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Whither mammalian ecology?

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The critical agenda for mammalian ecologists over this century is to obtain a synthetic and predictive understanding of the factors that limit the distribution and abundance of mammals on Earth. During the last 100 years, a start has been made on this agenda, but only a start. Most mammal species have been described, but there still are tropical areas of undisclosed species richness. We have been measuring changes in distribution and abundance of many common mammals during the last century, and this monitoring agenda has become more critical as climate change has accelerated and habitat destruction has increased with human population growth. There are a small number of factors that can limit the distribution and abundance of mammals: weather, predation, food supplies, disease, and social behavior. Weather limits distribution and abundance mostly in an indirect manner by affecting food supplies, disease, and predation in the short term and habitat composition and structure in the longer term. A good starting point for all studies of mammals is to define them within a well-structured trophic web, and then quantify the major linkages within that web. We still are far from having data on enough model systems to develop a complete theory and understanding of how food webs are structured and constrained as climate shifts and humans disturb habitats. We have many of the bits and pieces for some of our major ecosystems but a poor understanding of the links and the resilience of our mammalian communities to changes in trophic webs driven by climate change and human disturbances.

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Ecologists would like to develop a complete theory of ecology to closely mimic the theories of chemistry and physics, which, while not complete, are close enough to completion that a manager with enough insight ought to be able to manage problems in areas of physical science such as atmospheric chemistry or glacier and snow dynamics, and suggest solutions that are essentially applied physics and chemistry. Failures to solve problems in these physical science disciplines largely are political and social rather than scientific. The contrast with ecology could not be greater. I would guess that in my lifetime, ecologists have failed to provide the correct guidance to 30–50% of the management problems we have faced. This is not because we have poor managers, but rather because we have incomplete knowledge of how ecological systems operate and how they can be manipulated successfully. At the same time ecologists work in a moving landscape of global change so that the answers of yesterday need not be the answers of today or tomorrow. The present state of poor management of ecosystems calls for stronger ecological theory and understanding of the processes causing change. Better management can be achieved by ecologists recognizing that we have inadequate knowledge of community and ecosystem dynamics. My purpose here is to try to dissect why we have inadequate knowledge of mammalian populations, communities, and ecosystems, and what we can do about it in this century.

We gain knowledge in ecology by making careful observations, developing clear hypotheses, and doing experiments, and this has been demonstrated for more than 60 years (Popper 1963; Platt 1964). But the experimental approach is possible only if it is founded on a solid basis of natural history data. While descriptions and identifications of mammalian species are becoming more complete, thanks to the advances in taxonomy that have arisen from DNA technology (Cook and Light 2019), we lack basic ecological information on many—if not most—of these species. Given good taxonomic descriptions, we have spent much effort in the last century on understanding the natural history and ecology of many mammals in communities from the poles to the tropics. Ideally, we have imagined defining the niche of all our mammal species, their distribution and abundance, and then analyzing the mechanisms that limit both these seemingly simple descriptors. In the 1950s, we believed in a much simpler ecological world than we do today.

We imagined a balance of nature, an equilibrium of both distributions and abundances, and our job was to map these distributions and define the expected abundances of all the species that by then we had described. This world view was based on a static perspective of nature, the balance of nature. But this oversimplified view of the ecological world began to shatter by the 1960s and 1970s, when we recognized that the ecological world is not static but in constant change. Paleoecological studies have shown us the way the Earth has changed through glacial cycles and megafauna extinctions, and more recently ecologists have investigated changes wrought by human influences on landscapes and the resulting changes in climate, species interactions, and habitat loss.

The agenda of mammalian ecologists shifted slowly to a new paradigm that required more understanding of ecological processes, based on four general steps:

1. *A focus on individual species*: Defining the limiting factors on their distributions in mechanistic terms, with a foundation in both animal physiology and behavior, and their interactions with other species.
2. *A focus on population change*: Monitoring changes in abundance in detail over several generations to determine population stability, and if a change has occurred, why?
3. *A focus on the communities within which each species functions*: Determining the food web and the species interactions that structure the trophic dynamics of the community.
4. *A focus on community change*: Continually updating changes by focusing on the processes causing plant communities to change as the climate shifts and human domination of the Earth increases.

This new paradigm applies to ecologists in four major subgroups—biogeographers and biodiversity specialists, population ecologists, community and ecosystem ecologists, and conservation biologists. My research has been involved with population and community ecology; as such, this review will touch mainly on the second and third of these groups. I appreciate that much of the research on mammals now involves conservation biology, which I will not review, and my belief is that we cannot do conservation well without a good ecological understanding of population and community dynamics. There is a problem with this separation into four major groupings because what we need is integration in the science of ecology, a Solomon for all four groups. But we are not there yet, hence this overview should be viewed as a milepost along a continuing road to increasing ecological understanding of the Earth in all these subdisciplines of ecology.

I will discuss in turn each of the four steps—distribution, abundance, food webs, and global change—to evaluate where we are now and suggest some directions needed for future research.

What Limits Mammalian Distributions?

During much of the last century mammalian distributions were assumed to be static; once you had a map of good collections you had the geographic distribution in final form. Then interest shifted to local distributions among habitats and more research was required. But the largest change in this research question occurred when climate change erupted on the scene and ecologists realized we humans were doing a very large-scale experiment with the Earth, admittedly with $n = 1$. And the simple paradigm that all geographical distributions are limited by temperature and rainfall was temporarily revived (Shelford 1932, 1945; Whittaker 1975; Parmesan and Yohe 2003; Parmesan et al. 2013).

While climate change was coming to the fore, the importance of spatial scale and landscape ecology were being recognized. Although species distributions at the global scale might simply map to temperature or rainfall, on a local scale distributions were much more complicated, species, and habitat-specific (Wogan 2016; Morán-Ordóñez et al. 2017). Species distribution modeling has become popular and while it shed some light on the past, it provides a very narrow window of the past, and it is not yet clear that it is a very good predictive model for the future (Hewett 1999).

Two major problems limit progress in distributional ecology. First, most species are rare, and it is these species whose distribution at all spatial scales is poorly known and most difficult to quantify because of small sample sizes. Yet some of these rare species are the very species that conservation biologists most are concerned about. Other rare species are not endangered but are rare and thus difficult to study with short-term projects. Second, sampling techniques can be biased in ways that confound occupancy estimates (e.g., Soininen et al. 2015). One example from our 47 years of Yukon boreal forest studies will illustrate the problem. From extensive live- and snap-trap sampling, we have found there are 10 species of small rodents in the Kluane National Park region (Krebs and Wingate 1976). We have maintained 3–12 livetrapping grids since 1973 in this boreal forest area. We catch two dominant species and four other less common species (Boonstra et al. 2018), and virtually never have caught four of the other species in live traps. We have seen one species in camera footage once in 5 years of camera trapping. Thus, by any measure four rodent species are rare and we have no simple way of determining if they have gone extinct or are endangered in this region of boreal forest that is virtually undisturbed except by climate change. The rareness of these particular species may be the result of the slow processes of colonization—from the north and south, because we are still in the postglacial time window of expansion in northern Canada. For many mammals, the distribution model might be simplified as “build it (the vegetation) and they will come”—i.e., dispersal is not the issue, but rather vegetation is. The critical point here is that understanding the ecology of rare mammals is a major gap in our science. A good example of the difficulty of resampling older surveys for both rare and common mammals is described by Moritz et al. (2008) for Yosemite National Park in California.

Comparisons of changes in geographical distributions are relatively simple for easily observable large mammals, but difficult for many of the smaller species. The solution to this problem is to improve monitoring programs both in frequency and in sampling methods. New methods such as camera trapping can provide data that were previously impossible to obtain, but again there can be problems of sampling (Neilson et al. 2018; Abolaffio et al. 2019). The advent of eDNA techniques can also open new opportunities for sampling rare fauna. The major problem in my opinion is the short-term nature of many studies of distributional change and the lack of clear mechanistic hypotheses so that the explanatory variables are correlations with all the problems that "correlation ecology" contains (McKelvey et al. 2011; Keith et al. 2015).

The current approach to studying distributions is to use species distribution models, and the literature on these is growing rapidly (Briscoe et al. 2019). This approach in my opinion leads to the identification of many correlation-based models for explaining the limiting factors for species geographical ranges, and thus their future ranges under expected climatic change, but virtually all these model projections are untestable in anything like real time. Surrogate correlations may provide some insight into range shifts, but the most serious issue with distributional ecology is how to test the models that best fit current range limits. Recent reviews have suggested methods to amalgamate mechanistic models involving physiological and ecological data into predictions of how species ranges might shift under climate change (Johnston et al. 2019; Peterson et al. 2019). The problem with all predictive distribution models is the reliability of the current climate models to predict future climatic conditions at the local level, and the problematic assumption that correlation indicates causation. Caution is best advised (Journé et al. 2020).

What Limits Mammalian Abundances?

We have had major success in studying changes in population size of individual mammal species, particularly the charismatic megafauna and the graduate-thesis-convenient smaller mammals (Hayes et al. 2017; Bradley and Dowler 2019). There now are a series of classic books particularly on large mammals that illustrate well the findings of what controls populations of the larger mammals (e.g., Schaller 1972; Sinclair 1977; and many more) as well as excellent reviews (e.g., Gaillard et al. 1998). Following Wolff (1997), I tried to put together a sketchy overview of the factors limiting populations of large and small mammals (Krebs 2009). The potential importance of weather, predation, food supplies, disease, and social behavior, in limiting mammal populations now is well recognized, and while we can state that we have a general theory of what limits mammalian abundance, we are far from having the details well understood for very many species. Of all the demographic components, immigration and emigration for too long have been dismissed as unimportant components of dynamics in spite of the early work of Lidicker (1962, 2015; review in Millon et al. 2019). This contrasts to the important role assigned to immigration and emigration in conservation ecology and biogeography.

The example of food supplies as a cause of population limitation is a good example. While we have a general idea of the diet of many of the mammals of the world, specifics are weak because the database is constrained and often consists of samples collected only one season of the year in small numbers. One classic example is the assumed diet of the Norwegian lemming (*Lemmus lemmus*), completely revolutionized by DNA-based research (Soininen et al. 2017). There is a great deal of basic descriptive ecology that needs to be done to describe adequately the diet of most mammalian herbivores. Similar points may be made about carnivore diets. Some are clearly well defined, others are based on restricted seasonal data in limited landscapes, and the role of carrion in carnivore diets needs further research (Sivy et al. 2018; Barton et al. 2019; Peers et al. 2020). Precise diet data for taxa are necessary for reconstructing trophic dynamic models of communities and ecosystems.

Predator–prey theory was among the earliest theories in ecology and again, while we should celebrate our progress in understanding the roles of predators in affecting prey, there still is much to learn. There is much discussion of the role of apex and mesopredators in mammalian communities (Forsyth et al. 2018; Sivy et al. 2018). Our understanding of the effects of apex predators has largely resulted inadvertently from human interference in food webs, for example, from wolf culls and reintroductions (Boyce 2018), and our improving understanding of apex predator effects has important consequences for conservation. Recent work on the indirect effects of predators on prey reproduction is another example of discoveries that have enriched predator–prey theory (Abrams and Cortez 2015; MacLeod et al. 2018; Boudreau et al. 2019).

Social interactions involving spacing behavior have been one possible component of population changes in mammals, and recent work on small mammals has illustrated how social behavior can affect both reproduction and mortality rates in mammals (Sheriff et al. 2017; Edwards et al. 2019). Stress generated from a variety of ecological causes can impact brain function and in company with hormonal effects generate demographic effects in mammals (Boonstra 2013; Weidt et al. 2018; Lavergne et al. 2019). While much information is available on the individual physiological and behavioral effects of social interactions, tying these clearly to population- and community-level effects is incomplete (Sheriff et al. 2020). The interaction between social behavior and mortality agents such as predators and diseases in mammal populations needs much more study.

I will not detail further the answers we already have to the question of what limits abundance in mammalian populations. Among all the ecological subdisciplines in mammalogy, it is among the most solid. Yet there is much to be discovered, particularly for tropical mammals, marine mammals, and bats.

What Structures Food Webs and Limits Trophic Dynamics?

Despite the great theoretical and practical interest in who eats whom in mammalian communities, there has been surprisingly little cohesive understanding of the functioning of mammalian food webs. Paine (1980) reviewed the historical development of trophic ecology and explored how intertidal food webs could be disarticulated into functional units. Food webs dominated by mammals have typically focused only on the strong interactors in an ecosystem and have ignored the minor species. The literature on food webs is rich when it deals with single species or small groups of mammalian species, often apex predators and large mammals (e.g., Sinclair and Arcese 1995; Lee et al. 2016; and many other examples). But it fails when we reach the level of the rare species, typically those species of conservation concern. Rare or cryptic species are typically ignored in food web research because they have little impact on the energetics of the system, but this is an assumption that perhaps needs reevaluation for mammals.

While I cannot review the extensive literature on mammalian food webs here, I make the following general points:

1. There is a focus in much food web research on the stability properties of the species interactions that comprise the web. Long-term studies again are in short supply, and stability may be misconstrued with short-term observations.
2. There is simultaneously too much anthropogenic manipulation of mammal communities with no adequate controls for understanding the interactions. Adaptive management often is flagged but too rarely followed (Geary et al. 2020; Richardson et al. 2020). This is seen most clearly in aquatic mammals and their role in fisheries collapse (e.g., Kiszka et al. 2015; Neuenhoff et al. 2019). The result is considerable argument about trophic cascade generalizations (Wade et al. 2007; Peterson et al. 2014; Allen et al. 2017).
3. Given climate change and human alterations of habitat, it may not be possible to build predictive models of how food web organization will change so that management can be proactive. Trophic dynamics may be more opportunistic than predictable.
4. If it is correct that the climate niche of species provides little predictability about the abundance of a species, as was argued by Dallas and Hastings (2018), the emphasis on niche metrics may not lead into more understanding of trophic dynamics.

None of these reservations should reduce our investigations into trophic dynamics and food webs but should focus our efforts on local communities with predictable patterns and clear hypotheses that can lead us toward a global theory of food web dynamics. Rather than dichotomizing food webs simply as top-down or bottom-up, Humphries et al. (2017) have suggested to change our focus to recognize alternative configuration of seasonal food webs in which the same species may change from specialists in the food web to generalists depending on season, and may migrate to new habitats. A combination of better data and a more seasonal focus may help us to further our understanding of trophic dynamics in mammalian communities.

CAN WE PREDICT HOW GLOBAL CHANGE WILL ALTER MAMMALIAN COMMUNITIES?

There is much interest now in trying to decipher how the mammalian communities of the world will look in a century or two. Given that the two main forces for change are climatic alterations and habitat destruction, predicting the confounded possible changes would seem unlikely and risky. The current overview seems to be that species have restrictive climatic tolerances that can be changed slightly—but not dramatically—at the margins. Consequently, rapid evolution will not save our charismatic communities. If we then have a rigorous and predictive model of how temperature and rainfall will change, we should be able to model what to expect, at least for land-based mammals. This will depend on how global change impacts plant communities, so we have two steps of complexity: climate → plant communities → mammal communities. These steps alone are complex and ignore the additional complexity of insects and other vertebrates (e.g., Jepsen et al. 2013), as well as the diseases that impact on all these organisms. At least at the present time, this complexity should mean that any extrapolations to future states should be viewed as suggested, but untested, hypotheses and are best constrained to short-term predictions. For many herbivores, it is not the “community” that is the relevant metric, but specific food species that are only a small part of the community. An example would be the crucial role of bilberry (*Vaccinium myrtillus*) in the boreal forest community in Scotland, Norway, Finland, and Sweden, to small mammal and capercaillie (*Tetrao urogallus*) dynamics (Boonstra et al. 2016).

One alternative strategy we should consider is to design a global monitoring system that will give us data on representative model ecosystems for changes in mammal distributions and abundances as climate shifts. We are partly on our way to this goal. The two large problems facing mammalogists around the world are to select the nominated ecosystems for intensive monitoring, and to standardize the monitoring data coming in from different studies that might use different monitoring methods. We cannot monitor all ecosystems on Earth, and in the short term we will have to select the major ecosystems that we can study. We do not have gold standard monitoring methods for all mammal species. Estimates of changes in the global abundance of birds, which are much more intensively studied than mammals, have serious methodological problems in how to estimate global abundance changes (Rosenberg et al. 2019; Sugai et al. 2020). The literature on estimating abundance of mammals is highly taxon-specific, and the resulting biases are rarely known. Continued improvement in monitoring methods is highly desirable, but for the first steps we can design consistent methods only for local populations in long-term studies (Ims and Yoccoz 2017).

For the present, only single-species or small-group studies will be able to achieve the level of precision required such that we can estimate accurately the changes in mammal populations at a landscape level. Major success can be achieved for large mammals via aerial surveys. As the mammals of interest decrease in size, the study area shrinks in size even more rapidly. The use of camera technology may offer one approach that can expand the scale of survey. Camera traps can estimate occupancy readily and, in some cases, occupancy can be translated into population density (Steenweg et al. 2016; Villette et al.

2017; Nakashima et al. 2018). Much more detailed evaluation needs to be done on this technology, but it holds promise for expanding the spatial scale of mammalian census and providing abundance data for many species in the community. In particular, conservation biology demands data on rare species that in general raise the level of difficulty in census work by another order of magnitude (Dee et al. 2019).

A corollary of the climatic control of ecosystem changes is that population, community, and ecosystem studies must have a long time frame (Hughes et al. 2017). To achieve this goal in the present funding model, we must design studies that can be a concatenated sequence of short-term experiments with continuing unmanipulated controls. These major studies must have a life span that is longer than the career of single research scientists. We have made a start in designing some of these kinds of research programs, particularly for specific populations of charismatic species, but few programs look at changes in community or ecosystem dynamics for time periods of more than 30 years.

Conclusions

I distill my brief review with a synopsis of my opinions and recommendations about the future of mammalian ecological research.

1. The devil is in the details. Strive for generality but distrust it.
2. Study mammals within the context of their evolutionary history and of long-term changes that have occurred since the Mid- to Late Miocene.
3. Investigate mammals within the context of the present-day plant and animal communities and how landscapes are changing with climate change and human disruptions.
4. Design specific hypotheses for your particular question or problem and make risky predictions. Vague statements do not advance understanding.
5. Never stop worrying about methods, their reliability, their precision, and the limits of inference from your experiments.
6. Climate change and human alterations of the environment may change much of the wisdom provided from earlier studies. Admire your predecessors but do not venerate their ecological conclusions.
7. Collaborate with experts in all disciplines that impinge on the study of mammals: plant ecologists, insect ecologists, animal physiologists, evolutionary biologists, epidemiologists, mathematicians, and geographers.
8. Ecology is a contingent science under the broad control of climate and evolutionary change. It is an essential science if we are to achieve conservation successes. There is much left to do.

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