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REVIEW

OneARK: Strengthening the links between animal production science and animal ecology

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Summary

1. Wild and farmed animals are key elements of natural and managed ecosystems that deliver functions such as pollination, pest control and nutrient cycling. They are submitted to global changes with a profound impact on natural range and viability of animal species, emergence and spatial distribution of pathogens, land use, ecosystem services and farming sustainability. We urgently need to improve our understanding of how animal populations can respond adaptively and therefore sustainably to these new selective pressures.

2. In this context, we explored the common points between animal production science and animal ecology to identify promising avenues of synergy between communities through the transfer of concepts and/or methodologies, focusing on seven concepts that link both disciplines. Animal adaptability, animal diversity, selection, animal management, animal monitoring, agroecology and viability risks were identified as key concepts that should serve the cross-fertilization of both fields to improve ecosystem resilience and farming sustainability.

3. The need for breaking down interdisciplinary barriers is illustrated by two representative examples: i) the circulation and reassortment of pathogens between wild and domestic animals and ii) the role of animals in elementary cycles

4. *Policy implications.* Our synthesis identifies the need for knowledge integration techniques supported by programs and policy tools that reverse the fragmentation of animal research towards a unification into a single Animal Research Kinship, OneARK, which sets new objectives for future science policy.

5. At the interface of animal ecology and animal production science, our article promotes an effective application of the agroecology concept to animals and the use of functional diversity to increase resilience in both wild and farmed systems. It also promotes the use of novel monitoring technologies to quantify animal welfare and factors affecting fitness. These measures are needed to evaluate viability risk, predict and potentially increase animal adaptability, and improve the

management of wild and farmed systems, thereby responding to an increasing demand of the Society for the development of a sustainable management of systems.

Keywords Adaptation, Agroecosystem, Bio-logging, Emergence, Functional diversity; Livestock, Phenotypic plasticity, Resilience, Sustainability, Zoonotic disease.

Introduction

Our planet is undergoing major global environmental changes mainly caused by a rapid increase in human population and the concomitant agriculture industrialisation (specialization, concentration, intensification). These changes have a profound impact on biodiversity, on land use due to modified resource availability, as well as on emergence and spatial distribution of pathogens (Keesing et al. 2010). A primary concern is the extremely rapid rate of these changes, which applies strong and often novel selective pressures on animals, at scales rarely encountered over evolutionary time scales. These challenges are placing new demands on physiological and adaptive capacities (particularly phenotypic plasticity which permits compensation of rapid environmental changes when genetic adaptation is too slow), on the interactions among species, and ultimately on species persistence and biodiversity. The consequences are major in terms of conservation of biodiversity but will also have impacts on every category of ecosystem services: support (e.g. soil formation), production (e.g. milk and meat), regulation (e.g. pest control) and cultural (e.g. ecotourism). Thus, we have a responsibility to find new ways to better understand and preserve the functional diversity of ecosystems. These have been, and will continue to be, a major support of human endeavours.

Animals represent an enormous part of biodiversity, contributing 1.12 million catalogued species from a total of 1.43 species throughout eukaryotic kingdoms (Mora et al., 2011). Only a very limited number of species are farmed but they contribute a significant amount of biomass. Wild and farmed animals are landscape shapers and ecosystem engineers that control the availability of resources to other organisms by causing changes in biotic or abiotic materials. However, animals are also important vectors, intermediate hosts and reservoirs for microorganisms causing major infectious diseases (Woolhouse et al., 2005). Additionally, wild and farmed animals have always been a major source of proteins for human consumption.

It is increasingly recognized that there is a continuum between animals in managed ecosystems and animals in natural environments. No production system whatever its level of biosecurity is completely isolated from the surrounding environment. Likewise, today, no ecosystem is completely isolated from human influence, and increasingly ecosystems are subject to some degree of human management, or have limits imposed on them by human activity. Therefore, it is highly relevant to consider what the cross-fertilisation between the two communities of animal production science and animal ecology can bring.

A number of basic concepts appear at first sight to be fundamentally different between animal production science and ecology. However, when these concepts are given due consideration it transpires that they are actually more similar and not really in opposition. The aim of this paper is to explore the common points between animal production science and animal ecology. Better recognizing the similarities between the two communities will identify promising avenues of synergy by concept and/or methodology transfers between communities. This prospective thinking for a community unification into a single Animal Research Kinship, i.e. OneARK, sets new objectives for future science policy.

Artificial selection versus natural selection

Selection denotes the fact that, among individuals born at a given generation, those that will survive to mate and procreate a new generation can be considered as "chosen" according to some of their characteristics. These characteristics typically impact on their survival, mating probability and their number of descendants. For domestic species, **artificial selection** depends on decisions taken by humans (breeding managers). For wild species, **natural selection** emerges from interactions with conspecifics, other species and the abiotic environment.

Natural selection can act simultaneously on multiple traits, so that trade-offs are an important part of understanding adaptation and response to selection: natural selection maximises average fitness of the population, not trait values (Stearns, 1977). Another fundamental aspect is that natural selection varies spatially and temporally depending on the environment (Siepielski et al., 2013, 2017) so that traits may be positively selected in one environment and counterselected in another. Investigating selection is thus complex notably because we need to assess the actual target of selection but also make sure that the covariances between trait and fitness are not only due to environmental covariance (Morrissey et al., 2010).

It is generally admitted that artificial selection started in the early stages of domestication, the first selected traits being favourable to the domestication process itself, e.g. docility. During the last three centuries, and especially during the last six decades, this artificial selection was more and more organized and intense, targeting and maximising specific traits (e.g. dairy production, body mass). Another consequence of domestication was to decrease the natural selection pressure because humans increasingly controlled the environment of animals. This is typified by the strong intensification of animal production.

Whereas domestication first led to a huge increase in diversity between populations (Darwin, 1859), the recent changes in livestock production led to the opposite, with a decrease in the number of breeds for a given species (Sherf, 2000) and a reduction of within-population genetic variability in intensively selected populations (Danchin-Burge et al., 2012). The selection of highly specialised and homogeneous individuals led to (i) decreased robustness and lower adaptive potential (e.g. lower resistance to environmental variability, particularly stress and disease) and (ii) the exacerbation of trade-offs such as milk production *vs* fertility (Oltenacu & Broom, 2010). The multivariate nature of selection acknowledged by animal ecologists (Lande & Arnold, 1983) has promoted the development of artificial selection programs which include the use of selection on multiple traits (Puillet et al., 2016).

Such collorative efforts are increasingly needed because the rapid and strong changes of environmental conditions generate strong selective pressures, so much so that humans are now considered as the greatest evolutionary force (Palumbi, 2001). Understanding how populations respond to these new selective pressures is a key issue in applied evolution and conservation. It is also a key issue for artificial selection since global changes are altering the environmental conditions under which artificial selection is operating. A major challenge is to understand how global environmental changes are going to affect selective pressures acting on both wild and domesticated populations and whether populations are able to respond adaptively (and therefore, sustainably) to these new selective pressures.

Agro-ecosystems and farmed animal management versus ecosystems and wild animal management

In contrast to wild animals in natural ecosystems that are fully in interaction with the environment, the magnitude of interactions of farmed animals with the environment spreads along a continuum, ranging from agro-ecosystems to landless livestock production. This gradient is driven by the form of the feeding system, opposing land sharing to land sparing, and the level of interaction the livestock population has *vis-a-vis* agricultural and natural system components (crops, forest, water, wildlife, etc.). Agro-ecosystems are defined by a high dependence on local resources, like land and water (pastoralism being its apogee). At the opposite end of the scale, landless livestock systems maximize their direct independence from environmental constraints by means of feed trade, thus establishing production systems with almost no direct relation (excluding by the market) between the places and times where livestock are reared, their food is produced, and where their products are consumed.

Gradients in degree of human intervention are also a common element of wild animal and natural ecosystem management. Indeed, not a single natural ecosystem is human-proof, at least since climate change started. More direct wild animal ecosystem management profiles can range from biodiversity reserves through natural parks, run as wildlife sanctuaries, to wildlife areas managed by local communities, which recognize combined wildlife, livestock, and rangeland services as essential for human groups, a vision emphasized in Southern Africa (Chomba et al., 2014; Jones et al., 2015).

In the latter case there is a strong interaction between agricultural activity and ecosystem management. More generally, the frontier between the “wild” and the “farmed” animals is progressively being eroded, changing to situations where more coexistence and interactions are inevitable if we wish to reconcile preserving biodiversity and better resource sustainability. Achieving this in the design of these re-expanding agro-ecosystems imposes a tightening of the collaboration between animal production scientists and animal ecologists. An example of this is the “Natura 2000” policy to preserve biodiversity in Europe, often in human-made ecosystems.

Furthermore, and in line with societal considerations, there is a visible shift in livestock and wildlife policy dialogue, moving beyond the simple support of resource sufficiency and food provision to now provide incentives for conservation and rehabilitation of functional integrity, and payment for environment services in production areas and at global Earth scale (Frost et al., 2008; Kammli et al., 2011).

Viability risks for farmed systems versus natural ecosystems

Global changes pose a viability risk for both natural and farmed systems, although the “currencies” by which viability is judged have traditionally differed; being largely about economics for farmed systems and about biodiversity and population persistence for natural ecosystems. The most commonly used currency to assess viability in wild populations is the probability of extinction of a population over an arbitrarily chosen time period (e.g. 100 years in the UICN red list) or the median time to extinction. Several components of global change will affect viability of both natural and farmed systems.

The impacts of **climate change** emerge through both long-term changes in average conditions within local environments and an increase in the frequency of extreme events (Ummenhofer & Meehl, 2017). The former has received more attention so far. The effects of climate change can be mediated through many indirect effects such as the disruption of interaction between species because of changes of phenology or morphology (van Gils et al., 2016). A typical example is the earlier breeding of insectivorous birds so that the peak of offspring energetic needs coincides with the peak of food abundance (caterpillars, Visser et al., 1998): if the timing is mismatched then breeding success is low. These effects are more likely to be encountered in wild than farmed system where long-term changes in average environmental conditions will more frequently be experienced in terms of direct effects that reduce resource availability. In farmed systems, these will typically impact the stocking densities of animals that are sustainable in extensive systems, and incur greater costs for intensive systems (e.g. cooling systems). In managed populations, extreme events such as drought or flooding require the farmer to make costly, unplanned interventions (buying food, transporting animals) where possible. These clearly have economic consequences especially if possible interventions are limited and loss of animals occurs (e.g. rangeland grazing). In wild populations, effects of extreme events include both decreased survival (e.g. die-offs, McKechnie & Wolf, 2010) and reduced breeding success (Jenouvrier et al., 2015). Extreme events may generate very strong selection pressures leading to marked evolutionary shifts in wild populations (Grant et al., 2017). However the impact of extreme events is particularly complex to anticipate, as they engage non-linear shifts in multi-species interactions.

Introduced exotic species, which may be pathogens, pathogen carriers, predators or directly competing species, represent another major viability risk to both farmed and wild populations (Bellard et al., 2016; Paini et al., 2016; see section on circulation of zoonotic pathogens). They are particularly prevalent and successful in highly anthropized habitats such as peri-urban and agricultural lands, and species of tropical origin benefit from the warming climate in temperate and boreal regions.

Land use is another class of viability risks. There are direct economic impacts of human movement in terms of (i) the value of land or other shared resources such as water in zones where agricultural land is in competition with urban development, and (ii) in terms of rural depopulation (difficulties in recruiting labour, human isolation, costly supply chains) affecting ecological function of agro-landscapes (Sabatier et al., 2014). Extinction risks are further increased for wild populations due to competition with urban and agricultural land (e.g. palm oil, cocoa), and non-sustainable harvesting (Maxwell et al., 2016). To fully understand viability risks, all these factors and their interactions need to be taken into account.

There are also viability risks due to rigidity of **human behavior**. In farming this translates to, for example, continued use of inappropriate animal genetics through a failure to recognize the traits needed for durability in new conditions, or lack of flexibility in day-to-day farm management. The loss of genetic diversity of domesticated breeds due to rigid selection of a very few breeds is a major issue being addressed by the FAO (FAO, 2015). Rigidity of behaviour can also apply to animal species if we look at generalists/specialists or plastic/non-plastic species. One issue is the existence of ecological traps where species respond to cues that were supposed to signal high quality environment but that got uncorrelated from this environment, for example asphalt roads may reflect light in the same manner as water bodies attracting some insects to breed (Schlaepfer et al., 2002). Ultimately, population viability will depend on the ability of organisms to respond adaptively to complex environmental changes inducing novel selective pressures.

Both farmed and wild populations share some of the same viability risks and ultimately must respond by adaptation (microevolution and/or plasticity). The degree of management of the animal populations within a given ecosystem will mainly affect the extent to which risks can be buffered by human intervention, e.g. deploying reproductive technologies developed in animal production science to aid in rewilding and to overcome habitat fragmentation. Biodiversity and economics are connected across the spectrum from farmed to natural ecosystems. Tools developed in ecology, such as coviability analyses (Mouysset et al., 2014), which aim at finding compromises where viability of both farmed and natural systems can simultaneously satisfy different constraints, will be important for the future.

The key role of animal adaptability to connect evolutionary and animal production sciences

Adaptation processes are multifaceted, taking place at different scales with different temporal modalities (Gould & Lloyd, 1999). Evolutionary biologists, who mainly deal with natural populations, have focused on adaptation as a trait increasing relative fitness, *i.e.* which evolved via natural selection. Physiologists, who deal with laboratory and farmed strains, have focused on within lifetime reversible processes that allow individuals to adjust to their environment, with less focus on their heritability. These biological processes depend on the variability of the environment and adaptation can be described by the following continuum: (i) phenotypic flexibility of individuals leading to temporary/reversible changes, (ii) developmental plasticity leading to more permanent changes of phenotypes through physiological and/or epigenetic mechanisms, and (iii) intergenerational modification of allele frequencies through natural selection (Chevin & Beckerman, 2011). Integrating these different adaptive mechanisms has to be developed together with the interface with animal production science. Studying performance and behavioral changes induced by modifications in the farming environment would provide a great opportunity for evolutionary biologists to investigate the key mechanisms allowing individuals to maintain their performances over different abiotic conditions, complementing and providing a bridge between approaches in the lab and in the wild.

The complex phenotypes underlying adaptability are forcing scientists to develop an integrated approach looking at multiple characters. The recent expansion of genomics, and other -omic data, offers new avenues to understand the mechanisms that shape adaptability (Valcu & Kempenaers, 2014). Studying organisms as a whole, taking into account functional links between traits is now made possible by combining –omic data with the characterization of physiological and performance traits (Prunet et al., 2012). This should uncover cell or physiological processes important for adaptability in both wild and farmed animals. However, such approaches often produce big data on cell and physiological pathways concomitantly affected. Building an integrated phenotyping (Headon, 2013) that sorts out mechanisms underlying adaptability in an order of importance now needs to combine biological, bioinformatics and statistic knowledge.

Important questions remain regarding the role of transgenerational adaptation pathways in fitting, in the long term, populations to their environment. Such phenotypic modulation has a predictive power and may help the offspring to be better adapted to future environmental conditions. Intergenerational plasticity encompasses various mechanisms, including epigenetic changes. These mechanisms are likely to sustain rapid adaptation and to promote survival of the next generation (Rey et al., 2016). Their understanding is also a key element for animal production science: it opens an innovative way to optimize productivity, *via* the modulation of farming conditions during reproduction and offspring growth.

This is not an exhaustive list of the research of interest that remains to be conducted on animal adaptability. However, it emphasizes that promoting the understanding of the link between adaptation and fitness (survival or health state) and of the inheritance of related processes will enhance our ability to predict adaptability of animal populations, living in the wild or under farming conditions.

The importance of animal diversity for system resilience

Ecological resilience focuses on the adaptive capacity of an ecosystem and is defined as the amount of disturbance this system can absorb while remaining within the same stability range and retaining the same function(s), achieved through reinforcing within-system structures, processes and reciprocal feedbacks (Holling, 1996; Kaarlejärvi et al., 2015).

Resilience strongly depends on the initial composition of the local ecological assemblage and the degree of disturbance (Sasaki et al., 2015). In highly disturbed areas, differences in the recovery trajectory of assemblages have been related to differences in the composition and the dispersal capacities of the surrounding species pool of colonists and the level of connectivity among populations, species and ecosystems (Allison, 2004). These factors influence both probability of species persistence by increasing the genetic diversity of local populations (Bach & Dahllöf, 2012) and capacity for recovery by providing sources of propagating organisms (de Juan et al., 2013).

Biodiversity, a key factor for improving the long-term resilience of ecosystems (Awiti, 2011; Mori et al., 2013; Oliver et al., 2015), is frequently associated with high functional redundancy (*i.e.* presence of several species able to perform similar functions) (Sasaki et al., 2015; Kaiser-Bunbury et al., 2017) and high species complementarity (Lindegren et al., 2016). Both taxonomic (TD) and functional (FD) diversities, but not species richness, adequately capture the aspects of biodiversity most relevant to ecosystem stability and functionality (Mori et al., 2013). TD enhances resilience because most of the rare species within an assemblage are considered as functionally similar to the dominant ones and able to compensate their potential loss under changing environmental conditions, thus maintaining ecosystem functions. FD improves resilience because a more diverse set of traits increases the variety of potential responses to disturbance. This then increases the likelihood that species can compensate function(s) for one another lost during disturbance events (Moretti et al., 2006; Kühsel & Blüthgen, 2015). However, resilience is also likely to be scale-dependent (Shippers et al., 2015), *i.e.* a combination of traits providing resilience to small-scale disturbance can be ineffective against disturbance acting at largest scale. As a result, the link between biodiversity and resilience is sometimes weak

(Bellwood et al., 2003). If the trait structure of highly diverse animal assemblages remains rather stable after moderate stress, further intensification of human pressure can substantially reduce the variety of traits and results in significant alteration of functional diversity (Bregman et al., 2017). This raises the question of how to manage resilience and ecosystem services in socio-ecological systems?

Conceptual frameworks, tools and indicators (Sasaki et al., 2015; Oliver et al., 2015) have been defined for quantifying the resilience of coastal fisheries, estuaries or agricultural landscapes (de Juan et al., 2013; Mijatović et al., 2013) based on structural and functional attributes; *e.g.* ecosystem elasticity or sensitivity and adaptive capacity (López et al., 2013). Trends in the frequency of animal species that provide key ecosystem functions in Great Britain, have highlighted that key ecosystem functions are not equally impaired by global change, and conservation actions should focus on the functional groups for which there is clear evidence of resilience erosion (Oliver et al., 2015). Moreover, community field experiments have clearly shown that vegetation restoration can improve pollination, suggesting that the degradation of ecosystem functions is at least partially reversible (Kaiser-Bunbury et al., 2017) and that severe disturbance-driven reduction in ecosystem function does not preclude rapid ecosystem recovery. Several pattern- or process-oriented strategies have been suggested (Pauly et al., 2002; Fischer et al., 2006) to enhance biodiversity and ecosystem resilience for an improved management of marine and terrestrial production systems including: (i) promoting structurally complex patches of resources throughout the system, and species of particular concern for functional diversity, but (ii) controlling over-abundant and alien species and minimizing threatening ecosystem processes. Implementing those strategies will result in more heterogeneous production areas, with structurally more complex mosaics of habitats. The resulting production areas are likely to sustain higher levels of animal diversity and will be more resilient to external disturbances.

The concept of agro-ecology as a sustainable and responsible way forwards

Agro-ecology, a concept originally defined as “the application of ecological theory to the design and management of sustainable agricultural systems” (Altieri, 1987), has recently become a hot topic with the aim to optimize economic, ecological, and social dimensions to achieve sustainable food production. Understanding the mechanisms underlying the resilience of agro-ecosystems is critical for conserving biodiversity and ecosystem functions in the face of disturbances (Moretti et al., 2006) and for securing the production of essential ecosystem services. Surprisingly, the majority of research on agro-ecology has been in done in plant production. This concept now calls scientists from animal ecology and animal production domains to readily interact by developing more interdisciplinarity.

Thus, five key ecological processes were proposed to be adapted to the animal context (Dumont et al., 2013): 1) adopting management practices, including breeding, to improve animal resilience and health; 2) decreasing the external inputs needed for production, particularly use of resources that are directly useable by humans; 3) decreasing pollution by optimizing the metabolic functioning of farming systems, including consideration of animal manure as a resource; 4) enhancing diversity within animal production systems to strengthen farm resilience, and 5) preserving biological diversity in agroecosystems.

Even if agro-ecosystem resilience has been considered as a key driver of sustainable agriculture under increasing environmental uncertainty, only a very few studies have explicitly tested the resilience of productivity to disturbance. Taking agroecology forward as a shared discipline needs a number of challenges to be overcome; these relate to scientific problems (Carlisle, 2014; Dumont et al., 2013) and cultural issues. From an ecologist perspective, agroecosystems are often seen as being a special case study that offers the opportunity to test ecological principles in conditions that are less complex and more clearly controlled than purely natural ecosystems. From the perspective of an animal production scientist, agroecology is often perceived as a constraint problem, i.e. how to achieve economic performance without breaking some environmental “rules”. An important objective to better understand the interactions between environmental and biological processes that control community resistance and resilience will be to move beyond these viewpoints and exploit the synergies that the biodiversity within agroecosystems can bring (Tabacchi et al., 2009). One example of a useful synergy is to view climatic events as manageable phenomena resulting from processes whose effects could be much more mitigated through the use of integrated ecosystem management and flexible diversification than through adaptation to severe stress (Carlisle, 2014).

Thus, the notion of eco-efficiency may be a powerful tool (Keating et al., 2010). This implies enlarging traditional production-related efficiency definitions to include environmental (land, water, energy), ecological (biodiversity, resilience, conservation) and economic (labour, capital) dimensions. This eco-efficiency approach creates significant challenges for the integration of these multiple dimensions but there are promising avenues of research tackling this issue (Soteriades et al., 2016).

The commonality in the use of advanced technologies to monitor animals

Animal ecology and production science are both interested in explaining the variability with which individuals respond to their environment. These research fields, which both rely on methodologies to monitor animals in their living environment, have a lot to win from merging methodological approaches.

Recent technological advances allow ecologists studying free-ranging animals access to multiple parameters encompassing foraging patterns, social interactions, physiological parameters but also to environmental variables. These bio-logging technologies, recording from a distance several variables many times per seconds over periods up to years, now allow the quantification of energetic and behavioral variability between individuals (*e.g.* accelerometry, Gleiss et al., 2011).

Bio-logging is extensively used, as well, in animal production science and now recognized as field in its own right, in precision livestock farming (Wathes et al., 2008). It permits the monitoring of animals for signs of health problems, allowing timely intervention by the farm manager. The broad nature of the bio-logging data is increasingly useful, particularly with respect to phenotyping complex traits such as resilience and efficiency. Being able to achieve a sustainable balance between resilience and efficiency is a key goal of selection programs for agro-ecology. For instance, the efficiency with which farmed animals transfer energy towards body mass production could be evaluated from bio-logging measurements based on the time-budget devoted to feeding, locomotion, sleeping or social interactions at a daily scale. Such proxy measurements allow the phenotyping of efficiency (and other complex traits) in large populations, and thereby open up for incorporation of such traits in genomic selection (e.g. www.gentore/eu). From a husbandry perspective, finding fine-tuned modifications of farming environment to positively influence this productivity is also conceivable, e.g. detection of circadian optimal conditions in food access or ambient temperature. Those methodologies may change our view of how farmed animals are able to adapt their energy balance in response to changes in farming environments, as they did for wild animals or humans (Villars et al. 2012).

This offers the potential to integrate multiple markers over long-time scales to quantify factors affecting overall fitness. One promising step will be to combine diverse biomarkers to evaluate how environmental variations impact fitness and productivity over ages (a fundamental factor for selection in the wild) or over life stages (a key parameter to improve animal productivity). The use of non-invasive methodologies (using hairs, feathers, blood…) including biosensors raises the issue of integrating all this information in a valuable way. Consider for example animal resilience, the capacity to cope with short-term environmental fluctuations. There is no direct measure that encompasses all the facets of resilience, in other words it is a latent variable that can only be deduced by combining multiple (proxy) measures of its different aspects (see Højsgaard & Friggens, 2010 for a health-related example). This issue requires the development of new mathematical models on the ultimate consequence of, within and between individual differences in ecology (*e.g.* habitat use) and physiology (*i.e.* energy demands over different time scales).

An important challenge for ecology and animal production science is to safeguard animal welfare and thus health status across the wide range of husbandry and production environments, and also among individuals of different sizes and/or ages. This can range from the surveillance of animals scattered across very extensive rangelands to the monitoring of stress within groups in indoors environments. Currently, most protocols for welfare assessment rely on human observation (i.e. limited duration and potentially subjective). In this context, bio-logging technologies developed to be implemented in large or small animals have considerable potential to provide continuous monitoring of welfare status, allowing early and rapid identification of changes in behavioral and physiological components (Borchers et al., 2016; Sadoul et al., 2014; Ripperger et al., 2016). We suggest that combining these different types of parameters offers a more complete way to quantify animal welfare, which better integrates animal coping ability to changing environments both in wild and farmed conditions.

Two topical examples of breaking down the interdisciplinary barriers

Elaboration of the above points, and the commonalities that emerge, reinforces the call to more explicitly link these two disciplines for a better understanding of animals as systems, and animals within ecosystems. The importance of making such links, and the benefits arising, is illustrated by considering the following examples:

CIRCULATION AND REASSORTMENT OF POTENTIAL ZOONOTIC PATHOGENS BETWEEN WILD AND DOMESTIC POPULATIONS

Historically, animal domestication has indirectly mediated the transfer of infectious agents between wildlife and humans (Morand et al., 2014). If cases of domestic emergence are not refuted (Pearce-Duvet, 2006), almost three-quarters of emerging infectious diseases significant in terms of public health originate in wild animals (Woolhouse et al., 2005). The recent outbreak of highly pathogenic avian influenza (HPAI) H5N8 clade 2.3.4.4 in both wild and domestic birds in Europe is a major example of the “round trips” of viruses between wild and domestic populations. The ancestor of the H5N8 virus was first identified in January 2014 in domestic poultry in South Korea., then adapted to wild migrating aquatic birds and rapidly spread in 2014–2015 (Lycett et al., 2016). This virus affected poultry worldwide from fall 2016 to spring 2017. It caused a few domestic cases in northern Europe, mainly in gallinaceous populations and more rarely in domestic or wild ducks and geese population, which are commonly resistant to HPAI. A H5N8-related virus appeared in June 2016 in Touva Republic (southern Siberia) causing high mortality in waterfowl (OIE 2016).

Crossing the species barrier favors transmission and circulation of pathogens and constitutes a major advantage for multi-host pathogens (generalists). Host switches rely on genetic changes including nucleotide substitutions, acquisition of mobile genetic elements, or important genome rearrangement through recombinations and reassortments. Influenza viruses are a remarkable example of genetic material exchange between viruses issued from domestic and wild animals. H5N8 is itself a long lasting descendant of the HPAI H5N1 virus, first detected in China in 1996 and responsible for epizootics in domestic birds and some human cases since 2003 (Lycett et al., 2016). The complete sequence of the H5N8 Siberian strain isolated from wild birds in June 2016 revealed many reassortments with other poultry viruses. This virus infected northern European wild and domestic whereas other reassortants infected birds in southern Europe birds in fall 2016 to spring 2017 (Anses, 2017). The emergence of novel pathogenic strains within a region concentrating high densities of a receptive population (fat liver ducks) made possible (i) the dissemination of the virus within domestic and wild bird populations (abundant opportunities for cross-species transmission) and (ii) its reassortment with other low pathogenic strains of influenza virus circulating in the domestic and wild bird populations, thereby creating high levels of genetic diversity that can in turn broaden host-spectra.

Production of genetic variants is a mechanism predicted to favor the emergence of zoonotic strains. Fortunately, most of the time this has not led to pandemic viruses as avian influenza strains do not transfer easily from human to human due to the absence of important receptors in human bronchial tubes. Pigs are an exception to that as they are receptive to influenza viruses specific for pigs, humans and birds (Kaplan et al., 2017). As a consequence, when pigs are co-infected with viruses from different animal origins, they become gene reservoirs with the potential to facilitate reassortments and the emergence of pandemic viruses. Therefore, traditional farming systems mixing free range poultry and pigs in the same backyard close to human populations presents a risk for the emergence of new reassortants of influenza virus able to spread within human populations as pandemic viruses.

Together with emblematic examples of emerging and re-emerging vector-borne diseases in which wild and domestic animals play a key role as vectors, intermediate hosts and/or reservoirs (Boissier et al., 2016), influenza highlights the increasing globalization of health risks and the importance of the human-animal-ecosystem interface in the evolution and emergence of pathogens. It illustrates how a better knowledge of causes and consequences of certain human activities, lifestyles and behaviors in ecosystems is crucial for understanding disease dynamics and driving public policies. Therefore health security must be understood on a global scale integrating human health, animal health, plant health, ecosystems health and biodiversity. This ambition requires breaking down the interdisciplinary barriers that separate human and veterinary medicine from ecological, evolutionary and environmental science. It calls upon the development of integrative approaches linking the study of proximal factors underlying pathogen emergence and host physiological and adaptive responses to stress to their consequences on ecosystems functioning and evolution (Destoumieux-Garzón et al., 2018).

THE ROLE OF ANIMALS IN THE ELEMENTARY CYCLES IN TERRESTRIAL AND AQUATIC AGROECOSYSTEMS

Pushed by a dynamic political agenda on climate change, the roles of animals on biogeochemical cycles, the livestock sector contribution to global anthropogenic GHG emissions (14,5% of CO_2, CH_4 and N_2O emission) and mitigation options were highlighted (Gerber et al., 2013). This incited animal production research to collaborate with environment science. Initial studies were restricted to closed farm systems and animals were seen as "*a system*" emitting nutrients and gases in the atmosphere. Moreover, some effort was given to modelling nutrient emissions associated to waste management (Génermont et al., 1997), proposing some treatment options (Martinez et al., 2009) and practices (Thu et al., 2012).

However, this first era of research focussed on partial and segmented analysis of systems, neglecting more complex sets of interactions and flows between ecosystem compartments (not only exchanges with the atmosphere). Research somehow neglected the role of animals in contributing to nutrient and carbon recycling to other compartments of the ecosystem like soil or crops, i.e. considering "*animals in their systems*".

More recently there has been a marked increase of holistic and interdisciplinary research addressing biomass, nutrient and carbon recycling in soil-crop-animal systems at various scales, and their ecological, agronomic, environmental and economic impacts (Vayssières et al., 2009). Accordingly, animal science has adopted more holistic models, developing multi-dimensional impact assessment with metrics and methods derived from other disciplines including ecology, biogeochemistry, sociology and economics. Meanwhile, animal ecology and animal science have increasingly stressed the importance of considering the role of humans in their research, i.e. addressing sustainability and functioning of social ecological systems, a concept derived from new institutional economics (Ostrom, 2009).

In the terrestrial production context, research is now addressing animal effects on nutrient and carbon cycles in diverse agroecosystems. There are studies of the influence of specific management factors (e.g. ruminant grazing intensity) on nutrient recycling pathways, soil compaction and carbon stocks (de Faccio et al., 2010). In systems research on carbon balance, the use of pasture as the main source of feed was shown to be a non-negligible carbon sink under both semi-arid (e.g. Sahel) and humid environments (e.g. Amazonia) (Assouma et al., 2017; Stahl et al., 2016) addressed the importance of developing an ecosystem approach to better assess the real contribution of livestock. Enteritic methane from ruminants, emission from manure deposition, emission by termites, and savannah fire have been accounted for as well as carbon sink function of soils and perennial ligneous vegetation in an annual cycle. The carbon balance was ultimately found to be slightly negative, i.e. emissions due to livestock activities are compensated by carbon sequestration in soil and trees at landscape level. Thus, when environmental impact assessments integrate all the compartments of the agro-ecosystem (biomass, soil, plants and animals in relation to the atmosphere), and both emission and sequestration, the results contrast with partial analysis that classed African pastoral ecosystems as high GHG contributors.

In the aquatic production context, waste accounts for up to 75% of the nutrient discharge for Nitrogen and Phosphorus in conventional salmon and shrimp aquaculture. Therefore, biological and chemical filters have been developed to partially remove dissolved nutrients from waste. These various pathways of nutrient bioremediation have been increasingly embedded in diverse Integrated Multitrophic Aquaculture systems (IMTA), which are mostly adapted for land-based intensive aquaculture (fish, shrimp in ponds) (Troell et al., 2003). In such systems the addition of extractive organisms like seaweeds (macroalgae, culture of microalgae) (Milhazes-Cunha et al., 2017) or bivalves (shellfish) as biofilters to recycle wastewater, and reduce discharge and particulate and dissolved nutrient concentration was found promising (from 35 to 100% nitrogen removal). In open culture systems (fish cages) the setting up of IMTA is more complex and results are less clear. Accordingly, research is still on-going.

Such research needs continuity on the long term and design of new models (Lamprianidou et al., 2015). In particular, study of factors influencing reduction efficiency (seaweed species, capacity to uptake beyond physiological requirement, characteristics of production system and the environment, etc.) requires an interdisciplinary research approach (Troell et al., 2003). Similarly, increasing biomass recycling in terrestrial systems, or increasing carbon sequestration by soils and crops, is a long run and complex effort that argues for more global scientific collaboration.

Conclusions

This review highlights seven basic concepts that require cross-fertilization to respond to important societal challenges such as ecosystem resilience and farming sustainability. At the interface of animal ecology and animal production science, our article promotes an effective application of the agroecology concept to animals and the use of functional diversity to increase resilience in both wild and farmed systems. It also promotes the use of novel monitoring technologies to quantify animal welfare and factors affecting fitness. These measures are needed to evaluate viability risk, predict and potentially increase animal adaptability, and improve the management of wild and farmed systems, thereby responding to an increasing demand of the Society for the development of a sustainable management of systems

This ambition requires interdisciplinary research: we need a new era of translational research before application of results. Animal ecology has particular strengths in the study of interactions between species, biodiversity, adaptive evolution in natural populationsand ecosystem resilience. Animal production science has disciplinary strengths in selective breeding, production chains, economics and management. Therefore the two disciplines have many complementary skills but a stronger synergy is lacking due to old habits, i.e. perceived differences in viewpoints on the goal of each discipline, different knowledge and scientific vocabulary (e.g. in quantitative genetics), and different policy masters. Nevertheless, there are substantial advantages to be gained for animal-related research and for society's interaction with animals, from an enhanced cross-fertilization between disciplines.

Modelling approaches have the power to integrate disciplinary visions and knowledge and to translate them into actionable research. However, so far, research has not reached the level of operationality required to fully "pilot" animal systems and agroecosystems and has often socio economic factors and innovation processes, which hampers the adoption of any proposed changes. Integration of knowledge holders from the society in the process of research is also needed to tackle anticipated challenges at the interface between science, policy and society. This needs the development of knowledge integration techniques and enhanced collective expertise backed by participatory modelling and science. Such a process begins by breaking down the disciplinary boundaries. Substantial advantages will be gained for animal science, and for society's interaction with animals, from cross-fertilization between the animal ecology and animal production science disciplines. This should be accompanied by scientific vision, programs and policy tools that reverse the fragmentation of animal research across other themes, and instead create critical mass for animal science. The analogy to the emergence of One Health seems highly relevant, it is time for One Animal-Research Kinship, one ARK!!

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