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Ecophysiology of mammals

Thomas Tomasi,* Briana Anderson, and Theodore Garland, Jr.

Department of Biology, Missouri State University, Springfield, MO 65897, USA (TT, BA)
Department of Evolution, Ecology, and Organismal Biology, University of California – Riverside, Riverside, CA 92521, USA (TG)

Correspondent: tomtomasi@missouristate.edu

Ecophysiology is a relatively recent interdisciplinary field, and although active prior to the 75th anniversary of the American Society of Mammalogists (ASM), it has grown in breadth since then. This growth is in part a result of advances in technology that have reduced the size and improved the portability of key instrumentation, and also made sequencing of proteins and nucleic acids faster and less expensive. Here, we demonstrate the breadth of recent research on the ecophysiology of mammals, quantify the research activity of the past 25 years, and consider future research needs. Some of the most active areas of research have related to maintenance of homeostasis, associations of physiological traits with the evolution of varied life styles and life histories, and reproductive physiology. Key findings involve allometry and scaling, energetics and thermoregulation, phenotypic plasticity and epigenetics, and the importance of microbial symbionts. With respect to predictions of trends in mammalian ecophysiology, the strongest

themes relate to conservation biology, in large part related to rapid climate change, habitat destruction, and other anthropogenic factors. How our mammalian fauna adapts (or not) to these changes will be of great interest, and has the potential to affect the science of mammalogy in the future.

La ecofisiología es un campo interdisciplinario relativamente reciente, y a pesar de que era un área vigorosa antes del septuagésimo quinto aniversario de la Sociedad Americana de Mastozoología (ASM), desde entonces ha crecido en envergadura. Este crecimiento es en parte el resultado de los avances tecnológicos en donde el tamaño de los instrumentos se ha reducido facilitando de ese modo la portabilidad de instrumentos claves, y al mismo tiempo, permitiendo que la secuenciación de proteínas y ácidos nucleicos sea más rápida y menos costosa. En este trabajo, se demuestra el alcance de la investigación reciente sobre la ecofisiología de los mamíferos, se cuantifica la actividad científica de las investigaciones de las últimas dos décadas y se hacen predicciones para los próximos 25 años. Algunas de las áreas más activas de investigación se han asociado con el mantenimiento de la homeostasis, la relación entre los rasgos fisiológicos con la evolución de diferentes estilos e historias de vida, y la fisiología reproductiva. Los hallazgos clave incluyen la alometría y la escala, la energética y la termorregulación, la plasticidad fenotípica y la epigenética, y la importancia de los simbiontes microbianos. Con respecto a las predicciones sobre las tendencias de la ecofisiología de mamíferos, los temas más comunes están relacionados con la biología de la conservación, en su mayor parte a consecuencia del rápido cambio climático, la destrucción del hábitat y otros factores antropogénicos. La forma en que nuestra fauna de mamíferos se adapta (o no) a estos

cambios, a nivel fisiológico y de otro tipo, será de gran interés en el futuro, teniendo el potencial de influir a la ciencia de la mastozoología.

Key words: allometry, climate change, ecophysiology, energetics, evolution, homeostasis, microbiome, phenotypic plasticity, physiology, reproduction

SCOPE, PROCEDURES, AND LIMITATIONS

Following the model provided by (Wunder and Florant 1994) in *Seventy –five Years of Mammalogy* (Birney and Choate, eds.), we focus on the sub-discipline of physiology known as ecophysiology or physiological ecology. We focus primarily on basic physiological research that is relevant to mammals living under natural conditions, including studies that take place in a laboratory or in captivity under simulated natural conditions. Physiology is a major component of adaptation, and although physiology is a distinct discipline, it is inseparable from the related fields of biochemistry, anatomy, behavior, population biology, community ecology, biogeography, and evolution (for a specific example of physiological adaptation, see Storz et al. 2019).

Aspects of ecophysiology that are relevant to mammalogy include: 1) physiological acclimation and acclimatization (flexibility to adjust to environmental variation during the life of an individual), 2) epigenetic modifications that produce acclimation across generations without changing gene structure, and 3) evolutionary adaptations to ecological conditions (genetically based changes across generations). The emphasis on ecological benefits of physiological adaptations distinguishes this field from traditional comparative physiology (Karasov and Douglas 2013; Carey 2015). With over 6,500 currently recognized mammalian species living in diverse habitats across the planet (Burgin et al. 2018), it seems self-evident that mammals function physiologically in diverse ways. Much of this article is devoted to the ecological and comparative aspects of physiology that help mammalogists understand wild species of mammals.

Although we have not attempted an exhaustive review of recent literature, we include references that are representative of what is known about the ecophysiology of wild mammals. For book-length treatments, readers are referred elsewhere (Karasov and Martinez Del Rio 2007; McNab 2012; Withers et al. 2016; Hayssen and Orr 2017). We highlight the breadth and depth of research activity in the last 25 years, while admitting some bias in sub-disciplines. It should also be noted that historical biases exist relative to which mammal species and what aspects of their lives have been studied. Taxa in some regions of the world have been studied more intensively than those in other regions. Historically, the categories of mammal species that have received more attention include large charismatic mammals, species living in areas where collecting permits were not required or were easy to obtain, and species living closer to research centers as opposed to those in remote locations. Low-tech methods dominated until technology could be developed and miniaturized for use on smaller mammals and in remote locations. These technological advancements in ability to measure physiological traits have enabled mammalian physiologists to address questions that could only be envisioned by their predecessors. Since Wunder and Florant (1994) and contemporaries (McNab 1992; Hayes and Kenkins 1997) reviewed the state of ecophysiology, advances have occurred by using old techniques to address previously unasked questions (often using a comparative approach applied to species not previously studied) and by developing new methods to help answer these questions.

We surveyed the recent literature on mammalian ecophysiology, using Ebsco Host (Academic Search Complete), limited to peer-reviewed publications between January 1992 and January 2018. We also sought input from colleagues around the world to identify key questions, critical methods, and major findings since 1990. Finally, we projected these recent trends into the future in an attempt to identify the most critical questions and the techniques needed to be developed or perfected to address them (the next generation of mammalogists will undoubtedly comment on how well we did). We also tracked publication and presentation trends related to mammalian ecophysiology over the past 25 years in what we consider to be key periodicals and conference proceedings. These are compared to trends identified by Wunder and Florant (1994) for the preceding 75 years.

The following summary of ecophysiological research over the last quarter century is organized in three themes. To function under a wide variety of conditions, both abiotic and biotic, mammals must maintain relatively constant internal conditions (homeostasis). Multicellular animals do this to provide their cells with the appropriate intercellular environment to maintain cellular function, with each cell contributing to the success of the whole animal. Hence, homeostasis is the first and largest theme. However, many physiological traits are related to ways in which mammals interact with their environments to delineate their ecological niche; this second theme is designated “life styles.” For both of these themes, success is generally measured in terms of short-term survival of the individual animal. In contrast, for reproductive function, success is defined as the contribution of offspring to the next generation, which can be detrimental to individual survival but is necessary for Darwinian fitness. Hence, reproduction constitutes our third theme.

HOMEOSTASIS

Maintaining homeostasis requires balancing gains and losses. One pervasive component of animal survival is an energy budget: how (and how much) energy is acquired, and how energy is used at different stages of its life. This continues to be an active area of research across taxa representing three orders of mammals (e.g., western black-and-white colobus [*Colobus polykomos*]—Dasilva 1992; polar bear [*Ursus maritimus*]—Molnár et al, 2009; insectivorous bats [*Myotis nattereri, M. bechsteinii, Plecotus auritus*]—Becker et al. 2013). Other approaches to energy balance are exemplified by studies on the neural regulation of energy balance (Donovan and Tecott 2013), and comparisons of mammals and birds (Weiner 1992).

Recent studies related to energy intake include milk energy and its conversion to growth of young (Riek 2007), maximizing energy intake (Van Wieren 1996), and social hierarchy effects on food intake (Gende and Quinn 2004). The challenges of specializing on an herbivorous diet include maximum body size and adaptations for dealing with secondary plant compounds (Clauss et al. 2003; Sorensen et al. 2005). Similarly, there are adaptations for specialized carnivorous diets in marine systems; for example, different prey preferences for resident versus transient killer whales (*Orcinus orca*—Ford et al. 1998) and greater individual variation in the diet of sea otters (*Enhydra lutris*) in habitats with rocky substrates (Newsome et al. 2009). Related to energy intake are physiological adaptations for securing sufficient food, which are discussed below (Life Style). The capacity to process food in the digestive tract isn't fixed, but changes with the energy needs of the animal; for example, during winter or during reproduction when caloric requirements are elevated. This was first demonstrated by Voltura and Wunder (1998) and is still being studied (Ji-Ying et al. 2016). The role of the gut microbiome is just starting to be understood in this regard.

The other side of energy balance is expenditure, a topic that has recently been studied in more taxa living in a greater array of environmental conditions (e. g., White and Seymour 2004). As expected in this period of drastic climate change, the coadaptation of basal metabolic rates (BMR— Lovegrove 2003; Rezende et al. 2004), and of thermoregulatory patterns more generally (Levesque et al. 2016) with climate, has been of particular interest. To fully understand the effects of climate change on a species, we also need to know about any specialized or unique mechanisms and abilities that a species has to thermoregulate (Mitchell et al. 2002; Mauck et al. 2003; Briscoe et al. 2014; Rezende and Bacigalupe 2015).

Many mammals have food resources that vary in availability in space and time, or regularly encounter periods of insufficient food to balance their energy budget. As a consequence, they sometimes suspend homeothermy (becoming heterothermic) and enter torpor to reduce energy expenditure on a daily or seasonal basis (Geiser et al. 2005; Ruf and Geiser 2015; Evans et al. 2016; Levesque et al. 2017; Turner and Geiser 2017). The use of torpor is more widespread than previously known, with recent examples including house mice (*Mus musculus*—Swoap et al. 2012) and lemurs (*Cheirogaleus medius, Galago moholi, Microcebus griseorufus*—Dausmann et al. 2012). Much of this work has been described at a series of conferences of the International Hibernation Society (Geiser and Ruf 1995; Geiser 2004; Stawski et al. 2015; also see symposium volumes of the International Hibernation Society and an edited book by Frank 2019). The effect of climate change on mammalian hibernation is starting to be addressed (Humphries et al. 2002; Nemeth 2012). Other factors (e. g. precipitation, reproductive status, precipitation, etc.) also influence the use of torpor (Adams 2010; Rintoul and Brigham 2014). The control of hibernation and daily torpor is one area of ongoing interest, particularly related to neural regulation and brain function (Schwartz et al. 2013; Scherbarth et al. 2015;

Jansen et al. 2016), bone loss due to inactivity (Doherty et al. 2014; Ma et al. 2015; Wojda et al. 2016), fat storage and use (Frank and Storey 1995; Contreras et al. 2014), maintaining cellular functions (Zhang et al. 2014b; Yuan et al. 2015), and the microbiome (Carey and Assadi-Porter 2017). Not all mammals adjust their torpor use the same way in response to environmental perturbation; Doty et al. (2016) recently reported that daily torpor use after a wildfire decreased in lesser long-eared bats (*Nyctophilus geoffroyi*), in contrast to increased torpor use reported for terrestrial small mammals.

In conjunction with metabolic rates, the act of supplying oxygen and removing carbon dioxide requires appropriately sized and regulated respiratory and cardiovascular systems (Powell and Hopkins 2004; Hillman et al. 2013). Although gas exchange has not been as extensively studied, a comparative approach includes research on intraspecific and interspecific elevational differences (Ivy and Scott 2015; Storz 2016; Storz et al. 2019), diving physiology (Hooker et al. 2009; Gerlinsky et al. 2014), hemoglobin and myoglobin characteristics (Janecka et al. 2015; Wright and Davis 2015), and fetal gas exchange (Mess and Ferner 2010).

Also related to metabolic rate (and homeostasis in general) is water balance, the acquisition or production of water and rates of water loss. Water is produced during aerobic metabolism in mitochondria and is lost in the processes of respiration and evaporative cooling. Additional components of water balance include cutaneous water loss, renal function (Beuchat 1996; Al-kahtani et al. 2004), and the neural regulation of water intake. Both desert and marine mammals continuously face dehydration as the water gradient pulls water out of their bodies. Recent research on water balance has been conducted mostly on tropical bats (*Glossophaga soricina*—Hartman Bakken et al. 2008; *Epomophorus wahlbergi*—Minnaar et al. 2014), South American desert rodents (sigmodontine species—Bozinovic et al. 2007), desert ungulates (*Ovis* *canadensis nelson*—Gedir et al. 2016), and pinnipeds (*Mirounga angustirostris*—Lester and Costa 2006). Water loss in hibernating mammals (Thomas and Geiser 1997; Ben-Hamo et al. 2013) has also been of recent interest, particularly in regard to periodic arousal

Some mammals undergo marked seasonal changes (Tighe et al. 2016), usually mediated by changes in photoperiod and physiologically regulated via melatonin. Research in the 1970s and 1980s identified the importance of melatonin and the pineal gland in photoperiod-related phenomena (Arendt 1994; Gorman et al. 2001), and this work has been extended by recent research only possible with the advent of laboratory tools such as rapid sequencing of biopolymers (amino acids and nucleic acids). For example, our understanding of the role of photoperiod on annual cycles of reproduction (Ninomiya-Alarcón et al 2004; Hoole et al. 2016), feeding and body mass (Helwig et al. 2009; Wan-Long et al. 2013), immune function (Prendergast et al. 2004; Xu and Hu 2017), and thermoregulation (Zhang et al. 2014a) have been enhanced by these methods. Another area in which research on seasonal changes has been conducted, though more limited in scope, is migration (often an alternative to hibernation), as demonstrated by bats (McGuire et al. 2014). Although most recent research has focused on annual cycles, work also continues on the control of daily cycles, for example in rodents (*Cryptomys damarensis*—Richter et al. 2003; *Psammomys obesus*—Neuman et al. 2005; *Microtus arvalis*—van der Veen et al. 2006) and primates (*Lemur catta*—Donati et al. 2013).

LIFE STYLES

In addition to maintaining homeostasis, suites of behavioral and physiological adaptations have evolved or coadapted with other traits (e.g., behavioral) in ways that enhance survival and reproductive ability in a variety of niches (Brashares et al. 2000; Storz et al. 2019). The existence of different niches allows organisms to diversify with reduced competition, and specialization is required to best fit particular niches. Although physiology is often hard to separate from associated anatomy, biochemistry and genetics, many physiological adaptations that help mammals fit into their niches have been identified (e.g., enhanced renal function in species from arid habitats—Beuchat 1996; Al-kahtani et al. 2004). In turn, these adaptations affect the ecology of the species (see Storz et al. 2019). In this section, we organize these adaptations by life style. For example, mode of locomotion and diet specializations strongly influences niche definition, and these may overlap (Verde Arregoitia et al. 2017).

Life style is closely associated with locomotion (Schaeffer and Lindstedt 2013; Bertram 2016), and recent research on the physiology of locomotion includes: 1) maximal aerobic capacity and performance ability (Djawdan 1993); 2) energetics (Chappell et al. 2004; Garland and Albuquerque 2017; Halsey and White 2017); 3) biomechanics (Michilsens et al. 2009; Wilson et al. 2018); 4) ecomorphology (Spoor et al. 2007; Panciroli et al. 2017); 5) interactions with reproduction (Noren et al. 2012; Andrew et al. 2016); and 6) the evolution of the "runner's high" (Raichlen et al. 2012).

Aquatic mammals have special adaptations of the respiratory and cardiovascular systems that are associated with diving (Mottishaw et al. 1999; Bostrom et al. 2008; Mortola 2015), and that confer increased hypoxia tolerance (Sergina et al. 2015; Hoff et al. 2017) and oxygen storage (Nery et al. 2013). Interest in conservation of marine mammals, in regard to anthropogenic stress, has also generated studies of their stress physiology (Wright et al. 2007; Atkinson et al. 2015), and the effect of climate change on marine mammals (Thiemann et al. 2008).

Fossorial mammals can also face hypoxic (and hypercapnic) conditions and muted temperature fluctuations, allowing comparative studies of their physiological adaptations to these conditions. Subterranean coruros (*Spalacopus cyanus*) increase ventilation when exposed to hypoxia, while fossorial degus (*Octodon degus*) do so in response to hypercapnia (Tomasco et al. 2010). Much fossorial mammal research is on mole-rats, which have seasonal cycles in activity and reproduction, apparently related more to rainfall than to temperature (*Heliophobius argenteocinereus*— Zelová et al. 2011; Ngalameno et al. 2017), and extremely long life-spans (*Heterocephalus glaber*—Kim et al. 2011).

Aerial species of mammals also require special adaptations. Mammals that glide have been studied in relation to energy requirements (Flaherty et al. 2010; Byrnes et al. 2011). Chiropteran flight has been described from the perspective of biomechanics and kinematics (*Cynopterus brachyotis*—Iriarte-Diaz et al. 2012), in regard to the function of their small digestive systems (less weight to carry; *Artibeus lituratus*—Caviedes-Vidal et al. 2007, 2008), and the need for a prolonged lactation period (*Eptesicus fuscus*—Hood et al. 2011). An important component of bats' nocturnal flight, echolocation, may have evolved from fossorial mammals (Panyutina et al. 2017).

Herbivorous mammals often encounter toxins in their diet (especially in tree leaves) that need to be detoxified or that decrease the energy they can obtain from their food. Wunder and Florant (1994) correctly predicted that we would see more research on how herbivores use their plant resources. Studies since then address adaptations to use these plants despite the toxins and their associated energetic limitations (Min et al. 2005; Pauli et al. 2016); other studies consider detoxification, such as research on woodrats (*Neotoma stephensi*, *N. albigula*—Sorensen et al. 2004) and rabbits (*Sylvilagus nuttallii, Brachylagus idahoensis*—Crowell et al. 2018).

Carnivorous mammals obviously have anatomical and behavioral traits that make them successful, but they also possess physiological adaptations associated with this life style. These include sensory adaptations that aid in finding prey (see below), the use of venom (Kowalski and Rychlik 2018), and the ability to digest specific dietary components (chitin, wax, etc.). Several studies have used captive carnivores to address the issue of diet breakdown (*E. lutris*, *Leptonychotes weddellii*—Williams and Yeates 2004; *Mustela vison*—Mayntz et al. 2009; *Myrmecophaga tridactyla*—Gull et al. 2015) or to develop and compare methods of diet analysis (*E. lutris*—Tyrrell et al. 2013). Although prey species of mammals have evolved anti-predator strategies, we didn't identify any recent research on physiological defense mechanisms.

Similar to predator-prey relationships, mammals are involved in host-parasite relationships (always as the host), and research continues on the associated physiological costs of parasitism (Schwanz 2006; Olifiers et al. 2015; Simpson et al. 2016), and how this might change throughout the year (Kristan and Hammond 2003; Cizauskas et al. 2015). Some work on immune function, mostly in regard to parasites, has also been conducted recently, including models of immune function (Garnier et al. 2013; Jolles et al. 2015), host-parasite interactions (Lopez-Romero et al. 2015; Zhang et al. 2017), and how social factors affect immune function (Flies et al. 2016).

Beneficial interspecific relationships (from the mammals' perspective) also continue to be studied, including symbiotic relationships between vertebrate classes (Zdunkiak et al. 2017), between small mammals and pitcher plants (Greenwood et al. 2011), and among three-toed sloths (*Bradypus* spp.), moths, and algae (Pauli et al. 2014). The ecological interactions in these examples involve food acquisition or ectoparasite reduction, and so could be considered more behavioral than physiological, but are included here because we use a broad definition of ecophysiology, and most behaviors include physiological components. A special type of symbiotic relationship involves gut microbes (Leser and Mølbak 2009; Amato et al. 2014). This research includes comparative microbiome studies, using high-throughput sequencing platforms to identify the thousands of microorganism taxa that occupy the gut, as exemplified by Carey et al. (2013) and Kohl and Carey 2016).

To be successful in their various life styles, mammals must be able to sense the world around them and communicate with others. Therefore, sensory physiology remains of interest, and recent research in this subdiscipline covers vision (Williams et al. 2005; Pessoa et al. 2014) and hearing (Mariappan et al. 2013; Wahlberg et al. 2017). For example, Charlton et al. (2017) expanded our understanding of koala (*Phascolarctos cinereus*) vocalizations. In addition, research on tactile abilities (Pacheco-Cobos et al. 2003; Gaspard et al. 2017), electroreception (Ashwell and Hardman 2012; Czech-Damal et al. 2013), and echolocation (Gonzalez-Terrazas et al. 2016; Luís et al. 2016) are also producing new insights.

Olfactory studies were not present in our subset of published articles, suggesting this has not been an area of active research in the last 25 years. However, the use of pheromones, which share some characteristics with olfaction, is an important aspect of mammalian chemical ecology (a relatively new sub-discipline), and this has continued to be an area of active research, especially in primates (Evans 2006; *Mandrillus sphinx*—Charpentier et al. 2013). Mammals use pheromones for scent marking (Blank et al. 2014), influencing the reproductive status of the opposite sex (Anand et al. 2002; Lazar et al. 2004; de Catanzaro et al. 2014), and male-male competition (Bian et al. 2013; Rendon et al. 2016).

REPRODUCTION

As indicated above, most sub-disciplines of physiology focus on the short-term survival of the individual, but reproduction is a risky and resource-demanding process, often detrimental at the level of the individual, and not contributing to homeostasis. Nonetheless, reproduction is by definition required for species persistence, leading to evolutionary trade-offs (Martin 2015), and reproductive isolation is a key driver of speciation. Although this isolation is generally considered to be geographic, genetic, or anatomical in nature, physiological differences often contribute as well. In addition, understanding a species' reproductive processes (timing, behaviors, physiology, etc.) is important in conservation efforts.

Recent publications on reproductive physiology include multiple integrated aspects of reproduction, and by necessity overlap with morphology and behavior (Dixson and Anderson 2004). For example, although reproductive events such as implantation and parturition involve physiological changes, they are also life-history events, and timing of these events may depend on ecological factors (Friebe et al. 2014). Even when research on reproductive timing doesn't measure physiological traits (Ciuti and Apollonio 2016), underlying changes in endocrine and gonadal function are implied, and these functions can be profoundly different between breeding and nonbreeding periods of the year (Teodoro et al. 2012). Most of the timing of mammalian reproduction is based on photoperiod, and the possibility of anthropogenic light interfering with reproduction of wild mammals has recently been demonstrated (Robert et al. 2015).

Reproduction is regulated by endocrine cycles, either regular (spontaneous ovulation) or arrested (induced ovulation), and much of this was described prior to the period covered by this review. However, we continue to add details, find differences among taxa, improve on non-invasive methods to monitor hormones (Dehnhard et al. 2008), determine interactions with hormones that are not reproductive steroids (Saltzman and Ziegler 2014; Fanson and Parrott

2015), and investigate ecological factors that influence basic reproductive function (Cizauskas et al. 2015). Interesting work is also being done on hormones of one individual that affect another, e.g., maternal-offspring effects (Horton 2005; Ryan et al. 2014; Hinde et al. 2015).

A primary way in which mothers impact their offspring is via milk production, but the nutritional content of milk varies among taxa (Skibiel et al. 2013; Power et al. 2018) and the immunological components vary between individuals (Roulin and Roulin 1999). The production of milk is energetically expensive, particularly when required by fast-growing pups of species such as marine mammals (Thometz et al. 2014; Fowler et al. 2016). Uniquely, milk production in males has recently been demonstrated in two species of bats (*Dyacopterus spadecius* and *Pteropus capistrastus*—Kunz and Hosken 2009), which presumably helps distribute the cost of lactation. In all other mammalian species, the primary physiological contribution to reproduction by males is sperm production, the cost of which seems to increase when sperm competition exists (Jean-François 2011). Other reproductive costs incurred by males (which may exceed the cost of sperm production) are associated with access to estrus females, including territorial defense, maintaining a position in a hierarchy, and growing accessory reproductive structures (antlers, etc.)

The energetic cost of reproduction often limits the number of offspring produced (Thompson et al. 2012), and constitutes a trade-off with other energy-demanding processes, such as growth, maintenance of tissues (including large brains), thermoregulation, migration, etc. (Bårdsen et al. 2009; McAllan and Geiser 2014). These costs also vary based on environmental factors (Bergeron et al. 2011). Recent work has also begun examining the costs of reproduction for males in biparental species (Zhao et al. 2018).

PUBLICATION TRENDS

As was done by Wunder and Florant (1994), we assessed trends over time in mammalian ecophysiology research. Specifically, we analyzed journal publications for selected years over the last quarter century. For the *Journal of Mammalogy* (*JM*), we counted physiology articles (assuming 100% mammals), and broke these down by subdiscipline. For *Physiological and Biochemical Zoology* (*PBZ*) and *Comparative Biochemistry and Physiology* (*CBP*), we counted the number of publications on mammals (assuming 100% physiology) and broke these down into a few subject categories. Similarly, we counted the publications in the symposia volumes of the International Hibernation Society (IHS) over the same time period. As the IHS meets every four years, the journal data are matched.

From 1996-2016 (every fourth year), the number of articles published in *JM* on physiology has remained relatively constant. Over this time, an average of 18% of the articles in *JM* were physiological in nature, but this has decreased from 27% in 1996 to 13% in 2012 (Table 1; Fig. 1) because the total number of articles published in *JM* has increased by about 50%, but the absolute number of articles on physiology did not change. This decrease in percentage could be due to a relative decrease in physiological research on wild mammal species (particularly concerning reproduction), or to the existence of journals that are viewed as better options for this research (a "dilution effect"). Of the 143 physiological articles, the top five categories included 33% on aspects of reproductive physiology, followed by 10% on torpor-arousal research, 8% on digestion-storage of foods, 7% on communication, and 6% on energetics. Other kinds of research were published in smaller numbers. These align with what Wunder and Florant (1994) found for *JM* publications in the 1980s: their top four categories (over 10% each) were 1) energetics, 2) digestion-nutrition, 3) temperature regulation, and 4) reproduction.

Over the last 20 years (every fourth year), *PBZ* has consistently published about 24% (21-27%) of their articles on mammals (Fig. 1, Table 2), with another 2% involving mammals as part of a comparison (Table 2). Thus, mammals were the most popular taxon, with articles on birds and fish each representing about 18% of the published articles in our sampling. In this journal, virtually all the articles on mammals involved ecophysiology. This observation, and the constant number of mammal ecophysiology articles despite these numbers decreasing in other journals, suggests that this is the journal of choice for ecophysiology research.

Over the same time period, *CBP* (which publishes nearly five times as many articles per year as *PBZ*), published 15% of its articles solely on mammals (just over half the proportion of articles as *PBZ*), with another 1% including mammals in mixed-taxa studies (Table 3). This has decreased from 23% in 1996 to just 7% in 2016 (Fig. 1), and occurred in parallel with other terrestrial vertebrate groups. The majority of articles published in this journal are now on fish and invertebrates (about 30% each), and of the *CBP* publications on mammals, the slightly larger proportions involved molecular physiology or were integrative in nature. One possible factor responsible for some of this decline in research on live mammals could be taxon-based differences in government regulations, restrictions, and oversight (enforced via Institutional Animal Care and Use Committees) that is more stringent for mammals than other taxa. This may have led some researchers to use other taxa in their studies. If increasingly onerous regulation is a factor inhibiting physiological research on mammals, developing and implementing more non-invasive or minimally invasive field methods for studying mammals may help to reduce IACUC concerns. For a detailed treatment of use of wild mammals in research, with a consideration of issues relating to field research, see Sikes et al. (2019).

A final indicator of research publications in mammalian ecophysiology we included are the symposium volumes from the International Hibernation Society (symposia held every fourth year). In the last six volumes, about 88% of the chapters involved mammals, and of these, more than four of five fit into the subject categories of energetics, thermoregulation, torpor, rhythms, cellular mechanisms, neuroendocrinology, dietary, or other physiological categories (Table 4). Even those chapters that were mostly descriptive involved processes that had a physiological basis. Because of the emphasis of this society on mechanisms for coping with inclement weather and energy shortages, reproductive physiology was not represented in this data set. Other than this, however, we see similar patterns of active publication in physiology since 1992 across all the sources we investigated, and the topics are a continuation of the areas emphasized prior to that date. Unfortunately, in the last two decades, the proportion of articles on physiology published in *JM*, and the proportion of articles on mammals published in *CBP*, have slowly been declining.

KEY FINDINGS

One of the questions we asked when preparing this article was "What are the most significant research findings in mammalian ecophysiology over the last 25 years?" Based on our own experience and responses from queried colleagues within the discipline, we suggest that the most significant findings (and significant publications) can be separated into five broad categories, some of which overlap. We note that Wunder and Florant (1994:269) made two predictions for areas of future research that not only proved to be accurate, but are still valid as we look beyond 2019: 1) “cell and molecular approaches” will be revealing, and 2) we need to understand how mammals “adjust . . . as we witness climatic and other environmental changes.”

Allometry and scaling.—Databases related to body size and its correlates with ecophysiological parameters underwent tremendous expansion, and sharing of these via publication, including online supplemental materials and data repositories, became routine, thus greatly advancing research. Allometry and scaling showed continued development of grand theories, often tested with empirical studies to address why physiological traits co-vary with body size in particular ways (Brown et al. 2004; White and Kearney 2014; Glazier 2015).

Energetics and thermoregulation.—The ways in which basal, maximal, and field metabolic rates have coadapted with other aspects of physiology, morphology, behavior, and life history continued to be illuminated (Nagy 2005; McNab 2015). Torpor and hibernation were shown to be much more widespread than previously thought, and to occur not only in cold climates. Moreover, torpor and hibernation are now accepted as being as old as endothermy itself (Lovegrove 2016). The evolution of endothermy continued to attract attention from comparative, ecological, and evolutionary physiologists (Wone et al. 2015; Lovegrove 2016; Garland and Albuquerque 2017; Nespolo et al. 2017; Nicol 2017).

Genetics and evolution.—Individual variation, repeatability, and covariation of physiological and behavioral traits have now been demonstrated multiple times (e.g., Djawdan 1993; Hayes and Jenkins 1997; Szafrańska et al. 2007; Andrew et al. 2016). Subsequently, the mechanistic underpinnings of individual variation were explored (reviews in Careau and Garland 2012; Konarzewski and Książek 2012). As a key component of this individual variation, additive genetic variance of physiological traits was documented (Sadowska et al. 2005). Direct measurements of natural selection acting on physiological and behavioral traits in wild populations have also been made (Hayes and O’Connor 1999; Boratyński and Koteja 2009).

Thus, the components of adaptive, cross-generational changes that we all knew existed (variation, heritability, selection), were demonstrated empirically in mammals.

Results of artificial selection experiments on metabolic rate and on behavior demonstrated many correlated responses (or, sometimes, the lack of such predicted responses) at multiple levels of biological organization (along with cell size; Sadowska et al. 2015; Wone et al. 2015; Wallace and Garland 2016). This selection can even alter the mammal's microbiome (Kohl et al. 2016). "Omics" approaches started being applied to ecophysiological traits to elucidate the genetic and molecular basis of responses to selection (Konczal et al. 2015). Application of phylogenetically based statistical methods to classic ecophysiological questions showed that these approaches can lead to substantially altered conclusions, including with regard to scaling relationships (Garland and Carter 1994; Brashares et al. 2000; White and Seymour 2004; Dlugosz et al. 2013; White and Kearny 2014).

Phenotypic plasticity and epigenetics.— Phenotypic plasticity received increasing attention (Kelly et al. 2012), following the long tradition of studies on acclimation and acclimatization in mammalian ecophysiology. Responses to a wide array of environmental factors have been examined. Epigenetic mechanisms that may underlie phenotypic plasticity and may in some cases be transmitted across generations received increasing attention, especially as new molecular tools appeared (e.g., DNA methylation sequencing). Although the potential role of early-life effects in developmental programming of adult traits has been recognized based on numerous studies of humans and laboratory rodents, studies of such phenomena in wild mammals are scarce (Garland et al. 2017; Laubach et al. 2018).

Microbiomes.— The activity of host microbiomes, and particular the relationships between host animals and microbial symbionts, emerged as being potentially integrated into most aspects of animal physiology, behavior, and general biology (McFall-Ngai et al. 2013; Carey and Assadi-Porter 2017). This is particularly true in relation to gut microbes, and the impact they can have on realms of biology not previously envisioned.

PREDICTIONS

Attempts to predict the future in a scientific field, even with an understanding of the past, are as challenging as they are for predictions of the weather, sports, and politics. Nonetheless, we attempt here to make predictions of how ecophysiology will contribute to the next 25 years of mammalian biology, based on: 1) our understanding of current status; 2) trends observed in the recent past; 3) an appreciation for the pace and direction of technological advancements; 4) familiarity with some of the leading scientists in mammalian ecophysiology; 5) informal input from colleagues in mammalian ecophysiology; and 6) a bit of (admittedly non-scientific) intuition.

These factors allowed us to generate a list of research themes ("key words") and then assign a weight to these themes relative to the number of times each was encountered. Fig. 2 presents a word-cloud created using Wordle (www.wordle.net) that illustrates these weighted themes, with font sizes proportional to predicted research effort. The dominant themes are related to global change and conservation physiology, which is unsurprising in this time of perceived environmental crisis. Next are evolution, adaptation, and related topics, reflecting the ascendancy of evolutionary physiology in the last 25 years (Garland and Carter 1994; Carey 2015; Storz et al. 2019). Third, we see such terms as energetics, behavior, and plasticity, which are classic topics within the sphere of ecophysiology. The study of microbiomes also has the potential to change the way we think about many aspects of mammalogy that we don't currently connect to our microbes, particularly the (chemical) interactions with those evolved to live in the gut.

Although Wunder and Florant (1994) covered over 100 years in their review of the history of physiological research, we might argue that the advancements made in the last 25 years rival those made in the preceding century. Those pioneers of mammalian ecophysiology laid the groundwork, and developed explanatory theories, but these were based on a few species, and techniques and equipment that were advanced for their day but primitive by today's standards. Wunder and Florant (1994) mention that some equipment was developed by scientists who became entrepreneurs and started making equipment for sale to colleagues. This practice continued during the past 25 years; for example, Sable Systems^{TM} for precise measurements of gas exchange, and bat detectors and associated software to hear and identify echolocation calls.

However, the major technological advancements in biology over the last 25 years may well be in the area of sequencing polymers. In the recent past, it was predicted to take ten years to sequence the genome of one human. Now we can sequence the amino acids in a protein or the nucleic acids in RNA and DNA by the billions in a single day. Genomics, transcriptomics, proteomics, metabolomics, and microbiomics are new scientific approaches to address questions that up until now were just hypothetical (e.g., Konczal et al. 2015). The massive amount of sequence data has led to the development of software to handle it, and the field of "bioinformatics" was born. Databases for these sequences are growing exponentially, such that a new sequence from an unknown source can often be matched to a gene and a species in seconds.

The use of sequence data to discern taxonomic differences and phylogenetic relationships has clarified (and sometimes muddied) mammalian systematics, but has only recently been moving into ecophysiological studies. The explosion of sequence data has led to the development of research "tools" that allow us to dig deeper into "how mammals work" (e.g., Kitanovic et al. 2018). For example, quantitative polymerase change reaction (qPCR) assays allow us to identify microscopic bits of evidence, such as a diet analysis by examination of fecal materials. Prior to PCR, one had to sift through fecal matter under a microscope hoping to find an identifiable remnant of a food item, and then perhaps only be able to identify that item to the family level. Food items that were hard to digest were over-represented in data collected this way. Today, one can "search" for DNA in the feces with a qPCR assay, and probably identify the food item to species. Using qPCR, one can even determine the fraction of the diet made up by each food item identified.

Other techniques using sequence data allow us to "view" how our research subjects respond to their environment. For example, exposure to a pathogen or chemical, or to temperature extremes, can stimulate certain cells to turn on particular genes (for example, heat shock proteins) in response to this exposure. Differential expression of genes (up-regulation and down-regulation) can be determined by analysis of the sequenced genes which were transcribed (messenger RNA via "transcriptomics"). As not all transcribed genes actually end up making new proteins, one can also assess the viable proteins in a sample ("proteomics") to further delineate the animal's response to an environmental exposure or change. Other examples exist for new uses of sequence data now, and we have to assume that: 1) more techniques will be developed in the next 25 years; and 2) the cost of doing the sequencing will drop further and allow even more mammalogists to incorporate these methods into their inquiry.

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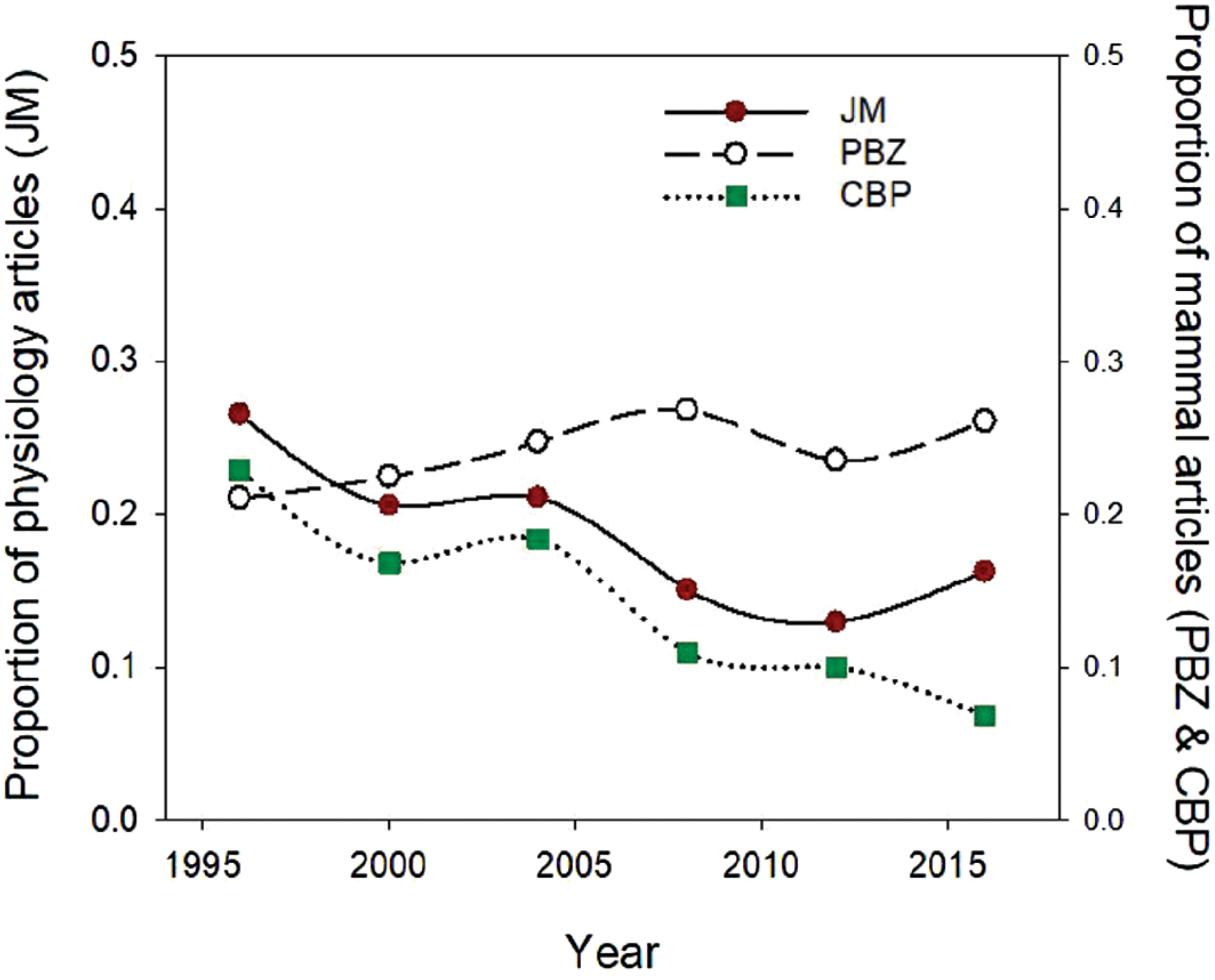
Special Issue Editor was Ronald A. Van Den Bussche.

Figure Legends

Fig. 1.—Fraction of articles that involve mammalian ecophysiology published in key journals over the last two decades. Articles in the Journal of Mammalogy (*JM*) are presumed to all be about mammals, with a fraction of these physiological in nature. In contrast, articles in Physiological & Biochemical Zoology (*PBZ*), and in Comparative Biochemistry and Physiology (*CBP*) are all presumed to be physiological (including cellular biochemistry), with a fraction of these studies on mammals.

Fig. 2.—Wordle diagram illustrating the dominant themes identified when we pondered the question "What will be the most significant research findings in the next 25 years, in terms of ecophysiology contributing to our understanding of wild mammals (e.g., their behavior, conservation, evolution, morphology, natural history, and taxonomy/systematics)?" The sizes of words and phrases reflect their frequency of occurrence in our examination of the literature and discussions with colleagues.


Proportion of physiology articles (JM)
Proportion of mammal articles (PBZ & CBP)
0.5
0.4
0.3
0.2
0.1
0.0
JM
PBZ
CBP
1995
2000
2005
2010
2015
Year


adaptation
conservation physiology
natural disasters
mechanisms
genetics
individual variation
geographic ranges
heritability
competition
evolutionary success
fluctuating selection
levels of organization
multiple solutions
epigenetics
species
temperature
integration
constraints
heterothermy
trade-offs
physiological diversity
free-ranging
reproduction
molecular
torpor
ecology
natural selection
diversity
integrative physiology
hibernation
aquatic
evolution
behavior
speciation
extreme environments
genomics
plasticity
stress
hormones
behavioral ecology
omics
promoting
field
population abundance
limits
anthropogenic change
adaptive potential
macrophysiology
energetics
regulation
microbiome
statistics
development
phylogeny
geographic distribution
community ecology
contamination
organism
natural history
macroevolution
diversification rates
chemical signaling
extinction
modelling
global change
geographic range
climate change

Table 1.— *Journal of Mammalogy* publications on research in ecophysiology.

	1996	2000	2004	2008	2012	2016	Total	Proportion
Energetics	1	2	2	2	0	2	9	0.06
Thermoregulation	0	2	0	0	0	0	2	0.01
Torpor, arousals	3	1	2	1	4	4	125	0.10
Energy, food intake and digestion-storage	2	1	3	1	0	4	11	0.08
Renal and water balance (osmoregulation)	0	0	1	0	0	2	3	0.02
Cardio and respiration (O_2 delivery)	0	0	1	0	0	0	1	0.01
Reproduction	10	9	9	11	4	4	47	0.33
Communication	0	1	2	5	1	1	10	0.07
Sensory physiology	0	0	3	0	1	2	6	0.04
Biotic interactions	1	1	1	0	0	0	3	0.02
Timing, rhythms	1	1	2	0	2	1	7	0.05
Muscle	0	0	0	0	0	2	2	0.01
Neuro and endocrinology mechanism	2	0	0	1	0	2	5	0.03
Cell-molecular mechanisms	0	0	0	0	0	0	0	0.00

Other physiology	6	3	5	1	6	1	22	0.15
Total physiology	26	21	31	22	18	25	143	0.18
Non-physiology	72	81	116	124	121	129	643	0.82
Total articles	98	102	147	146	139	154	786	

Table 2.—*Physiological and Biochemical Zoology* (previously named *Physiological Zoology*) publications. Mammals ++ = studies of mixed taxa including mammals. Mammals -- = studies of mixed taxa not including mammals.

	1996	2000	2004	2008	2012	2016	Total	Proportion
Mammals	16	20	23	22	16	12	109	0.24
Birds	9	17	10	20	14	11	81	0.18
Reptiles	10	10	13	14	8	3	58	0.13
Amphibians	6	7	7	5	2	5	32	0.07
Fish	11	11	18	14	17	10	81	0.18
Invertebrates	20	18	12	5	8	2	65	0.14
Mammals ++	0	3	6	0	0	1	10	0.02
Mammals --	0	2	2	0	0	0	4	0.01
Miscellaneous	4	1	2	2	3	2	14	0.03
Total articles	76	89	93	82	68	46	454	

Table 3.—*Comparative Biochemistry and Physiology* (*parts A & B*) publications. Mammals ++ = studies of mixed taxa including mammals. Mammals -- = studies of mixed taxa not including mammals.

	1996	2000	2004	2008	2012	2016	Total	Proportion
Mammals	90	54	69	60	36	15	324	0.15
Molecular physiology	22	18	21	16	12	4	93	0.05
Integrative physiology	17	15	29	19	21	5	106	0.05
Biochemistry	22	10	8	13	0	2	55	0.03
Molecular biology	29	11	11	12	3	4	70	0.03
Birds	43	25	44	59	21	14	206	0.09
Reptiles	13	19	16	27	15	8	98	0.04
Amphibians	20	23	12	17	7	7	86	0.04
Fish	76	59	101	158	133	106	633	0.29
Invertebrates	112	104	99	191	120	59	685	0.31
Mammals ++	10	1	4	4	1	2	22	0.01
Mammals --	4	3	6	5	4	0	22	0.01
Miscellaneous	25	33	24	28	23	10	143	0.06

Total articles	393	321	375	549	360	221	2219

Table 4.—International Hibernation Society symposium publications.

	1996	2000	2004	2008	2012	2016	Total	Proportion
Energetics and thermoregulation	9	7	8	5	4	5	38	0.12
Dietary	3	3	1	1	3	8	19	0.06
Cell-molecular mechanisms	6	9	10	7	8	13	53	0.16
Neuroendocrinology	8	9	6	9	4	5	41	0.12
Other physiology	4	9	2	1	6	13	35	0.11
Ecology-evolution-behavior	4	2	5	4	6	9	30	0.09
Torpor and arousals	4	4	2	5	6	5	26	0.08
Timing and rhythms	7	3	4	3	4	4	25	0.08
Miscellaneous	6	4	6	2	2	4	24	0.07
Total mammals	51	50	44	37	43	66	291	0.88
Non-mammals	5	5	14	5	4	5	38	0.12
Total articles	56	55	58	42	47	71	329	