DISSERTATION / DOCTORAL THESIS

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„Reproductive strategies in the wild boar (*Sus scrofa*) in the context of pulsed food availability“

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1 INTRODUCTION

1.1 BACKGROUND

Pulsed (i.e., erratic and short-term) availability of high quality and quantity food resources is widespread and occurs in a large variety of ecosystems (Ostfeld & Keesing 2000). Apart from the intensively studied consequences for populations and communities (Ostfeld & Keesing 2000, Boutin *et al.* 2006, Ruf *et al.* 2006, Yang *et al.* 2010), there could also be significant effects on individual life-histories in species relying on such pulsed resources (e.g. Monaghan 2008, Millon *et al.* 2010). Life-histories describe the age-, size, or stage-specific patterns of development, growth, maturation, reproduction, and survival of individuals (Fabian & Flatt 2012). It has been shown, for example, that juveniles growing up under favourable conditions (i.e., at the time of a resource pulse) can have an advantage throughout life, in terms of reproductive success or survival (Lindström 1999, Festa-Bianchet *et al.* 2000, Weladji *et al.* 2008), a phenomenon recognised as the “silver spoon effect” (Grafen 1988). Additionally, heterogeneous selection pressures in varying environments might favour the evolution and persistence of different life-history tactics within populations (Roff 2002, Careau *et al.* 2009, Réale *et al.* 2010). In particular, the persistence of different animal personalities, which have been shown to be linked to different life-history strategies (Careau *et al.* 2009, Réale *et al.* 2010), has been discussed in this context only recently (Dingemanse & Réale 2013). Different personality traits like boldness, aggressiveness or activity have been shown to be associated with different life-history traits in various animals (reviewed in Biro & Stamps 2008). In fact, in some pulsed resource consumers the benefits of different personality phenotypes alter with food availability (Dingemanse *et al.* 2004, Boon *et al.* 2007). Although the occurrence of different personality phenotypes with associated life-history strategies seems plausible in species relying on pulsed resources, empirical studies investigating this question are scarce within the published literature.

In central Europe acorns (*Quercus spec.*) and beechnuts (*Fagus sylvatica*) represent classic pulsed resources as they occur in vast amounts at irregular time intervals in so-called mast years, whereas their abundance is only intermediate or even very low in years between these pulses (König & Knops 2000, Hilton & Packham 2003). Most mammal species relying on these tree seeds are small rodents (reviewed in Ostfeld & Keesing 2000) but there is an interesting exception to this pattern: The omnivorous wild boar (*Sus scrofa*) feasts on these seeds (Schley & Roper 2003, Briedermann 2009, Gamelon *et al.* 2013a) and is affected by their pulsed availability at the population level (Jędrzejewska & Jędrzejewski 1998, Bieber & Ruf 2005).

1.2 THE WILD BOAR - RESPONSES TO FLUCTUATING ENVIRONMENTS

Interestingly, the wild boar does not only heavily consume pulsed resources (acorns and beech nuts) but also has a very unusual life-history tactic for a mammal of its size (Focardi *et al.* 2008). Wild boar reproduction is characterized by a large average litter size of more than five juveniles in central Europe (Bywater *et al.* 2010), with a high variation of 1-14 juveniles per litter (Servanty *et al.* 2007). Further, reproduction can start even at the juvenile stage (< 1year) at only ~ 33 - 41 % of the adult body mass (Servanty *et al.* 2009). Thus, its reproductive characteristics more resemble those of small terrestrial mammals than those known from other large ungulates (Focardi *et al.* 2008).

Age and body mass strongly affect the proportion of females breeding as well as litter size in the wild boar (e.g. Mauget 1972, Gaillard *et al.* 1993, Fernández-Llario & Mateos-Quesada 1998, Náhlik & Sándor 2003, Gethöffer *et al.* 2007, Briedermann 2009 and citations therein, Servanty *et al.* 2009, Bywater *et al.* 2010, Fonseca *et al.* 2011, Gamelon *et al.* 2012, Rosell *et al.* 2012). Additionally, reproductive output in the wild boar is strongly affected by food availability: In years with high food availability a higher proportion of juvenile and yearling wild boars reproduce (Servanty *et al.* 2009, Linderoth & Pegel 2010), and adult females can reproduce twice in years following full mast events (Mauget 1978). Also, litter size is strongly affected by food availability in the wild boar, with higher litter sizes after mast years (Briederman 1971, Aumaitre *et al.* 1982, Groot Bruinderink *et al.* 1994, Massei *et al.* 1996, Rosell Pagès 1998, Servanty *et al.* 2009, Linderoth & Pegel 2010). Besides the effects of food availability, climatic conditions also affect reproduction (Servanty *et al.* 2009) and survival (Jędrzejewski *et al.* 1992). However, although effects of food availability and climate have been modelled to explain population dynamics and to recommend suitable management strategies (Bieber & Ruf 2005, Gamelon *et al.* 2012), we still lack studies disentangling these effects and their interaction in this species.

Despite a vast amount of studies on wild boar reproduction and population dynamics (see above) our knowledge on individual life-histories is still lacking. The main reason is most of the previous studies evaluated hunting bag data (for the only exceptions see Pépin & Mauget 1989, Massei *et al.* 1996), which reveal only very limited information on important longitudinal effects of, for instance, reproductive output or body mass. Consequently, the currently available data do not allow for assessing early life effects (Monaghan 2008) or effects of other factors, such as animal personality (Réale *et al.* 2010), on life-history strategies and future reproductive success in the wild boar. For the same reason only little is known about early life effects on important life-history trade-offs. Such trade-offs include those between current and future reproduction or between growth and reproduction (e.g. Williams 1966, Stearns 1989, Roff 1992, Stearns 1992), even though they sometimes might be masked by differences in individual quality (Noordwijk & de Jong 1986, Reznick *et al.* 2000).

Female wild boars live in matrilineal groups (Mauget 1981) whereas males live solitary for most of the year and only associate with the female groups during the breeding season (Briedermann 2009). Although males defend female groups against competitors, there is increasing evidence that multiple paternity in wild boar litters occurs more frequently (e.g. Costa *et al.* 2012, Gamelon *et al.* 2013b) than previously expected (Delgado *et al.* 2008). These findings are strengthened by various signs of intense sperm competition (Møller 1989), like large relative testis size and ejaculate volume (Kozdrowski & Dubiel 2004, Briedermann 2009), the placement of a mating plug after copulation (Hafez 1987) and multiple copulations of boars with the same female (Fraser 1968). In other species it was shown that multiple paternity could be a female strategy to diversify offspring within litters (reviewed in Fox & Rauter 2003). Such a diversification could potentially represent a strategy to produce offspring showing different life-history strategies and thus to maximize inclusive fitness in variable and unpredictable environments, also known as diversified bet-hedging (Philippi & Seger 1989, Crean & Marshall 2009). Gamelon *et al.* (2013a, 2013b) found evidence that heavier or adult female wild boars diversify their offspring within litters, but only in mast years. The mechanism of this diversification in the wild boar, however, is as yet unknown. Further, it is unclear whether this diversification in fact represents a diversified bet-hedging strategy used by female wild boars as argued by the authors (Gamelon *et al.* 2013b). Alternatively, offspring diversification stemming from multiple paternity could also be a by-product of a female strategy to avoid male harassment (Rowe *et al.* 1994) or male infanticide (Agrell *et al.* 1998, Wolff & Macdonald 2004). Finally it may represent a way to reduce the negative effects of sibling rivalry by facilitating the formation of a stable hierarchy (Fraser & Thompson 1991, Mock & Parker 1997, Forbes & Glassey 2000).

1.3 AIMS OF THE STUDY

The aim of this project was to investigate how pulsed availability of high amounts of high quality food affects the wild boar on the population level as well as on the individual level. First, to analyse effects of pulsed resource availability on the population level, I investigated, together with my colleagues, which factors mediated the recent dramatic increase of wild boar populations all over Europe (Sáez-Royuela & Tellería 1986, Massei *et al.* 2015). In doing so, I aimed to disentangle the effects of climate and food availability on population growth and hypothesised that climate change affected population dynamics twofold; i) related to an increase in average winter temperatures (direct effect), and ii) by a climate change related increase in mast frequencies (indirect effect) (Övergaard *et al.* 2007). I did this by evaluating a long-term hunting bag data set (up to 150 years from 69 regions across Europe) and a long-term data set on beech masting patterns in Austria.

Second, to investigate individual reproductive strategies, I collected longitudinal data on life-history parameters of female wild boars kept under semi-natural conditions. By applying different feeding regimes I focused on the question how individual traits, such as body mass and animal personality, affect the reproductive success under varying food availability. Based on the modified pace-of-life-syndrome concept (Réale *et al.* 2010) and the review of Dingemanse and Réale (2013) on the persistence of different animal personalities within populations, I hypothesised that in the wild boar different life-history strategies are similarly linked to different animal personalities. Therefore, I expected the benefits (i.e., the reproductive success) of a personality phenotype to change with food availability.

I further analysed paternal and maternal effects on offspring traits as well as male and female mating behaviour and promiscuity. I hypothesised that multiple paternity in the wild boar provides an important mechanism for offspring diversification and is used by female wild boars for this purpose. Consequently, I expected to find strong paternal effects on juvenile body mass and potentially even on subsequent reproductive success.

Finally, integrating my findings on individual reproductive strategies and offspring diversification, I discuss whether offspring diversification of female wild boars in fact constitutes a diversified bet-hedging strategy in response to the unpredictability of food availability or might be rather caused by one of the alternative mechanisms mentioned above.

2 EFFECTS OF PULSED RESOURCES ON POPULATION DYNAMICS IN THE WILD BOAR

2.1 WHAT IS A MILD WINTER? REGIONAL DIFFERENCES IN WITHIN-SPECIES RESPONSES TO CLIMATE CHANGE

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Climate change is known to affect ecosystems globally, but our knowledge of its impact on large and widespread mammals, and possibly population-specific responses is still sparse. We investigated large-scale and long-term effects of climate change on local population dynamics using the wild boar (*Sus scrofa* L.) as a model species. Our results show that population increases across Europe are strongly associated with increasingly mild winters, yet with region-specific threshold temperatures for the onset of exponential growth. Additionally, we found that abundant availability of critical food resources, e.g. beech nuts, can outweigh the negative effects of cold winters on population growth of wild boar. Availability of beech nuts is highly variable and highest in years of beech mast which increased in frequency since 1980, according to our data. We conclude that climate change drives population growth of wild boar directly by relaxing the negative effect of cold winters on survival and reproduction, and indirectly by increasing food availability. However, region-specific responses need to be considered in order to fully understand a species' demographic response to climate change.

Sus scrofa, climate change, body mass, beech mast, seasonality, thermoregulation

Introduction

Despite an increasing understanding of the impact of global climate change on a broad range of ecosystems (Walther *et al.* 2002) there is a lack of long-term and large-scale biological data-sets necessary to gain a more complete understanding of how ecosystems are affected by climate change (Staudinger *et al.* 2013). Additionally, most studies dealing with the impact of climate change on animals are distributional studies (Parmesan 2006), showing that many species respond to increasing ambient temperatures with range shifts (Perry *et al.* 2005, Staudinger *et al.* 2013). Some studies, however, also found that local populations of non-migratory species of birds and fishes differ in their thermal tolerance and their response to temperature changes (Kendeigh & Blem 1974, Jensen *et al.* 2008). Such differences between different populations might be due to physiological differences caused by local adaptation or phenotypic plasticity. In fact, it is known that body mass is affected by the general climatic conditions with individuals living in cold climates being larger (Bergmann 1848). Some studies on bird species even reported changes in body mass in response to climate change (Teplitsky *et al.* 2008, Husby *et al.* 2011). However, very little is known on how large mammals with a wide distribution range respond to climate change and whether those responses differ between populations (Gaillard *et al.* 2013, Morellet *et al.* 2013). Thus, it is unclear whether results of studies on the impact of climate on single populations can be generalized throughout a species' distribution range.

The wild boar is an excellent model to investigate this topic. First, it is one of the most widely distributed mammals in the world (Massei & Genov 2004, Ballari & Barrios-García 2014), with recent significant growth documented for many populations (Sáez-Royuela & Tellería 1986, Massei *et al.* 2015). As wild boars occupy a broad range of habitat types and climatic zones with a number of genetically distinct ecotypes (Scandura *et al.* 2008, Scandura *et al.* 2011), there is a high potential for region-specific responses to climate change in this species. Second, the wild boar has an enormous reproductive capacity, and thus the potential for remarkable population growth when environmental conditions become more favourable (e.g., Bieber & Ruf 2005). Given an average litter size in Europe of ~ 5 juveniles (Bywater *et al.* 2010), reproductive output in the wild boar is much larger than in other ungulates of similar size (Focardi *et al.* 2008). Furthermore, if food availability is high, female boar can reach sexual maturity yet in their year of birth (Servanty *et al.* 2009), and maximum life-span is high, i.e. up to 12 years in natural habitats (Massei & Genov 2004). Third, climatic conditions are known to affect reproduction (Servanty *et al.* 2009), as well as survival (Jędrzejewski *et al.* 1992) of wild boar.

Climate change, however, could affect wild boar populations not only directly through changes in temperature and precipitation, but also indirectly by affecting important biotic factors such as food availability. Such ecological impacts of climate change at the community level have received less attention than direct responses to abiotic changes but are important for a holistic understanding of how climate change affects both, species and communities (Staudinger *et al.* 2013). Although an omnivorous species, the wild boar strongly relies on tree seeds like beech nuts, *Fagus sylvatica* L., or acorns, *Quercus spec*. L. in large parts of its distribution range in Europe (Schley & Roper 2003). Fructification in these trees is highly pulsed (seed masting), but the frequency of masting events has significantly increased over the past decades in parts of Europe (e.g., Austria, see below), probably as a consequence of climate change (Övergaard *et al.* 2007).

In this study, we investigated the effect of seasonal mean temperatures and seasonal precipitation sums on the relative change in annual wild boar population size (i.e., rate of growth, λ) using long-term data on wild boar hunting bags from a major part of the wild boars' European distribution range (Fig. 1a; details in S1 Table, Supporting Information). We further tested the effect of food availability on λ in a subsample of our data for which information on beech masting and areas under cultivation of corn and potatoes was available. We focussed on these fruits because they are known to play a major role in the food composition of wild boar (Briedermann 2009).

We hypothesized that (1) major increases in the size of wild boar populations are linked to milder winter temperatures and changes in precipitation. If wild boar population dynamics are indeed affected by climate, particularly temperature, we envisioned two alternative scenarios: (i) There is a single critical species-specific winter temperature threshold for population growth for all European wild boar populations. (ii) Physiological trade-offs generate locally differing responses to ambient temperatures leading to population-specific winter temperature thresholds for population growth. (2) We further hypothesized that, in addition to direct climatic effects, increased abundance of food accelerates wild boar population growth by compensating the negative effects of severe winters.

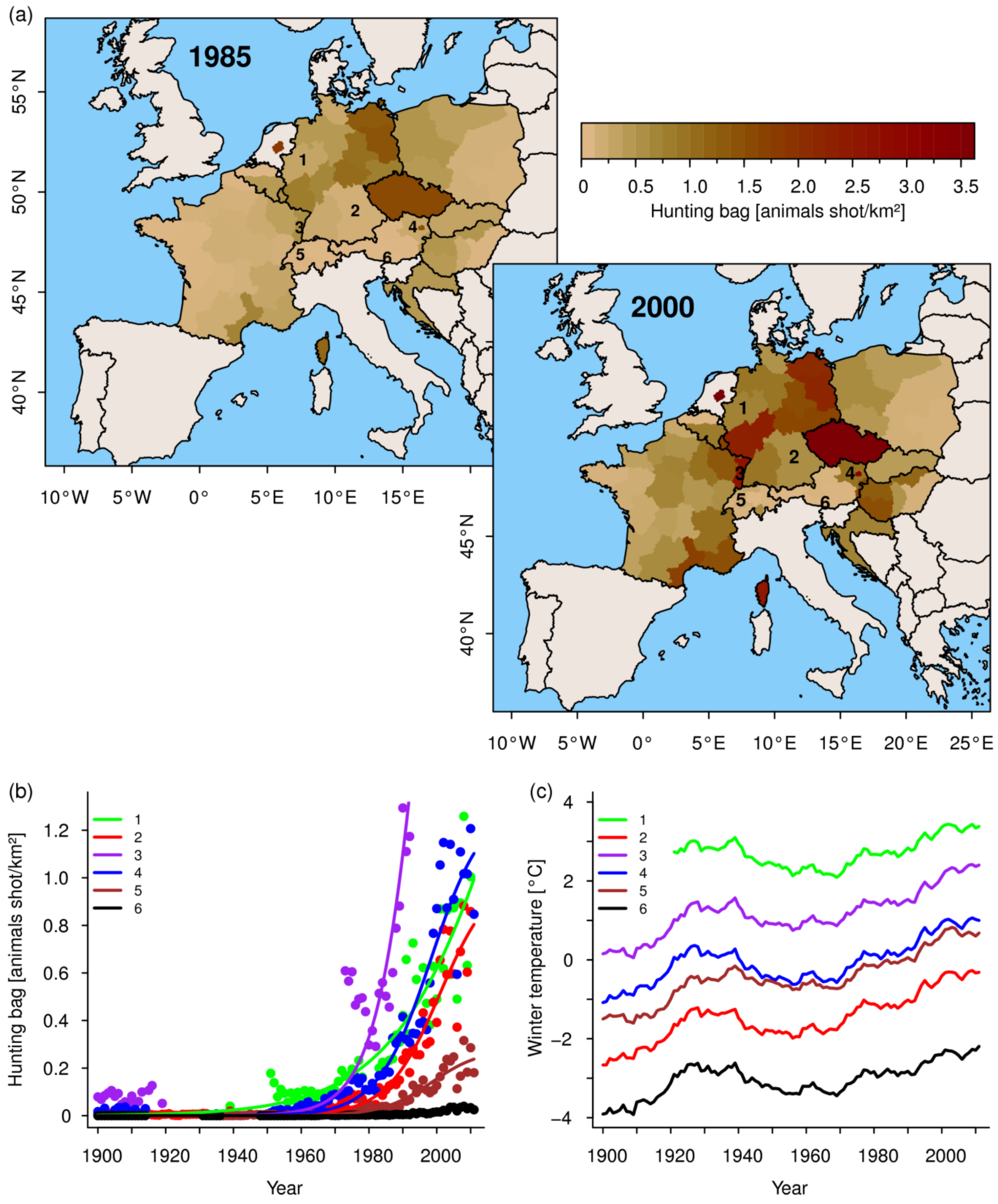

Figure 1 Increase of European wild boar populations and mean winter temperatures. (a) Color-coded wild boar densities in various regions 1985 and 2005, respectively. For six exemplary regions time courses of wild boar hunting bags (b) as well as corresponding changes in long-term mean winter temperatures (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).

Materials and Methods

Data collection

Long-term (15-150 years) annual wild boar hunting bag data were acquired for 69 regions from 12 European countries. The relative change in the hunting bag from one year to another ($\lambda = bag_t/bag_{t-1}$) was calculated after excluding hunting bags smaller than 0.01 animals shot/km² (799 data points), as such small values cause large uncertainty in estimating λ. This procedure yielded a data set in which most data points prior to 1950 were excluded, allowing us to focus mainly on the period showing exponential wild boar population growth (see Fig. 1b for some examples). Further, 87 data points were excluded that could have been affected by the political situation at that time (World War 2, Balkan War, split of Czechoslovakia). The final data set included 64 regions out of 12 European countries (Fig. 1a; details in S1 Table, Supporting Information). In sum we analysed a total of 2075 annual hunting bags (mean: 32.5 years per region).

Monthly precipitation sums and mean temperatures were acquired for the respective regions and periods (S2 Table, Supporting Information). Seasonal (3 months) precipitation sums and temperature means (weighted by the number of days per month) were calculated from the monthly data for spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). Spatial autocorrelation analysis of the climatic data revealed that in none of the climatic variables the difference between climate stations increased below a distance of 300 to 400 km (S3 Fig., Supporting Information). However, climate stations used were not separated by more than 268 km to the next climate station in the data set. Thus, climate data can be considered representative even for the largest regions in our data set.

Effects of food availability on population dynamics were investigated using the Austrian subsample (*n* = 135 years, 6 regions (S1 Table, Supporting Information), mean: 22.5 years per region). Rank data on beech mast intensity (0 < 30% pollination, mast failure; 1 = 30-50 % pollination; 2 = 50-70% pollination; 3 = 70-85 % pollination; 4 = 85-100 % pollination, full mast) were obtained from the Austrian Federal Office and Research Centre for Forests (BFW, bfw.ac.at/rz/pollen.main) for 1976-2013. In years where multiple measurements were available per region the rank data were averaged in order to obtain a more accurate measurement for the whole region. Data on areas under cultivation of corn (*Zea mays* L.) and potatoes (*Solanum tuberosum* L.) were acquired from Statistics Austria (www.statistik.at) and were available from 1960 to 2011 and from 1966 to 2011, respectively.

Male and/or female adult (> 2 years) wild boar body mass data were obtained for one Italian region (Arezzo, Tuscany; M. Apollonio, pers. com.), three French regions (Gaillard *et al.* 1993, Toïgo *et al.* 2008), three German regions (Gethöffer 2005), one Spanish region (Fernández-Llario & Mateos-Quesada 1998), one region from the Netherlands (Groot Bruinderink *et al.* 1994), three regions of the former Soviet Union (reviewed in Briedermann 2009), and one Austrian region (own data). It has been shown recently that in many species body size decreases as a response to climate change (Sheridan & Bickford 2011). Consequently, in order to include only data for comparable periods, data published before 1970 were excluded from the analysis of body mass. If only dressed body mass was available, live body mass was estimated by multiplying dressed mass by 1.25 (for Central European data) and 1.15 (for Eastern European data), respectively, to account for different ways of dressing in these areas (Briedermann 2009).

National data on the number of traffic accidents involving wild boar and the number of cars and trucks registered were acquired for Austria (1974-2011; Source: Statistics Austria, www.statistik.at), Germany (2007-2011; Sources: German Hunting Association, and German Federal Office of Statistics, www.destatis.de), and Switzerland (1992-2011; Source: Swiss Federal Office of Statistics, www.bfs.admin.ch). In these three countries every accident involving a game animal has to be reported to the police and is therefore well documented.

Data analysis

To test the reliability of wild boar hunting bags as a proxy for wild boar population size, we computed Pearson’s correlation coefficients for the relationship between the number of traffic accidents involving wild boar (corrected for the number of cars and trucks registered) and the hunting bag (S1a-c Fig., Supporting Information) as well as those between the relative year-to-year changes in the number of traffic accidents and λ (S1d-f Fig., Supporting Information). This was done for Austria, Germany and Switzerland (i.e., countries where reliable traffic accident data were available), with the latter in parts employing a different hunting system (S1 Fig., Supporting Information).

To test climatic effects on λ, temperature means and precipitation sums were considered during six seasons, spring (March-May), summer (June-August) and autumn (September-November) of the previous year, winter (December-February), and spring and summer of the census year. This large number of climatic variables and their interactions rendered statistical models computationally unfeasible. We therefore used the random forest method (a combination of binary decision trees created of bootstrapped samples of the data set and choosing randomly a subset of explanatory variables at each split (Breiman 2001, Genuer *et al.* 2010)) to pre-select important variables among all possible climatic variables. The number of variables randomly sampled as candidates at each split was set to 4 (number of predictor variables divided by 3) and the number of trees in the forest was set to 2000. The result of this analysis was very robust to changes of these parameters and showed that seasonal precipitation data contributed little to explaining the observed variance in λ (S2 Fig., Supporting Information). Therefore, only seasonal temperature data were included in subsequent analysis. Additionally, regional long-term mean winter and summer temperatures as well as their interactions with current mean winter and summer temperatures were included in the model in order to test for the effect of long-term thermal conditions. We chose the 30-year period from 1973 to 2002 to calculate average long-term temperatures because data were available for all regions without missing values for that period. We further included the long-term average of summer and yearly precipitation sums in the model, which were calculated over the same period as the long-term temperatures. Further, to test whether population density affected λ, 5-year averages of hunting bags (animals shot per km²) preceding the census year were included in the model, as a proxy of density, along with its interaction with mean winter temperature. The use of hunting bag data as a proxy of density is justified by the strong correlation of hunting bag data and number of traffic accidents involving wild boar (see S1a-c Fig., Supporting Information). The average of the previous 5-years was chosen instead of a single measure from the respective previous year to avoid “regression to the mean” effects (Bland & Altman 1994), because the chance of a high λ occurring at random is much higher after a year with a low population density. To ease comparisons all variables were standardized to a mean of 0 and a SD of 0.5 (Grueber *et al.* 2011). Finally, country and region were included in all models as nested random effects in order to correct for potentially consistent regional influences on hunting bags (e.g., differences in overall hunting pressure). Inspection of the distribution of residuals of this full linear mixed effects (lme) model by means of histograms and quantile-quantile plots gave no evidence for serious deviations from normality. This also applies to all models described below. We used linear mixed effects models because the pre-analyses showed that those were superior in describing the data, according to the Akaike Information Criterium corrected for small sample size (AICc), compared to additive mixed effects models.

The full lme model was further analysed using a multi-model averaging approach (Burnham & Anderson 2002). Hereby, the multi-model average was calculated by including all possible nested models. However, the averaged estimates did not differ essentially when only certain subsets of models (i.e., with a delta AICc of below 4 and 10, respectively) were used for calculating the model-averaged parameter estimates (data not shown). Model-averaged parameter estimates were calculated with the natural average method, in order to avoid shrinkage towards zero, especially of weak effects (Grueber *et al.* 2011, Nakagawa & Freckleton 2011). As we further aimed to determine which variable had the strongest impact on λ we also calculated model averaged estimates using the zero-method (Grueber *et al.* 2011). However, the order of effect sizes of significant variables was identical for both model-averaging methods (compare Table 1 vs. S3 Table, Supporting Information). To obtain correct parameter estimates for main effects of variables involved in interactions, we selected models used for averaging as follows: If an interaction was significant in the model-average we selected only models where this interaction also was significant to calculate the weighted averages of the parameter estimates (i.e., annual and long-term winter temperature; Table 1a). In contrast, if an interaction was not significant in the model-average, we selected only models not containing this interaction, and models in which this interaction was not significant, to calculate weighted averages (i.e., annual and long-term summer temperature, and density; Table 1). This procedure of averaging also was applied in all further multi-model averages described below. Model-averaged residuals were subsequently checked for spatio-temporal autocorrelation by means of semivariograms which showed that residuals were neither temporally nor spatially autocorrelated (S4 Fig. and S5 Fig., Supporting Information).

Due to smaller sample size only those variables were included in the full lme model of the Austrian multi-model average that were found to be important in the European wide analysis (Table 1a). To assess effects of food availability, beech mast of the previous year (binary coded; 1: moderate or full beech mast (categories 3 or 4; pollination ≥ 70%), 0: less than moderate beech mast (categories 0-2; pollination < 70%), as well as areas under cultivation (% of total area of a region) of corn and potatoes during the previous year were

Table 1 Impact of climate and food availability on wild boar population growth rate (λ).

(a) European data set (*n* = 2075)

term	estimate	SE	*P*	RVI
winter temperature	**0.180**	**0.025**	**< 0.001**	**1.00**
long-term winter temperature	**-0.252**	**0.033**	**< 0.001**	**1.00**
prior autumn temperature	**0.179**	**0.027**	**< 0.001**	**1.00**
population density	**-0.065**	**0.016**	**< 0.001**	**1.00**
summer temperature	**-0.050**	**0.023**	**0.031**	**0.82**
winter temperature: long-term winter temperature	**-0.059**	**0.027**	**0.030**	**0.80**
prior spring temperature	0.039	0.023	0.09	0.62
prior summer temperature	-0.027	0.026	0.29	0.41
long-term summer temperature	-0.012	0.029	0.67	0.39
long-term summer precipitation	0.021	0.024	0.40	0.37
winter temperature: population density	0.029	0.033	0.37	0.37
long-term yearly precipitation	0.012	0.025	0.65	0.34
spring temperature	-0.011	0.025	0.64	0.30
summer temperature: long-term summer temperature	-0.022	0.029	0.44	0.10

(b) Austrian data set (*n* = 135)

term	estimate	SE	*P*	RVI
winter temperature	**0.237**	**0.064**	**< 0.001**	**1.00**
mast	**0.284**	**0.112**	**0.012**	**1.00**
mast: winter temperature	**-0.926**	**0.247**	**< 0.001**	**0.98**
prior autumn temperature	**0.173**	**0.062**	**0.005**	**0.94**
long-term winter temperature	**-0.172**	**0.084**	**0.044**	**0.82**
population density	-0.133	0.113	0.24	0.50
area under cultivation of potatoes	-0.096	0.071	0.18	0.45
area under cultivation of corn	-0.092	0.088	0.30	0.38
summer temperature	-0.063	0.061	0.31	0.34
prior spring temperature	-0.022	0.055	0.70	0.25
winter temperature: long-term winter temperature	-0.045	0.104	0.67	0.21
mast: long-term winter temperature	-0.098	0.664	0.88	0.19
mast: population density	-0.097	0.291	0.74	0.13

Parameters estimate, standard error (*SE*), p-value (*P*), and relative variable importance (*RVI*) for each term included in the multi-model averages of the European data set (a) and the Austrian subset (b). Interaction terms are indicated by colons, significant predictor variables are highlighted bold. See methods for the definition of seasons.

included. Furthermore, the interaction between beech mast and winter temperature was included, because the vast amount of energy provided by tree seeds might have compensated for unfavourable climatic conditions. In addition to region, beech mast in the respective census year was added as a random factor to the Austrian subset models, to account for possible effects of mast intensity on hunting success.

Further, we tested whether the frequencies of mast failure (mast category ≤ 1), moderate (1 < mast category ≤ 3) and full beech mast (mast category > 3; each coded 1/0) have changed in Austria since 1976 by computing three binomial linear mixed effects models, respectively, each with year as fixed and region as random effect (*n* for all three models = 165 years, 6 regions, mean: 27.5 years per region).

In order to test for an association of body mass with regional climate we computed the multi-model average of a linear model with adult (> 2 years) wild boar body mass as a function of the long-term mean winter-temperature (see below), sex and their interaction (*n* = 22 European regions).

All statistical analyses were performed in R.3.0.2 (R Core Team 2013). Linear mixed-effects models were computed using the package lme4 (Bates *et al.* 2014a), for multi-model averaging we used the package MuMIn (Barton 2013) and own functions. The random forest analysis was performed using the package randomForest (V 4.6-10) (Liaw & Wiener 2002). Spatio-temporal autocorrelation of the residuals was checked using the package gstat (Pebesma 2004).

Results

Validity of hunting bag data

We observed strong correlations between hunting bags and the number of traffic accidents involving wild boar (corrected for the number of cars registered) in Austria, Germany, and Switzerland (Austria (AT): $r = 0.96$, $P < 0.001$; Germany (DE): $r = 0.99$, $P < 0.001$; Switzerland (CH): $r = 0.84$, $P < 0.001$; S1a-c Fig., Supporting Information). Further, we found similarly strong correlations between the λ calculated from hunting bags and year-to-year change in car accidents involving wild boars in Austria, Germany, and Switzerland (AT: $r = 0.73$, $P < 0.001$; DE: $r = 0.99$, $P < 0.001$; CH: $r = 0.90$, $P < 0.001$; S1d-f Fig., Supporting Information). These strong correlations indicate that hunting bags are a reliable proxy for changes in population size, as car accidents represent a random sample (Geisser & Reyer 2005).

Climatic effects

As determined by our initial analysis using the random-forest approach (see Materials and Methods), seasonal precipitation data had no significant effect on wild boar population growth (S2 Figure, Supporting Information). Long-term summer precipitation and long-term yearly precipitation also had no effect on λ (Table 1a).

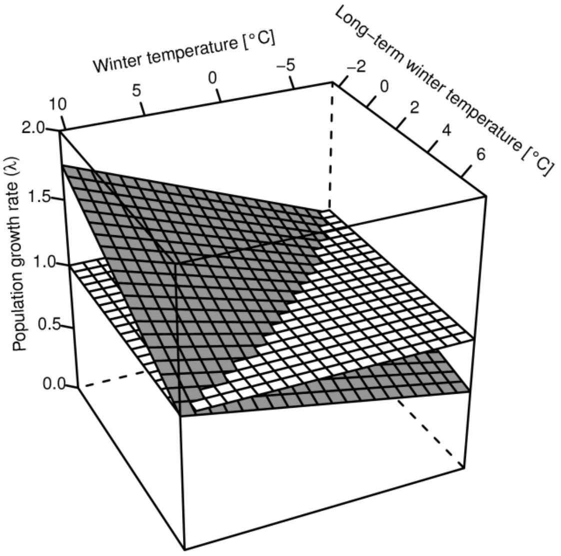

Figure 2 European-wide effect of winter temperature on subsequent wild boar population growth (λ). Long-term mean winter temperature refers to the 30-year average of winter temperature (December to February) from 1973 to 2002 and indicates how cold or warm a specific region in general is. The grey plane shows model predictions for λ, the white plane represents λ = 1, i.e., no change in population size.

Population growth in European wild boars was positively affected by annual and negatively by long-term winter temperature (Table 1a, Fig. 2). Importantly, these two variables showed a significant interaction (Table 1a, Fig. 2), indicating that wild boar populations in cooler regions were more strongly affected by an increase in annual winter temperature than populations in warmer regions (Fig. 2). Additionally, this interaction reflected that populations began to grow (λ > 1) already at much lower winter temperatures in cooler regions compared to warmer areas (Fig. 2). Further, autumn temperature of the previous year had a strong positive effect on population growth (Table 1a), in contrast to summer temperature in the census year, which had a much weaker negative effect (Table 1a, Fig. 3a). We found no significant effect of long-term summer temperature on λ (Table 1a).

Apart from climatic variables, population density, as indicated by the mean hunting bag during the 5 years prior to the census, had also a slightly negative effect on λ (Table 1a, Fig. 3b). However, there was no significant interaction between density and winter temperature (Table 1a), indicating that density effects did not differ between warmer and colder regions.

Food availability and mast frequency

The effect of beech masting events and other food sources was explored in the Austrian subset of our data. We found that moderate or full mast in the previous autumn, i.e., high food availability during winter, completely outweighed the negative effects of cold winter conditions on population growth (Table 1b, Fig. 4a). There was no significant interaction between beech mast and population density or beech mast and long-term winter temperature (Table 1b). Further, we did not find any effects of areas under cultivation of corn and potatoes on population growth (Table 1b).

The frequency of mast failure years in Austria decreased significantly since 1976 (slope = -0.054, se = 0.019, *P* = 0.004, Fig. 4b). Accordingly, both intermediate masting events (slope = 0.038, se = 0.020, *P* = 0.052, Fig. 4b) and full masting events (slope = 0.077, se = 0.040, *P* = 0.053, Fig. 4b) showed strong trends of increase.

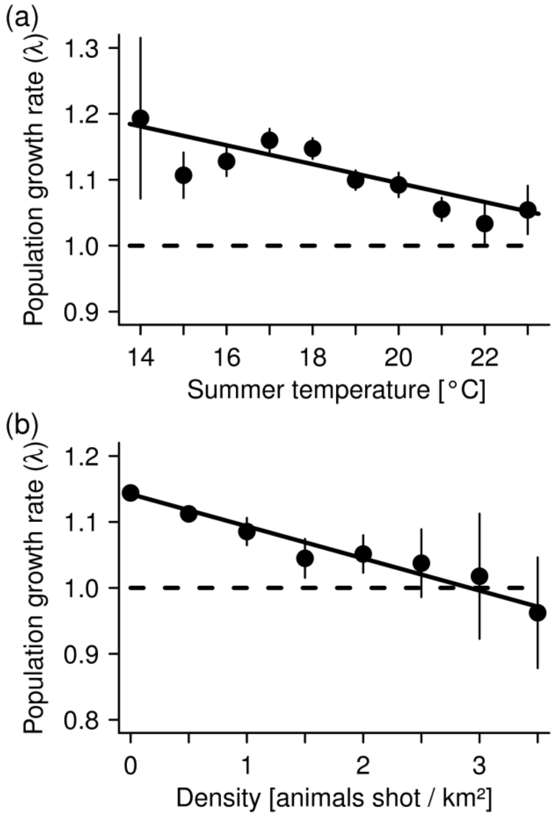

Figure 3 Effect of (a) summer temperature and (b) previous population density on wild boar population growth (λ). Means and standard errors of the means for bins of summer temperature (ranges of 1 degree) and density (ranges of 0.5 animals shot per km²) are plotted with the model prediction of the respective variable.

Body mass

Adult wild boar body mass correlated negatively with long-term (30-year) regional mean winter temperature (slope = -3.9, se = 1.1, *P* < 0.001; Fig. 5). Males and females showed different intercepts (estimate = 25.7, se = 5.6, *P* < 0.001; Fig. 5) but no difference concerning the slope of the relationship (*P* = 0.38; Fig. 5). Wild boars in the coldest region were about 30-40 kg (~ 30 %) heavier than in the warmest region investigated.

Discussion

It has been shown in previous studies that ungulate traffic collisions in Europe accurately reflect the population size and therefore can be regarded as random sampling (Groot Bruinderink & Hazebroek 1996, Geisser & Reyer 2005). The strong correlations between the relative year-to-year changes in the number of traffic accidents and the λ calculated from hunting bags in all regions investigated (S1d-f Fig., Supporting Information) show that fluctuations in hunting bags largely reflect those in population size and, consequently, are a good proxy for relative changes in wild boar population size, at least at the coarse scales considered here.

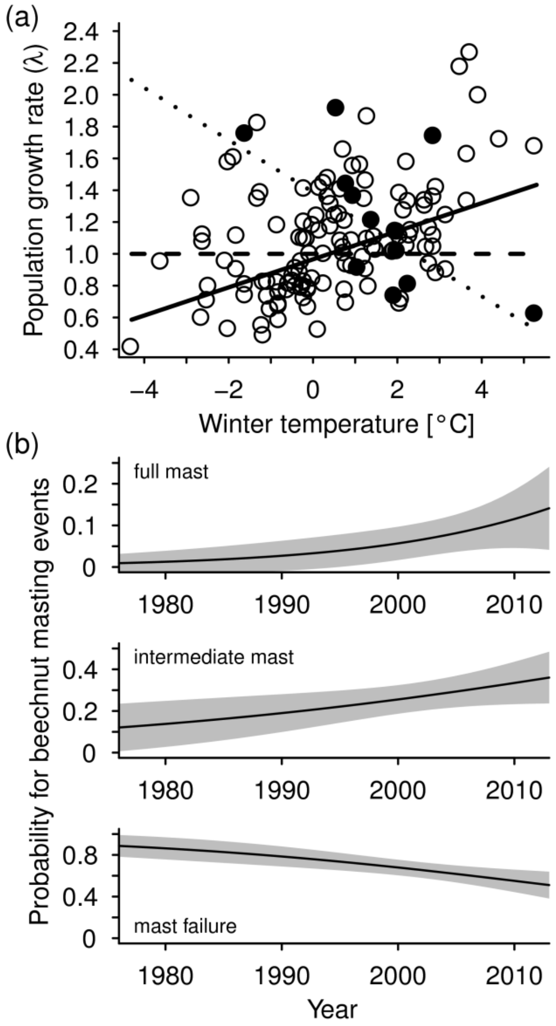

Figure 4 Wild boar population growth and beech masting. (a) The effect of winter temperature on population growth rate (λ) in years after full or moderate mast (•, ···), and in years after mast failure (◦, —). The horizontal dashed line indicates no change, i.e. λ = 1. (b) Probability of beech mast events in Austria from 1976 to 2013. Lines represent predicted values from binomial models (see Methods for details), shaded areas 95 % confidence limits.

Our analysis shows that wild boars are apparently highly susceptible to cold winter conditions (Fig. 2), as those were consistently followed by population declines. Cool autumns also had a negative impact on population growth, which may simply reflect an early onset of winter. It is known that cold winters lead to increased juvenile mortality (Geisser & Reyer 2005), which is a major driver of wild boar population dynamics (Bieber & Ruf 2005). Susceptibility to low winter temperatures can also explain why wild boars occur at higher densities in warmer regions (Melis *et al.* 2006). Of course, we cannot exclude that other factors such as changes in agricultural practices or changes in hunting pressure (Servanty *et al.* 2009, Gamelon *et al.* 2011, Servanty *et al.* 2011) also influence growth of wild boar populations. However, although it was reported that hunting pressure affects life-history traits and demography in the wild boar (Servanty *et al.* 2009, Gamelon *et* *al.* 2011, Servanty *et al.* 2011), no study so far has actually shown that population growth rate in wild boar is significantly affected by hunting pressure. Moreover, a recent study underlines that recreational hunting has no influence on wild boar population growth (Massei *et al.* 2015). Wild boar populations across Europe have been growing irrespective of whether the number of hunters have increased, decreased or remained stable (Massei *et al.* 2015). Furthermore, even though such factors may well have contributed to the considerable noise in λ, they were not strong enough to mask the dominant effect of winter temperature. Increasingly milder winters as a result of climate change (Fig. 1c; see also (Luterbacher *et al.* 2004)) must therefore be considered as a major reason for the European-wide massive increase of wild boar during the last decades (Fig. 1b).

Flexible and generalist species like the wild boar are generally more likely to cope with or even benefit from climate change compared to specialist and less flexible species (Staudinger *et al.* 2013). The positive effect of warming climate on wild boar population growth identified here, together with results from previous studies on other ungulates (Forchhammer *et al.* 1998, Pettorelli *et al.* 2005, Gaillard *et al.* 2013), is in line with this. Population size is positively associated with milder winters and an early onset of spring in red deer (*Cervus elaphus* L.) (Forchhammer *et al.* 1998, Pettorelli *et al.* 2005), an ungulate species with flexible birth dates (Coulson *et al.* 2003). In contrast, in roe deer (*Capreolus capreolus* L.), where females have inflexible birth dates, an earlier onset of spring has a negative impact on population growth (Gaillard *et al.* 2013). The latter is apparently caused by an increasing phenological mismatch between onset of vegetation growth and birth (Gaillard *et al.* 2013). Furthermore, being an income breeder (Andersen *et al.* 2000), the roe deer can be expected to be more severely affected by such a phenological mismatch than wild boar or red deer.

Surprisingly, climate change associated wild boar population increases were not restricted to the coldest regions. In fact, we show for the first time that a positive relation between winter temperature and wild boar population growth exists over a large climatic range, but the effect is weaker in warmer regions. Further, in warmer areas there was a higher threshold-temperature for the onset of population growth (Fig. 2). Therefore, population-specific temperature thresholds can explain why changes in average winter temperature have led to almost concurrent increases in wild boar population sizes all over Europe (Fig. 1a,b; (Sáez-Royuela & Tellería 1986)), despite differences in local climates.

The lack of a common threshold winter temperature initiating population growth could be either due to local adaptation, phenotypic plasticity, or to a density-climate interaction, as population densities in cooler regions are generally lower (Melis *et al.* 2006). Density-dependent mechanisms have been shown to affect life-history traits and consequently population growth in several other ungulate species (Clutton-Brock *et al.* 1992, Forchhammer *et al.* 1998, Grenfell *et al.* 1998, Milner *et al.* 1999, Forchhammer *et al.* 2001, Patterson & Power 2002). However, the effect of density in the present analysis was relatively small compared with the impact of long-term winter temperature (Table 1a). Additionally, our results gave no evidence for a significant interaction of density with annual winter temperature (Table 1a), which might have been expected because environmental fluctuations are likely to affect animals more strongly at higher population densities (Grenfell *et al.* 1998, Milner *et al.* 1999). Further, as yet there is no flattening of the exponential population growth curves (see Fig. 1b for some examples), and a previous study indicates that density dependence in general plays a minor role in wild boar population dynamics (Choquenot 1998). Overall, this suggests that the locally differing temperature-thresholds for the onset of population growth identified here are probably not caused by a density-climate interaction but are rather due to phenotypic plasticity or local adaptation. With our data, we cannot differentiate between these two mutually not exclusive alternatives. However, wild boar populations in Europe have been shown to be genetically distinct (Scandura *et al.* 2008), rendering at least some degree of genetic adaptation likely. Such genetic differentiation of populations and adaptation to local climatic conditions has been shown in several fish species (e.g., Koskinen *et al.* 2002, Jensen *et al.* 2008), whereas changes in body size of red-billed gulls (*Chroicocephalus scopulinus* F.) and great tits (*Parus major* L.) in response to climate change seemed to be due to phenotypic plasticity (Teplitsky *et al.* 2008, Husby *et al.* 2011).

If differences in the local responses to climate in wild boar are due to local adaptation or phenotypic plasticity, one would expect regional clines in morphological or physiological characteristics. One important trait to consider in this context is body size. Body size is known to be a major factor affecting thermoregulation, energy requirements, and ultimately survival in different climates by changing the surface to volume ratio and thus relative heat loss (Bergmann's rule (Bergmann 1848)). Our results confirm previous indications for the applicability of Bergmann's rule to the wild boar (e.g., Davis 1981), as animals of this species

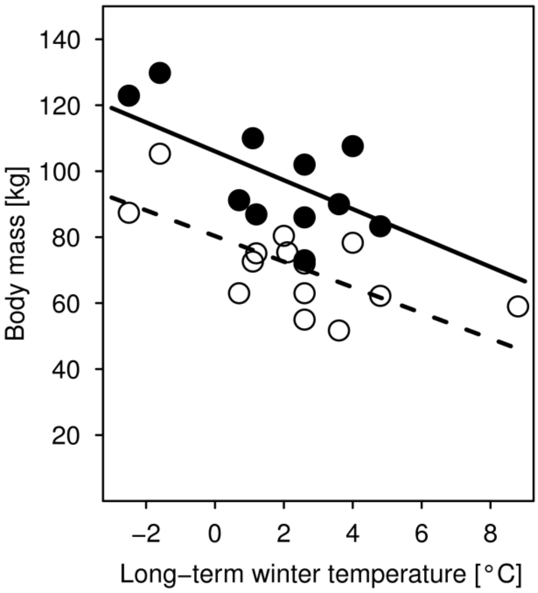

Figure 5 Body mass of adult wild boar in relation to local long-term winter temperatures. Males (•, —), females (◦, - -), long-term mean winter temperature is for each region the 30-year average of December to February from 1973 to 2002.

in colder regions are indeed heavier (Fig. 5). While larger body size in cool climates reduces the relative heat loss, small body size in warmer regions, on the other hand, leads to lower total metabolic rates and higher rates of heat loss. Hence, smaller body size may help wild boar to withstand high summer temperatures despite its limited ability to use evaporative cooling, and potentially serve to reduce reproductive constraints due to the limits of heat dissipation during lactation (Speakman & Król 2010). However, smaller body size does not seem to entirely offset adverse effects of heat, as underlined by our finding that wild boar population growth generally decreased, though only slightly, with higher summer temperatures. Consequently, it seems plausible that regionally differing body mass of wild boars, no matter whether it is due to local adaptation or a common reaction norm, evolved because of trade-offs between the benefits of large size in winter and of small size in summer. These locally different phenotypes in turn could have caused the region-specific temperature thresholds observed here.

Several studies on birds (e.g., Teplitsky *et al.* 2008) and mammals (e.g., Smith *et al.* 1995, Guthrie 2003) showed that the average body size in populations often changes in response to climate change. So far it is not known whether this is also the case in the wild boar and how this might affect the impact of rising temperatures on wild boar populations. This question needs to be targeted in further studies.

The negative effect of summer temperature on wild boar population growth, however, was very small in the European-wide data set (Table 1a) and even absent in the Austrian subset (Table 1b). Therefore, higher than average summer temperatures probably play an important role only in specific habitats, whereas warm and rainy summers may even have a positive effect on reproduction in certain populations (Servanty *et al.* 2009). It remains unclear however, which habitats that might be as the effect of summer temperature, in contrast to winter temperature, was apparently independent of the local long-term climate (Table 1a).

In addition to these direct abiotic effects of climate change on wild boar populations we also identified indirect effects via food availability. Beech nuts and acorns are the most important food resource for wild boar (Jędrzejewska *et al.* 1997, Briedermann 2009) but seed production in these species is highly variable and can cease entirely over large areas. This mechanism is commonly viewed as a strategy of trees to swamp seed-predators at unpredictable intervals (Ostfeld & Keesing 2000). Our analysis showed that the frequency of beech masting years has increased over the last decades (Fig. 4b), presumably due to climate change (Övergaard *et al.* 2007). This finding, together with the fact that cold winters had no negative effect on population growth when food resources were abundant, shows that the effect of climate change on population growth of wild boar is two-fold: Cold winters have become rarer and, on top of this, the remaining severe winters became increasingly ineffective in diminishing wild boar populations because of the increasing frequency of masting years. In such years, beech or oak trees produce vast amounts of energy rich seeds that are available from autumn until spring in the following year (Schley & Roper 2003, Bieber & Ruf 2005). If abundant, this food source likely enables juveniles to cope even with high thermoregulatory costs in a severe winter, and adults to accumulate high amounts of body energy reserves for reproduction in the following year. This result also indicates that low survival in cold winters is apparently not caused by a limited thermogenic capacity. Instead, increased winter mortality seems to be caused by a negative energy balance, i.e., when high thermoregulatory costs, due to severe cold, cannot be matched by the available food, especially when high caloric seeds are absent.

In addition to tree seeds, increased crop availability in a human-shaped landscape has previously been assumed to provide an important source of energy for wild boars (Schley & Roper 2003). However, the lack of significant effects of areas under cultivation of corn and potatoes on wild boar population dynamics indicates that this is apparently not the case, presumably because significant quantities of these crops are available only during a short period prior to harvesting.

Conclusions

It has been shown recently that, even for closely related species with similar ecological niches, responses to climate change cannot be extrapolated easily from one species to another (Tafani *et al.* 2013). Our results show for the first time that this holds even for separate populations within a species and therefore questions any predictions of the consequences of climate change for population dynamics if they are based on responses to environmental factors, such as ambient temperature, in a single or just a few local populations. Our results further underline the need to take indirect ecological effects into account, such as increasing food availability (e.g. accelerated tree-masting frequency), when studying the impact of climate change on species or ecosystems.

Data accessibility

All data are available from Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.11962.

Acknowledgements

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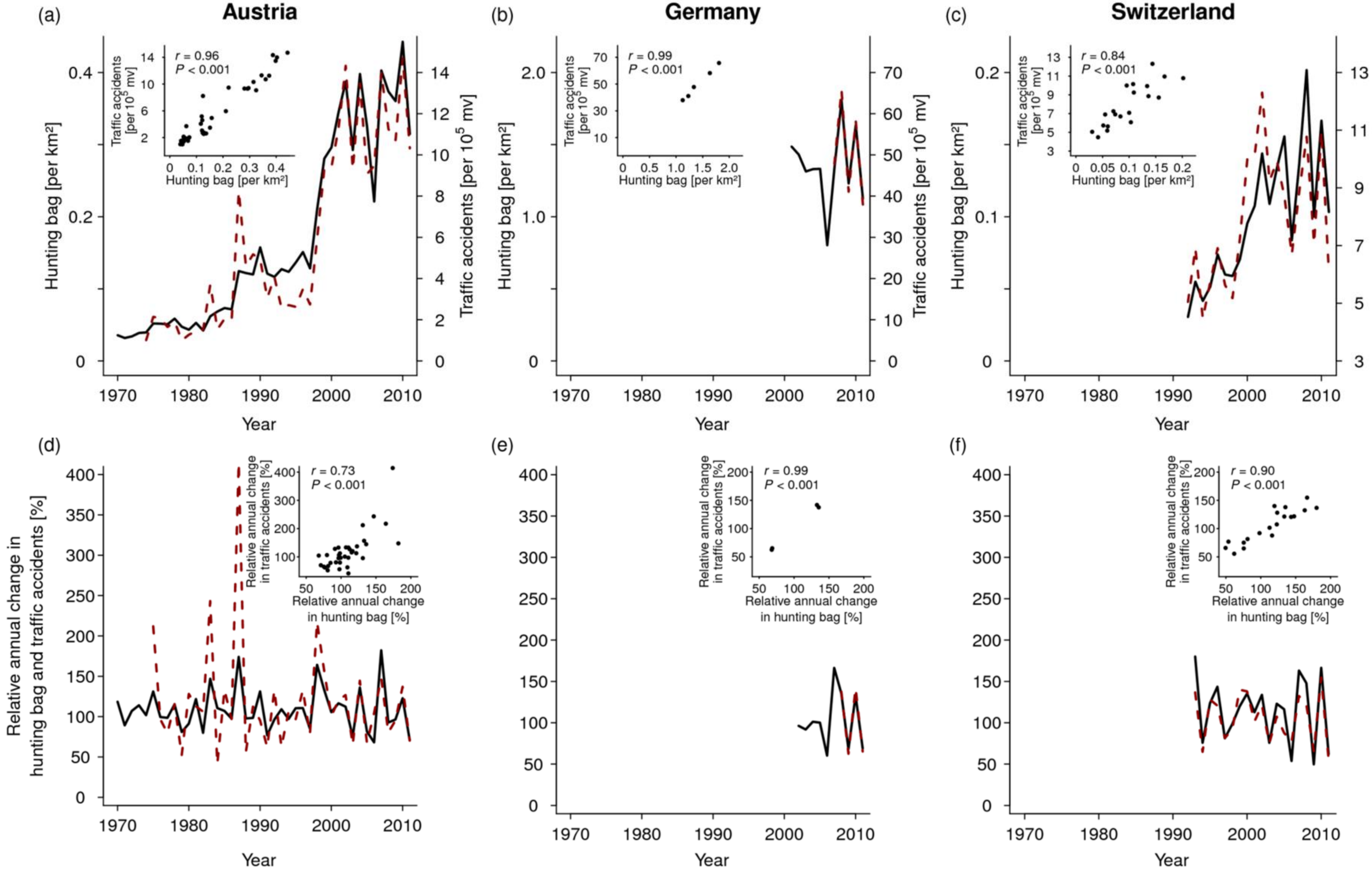
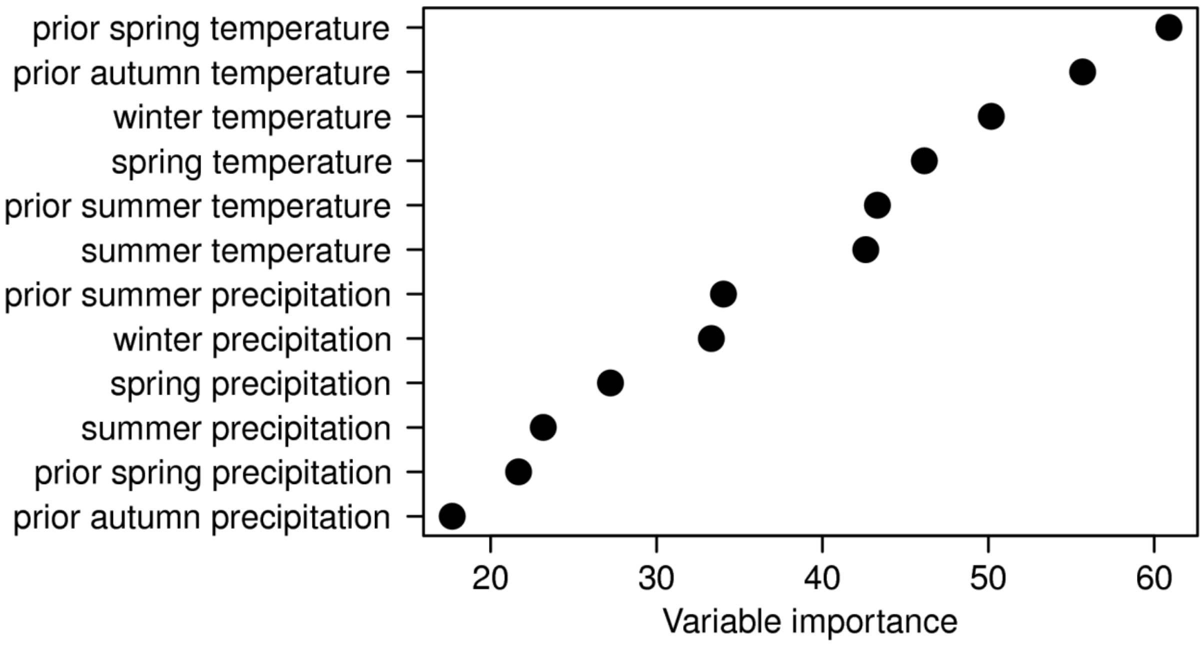
Author contributions

SGV collected data and performed the analyses. TR helped with the statistical analyses. CB directed the work. WA conceived the study and collected data. SGV, TR and CB wrote the manuscript. All authors discussed the results and commented on the manuscript text.

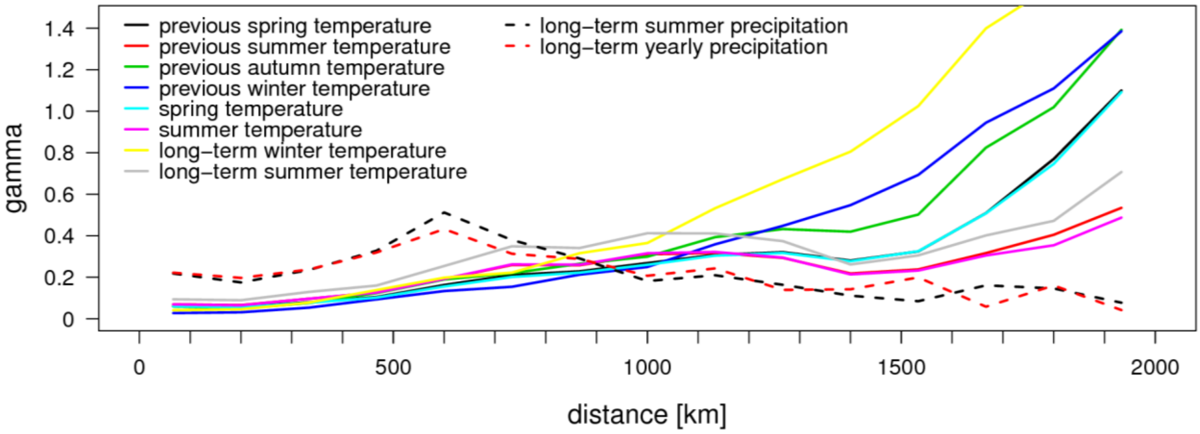
Supporting Information



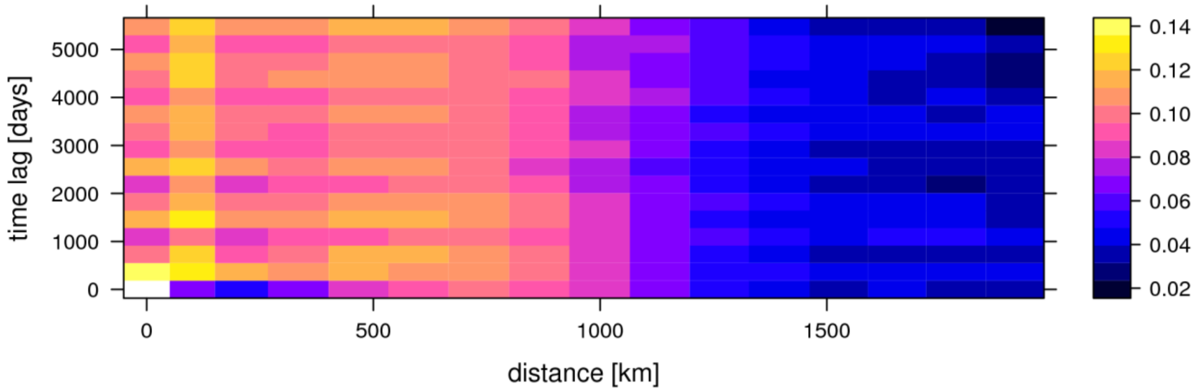
S1 Figure Wild boar hunting bags and traffic accidents involving wild boar. Data are shown for (a, d) Austria (b, e) Germany, and (c, f) Switzerland. In a, b, c — shows the hunting bag (left axis) and - - shows the traffic accidents corrected for the number of motor-vehicles (mv = cars and trucks) registered (right axis). The insert plots show the correlations between these two variables. In d, e, f — shows the relative change in the hunting bag and - - shows the relative change in traffic accidents (also corrected for the number of motor-vehicles registered). In both analyses (a-c vs. d-f) very high correlation coefficients were obtained for all three countries, despite the fact that there is a different hunting system in some parts of Switzerland. These findings justify the use of wild boar hunting bags as a proxy for population size, since traffic accidents can be regarded as a random sampling of population size.



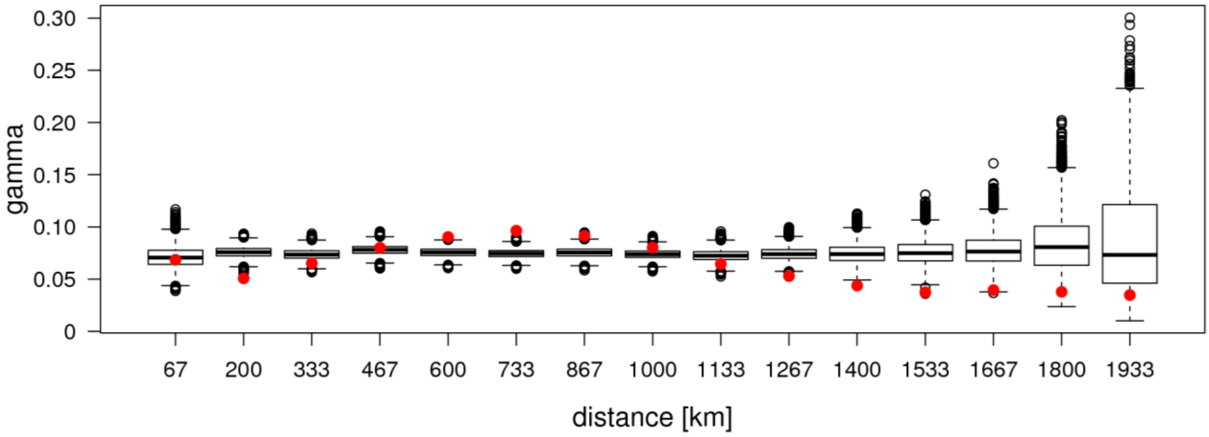
S2 Figure Importance of climatic variables according to a 'random forest' analysis. Variable importance is given as the percental increase of the mean standard error under random permutation of the respective variables. See methods for the definition of seasons.



S3 Figure Semivariogram showing the spatial autocorrelation structure of the climatic variables.



S4 Figure Spatio-temporal semivariogram of the residuals of the European multi-model average. Colour codes refer to γ-values indicated by the legend.



S5 Figure Bootstrapped spatial autocorrelation structure of the residuals of the European multi-model average. Bootstrapping was performed by randomly sampling 75% of the residuals and calculating the respective spatial autocorrelation structure without any time lag for 10,000 times. Red points show the original semivariogram including the full data set.

S1 Table Overview over the wild boar hunting bag data.

Country	Region	area	earliest	latest	min	max	winter	Source
Austria	Burgenland	3,966	1931	2011	0.012	2.375	0.7	Stat. Austria
Austria	Carinthia	9,536	1874	2011	0.016	0.039	-2.3	Schwenk, S. (1985); Stat. Austria
Austria	Lower Austria	19,178	1868	2011	0.012	1.207	1.0	Schwenk, S. (1985); Stat. Austria
Austria	Styria	16,392	1874	2011	0.013	0.127	0.0	Schwenk, S. (1985); Stat. Austria
Austria	Upper Austria	11,982	1874	2011	0.011	0.075	0.4	Schwenk, S. (1985); Stat. Austria
Austria	Vienna	415	1935	2011	0.080	5.465	1.0	Stat. Austria
Belgium	Wallonia	16,844	1974	2011	0.293	1.442	2.4	FAB
Croatia	-	56,538	1972	1990	0.119	0.803	2.4	Schwenk, S. (1984)
Czech Republic	-	7,969	1902	1977	0.010	0.796	-0.6	Schwenk, S. (1985); Bartos (pers. com.)
France	Alsace	14,522	1884	2011	0.029	4.702	2.3	Schwenk, S. (1982); ONCFS
France	Aquitaine	41,309	1975	2011	0.017	0.679	5.9	ONCFS
France	Auvergne	26,013	1975	2011	0.052	0.514	4.4	ONCFS
France	Brittany	27,209	1976	2011	0.010	0.150	5.9	ONCFS
France	Burgundy	31,582	1975	2011	0.049	1.059	2.8	ONCFS
France	Centre	39,151	1975	2011	0.065	1.348	4.1	ONCFS
France	Champagne-Ardenne	25,606	1975	2011	0.111	1.671	3.5	ONCFS
France	Corsica	8,680	1980	2011	0.945	3.165	8.9	ONCFS
France	Franche-Comté	16,202	1977	2011	0.070	0.985	2.6	ONCFS
France	Île-de-France	11,494	1977	2011	0.074	1.570	4.4	ONCFS
France	Languedoc-Roussillon	27,376	1977	2011	0.348	2.505	6.7	ONCFS
France	Limousin	16,942	1975	2011	0.016	0.743	4.6	ONCFS
France	Lorraine	23,547	1975	2011	0.126	2.636	2.6	ONCFS
France	Lower Normandy	17,589	1975	2011	0.070	0.976	5.6	ONCFS
France	Midi-Pyrénées	45,348	1975	2011	0.036	0.824	6.3	ONCFS
France	Nord-Pas-de-Calais	12,414	1975	2011	0.011	0.385	3.8	ONCFS
France	Pays de la Loire	32,082	1977	2010	0.014	0.385	5.6	ONCFS
France	Picardy	19,399	1977	2011	0.040	0.935	3.9	ONCFS
France	Poitou-Charentes	25,809	1975	2011	0.015	0.427	6.3	ONCFS
France	Provence-Alpes-Côte d'Azur	31,400	1977	2011	0.229	1.532	4.3	ONCFS
France	Rhône-Alpes	43,698	1975	2011	0.092	1.215	3.2	ONCFS
France	Upper Normandy	12,318	1975	2011	0.026	0.406	4.0	ONCFS

S1 Table (continued) Overview over the wild boar hunting bag data.

Country	Region	Area	earliest	latest	min	max	winter	Source
Germany	Baden-Württemberg	35,751	1956	2010	0.038	1.453	2.1	DJV
Germany	Bavaria	70,553	1909	2010	0.010	0.882	-0.3	Schwenk, S. (1983); DJV
Germany	Brandenburg & Berlin	30,370	1984	2010	1.273	2.752	1.2	DJV
Germany	Hesse	21,114	1953	2010	0.085	3.691	2.2	DJV
Germany	Lower Saxony & Bremen	48,004	1958	2010	0.066	1.200	2.0	DJV
Germany	Mecklenburg-Vorpommern	23,167	1984	2010	1.121	3.275	1.7	DJV
Germany	North Rhine-Westphalia	34,070	1953	2010	0.056	1.258	3.4	DJV
Germany	Rhineland-Palatinate & Saarland	22,416	1955	2010	0.120	3.866	2.1	DJV
Germany	Saxony	18,338	1984	2010	0.677	1.850	1.0	DJV
Germany	Saxony-Anhalt	20,443	1984	2010	0.810	1.767	1.1	DJV
Germany	Schleswig-Holstein & Hamburg	16,486	1956	2010	0.039	0.987	1.5	DJV
Germany	Thuringia	16,175	1984	2010	0.656	1.981	0.3	DJV
Hungary	Central Hungary	14,839	1962	2002	0.018	0.684	0.6	OVA
Hungary	historical Hungary	93,036	1896	1909	0.032	0.064	0.6	Schwenk, S. (1985)
Hungary	Northern Hungary	13,428	1974	1992	0.102	0.635	-1.1	OVA
Hungary	Northern Transdanubia	18,662	1962	2002	0.047	1.535	0.2	OVA
Hungary	Southern Transdanubia	17,953	1962	2002	0.032	1.719	0.9	OVA
Hungary	Trans-Tiszanian Region	27,623	1981	2002	0.012	0.116	-0.4	OVA
Luxemburg	-	2,586	1950	2003	0.085	1.842	1.3	ANF
Netherlands	Veluwe	621	1978	2011	0.628	8.744	3.6	Spek (pers. com.)
Poland	Central Poland	53,777	1977	2011	0.068	0.306	-1.2	GUS; Fruziński, B. (1992)
Poland	Eastern Poland	74,866	2001	2011	0.067	0.280	-0.9	GUS; Fruziński, B. (1992)
Poland	Northern Poland	60,455	2001	2011	0.410	0.852	-1.1	GUS; Fruziński, B. (1992)
Poland	North-western Poland	66,707	1977	2011	0.334	1.147	-0.2	GUS; Fruziński, B. (1992)
Poland	Podlaskie	20,187	1977	2011	0.069	0.309	-2.5	GUS; Fruziński, B. (1992)
Poland	Southern Poland	27,516	1977	2011	0.076	0.389	-1.3	GUS; Fruziński, B. (1992)
Poland	Southwestern Poland	29,359	1977	2011	0.285	1.132	0.2	GUS; Fruziński, B. (1992)
Slovakia	-	49,034	1894	1971	0.017	0.076	0.4	Findo (pers. com.)

S1 Table (continued) Overview over the wild boar hunting bag data.

Country	Region	Area	earliest	latest	min	max	winter	Source
Switzerland	Eastern Switzerland	12,225	1952	2011	0.016	0.086	0.2	FOEN
Switzerland	Espace Mittelland	4,621	1979	2011	0.027	0.316	0.8	FOEN
Switzerland	Lake Geneva region	8,719	1977	2011	0.013	0.089	0.7	FOEN
Switzerland	North-western Switzerland& Zurich	9,129	1985	2011	0.014	0.363	1.1	FOEN
Switzerland	Ticino	991	1990	2011	0.146	1.738	4.0	FOEN

For each region the area (*Area*) [km²], the earliest (*earliest*) and the latest (*latest*) hunting bag data point, the minimum (*min*) and the maximum (*max*) hunting bag [animals shot/km²] as well as the 30-year (1973-2002) winter mean temperature [°C] (*winter*) is shown. The last column specifies the sources of the hunting bag data. The data were acquired from the Federal Office for the Environment, Switzerland (FOEN, www.wild.uzh.ch/jagdst/), the Research Institute for Nature and Forest, Flanders, Belgium (INBO, through T. Scheppers), the Forestry Administration, Belgium (FAB, through A. Licoppe), the Nature and Forestry Agency, Luxemburg (ANF, through S. Cellina), the National Office for Hunting and Wildlife, France (ONCFS), the Annual Handbook of the German Hunting Association (DJV), Statistics Austria (Stat. Austria, www.statistik.at), and the Central Statistical Office, Poland (GUS, www.stat.gov.pl), and the National Game Management Database, Hungary (OVA, www.vvt.gau.hu). Further data for the Czech-Republic, the Netherlands, and Slovakia were kindly provided to us by Bartos, Spek, and Findo, respectively (all pers. com.). Historical data were taken from Schwenk (1982, 1983, 1984, 1984, 1985) and Fruziński (1992).

S2 Table Overview over the climatic data.

Country	Region	No.	Name	Lat.	Long.	Alt.	Temp.	Prec.	Source
Austria	Burgenland	128	Sopron	47.68	16.6	234	1871	1865	AlpImp; ZAMG
Austria	Carinthia	64	Klagenfurt-Airport	46.65	14.33	459	1813	1813	AlpImp; ZAMG
Austria	Lower Austria	152	Vienna-Hohe Warte	48.22	16.35	209	1775	1841	AlpImp; ZAMG
Austria	Salzburg	122	Salzburg-Airport	47.80	13.00	430	1842	1839	AlpImp; ZAMG
Austria	Styria	53	Graz-University	47.08	15.45	377	1837	1837	AlpImp; ZAMG
Austria	Tyrol	59	Innsbruck-University	47.27	11.38	609	1777	1858	AlpImp; ZAMG
Austria	Upper Austria	75	Linz	48.30	14.28	263	1816	1852	AlpImp; ZAMG
Austria	Vienna	152	Vienna-Hohe Warte	48.22	16.35	209	1775	1841	AlpImp; ZAMG
Austria	Vorarlberg	42	Feldkirch	47.27	9.62	440	1875	1876	AlpImp; ZAMG
Belgium	Flanders	64280	Munte	50.93	3.37	55	1973	1973	TUT
Belgium	Wallonia	64560	Florennes	50.23	4.65	279	1973	1973	TUT
Croatia	-	153	Zagreb-Gric; Split	45.82	15.98	162	1861	1862	AlpImp; TUT
Czech Republic	-	165	Brno-Turany	49.16	16.7	241	1848	1805	AlpImp; TUT
France	Alsace	135	Strasbourg-Entzheim-Airport	48.55	7.64	150	1973	1973	AlpImp; TUT
France	Aquitaine	75240	Agen	44.18	0.60	61	1973	1973	TUT
France	Auvergne	74600	Clement-Ferrand	45.78	3.16	332	1973	1973	TUT
France	Brittany	71300	Rennes	48.06	-1.73	37	1973	1973	TUT
France	Burgundy	72800	Dijon	47.26	5.08	222	1973	1973	TUT
France	Centre	72490	Orleans	47.98	1.75	126	1973	1973	TUT
France	Champagne-Ardenne	70700	Reims	49.30	4.03	95	1973	1973	TUT
France	Corsica	77610	Ajaccio	41.91	8.80	6	1973	1973	TUT
France	Franche-Comté	72880	Besancon	47.25	5.98	307	1973	1973	TUT
France	Île-de-France	71490	Paris-Orly	48.71	2.40	89	1973	1973	TUT
France	Languedoc-Roussillon	76350	Carcassonne	43.21	2.31	130	1973	1973	TUT
France	Limousin	74340	Limoges	45.86	1.18	396	1973	1973	TUT
France	Lorraine	93	Nancy-Essey-Tomblaine-Airport	46.00	8.97	273	1973	1973	AlpImp; TUT
France	Lower Normandy	70270	Caen	49.18	-0.45	78	1973	1973	TUT
France	Midi-Pyrénées	76300	Toulouse-Blagnac	43.63	1.36	152	1973	1973	TUT
France	Nord-Pas-de-Calais	70150	Lille	50.56	3.10	48	1973	1973	TUT

S2 Table (continued) Overview over the climatic data.

Country	Region	No.	Name	Lat.	Long.	Alt.	Temp.	Prec.	Source
France	Pays de la Loire	72300	Angers	47.48	-0.56	57	1973	1973	TUT
France	Picardy	70550	Beauvais-Lille	49.46	2.11	109	1973	1973	TUT
France	Poitou-Charentes	74120	Cognac	45.66	-0.31	30	1973	1973	TUT
France	Provence-Alpes-Côte d'Azur	75880	Saint-Auban-sur-Durance	44.06	6.00	460	1973	1973	TUT
France	Rhône-Alpes	74860	Grenoble	45.36	5.33	384	1973	1973	TUT
France	Upper Normandy	70370	Rouen	49.38	1.18	157	1973	1973	TUT
Germany	Baden-Württemberg	136	Stuttgart	48.83	9.20	311	1792	1807	AlpImp; DWD
Germany	Bavaria	193	Regensburg	49.03	12.10	366	1773	1800	AlpImp; DWD
Germany	Brandenburg & Berlin	403	Berlin-Dahlem	52.46	13.30	51	1876	1848	DWD
Germany	Hesse	1420	Frankfurt am Main	50.05	8.60	112	1757	1826	DWD
Germany	Lower Saxony & Bremen	2014	Hannover	52.47	9.68	55	1856	1856	DWD
Germany	Mecklenburg-Vorpommern	4271	Rostock	54.18	12.08	4	1947	1947	DWD
Germany	North Rhine-Westphalia	3	Aachen	50.78	6.09	202	1891	1891	DWD
Germany	Rhineland-Palatinate & Saarland	5100	Trier	49.75	6.66	265	-	1806	DWD
Germany	Saxony	1048	Dresden	51.13	13.76	227	1960	1960	DWD
Germany	Saxony-Anhalt	2932	Halle	51.44	12.24	131	1972	1972	DWD
Germany	Schleswig-Holstein & Hamburg	4466	Schleswig	54.53	9.55	43	1947	1947	DWD
Germany	Thuringia	1270	Erfurt	50.98	10.96	316	1951	1951	DWD
Hungary	Central Hungary	215	Budapest-Lörinc-Airport	47.45	19.22	130	1780	1841	AlpImp; TUT
Hungary	historical Hungary	215	Budapest-Lörinc-Airport	47.45	19.22	130	1780	1841	AlpImp
Hungary	Northern Hungary	127720	Miskolc	48.10	20.76	232	1973	1973	TUT
Hungary	Northern Transdanubia	137	Szombathely	47.27	16.63	221	1874	1865	AlpImp; TUT
Hungary	Southern Transdanubia	104	Pécs	46.06	18.17	150	1871	1854	AlpImp; TUT
Hungary	Trans-Tiszanian Region	128820	Debrecen	47.48	21.60	108	1973	1973	TUT
Italy	Tuscany	6	Arezzo	43.45	11.88	274	1973	-	AlpImp

S2 Table (continued) Overview over the climatic data.

Country	Region	No.	Name	Lat.	Long.	Alt.	Temp.	Prec.	Source
Luxemburg	-	65900	Luxembourg	49.61	6.21	376	1949	1949	TUT
Netherlands	Veluwe	62400	Amsterdam_Airport_Schiphol	52.30	4.76	-4	1973	1973	TUT
Poland	Central Poland	123750	Warszawa-Okecie	52.16	20.96	106	1973	1973	TUT
Poland	Eastern Poland	125850	Sandomierz	50.70	21.71	218	1989	1989	TUT
Poland	Northern Poland	122720	Olsztyn	53.76	20.41	137	1973	1973	TUT
Poland	Northwestern Poland	123300	Poznan	52.41	16.38	86	1973	1973	TUT
Poland	Podlaskie	122950	Bialystok	53.10	23.16	151	1973	1973	TUT
Poland	Southern Poland	125660	Krakow	50.08	19.8	237	1973	1973	TUT
Poland	Southwestern Poland	124240	Wroclaw_Ii	51.10	16.88	120	1973	1973	TUT
Slovakia	-	57	Hurbanovo	47.87	18.20	124	1872	1871	AlpImp; TUT
Spain	Villuercas	82610	Cáceres	39.46	-6.33	405	1973	-	TUT
Switzerland	Central Switzerland	4	Altdorf	46.87	8.63	449	1864	1864	AlpImp; TUT
Switzerland	Eastern Switzerland	50	Glarus	47.04	9.07	515	1864	1872	AlpImp; TUT
Switzerland	Espace Mittelland	17	Bern-Liebefeld	46.93	7.42	565	1777	1856	AlpImp; TUT
Switzerland	Lake Geneva region	126	Sion	46.23	7.37	482	1864	1861	AlpImp; TUT
Switzerland	Northwestern Switzerland & Zurich	157	Zürich-Meteo-Schweiz	47.38	8.57	556	1830	1830	AlpImp; TUT
Switzerland	Ticino	80	Lugano	46.00	8.97	273	1864	1861	AlpImp; TUT

The table gives the number of the climate station used (*no.*; corresponding to the respective source) and its name (*name*) for each region as well as the latitude (*lat.*), longitude (*long.*), and altitude (*alt.*) of the station. Further, the year of the oldest data point for monthly mean temperature (*temp.*) and monthly precipitation sum (*prec.*) is given. In the last column the *source* of the data is shown. The climatic data were acquired from the AlpImp-Project (Auer *et al.* 2007), the Central Institute for Meteorology and Geodynamics (ZAMG, www.zamg.ac.at), the German weather service (DWD; www.dwd.de), and from www.tutiempo.net (TUT). Data from the AlpImp-Project (Auer *et al.* 2007) were homogenized and only available until 2006 so that a second source was used for newer data. For incomplete monthly data points from TUT the mean temperature was calculated anyway and monthly precipitation sum was extrapolated to the full month if there were at least 20 days of data available in the respective month.

S3 Table Model-averaged parameters calculated with the zero-method.

(a) European data set (n = 2075)

term	estimate	SE
winter temperature	**0.188**	**0.025**
long-term winter temperature	**-0.263**	**0.033**
prior autumn temperature	**0.179**	**0.027**
population density	**-0.065**	**0.016**
summer temperature	**-0.041**	**0.022**
winter temperature : long-term winter temperature	**-0.047**	**0.026**
prior spring temperature	0.024	0.022
prior summer temperature	-0.011	0.019
long-term summer temperature	-0.005	0.019
long-term summer precipitation	0.008	0.017
winter temperature : population density	0.011	0.023
long-term yearly precipitation	0.004	0.015
spring temperature	-0.003	0.014
summer temperature : long-term summer temperature	-0.002	0.011

(b) Austrian data set (n = 135)

term	estimate	SE
winter temperature	**0.237**	**0.064**
mast	**0.284**	**0.112**
mast : winter temperature	**-0.910**	**0.245**
prior autumn temperature	**0.162**	**0.061**
long-term winter temperature	**-0.141**	**0.081**
population density	-0.065	0.092
area under cultivation of potatoes	-0.043	0.059
area under cultivation of corn	-0.035	0.065
summer temperature	-0.022	0.043
prior spring temperature	-0.005	0.029
winter temperature : long-term winter temperature	-0.009	0.050
mast : long-term winter temperature	-0.098	0.294
mast : population density	-0.012	0.108

Parameters estimate and standard error (SE) for each term included in the multi-model averages of the European data set (a) and the Austrian subset (b), calculated with the zero-method ADDIN EN.CITE (Grueber *et al.* 2011, Nakagawa & Freckleton 2011

3 EFFECTS OF PULSED RESOURCES ON INDIVIDUAL REPRODUCTIVE PERFORMANCE IN THE WILD BOAR

3.1 SHY IS SOMETIMES BETTER: PERSONALITY AND JUVENILE BODY MASS AFFECT ADULT REPRODUCTIVE SUCCESS IN THE WILD BOAR (*SUS SCROFA*)

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There is increasing evidence that animal personalities are linked to different life-history strategies. However, studies investigating whether these effects differ under varying environmental conditions are rare. We investigated how animal personality affects reproductive success in a pulsed resource consumer, the wild boar. We determined the exploratory behaviour of 57 female wild boars in nine novel object tests and additionally assessed their aggressiveness. Latency to the first approach of the object and total investigation duration as well as aggressiveness were repeatable within individuals and therefore combined in one personality score using principle component analysis. Afterwards the females were kept together with 28 male wild boars under semi-natural conditions in two large breeding enclosures from 2011 to 2014. Over winter 2013/2014 we applied high versus intermediate feeding regimes to the two enclosures. Our results show that adult body mass and reproductive success were affected by juvenile body mass and thus already determined early in life, which may point to a silver spoon effect in the wild boar. The decision whether to invest into reproduction or not, as well as the litter size shortly after birth, was only affected by female body mass, whereas the post-weaning litter size (i.e., at the time of independence at the age of ~ 6 months) was additionally affected by personality. We conclude that lower aggressiveness and reduced exploratory tendency of the mother leads to lower juvenile mortality and hence has a positive impact on post-weaning litter size. However, less aggressive and explorative individuals raised more juveniles to independence only under high food availability whereas this effect vanished under less favourable food availability. Thus, the impact of personality on life-history traits, such as reproductive success, differed between changing environmental conditions. Our results support the hypothesis that different personality phenotypes are evolutionarily maintained by changing selection pressures in heterogeneous environments.

life-history strategy, litter size, feeding experiment, personality, individual quality, silver spoon effect

Introduction

Animal personality describes the existence of a suite of correlated behavioural traits, which differ consistently among individuals over time and across different contexts (e.g. Sih *et al.* 2004, Réale *et al.* 2007, Bergmüller & Taborsky 2010, Carere & Maestripieri 2013). Such personality traits include aggressiveness, exploratory behaviour, willingness to take risks (boldness), activity and sociality (Réale *et al.* 2007). An animal's 'personality' or 'coping style' thus determines its response to different social and environmental challenges, like how to forage, deal with predators, or interact with conspecifics (Bergmüller & Taborsky 2010). It is easy to envision that these personalities may have far-reaching consequences, potentially affecting variation and trade-offs in life-history strategies (Biro & Stamps 2008, Smith & Blumstein 2008, Réale *et al.* 2010, Sih *et al.* 2012). Indeed, various personality traits have been shown to be associated with different life-history traits such as dispersal (Dingemanse *et al.* 2003), maternal performance (Boon *et al.* 2007, Monestier *et al.* 2015), growth (reviewed in Stamps 2007, Cote *et al.* 2008), survival (Dingemanse *et al.* 2004, Cote *et al.* 2008), or fecundity (Cote *et al.* 2008). However, the link between personality traits and life-history traits, such as reproduction and survival, may not always be easy to detect and might differ according to environmental conditions (Réale *et al.* 2010). For instance, aggressiveness and activity in North American red squirrels (*Tamiasciurus hudsonicus*) were found to affect reproductive success and juvenile survival differently in different years (Boon *et al.* 2007). Heterogeneous selection pressures in temporally or spatially varying environments are thought to be an important mechanism in maintaining different life-history strategies and animal personalities in a population as they can cause net selection on these strategies to be close to zero (Dingemanse *et al.* 2004, Réale *et al.* 2010, Dingemanse & Réale 2013). However, up to now there are very few empirical studies investigating effects of personality on life-history traits, such as reproductive success, under changing environmental conditions or in different habitats (but see Dingemanse *et al.* 2004, Boon *et al.* 2007, Cote *et al.* 2008, Monestier *et al.* 2015).

The wild boar (*Sus scrofa*) is an interesting model species to investigate this topic. Similar to the red squirrel, the wild boar strongly relies on tree seeds in its diet (for the wild boar these are acorn, *Quercus spec.*, and beech seeds, *Fagus sylvatica*) (Schley & Roper 2003). Thus, due to the variability in tree seeding, the wild boar faces high variation in food abundance from year to year, which is known to affect its population dynamics considerably (e.g. Bieber & Ruf 2005, Vetter *et al.* 2015). Living in such a highly variable and unpredictable environment, diversity in reproductive strategies may have evolved in the wild boar, potentially associated with personality, to maximise fitness. For instance, aggressiveness has been shown to positively affect competitiveness but negatively affect maternal care (e.g. Veiga & Polo 2008, Rosvall 2013).

In wild boars body mass has a strong impact on reproductive performance. Even juvenile females can start to reproduce once they reach a body mass threshold of 20 to 30 kg (e.g. Gethöffer *et al.* 2007, Servanty *et al.* 2009). Further, litter size as well as breeding probability are positively associated with body mass in this species (e.g. Briedermann 2009, Rosell *et al.* 2012, and citations therein). Consequently, body mass is expected to be a good indicator for individual quality in the wild boar. In other ungulates adult quality is also well predicted by juvenile quality (red deer (*Cervus elaphus*): Albon *et al.* (1992), Soay sheep (*Ovis aries*): Clutton-Brock *et al.* (1992), roe deer (*Capreolus capreolus*): Pettorelli *et al.* (2002). Indeed, differences in individual quality might even mask the cost of reproduction (Noordwijk & de Jong 1986, Reznick *et al.* 2000, Weladji *et al.* 2008). In the wild boar, however, data on reproductive success are mainly based on foetus counts evaluated from hunting bags (e.g. Briedermann 2009, Rosell *et al.* 2012, and citations therein). Therefore these data are not suitable for determining the costs of reproduction or considering long lasting effects of juvenile body mass on future reproduction. Effects such as body mass need to be taken into account and corrected for, however, when investigating potential impacts of personality on reproductive success, especially as recent studies indicate that differences in animal personality are linked to differences in body mass early in life (Rödel & Meyer 2011, Guenther & Trillmich 2015).

Therefore, we investigated effects of personality, including longitudinal effects of individual quality in terms of body mass and previous reproductive success, on female reproductive success in a wild boar population housed under semi-natural conditions. As raising juveniles successfully might not only depend on the body mass or personality of a mother but also on her experience we chose an experimental setting with all females being of the same age and thus having the same experience. Additionally, we manipulated food availability experimentally by providing different supplementary feeding regimes to investigate whether the effects of personality change under different food availabilities. By recording litter sizes shortly after birth and post weaning (i.e., at the time of independence at the age of ~ 6 month), as well as frequencies of suckling bouts during lactation, we focused on the time period when differences between mothers are expected to have a high impact on growth and thus potentially survival of their offspring (English *et al.* 2014). Although, we are not aware of any studies directly investigating animal personality in the wild boar, some studies show consistent behavioural differences in domestic pigs, including aggression, sociality, and exploration behaviour (e.g. Lawrence *et al.* 1991, Hessing *et al.* 1993, Hessing *et al.* 1994, Ruis *et al.* 2000). Aggression and exploration behaviour are known to be linked to maternal care or offspring survival and therefore are likely to affect the number of offspring reared (Murphy *et al.* 1994, Both *et al.* 2005, Sandell 2007, Veiga & Polo 2008, Rosvall 2013).

We hypothesised (i) that wild boars show consistent differences in correlated personality traits (i.e., aggression and exploration behaviour) and (ii) that juvenile body mass is linked to this personality. We further hypothesised that, as in other ungulates, juvenile body mass in the wild boar has long lasting effects on adult quality (i.e., in terms of body mass and reproductive success), possibly masking costs of reproduction. We finally hypothesised that (iii) reproductive performance (i.e., breeding probability and litter size) of females is strongly affected by body mass, as previously shown, but also by their personality. In this context we expected the effect of personality on reproductive success to be most pronounced after weaning but to change under different food availabilities.

Methods

Ethical Note

The present study was discussed and approved by the ethics and animals welfare committee of the University of Veterinary Medicine, Vienna, Austria, in accordance with good scientific practise and national legislation (GZ: 06/11/97/2011 and GZ: 15/03/97/2012).

Animal breeding

We obtained 118 female wild boars from four different source populations, Iszkáz and Ásotthalom (both in Hungary), and Vienna and Eisenstadt (both in Austria). They were brought to the study site at the age of around six months in autumn 2011 (born in April 2011). Animals were transported with professional livestock carriers (Örkény-Med LTD., Kaposvár-Fészerlak 324/5, Hungary) in groups of up to 31 individuals; maximum journey time was 4h. Animals had room to move in the carriers, sufficient air circulation was ensured, and a thick layer of straw was provided. Because of the short journey time water was offered directly before and after the journey. All animals were used to the presence of humans and were not sedated for transport. They were led over wooden corridors from their stables/enclosures into the livestock-carrier. The journeys were carried out during the afternoon to prevent the animals from heat exposure in the truck. All animals were individually marked with ear tags (left ear: coloured and numbered ear tag (Supertag Hog 55 mm x 50 mm) for visual observation, right ear: RFID I-Tag Button (∅ 25 mm) for recognition via a RFID reading station, both from Dalton, Lichtenvoorde, Netherlands) at their arrival. Both markings were applied with specific marking-pliers (Dalton, Lichtervoorde, Netherlands). Additionally, common ID ISO-transponder (2 x 12 mm Virbac, Barnevelden, Netherlands or Dasmann Tecklenburg, Germany) were injected subcutaneously caudal/dorsal in the abdomen for life-long identification (animals from the breeding enclosure Ásotthalom were already marked with ISO-transponders and were not marked again). For the individual marking juveniles were separated, after they were led one by one through a wooden corridor (4 m length x 0.4 m width x 1 m height), into a wooden box (1.2 m x 0.7 m x 1.1 m). Animals were then grabbed at their hind legs and fixed sideways on the floor with manpower. After marking the ears and taking the hair samples for genetic analysis (~ 1-2 min. handling time) animals were released into habituation enclosures (HE). Animals were kept for eight weeks in four HEs, each of about 350 m², separated according to their origin (27-31 animals per HE). Because of this handling regime we could prevent severe aggressions within the HE. Animals were aggressive against unknown conspecifics in the neighbouring HE, but this aggression through the fence vanished within a week. After eight weeks of habituation period the animals were released pseudo-randomly with respect to origin, body mass and density into two large experimental enclosures (E1, ~ 33 ha; E2, ~ 22 ha) resulting in a density of ~ 2.1 females/ha in both enclosures. In all enclosures (HE, E) water, shelter and trees were available. Additionally, all animals had continuously access to an open water body allowing wallowing. Animals were monitored and supplementary fed daily (see below). We did not observe any stereotypies in the enclosures. The animals experienced ambient temperatures between -9.5°C (2014) and +39.3°C (2013) during the study period (HE/E). The enclosures also housed 17 males (E1) and 11 males (E2) aged between 1 and 5 years to allow mating. The two experimental enclosures were very similar with respect to vegetation and were covered by an oak (*Quercus cerris*) forest interspersed by some open areas.

All animals were under supervision of a veterinarian who handled and treated the animals. Veterinary care included annual deworming (Ivermectin, 0.1 mg kg^{-1} day^{-1} was administered orally, together with the food, for five consecutive days), treatment of six minor infections or injuries within the study period, and overseeing the general health of the individuals. Despite the intensive veterinary care, eight females died over the course of the study. Seven females failed to survive the first winter (i.e., 2011/2012) and one during the second winter (i.e., 2012/2013). No study animals died over the third winter of 2013/2014 and thus as a result of the manipulated food availability. We could not determine the cause of death (animals no longer came to the feeding station). However, winter mortality in young wild boars is well-known (Howells & Edwards-Jones 1997, Leaper *et al.* 1999) and the observed mortality rate in our study was negligible compared with those observed in wild populations of wild boars (e.g. Jezierski 1977, Moretti 1995, Briedermann 2009). Given the growth of the animals and the concomitant space demands, we removed 8 animals in autumn 2012 from the population, resulting in 102 females from spring 2013 onwards (i.e., ~ 1.9 females/ha). Animals that were removed from the study site were released into an adjacent game reserve (2-3 adult or 3-8 juveniles (see below) were transported together in a wooden box (2 m x 1 m x 2 m) on a pickup (< 1 km)). Ear tags were removed prior to release without sedating the animals (by cutting the plastic-base between the tags with pliers).

Assessment of body mass

Prior to the release from the HE's into E1 and E2 the body mass of each animal was recorded (i.e., at the age of ~ 8 months; juvenile body mass; Gallagher SmartScale® 600 and Gallagher Loadbars (accuracy: 0.2 and 0.5 kg for weights below and above 50 kg respectively), Gallagher Europe, Groningen, Netherlands). Body mass was recorded again preceding the reproductive season in 2012 at the age of ~ 19 months (pre-rut body mass 2012) and in 2013 at the age of ~ 29 months (pre-rut body mass 2013) as well as in late winter 2014 at the age of ~ 34 months (winter body mass 2014). At these occasions on average ~ 70 % of the females could be captured and weighed after 3-4 capture events within 10 days. All capture events in E1 and E2 were carried out by locking the animals in the corresponding feeding area. To minimise the recapture frequency within one capture season, the doors were closed selectively if the target groups were in the feeding station. The animals were then led through a wooden corridor (see above) and separated into a wooden box placed on load bars (Gallagher Europe, Groningen, Netherlands). After recording the body mass, the box was opened and the animals were released back into their enclosure. Through the top of the wooden corridor we had access to the animals and could remove or re-mark single animals. To this end the animal was fixed with a plank at one side of the corridor, if necessary. The same capture and separation procedure was used to remove juveniles from the study site.

Food availability and feeding regimes

Naturally occurring food resources were intermediate (25-50 % of the trees provided acorn) during all study years. However, the seed abundance was not sufficient to maintain the animals. The animals therefore received supplementary feeding *ad libitum* on a daily basis. We fed a high-fat wild boar food mixture (Type H9483, Hoferfutter, Herbert Lugitsch u. Söhne GmbH, Eggendorf, Austria) during winter (October to March), and corn as a summer diet (April to September). To reduce the risk of rotten food leftovers, *ad libitum* feeding was performed by providing the maximum amount of food which could be consumed within 24h. Following this, the wild boars consumed on average 0.74 kg*animal^{-1}*day^{-1} until March 2012, and 0.91 kg*animal^{-1}*day^{-1} from March to November 2012. From November 2012 until November 2014 the animals consumed on average ~ 1.2 kg*animal^{-1}*day^{-1} which accounts for ~ 160 % of the basal metabolic rate of a 60 kg wild boar (Briedermann 2009). This feeding regime is thus assumed to resemble a mast situation with high food availability. Animals in E1, however, received a moderately reduced supplementary feeding of

~ 1.0 kg*animal^{-1}*day^{-1} (resembling an intermediate mast year) between November 2013 and March 2014. We did observe a body mass gain under both feeding regimes (see Fig. 1). Thus, our feeding regime did not severely restrict the food uptake of the animals.

Assessment of reproductive success

Each spring, intensive observations were carried out in order to determine which females reproduced (yes/no). Under the semi natural conditions of the enclosure it was not possible to determine litter sizes at birth for all females as mothers tend to hide around the time of parturition (see the results for the timing of parturition). However, in spring 2013 we obtained reliable observational data on the litter size approximately one week after birth for 14 females in E2. Although these counts probably slightly underestimate the litter size at birth, we believe the proximity to the time of birth negates any minor effects of post-natal mortality. Between April and June 2013, we additionally recorded the lactation behaviour (i.e., time and duration of suckling events) of a subsample of 12 females in E2 during daytime. We chose this variable, as it accurately reflects the intensity of maternal care, which is not only important in terms of food provisioning, but also in terms of time spent warming the offspring, which are strongly affected by cold temperatures (Howells & Edwards-Jones 1997, Geisser & Reyer 2005). Additionally, it provided the most accurate data compared with other variables like total lactation duration or the time offspring spent with their mother, which were difficult to assess in our semi-natural setting. Due to logistical reasons we restricted our observations of lactation behaviour to E2. In fact, one group of females in this enclosure started to lactate regularly directly at the feeding area and could therefore be observed without any distress for the animals. Finally, every year all juveniles were caught as described above at the age of about six months and hair samples were collected. The juveniles were removed from the population at this stage and released into a game enclosure (see above). Maternity and consequently weaned litter size of each female was determined via microsatellite analysis using the program COLONY (v2.0.4.7, Jones & Wang 2010) (for a detailed description of the microsatellite analysis see Supplementary Material S1).

Assessment of animal personality

In order to determine possible personality differences, nine novel object tests (objects: bucket, football, booster seat, toy tube, plastic basket, traffic cone, plastic crow, potato bag, and watering can) were performed over a period of 14 days while the animals were still in the habituation enclosures but after an acclimation-period of three weeks. Due to logistical reasons, the tests were restricted to two habituation enclosures (57 individuals, 55 %). Since wild boars are highly social and live in groups, the novel objects were presented to the whole group simultaneously. After the object was placed into the enclosure the investigation behaviour of the animals was videotaped for ten minutes using a hand held camera (HDC-SD9, Panasonic Germany GmbH). Videos were analysed afterwards by recording the timing of first contact with the novel object and total investigation duration per object. Investigation behaviour was defined as the animal sniffing at the object or manipulating (i.e., biting, moving) it. To also consider animals which did not approach the novel object, the timing of the first contact was transformed into a rank variable (1: no contact, 2: 300-600 s, 3: 200-300 s, 4: 100-200 s, 5: < 100 s).

After the acclimatisation period of three weeks, we also regularly recorded aggressive interactions (for a definition of aggressive behaviours see Table 1) until the end of the habituation period using ten-minute intervals of event sampling (Martin & Bateson 1993). The entire group was observed and for each aggressive interaction the aggressor, the victim, and the respective winner of the interaction was recorded. In order to avoid autocorrelation, two intervals in the same enclosure had to be separated by at least one hour. Total observation time was 35 h for both enclosures. The total number of aggressive actions shown by each individual was standardised by observation time (i.e., 35 h). Further, based on the aggressive interactions, the social rank was calculated for each individual using the Batchelder-Bershad-Simpson scaling method (BBS; Batchelder & Bershad 1979). Due to slight differences in group size (i.e., 27 individuals in HE1 vs 30 individuals in HE2) we standardised this BBS score by group size to obtain a comparable social rank variable.

Table 1 Definition of aggressive behaviours.

Behaviour	**definition**
Threatening	Erection of the back fur, snapping The inferior animal avoids the aggressor
Attacking	Biting or Hitting with the snout The inferior animal immediately gets out of the way of the aggressor
Chasing	One individual chases another away by running after it; The inferior animal runs away
Fighting	Both animals show attacks The defeated animal runs way
Mounting	Mounting another individual The dominated animal does not fight back

We tested the repeatability (R; i.e., the proportion of the total variance accounted for by differences among individuals (Nakagawa & Schielzeth 2010, Sokal & Rohlf 1995) of the timing of the first contact and the investigation duration over the nine novel object tests with multiplicative overdispersion models for count data (Nakagawa & Schielzeth 2010) using the R-package rptR (Schielzeth & Nakagawa 2013). In order to assess repeatability of aggressiveness (i.e., using the same method), aggressive actions were recorded again from March to Mai 2012 during daytime (i.e., 8:30 am until 16:30 pm) in both experimental enclosures using event sampling (Martin & Bateson 1993) and corrected by the time each individual was observed. Individual observation times for this period ranged from 10.1 h to 33.3 h.

As the timing of the first contact and total investigation duration were significantly repeatable (see results) we averaged these variables for each individual and performed a normalised principal component analysis (PCA) including the two averaged variables and aggressiveness as obtained in autumn 2011. This PCA yielded a single personality score for each of the 57 animals tested in the novel object tests (see results), including two of the five major personality traits (i.e., aggression and exploration; Réale *et al.* 2007).

Statistical analyses

An overview of all models, including the respective response and predictor variables of the full models, included random effects, as well as sample sizes is given in Table 2. All statistical analyses were performed in R.3.0.2 (R Core Team 2013). Linear mixed effects models and mixed effects poisson models were calculated using the R-package lme4 (Bates *et al.* 2014a). The zero-inflated mixed effects poisson model was calculated using the R-package glmmADMB (Fournier *et al.* 2012, Skaug *et al.* 2014).

As we performed the novel object tests within groups, the social hierarchy could have had affected the behaviour of the animals in the tests. Thus, we tested which factors had an impact on the averaged timing of the first contact and on the averaged investigation duration (Table 2a). Additionally, we tested whether the first principal component of the PCA, which we used as a measure for animal personality (see results), was affected by juvenile body mass and linked to social status (Table 2a).

To test for long-term effects of juvenile condition and potential costs of reproduction, we tested which factors (e.g., juvenile body mass, personality, previous post weaning litter size, or food availability) affected the body mass at different stages of female wild boars as well as body mass gain over winter 2013/2014 (Table 2b).

Table 2 Overview over statistical analyses for testing (a) reliability of the novel object tests for determining animal personality, (b) effects on body mass development, (c) effects on the reproductive performance, and (d) testing maternal care behaviour. Response variables include timing of the first contact with the novel objects (*$1^{st}c$*), total investigation duration of the novel objects (*InvDur*), pre-rut body mass 2012 and 2013 (*PRbm12*, and *PRbm13*, respectively), winter body mass 2014 (*Wbm14*), Reproduction (yes/no; *Repro*), initial litter size (*iLS*, i.e. within 7 days after birth), post-weaning litter size (*pwLS*), time interval between two lactation events as a measure of lactation frequency (*Lact*). Further predictor variables include social rank (*SR*), aggressiveness (*Aggr*), personality score from the PCA (*Pers*), juvenile body mass (*Jbm*), pre-rut body mass of the respective reproductive season (*PRbm*), post-weaning litter size of the previous reproduction (*ppwLS*), as well as food availability (*FA*). Random factors include habituation enclosure (HE), experimental enclosure (EE), animal (ID), and Year. Sample size are given as number of individuals (N_{ind}) and, if the analysis included several measurements per individual, total number of data points (N_{tot}).

Hypothesis / Scientific question	**Statistical test**	**Response variable**	**Predictor variables**	**Random effect(s)**	**N_{ind} (N_{tot})**
(a) Reliability of the novel object test					
Is the behaviour in the novel object test affected by social rank?	Linear mixed effects model	1^{st}c	SR, Aggr, InvDur, Jbm	HE	57
	Linear mixed effects model	InvDur	SR, Aggr, 1^{st}c, Jbm	HE	57
Juvenile body mass is linked to animal personality.	Linear mixed effects model	Pers	Jbm, SR	HE	57
(b) Body mass development					
Juvenile body mass has long-lasting effects on adult body mass and body mass gain after reproduction, indicating differences in individual quality.	Linear mixed effects model	PRbm12 (19 month)	Jbm, Pers	HE, EE	44
	Linear mixed effects model	PRbm13 (29 month)	Jbm, Pers, ppwLS	HE, EE	46
	Linear mixed effects model	Wbm14 (34 month)	Jbm, Pers, ppwLS, FA, Pers:FA	HE, EE	44
	Linear mixed effects model	Wbm14 (34 month)	Jbm, Pers, ppwLS, FA, Pers:FA, PRbm13	HE, EE	44
(c) Reproductive performance[1]					
Probability of reproduction and litter size shortly after birth are affected by body mass.	Binomial mixed effects model	Repro	Jbm, PRbm, ppwLS, Jbm:PRbm	HE, EE, Year, ID	92 (137)
	Mixed effects poisson model	iLS[2]	Jbm, PRbm, Jbm:PRbm	HE	13
Post-weaning litter size is also affected by animal personality but this effect is altered by food availability.	Zero-inflated mixed effects poisson model	pwLS	Jbm, Pers, ppwLS, FA, Pers:FA, Jbm:FA, ppwLS:FA	HE, EE, Year, ID	47 (94)
(d) Maternal care					
Is maternal care affected by personality?	Linear mixed effects model	Lact[2]	Jbm, PRbm, Pers, Jbm:PRbm	HE, ID	12 (145)

[1] For all three models on reproductive performance a random forest analysis including Jbm, PRbm, pPWLS, Pers was carried out beforehand to avoid overfitting of the full models. For details see text.

[2] Data only available for some mothers in EE2 in 2013. Year and experimental enclosure are therefore not included as random effects.

In order to test for effects of juvenile and current body mass, personality, and food availability on the reproductive performance, we tested their effects on whether a female reproduced or not, the initial litter size (i.e., within 7 days after birth), and the post-weaning litter size (Table 2c). To avoid overfitting of the full models, we used a random forest analysis for variable pre-selection (i.e, a combination of binary decision trees created from bootstrapped samples of the data set and randomly choosing a subset of explanatory variables at each split (Breiman 2001, Genuer *et al.* 2010)), using the R package randomForest (Liaw & Wiener 2002). For these tests we included juvenile and pre-rut body mass, previous post-weaning litter size (i.e., from the previous reproductive season) and the personality score for all three analyses on reproductive success. As the results of these random forest analyses were very robust to changes in the number of candidate variables randomly sampled at each split, this parameter was kept as the default (i.e., 2). The number of trees in the forest was set to 5000 in order to increase the stability of the random forest analysis. If the random forest analysis showed a high importance for food availability we also included the interactive effects of food availability with personality, juvenile body mass and previous post-weaning litter size as we expected potential effects of these variables to be altered by food availability. If both, juvenile and pre-rut body mass, proved to be important in the random forest analysis we additionally included the interaction of those two variables in order to test whether lighter juveniles are able to catch up with heavier ones. The resulting full models on reproductive performance are given in Table 2c.

Finally, we tested whether maternal care behaviour (i.e., the boxcox-transformed timespan between two successive lactation events) was affected by individual personality or body mass of a female (Table 2d).

For all models, relevant explanatory variables were selected by comparing all nested models in a model selection table based on Akaike's Information Criterion (AICc; Akaike 1973) corrected for small sample size (Hurvich & Tsai 1989), which are shown in the Supplementary Material S2. As some predictor variables were obviously correlated (e.g. juvenile and adult body mass, etc.; see results) for all full models (see Table 2), we calculated variance inflation factors of the predictor variables using the corvif function (Zuur *et al.* 2009). According to these analyses, none of the models showed serious collinearity issues (all values well below 10 (Menard 1995); results are reported in Supplementary Material S2 along with the respective model selection tables). Full models of all linear mixed effects models showed no evidence for serious deviations from normality according to the inspection of the distribution of residuals by means of histograms and quantile-quantile plots. (Zero-inflated) mixed effects Poisson models showed no signs of serious overdispersion.

Results

Personality assessment

The timing of the first contact (R ± SE = 0.17±0.05, P = 0.001, N = 57) and the total investigation duration (R ± SE = 0.17±0.09, P = 0.001, N = 57) of the novel objects were both significantly repeatable within individuals. The best models for the timing of the first contact only contained investigation duration and aggression, the best model for investigation duration only contained timing of the first contact (ΔAICc to the next best models was 2.18 and 2.24, respectively; Supplementary Material S2, Table S3-S4). Individual aggressiveness was repeatable between autumn 2011 and spring 2012 (R ± SE = 0.50±0.17, P = 0.005, N = 51 animals).

In the PCA the first principal component (PC1) proved to be the only principle component with an eigenvalue > 1 (i.e., 2.03) (Kaiser-Guttman rule; Kaiser 1991). It explained 67.7 % of the variation and was negatively linked to all three behavioural variables (Table 3). Consequently, the PC1 was then used as individual personality score with more explorative (i.e., shorter latency to approach a novel object and longer investigation duration) and more aggressive individuals having a lower personality score, and less explorative, less aggressive individuals having a higher score.

Table 3 PCA loadings of behavioural traits for the three principal components of the normalized principal component analysis (N = 57), together with their Eigenvalues and the amount of variance they explained.

Behavioural trait	PC1	PC2	PC3
Timing of the 1st contact	-0.63	0.18	0.75
Investigation duration	-0.59	0.51	0.62
Aggressiveness	-0.50	-0.84	0.21
Eigenvalue	2.01	0.69	0.28
Variance Explained (%)	67.67	22.90	9.43

This personality score was positively linked to juvenile body mass (slope ± SE = 0.05 ± 0.02) as well as to the social rank of an individual (slope ± SE = 2.13± 0.58) as indicated by the fact that the best model contained both variables (ΔAICc to the next best models was 2.20; Supplementary Material S2, Table S5).

Body mass development

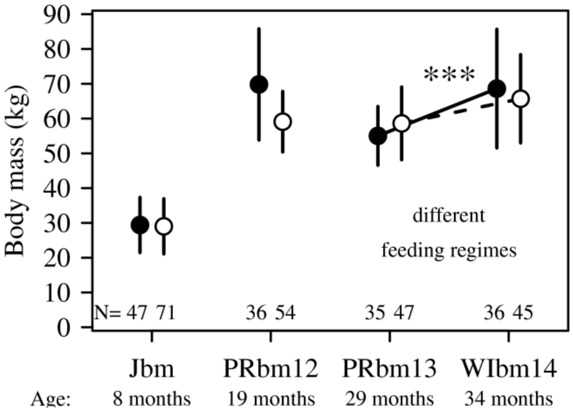

Figure 1 Body mass of female wild boars at the age of 8 months (juvenile body mass, Jbm), 19 months (pre-rut body mass 2012, PRbm12), 29 months (pre-rut body mass 2013, PRbm12), and in late winter 2014 (WIbm14) at the age of 34 months. Black circles (E2) and white circles (E1) show means ± sd. The slopes between ages 29 and 34 months indicate the significant difference in body mass gain over winter 2013/2014 during the different feeding regimes (E2: solid line, E1: dashed line).

Only juvenile body mass was included in the best models on pre-rut body mass 2012 and winter body mass 2014 (ΔAICc to the next best models were 2.58 and 2.28, respectively; Supplementary Material S2, Table S6-S8) and positively affected these subsequent body mass measurements (pre-rut body mass 2012: slope ± SE = 0.66 ± 0.20; winter body mass 2014: slope ± SE = 0.42 ± 0.21). Thus, on average, lighter juveniles remained lighter as adults, even more than two years later. Juvenile body mass also positively affected the pre-rut body mass 2013 (slope ± SE = 0.56 ± 0.20). The best model on pre-rut body mass 2013 (i.e., after the first lactation; ΔAICc = 1.79), however, additionally contained the previous post-weaning litter size (Supplementary Material S2, Table S7), which negatively affected this body mass measurement (slope ± SE = -3.35 ± 1.42). This was also reflected by the fact that the mean body mass at the age of 29 months was considerably lower compared to that at 19 months (Fig. 1). The best model on body mass gain (ΔAICc of 1.59; Supplementary Material S2, Table S9) from autumn 2013 to late winter 2014 again contained juvenile body mass, which showed a positive effect (slope ± SE = 0.69 ± 0.19). Additionally, feeding regime (slope ± SE = 6.90 ± 2.28; Fig. 1) and previous post-weaning litter size (slope ± SE = 2.50 ± 1.14) were included in this best model (Supplementary Material S2, Table S9) and positively affected the body mass gain.

Reproductive performance

There was no reproduction in 2012, but in spring 2013 and 2014 successful reproduction was observed. In 2013 86 % (N = 60) of the observed females reproduced. Altogether, 40 % of females (N = 41) successfully raised a total of 92 juveniles (49 % male, 51 % female), resulting in an average post-weaning litter size of 2.2 ± 1.4 juveniles. In 2014, 55 % (N = 54) of the observed females reproduced and 21 % (N = 21) of all females successfully weaned a total of 45 juveniles (40 % male, 60 % female). Post-weaning litter size in 2014 was on average 2.1 ± 1.5. Mean parturition took place on calendar week 12.8 ± 3.1 (mean ± sd) in 2013 and 18.4 ± 2.2 (mean ± sd) in 2014.

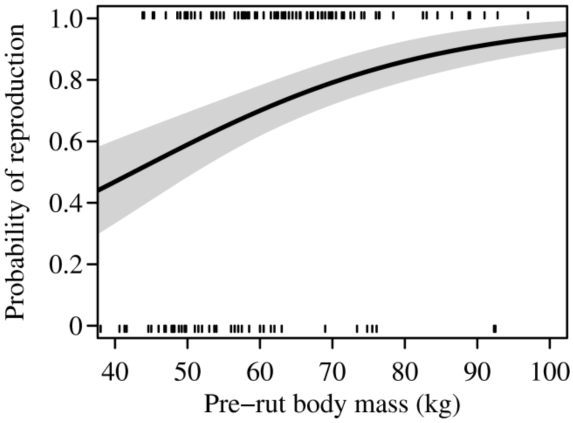

Figure 2 Partial effect of pre-rut body mass of females on their probability to reproduce (N = 137 data points from 92 animals).

According to the random forest analysis, the personality score and the food availability were of minor importance in explaining variation in the probability to breed in female wild boars (see Supplementary Material S3, Fig. S1a), and therefore were not included in the full model. The best model on female probability of reproduction only contained pre-rut body mass (Supplementary Material S3, Table S10; slope ± SE = 0.05 ± 0.02; Fig. 2). The second best model, containing additionally the interaction of pre-rut body mass with juvenile body mass, was almost equally likely (ΔAICc = 0.39; Supplementary Material S2, Table S10). According to this model, females that were heavy as juveniles were more likely to reproduce, even with a lower pre-rut body mass.

The random forest analysis revealed that only body mass was important for explaining variation in initial litter size (recorded within 7 days after birth; see Supplementary Material S3, Fig. S1b). Therefore previous post-weaning litter size and the personality score were not included in the full model. The litter size shortly after birth was 4.2 ± 1.8 (mean ± sd) juveniles per female and was only affected by juvenile body mass with no other variables occurring in the best model (Supplementary Material S2, Table S11; slope ± SE = 0.04 ± 0.02). The second best model only contained pre-rut body mass and had a ΔAICc of 0.23 (Supplementary Material S2, Table S11).

According to the random forest analysis pre-rut body mass was not included in the full model on post-weaning litter size (see Supplementary Material S3, Fig. S1c). Juvenile body mass was present in the best model, and positively affected post-weaning litter size (slope ± SE 0.08 ± 0.04; Fig 3a; Supplementary Material S2, Table S12) The personality score was also included in the best model as there was an interaction between personality and food availability (Supplementary Material S2, Table S12). Under high food availability females that were less aggressive and less explorative had a higher post-weaning litter size than females that were more explorative and aggressive (slope ± SE = 0.48 ± 0.20, Fig. 3b), whereas the personality score had no effect under less favourable food availability (slope = -0.12 ± 0.22, Fig. 3c). The second best model only contained juvenile body mass (heavier females raised more juveniles) and the personality score (less aggressive and less explorative females raised more juveniles) and had a ΔAICc of 0.03 (Supplementary Material S2, Table S12).

Maternal care

The Null-model was the best model explaining the time between two lactation events (Supplementary Material S2, Table S13). The three next best models were all within a ΔAICc below 1.3 (i.e., 1.15., 1.23, and 1.28, respectively) and contained the personality score and/or pre-rut body mass (both variables: ΔAICc = 1.15, only the personality score: ΔAICc = 1.23, and only pre-rut body mass: ΔAICc = 1.28; Supplementary Material S2, Table S13). According to the second best model, the time between successive lactation events was shorter in less explorative and aggressive mothers (model prediction for less aggressive/explorative mothers: mean ± SE = 44.5 ± 1.4 min; model prediction for more explorative/aggressive mothers: mean ± SE = 64.9 ± 1.6 min; slope ± SE = -0.25 ± 0.19). Pre-rut body mass in this model showed a weak negative effect on the time between two successive lactation events (coefficient from the second best model: slope ± SE = -0.02 ± 0.02).

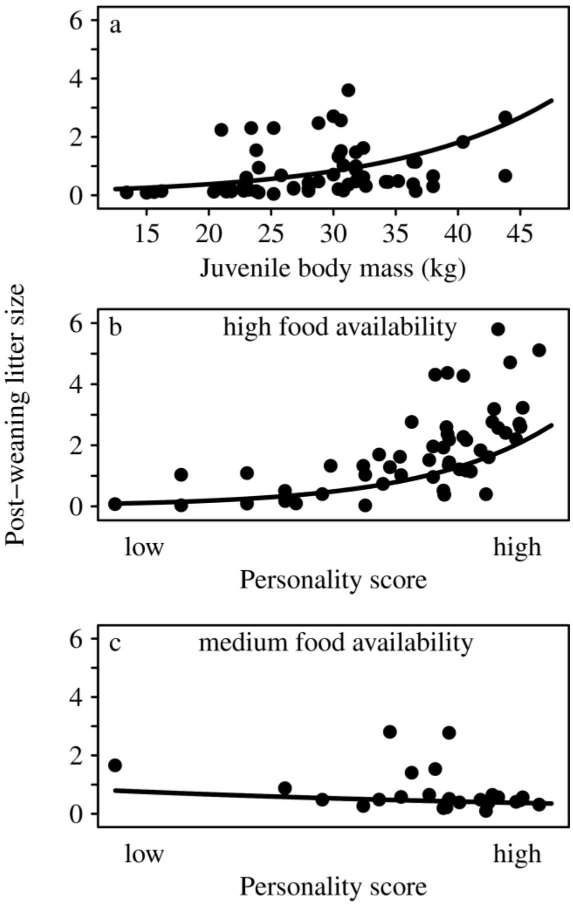

Figure 3 Partial effects on the post-weaning litter size of female wild boars (N = 94 data points from 47 animals). (a) The effect of juvenile body mass (i.e., at the age of eight months) on post-weaning litter size. The effect of personality on post-weaning litter size is shown for (b) high food availability and for (c) medium food availability.

Discussion

Overall, our study shows an interactive effect of female personality and food availability on reproductive success. Less aggressive and explorative females raised more juveniles under high food availability but not under moderate food restriction (Fig. 3). As we did not observe effects of personality on either breeding probability or litter size shortly after birth, we conclude that the personality of the mother directly affected the survival of her offspring. Thus, our findings further strengthen the hypothesis that different personality phenotypes are evolutionarily maintained by heterogeneous selection pressures (Dingemanse & Réale 2013). Additionally, we found strong and long-lasting effects of juvenile body mass on adult body mass, as well as on reproductive success in the wild boar. As a major outcome of our study we can show that differences in juvenile body mass caused differences in individual quality in adult females, hampering the detection of long-term costs of reproduction and trade-offs between reproductive effort and other life-history variables (e.g. compare Noordwijk & de Jong 1986, Reznick *et al.* 2000, Weladji *et al.* 2008). These effects of juvenile body mass also emphasise the importance of taking body mass into account when testing for effects of personality on reproductive parameters, especially as we found that juvenile body mass was linked to personality in the wild boar. A similar association between personality and body mass was recently found in guinea pigs (*Cavia aperea*) (Guenther & Trillmich 2015) and laboratory rats (*Rattus norvegicus*) (Rödel & Meyer 2011).

Effects of Body mass on reproductive success

The numbers of juveniles raised by 2-3 year old females in our study (2.2 ± 1.4) are in line with field observations showing that younger animals raise on average 1.3 juveniles, while older females raise 3.0 juveniles (Ahmad *et al.* 1995). Our study revealed that the decision of whether to invest into reproduction was mostly affected by the body mass of females shortly before breeding (Fig. 2). Similar effects of body mass on the breeding probability have been shown previously in several wild boar populations across Europe (e.g. Gaillard *et al.* 1993, Boitani *et al.* 1995, Náhlik & Sándor 2003, Gethöffer 2005, Rosell *et al.* 2012). However, in our analysis the second best model on breeding probability, which was only marginally worse (ΔAICc = 0.39), additionally included interactive effects of pre-rut and juvenile body mass. According to this model, even lighter females had a higher probability of reproduction when they had been heavy as juveniles. This points to the importance of juvenile body mass, and, in fact, we also found that juvenile body mass positively affected all subsequent body mass measurements in adults (i.e., at the age of 19, 29, and 34 months). The importance of juvenile body mass for adult quality was further reflected by its positive effect on litter size, both at birth and post weaning. Although this is the first study showing these strong early life effects in wild boar, previous studies identified similar effects in other ungulate species (e.g. Albon *et al.* 1992, Clutton-Brock *et al.* 1992, Festa-Bianchet *et al.* 2000, Pettorelli *et al.* 2002, Weladji *et al.* 2008).

In line with this finding, we could identify only short-term costs of reproduction in the wild boar. Litter size at independence (i.e., post-weaning) did not affect reproductive success in the following year and had an impact on body mass only shortly after weaning (pre-rut body mass 2013) but not longer than 5 months later (winter body mass 2014). Although one might assume that the latter was due to the supplementary feeding in our enclosures, the analysis of body mass gains over winter 2013/2014 showed that individuals with a higher previous post-weaning litter size in fact gained more weight, independent of the food supply. Additionally, the body mass gain over winter was positively affected by juvenile body mass, once more underlining the significant impact of juvenile body mass on adult quality. These results indicate that differences in female quality are determined early in life and may override trade-offs between reproduction and other life-history traits (Noordwijk & de Jong 1986, Reznick *et al.* 2000).

Long lasting effects of juvenile condition on later reproductive success and other life-history traits are known from several bird and mammal species (reviewed in Lindström 1999). Such consequences are often associated with the so-called silver spoon effect, describing the phenomenon that individuals that grow up under good environmental conditions have a life-long advantage (Grafen 1988). Our data are not sufficient to differentiate between a genuine silver spoon effect and a heritable genetic basis of individual quality, although these two possibilities are not necessarily mutually exclusive. Another alternative, which is mutually exclusive to a silver spoon effect, is the so-called environmental matching, where individuals are best adapted to and have the highest fitness under the environmental conditions in which they grew up (Monaghan 2008). The variation in juvenile body mass we observed, however, is unlikely to be solely explained by genetic differences but might also be influenced by environmental factors such as differential access to food due to sibling rivalry (Fraser & Thompson 1991). Assuming that female wild boars show environmental matching (Monaghan 2008), one would therefore expect lighter juveniles to have developed under less favourable conditions and thus to perform better under reduced food availability as adults, whereas heavier juveniles would be expected to have developed under favourable conditions and consequently to perform better under high food availability. We did not, however, observe such an interactive effect of juvenile body mass and food availability and therefore conclude that a silver spoon effect is more likely in this case than environmental matching. Nevertheless, further longitudinal studies are needed to clarify which of these strategies best applies to the wild boar.

We included body mass as a covariate in all analysis, since juvenile body mass was also linked to personality (compare Rödel & Meyer 2011, Guenther & Trillmich 2015). Indeed, this, together with the long-lasting effects of juvenile body mass on adult body mass and reproductive success, underlines the importance of taking body mass into account when testing for effects of personality.

Personality in the wild boar

Latency of the first contact with the novel object, total investigation duration, and aggression were all significantly repeatable within individuals and correlated to each other, which demonstrates the existence of different animal personalities (Réale *et al.* 2007, Biro & Stamps 2008, Carere & Maestripieri 2013) in wild boars. We are not aware of any study investigating personality in the wild boar but there are several studies on domestic pigs (*Sus scrofa domestica*). Although, some of these studies found no support for correlated consistent behavioural traits (Forkman *et al.* 1995, Jensen *et al.* 1995, Spoolder *et al.* 1996), the majority identified various relevant correlations (Lawrence *et al.* 1991, Hessing *et al.* 1993, Hessing *et al.* 1994, Erhard & Mendl 1999, Thodberg *et al.* 1999, Ruis *et al.* 2000) and are therefore consistent with our finding.

We found that more aggressive individuals approached novel objects faster. Additionally, individuals with a shorter latency to approach a novel object also investigated the object for a longer time. This seems odd at the first glance, as one usually would expect individuals that quickly approach a novel object to investigate it only superficially, whereas more cautious animals may approach the object later but investigate it more thoroughly (Wilson 1998). This negative link was also found in domestic pigs (Hessing *et al.* 1994). One possible explanation for our contrasting finding might be that we assessed exploration behaviour of individuals while they were in a group, causing lower ranking individuals to have limited access to the object. However, we found that the social rank had no effect on the animal's behaviour in the novel object tests. Nevertheless, encountering the novel objects in the group might have affected exploratory behaviour by pathways other than social hierarchy. A recent study showed that in the wolf (*Canis lupus*), a highly social animal, the duration individuals investigated a novel objects increased when other pack members were present (Moretti *et al.* 2015). We cannot exclude that the wild boars would have behaved differently when tested alone but our results are in fact in line with another study on domestic pigs (Forkman *et al.* 1995). However, estimates of exploration behaviour of highly social animals like female wild boars are likely more realistic when assessed with group members being present. Female wild boars in natural habitats are unlikely to face a novel situation alone and such an experimental setup would therefore be highly artificial, potentially causing misleading results.

Effects of personality on reproductive success

Our results indicate that, in the wild boar, personality does not affect the decision of females to invest into reproduction or litter size shortly after birth. Data on effects of personality traits on the probability of reproduction are very rare and we are aware of only one study investigating this question in wild female common lizards (*Lacerta vivipara*). In this species only social tolerance, but not boldness, affected the probability of reproduction (Cote *et al.* 2008). Previous studies on associations between personality traits and the number of offspring initially produced, however, gave varying results. In minks (*Mustela vison*), for instance, confident females (compared to fearful individuals) had larger litters already at parturition (Korhonen *et al.* 2002). In contrast, clutch size in great tits (*Parus major*) was not related to female exploration behaviour, whereas slow-exploring females had a higher probability to fledge at least one chick (Both *et al.* 2005). This is in line with our results showing that personality affected litter size only post-weaning but not shortly after birth. The lack of an effect of personality on initial litter size, however, needs to be interpreted with caution. First, sample size in this test was small (N = 13), and second, initial litter size was recorded within the first week after birth but not directly at parturition. Nevertheless, as we observed a larger litter size shortly after birth than post-weaning, our results indicate that differences in reproductive success of personality phenotypes are caused by differential offspring survival. Indeed, postnatal mortalities (up to the age of 8 months) are generally high in wild boars and vary from 5 – 70 % between populations and years, and even in enclosures reach up to 30 % (Briedermann 2009, Andersson *et al.* 2011). High postnatal mortality is also common in other large ungulates and can be caused by thermoregulatory costs, disease or predation (e.g. Monestier *et al.* 2015). Consequences of the personality phenotype of mothers on the survival probability of their offspring are known from a variety of species (e.g. mink (Korhonen *et al.* 2002), silver fox (*Vulpes vulpes*) (Korhonen & Niemelä

1996), great tit (Both *et al.* 2005)). There are two not mutually exclusive explanations for such a personality-affected difference in survival probabilities. First, as less aggressive and explorative animals usually also show less risk-taking behaviour (Sih *et al.* 2004), offspring of those animals might grow up in a safer environment. We cannot test this hypothesis with the data analysed here but it is known that juvenile wild boars are especially prone to intra- and interspecific predation (Jędrzejewski *et al.* 2002, Andersson *et al.* 2011). Consequently, avoidance of potentially risky situations by those mothers might, in fact, decrease mortality rates in their litters. Second, less aggressive females might show higher levels of maternal care. Several studies have shown that increased boldness or aggression levels were associated with a reduction of maternal care (e.g. Merino sheep (*Ovis aries*) (Murphy *et al.* 1994), European starling (*Sturnus vulgaris*) (Sandell 2007), spotless starling (*Sturnus unicolor*) (Veiga & Polo 2008), tree swallows (*Tachycineta bicolor*) (Rosvall 2013)). We were not able to identify clear personality-related difference in maternal care, as the best model explaining inter-lactation bout durations, as a measure of maternal investment, was the Null-model containing only the intercept. This might be due to fact that only data from 12 animals could be included in this analysis. The second best model (ΔAICc = 1.15) included, apart from pre-rut body mass, also the personality score and therefore might give a hint for an effect of personality on maternal care behaviour also in the wild boar. This, however, needs to be validated in future studies. According to this model, time intervals between successive lactation bouts were shorter in less aggressive and explorative females, indicating an increased effort into lactation. Shorter time intervals between suckling bouts may, however, not only reflect increased milk transfer but might additionally prevent increased heat loss in juveniles (i.e., by having close body contact more frequently), which is one of the most important reasons for postnatal-mortality in juveniles (Howells & Edwards-Jones 1997, Leaper *et al.* 1999).

Context-dependent selection on animal personality

Less aggressive and explorative females raised more juveniles only under conditions of high food supply, simulating a mast situation. Our finding of a context-dependent effect of personality is in line with a meta-analysis, in which the authors hypothesised that the large variation in the effects of personality on reproductive success in wild animals might be caused by context-dependent variation in the fitness associated with a certain personality (Smith & Blumstein 2008). Such context-dependent variation and resulting heterogeneous selection pressures are, in fact, assumed to be an important mechanism in the evolution and maintenance of different personalities within populations (Dingemanse & Réale 2013). A recent study on roe deer, for instance, showed that juveniles of proactive mothers survived better in open habitats, whereas those of reactive mothers had highest survival in closed habitats (Monestier *et al.* 2015). In the common lizard, 'asocial' individuals had an increased survival in low-density populations, whereas 'social' individuals were more likely to breed and had higher clutch sizes (Cote *et al.* 2008). With respect to temporal variation in food availability, as encountered by wild boar, Dingemanse *et al.* (2004) found that in great tits certain personality types survived better in mast failure years, whereas other types had better survival in a mast year. Additionally, in North American red squirrels offspring of more active females showed higher growth rates after mast years, whereas offspring growth rate was negatively correlated to the activity of the mother in a year following two mast failure years (Boon *et al.* 2007). Our finding of food dependent effects of personality on reproductive success indicates that in the mast-adapted wild boar (Schley & Roper 2003), context-dependent selection pressures might have supported the evolution and maintenance of different personalities. However, we observed only positive effects of being less aggressive and explorative but not of being more aggressive and explorative. Arguably, this may be due to the fact that in our experiment food restriction was only moderate. Indeed, the wild boar as a typical pulsed resource consumer is known to face extreme differences in the food availability (beech-nuts and acorns) between years, whereas, for ethical reasons, we never subjected animals to severe food restriction. Alternatively, positive selection on aggressiveness and exploratory tendency could also be caused by factors other than litter size, which we did not investigate, such as higher litter quality (e.g. in terms of litter mass or sex ratio Servanty *et al.* 2007) or increased survival rates. We found that more aggressive and explorative juvenile females have a higher social rank as well as a higher juvenile body mass. Therefore, positive selection for increased aggressiveness and exploratory tendency might be due a higher competitiveness during the juvenile stage and the resulting long lasting effects of juvenile body mass on adult female quality. Further, as more aggressive and explorative individuals also have a higher social rank at the adult stage, it seems plausible that the resulting competitive advantage might translate into increased fitness under severe food shortage. Thus, further studies focusing on unfavourable environmental conditions are needed to uncover possible selective advantages of being more aggressive and explorative in wild boar.

Acknowledgements

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Author contributions

SGV, CoB, MM and HG collected the data. SGV and FS performed the genetic analysis. SGV performed the statistical analyses. ClB conceived the study. SGV and ClB wrote the manuscript. All authors discussed the results and commented on the manuscript.

Supplementary Material

Supplementary Material S1 – Description of the microsatellites used and the genetic analysis

We analysed 17 microsatellite loci that have been used successfully in *Sus scrofa* previously (supplementary Tab. S1; (Laval *et al.* 2000, Vernesi *et al.* 2003, Schwarz *et al.* 2005, Scandura *et al.* 2008)). DNA was purified from 3 hair roots using the GeneElute^{TM} Mammalian Genomic DNA Miniprep Kit (Sigma-Aldrich® Handels GmbH, Vienna, Austria). Each PCR was performed in a 25 µl reaction volume containing 1 µl of DNA template solution (~20 ng/µl), 0.5 U of *Taq* DNA Polymerase (BioTherm^{TM}, Biozym® Biotech Trading GmbH, Vienna, Austria), 1 x PCR Buffer (BioTherm^{TM}, Biozym® Biotech Trading GmbH, Vienna, Austria), 160 µM of each dNTP, and 0.6 µM of each primer. The reverse primer of each pair was labelled with a fluorescent dye (ATTO 550, Yakima Yellow^{TM}, or 6-FAM; see supplementary Tab. S1). The amplification profile was set up as previously described in Scandura *et al.* (2008). Annealing temperatures (T_a) of each primer pair are specified in supplementary Tab. S1. For some loci it was necessary to dilute the PCR product with dist. H_2O according to the ratio given in the supplementary Tab. S1. Subsequently the (diluted) PCR products were analysed on a 3130xl Genetic Analyzer (Applied Biosystems®, Fischer Scientific (Austria) GmbH, Vienna, Austria) in six multiplex sets consisting of max. three microsatellite loci with non-overlapping ranges and different dyes (see supplementary Tab. S1 for multiplex sets). As an internal standard, an in-house ROX-standard was used that was produced according to DeWoody *et al.* (2004) using pUC-19 template, the ROXF1 forward primer and six labelled reverse primers (NAUROX105, NAUROX201, NAUROX254, NAUROX306, NAUROX362) to give a size range from 105 bp up to 362 bp. Microsatellite allele lengths were analysed using the program GeneMapper® (v4.0, Fischer Scientific (Austria) GmbH, Vienna, Austria).

Microsatellite loci were checked for null-alleles (Micro-Checker v2.2.3 (Van Oosterhout *et al.* 2004)), linkage disequlibrium (GenePop v4.2.2 (Rousset 2008)) as well as for deviations from Hardy-Weinberg equilibrium (Genetix v4.05.2, (Belkhir *et al.* 1996-2004)) and signs of inbreeding (Fstat v2.9.3.2 (Goudet 1995)) for each origin separately.

Parenthood assignment was done using the program COLONY (v2.0.4.7 (Jones & Wang 2010)) using the following specifications. Mating system was set to male and female polygamy without inbreeding. Length of run was set to medium and the full likelihood approach was used as analysis method. We did not set any sibship prior and did not update allele frequencies over runs as they were supplied externally.

Table S1 Description of microsatellites used.

Microsatellite		Chromosome	range	fluorescent dye	T_a	dilution	multiplex
S0002	(Laval *et al.* 2000)	3	198-216	ATTO 550	59	-	A
S0005	(Laval *et al.* 2000)	5	204-252	AT550	55	-	B
S0097	(Schwarz *et al.* 2005)	4	216-238	Yakima Yellow™	57	-	A
S0101	(Laval *et al.* 2000, Schwarz *et al.* 2005)	7	199-219	ATTO 550	55	1:5	C
S0155	(Laval *et al.* 2000)	1	144-160	6-FAM	55	-	A
S0215	(Laval *et al.* 2000, Scandura *et al.* 2008)	13	148-166	6-FAM	55	1:10	B
SW24	(Laval *et al.* 2000)	17	94-114	6-FAM	55	1:10	C
SW72	(Laval *et al.* 2000, Schwarz *et al.* 2005, Scandura *et al.* 2008)	3	96-110	6-FAM	55	1:10	D
SW122	(Laval *et al.* 2000, Schwarz *et al.* 2005)	6	113-127	6-FAM	55	-	E
SW240	(Laval *et al.* 2000)	2	91-121	Yakima Yellow™	55	-	B
SW461	(Vernesi *et al.* 2003, Scandura *et al.* 2008)	2	135-153	ATTO 550	59	-	D
SW857	(Laval *et al.* 2000, Scandura *et al.* 2008)	14	146-150	Yakima Yellow™	55	1:5	C
SW936	(Laval *et al.* 2000)	15	96-114	ATTO 550	55	1:10	E
SW1492	(Vernesi *et al.* 2003, Scandura *et al.* 2008)	4	112-120	Yakima Yellow™	55	-	F
SW2021	(Vernesi *et al.* 2003, Scandura *et al.* 2008)	3	105-133	ATTO 550	55	-	F
SW2496	(Vernesi *et al.* 2003, Scandura *et al.* 2008)	14	184-224	Yakima Yellow™	55	-	F
SW2532	(Vernesi *et al.* 2003, Scandura *et al.* 2008)	3	167-193	6-FAM	59	1:10	D

Microsatellites are shown with their respective range of alleles, the fluorescent dye the primers were labelled with, the annealing temperature during the PCR (T_a), the dilution of the PCR product before the multiplexing, and the multiplex set.

Supplementary Material S2 – Model selection tables for all analyses

In the model selection tables models with a AICc < 4 are shown. Variance inflation factors have been calculated for the respective full models and are presented in the legend of the model selection tables. The following variable abbreviations are used for the description of the models:

Aggr	Average number of aggressions per hour the individuals showed in autumn 2011.
1^{st}c	Timing of the first contact with the novel objects averaged over the nine novel object tests.
InvDur	Total time animals spend investigation a novel object averaged over the nine novel object tests.
SR	Social rank of the individuals estimated according to the Batchelder-Bershad-Simpson method and relativized for group size.
Pers	Personality score as given by the first principle component of the PCA.
Jbm	Juvenile body mass (i.e., the body mass at the age of eight months).
PRbm	Pre-rut body mass (i.e., the body mass at the age of 19 month, for data on the reproduction in 2013, and 29 month, for data on the reproduction 2014, respectively).
pLSaI	Previous litter size at independence (i.e., from the previous reproductive season).
FC	Food condition indicating moderate or good food availability.
NULL	The Null-model only containing the intercept.

Model selection tables:

Table S3 Model selection table for models testing effects on the latency of the first contact in the novel object tests (N = 57). Variance inflation factors: Aggr: 2.02, InvDur: 1.26, SR: 2.10, Jbm: 1.38.

Model	df	AICc	ΔAICc
Aggr + InvDur	5	105.75	0.00
Aggr + InvDur + SR	6	107.93	2.18
InvDur + SR	5	108.06	2.31
Aggr + InvDur + Jbm	6	108.25	2.50

Table S4 Model selection table for models testing effects on the total investigation duration in the novel object tests (N = 57). Variance inflation factors: Aggr: 2.15, 1^{st}c: 1.37, SR: 2.10, Jbm: 1.29.

Model	df	AICc	ΔAICc
1stc + Jbm	5	497.64	0.00
1stc	4	498.00	0.36
1stc + Jbm + SR	6	499.93	2.29
1stc + Jbm + Aggr	6	500.14	2.50
1stc + Aggr	5	500.24	2.60
1stc + SR	5	500.39	2.75

Table S5 Model selection table for models testing effects on the personality score (i.e., the PC1 of the PCA; N = 57). Variance inflation factors: Jbm: 1.24, SR: 1.24.

Model	df	AICc	ΔAICc
Jbm + SR	5	187.17	0.00
Pers	4	189.37	2.20

Table S6 Model selection table for models testing effects on pre-rut body mass 2012 (i.e., at the age of 19 months; N = 44). Variance inflation factors: Jbm: 1.20, Pers: 1.20.

Model	df	AICc	ΔAICc
Jbm	5	330.27	0.00
Jbm + Pers	6	332.86	2.58

Table S7 Model selection table for models testing effects on pre-rut body mass 2013 (i.e., at the age of 29 months; N = 46). Variance inflation factors: Jbm: 1.38, Pers: 1.26, pLSaI: 1.17.

Model	df	AICc	ΔAICc
Jbm + pLSaI	6	345.63	0.00
Jbm + pLSaI + Pers	7	347.42	1.79
Pers	5	347.95	2.32
Jbm	5	348.26	2.63
Jbm + Pers	6	348.79	3.16
Pers + pLSaI	6	348.82	3.19

Table S8 Model selection table for models testing effects on winter body mass 2014 (i.e., at the age of 34 months; N = 44). Variance inflation factors: Jbm: 1.56, Pers: 1.26, pLSaI: 1.18, FC: 1.17.

Model	df	AICc	ΔAICc
Jbm	5	352.84	0.00
Jbm + pLSaI	6	355.12	2.28
Jbm + FC	6	355.16	2.32
Jbm + Pers	6	355.19	2.35

Table S9 Model selection table for models testing effects body mass gain over winter 2013/2014 (N = 44). Variance inflation factors: Jbm: 1.79, Pers: 1.27, pLSaI: 1.32, FC: 1.23, PRbm2013: 1.32.

Model	df	AICc	ΔAICc
bmJ + FC + pLSaI	8	313.25	0.00
bmJ + FC	7	314.84	1.59
bmJ + pLSaI	7	315.56	2.31
bmJ + FC + Pers + pLSaI	9	316.41	3.15
bmJ	6	316.92	3.67

Table S10 Model selection table for models testing effects on the probability of reproduction (N = 137 data points from 92 animals). Variance inflation factors: Jbm: 1.37, PRbm: 1.38, pLSaI: 1.22.

Model	df	AICc	ΔAICc
PRbm	6	171.61	0.00
PRbm + Jbm + PRbm:Jbm	8	171.99	0.39
PRbm + pLSaI	7	173.45	1.84
PRbm + Jbm+ pLSaI + PRbm:Jbm	7	173.75	2.15
PRbm + pLSaI + PRbm: pLSaI	9	174.22	2.61
Bold + SR	8	175.28	3.68

Table S11 Model selection table for models testing effects on the initial litter size (within 7 days after birth; N = 13 animals). Variance inflation factors could not be estimated due to the small sample size.

Model	df	AICc	ΔAICc
Jbm	3	55.57	0.00
PRbm	3	55.80	0.23
NULL	2	56.53	0.96
Jbm + PRbm	4	58.64	3.06

Table S12 Model selection table for models testing effects on the litter size at independence (N = 94 data points from 47 animals). Variance inflation factors: Jbm: 1.37, Pers: 1.23, FC: 1.10, pLSaI: 1.12.

Model	df	AICc	ΔAICc
Jbm + Pers + FC + Pers:FC	10	188.81	0.00
Jbm + Pers	8	188.84	0.03
Jbm + Pers + FC	9	189.87	1.06
FC	7	190.20	1.39
Jbm + Pers + FC + Pers:FC + Jbm:FC	11	190.40	1.59
Pers + FC + Pers:FC	9	190.59	1.79
Pers + FC	8	190.91	2.11
Jbm + FC	8	190.94	2.13
Jbm + Pers + pLSaI	9	191.09	2.29
Pers	7	191.11	2.31
Jbm	7	191.24	2.44
Jbm + Pers + FC + pLSaI + Pers:FC	11	191.34	2.54
NULL	6	191.66	2.85
Jbm + Pers + FC + pLSaI	10	192.33	3.52
Jbm + Pers + FC + Pers:FC	10	192.37	3.56
FC + pLSaI	8	192.58	3.78

Table S13 Model selection table for models testing effects on lactation behaviour (N = 145 data points from 12 animals). Variance inflation factors: Jbm: 6.02, PRbm: 2.67, Pers: 3.47.

Model	df	AICc	ΔAICc
NULL	4	638.27	0.00
PRbm + Pers	6	639.42	1.15
Pers	5	639.50	1.23
PRbm	5	639.56	1.28
Jbm + Pers	6	639.73	1.45
Jbm	5	640.41	2.14
Jbm + PRbm	6	641.04	2.77
Jbm + PRbm + Pers + Jbm:PRbm	8	641.24	2.96
Jbm + PRbm + Pers	7	641.37	3.10

Supplementary Material S3 – Results of the random forest analyses

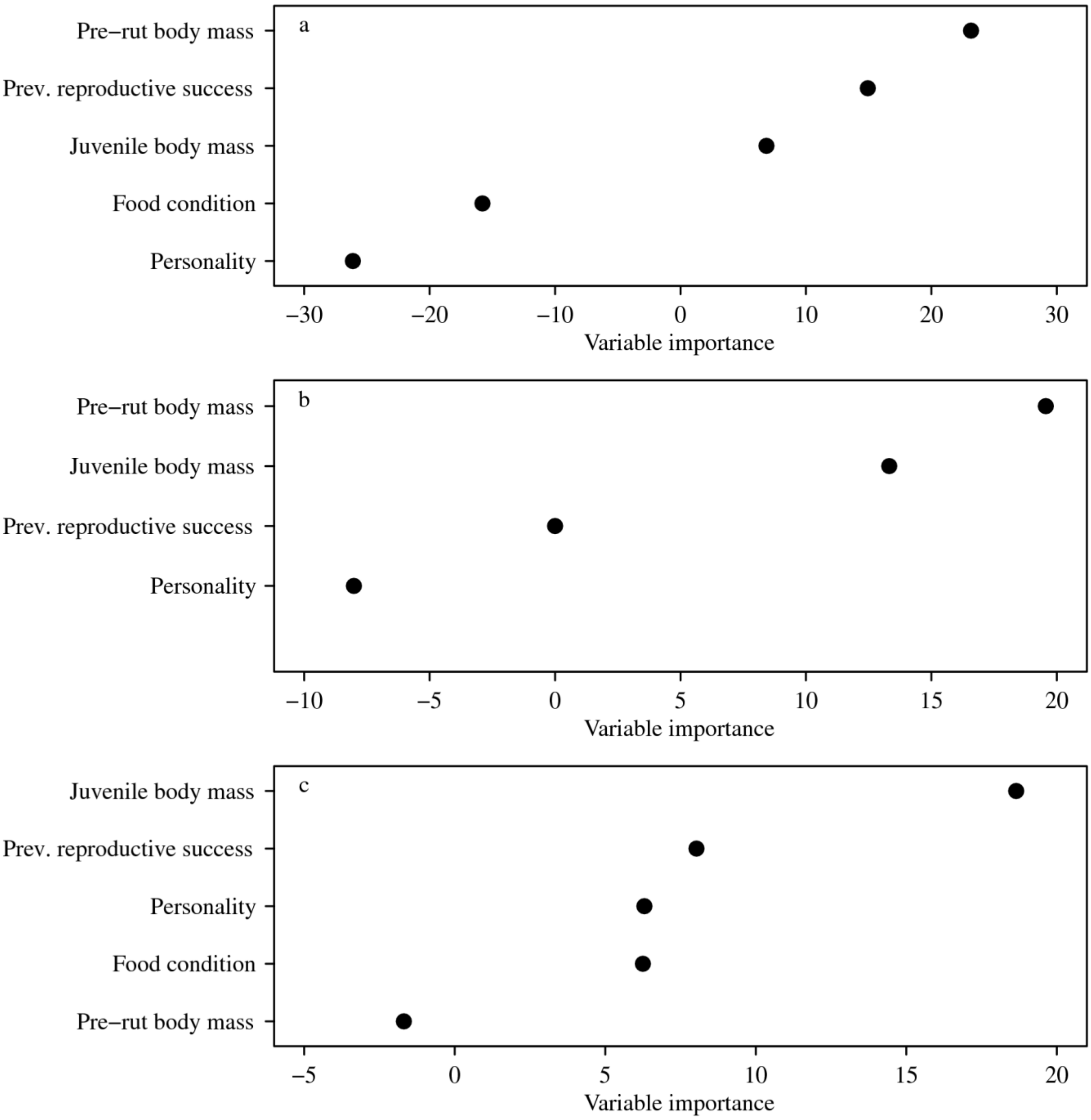

Figure S1 Results of the random forest analyses on (a) whether a female reproduced or not (N = 71 data points from 47 animals), (b) initial litter size (within 7 days after birth; N = 13 animals, only data from one year) and (b) litter size at independence (N = 86 data points from 47 animals).

3.2 MULTIPLE PATERNITY AS A POSSIBLE MECHANISM FOR OFFSPRING DIVERSIFICATION IN WILD BOARS (*SUS SCROFA*)

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Heavier, adult female wild boars have been shown to produce more variable litters compared to lighter, younger females concerning offspring body mass. The mechanism of this size diversification, however, is unknown but multiple paternity was discussed as a possible mechanism. Here we investigated whether multiple paternity provides a mechanism for diversification of juvenile body mass within litters in the wild boar. Besides investigating paternal and maternal effects on juvenile body mass of female wild boars, we also evaluated parental effects on their reproductive success. Our results show (i) a high frequency of multiple paternity in the wild boar (> 70% of litters with more than one offspring); (ii) that up to 4 males fathered one litter (litter size = 5); (iii) that paternal half-siblings and full-siblings were more similar in terms of juvenile body mass (at ~ 8 month) compared with maternal half-siblings and unrelated animals, indicating strong paternal effects; (iv) that the litter size (first litter at 2 years of age) was also affected by a dam's father, again resulting in a lower diversity among paternal half-siblings compared with unrelated females. In contrast, (v) similarity in juvenile body mass and reproductive success was low in maternal half-siblings and did not differ from that found in unrelated females. These strong paternal effects and the high degree of multiple paternity show that multiple mating is an important mechanism for offspring diversification in the wild boar. Additionally, we discuss potential ultimate causes for offspring diversification and argue that diversification of offspring body mass via multiple paternity in the wild boar functions to reduce sibling rivalry within large litters by facilitating the formation of a stable hierarchy and teat fidelity.

mating, reproductive success, juvenile body mass, multiple paternity, paternal effects

Introduction

Female promiscuity has been shown to have several evolutionary benefits (Jennions & Petrie 2000, Wolff & Macdonald 2004). For example, mating with multiple males could be an effective counter-strategy against male infanticide (Agrell *et al.* 1998, Wolff & Macdonald 2004) or reduce male harassment (Rowe *et al.* 1994). Not mutually exclusive, multiple paternity might function to enhance offspring diversity (Jennions & Petrie 2000, Fox & Rauter 2003). Such a diversification might, for instance, be adaptive in the context of a diversified bet-hedging strategy, with females producing offspring of different phenotypes which are best adapted to different environmental conditions in response to environmental unpredictability (Slatkin 1974, Philippi & Seger 1989, Crean & Marshall 2009). Further, diversification of offspring size might function as a female strategy to minimise the negative effects of sibling rivalry, at least for larger offspring (Nilsson & Svensson 1996, Forbes & Glassey 2000). It was shown that earlier hatched, larger chicks are not affected by the presence of smaller, later hatched chicks and that they are less affected by food shortage than the smaller chicks (Forbes & Glassey 2000). Sibling rivalry is also common in mammals, especially in species producing large litters where juveniles heavily compete for the best teats (Mock & Parker 1997, Stockley & Parker 2002). However, studies investigating such an effect of increased variation in offspring size so far were mostly restricted to birds producing surplus chicks and diversifying these by hatching asynchrony (reviewed in Ricklefs 1993).

For their size (mean female body mass: 84 - 102 kg; reviewed in Briedermann 2009), wild boars produce large (i.e., mean: > 5 offspring per litter; Bywater *et al.* 2010) and highly variable litter sizes (i.e., 1 to 14 juveniles per litter; Servanty *et al.* 2007). Additionally, it was recently shown that heavier, adult females produce more diverse litters compared with smaller, younger females in terms of foetus mass, and multi-male mating was discussed as a potential mechanism in this context (Gamelon *et al.* 2013a, 2013b).

Female promiscuity and multiple paternity, however, were assumed to rarely occur in wild boar (Delgado *et al.* 2008, Briedermann 2009). During the breeding season the solitarily living male wild boars associate with the matrilineal groups the females live in (Mauget 1981), barely feed, and defend these “sounders” against competitors. This behaviour is very costly, causing severe body mass losses in the males (15 – 20 %), and was thought to limit the females' chances to mate with multiple males effectively (Briedermann 2009). To our knowledge, however, there are no studies investigating reproductive success in male wild boars justifying this assumption. In contrast, more recent studies indicated that multiple paternity in the wild boar might in fact be more common than previously expected (Poteaux *et al.* 2009, Costa *et al.* 2012, Gamelon *et al.* 2013b). This finding is strengthened by various indices of pronounced sperm competition in the wild boar. For instance, male wild boars have a large relative testis size and ejaculate volume (Kozdrowski & Dubiel 2004, Briedermann 2009) compared with other ungulates (e.g. the red deer (*Cervus elaphus*) (Hochereau-de Reviers & Lincoln 1978, Malo *et al.* 2005)). Further, a mating plug is placed in the vagina of mated sows after copulation (Hafez 1987), and males copulate multiple times with the same female (Fraser 1968).

In female wild boars juvenile body mass has major effects on adult quality (Vetter *et al.* submitted). Heavier juveniles become heavier adults and raised significantly more offspring (i.e., litter size recorded at independence when offspring were ~ 6 months of age) compared with individuals that had a lower juvenile body mass (Vetter *et al.* submitted). This, together with the fact that, corrected for litter size, heavier female wild boars produced more diverse litters regarding foetus mass than lighter females (Gamelon *et al.* 2013b), suggest that lighter females that were small as juveniles show a more conservative strategy by producing smaller litters with lower diversification (i.e., optimising the trade-off between number of offspring and offspring size; Smith & Fretwell 1974, Lloyd 1987). Females that were heavy as juveniles, in contrast, might produce larger litters with a high degree of diversification, possibly representing a diversified bet-hedging strategy (Slatkin 1974, Philippi & Seger 1989, Crean & Marshall 2009). The mechanism, however, how females might diversify offspring body mass within litters is yet unknown (Gamelon *et al.* 2013b) but multiple paternity was discussed as a possible explanation.

To test whether multi-male mating causes increased offspring diversity in wild boars, we investigated parental effects on juvenile body mass of 118 female wild boars (cohort 2011) and, later in their life (2013), on their reproductive success. Assuming that multiple paternity provides a mechanism for offspring diversification, we expected to find strong paternal effects on juvenile body mass and potentially on later reproductive success, and, therefore, females sharing the same father to be more similar in these traits compared with maternal-half-siblings or unrelated females. We also assessed the degree of multiple paternity in the first litter of these females and tested whether it was affected by their juvenile or adult body mass, indicating potentially different reproductive strategies. Based on previous findings that lighter females produce less diverse litters (Gamelon *et al.* 2013a, 2013b), we expected lighter females to show a reduced degree of multiple paternity compared with heavier ones. Finally, we analysed which factors affected the reproductive success of male wild boars and whether there are hints for male mate choice in the wild boar in terms of female body mass. We expected older and heavier males to be more competitive and therefore to mate with more females and sire more offspring than younger, smaller males.

Methods

The study animals

118 female wild boars, born in 2011 (cohort 2011), were kept in two large enclosures (E1: ~ 32 ha, E2: ~ 22 ha) under semi-natural conditions and observed for two years from the age of around six months until after their first reproduction. The large size of the enclosures allowed females to build social groups of 19 ± 3 individuals (Rauchenschwandtner 2014), which is in line with observations in free-ranging wild boars (Mauget 1981).

All animals were marked with ear tags (left ear: coloured and numbered ear tag (Supertag Hog 55 mm x 50 mm) for visual observation, right ear: RFID I-Tag Button (∅ 25 mm) for recognition via a RFID reading station, both from Dalton, Lichtenvoorde, Netherlands) and an implant common ID ISO-transponder (lifelong marking, Virbac, Barnevelden, Netherlands) for individual identification. Additionally, hair samples were collected once from all individuals in our enclosures for genetic analysis (see below).

The number of males in E1 and E2 was 12 and nine, respectively, over the breeding season 2012/2013 (0.2 males per female in both enclosures). Male age did not differ significantly between the two enclosures (E1: range = 2-5; mean ± sd = 3.1 ± 1.4; E2: range = 2-7, mean ± sd = 3.6 ± 1.7). The age distribution in the reproductive season 2012/2013 including all males from both enclosures is shown in Fig. 1 (females were all 2 years of age at that time).

The animals received supplementary feeding *ad libitum* on a daily basis. During winter (October to March) we fed a high-fat wild boar food mixture (Type H9483, Hoferfutter, Herbert Lugitsch u. Söhne GmbH, Eggendorf, Austria) during summer (April to September), corn was fed. The wild boars consumed on average 0.74 kg*animal^{-1}*day^{-1} until March 2012, and 0.91 kg*animal^{-1}*day^{-1} from March to November 2012. From November 2012 onwards the animals consumed on average ~ 1.2 kg*animal^{-1}*day^{-1}. This feeding regime is assumed to resemble a mast situation with high food availability.

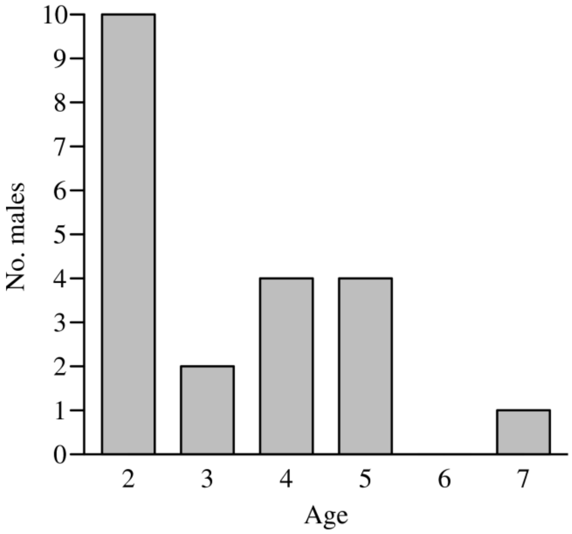

Fig. 1 Age distribution in the reproductive season 2012/2013 of all males included in the study (i.e., from both enclosures; N = 21).

Assessment of sibship

Sibship between females of the cohort 2011 was determined by inferring parents via microsatellite analysis using the program COLONY v2.0.4.7 (Jones & Wang 2010). For more detailed information on the microsatellites used and the analysis see the supplementary information in Vetter *et al.* (submitted). From the inferred parents (of unknown identity) we determined whether the females were full-siblings (i.e., litter mates sharing the same father and the same mother), maternal half-siblings (i.e., from the same litter but different fathers), paternal half-siblings (i.e., from different litters but the same father), or unrelated.

Parental effects on juvenile body mass of the females (cohort 2011) and on post-weaning litter size (i.e., at ~ 6 months at independence) of their first reproduction (i.e., in 2013) were analysed by comparing pairwise differences in these variables in full- and half-sibling dyads (i.e., maternal and paternal) to those in dyads of unrelated animals (see below). We here focused on juvenile body mass as it is known to have long lasting effects on adult body mass in female wild boars (Vetter *et al.* submitted). Data from both enclosures were pooled for this analysis as juvenile body mass was measured before the animals were released into the two enclosures and reproductive success in 2013 did not differ between the two enclosures (E1: mean ± sd = 2.2 ± 1.3; E2: mean ± sd = 2.0 ± 1.4).

Assessment of body mass, reproductive success and multiple paternity

Body mass of the females (cohort 2011) was assessed at the age of about eight months (juvenile body mass; autumn 2011) and 19 months (adult body mass prior to the breeding season; autumn 2012). Male body mass was measured in autumn 2013. To measure body mass and collect hair samples/mark individuals animals were confined within the feeding area while feeding. Animals were then led individually through a wooden corridor (4 m x length 0.4 m width x 0.9 m height) into a wooden box (1.2 m x 0.7 m x 1.1 m) placed on loadbars (Gallagher SmartScale® 600 and Gallagher Loadbars (accuracy: 0.2 and 0.5 kg for weights below and above 50 kg respectively), Gallagher Europe, Groningen, Netherlands) and subsequently released into their enclosures.

After the first reproduction in 2013, parenthood, and thus female and male reproductive success (of cohort 2011 and their mates), as well as the degree of multiple paternity of each litter, was assessed via microsatellite analysis after collecting hair samples of all offspring that survived until the age of about six months (i.e., around independence) in autumn 2013 (cohort 2013). After acquiring the hair samples juveniles were removed from the study site.

Statistical analysis

To analyse parental effects on juvenile body mass, we ran a generalised least squares model, corrected for heterogeneity in the variances between the four relatedness classes using the varIdent() function, on boxcox-transformed pairwise differences in juvenile body mass, using the nlme package (Pinheiro *et al.* 2012). Further, we ran a generalised linear model with a quasi-Poisson error distribution on pairwise differences in post-weaning litter size using the package stats (R Development Core Team 2013). In both models degree of relatedness was the only predictor variable. Additionally, we performed post-hoc analyses for both models comparing pairwise differences in dyads of maternal half-siblings to those found in dyads of paternal half-siblings using the package multcomp version 1.4-1 (Hothorn *et al.* 2008).

In order to test for potentially different reproductive strategies in females we tested whether the number of males mated with was affected by a female's juvenile or adult body mass. We did this using a mixed effects Poisson model where we additionally included litter size as another fixed effect, in order to correct for different litter sizes, and enclosure as random effect (N = 29).

We tested whether age and body mass were correlated in male wild boars using a Spearman correlation test (N = 11). Concerning male mating success, we tested whether number of offspring sired and number of females fertilised was affected by male age by running two mixed effects negative binomial models containing enclosure as a random effect (N = 21 for both). We only included age in these models but not body mass as those two variables were highly correlated (see results) and age was available for all males in 2012/2013 whereas body mass was only available for the subsequent reproductive season and not for all males. To test whether the number of offspring sired per female was also affected by age we ran a second negative binomial model on the number of offspring sired and included, besides male age and the random effect of enclosure, the number of females mated with as another fixed effect. To test for male mate choice, we analysed whether older males (i.e., heavier, more competitive males; see results) mated more often with heavier females by running a linear mixed effects model on adult female body mass including age of the mating partners as fixed effect and enclosure and male ID as random effects ($N = 45$ mating dyads including 15 males and 29 females).

Inspection of the distribution of residuals of generalised least squares and linear (mixed effects) models by means of histograms and quantile-quantile plots gave no evidence for serious deviations from normality. No Poisson and negative binomial models showed serious overdispersion. All statistical analyses were performed in R.3.0.2 (R Development Core Team 2013). All mixed effects models were calculated using the package lme4 (Bates *et al.* 2014b).

Results

Parental effects

Juvenile body mass of the study individuals (118 females; cohort 2011) ranged from 20.0 to 48.8 kg (mean ± sd = 29.2 ± 7.9) and differed not essentially from the range found in free-ranging animals (9.4 - 61.0 kg; Briedermann 2009). In line with our expectation, females of the cohort 2011 sharing the same father, that is full-siblings (mean difference ± standard error of the mean (sem) = 5.3 ± 0.6, $N = 51$ dyads, $t = -4.95$, $P < 0.001$) and paternal half-siblings (mean difference ± sem = 6.4 ± 0.4, $N = 211$ dyads, $t = -5.96$, $P < 0.001$), were more similar in juvenile body mass than unrelated females (mean difference ± sem = 8.9 ± 0.2, $N = 1380$ dyads; Fig. 2a). Paternal half-siblings were also more similar in juvenile body mass than maternal half-siblings (mean difference ± sem =8.4 ± 0.6, $N = 120$ dyads, $z = -2.70$, $P = 0.006$), with the latter not differing from unrelated females ($t = -0.94$, $P = 0.349$; Fig. 2a) in terms of similarity in juvenile body mass.

In 2013 41 females (40 %, cohort 2011) successfully raised 92 piglets (49 % males, 51 % females). The average litter size was 2.2 ± 1.4 offspring raised to independence. Again in line with our expectation, the number of offspring raised to independence was more similar between paternal half-siblings (mean difference ± sem = 0.9 ± 0.1, N = 159 dyads, t = -3.51, P < 0.001) than between unrelated animals (mean difference ± sem = 1.4 ± 0.05, N = 1035 dyads; Fig. 2b). In contrast, full-siblings (mean difference ± sem = 1.2 ± 0.2, N = 34 dyads, t = -0.74, P = 0.459) and maternal half-siblings (mean difference ± sem = 1.4 ± 0.2, N = 87 dyads, t = -0.26, P = 0.792) were not more similar than unrelated animals (Fig. 2b). Paternal half-siblings were also more similar than maternal half-siblings concerning litter size at independence ($z = -2.74$, $P = 0.006$).

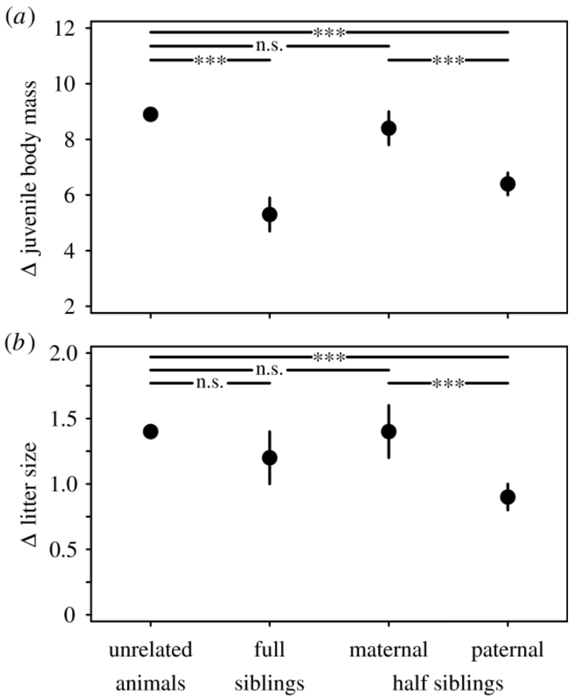

Fig. 2 Parental effects shown as pairwise differences (Δ) in (a) juvenile body mass and (b) litter size at independence in dyads of unrelated animals, full-siblings and maternal and paternal half-siblings. Lines show the analysed comparisons with '***' indicating a p-value < 0.001 and 'n.s.' indicating non-significance.

Female reproduction

Body mass of our study animals (cohort 2011) prior to their first reproduction (autumn 2012, adult body mass at the age of two years) ranged from 49.0 to 92.8 kg, (mean ± sd = 68.0 ± 10.8 kg), covering a major part of the range found in wild animals of the same age and sex (37.5 - 95.0 kg; Briedermann 2009). Multiple paternity was found in 72 % of litters with more than one offspring, with a maximum of four fathers within a litter of five juveniles. In contrast to our expectations, the number of fathers per litter (i.e., degree of multiple paternity) was not affected by a female's juvenile (estimate ± se = 0.003 ± 0.03, $z = 0.10$, $P = 0.923$, N = 29 litters) or adult body mass (estimate ± se = -0.01 ± 0.02, $z = -0.28$, $P = 0.780$) when corrected for litter size (estimate ± se = 0.23 ± 0.11, $z = 2.06$, $P = 0.040$).

Male reproduction

In male wild boars, age and body mass (range = 76.0 – 122.5 kg, mean ± sd = 92.0 ± 13.8 kg) were significantly correlated (Spearman's rho = 0.80, $P = 0.003$, N = 11). Of the 21 males 5 (aged between 2 and 5 years) did not sire any offspring that survived to independence. As expected, older males fertilised more females (estimate ± se = 0.30 ± 0.13, $z = 2.26$, *P* = 0.024, N = 21, Fig. 3a) and consequently also sired more offspring (estimate ± se = 0.40 ± 0.15, *z* = 2.68, *P* = 0.007, N = 21, Fig. 3b) than younger males. Older males did not sire more offspring per female, however (estimate ± se = 0.05 ± 0.08, *z* = 0.60, *P* = 0.546, N = 21). We observed a strong trend that older males mated with heavier females (estimate ± se = 1.78 ± 0.89, *t* = 0.91, *P* = 0.052, N = 45 mating dyads including 15 males and 29 females) compared with younger males.

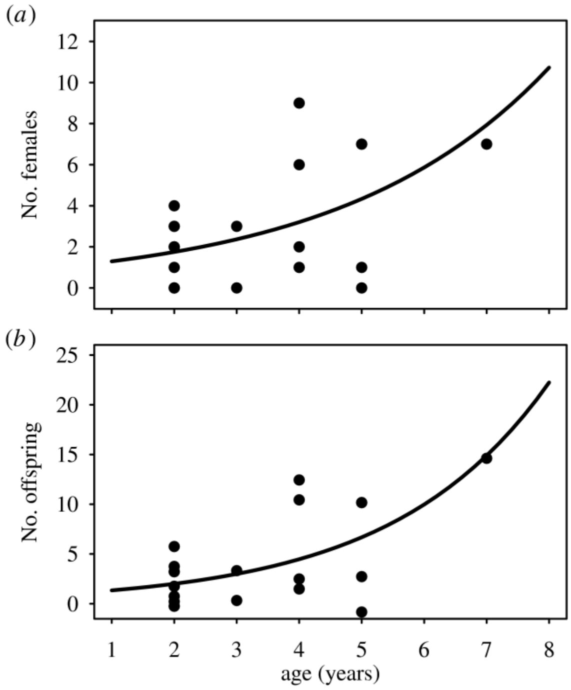

Fig. 3 Partial effects of age on male reproductive success in terms of (a) number of females fertilised and (b) number of offspring sired.

Discussion

Parental effects

The mean difference in juvenile body mass of female wild boars sharing the same father but not the same mother was about 3 kg (~ 10 % of the average body mass) smaller compared with maternal half-siblings or unrelated animals (Fig. 2a). Indeed, pair-wise differences of body mass in maternal half-sibling dyads did not differ from those found in dyads of unrelated individuals. This means that fathers had a much stronger impact on the juvenile body mass (i.e., at the age of 8 months) of the females compared with their mothers or the common environment they grew up in (i.e., maternal half-siblings are litter mates in contrast to paternal half-siblings). This shows that also in wild boars multiple paternity could provide an effective mechanism for the diversification of offspring body mass within litters (compare Fox & Rauter 2003) as hypothesised by Gamelon *et al.* (2013b). In fact, our results show that multiple paternity cannot not only affect diversity in foetus mass (Gamelon *et al.* 2013a, Gamelon *et al.* 2013b) but has long lasting effects that are still visible at the age of ~ 8 months in terms of body mass and even causes differences in reproductive success of adult females. The average difference in the number of offspring raised to independence was 0.5 offspring smaller (> 20 % of the average number of offspring raised) in paternal half-siblings than in maternal half-siblings and unrelated animals (Fig. 2b). This long-lasting paternal effects on adult reproductive success are most likely due to the long-lasting effects of juvenile body mass on adult body mass and reproductive success in these animals (Vetter *et al.* submitted). However, the fact that full-siblings were not more similar than unrelated animals (Fig. 2b) in terms of reproductive success (in contrast to juvenile body mass) indicates the presence of additional, father-independent factors (e.g. social status) affecting reproductive success of female wild boars growing up in the same litter. Although the proximate mechanisms of the strong paternal effects we identified need to be targeted in future studies, the fact that paternal half-siblings, sired by different mothers, were more similar already shows that they are not caused by different mating and thus implantation times (i.e., gestation durations) but more likely by genetic effects.

Female reproduction

We here identified a very high proportion (> 70 %) of multiple paternity in the wild boar. However, also in free-ranging populations of wild boars and feral pigs, there is increasing evidence that multiple paternity is more common (e.g. Delgado-Acevedo *et al.* 2010, Costa *et al.* 2012, Gamelon *et al.* 2013b) than previously expected (Delgado *et al.* 2008). This finding is consistent with various indices of pronounced sperm competition, like the large relative testis size and the large ejaculate volume (Kozdrowski & Dubiel 2004, Briedermann 2009) compared to other ungulates (e.g. the red deer (Hochereau-de Reviers & Lincoln 1978, Malo *et al.* 2005)), the placement of a mating plug (Hafez 1987), and multiple copulations with the same female (Fraser 1968). Although, we cannot exclude that the extraordinary high proportion of multiple paternity we identified in the present study might have been influenced by the semi-natural conditions in our enclosures, these findings indicate that female promiscuity and multiple paternity is also common in free-ranging populations of wild boars. This together with the strong paternal effects on juvenile body mass and even reproductive success of adult females shows that multiple paternity significantly contributes to the diversification of offspring in the wild boar. However, is not clear yet whether this diversification is adaptive or whether it rather results from mating with multiple males as a strategy to avoid harassment or infanticide.

Mating with multiple males has be shown to reduce male harassment (Rowe *et al.* 1994) or prevent male infanticide (Agrell *et al.* 1998, Wolff & Macdonald 2004). Our results on male mating success indicate a male preference for heavier females (see below), which could result in an increased risk for these females to be affected by male harassment or infanticide. In line with this assumption a previous study showed that heavier females produce more diverse litters than lighter females, potentially as a result of mating with more males (Gamelon *et al.* 2013b). However, investigating only females of the same age, we found that heavier females did not mate with more males than lighter ones, indicating that offspring size diversification in the wild boar seems to be affected by the age of a female rather than by her body mass (see also Gamelon *et al.* 2013a) and thus does not result from a male preference for heavier females. This, together with the fact that adult females only produce more diverse litters in years or high food availability (Gamelon *et al.* 2013a), indicates that multiple mating in female wild boars does not represent a strategy to avoid male harassment or infanticide.

Alternatively, female wild boars might benefit from producing diverse offspring. Wild boars strongly rely on tree seeds in their diet (Schley & Roper 2003) and thus face large and unpredictable annual variation in food availability. Facing such environmental unpredictability offspring diversification might be adaptive through diversified bet-hedging (Slatkin 1974, Philippi & Seger 1989, Crean & Marshall 2009), with females producing different offspring phenotypes which are best adapted to different environmental conditions. Accordingly, it was recently argued that diversification of offspring body mass in the wild boar represents a diversified bet-hedging strategy (Gamelon *et al.* 2013b). However, given a diversified bet-hedging strategy one would not necessarily expect females to produce diverse litters only in years with high food availability, as previously shown (Gamelon *et al.* 2013a). Further, if such a strategy is shown by female wild boars one would expect different phenotypes to have an increased fitness under differential food availability of to differ in their reproductive strategies. The impact of body mass on reproductive success in female wild boars, however, was not affected by food availability (Vetter *et al.* submitted). In contrast, juvenile body mass had long-lasting effects on adult quality in female wild boars and smaller females always were inferior compared with heavier females irrespective of the food availability (Vetter *et al.* submitted). Additionally, the fact that lighter females did not mate fewer males than heavier females indicates that lighter females did not show a more conservative reproductive strategy compared with heavier females as one could have expected (Gamelon *et al.* 2013a, Gamelon *et al.* 2013b), suggesting a lack of different body mass related reproductive strategies in the wild boar. Therefore, I argue that a diversification of offspring body mass by adult female wild boars in mast years (Gamelon *et* *al.* 2013a) does not represent a diversified bet-hedging strategy shown by females in response to unpredictable food availability.

The fact that diversification of offspring size is only shown by adult females and only in years with high food availability (Gamelon *et al.* 2013a) indicates that this diversification is in fact only shown by females producing large litters. Competition for the best teats is generally high within pig and wild boar litters and can result in severe fights between siblings (Fraser & Thompson 1991). After two to three weeks a stable hierarchy and teat fidelity develops within the litter (Hartsock *et al.* 1977, Fernández-Llario & Mateos-Quesada 2005). Size differences between siblings are known to reduce the negative consequences of such sibling rivalry, at least for the heavier offspring (Nilsson & Svensson 1996, Forbes & Glassey 2000). As sibling rivalry is directly related to the average number of juveniles per teat (Mock & Parker 1997) it seems plausible that females producing the largest litters seem to diversify their offspring the most (Gamelon *et al.* 2013a). Therefore, we assume that offspring diversification in the wild boar facilitates the formation of a stable hierarchy and teat fidelity, and thus results in an overall reduction of the negative effects of sibling rivalry when extra offspring are produced (Hartsock *et al.* 1977, Fraser & Thompson 1991, Fernández-Llario & Mateos-Quesada 2005, Gamelon *et al.* 2013a). This hypothesis, however, needs to be tested in further studies investigating the formation of a stable hierarchy within litters, offspring survival, or litter mass at weaning in the context of variation in offspring body mass.

Male reproduction

Concerning male reproductive success we found that body mass and age in male wild boars were highly correlated and that older and thus heavier males mated more females and sired more offspring. This finding is in line with observations that stronger males manage to defend females against competitors (Briedermann 2009). Nevertheless, the fact that 70 % of the youngest boars also reproduced successfully and the high degree of multiple paternity indicate that their mate guarding abilities are limited. Further, our results indicate that older males mated more often with heavier females compared with younger males. This effect, however, was only a strong trend, perhaps due to the small sample size and the fact that only two-year old females were included in the study resulting in a more narrow range of female body mass compared to wild populations containing all age classes. A male mating bias for heavier females might indicate male mate choice behaviour resulting in increased competition over heavy females and thus limited access to those females for younger males.

Positive effects of female body mass on litter size have been shown in our study population (Vetter *et al.* submitted), as well as in free-ranging wild boar populations (e.g. Mauget 1972, Gaillard *et al.* 1993, Fernández-Llario & Mateos-Quesada 1998, Náhlik & Sándor 2003, Gethöffer *et al.* 2007, Briedermann 2009, Servanty *et al.* 2009, Bywater *et al.* 2010, Fonseca *et al.* 2011, Gamelon *et al.* 2012, Rosell *et al.* 2012). A preference for mating heavier females might therefore increase a male's reproductive output as mating a heavier female most likely results in a larger number of offspring sired than mating a smaller female (e.g. compare Kraak & Bakker 1998, Preston *et al.* 2005). However, our finding that older males did not sire more offspring per female than younger ones is in contradiction to this assumption and further studies are needed investigating male mate choice in the wild boar.

Conclusions

Overall our results show strong paternal effects on juvenile body mass and reproductive success. Consequently, female promiscuity has long-lasting effects on the diversity of litter mates regarding these two traits. The high degree of male and female promiscuity in the wild boar identified here is in line with a previous study showing that adult female wild boars diversify their offspring under high food availability (Gamelon *et al.* 2013a). Based on our results, we argue that this diversification does, however, not represent a diversified bet-hedging strategy in response to unpredictable environmental conditions, as previously suggested (Gamelon *et al.* 2013b). We hypothesise that diversification of offspring body mass rather serves as a strategy to reduce the negative consequences of sibling rivalry when females produce extra offspring under good environmental conditions. In terms of male reproductive success we showed that older and heavier males had a higher reproductive success than younger males. Additionally, they mated more often with heavier females than younger males, which might indicate the presence of some male mate choice behaviour in the wild boar.

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accordance with good scientific practise and national legislation (GZ: 06/11/97/2011 and GZ: 15/03/97/2012). The authors declare no conflict of interest.

Author contributions

CB and SGV conceived the study. SGV and GS collected the data. SGV and FS performed the genetic analysis. SGV performed the statistical analyses. SGV wrote the first draft of the manuscript. CB contributed substantially to the manuscript. All authors discussed the results and commented on the manuscript.

4 CONCLUDING DISCUSSION

In this thesis I show that there are strong effects of the pulsed availability of food on population dynamics, as well as on individual reproductive performance in the wild boar. Analysing effects of climate and food availability on wild boar population growth, I, together with my colleagues, showed that one major driver for accelerated wild boar population growth throughout Europe is climate change (chapter 2.1). I found that climate change affected wild boar populations not only directly through increasing winter temperatures but also indirectly through increasing tree-masting frequency and hence food availability. Although several studies have already investigated effects of climate and food availability on wild boar population dynamics, interactive effects have not yet been considered. This is because in previous studies food and climate were either combined into one variable (e.g. Bieber & Ruf 2005, Geisser & Reyer 2005) or only additive effects have been included in the models (e.g. Jędrzejewska *et al.* 1997, Servanty *et al.* 2009). Here I show, for the first time, that these two effects were not simply additive but that the impact of winter temperature on wild boar population growth was modulated by food availability. Under low food availability cold winter temperatures attenuated population growth, whereas this was not true in mast years when food was abundant (chapter 2.1). This result indicates that the negative effects of cold temperatures on wild boars are not caused by a limited thermogenic capacity but rather by a negative energy balance when high thermoregulatory costs cannot be matched by the available food.

Comparable interactive effects of climate and density (indicating competition for food and thus per capita food availability; Messier 1991) on population growth rates have also been found in other ungulates (e.g. red deer (*Cervus elaphus*) (Benton *et al.* 1995), bighorn sheep (*Ovis Canadensis*) (Portier *et al.* 1998), and Soay sheep (*Ovis aries*) (Grenfell *et al.* 1998)). Also, in the European bison (*Bison bonasus*) and the elk (*Alces alces*) sufficient food availability was assumed to counterbalance negative effects of adverse winter conditions on winter survival (Jędrzejewska *et al.* 1997). My results therefore support the finding that interactive effects of climate and food availability can cause negative energy balances in ungulates. In pulsed resource consumers, like the wild boar however, this negative energy balance is overcome at irregular intervals in years of resource pulses, resulting in major population increases (e.g. chapter 2.1, Bieber & Ruf 2005). Although survival has been shown to have the highest impact on wild boar population growth (Bieber & Ruf 2005), various studies found that breeding probability of females as well as litter sizes were also increased after mast years (e.g. Briederman 1971, Aumaitre *et al.* 1982, Groot Bruinderink *et al.* 1994, Rosell Pagès 1998, Servanty *et al.* 2009, Linderoth & Pegel 2010). These studies, however, were mostly based on foetus counts and thus did not consider individual life-history variables other than current body mass or age. Following female wild boars over the course of three years and two reproductive events, I was able to show that already juvenile body mass and also personality affected the number of offspring raised to independence (chapter 3.1). The effect of personality, however, was altered by food availability. Under plentiful food availability less aggressive less and explorative individuals raised considerably more offspring than more aggressive and explorative females, whereas this was not the case under moderate food restriction (chapter 3.1).

The fact that only post-weaning litter size was affected by personality but not the breeding probability or the initial litter size shortly after birth (chapter 3.1) indicates that the increased reproductive success of less aggressive and explorative females was due to reduced offspring mortality in litters of these females. My results suggested that this decreased mortality was caused by an increased maternal effort of less aggressive mothers, which tended to lactate more frequently (chapter 3.1). In line with this finding, aggressiveness has previously been shown to be associated with reduced maternal care behaviour (e.g. Murphy *et al.* 1994, Sandell 2007, Veiga & Polo 2008, Rosvall 2013). The increased maternal effort of less aggressive female wild boars, however, seems to be costly and resulted in higher litter sizes at independence only under conditions of high food availability (chapter 3.1).

As more aggressive and explorative females did not have a higher reproductive success under reduced food availability (chapter 3.1), the benefits of the more aggressive phenotype remain unclear and need to be targeted in further studies. This, however, could be due to the fact that we reduced food availability only moderately. In contrast, free ranging wild boars, as typical pulsed resource consumers, are known to face extreme differences in food availability between years (Briedermann 2009). Another explanation could be that, besides variation in food availability, further factors are involved in the selection of personality phenotypes and associated life-history strategies. It was shown recently that shy roe deer (*Capreolus capreolus*) females raised more offspring in closed, forested habitats whereas bold females had an increased reproductive success in open habitats (Monestier *et al.* 2015). Alternatively, assuming that personality is heritable (Penke *et al.* 2007, Réale *et al.* 2007), more aggressive females could benefit indirectly from having more aggressive sons if aggressiveness was positively associated with male competitiveness and fitness also in wild boars (e.g. compare Réale *et al.* 2009, Ariyomo & Watt 2012). Finally, more aggressive and explorative individuals could have a competitive advantage during the juvenile stage when growing up under unfavourable food conditions. Boldness and aggressiveness have been shown to positively affect food intake, growth, and several other life-history parameters in a wide range of taxa (Biro & Stamps 2008) and also in domestic pigs (Geverink *et al.* 2004). This, together with my findings that more aggressive and explorative females also had a higher social rank in the juvenile group as well as a higher juvenile body mass (chapter 3.1), indicates that being bold and aggressive pays when food is scarce and competition for it is high. Such a potential advantage of more aggressive and explorative individuals during the juvenile stage would have long-lasting effects on adult quality, as juvenile body mass strongly affects body mass and reproductive success in adult females (see chapter 3.1).

Although these different hypotheses are yet to be tested, my results clearly indicate that selection pressures on different personality phenotypes are context-dependent. Heterogeneous selection pressures in variable environments are thought to be an important mechanism in maintaining different life-history strategies and animal personalities in a population as they might cause net selection on different phenotypes to be close to zero (Roff 2002, Dingemanse *et al.* 2004, Réale *et al.* 2010, Dingemanse & Réale 2013). So far, however, only few studies have tested this empirically (Dingemanse *et al.* 2004, Boon *et al.* 2007, Cote *et al.* 2008, Monestier *et al.* 2015). Only two of those studies actually investigated the effect of pulsed resource availability in this context and, in line with my results, found context-dependent selection pressures on personality traits (Dingemanse *et al.* 2004, Boon *et al.* 2007, Cote *et al.* 2008, Monestier *et al.* 2015). In great tits (*Parus major*) fast exploring males and slow exploring females showed increased survival in mast years whereas this effect was reversed in mast failure years (Dingemanse *et al.* 2004). In North American red squirrels (*Tamiasciurus hudsonicus*) high activity-levels of females affected the growth rate of their offspring positively in years following a mast year but negatively after mast failure years (Boon *et al.* 2007).

For the wild boar, like for most species, resource pulses are unpredictable (see Lebl *et al.* 2010 for an exception). Hence, wild boars respond to these pulses only after the masting events (Bieber & Ruf 2005, Servanty *et al.* 2009, Gamelon *et al.* 2013a, chapter 2.1). Given that the fitness of a certain phenotype is context-dependent and environmental conditions vary unpredictably, a female could maximise its inclusive fitness by producing a variety of offspring phenotypes which are best adapted to different environmental conditions (i.e., diversified bet-hedging; Slatkin 1974, Philippi & Seger 1989, Crean & Marshall 2009). Two recent studies found that heavy, adult female wild boars diversified the body mass of their offspring (within single litters; Gamelon *et al.* 2013a, 2013b) in contrast to smaller, younger females within the same population. This finding might indicate that heavier females followed a diversified bet-hedging strategy in response to the highly variable and unpredictable food availability (Gamelon *et al.* 2013b). Given such a strategy, one would expect different phenotypes to be adapted to differential food availability and thus an interactive effect of (juvenile) body mass and food availability on survival or reproductive success. According to my results, however, food availability does not alter the effect of body mass (juvenile and pre-breeding). In contrast, juvenile body mass had strong and long-lasting positive effects on adult body mass and even reproductive success (i.e., female quality) independent of food availability (chapter 3.1). In fact, most likely due to these persistent differences in individual quality (Noordwijk & de Jong 1986, Reznick *et al.* 2000), I could not detect trade-offs between previous and current reproduction as well as between body mass gain and reproduction (chapter 3.1). Similar long-lasting effects of juvenile condition have been shown for a wide variety of bird and mammal species (reviewed in Lindström 1999) and also for other ungulates (e.g. Albon *et al.* 1992, Clutton-Brock *et al.* 1992, Festa-Bianchet *et al.* 2000, Pettorelli *et al.* 2002, Weladji *et al.* 2008). Consequently, I conclude that, due to the persistent inferiority of smaller juveniles, the diversification of offspring body mass shown by adult female wild boars (Gamelon *et al.* 2013a) is unlikely to represent a diversified bet-hedging strategy. This conclusion is strengthened by the fact that adult females produce more diverse litters only under high food availability (Gamelon *et al.* 2013a), whereas they would be expected to produce diverse litters under any conditions given a diversified bet-hedging strategy.

I identified strong paternal effects on juvenile body mass and later reproductive success in female wild boars, as well as a high degree of multiple paternity in their litters. This indicates, in line with previous studies (reviewed in Fox & Rauter 2003), that multiple paternity is also an important mechanism for offspring diversification in wild boars (chapter 3.2). Therefore, an alternative explanation for high offspring variability could be that diverse litters are a consequence of females avoiding male harassment or infanticide by mating with multiple males (Rowe *et al.* 1994, Agrell *et al.* 1998, Wolff & Macdonald 2004). My results indicate a potential male preference for heavier females as older, and thus more competitive males, mated more often with heavier females (chapter 3.2). Such a preference might result in an increased risk for these females to be affected by male harassment or infanticide and thus could explain why heavy adult females produce more diverse litters (Gamelon *et al.* 2013a, 2013b). However, investigating only females of the same age, I found that heavier females were not fertilised by more males (chapter 3.2). This indicates that whether or not females produce diverse litters depends on their age rather than on body mass, and, together with the fact that adult females produce diverse litters only in mast years (Gamelon *et al.* 2013a), also renders the harassment or infanticide avoidance strategies as possible causes for offspring diversification unlikely.

A high diversity in offspring body mass has been shown to reduce the negative consequences of sibling rivalry, at least for the heavier offspring (Nilsson & Svensson 1996, Forbes & Glassey 2000). Sibling rivalry is generally high in domestic pigs and the wild boar and severe fights over the best teats occur (Fraser & Thompson 1991). After two to three weeks this results in a stable hierarchy between siblings and teat fidelity (Hartsock *et al.* 1977, Fernández-Llario & Mateos-Quesada 2005). Producing more offspring with a high variance in body mass might facilitate the formation of this hierarchy and teat fidelity, and could consequently result in an overall reduction of the negative effects of sibling rivalry. Litter size in the wild boar is known to increase with both age and food availability (e.g. Briederman 1971, Groot Bruinderink *et al.* 1994, Linderoth & Pegel 2010). Additionally, sibling rivalry is directly related to the average number of juveniles per teat and thus to litter size (Mock & Parker 1997). Therefore, it seems plausible that only adult females under high food availability (i.e., females producing particularly large litters) show offspring diversification (Gamelon *et al.* 2013a). Given these results, the most parsimonious explanation for large body mass variation within litters in the wild boar seems to be the reduction of sibling rivalry when females produce large litters after resource pulses. This, however, needs to be directly evaluated in further studies.

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6 APPENDIX

6.1 SUMMARY

Reliance on pulsed resources, that is, the erratic and short-term availability of high quality food resources, may have a strong impact on animals and their life-history strategies. Wild boars strongly rely on tree seeds, a typical pulsed resource, in central Europe. In this thesis I could show that the recently observed exponential growth of wild boar populations is not only caused by increasing winter temperatures but also by a climate change related increase in tree-masting frequencies. A high availability of tree seeds in mast years in fact completely outbalanced the negative effect of cold winter temperatures. This indicates that reduced population growth after cold winters is not caused by a limited thermogenic capacity but by a negative energy balance, when high thermoregulatory costs cannot be matched by the available food.

Being highly affected by tree mast, wild boars are likely to show reproductive strategies adapted to strong annual fluctuations in resource availability. Therefore, I, together with my colleagues, investigated in an experimental setting whether reproductive success of different phenotypes of female wild boars differed under changing feeding conditions. In one of the first studies investigating a link between animal personality and life-history strategies in a large mammal, I could show that less aggressive and less explorative female wild boars raised more offspring than more aggressive and explorative individuals. As neither breeding probability nor litter size shortly after birth was affected by personality, this was most likely due to differential offspring survival in litters of females with different personality phenotypes. This positive effect of lower aggressiveness and reduced exploration behaviour on the number of offspring raised, however, was only visible under high food availability, indicating context-dependent selection pressures on different personality phenotypes.

Although food availability did not alter the effect of body mass on reproductive success in our experimental setting, female wild boars seemed to diversify their offspring within litters. I found strong paternal effects on body mass and reproductive success (i.e., number of offspring raised) in female wild boars as well as high degrees of multiple paternity, indicating that multiple paternity is an important mechanism in this diversification of offspring body mass. I identified strong and long-lasting effects of juvenile body mass on adult body mass and reproductive success in female wild boars. This effect, together with the lack of an interactive effect of juvenile body mass and food availability, points to a silver

spoon effect in the wild boar. That is, there are long-lasting differences in individual quality with lighter juveniles always being inferior compared with heavier individuals for their entire life and irrespective of the food availability. Therefore, I argue that the diversification of offspring body mass does not represent a diversified bet-hedging strategy of females in response to environmental unpredictability, with females producing offspring of different phenotypes best adapted to different environmental conditions. Instead, the more parsimonious explanation for offspring diversification in the wild boar seems to be a reduction of the negative effects of sibling rivalry when females produce large litters in years of resource pulses and when competition for the best teats is high.

In conclusion, my results indicate that the adaptation to pulsed resources has far-reaching consequences, affecting behavioural traits as well as mating strategies in a large mammalian species, the wild boar.

6.2 ZUSAMMENFASSUNG

Die Abhängigkeit von hochwertigen Nahrungsressourcen deren Verfügbarkeit stark schwankt, sogenannte *pulsed resources*, hat weitreichende Folgen für Tiere und ihre Lebensstrategien. Zum Nahrungsspektrum der Wildschweine gehören Samen von Buchen und Eichen, deren Verfügbarkeit (Mast) ein klassisches Beispiel für eine gepulste Nahrungsressource in Mitteleuropa ist. In der hier vorgelegten Arbeit konnte ich zeigen, dass eine durch den Klimawandel bedingte Zunahme der Masthäufigkeit, neben einem Anstieg der mittleren Wintertemperatur, eine der Ursachen für das derzeit beobachtbare exponentielle Wachstum von Wildschweinpopulationen ist. Tatsächlich glich die hohe Nahrungsverfügbarkeit in Mastjahren die negativen Effekte eines kalten Winters völlig aus. Dies weist darauf hin, dass das reduziertes Populationswachstum nach kalten Wintern nicht durch eine eingeschränkte Fähigkeit des Wildschweins zur Thermogenese hervorgerufen wird, sondern durch einen negativen Energiehaushalt wenn hohe thermoregulatorische Kosten nicht mit der zur Verfügung stehenden Nahrung gedeckt werden können.

Dieser starke Effekt der Baummast auf die Populationsdynamik legt nahe, dass auch die Reproduktionsstrategien von Wildschweinen an eine jährlich schwankende Nahrungsverfügbarkeit angepasst sind. In Zusammenarbeit mit meinen Kollegeninnen und Kollegen habe ich daher unter Nutzung eines experimentellen Ansatzes untersucht, ob der Erfolg verschiedener Reproduktionsstrategien weiblicher Wildschweine abhängig von der Nahrungsverfügbarkeit ist. In einer der ersten Studien, die die Verknüpfung von Persönlichkeit und Lebenszyklusstrategien in einem größeren Säugetier untersucht, konnte ich zeigen, dass weniger aggressive und explorative Bachen mehr Nachkommen großzogen als aggressivere und explorativere. Da weder die Wahrscheinlichkeit überhaupt zu reproduzieren noch die Wurfgröße kurz nach der Geburt von der Persönlichkeit der Tiere beeinflusst war, ist es wahrscheinlich, dass dieser Effekt durch unterschiedliche Überlebenswahrscheinlichkeiten der Nachkommen verschiedener Persönlichkeitstypen verursacht wurde. Dieser positive Effekt einer reduzierten Aggressivität und Explorativität auf die Anzahl an großgezogenen Nachkommen zeigte sich jedoch nur unter Bedingungen besonders guter Nahrungsverfügbarkeit. Dies weist darauf hin, dass Selektionsdrücke auf verschiedene Persönlichkeitstypen je nach Bedingung variieren.

Obwohl die Nahrungsverfügbarkeit den Effekt des Gewichtes auf den Reproduktionserfolg in unserem experimentellen Ansatz nicht beeinflusste, schienen Bachen die Jungtiere innerhalb ihrer Würfe zu diversifizieren. Meine Daten zeigen einen starken väterlichen Einfluss auf das Gewicht und den Reproduktionserfolg (die Anzahl an großgezogenen Nachkommen) von Bachen, sowie einen hohen Anteil an *multiple paterniy* (das Vorhandensein mehrerer Väter innerhalb eines Wurfes). Dies weist daraufhin, dass mehrfaches Verpaaren einer Bache mit unterschiedlichen Keilern ein wichtiger Mechanismus zur Diversifizierung des Gewichts ihrer Nachkommen ist. Ich fand, dass das Juvenilgewicht einer Bache einen starken und langanhaltenden Effekt sowohl auf ihr Adultgewicht als auch ihren Reproduktionserfolg hatte. Dies, zusammen mit dem Fehlen eines interaktiven Effektes von Juvenilgewicht und Nahrungsverfügbarkeit, weist auf einen *silver spoon effect* hin, das heißt, auf langanhaltende Unterschiede in der Qualität von Bachen, wobei leichtere Jungtiere ihr Leben lang einen Nachteil gegenüber schwereren haben, unabhängig von der Nahrungsverfügbarkeit. Daher argumentiere ich, dass die Diversifizierung des Gewichts der Nachkommen nicht eine *diversified bet-hedging* Strategie der Bachen in Anpassung an die unvorhersehbaren Umweltbedingungen darstellt, bei der Bachen Nachkommen unterschiedlicher Phänotypen produzieren, die an verschiedene Umweltbedingungen angepasst sind. Die sparsamere Erklärung für die Diversifizierung der Nachkommen wäre stattdessen eine resultierende Verminderung der Rivalität zwischen Wurfgeschwistern wenn Bachen in Jahren guter Nahrungsverfügbarkeit große Würfe produzieren und die Konkurrenz um die besten Zitzen groß ist.

Zusammenfassend weisen meine Ergebnisse darauf hin, dass bei einer großen Säugetierart, dem Wildschwein, die Anpassung an schwankende Nahrungsverfügbarkeit weitreichende Folgen hatte und sowohl Verhaltensmerkmale als auch Paarungsstrategien beeinflusste.

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6.4 CURRICULUM VITAE

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RESEARCH INTERESTS

Evolutionary biology, life history strategies, population ecology, behavioural ecology, chemical communication

EDUCATION

Nov 2011 -	PhD Studies; University of Vienna, Austria Evolutionary Biology and Wildlife Ecology Degree: PhD (final result: tba)
Oct 2009 - Apr 2010	Internship; Wolf Science Center, Ernstbrunn, Austria Cognitive Biology
Oct 2004 - Mar 2011	Diploma Studies of Biology; University of Freiburg, Freiburg im Breisgau, Germany Evolutionary Biology and Animal Ecology, Wildlife Ecology and Management, Animal Physiology and Neurobiology, Anthropology, Geobotany Degree: Diploma (M.Sc. equivalent; final result: 1.1)

PROJECTS

Nov 2011 -	Reproductive strategies in the wild boar (*Sus scrofa*) (PhD Thesis) Research Institute of Wildlife Ecology, Department of Integrative Biology and Evolution, University of Veterinary Medicine Vienna, Austria Supervision: Dr. Claudia Bieber, Prof. Dr. Thomas Ruf, Prof. Dr. Eva Millesi
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EMPLOYMENT

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Genetic analysis for identification of parasite-markers from host-blood of *Sylvia atricapilla*

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Catching, measuring, and taking blood-samples of *Sylvia atricapilla*

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Measuring tannin and phenol level of different fruits and leaves

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Research Institute of Wildlife Ecology, Department of Integrative Biology and Evolution, University of Veterinary Medicine Vienna, Austria

WS 2014, WS 2015 Undergraduate course: "Introduction to statistical data analysis."
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AFFILIATIONS

2010 -	DZG (German Zoological Society) (member)
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2010 -	GzSdW (Society for the protection and conservation of wolves) (member)

AWARDS

2015	Frontiers in Zoology Award 2015 for the best short presentation in the symposium of the occupational group of evolutionary biology at the 108th Annual meeting of the German Zoological Society; SEP 09-13, 2015; Graz, Austria.

CONFERENCES

2015	108th Annual Meeting of the German Zoological Society, Graz, Austria
2015	Wild clocks 2015: Eco meets Chrono
2014	107th Annual Meeting of the German Zoological Society, Goettingen, Germany
2014	10th International Symposium on Wild boar and other Suids, Velenje, Slovenia
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2011	Chemical Signals in Vertebrates (ISCE-CSiV 2011), Berlin, Germany
2011	Meeting of the chemical-ecological workgroups of Baden-Wuerttemberg and Bavaria, Ulm, Germany
2010	103th Annual Meeting of the German Zoological Society, Hamburg, Germany
2010	4th ISEB (Italian Society of Evolutionary Biology) Congress, Milan, Italy
2010	2nd Canine Science Forum, Wien, Austria
2009	1st Interdisciplinary FRIAS Symposium EVOLUTION, Freiburg, Germany

6.5 PUBLICATION LIST

Journal Articles

in prep. Drescher, J; Blüthgen, N; Schmitt, T; Bühler, J; Vetter, SG; Feldhaar, H (in preparation) Worker aggression towards foreign sexuals restricts gene flow between supercolonies of the invasive yellow crazy ant *Anoplolepis gracilipes*

Vetter, SG; Buellesbach, J; Schmitt, T (in preparation) Differences in the reliance on cuticular hydrocarbons as sexual cues in the parasitic wasp family Pteromalidae

Vetter, SG; Suchentrunk, F; Stalder, G; Bieber, C (in preparation) Multiple paternity as a possible mechanism for offspring diversification in wild boars (*Sus scrofa*)

submitted Vetter, SG; Brandstätter, C; Macheiner, M; Suchentrunk, F; Gerritsmann, H; Bieber, C (submitted) Shy is sometimes better: Personality and juvenile body mass affect adult reproductive success in the wild boar (*Sus scrofa*)

2015 Vetter, SG; Ruf, T; Bieber, C; Arnold, W (2015) What Is a Mild Winter? Regional Differences in Within-Species Responses to Climate Change. PLoS ONE 10(7): e0132178. doi:10.1371/journal.pone.0132178

Conference talks and posters

2015 Vetter, SG; Brandstätter, C; Macheiner, M; Suchentrunk, F; Bieber, C (2015) Personality and individual quality in a pulsed resource consumer – the wild boar (*Sus scrofa*). 108th Annual meeting of the German Zoological Society; SEP 09-13, 2015; Graz, Austria.

Vetter, SG; Bieber, C; Ruf, T (2015) Seasonal timing of reproduction in the wild boar. Wild Clocks 2015: Eco meets Chrono; MAR 10-15, 2015; Texel, Netherlands.

2014 Vetter, SG; Bieber, C; Suchentrunk F (2014): Parenthood analysis and population assignment in wild boar (*Sus scrofa*): How many microsatellites to use? 107th Annual meeting of the German Zoological Society; SEP 11-14, 2014; Göttingen, Germany.

Vetter, SG; Bieber C; Suchentrunk F (2014): Evaluating commonly used microsatellites for parenthood analysis and population assignment in wild boar (*Sus scrofa*). 10th International Symposium on Wild Boar and other Suids; SEP 1-5, 2014; Velenje, Slovenia.

Vetter, SG; Ruf, T; Bieber, C; Arnold, W (2014): The burst of wild boar populations in Europe: how local adaptation mediates the effects of climate change in a widespread ungulate. 107th Annual meeting of the German Zoological Society; SEP 11-14, 2014; Göttingen, Germany.

Suchentrunk, F; Himmler, E; Habe, M; Zink, R; Bieber, C; Vetter, SG (2014): Spatial genetics for the management of wild boar (*Sus scrofa*) in peri-urban Vienna. 10th International Symposium on Wild Boar and other Suids; SEP 1-4, 2014; Velenje, Slovenia.

2013 Himmler, E; Habe, M; Vetter, SG; Bieber, C; Suchentrunk, F (2013) Spatial genetic patterns of the wild boar (*Sus scrofa*) in peri-urban Vienna. 87th Annual Meeting of the German Society of Mammalogy, Praha, Czech Republic. Mammalian Biology (78), S 12-12.

2012 Vetter, SG; Bieber, C (2012) Assessing body mass of wild boars (*Sus scrofa*) under semi-natural conditions. 9th International Symposium on Wild boar and other Suids, Hannover, Germany.

Walzer, C; Stalder, GL; Bieber, C; Miljkovic, V; Vetter, SG; Gerritsmann, H (2012) Seroprevalence of viral and bacterial pathogens in wild boar (*Sus scrofa*) in Austria. Joint WDA/EWDA Conference, Lyon, France.

2010 Vetter, SG; Büllesbach, J; Schmitt, T (2010) Differences in cuticular hydrocarbon-mediated mate discrimination behaviour between closely related genera of parasitic wasps. 103th Annual Meeting of the German Zoological Society, Hamburg, Germany.

Büllesbach, J; Vetter, SG; Echinger, F; Niehuis, O; Gadau, J; Schmitt, T (2010) Chemical communication mediated by species-specific cuticular hydrocarbon profiles in the jewel wasp Nasonia - from phenotypic to genetic architecture. 103th Annual Meeting of the German Zoological Society, Hamburg, Germany.

Theses

2011 Vetter, SG; Schmitt, T (2011) Cuticular hydrocarbons and their function in parasitic wasps of the family Pteromalidae (Hymenoptera). University of Freiburg, Freiburg im Breisgau, Germany.