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COMMENTARY

CENTENARY ARTICLE 100 YEARS OF DISCOVERY

Physiological differences between wild and captive animals: a century-old dilemma

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ABSTRACT

Laboratory-based research dominates the fields of comparative physiology and biomechanics. The power of lab work has long been recognized by experimental biologists. For example, in 1932, Georgy Gause published an influential paper in Journal of Experimental Biology describing a series of clever lab experiments that provided the first empirical test of competitive exclusion theory, laying the foundation for a field that remains active today. At the time, Gause wrestled with the dilemma of conducting experiments in the lab or the field, ultimately deciding that progress could be best achieved by taking advantage of the high level of control offered by lab experiments. However, physiological experiments often yield different, and even contradictory, results when conducted in lab versus field settings. This is especially concerning in the Anthropocene, as standard laboratory techniques are increasingly relied upon to predict how wild animals will respond to environmental disturbances to inform decisions in conservation and management. In this Commentary, we discuss several hypothesized mechanisms that could explain disparities between experimental biology in the lab and in the field. We propose strategies for understanding why these differences occur and how we can use these results to improve our understanding of the physiology of wild animals. Nearly a century beyond Gause's work, we still know remarkably little about what makes captive animals different from wild ones. Discovering these mechanisms should be an important goal for experimental biologists in the future.

KEY WORDS: Acclimation, Plasticity, Fluctuating environments, Laboratory, Captivity, Field

Introduction

Most experimental biologists work in labs. Sheltered from the unpredictability of the field, scientists working in the lab can carefully manipulate and measure the environment and physiology of their subjects. This high degree of control has resulted in tremendous scientific progress by allowing for critical tests of biological hypotheses (Benton et al., 2007). For example, almost a century ago R. F. Gause published a seminal paper in Journal of Experimental Biology that used clever lab experiments to provide the first rigorous empirical evidence for competitive exclusion theory (see Glossary; Gause, 1932). Gause cultured two species of yeast in isolation or in combination while varying the surrounding environment, which revealed that two species with similar niches cannot co-exist in perpetuity. This breakthrough was possible because of the control provided by the lab environment – tests of competitive exclusion in field conditions could not decisively isolate the role of competitive interactions in determining species distributions. Subsequent work, however, has discovered that simplified lab experiments do not reflect the complexity of natural ecosystems, where an organism's niche is dynamic and competing species often find ways to partition resources (Chesson, 2000; Schoener, 1974; Holt, 2009).

The debate about whether to conduct biological experiments in the laboratory or in the field predates Gause and continues to this day. Ecologists have frequently pointed out the drawbacks of relying on laboratory or microcosm experiments for testing hypotheses in ecologically relevant contexts (e.g. Schindler, 1998; Melvin and Houlahan, 2012; Salena et al., 2021). For example, the life history responses of guppies to predation pressure are opposite when comparing field versus laboratory populations (Reznick and Ghalambor, 2005). Comparative physiologists and biomechanists have similarly drawn attention to the drawbacks of working with animals in captivity (Costa and Sinervo, 2004; Calisi and Bentley, 2009; Maclean et al., 2018; Moore and Clifton, 2023). However, lab experiments continue to dominate these fields – in 2022, 85% (264/311) of the research papers published in Journal of Experimental Biology reported results entirely collected in the lab. When lab and field studies are integrated, they are often treated as separate experimental components that investigate different variables (e.g. habitat choice measured in the field, osmoregulatory physiology in the lab; Grosell et al., 2020) or ask whether lab-measured physiological responses scale to population-level patterns (e.g. Zani and Stein, 2018; Boyes et al., 2021). Few studies directly investigate how physiological processes differ between lab and field. This is concerning, because the results of physiological experiments can be dramatically different between the lab and the field (Costa and Sinervo, 2004; Calisi and Bentley, 2009; Table 1). Understanding when and why these differences occur can lead to fundamental insights into mechanistic links across levels of biological organization and help researchers design smarter and more decisive laboratory experiments. Furthermore, as the expertise of comparative physiologists is increasingly applied to conservation problems (Cooke et al., 2013, 2021), understanding how animals in nature will respond to anthropogenic disturbances is critical for accurately predicting population responses and informing species conservation. In this Commentary, we discuss several possible mechanisms (Fig. 1) that may cause the differences seen in lab versus field studies. While we focus on hypotheses that may explain physiological differences between captive and wild animals in the absence of selection, we note that these mechanisms may also influence the trajectory of selection in lab-bred organisms.

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Glossary

Acclimation potential
The ability of an organism to adjust their phenotype with environmental change.

Aerobic scope
An organism's capacity to increase aerobic metabolic rate above basal levels to perform critical functions (e.g. locomotion, digestion, reproduction).

Cardiac break point temperature
The temperature where cardiac function begins to drastically decline.

Character displacement
The evolutionary change in morphology, behaviour or physiology of similar species that inhabit the same ecological niche.

Competitive exclusion theory
Two species that share the same ecological niche cannot co-exist indefinitely without one out competing the other for the limited resource.

Social buffering
Affiliating with conspecifics can mitigate an organism's response to stressors.

Thermal performance
The effect ambient temperature has on various biological rates.

Thermal regimes
In stochastic thermal regimes, temperature fluctuations in a system are randomly determined every day. In predictable thermal regimes, temperature fluctuations in a system are exactly the same every day.

Why might lab and field differ?

Organismal physiology is the product of complex interactions between genes, the environment and epigenetics (Burggren and Dubansky, 2018). Each of these factors may influence physiological differences that occur between lab and field conditions. For example, many common experimental organisms have undergone unconscious selection that has improved fitness in lab environments and/or artificial selection for human-defined desirable traits such as faster growth or reduced aggression (Trut et al., 2009; Christie et al., 2012; Lachambre et al., 2017; Maclean et al., 2018; Morgan et al., 2019; Racicot et al., 2021). These evolved differences can directly affect physiology, and can also affect acclimation potential (i.e. gene×environment interactions; see Glossary; Hirakawa and Salinas, 2020; Morgan et al., 2022). Thus, the source of experimental organisms for lab studies (e.g. wild-caught versus lab-raised from wild-caught parents versus captive-bred semi-domesticated animals) and their evolutionary histories are important considerations. However, accumulating evidence indicates that physiological differences can occur between lab and field studies in the absence of evolutionary differences (Table 1). These differences have received much less attention and could be the result of phenotypic plasticity (West-Eberhard, 2003; Pfennig, 2021), parental effects (Badyaev and Uller, 2009; Bell and Hellmann, 2019) or epigenetic modifications (Burggren, 2014; Hu and Barrett, 2017; Perez and Lehner, 2019) that act on time scales ranging from minutes to several generations. While few studies have explicitly investigated why these differences occur, below we provide some hypotheses that we believe should be investigated further. We emphasize that this is not a comprehensive list of possible mechanisms, and many of these mechanisms likely interact. Furthermore, while we attempted to include both vertebrate and invertebrate examples throughout, we acknowledge that all authors of this Commentary are primarily vertebrate physiologists, which has shaped our perspectives.

Competitive interactions

Competitive interactions among species – which Gause identified as being fundamentally important for shaping population distributions – can also theoretically influence many physiological traits of individual organisms (Lawton, 1991). One likely mechanism driving these effects is character displacement (see Glossary) enabled by phenotypic plasticity (Pfennig and Pfennig, 2010; Turcotte and Levine, 2016; Stuart et al., 2017). For example, the presence of both conspecific and heterospecific competitors increases activity and, presumably, the metabolic rate of frog tadpoles (Relyea, 2002; Relyea, 2004; Castellano et al., 2022). In other frogs, competition results in dietary niche separation (Pfennig et al., 2007). The effects of competitive interactions are typically weaker under natural conditions (Skelly and Kiesecker, 2001), perhaps because laboratory animals typically live at much higher densities than they do in nature (Newman et al., 2015). For example, competition between tadpoles of two frog species decreased developmental rate in an artificial laboratory mesocosm, but not in a natural field environment (Skelly, 2002). Given that most lab experiments house animals only with conspecifics, the lack of competitive interspecific interactions may explain some of the differences that occur between lab and field experiments.

Parasite load

Parasites and their physiological consequences are widespread in natural systems (Dobson et al., 2008; Weinstein and Kuris, 2016). Parasites can impact many aspects of physiology including feeding (Parker et al., 2023), aerobic capacity (Simon et al., 2004), metabolic rate and haematocrit (Filipsson et al., 2017; Fellin and Schulte-Hostedde, 2022; Guitard et al., 2022), locomotor performance (Moretti et al., 2017), learning (Gómez-Moracho et al., 2022) and glucose uptake (Kristan and Hammond, 2000). As a result, parasites may be an important mechanism that causes differences between animals in the lab versus the field (Reznick and Ghalambor, 2005). However, the difference in parasite load between the lab and field requires further study. Lab specimens may exhibit decreased parasite loads due to antiparasitic treatment or may exhibit greater parasite loads if held at high densities and/or in flow-through systems where close proximity facilitates direct transmission of parasites. Furthermore, the influence of parasites on laboratory studies is not well known. In fact, a recent meta-analysis found that only 21.9% of laboratory studies acknowledged potential parasite effects and just 5.1% accounted for parasite loads (Chrétien et al., 2023). Sensitivity to parasites varies interspecifically and ontogenetically, adding additional uncertainty to our understanding of how parasites influence host physiology and, thus, how the presence of parasites may drive the differences between lab and field measurements (Grab et al., 2019; Knutie et al., 2016; Prati et al., 2020; Canel et al., 2021).

Stress

Stressful environments influence a broad range of physiological traits on both acute and chronic time scales (Kassahn et al., 2009; Schreck et al., 2016). Stress may thus explain some of the differences observed between captive and wild animals, a hypothesis that has been extensively reviewed elsewhere (Calisi and Bentley, 2009; Archard and Braithwaite, 2010). In short, although laboratory environments are generally designed to be non-threatening and comfortable (Boonstra, 2013), captive animals may still experience chronic stress (e.g. from confinement or human presence; Newman et al., 2015; Bailey, 2018). In contrast, wild animals are free living, but may experience stress caused by food scarcity, the presence of parasites, predators, competitors and/or suboptimal environmental conditions (Boonstra, 2013; Clinchy et al., 2013; Babic et al., 2023). Thus, the two environments impose different stressors, and it is unknown which environment is more stressful overall. The stress response of animals to captivity is also highly species specific, perhaps as a result of interspecific differences in the underlying

Table 1. Select examples of phenotypic differences in animals measured under laboratory versus field conditions, chosen to highlight the taxonomic and phenotypic diversity of studies that report differences between these conditions

Phenotypic trait	Species	Lab versus field difference	Hypothesized mechanism	Reference
Bone density	Felid cats	Reduced bone density in captive animals.	Decreased activity and mechanical strain on the skeleton of confined animals.	Chirchir et al., 2022
Transcriptome	Crown of thorns starfish *Acanthaster planci*	Captivity induced widespread changes to gene expression that persisted for 30 days. Genes upregulated in captivity were associated with metabolism and oxidative stress.	Chronic holding stress. Experimental evidence suggests nutrition plays only a small role.	Morin et al., 2023
Flight performance and flight muscle	Eurasian tree sparrow *Passer montanus*	Prolonged captivity decreased flight performance and increased fat content of pectoralis muscle.	Reduced exercise in captivity.	Kou et al., 2022
Glucocorticoid regulation	Daffodil cichlid *Neolamprologus pulcher*	In the lab, dominant individuals had lower cortisol levels than subordinates, but in the wild, cortisol levels were higher in dominant individuals.	Increased levels of social conflict and antagonistic interactions in the wild.	Culbert et al., 2018, 2021
Chemical defence	Little devil frog *Oophaga sylvatica*	Wild frogs had higher levels of toxic alkaloids and proteins involved in small molecule metabolism and sequestration.	Alkaloid content of diet.	Caty et al., 2019
Interaction between diet and aggression	Jumping spider *Phidippus audax*	High aggression was promoted by high-protein diets in wild spiders, while lab spiders were more aggressive when fed high-lipid diets.	Irreversible developmental plasticity of the digestive system caused by different food availability.	Wiggins et al., 2018
Metabolism and oxygen transport	Sunfishes *Lepomis* spp.	Compared with lab-acclimated fish, wild fish had lower metabolic rates and were more hypoxia tolerant, linked to larger gill surface area, higher haematocrit, and lower activity of metabolic enzymes.	Rapid phenotypic plasticity.	Borowiec et al., 2016
Developmental rate and colony growth rate	Paper wasp *Polistes fuscatus*	Larval development and colony growth were slower in lab than in the wild.	Increased food availability in the lab.	Jandt et al., 2015
Stress responsiveness (Δ plasma corticosterone)	Curve-billed thrasher *Toxostoma curvirostre*	Population differences measured in wild animals disappeared when animals were housed in the lab.	Plasticity in response to common garden laboratory conditions.	Fokidis et al., 2011
Fecal corticosterone	Tuco-tuco *Ctenomys sociabilis*	Corticosterone levels were higher and more variable in the field versus the lab.	Higher environmental variability and unpredictability in nature.	Woodruff et al., 2010
Brain size	Guppy *Poecilia reticulata*	Smaller relative brain size in lab-reared fish.	Complexity of rearing conditions, though follow-up studies that increased complexity did not recover brain size.	Burns et al., 2009

For additional historical examples, see Calisi and Bentley (2009).

cellular and molecular mechanisms involved (Fischer and Romero, 2019). Stress responses to captivity may also be life-stage specific. For example, animals migrating to spawning areas may be particularly stressed by confinement (Donaldson et al., 2011; Jeffries et al., 2012). This means that the effects of stress from captivity cannot be generalized across contexts. It seems likely that some differences between laboratory and field results may be largely due to stress, while in other cases stress has a negligible impact.

Diet

Lab and field organisms differ in dietary quality, quantity, variety and feeding schedule. Wild organisms generally consume a variety of food types that change based on ontogeny (Young et al., 2010), availability (Schulte-Hostedde et al., 2018), season (Spence et al., 2007; Twining et al., 2022) and nutritional needs (Hansson, 2001). However, laboratory animals typically receive a single type of food (often commercially prepared) fed *ad libitum* to improve experimental replication and simplify care requirements (Hoevenaars et al., 2012; Pellizzon and Ricci, 2020). Differences in the type of food animals eat can impact behaviour and physiology outright (Fowler et al., 2019; van Leeuwen et al., 2020), and can also influence physiological processes by affecting the gut microbiome (Falcinelli et al., 2017; Cabana et al., 2019; van Leeuwen et al., 2020; see ‘Microbiome’, below). For example, opaleye (*Girella nigricans*) fed an omnivorous diet had reduced cardiovascular thermal performance (see Glossary) and increased standard metabolic rate compared with opaleye fed a carnivorous diet (Hardison et al., 2021). The effects of diet can also vary between lab and field. Lab-reared wolf spiders won aggressive interactions more quickly if fed a high-lipid versus a high-protein diet, but wild-caught individuals performed better if fed the high-protein diet (Wiggins et al., 2018). Changes in diet quantity can also affect many aspects of physiological performance, including metabolism (Simon et al., 2004; Auer et al., 2016), thermal tolerance (Gilbert and Miles, 2016; Turko et al., 2020), circulating steroid levels (Fokidis et al., 2013), gonadal function (Valle et al., 2015, 2020) and parasite resistance (Knutie, 2020). Even when food is abundant, unpredictable variation in food availability can depress growth and increase circulating levels of stress hormones (Fokidis et al., 2012). Consequently, dietary differences between the lab and field may account for many physiological differences.

Microbiome

The microbiome influences many aspects of organismal physiology and behaviour (Hird, 2017; Cryan et al., 2019; Davidson et al., 2020; Knutie, 2020). For example, gut microbiome changes from

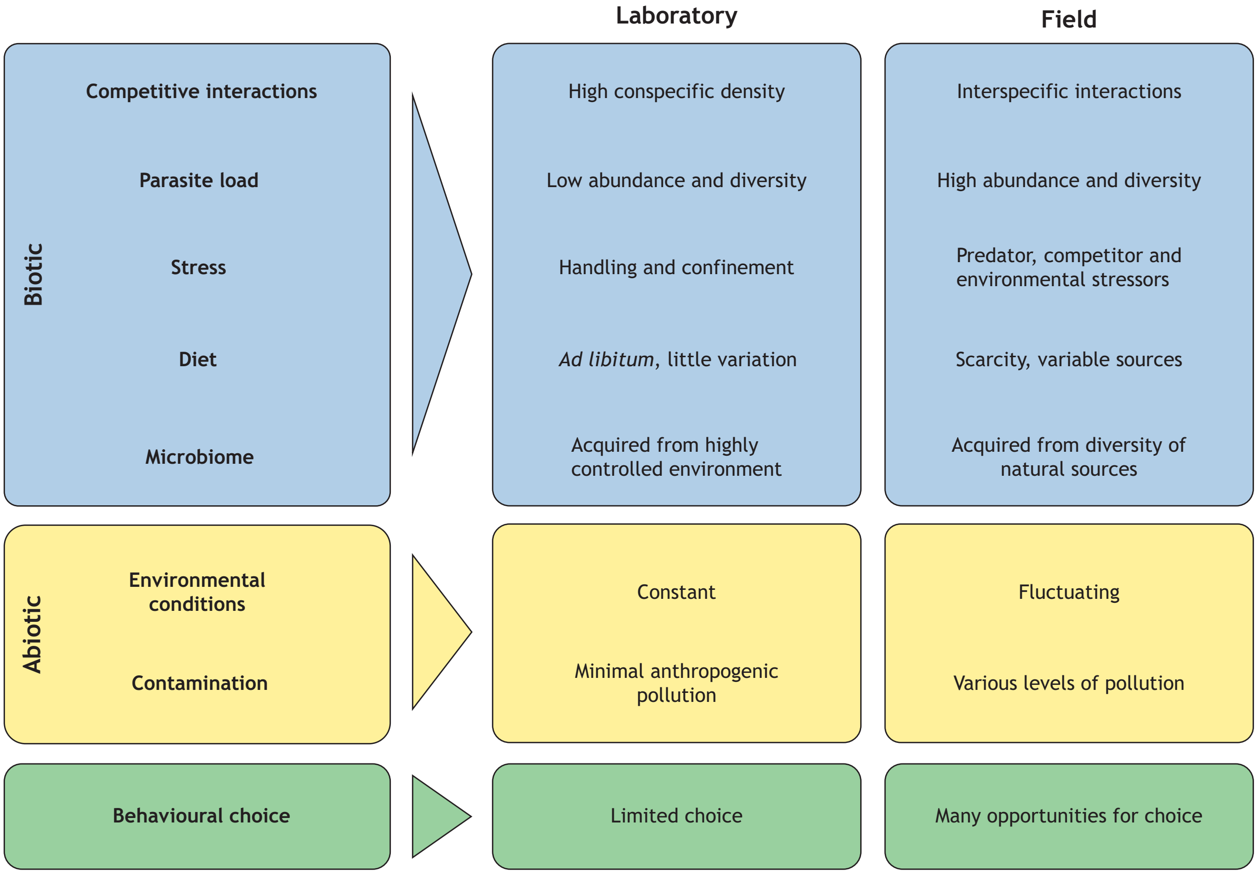

Fig. 1. Conceptual framework of some possible factors that influence differences between laboratory- and field-based studies in experimental biology. Wild animals experience different biotic (blue) and abiotic (yellow) conditions, and have different opportunities to make behavioural choices (green) compared with their captive counterparts.

food supplementation increased antibody response and decreased parasite abundance in eastern bluebird (*Sialia sialis*) nestlings (Knutie, 2020). Additionally, seasonal changes in the gut microbiome may affect thermal tolerance (Ferguson et al., 2018; Moeller et al., 2020; Fontaine and Kohl, 2023). Differences in the composition of the microbiome between captive and wild animals have recently become well established (Dallas and Warne, 2023; Kueneman et al., 2022) and have been described for numerous invertebrates (Roura et al., 2017; Mays et al., 2021), fishes (Givens et al., 2015; Eichmiller et al., 2016; Uren Webster et al., 2020; Restivo et al., 2021), reptiles (Eliades et al., 2022), mammals (Bowerman et al., 2021; Cabana et al., 2019; Schmidt et al., 2019) and birds (Salgado-Flores et al., 2019; San Juan et al., 2021; Madden et al., 2022; Kelly et al., 2022). However, we lack a general understanding of the links between environmental conditions, microbiome composition and animal physiology. This is an exciting area of research that has the potential to explain many differences between lab and field studies.

Fluctuating abiotic conditions

The complexity of nature has long been considered an important challenge for experimental design (Helmuth, 2002; Morash et al., 2018; Treberg et al., 2016). Nonetheless, organisms are typically held and tested at constant abiotic conditions (e.g. temperature, oxygen levels, osmolarity) in the lab to minimize experimental variability. However, these conditions are not ecologically realistic. Natural environments are complex, with abiotic variables fluctuating on both diurnal and seasonal time scales, and the magnitude, speed and predictability of short-term fluctuations often varies as well.

Environmental variability can directly affect physiological traits. For example, limpets (*Lottia digitalis*) exposed to simulated tidal conditions had higher cardiac break point temperatures (see Glossary) than limpets exposed to no tide (Drake et al., 2017). Red flour beetles (*Tribolium castaneum*) exposed to fluctuating temperature conditions had reduced offspring survival (Scharf et al., 2022). Environmental variability can also mediate interspecific interactions, such as altering rates of parasite transmission (Claar and Wood, 2020). One popular strategy for evaluating the importance of environmental variability in driving lab versus field differences is to vary conditions in the laboratory rather than holding organisms under stable conditions (e.g. Davis et al., 2019; Farless and Brewer, 2017; Nancollas and Todgham, 2022; Xing et al., 2015; Zhu et al., 2022). Further complicating the situation is the reality that many abiotic variables (e.g. temperature, dissolved oxygen) fluctuate simultaneously in natural systems. Moreover, many animals move through their environments, adding a further layer of variability. Consequently, lab studies that attempt to replicate natural variability of one abiotic variable will likely fail to incorporate the interactive effects of other abiotic variables that could lead to additive, synergistic or antagonistic impacts on physiological results. For example, tidepool sculpin (*Oligocottus maculosus*) exposed to a cycling temperature regime mimicking field conditions did not express the same level and pattern of heat shock proteins as did sculpin taken directly from the tidepool

(Todgham et al., 2006). This difference in protein response was hypothesized to be attributed to the concurrent fluctuations in dissolved oxygen and salinity with temperature in the field (Todgham et al., 2006).

Anthropogenic contamination

The number of 'pristine' ecosystems is diminishing, and most field sites are likely to contain contaminants that influence the animals that live there. Even field sites in the Arctic are contaminated by microplastics (Bergmann et al., 2022) and mercury (Dietz et al., 2009), while the deep sea is polluted by sewage, mining and radioactive waste, pharmaceuticals and other chemicals (Ramirez-Llodra et al., 2011). This widespread contamination can complicate physiological comparisons. For example, in a recent field study assessing the impacts of wastewater effluent on native fishes, even 'clean' reference sites were ultimately found to be polluted (Gauvreau et al., 2022). Anthropogenic contaminants have a wide variety of consequences for behaviour and physiology; discussing these wide-ranging effects is beyond the scope of this article and these effects have been extensively reviewed elsewhere (e.g. Saaristo et al., 2018; Dietz et al., 2019). However, lab-raised organisms are likely sheltered from most anthropogenic contamination because of the thorough decontamination and sterilization of a captive animal's environment, including housing, water and feed. The ubiquity of these contaminants in the wild could conceivably explain some differences between the lab and field.

Behavioural choices

In nature, animals can make choices that affect their physiological responses to environmental challenges (Odling-Smee et al., 2003; Sultan, 2015). For example, wild animals are often more active and devote more of their daily energy budget to movement compared with their captive counterparts (Yamanashi and Hayashi, 2011; Rose et al., 2022). These activity differences can directly affect numerous physiological and morphological traits such as migration speed (Hyvärinen and Rodewald, 2013) or bone density (Chirchir et al., 2022). Movement in the wild also allows animals to make decisions about the environmental conditions they experience. Habitat choice can buffer the magnitude of temporal environmental changes, thereby influencing the expression of physiological plasticity (Fey et al., 2019; Salachan et al., 2021; Turko and Rossi, 2022). For example, to conserve energy stores during hibernation or aestivation, many turtles and frogs select cold or hypoxic microhabitats that enhance energy-saving reductions in metabolic rate (Danks, 1991; Duman et al., 1991; Tattersall and Ultsch, 2008; Edge et al., 2009; Rossi et al., 2020). Choosing to interact with familiar conspecifics can also enhance physiological resilience, a phenomenon known as 'social buffering' (see Glossary; Kiyokawa and Hennessy, 2018). Interspecific interactions can also be important. For instance, the metabolic physiologies of anemones and anemonefishes is altered by the presence of each other (Szczebak et al., 2013; Norin et al., 2018). Therefore, laboratory studies that do not consider the role of habitat selection or the role that intraspecific and interspecific interactions play may underestimate the capacity of animals to withstand challenging environmental conditions.

In addition to choosing their habitats, many wild animals can also make choices about the amount and type of food they consume (Kyriazakis et al., 1999; Raubenheimer et al., 2009). Given the energetic demands of digestion, wild fishes exposed to predation risk may choose to eat small meals to preserve aerobic scope (see Glossary), even though digesting small meals is less efficient than digesting large ones (Norin and Clark, 2017; Jutfelt et al., 2021). In response to environmental changes (e.g. acute or seasonal temperature changes), animals may also alter their dietary preferences to improve growth and other aspects of physiological performance (Behrens and Lafferty, 2007; Carreira et al., 2016; Hardison et al., 2021). Experimental evidence from mice indicates that dietary preferences are also influenced by the gut microbiome (Trevelline and Kohl, 2022). The lack of dietary choice available to animals in the lab, possibly compounded by differences in the microbiome, may therefore contribute to differences in data collected in the lab versus the field.

How can we reconcile lab and field results?

Understanding the physiology of animals in nature is essential for understanding how they function, how they interact with their environment, and how they respond to changing conditions. This knowledge is also important for effectively conserving wildlife and ensuring sustainable practices in natural resource management. However, the assessment of animal physiology in the wild can be challenging because of the complex and dynamic nature of natural environments. Despite this complexity, we believe that differences between lab and field results can be reconciled with ingenuity, careful experimentation and the exciting potential offered by new technologies. Here, we outline several possible strategies including bringing the lab to the field, incorporating aspects of field conditions into lab experiments, and choosing to work with animals that most closely resemble their wild counterparts.

Bringing the lab to the field

Portable equipment allows animals to be studied in their natural environments, thus minimizing the effects of captivity. 'Field physiology' has provided important insights for decades, though these studies remain rare because of their inherent logistical challenges (Costa and Sinervo, 2004). However, recent technological advances have facilitated the ability to record numerous physiological parameters in free-living animals, which alleviates some of these challenges. For example, researchers can use implantable telemetry tracking devices to monitor location, heart rate, acceleration, body temperature and other physiological parameters in wild animals with minimal invasiveness and disruption to the study organism (e.g. Twardek et al., 2021). Electronic tags are being used to answer a wide variety of research questions, including tracking imperilled fishes for fisheries management (Brownscombe et al., 2022) and identification of critical habitat for endangered sea turtle species (Mansfield et al., 2021). Additionally, field-based respirometry equipment to assess the energetics and metabolism of field-caught organisms is now more accessible. For example, this technique was used to discover that silver haired bats (*Lasionycteris noctivagans*) employ torpor during periods of inactivity to help conserve energy during migration (McGuire et al., 2014). Field-based respirometry has similarly revealed the energetic trade-offs faced by numerous bee species (Billardon and Darveau, 2019; Duell et al., 2022). Others have exploited riverside experiments to measure the response of fishes to natural variation in water quality (Ste-Marie et al., 2020; Anlauf-Dunn et al., 2022), and to measure hypoxia tolerance (Firth et al., 2023) or thermal tolerance (Turko et al., 2020). Portable blood analysis equipment can provide rapid measurement of numerous metabolites and blood gasses, and the use of this equipment has been validated in a number of non-human organisms, such as moose (Barros et al., 2018), fishes (Harter et al., 2014; Talwar et al., 2017; Borissov et al., 2019), reptiles (Hamilton et al., 2016; Griffioen et al., 2020) and birds (Yaw et al., 2019; Anderson et al., 2022). Even highly advanced sequencing equipment has been converted into portable, field-based devices, such as the nanopore sequencing platform minION, which has been used for the identification of haematophagous insects and their blood meal hosts, providing valuable information on bloodborne parasites and disease mitigation (Kipp et al., 2023). However, the major drawback of bringing the lab to the field is that these experiments necessarily result in a loss of experimental control over the conditions the animals experience. Conducting robust physiological and biomechanical experiments in the field therefore requires researchers to be familiar with aspects of experimental design not usually considered by lab-based scientists. For example, field-based experiments require careful consideration of environmental variability, temporal and spatial replication and sampling bias, among other challenges. Fortunately, these challenges are well known to field ecologists who have developed many practical solutions (e.g. Scheiner and Gurevitch, 2001; Henderson, 2003; Fox et al., 2015) – though future field physiology will also likely create new challenges requiring clever experimental designs and technological advances.

Bringing the field to the lab

Much of what comparative physiologists attempt to measure is, at present, either difficult or impossible to measure accurately in free-ranging wild animals (Cooke et al., 2016). For example, there is no reliable way to quantify an individual's standard metabolic rate while it is at liberty in the wild. As a result, an increasing number of researchers are taking an 'environmental realism' approach when designing lab-based experiments by replicating the conditions that wild animals currently experience or the conditions they are likely to experience in the future (Steinberg, 2012; Côté et al., 2016; Cooke et al., 2022). One way to promote environmental realism is to expose captive animals to as many components of their natural environment as possible; for example, by using flow-through aquatic systems that draw water straight from natural systems or by providing terrestrial animals with access to enclosed outdoor environments. These housing strategies may reduce captivity-related changes to the microbiome or sensory systems, but conversely may also expose animals to a broader range of parasites and pathogens. Another strategy to promote environmental realism is to use environmental data such as long-term datasets of abiotic variables and telemetry data; researchers are designing ecologically realistic experiments, acknowledging that environmental conditions change on different temporal and spatial time scales. Numerous biotic and abiotic variables that could drive physiological differences between lab and field settings such as light intensity, temperature fluctuations, oxygen levels, pH, habitat choice, behavioural dynamics, seasonality, social and structural enrichment, and reproductive timing can be altered to replicate field conditions in the lab. Despite the benefits of this approach, only 5.3% (14/311) of research papers published in Journal of Experimental Biology in 2022 included both lab and field data. However, this is an improvement compared with 50 years ago when only 2.6% (3/120; data from 1972) of papers contained field data, and in the inaugural volume (1923–1924), all of the 22 research papers were based exclusively on laboratory work.

Another promising approach to increase the environmental realism of lab experiments is the use of mesocosms. Building mesocosms to replicate many terrestrial and aquatic habitats is logistically feasible, although technical difficulties increase as more environmental variables need to be controlled. Mesocosm experiments have been valuable for understanding interactions between temperature and pH (Wong and Hofmann, 2021), salinity and polychlorinated biphenyls (Holliday et al., 2009), and nutritional and social stress (Hansen et al., 2020). Increasingly, researchers are building greater environmental variability into these experiments; for example, by exposing animals to thermal regimes (see Glossary) that fluctuate predictably (Morash et al., 2018; Schwieterman et al., 2022) or stochastically (Nancollas and Todgham, 2022). Despite these advances, it is impossible to fully replicate wild conditions in the lab given that many natural abiotic and biotic conditions may be unknown/unknowable to the researcher (e.g. number/type of predators, competitors, microscale habitat temperature). Although mesocosms are not perfect replicas of the natural world (Melvin and Houlahan, 2012), they are valuable tools for increasing the environmental realism of physiological studies and testing hypotheses about which variables may be responsible for lab versus field differences.

Choosing the right animals

Careful selection of the experimental species used for lab studies can minimize many of the consequences associated with captivity. A major concern of studying lab-reared animals is that acclimation and/or domestication means that their physiological and behavioural responses no longer reflect wild animals. Most selection pressures are relaxed in a lab environment, where animals are protected from predation and frequently are fed *ad libitum*. This can lead to reduced territoriality/aggression (Metcalfe et al., 2003; Pearsons et al., 2007), reduced locomotor performance (Bellinger et al., 2018), reduced brain size (Burns et al., 2009) and impaired predator avoidance (Mineka et al., 1980; Alvarez and Nicieza, 2003) compared with wild conspecifics. Indeed, just a single generation of domestication was shown to heritably alter the expression of hundreds of genes in rainbow trout (Christie et al., 2016).

One solution to the effects of acclimation and/or domestication on lab-reared animals is to use wild-caught animals (Archard and Braithwaite, 2010; Salena et al., 2021). Wild animals captured in the field and transported to the lab or a field station bring with them their wild history and experience acquired through genetics, developmental plasticity and acclimatization. This appears to be a popular strategy among comparative physiologists – 41% (114/262) of lab studies published in Journal of Experimental Biology in 2022 used wild-caught animals [this has changed little through time – the figure was 37.5% (45/120 studies) in 1972 and 36.4% (8/22 studies) in 1924]. However, the benefits of using wild-caught animals are species specific and may depend on the conditions experienced prior to capture. There is also considerable interspecific variation in the stress associated with captivity – some animals readily adjust to lab environments, while other species experience permanent life-long stress in captivity (Fischer and Romero, 2019). Thus, just as comparative physiologists have long applied the Krogh principle to choose experimental animals based on the conditions they experience in nature (Green et al., 2018), we suggest that animals' rearing environments (e.g. lab raised or wild caught) and response to captivity should be important considerations when designing experiments and interpreting results.

Perspectives and conclusions

Almost a century after it was published, the insights provided by Gause's lab work continue to be foundational to our understanding of competitive exclusion theory, highlighting the advantages of a simple and controlled laboratory environment for hypothesis-driven, mechanistic research. However, more recent work has demonstrated that laboratory environments are not just simplified versions of the field, but often different environments altogether (Fig. 1). As a result, laboratory animals are inconsistently different from their wild counterparts (Table 1). Our view is that future work in experimental biology should address these issues head-on, including alterations in experimental design (e.g. acclimating animals to more realistic environments), incorporating new techniques (e.g. telemetry and other field tools), and pursuing new lines of research (e.g. testing hypothesized mechanisms that may explain laboratory versus field differences). Given the status of Journal of Experimental Biology as a leading journal in comparative physiology, we were surprised to find that it has published relatively few papers about lab versus field differences (e.g. only 2 of 12 studies featured in Table 1 are from this journal). Perhaps this is because studies to date of lab versus field physiology have often focused on documenting differences without explicitly testing mechanisms for why they occur. Understanding these mechanisms is a key next step for the field, with important implications for comparative and conservation physiology, and we hope to see many of these types of mechanistic studies in future issues of Journal of Experimental Biology.

One lingering question remains: how far do we need to go towards environmental realism? There are situations in which discrepancies between animals in the field and animals in the laboratory are vitally important, and situations when these can be ignored. Early comparative physiologists were able to make substantial progress in understanding fundamental physiological mechanisms using laboratory animals (see recent reviews by West, 2019; Larsen et al., 2021). Similarly, we have few reasons to doubt that wild animals increase their metabolic rate during digestion (e.g. Wang et al., 2001), or to think that the biomechanics of hagfish slime differ radically in nature from what has been characterized in the lab (e.g. Fudge et al., 2005). However, for fields that are centred on understanding how animals interact with their natural environments (e.g. ecophysiology, conservation physiology), differences between lab and field studies can dramatically affect the biological conclusions we draw, which is especially concerning for results that are used to shape regulations and policy. Ideally, we would fully replicate field conditions in the lab; however, this is impossible given the complexity of known (and unknown) factors in the wild. Experimental designs based on manipulation of even two or three factors become logistically challenging when a factorial design is applied, and these designs often push the limits of most existing lab infrastructure, personnel and statistical power. We suggest that in many cases, environmental realism can be increased without the need for fully factorial designs such as by altering control conditions to reflect those in nature and then adjusting the variable(s) of interest in each treatment. This approach can provide more meaningful data to resource management practitioners and other applied biologists who work to conserve species biodiversity and minimize anthropogenic disturbances.

We encourage more work investigating the underlying mechanisms responsible for variation in the physiology of laboratory versus wild animals. However, there may never be a clear delineation between when these differences matter and when they do not. Instead, we recommend that experimental biologists be aware of where their animals come from, how these places differ from a laboratory, and how that knowledge might influence ecologically relevant experimental design and data interpretation.

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Competing interests

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