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Short communication

Macronutritional consequences of food generalism in an invasive mammal, the wild boar

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ABSTRACT

We apply a recently established nutritional framework for defining dietary generalism to global populations of wild boar (*Sus scrofa*). Across its range, wild boar consume a diversity of foods that vary in nutritional composition. The macronutrient (carbohydrate, protein and fat) composition of the diets composed from those foods also varies substantially between countries, particularly in terms of proportion of energy from protein. These results suggest that as a species wild boar have a wide fundamental macronutrient niche, which likely contributes to the success of the species as an invader of novel environments.

Diet is commonly used to classify species along the generalist-specialist spectrum (Machovsky-Capuska et al., 2016a). However, dietary generalism has been coarsely defined historically, with the role of nutrition poorly considered (Machovsky-Capuska et al., 2016a). This is problematic, because nutrition is a fundamental determinant of the environments an animal is able to inhabit (Raubenheimer et al., 2012). Dietary macronutrient composition, in particular, has been shown to impact many fundamental biological traits, including foraging behaviour, lifespan and individual fitness (Le Couteur et al., 2015; Machovsky-Capuska et al., 2016b; Senior et al., 2015).

Recently, Machovsky-Capuska et al. (2016a) developed a framework for integrating nutrition and ecological niche theory, and provided a definition of dietary niche that allows a species to be classified as a generalist across three functional levels: 1) the range of dietary macronutrient compositions on which the animal is able to succeed, or its "fundamental macronutrient niche"; 2) the range of food nutritional compositions from which it is able to compose a diet that falls within the macronutrient niche, and 3) the range of ecological and physical attributes of foods that it is able to exploit. While these three levels interact to determine the diet of a species, the fundamental macronutrient niche has particular ecological relevance because animals that are nutritionally flexible are more likely to persist in the face of substantial changes to their nutritional environment (e.g. loss of a food, or translocation to a new environment).

The wild boar (*Sus scrofa*) is considered among the 100 world's most effective invasive species, now established on all continents except for Antarctica (Lowe et al., 2000). Wild boar prey on native wildlife, and their rooting behaviour destroys plant cover, seed banks and crops (Ballari and Barios-Garcia, 2014). Wild boar diets comprise a variety of foods that differ in their ecological, physical and nutritional properties, and as such the species is widely considered a generalist omnivore (reviewed in Ballari and Barios-Garcia, 2014). In the context of functional dietary generalism, wild boar can thus be classified as food exploitation and food composition generalist (i.e. a generalist at levels 2 and 3 above).

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However, to understand the relationship between the nutritional environment, adaptation and population persistence, it is important to also establish a species' fundamental macronutrient niche, as this represents the range of dietary compositions on which a population can actually persist (Machovsky-Capuska et al., 2016a). It is unclear whether wild boar consume a range of ecologically different foods in order to regulate macronutrient intake, as is seen in many other mammals (Raubenheimer et al., 2015; Simpson and Raubenheimer, 2012) including domesticated pigs (Kyriazakis and Emmans, 1991). It is also unclear whether wild boar populations are capable of persisting on diets that vary widely in macronutrient composition (i.e. have a broad fundamental macronutrient niche). We applied a recent framework using the right-angle mixture triangle (RMT; Machovsky-Capuska et al., 2016a; Raubenheimer, 2011), to infer the fundamental macronutrient niche of wild boar. Data were extracted from published reports of wild boar diets from geographically separated populations, following the approach previously applied to examine the diets of omnivorous predators (Remonti et al., 2015).

From a recent review of wild boar diets in native and introduced ranges (Ballari and Barios-Garcia, 2014), we collected studies that provided estimates of the percentage contribution (by mass) of foods to the diet of populations of wild boar (based on stomach contents). We also updated the previous search by using the same criteria to find material published between 2013 and 2016, and by searching within literature citing the aforementioned review. We were able to obtain a total of 16 articles that met our criteria, providing dietary data for 28 populations. "Populations" within articles were considered independent if samples were taken from different studies, countries, geographical regions, seasons, or segregated by sex (Appendices Files S1, S2 in Supplementary material).

Foods within diets were listed in published articles to varying specificity, e.g. some studies listed the contribution of leaves from specific plant species, while others gave broad categorisations of foods (e.g. "vertebrates"). To evaluate the percentage of macronutrients in the diet, we first estimated the percentage contribution of each food type to the total diet. We then estimated the nutrient composition (in terms of digestible content, then in terms of protein, carbohydrate and fat, assuming dry mass), of each food using published data and the USDA National Nutrient Database for Standard Reference (US Department of Agriculture, 2015) (Appendices Files S2, S3 in Supplementary material). We were unable to obtain proximate composition of reported foods using data that were temporally and spatially contemporary with the wild boar stomach contents sampled. While this might introduce error around estimates of the composition of specific foods (e.g. the nutritional content of a specific forage may vary spatially/temporally; Rothman et al., 2012), it is unlikely to substantially impact on differences in diet estimates between populations, which are driven by variable proportions and foods types (i.e. the ratio of different forages and animal matter) in the diet (Remonti et al., 2015). Following Raubenheimer and Rothman (2013), macronutrient masses of the foods obtained from the literature were converted to energy using protein/carbohydrate = 17 Kj/g and lipid = 37 Kj/g.

Our dataset included ten countries (Fig. 1A), although for analytical purposes we pooled data from France and Luxembourg. Of these countries wild boar are invasive in Australia, New Zealand and the USA. Data from seven countries were reported as being based on samples pooled over multiple seasons. For five countries data were available from discrete seasons enabling temporal examination of diet (Fig. 1A and B). Two studies did not clearly report sample size, but for the remainder the mean number of wild boar examined per population was 102.5 (range 3–1200). We recorded 43 food types present in the stomach contents of wild boar, which varied substantially in their nutritive content (round points shown on Fig. 1A and B); foods ranged from <1% to 91% protein (dry mass), 0–95% carbohydrates (dry mass) and <1–78% fats (dry mass). Researchers reported an average of 8.8 food types per population (range 5–13).

Where data were based on samples pooled from multiple seasons, the macronutrient composition of wild boar diets varied between countries. In New Zealand, diets had higher protein content than in other countries (Fig. 1A). The pattern of dietary variation among countries was also seen among those data that were recorded seasonally: in spring and summer, for example, New Zealand diets showed substantially higher protein content than those from USA and Ukraine (Fig. 1B). Across all seasons, intra-country variation in protein composition was relatively low in comparison to inter-country variation (Fig. 1B). Analyses using linear-mixed models confirmed a high degree of between-country variance in dietary proportions of protein (estimated between-country SD = 0.51, $\chi^2 = 55.8$, d.f. = 1, $p < 0.001$; see Appendix File S4, Tables A1 and A2 in Supplementary material). A moderate degree of between-country variation in carbohydrates was also estimated, although this was not quite statistically significant (estimated between-country SD = 0.31, $\chi^2 = 3.34$, d.f. = 1, $p = 0.07$). There was no between-country variation in proportion of energy from fat (estimated between-country SD = 0). Accordingly, residual variance of each model (interpretable as variation among populations within each country) was low for protein, moderate for carbohydrate, and high for fat (Tables A1 and A2 in Supplementary material).

The breadth of dietary compositions that we observed shows that wild boar are dietary generalists in terms of the diversity of food types exploited, the compositions thereof, and the composition of diets that can sustain a population. Previous synthesis of wild boar diet has focussed on food types, rather than the nutritional composition of foods and overall diet. Ballari and Barios-Garcia (2014) concluded that temporal/spatial variations in availability were major contributors to the foods selected by wild boar. Along with these variations, our analyses suggest that wild boar shows a wide tolerance of macronutrient dietary compositions across the whole range. For example, in New Zealand, wild boar diets were substantially higher in protein than in native ranges, a difference that seemingly persists across seasons. In New Zealand, it is likely that animals make up a larger component of wild boar diets than in native ranges (Ballari and Barios-Garcia, 2014). The extent to which the inter-population differences in diet that we observed result from food availability (e.g. habitat-type or proximity to human settlement) and/or selection (i.e. the regulatory behaviours of the species) is difficult to say based on our data. Additionally, the relative consistency that we observe in proportion of energy from protein across seasons in our dataset may not necessarily be ubiquitous. Studies on European wild boar populations have shown that animals adjust their foraging to take advantage of abundant agricultural crops in summer (Keuling et al., 2009). It remains to be seen how such changes in habitat use impact the macronutrient composition of the diet. Nevertheless, our results suggest that as a species, wild boar populations are not intrinsically constrained to diets of a narrow macronutrient range, and that other non-physiological processes are likely to influence the distribution of the species.

It is interesting to consider how variation in dietary composition influences life-history traits and population demography. Studies in model organisms indicate that higher-protein diets are associated with increased reproductive output (Lee et al., 2008; Solon-Biet et al., 2015). Furthermore, in production populations, sows on higher-protein diets are quicker to reach oestrous after weaning their first litter (King and Dunkin, 1986). There is abundant evidence that food intake influences reproduction in wild boar, with females tending to give birth to larger litters in seasons where food is more abundant (Frauendorf et al., 2016; Gamelon et al., 2013; Gethöffer et al., 2007; Servanty et al., 2009). The degree to which this is driven by an increase in total energy per se, or an increase in the intake of specific macronutrients (e.g. protein) that