour (e.g. dispersion, home range size) and distort their regular diet (e.g. when mast is available), which may give an inaccurate impression of their food selection (Eisfeld & Hahn 1998, Schley & Roper 2003, Keuling 2007, Linderoth 2010). In the introduced range, food availability and energy requirements are also reported as important factors that determine diet. For example, the availability of fruits has been reported as a key resource of the diet of the wild boar in environments such as rainforests and islands (Baber & Coblentz 1987, Desbiez 2007).

Several authors showed that food selection varies with seasons and geographical location (Challies 1975, Genov 1981a, Thomson & Challies 1988, Taylor & Hellgren 1997, Baubet et al. 2004, Herrero et al. 2004, Hafeez et al. 2011). For example, rooting is used when above-ground resources are scarce (e.g. in winter and early spring; Scott 1973, Barrett 1978, Baron 1982). In the native range, above-ground plant parts are important in the spring when new shoots of herbs are most luxuriant (Baubet et al. 2004). Fruits are consumed throughout the year but more predominantly in summer (Baubet et al. 2004, Herrero et al. 2004). In Europe, wild boars consume a large number of agricultural food items, particularly in summer and autumn (Briedermann 1976, Genov 1981a, Hahn & Eisfeld 1998, Wilson 2004, Herrero et al. 2006, Cellina 2008, Giménez-Anaya et al. 2008). Earthworms are also consumed year-round, but consumption decreases significantly in the winter months because of the snow cover (Genov 1981a, Baubet et al. 2004). In the introduced range, above-ground vegetable parts are consumed mostly in spring when grasses sprout and are tender (Wood & Roark 1980, Taylor & Hellgren 1997). Fruits are consumed throughout most of the year except in spring (Wood & Roark 1980, Baber & Coblentz 1987, Thomson & Challies 1988, Taylor & Hellgren 1997), and, as in Europe, acorns are one of the main foods during winter and autumn (Scott 1973, Everitt & Alaniz 1980, Wood & Roark 1980, Loggins et al. 2002, Solís-Cámara et al. 2008).

In both native and introduced ranges, geographical variation represented mainly by altitudinal gradients and differences in precipitation may also determine some aspects of food selection by the wild boar. For example, consumption of animal matter may depend on altitude (Challies 1975, Baubet et al. 2004), and pastures may be avoided in abnormally dry years (Everitt & Alaniz 1980).

Age and sex differences

A few records show dietary differences between ages and sexes of wild boars. In the native range, Dardaillon (1986) and Groot Bruinderink and Hazebroek (1996) reported a greater proportion of animal matter and greater diversity of food in juveniles than in yearlings and adults. Also, yearlings and adults eat larger proportions of rice and below-ground plant parts than do juveniles (Dardaillon 1986). These differences between age classes were attributed to different nutritional requirements or food availability (Dardaillon 1986). In the introduced range, Wilcox and Van Vuren (2009) found that predation of vertebrates is more pronounced in females than in males. Protein deficiency for females facing the physiological cost of reproduction is likely to be an important factor influencing predation on vertebrates (Wilcox & Van Vuren 2009). However, most of the reviewed studies showed no differences between age and sex in both the native and introduced ranges (Wood & Roark 1980, Durio et al. 1995, Loggins et al. 2002, Adkins & Harveson 2006, Skewes et al. 2007).

CONCLUSION

Wild boars are generalist feeders with a highly plastic diet that contributes to their wide geographical distribution (Barrios-Garcia & Ballari 2012, Baubet et al. 2004, Herrero et al. 2006, Nogueira-Filho et al. 2009). In this review, we found significant differences in the diets of wild

boars in their native and introduced ranges, though feeding behaviours including browsing and grazing, rooting, and preying seem to be similar in both ranges. We identified four factors that influence food selection: food availability, energy requirements, seasonal variation and geographical variation. This information in combination with knowledge of seasonal patterns of space and habitat use may help inform the design of management plans.

Animal matter and fungi were eaten in greater proportions in the introduced range than in the native range, whereas the opposite occurred with plant matter. This pattern might be explained partly by evolution. In the native range, animal species co-evolved with wild boars over thousands of years and developed strategies to avoid competition or predation. By contrast, in the introduced range, animal species are not adapted to the presence and feeding habits of wild boars and may therefore be more susceptible to predation. Similarly, plants in the native range may be adapted to the feeding behaviour of wild boars (rooting) for their establishment and development. Indeed, Welander (1995) showed that in Sweden, rooting enhances plant diversity and richness. Although rooting in the introduced range could replace suppressed natural events (e.g. wildfires; Kotanen 1995) or extinct ecological equivalents (e.g. *Ursus arctos* in California; Sweitzer & Van Vuren 2002), most studies show negative effects of rooting on plant species (Bratton 1975, Challies 1975, Singer et al. 1984, Hone 2002, Tierney & Cushman 2006), suggesting that plants are not adapted to wild boar disturbance.

As well as seasonal and geographic variation, energy requirements and food availability are major factors influencing wild boar diet in the introduced and native range. Energy requirements may drive wild boar behaviour and reproduction. For example, protein is essential in wild boar diet, and a deficiency can trigger higher animal predation rates, particularly in females facing the physiological cost of reproduction (Wilcox & Van Vuren 2009). Food availability is determined by environmental parameters (e.g. mast and climate) as well as by human activities (e.g. supplemental feeding and agricultural crops). Nevertheless, wild boars seem to adapt their diet to whatever is available (Challies 1975, Wood & Roark 1980, Cellina 2008). For example, wild boars rely strongly on acorns in good mast years but diversify their diet during poor mast years (Briedermann 1976, Fournier-Chambrillon et al. 1995, Massei et al. 1996). Availability not only influences the diet and feeding habits of wild boar but may also alter other features such as population dynamics, habitat use, dispersal, reproduction and interactions with other species (Massei et al. 1996, Bieber & Ruf 2005). For example, some authors suggested that under food scarcity, resource competition may occur between the wild boar and other mammals (Wood & Roark 1980, Massei et al. 1996).

Dietary studies should be more rigorous and consistent across ranges to allow better comparisons. The implications of some studies on wild boar diet should be treated with caution because of low sample sizes (Schley & Roper 2003) or because they are limited to certain times of the year. Furthermore, the frequency or volume of certain food items in the diet could be underestimated because the analysis of faeces may be less accurate than the evaluation of stomach contents, in which foods are preserved better. Moreover, the fast digestion of soft tissues (4–5 hours; Guerin et al. 2001) may result in underestimated volumes. Finally, Wood and Roark (1980) found that the use of some woody plants may be underestimated, as wild boars may chew the roots, swallow the sap and starches, and reject the woody tissue. The quality of wild boar diet studies could be improved by: (i) increasing the number of samples (many studies reported results based on fewer than 10 samples); (ii) reporting both frequency and volume values for food items; and (iii) assessing seasonal differences in wild boar diet based on food availability.

The effect of an invasive species can largely be inferred by its trophic position in the community (Skewes et al. 2007). Therefore, understanding what wild boars eat and how, when and where they feed is critical to the delineation of management and control plans in both ranges. Our findings suggest that animal species in the introduced range are at greater risk, both by virtue of being naïve and because they are consumed in a greater proportion than in the native range. A detailed study of diet could provide key information such as target species and susceptible habitats on which management efforts should focus.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. References relevant to wild boar diet found in the literature search.
Appendix S2. References used in this review to assess and compare wild boar diet in the native and introduced range.