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REVIEW

SPECIAL ISSUE
THE INTEGRATIVE BIOLOGY OF EXERCISE

A life-history perspective on exercise

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ABSTRACT

Exercise has been extensively studied in humans because of its multiple benefits, yet it is unclear how relevant 'exercise' is to non-human animals and whether the effects of exercise are identical to those in humans. One main difference is that humans rarely have chronic limited resources when exercising, whereas wild animals do. Nevertheless, because other species from fish to lizards have been shown to have similar responses to exercise, the generalized response is almost certainly very old evolutionarily. This means that the response to exercise evolved under conditions of limited resources, and the modern conditions under which humans use exercise are novel. If we view 'exercise' as increased locomotor activity above baseline levels, then locomotor performance and the response to exercise play a crucial role within the larger life-history strategies of animals. We consider exercise from a life-history perspective, where allocating finite resources towards the exercise response can create trade-offs with other traits. In this Review, we synthesize our work on green anole lizards (*Anolis carolinensis*) to show how complex trade-offs can occur when resources are forced to be allocated to performance via specialized exercise training. There is still much we do not know about the exercise response of vertebrates, and future studies would benefit by considering exercise from a life-history perspective.

KEY WORDS: Exercise response, Metabolism, Performance, Plasticity, Trade-offs

Ecological relevance of exercise

To the average person, 'exercise' is an activity that requires strenuous physical effort and is performed to sustain or improve health and athletic fitness (Lieberman, 2015). However, to readers of this Review, there is likely a more nuanced view of 'exercise' as a physiological concept – 'physical activity that involves movement supported by sustained locomotor performance, increased cardiac output, and increases in energy expenditure above basal levels' (Yap et al., 2017, p. 195). The former definition seems to make exercise irrelevant to non-human animals (Halsey, 2016a,b), but the latter definition applies to many activities of free-living, non-human animals (Killen et al., 2017), particularly those primarily locomotor activities termed whole-organism performance that are typically studied under the auspices of the ecomorphological paradigm (Arnold, 1983; Garland and Losos, 1994; Lailvaux and Husak, 2014). Even in our distant human past, the former definition would have been irrelevant to us, since early humans would not have performed strenuous physical exercise only to improve health, but instead to hunt and forage like other animals (Lieberman, 2015; Shirley et al., 2022). Nevertheless, strenuous physical effort, or 'exercise', causes a multitude of physiological changes in the short and long term (e.g. Bouchard et al., 2011a,b; Hoppeler et al., 2011; Atherton and Smith, 2012). These changes can be viewed as a special case of phenotypic plasticity to overcome an environmental challenge that involves increasing locomotion (Garland and Kelly, 2006). In this Review, we adhere to the view that exercise should be seen as a scenario of chronic increased activity of individuals in a population. 'Chronic increased activity' is probably a sufficient term for these situations in nature, but when that increased activity is used for experimental manipulation, 'exercise' is more appropriate. The semantics between the two is beyond the scope of this Review, but we encourage others to be clear about what they mean when using the term 'exercise' in their studies. In either case, the response to that increased activity (i.e. the 'exercise response') results in metabolic shifts and resources being re-allocated to cause a variety of phenotypic trade-offs (reviewed by Lailvaux and Husak, 2014; Husak and Lailvaux, 2022). In this light, exercise, when broadly defined, is very relevant to most animals, since all animals move at some point in their lives, have limited resources and must deal with environmental challenges (Williams and Fowler, 2015; Husak and Lailvaux, 2022). Acquired energy must also be allocated in light of these challenges over the long term.

In a 2014 review (Lailvaux and Husak, 2014), we encouraged integrative biologists to incorporate exercise and whole-organism performance traits more generally into life-history research questions (see also Killen et al., 2017). Even though the idea does not seem to have caught on, those interested in human exercise physiology have independently embraced the idea of incorporating life-history theory into their study of exercise, especially recently (Lieberman, 2015; Pontzer, 2018; Shirley et al., 2022; Areta, 2023). Indeed, studies of exercise effects during periods of low energy availability have capitalized on concepts from life-history theory, such as energetic trade-offs and allocation priorities. Areta (2023) even proposed the hypothesis that selection has prioritized allocation of resources to locomotor capacity during periods of low energy availability because locomotion is one of the only means of acquiring more energy. This hypothesis is consistent with human studies that have shown maintenance or improvement in athletic performance even under low energy conditions (reviewed by Areta, 2023; see also Husak et al., 2016 and Lailvaux et al., 2020, for examples in lizards). Whole-organism performance traits, such as sprinting, endurance running and jumping are both energetically expensive (reviewed in Halsey, 2016b; Brownscombe et al., 2022; Hedenström, 2025) and important to Darwinian fitness, making them key targets of selection (Arnold, 1983; Irschick et al., 2008; Husak, 2015; Matthews et al., 2023). Performance traits are also involved in a number of trade-offs with other phenotypic traits, including classic life-history traits, such as age at first maturity and longevity (reviewed in Lailvaux and Husak, 2017; Husak and Lailvaux, 2017; Husak and Lailvaux, 2022; Husak et al., 2024;

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Glossary

Development costs
Costs incurred when the physiology and morphology underlying a performance trait is being built.

Exertion capacity
Also sometimes termed ‘distance capacity’, exertion has historically been defined by the way it is measured, rather than in terms of the underlying physiology. The animal in question is chased, often around a circular track, at top speed until it becomes exhausted. Exertion capacity likely incorporates aspects of aerobic and anaerobic physiology.

Fast-slow life-history continuum
A conceptual framework organizing life histories along a continuum from ‘fast’ life histories, characterized by rapid growth and development, high reproduction, and short lifespans, to ‘slow’ life histories characterized by slow growth and development, low reproduction, and long lifespans.

Maintenance costs
Costs necessary to maintain the performance trait once it has been built, even when it is not in use.

Production costs
Costs incurred when a given performance trait is used.

Pontzer, 2025). For example, experimental immune challenges alter performance capacities (Zamora-Camacho et al., 2015; Husak et al., 2021; Hudson et al., 2021a,b), whereas increasing investment in locomotion via exercise training reduces reproductive output (Husak et al., 2016; Minter et al., 2018) and alters immunocompetence (Chapman et al., 2015; Wang and Husak, 2020; Altizer et al., 2011). From this perspective, intense strenuous activity, or exercise, is not an extraneous or peripheral activity, but rather a central component of life-history strategies that drives crucial variation in resource acquisition and allocation.

Despite the lack of broadly incorporating exercise into integrative biology research, there is a large comparative literature that uses ‘exercise’ as an experimental tool. Exercise is used in these studies to determine two very different types of effects of increased locomotion in non-human subjects: acute short-term effects and chronic long-term effects. Acute effects are typically measured in a laboratory setting in animals that have not had previous experience with the ‘exercise’ performed during the study, so any effects are direct consequences of performing the exercise in that moment. For example, a group of animals could be maintained in the laboratory or brought to the laboratory from the wild, and exercised to exhaustion, during and after which metabolic, cardiovascular or hormonal changes due to that exhaustive exercise are measured (e.g. Poole et al., 2020; Hastings et al., 2022). This is distinct from long-term effects that occur with repeated bouts of the same exercise (i.e. exercise training). Such long-term studies (see the section ‘Phylogenetic distribution of exercise effects’) reveal different types of plastic responses to increased activity, including significant phenotypic trade-offs. Indeed, we argue here that these long-term responses constitute distinct strategies, with disparate physiological consequences and mechanisms. Importantly, these strategies are most apparent under conditions of limited resources, and they can be contrary to the ‘health benefits’ found with exercise in humans where resources are not limited. Even though we do not suggest that free-living, non-human animals ‘exercise’ to sustain or improve health and athletic fitness in human terms (e.g. Halsey, 2016a,b), individuals in natural populations do vary in their activity levels (Yap et al., 2017) and their responses to chronic increased activity (Husak et al., 2016, 2017), and they are susceptible to similar consequences of increased activity as seen in humans.

Our goal in this Review is to highlight studies that place exercise within an appropriate life-history framework, and to synthesize the literature regarding the relevant physiological mechanisms and genetic variation enabling the exercise response from an explicitly evolutionary perspective. Within that life-history framework, we discuss the costs and benefits of responding to exercise, and what the fitness consequences may be. We highlight our work on green anole lizards (*Anolis carolinensis*) as a framework to ask how investing more limited resources in performance impacts the rest of the integrated phenotype. We discuss the phylogenetic distribution and conserved nature of many aspects of the exercise response, with an emphasis on vertebrates. Finally, we conclude with an extensive list of questions that need further study if we are to properly understand the selective value of the exercise response within an ecological, evolutionary and life-history framework.

Costs of performance and exercise

From a purely physiological perspective, exercise has both short-term and long-term, chronic costs (e.g. Bennett, 1980). In the short-term, exhaustive exercise results in a 10-fold, or greater, increase in oxygen consumption above basal or standard metabolic rates (BMR or SMR, respectively; Weibel et al., 2004). In fishes, enhanced gas exchange capacity to match demands from swimming results in an increased passive movement of ions that can be osmotically disruptive (the ‘osmorespiratory compromise’, reviewed by Wood and Eom, 2021; also seen in sharks, Giacomin et al., 2022). In this case, gills with increased functional surface area and low diffusion distance to favor gas exchange will result in a cost of compromised osmotic balance. For all vertebrates, after the cessation of exercise, oxygen consumption remains elevated for hours to days (e.g. excess post-exercise oxygen consumption, EPOC; Gaesser and Brooks, 1984), and reactive oxygen species increase as a result of increased mitochondrial activity (Koch et al., 2021; Powers et al., 2024). For example, increased oxidative stress is associated with migratory flight in bats (Costantini et al., 2019) and elevated physical activity in humans (Pontzer, 2025). Circulating glucocorticoid and epinephrine concentrations increase to mobilize glucose from glycogen and non-carbohydrate sources (Howlett et al., 1999; Chen et al., 2017), and also elevate heart rate and blood pressure. All of these costs – which are accrued while doing the exercise and shortly thereafter – are what we refer to as production costs (see Glossary) (Husak and Lailvaux, 2017), and they are known from all vertebrate species studied (see below).

Additionally, the tissues necessary for activity and exercise (e.g. muscle, bone, cardiovascular system, etc.) must be actively maintained, and these metabolic processes are referred to as maintenance costs (see Glossary), typically measured as BMR or SMR. The effects of exercise training on BMR/SMR are equivocal, with some studies showing an increase and others showing a decrease (Speakman and Selman, 2003). If exercise results in building more tissue, such as muscle or blood cells (see below), then the extra tissue will also have maintenance costs. Exercise training can result in higher mitochondrial densities to increase ATP production (Heine and Hood, 2020), but if they have ‘leaky’ membranes, then BMR/SMR will be higher than for those with more efficient mitochondria, because leaky membranes result in more oxidative cycles but less ATP output (Else and Hulbert, 1981; Else et al., 2004; Konarzewski and Książek, 2013). However, exercise can affect mitochondria in other ways, such as mitochondrial fusion (Arribat et al., 2019) or increased mitochondrial efficiency at ATP synthesis, which increases ATP production without an increase in mitochondrial number or ‘leaky’ membranes (Treberg et al., 2018;

Boël et al., 2020). The direction in which exercise takes BMR/SMR among different species and why is unclear, as different lifestyles and energetic demands will influence the outcome (Koch et al., 2021).

Finally, as performance is enhanced by exercise training, existing tissues are modified and new tissues are built, resulting in development costs (see Glossary). Skeletal muscle hypertrophy, angiogenesis, increased hematocrit and cardiac modifications all require increased investment of acquired protein (Hoppeler et al., 2011). This can happen by increasing resource acquisition or diverting protein from other functions, or a combination of the two strategies (van Noordwijk and de Jong, 1986; Stearns, 2000; Tomkins et al., 2004). Development costs can be difficult to quantify, as they are transient and likely most apparent during the 'acclimation' period, when physiological capacities are in the process of being enhanced to match the new activity level, but studies that sample individuals frequently may be able to capture increases in metabolism that are independent of maintenance costs (Brook et al., 2016; MacKenzie-Shalders et al., 2020; but see MacKenzie-Shalders et al., 2019). Stable isotope studies may also reveal development costs by tracking the routing of macronutrients during the course of training. For example, Husak and Lailvaux (2024) fed endurance- and sprint-trained green anole lizards (*Anolis carolinensis*) an isotopically labelled essential amino acid (^{13}C-leucine) after 9 weeks of training to track its routing to four tissues (muscle, liver, gonads and spleen) under different combinations of resource availability (high- and low-calorie diets) and exercise training modalities (sprint and endurance training). Increased routing to muscle tissue compared to sedentary controls would have been an example of development costs. Unexpectedly, routing increased to the liver and spleen, not muscle, suggesting that, after extensive training, metabolic requirements (production costs) and blood cell turnover (development costs) were prioritized. Muscle hypertrophy had likely plateaued, but future studies that sample during the course of training will help to resolve this pattern.

In the long-term, chronic increased activity may result in trade-offs that result from increased allocation to performance that is shifted from other functions. All of these costs of responding to exercise are important, because they must be outweighed by fitness benefits to be maintained over evolutionary time. For example, if the immune system is suppressed, the survival advantage of enhanced locomotion should outweigh the survival detriment of the altered immune response. It is unclear which of the costs above (production, maintenance and development) are most important for causing phenotypic trade-offs, and it may be that they all are involved to some degree. An important unanswered question is how aspects of a species' life history impact plasticity to increased activity and its associated costs.

Specialized training of green anole lizards

Training lizards

Although mammals have served as the most common subjects for studies of exercise, lizards have emerged as a promising model system. Early studies on lizard exercise were fraught with difficulties and did not demonstrate significant training effects, though the reasons why differed across studies. *Sceloporus occidentalis* from the family Phrynosomatidae trained for 6 or 8 weeks with an increasingly intense endurance training regimen on a circular track did not have significantly better running performance or its presumed metabolic correlates (Gleeson, 1979). These results were initially attributed to a fundamental physiological difference between mammalian and saurian metabolic flexibility, but Garland et al. (1987) suggested that the training regimen may not have been intense enough above baseline movement patterns in nature to elicit a response. Garland et al. (1987) trained *Amphibolorus nuchalis* agamid lizards 5 days a week for 8 weeks (with increased intensity) on a treadmill and found no effect on endurance capacity compared to sedentary controls. However, trained lizards showed evidence of joint degradation, which the authors speculated was due to the excessive training regimen. O'Connor et al. (2011) trained teiid *Aspidoscelis sexlineata* with a training regimen that included treadmill endurance, maximum run time on a circular track and maximum burst speed. There were no training effects on performance traits, muscle fiber size or composition, or hematocrit. This lack of an effect was likely due to the simultaneous combination of different types of exercise, which prevented locomotor specialization because of an interference in the cellular pathways involved with protein turnover in the different types of exercise, as is the case in mammals (Coffey et al., 2009a,b; Hoppeler et al., 2011).

Despite these 'negative' findings with lizard exercise, our laboratories used these earlier studies to design specialized exercise training regimes that were meant to be strenuous enough, but not too strenuous, to cause an exercise response. We trained lizards for endurance on a small treadmill and for sprint speed on a wooden dowel that approximated a tree branch. Over the course of our studies, we changed how we increased intensity. Initially, we ran lizards more frequently to increase sprint intensity and increased the angle of the treadmill to increase endurance intensity (Husak et al., 2015). In later studies, we increased sprint intensity by tying successfully heavier weights to the lizards' waists when they ran, similar to human athletes (Lailvaux et al., 2018). We have not quantified how these different training regimes affect lizards differently, but in each case we obtained significant training effects, which we discuss below. By contrast, exertion capacity (see Glossary), the physiological basis of which is unclear (Baxter-Gilbert et al., 2017; but see Garland, 1984; Bennett and Huey, 1990), was not affected by sprint training or endurance training (Sorlin et al., 2022). Our goal with training was to force activity at the high ends of locomotor performance seen in nature. Each 30 min endurance training session equaled 90 m of slow traveling by each lizard. This is relevant to male and female green anoles in nature (Irschick, 2000), where ∼25% of their time budget (Jenssen et al., 1995) and a significant proportion of their energy budget (Orrell et al., 2004) are spent traveling through their territories and home ranges, with much of this time spent 'creeping' in trees at lower speeds. Green anoles use slow, sustained locomotion for territory patrolling and foraging, and there is great variation among individuals in the use of locomotion (Jenssen et al., 1995; Irschick and Losos, 1998; Irschick, 2000). For example, green anoles from southern Louisiana, USA, near where all of our subjects were collected, moved, on average, 60.6±9.6 m (mean±s.e.m.) daily, with a large range of 1.3–279.2 m (Irschick, 2000). In contrast, green anoles are sit-and-wait foragers that also rely on sprinting to capture prey and avoid predators, contexts in which they use near-maximal capacities (Irschick and Losos, 1998; Irschick, 2000). Sprints in nature can approach a meter in length per run in green anoles (Irschick, 2000), but sprinting distances have not been systematically studied in this species. Our training regimen at the high end of distance traveled in a day and at speeds used in nature was meant to determine how levels of performance towards the upper limits of use (and investment) might lead to phenotypic trade-offs. To that end, it is important to note that lizards were not fed *ad libitum* during training – instead, they were fed a diet that we empirically determined to result in trade-offs when lizards were energetically challenged (Lailvaux et al., 2012; Husak et al., 2016).

Endurance training

Endurance training had many effects consistent with those seen in humans and other mammals (Table 1). Interestingly, we found increased growth in body length (SVL), even when calories were restricted (Husak et al., 2016). Training generally decreased reproduction in females. Even though female corticosterone increased with training, the levels of corticosterone in the eggs of trained mothers was no different from control eggs (Hanover et al., 2019). Neither testis size nor maximum bite-force performance was affected by training in males (Husak et al., 2016). We found complex trade-offs with immune function, with the swelling response to phytohemagglutinin (PHA) and bacterial killing ability of plasma being reduced, but wound healing and acquired immunity (antibody production after exposure to sheep red blood cells) being unaffected (Table 1). Interestingly, the reduction in PHA swelling response due to training was rescued with leptin supplementation, but the trade-off with reproduction was not (Wang et al., 2019), emphasizing the complex nature of trade-off regulation. Stable isotope analysis revealed that long-term endurance training resulted in leucine being routed to the spleen and liver for blood cell turnover and metabolic substrate shifts, respectively (Husak and Lailvaux, 2024). One of the more interesting findings was the large range of responses to exercise. Endurance increased >250% on average (pre- to post-treatment measures), with a range of no increase to >1300% increase (data from Husak et al., 2016).

The vast majority of our studies were conducted on adult lizards, but we examined how trade-offs would differ in juveniles with different allocation priorities. Without investment in egg production or finding and acquiring mates, juveniles were expected to prioritize growth. Endurance training increased heart ventricle mass, hematocrit and baseline corticosterone levels, as in adults, but there was no effect on growth (Husak et al., 2017). The PHA swelling response was reduced in juvenile females but not in males (Husak et al., 2017). The lack of effect on growth was surprising and may be due to already-maximal growth rates or reduced plasticity from external stimuli because of the importance of growth at this life stage. More studies of exercise on juveniles are needed across species to test whether this pattern is consistent or co-varies with other factors, such as growth rate, age at maturity or longevity.

Sprint training

As with endurance training, effects from sprint training were similar to those seen in humans and other mammals (Table 1). We rarely found an increase in sprint performance itself after training. Although this seems counter-intuitive, it is almost certainly due to lizards acclimating to handling over the course of 2 months so that their motivation has decreased by the end of training (Losos et al., 2002). Nevertheless, they always completed training, which was rigorous for their daily activity patterns, and we did detect a significant increase in sprint speed in one study (Husak and Lailvaux, 2019). Despite our inability to consistently detect sprint performance enhancement, we did detect physiological changes that suggest it did occur, including increases in muscle cross-sectional area (Table 1). Contrary to studies on humans where resistance training increases BMR (Stavres et al., 2018; Mackenzie-Shalders et al., 2020), we found that sprint training reduced SMR (Lailvaux et al., 2018). However, sprint training resulted in a higher increase in metabolic rate (MR) after exhaustive exercise (EPOC) on a treadmill, as well as longer recovery time to return to baseline MR compared to sedentary controls and endurance-trained lizards, suggesting an increased anaerobic capacity (Lailvaux et al., 2018). Interestingly, sprint-trained lizards that were diet-restricted did not have decreased sprint speed compared with controls (Lailvaux et al., 2019), suggesting that the importance of sprint speed to fitness, especially foraging (Irscshick et al., 2008), may 'protect' it from trade-offs. Sprint training had complex trade-offs with immune function (Table 1), but it is unknown how it impacts reproduction. Like endurance training, sprint training had no effect on acquired immunity (antibody response to sheep red blood cells; Wang and Husak, 2020). Stable isotope analysis revealed that long-term sprint training resulted in leucine being routed to the spleen and liver for blood cell turnover and metabolic shifts, respectively, as seen in endurance training (Husak and Lailvaux, 2024). Surprisingly, leucine was not routed to muscle, compared to sedentary controls,

Table 1. Effects of specialized exercise training on green anole lizards (*Anolis carolinensis*)

Effect of endurance training	Effect of sprint training
Physiological traits	
Reduced SMR[1,2]	Reduced SMR[1]
Increased mitochondrial efficiency[2]	Increased EPOC[1]
Increased hematocrit[3,4]	
Increased heart ventricle size[4]	
Increased cross-sectional area of slow-oxidative fibers in gastrocnemius and iliofibularis muscles[3]	Increased cross-sectional area of fast-glycolytic muscle fibers in gastrocnemius and iliofibularis muscles[3]
Increased baseline corticosterone[4]	
Increased growth rate[4]	
Reproductive traits	
Decreased probability of laying eggs[4]	Fewer eggs[8]
No effect on average size of eggs[4]	Heavier eggs[8]
No effect on corticosterone levels in eggs[5]	Increased hatchling body length[8]
No effect on testis size[4]	
No effect on male maximum bite-force performance[4]	
Immunological traits	
Reduced PHA swelling response[4,6,7]	Mixed effects on PHA swelling response[6,7]
Reduced bacterial killing ability of blood[4]	
No effect on wound-healing ability[4]	Reduced wound-healing ability[6]
No effect on production of antibodies to sheep red blood cells[7]	No effect on production of antibodies to sheep red blood cells[7]

Summary of how endurance and sprint training affected multiple aspects of the phenotype. Directions of change are relative to sedentary control lizards. EPOC, excess post-exercise oxygen consumption; PHA, phytohemagglutinin; SMR, standard metabolic rate. [1]Lailvaux et al. (2018); [2]Reardon et al. (2023); [3]Husak et al. (2015); [4]Husak et al. (2016); [5]Hanover et al. (2019); [6]Husak and Lailvaux (2019); [7]Wang and Husak (2020); [8]Marks et al. (2023).

after the 8 weeks of training, likely because the lizards had plateaued in their muscle hypertrophy, as seen in human bodybuilders (Husak and Lailvaux, 2024).

The increased investment in muscle cross-sectional area in sprint-trained animals has potential consequences not only for the proximate phenotype of the organism in question, but also for that organism's subsequent investment in reproductive effort. The mechanistic life-history 'decision' to invest in survival versus reproduction is governed by the insulin and insulin-like signaling network (ILS). The activation of specific components of these networks is associated with investment in survival, reproduction and growth (reviewed by Regan et al., 2020). Increased investment in skeletal muscle growth via resistance training is typically associated with an increase in a key ILS agonist called insulin-like growth factor 1 (IGF1); however, decreases in circulating IGF1 are associated with dietary restriction (defined as caloric restriction without malnutrition) and investment in survival-related mechanisms at the cellular level, with a consequent decrease in reproductive investment. Marks et al. (2021) showed that gene expression of *IGF1* is mediated by changes in body mass in diet-restricted green anole females, and Marks et al. (2022) found that sprint training also affected *IGF1* expression in a size-dependent manner, such that larger sprint-trained females expressed hepatic *IGF1* at the highest levels. Finally, these effects on the maternal phenotype also correlated with changes in the phenotypes of offspring, such that hatchlings from sprint-trained mothers were significantly larger than those from untrained mothers.

Synthesis

Studies of green anole lizards suggest a myriad of phenotypic trade-offs with performance capacities when resources are limited during training. We have previously predicted that forced allocation to performance, and its underlying biochemical, morphological and physiological predictors, would result in trade-offs when resources are limited (see figure 3 in Lailvaux and Husak, 2014). At that time, only a partial test of those predictions was possible for any species; adult male field crickets (*Teleogryllus commodus*) showed complex trade-offs among performance and classic life-history traits (Figure 4 in Lailvaux and Husak, 2014). We can now greatly expand those links with our studies of green anoles. Fig. 1 shows how forced investment into endurance capacity via exercise training results in trade-offs with a variety of phenotypic traits. We discuss the fitness implications of these trade-offs in the section 'Selection on the exercise response'. Additionally, since we controlled diet in the laboratory, daily energy intake was kept constant to give us a better idea of which components of their energy budgets were increasing or decreasing after training. Savings in maintenance costs (lowered SMR) were not sufficient to protect reproduction and components of immune function from increased production and presumed development costs associated with training (Fig. 2). Perhaps most surprising is that, even when training was coupled with diet restriction, performance capacities were maintained (Lailvaux et al., 2019) and usually enhanced (Husak et al., 2016, 2017).

Another key takeaway from our studies on green anoles is that trade-offs seem to depend on the type of exercise (i.e. endurance versus sprint). As expected, based on mammalian studies, sprint training increased muscle hypertrophy and endurance training resulted in changes to increase oxygen delivery to tissues. More interesting from a life-history perspective is that components of the immune response were differentially affected by the two types of training. Worthy of note is that our measure of acquired immunity (antibody production in response to sheep red blood cell injection) was unaffected by either type of training. Further research is necessary to understand the ultimate reason for these performance-immunity trade-offs, or lack thereof. With such clear trade-offs present between performance and other traits presumably important for survival (immune function) and reproduction, the obvious question is what selective pressures maintain the exercise response in green anole lizards and other species? Although that question cannot currently be answered with certainty, studies of the genetic variation underlying the exercise response offer potential insights into the relevant factors at play.

Evolution of the exercise response

Heritability and genomics of the human exercise response

Performance traits that are linked to fitness in key ecological contexts, like many other continuous traits, have both genetic and environmental components. The quantitative genetics of performance is understudied in the vast majority of animal species, likely due to a combination of the difficulty of obtaining these data within the context of a rigorous breeding design or well-resolved pedigree, and a general lack of

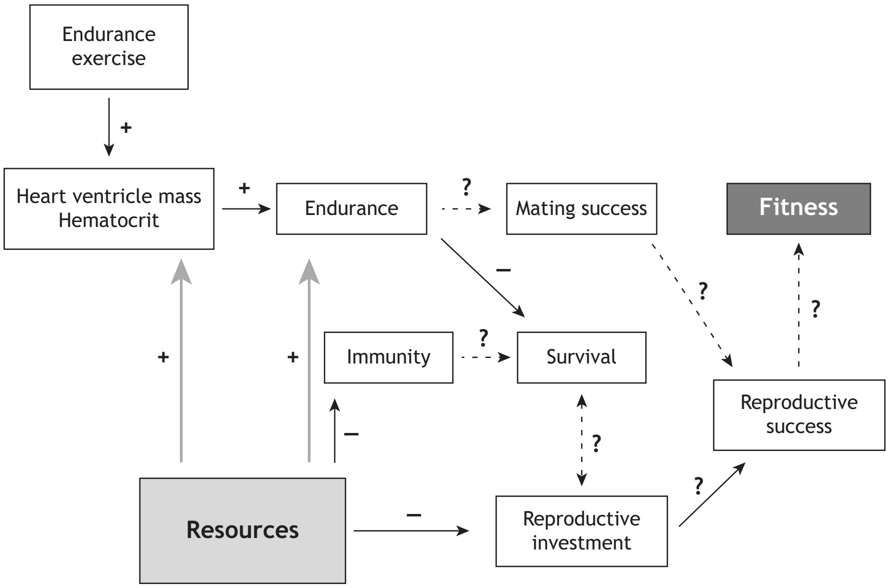

Fig. 1. Summary of endurance training studies on green anole lizards. Empirical results from our studies of green anole lizards that have filled in the conceptual diagram (modified from figure 3 of Lailvaux and Husak, 2014). Although not all links are derived from a single study, many of these effects have been replicated across different studies (see Table 1 and text for details). Arrows indicate allocation of resources to traits and relationships between traits after endurance training, in comparison to sedentary controls. Solid lines represent empirically confirmed links, whereas dashed lines represent likely links that have not been empirically tested. +, positive relationship; –, negative relationship; ?, untested relationship. For example, after training, resources are allocated to heart ventricle mass and endurance, but away from reproduction and components of immunity. Not all possible links are shown, only those empirically detected and suspected based on empirical findings.

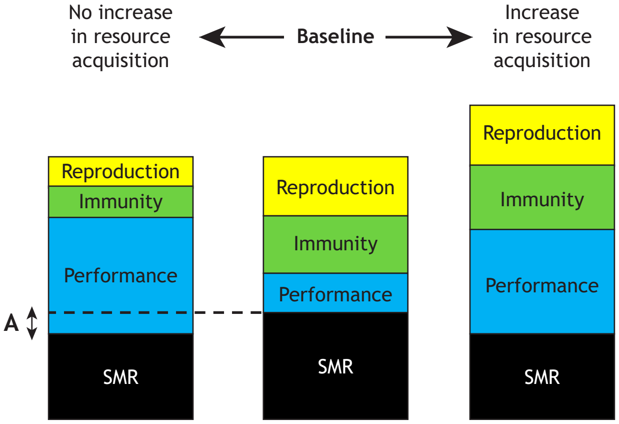

Fig. 2. Endurance training in green anoles without increased food availability resulted in significant phenotypic trade-offs. Significant increases in activity, without increases in food availability (left), resulted in higher production costs (blue; performance), as well as performance enhancement. Performance enhancement occurred by alterations to morphology (development costs) and physiology that lowered maintenance costs (indicated by A). Despite savings in maintenance costs, the increased production (and possibly development) costs of endurance training reduced allocation to reproduction and components of the immune system. Alternatively, with increased food availability (right), not only can trade-offs be mitigated, but there could be increases in allocation to immunity and/or reproduction along with increased performance. The size of boxes is not based on quantitative measures of energy costs for each, but are intended for qualitative comparisons (see Careau et al., 2008). SMR, standard metabolic rate.

interest in the genetics of animal performance from more than a few researchers (but see Garland et al., 1990; Dohm et al., 1996 for some key examples). However, the relatively few published studies that have attempted to quantify the heritability of performance typically show moderate and significant additive genetic variation for such traits, including narrow-sense heritabilities of 0.15 for flight duration in the fly *Drosophila aldrichi* (Gu and Barker, 1995), 0.21 for mean take-off acceleration in the butterfly *Pararge aegeria* (Berwaerts et al., 2008), 0.3 for jump power in *Teleogryllus commodus* crickets (Lailvaux et al., 2010) and 0.46 for endurance in *Zootoca vivipara* (although the heritability for sprint speed in this same species was not significant; Sorci et al., 1995). The genomic basis of animal performance is also poorly understood, although several recent studies have connected candidate genes to performance variation in some species. For example, genes such as *PPL* that regulate the keratin cytoskeleton are associated with climbing and grasping in Asian flying tree frogs (*Rhacophorus* spp) (Wu et al., 2022); however, here it should be noted that, in some cases where traits are labelled by authors as locomotion, they are more plausibly considered to be measures of behavior instead (e.g. exploratory locomotion; Chitre et al., 2023).

By contrast, the genomic basis of exercise within the context of human performance is at least moderately well-studied, with several candidate loci being linked to various forms of superior human athletic performance, especially endurance and strength (reviewed by Yao et al., 2025). The *R* variant of the gene *ACTN3*, which encodes the protein alpha-actinin-3, is considered to be associated with increased sprint speed – likely through its effects on muscular contraction – at least in comparison to the *X* variant, which does not produce alpha-actinin-3 (Berman and North, 2010). A variant of the *COL5A1* gene, which encodes proteins that make up collagen, is also associated with less flexible Achilles tendons and enhanced performance in the running component of Ironman competitions (but may also make bearers more prone to injury) (Posthumus et al., 2011). Other candidate genes, such as the angiotensin converting enzyme in/del (*ACE* I/D) polymorphisms, exhibit more controversial relationships with both endurance and sprinting (Kritchevsky et al., 2005; Minami et al., 2007). However, associations with elite athletic performance are often tentative at best, limited primarily by the small absolute number of elite athletes and the consequent low historical power of such association tests.

Although the exercise response is a form of phenotypic plasticity, that response is itself likely to have both genetic and environmental components in many animal species. Indeed, in human studies, there are individuals that do not appear to respond to exercise, but the reasons why are controversial (Pickering and Kiely, 2019). Consequently, both the capacity to perform a given athletic feat and the ability to respond to training specifically targeted at that feat are both underpinned by distinct patterns of genomic variation. The HERITAGE (HEalth, RIsk factors, exercise Training And GEnetics) study, a large-scale investigation of cycling exercise across 228 families in North America, quantified the heritability of human cycling endurance (0.42), but also showed that the individual capacity to respond to cycling training exhibited a heritability (h^2) of 0.47 (Bouchard, 2012). Furthermore, Bouchard et al. also identified 21 candidate genes that are implicated in the cycling exercise response (Bouchard et al., 2011a,b; Bouchard, 2012). Comparable studies for power-based athletic capacities such as sprinting are lacking, although phenotypic variation in the response to standardized resistance training has also been noted in humans (Hubal et al., 2005).

Despite this detailed work on human exercise training, no comparable genetic or genomic studies to our knowledge have investigated the training response in animal species. Swallow et al. (2009) described the results of a long-term study considering artificial selection on voluntary wheel-running performance in mice, which revealed insights into morphology, physiology and genetic factors affecting the evolutionary response to increased activity levels (see also Hillis and Garland, 2023). Importantly, this study also demonstrated the effect of neurochemical factors driving increased voluntary activity, including dopamine (see also Bubak et al., 2022; Adeola and Lailvaux, 2023 for discussion of the neurochemical basis of performance motivation in insects). Nonetheless, the genetic factors underlying both the exercise response and enhanced locomotor performance remain understudied in the vast majority of animal species.

Among the various factors that influence muscle growth, IGF-1 and myostatin have received the most attention. A product of the *MSTN* gene, myostatin is a myokine protein that inhibits muscle growth via its regulatory action on both developmental and post-natal muscle fiber number and growth. Within the context of animal breeding, mutations in *MSTN* are associated with 'double-muscled' phenotypes – extreme muscularity – in animals such as cattle and some domestic dogs (Rodgers and Garikipati, 2008). 'Bully' whippets harboring two copies of a two base-pair deletion in the third exon of *MSTN*, have extreme muscularity that renders them unsuitable for racing, whereas individuals exhibiting only one such copy are significantly faster in competitive racing events than those carrying the wild-type genotype (Mosher et al., 2007). Similarly, *MSTN* polymorphisms also predict sprinting ability and racing stamina in thoroughbred horses (Hill et al., 2010). Myostatin is deeply conserved within vertebrates (albeit comprising two sister clades within teleost fish, Rodgers and Garikipati, 2008) and is generally considered to be under purifying – as opposed to positive – selection in most vertebrates, so as to optimize muscle size and function (Pie and Alvares, 2006). However, the known interaction between myostatin and muscle fiber type (Lee, 2010) suggests a potential role for myostatin in regulating muscle growth in response to training that is likely unequally distributed across the vertebrate phylogeny, depending on the activity levels and evolved performance-based strategy of the species in question. This notion has received no attention from evolutionary physiologists, and the role of myostatin in regulating the training response in various organisms, if any, is unknown. The very existence of myostatin and its regulation of muscle growth emphasize the energetic costs of increasing muscle mass and position locomotor performance capacities as central components of animal life-history strategies. Myostatin in fishes appears to be a more general inhibitor of cell proliferation and growth in numerous tissues instead of a specific regulator of only muscle (Gabillard et al., 2013). Whether this is an ancestral or derived function may shed light on how the exercise response evolved, although we note that there is both determinate and indeterminate growth present in fishes (Dutta, 1994; Johnston et al., 2011). This is an especially important question given the phylogenetic distribution of exercise responses across vertebrates.

Phylogenetic distribution of exercise effects

Available data suggest that much of the response to exercise is conserved across vertebrates (Bennett, 1980, 1991), though comparable data across taxa are scarce. All vertebrates seem to increase metabolic rates after acute exhaustive exercise (EPOC), suggesting that this form of plasticity is ancestral in vertebrates (Gleeson, 1991; Hedrick et al., 2015). Post-exercise metabolic changes are well-documented in bony fishes (reviewed by Magnoni et al., 2013; Holder et al., 2022) and have been found in sharks (Pacific spiny dogfish, *Squalus suckleyi*, Giacomin et al., 2022). Similar effects have also been found in jawless fishes [sea lamprey, *Petromyzon marinus* (Boutilier et al., 1993); Pacific lamprey, *Lampreta tridentata* (Mesa et al., 2003)]. Given that muscle evolved early in Metazoan history (Seipel and Schmid, 2005), it is almost certain that metabolic plasticity due to increased activity is also ancient (reviewed by Husak and Lailvaux, 2022). Indeed, insects (and even spiders; Anderson and Prestwich, 1985) have been good model systems for exercise physiology (Wegener, 1996; Lorenz and Gäde, 2009) despite their cardiorespiratory systems being very different from vertebrates. An ancient origin of acute response to exercise makes sense given that most, if not all, animals must alter their movement to deal with environmental challenges at some point in their life, thus favoring plasticity in the physiological underpinnings of locomotion. What is less clear is whether responses to chronic exercise are evolutionarily conserved. We focus our discussion on vertebrates, since they share many similarities in cardiorespiratory function, as well as homeostatic mechanisms.

Most vertebrates that have undergone exercise training show effects that are generally similar, but not identical, to mammals. It is beyond the scope of this Review to point out every similarity and difference; instead, we refer readers to the individual papers and indicate their relevance to a life-history perspective. Most studies that use exercise training have been interested in determining the specific physiological responses to acute and chronic exercise. These are important questions, but they impact how the studies were conducted. In the vast majority of cases, individuals were fed *ad libitum*, thus precluding energetically based trade-offs because of increased available energy (Careau et al., 2008). This makes sense in studies of fish exercise physiology if the goal is to increase muscle growth for aquaculture purposes. However, to detect trade-offs that might occur in nature with increased activity, diets of experimental animals must be carefully controlled and resources limited (Reznick et al., 2000; Garland et al., 2022). Nevertheless, the fact that a diverse group of vertebrates show similar responses to exercise suggests that much of the plasticity is evolutionarily conserved with some specialized adaptations to fit the lifestyle of the species. It remains unknown what aspects of life history determine which aspects of the exercise response, but there are some clues in comparative studies. A phylogenetic comparative analysis of 25 phrynosomatid lizard species revealed that species with high endurance capacity also have low relative clutch masses and a small size at maturity, but have higher SMRs, live longer and have larger offspring (Husak and Lailvaux, 2017). No relationships were found between any life history trait and sprint speed in these lizards. A phylogenetic comparative analysis of 72 mammal species showed that species on the 'fast' end of the fast–slow life-history continuum (see Glossary) also spend less of their total daily energy budgets on locomotor performance, suggesting that performance likely trades off against growth, reproduction and, possibly, longevity (Lailvaux and Husak, 2017). In an extended comparative analysis on the same mammal species, mammals with non-monogamous mating systems were associated with larger testes, faster life histories and lower costs of locomotion compared to monogamous species (Husak et al., 2024). Such comparative studies are revealing because, despite variation in data collection across studies used in such analyses, clear links have still been found between performance and other aspects of life history. This highlights the importance of locomotion to fitness, but also its costs. Thus, we expect the response to exercise, and trade-offs with other traits, to be widespread across vertebrates.

Generally, studies that use exercise training regimes result in increased performance. As we noted above for green anole lizards, though, motivation often decreases after prolonged handling in a laboratory setting, resulting in a decrease in apparent maximum performance despite physiological changes that should enhance it (e.g. Husak et al., 2015). Outside of mammals, fish are the best-studied group for how long-term exercise training affects morphology and physiology, largely due to demands in the aquaculture industry (He et al., 2013; Huang et al., 2021; Palstra and Planas, 2013). Perhaps the most well-known effect of exercise in fish is increased growth (reviewed by Davison, 1997; Palstra and Planas, 2013), especially in species with active lifestyles, such as salmonids, and those that have a large metabolic scope (Randall and Brauner, 1991; Davison and Herbert, 2013; Fu et al., 2022; Rodgers and Gomez Isaza, 2024). The lifestyle of the fish species appears important, with sedentary species having little response. In perhaps one of the most entertaining studies ever performed, attempts to train Japanese flounder resulted in fish just being blown away by the flowing water (Ogata and Oku, 2000).

Growth promotion via sustained swimming has also been found in sharks, even when other effects of training are not detected (leopard shark, *Triakis semifasciata*; Gruber and Dickson, 1997). However, the hypertrophy of skeletal muscle, increase in aerobic capacity, cardiac hypertrophy and beneficial effects on the immune system (reviewed by Palstra et al., 2013) found in fishes were not found in leopard sharks that were exercised for 6 weeks (Gruber and Dickson, 1997). Training increased growth, white myotomal fiber diameter, citrate synthase activity in white and red myotomal muscle, and lactate dehydrogenase activity in white myotomal muscle, but there was no effect of training on maximal sustainable speed, oxygen consumption rate, liver mass, liver lipid, glycogen and protein concentrations, white muscle protein content, heart ventricle mass, or the activities of heart ventricle enzymes. The authors speculated that endurance capacity may have increased (although it was not measured), but proposed no hypotheses as to why so many traits did not respond to training. More studies on sharks will be very helpful to understand why plasticity in the face of increased activity may vary so much, especially in light of the fact that sharks are mostly restricted to saltwater, whereas many bony fishes are not, making the groups physiologically distinct. Sharks in particular will be useful, since some have obligate ram ventilation that requires constant locomotion for respiration, while others can use buccal pumping (like the leopard sharks mentioned above) or a combination of both (Carlson et al., 2004).

Does the opportunity for variable locomotion promote the evolution of greater plasticity in those species that are not dependent on ram ventilation? Among bony fishes, tuna species are obligate ram ventilators with high-performance swimming and high metabolic rates (Magnuson, 1978). Like other fishes, tuna increase oxygen consumption with increasing swimming speeds (Korsmeyer et al., 1997) during acute exercise, but it is unknown how they respond to long-term exercise. Brill and Bushnell (1991) argued that tuna, living in the vast pelagic zone, have evolved physiological adaptations for exceptional aerobic capacities that promote continuous swimming. As pelagic fish ‘can run but cannot hide’ (Brill and Bushnell, 1991, p. 2002) in open ocean, there should be little selection to reach high maximum burst speeds. Indeed, Brill (1996, p. 3) hypothesized that ‘the ability of high-performance pelagic species (tunas, billfishes, and dolphin fish) to deliver oxygen and metabolic substrates to the tissues at high rates evolved to permit rapid somatic and gonadal growth, rapid digestion, and rapid recovery from exhaustive exercise (abilities central to success in the pelagic environment), not exceptionally high sustained swimming speeds’. Here, locomotion and the response to increased locomotion is central to life history. Long-term training studies on these species would be very illuminating, but admittedly difficult to accomplish given their relatively large body sizes and large space requirements.

Among amphibians, leopard frogs [*Lithobates* (*Rana*) *pipiens*] that were endurance trained on a treadmill increased performance (hops to fatigue), citrate synthase activity and lactate clearance rates similar to mammals (Cummings, 1979). African clawed frogs (*Xenopus laevis*) showed slightly different results. Frogs were trained for either sprinting or endurance swimming, and significant performance enhancement was observed with both (Miller and Camilliere, 1981). Endurance training decreased lactate accumulation after exercise, but neither citrate synthase activity nor heart mass were affected by training. In both species, individuals were fed *ad libitum*, and other phenotypic traits that might represent trade-offs were not measured. The acute effects of exercise have been studied in several salamander species, revealing typical patterns of increased oxygen consumption, even among lungless species (Full et al., 1988). However, we are unaware of any studies that have exercised salamanders for extended periods of time.

Two crocodilian species have been studied. Juvenile estuarine crocodiles (*Crocodylus porosus*) were trained to run on a treadmill for 16 weeks (Owerkowicz and Baudinette, 2008). Training increased endurance capacity and VO_2max, but it had no effect on SMR. Juvenile American alligators (*Alligator mississippiensis*) were regularly trained for 15 months, either running on a treadmill or swimming in a flume (Eme et al., 2009). Compared to sedentary controls, trained alligators had higher peak oxygen consumption rates, and increased heart ventricular mass and hematocrit. There was no effect of training on skeletal muscle mass or the activities of citrate synthase and lactate dehydrogenase. These studies also fed subjects *ad libitum*. Although acute effects of exercise have been shown to increase oxygen consumption and heart rate in turtles (e.g. Chessman, 2019; Okuyama et al., 2020), we are unaware of any studies that have exercised turtles over long periods of time.

Bird migration is, energetically, probably the closest thing in free-living animals to exercise in humans (Butler, 2016; McWilliams et al., 2021; Hawkes, 2025; papers in this special issue), but that phenomenon is beyond the scope of this Review. Instead, we focus on studies that have used laboratory-based exercise training (see also Butler, 1991). Starlings (*Sturnus* spp.) that were exercised for 2 weeks in a wind tunnel showed increases in flying endurance (*S. roseus*, Engel et al., 2006; *S. vulgaris*, Price et al., 2011) and flight muscle mass (Price et al., 2011). While acute exercise in European starlings increased expression of *IGFI* mRNA, long-term exercise did not, and *myostatin* expression was unaffected by training (Price et al., 2011), as were lipid transporters in another study of the same species (Price et al., 2022). House sparrows (*Passer domesticus*) that were endurance trained for 24 days to continuously fly between two perches showed increased pectoralis muscle mass and heart mass, as well as reduced BMR and increased MMR (Zhang et al., 2015). Tufted ducks (*Aythya fuligula*) endurance trained for 9 weeks to swim in flowing water had increased maximal oxygen consumption compared to controls, but no change in BMR (Butler and Turner, 1988). Increased oxidative capacity was likely due to the increased muscle capillarity and citrate synthesis activity. Resting heart rate was also significantly lower in trained ducks compared to controls, but heart mass did not differ between groups. Muscle fiber types were apparently altered by training, with an increase in oxidative fibers in the lateral gastrocnemius (slow oxidative fibers in the red region and fast-oxidative-glycolytic in the white region), although no differences in fiber type were found in the semitendinosus. Although not conducted in a laboratory setting, Eared grebes (*Podiceps nigricollis*) in eastern California, USA, voluntarily ‘train’ by performing flapping exercises before migrating (Gaunt et al., 1990). During the summer months when food is plentiful, flight muscles can atrophy up to 50% in mass. The flapping exercise serves to stimulate hypertrophy, boosting the muscles back to an appropriate mass to sustain migration. This is similar to the ‘self-induced adaptive plasticity’ originally described for laboratory mice that voluntarily run at high frequency, benefitting from the exercise (Swallow et al., 2005). In the laboratory studies, individuals were fed *ad libitum*, and in the study of eared grebes, other phenotypic traits that may trade off were not measured.

Selection on the exercise response

The widespread distribution of exercise responses across vertebrates (and invertebrates) suggests that there is selection to maintain this form of phenotypic plasticity. This means that the response to exercise is part of a system of mechanistic pathways that extend to all major systems in the body and have evolved to maximize fitness under environmental conditions where chronic increased activity is necessary. Given the presumably high costs of increasing performance, the benefits must outweigh those costs for selection to maintain it. Not surprisingly, this idea remains largely untested.

A foundational component of the influential ecomorphological paradigm is the assumption that performance affects fitness (Arnold, 1983; Garland and Losos, 1994; Irschick et al., 2008). This link has been the subject of numerous correlational and experimental studies (Husak, 2015), and the finding that selection alters performance in nature has been demonstrated repeatedly. One important and testable prediction arising from the general relationship between enhanced performance and fitness is the suggestion that individuals that enhance their performance capacities via the exercise response may accrue fitness or survival benefits through those enhanced capacities.

Husak and Lailvaux (2019) tested this prediction directly by training green anoles for sprinting or endurance, releasing those trained animals into an urban space that had been emptied of resident animals and tracking their survival alongside that of untrained controls. Counter-intuitively, instead of increased survival, they found that enhanced endurance and sprint speed achieved through exercise actually compromised survival in the wild compared to control lizards. Admittedly, we do not know how much 'de-training' there was after the cessation of training. Nevertheless, these results suggest that forcing re-allocation of resources due to exercise moves individuals away from an optimal phenotype, hinting at fitness costs to the exercise response beyond those energetic development, maintenance and production costs already discussed.

Although the ability to plastically alter one's physiological capacities might be beneficial to certain species in specific contexts (Huey et al., 1999; Deere and Chown, 2006; Garland et al., 2022), a further possibility that has received relatively little consideration in the literature is that those performance phenotypes might be canalized by selection in some cases. If the costs associated with the training response outweigh the selective benefits of altering one's performance abilities, then selection might be expected to purge that plasticity (Murren et al., 2015), resulting in a performance phenotype that does not respond to any training regimes that would otherwise induce an exercise response in other species. Performance is likely generally important to a majority of animal taxa; however, species that routinely or obligately perform at exceptionally high levels might be especially expected to exhibit canalized performance phenotypes. For example, laboratory mice selected for high voluntary running have evolved higher endurance capacity, with a trade-off for lower sprint speed in some lines (Dlugosz et al., 2009). In aquatic fishes such as sharks and tuna, which rely on ram ventilation – requiring constant locomotion to move oxygenated water over their gills – little evidence exists for responses to that training other than sharks showing enhanced growth as a consequence of exercise training (see the section 'Phylogenetic distribution of exercise effects'). Terrestrial species that exhibit exceptional locomotor capacities, such as cheetah, pronghorns and wild dogs, might also be expected to exhibit limited plasticity in their respective locomotor specialities. Any such investigations would ideally be accompanied by rigorous measures of selection on those capacities in nature – a particular challenge for certain species where acquiring either of those types of data (training or selection) alone might be difficult, at best.

What is still unknown?

Many questions remain about the ecology and evolution of exercise, as well as how locomotor performance in general fits within a life-history perspective. However, what is clear is that such a perspective offers valuable insights into the evolutionary and physiological ecology of exercise. Given that the exercise response is generally conserved across vertebrates and is almost certainly ancestral, more studies across more taxa are warranted, if not required, to better understand the evolution of energy budgets, metabolism and life histories. Here, we offer several suggestions for future research that will help with this knowledge gap. Perhaps the most important, but easiest, is to conduct more studies of exercise training with limited energetic resources while measuring a multitude of key phenotypic traits (e.g. reproduction and immune function). These will allow a better understanding of how different trade-offs are associated with life-history strategy. Perhaps trade-offs are conserved regardless of life history because of conserved mechanisms of plasticity (Husak and Lailvaux, 2022), or perhaps it varies according to lifestyle.

There is still a great deal unknown about the nature of performance-life-history trade-offs. Do the same traits consistently trade off in all taxa, or are allocation priorities labile due to differential selection pressure and independent evolution of plastic response systems? How much exercise is necessary to cause trade-offs? Our work on green anoles, for example, discerned trade-offs at the end of a relatively long training regime, but the time course of those trade-offs is still unknown. Do they occur early in training when development costs are high and persist due to constant increased production costs, or do they slowly develop over time? Our stable isotope results showing little routing of leucine to muscle at the end of training (Husak and Lailvaux, 2024) suggest that the former may be true in green anoles, at least for sprint training. Similarly, we still know little about the exact mechanisms responsible for the trade-offs. We can speculate about many, but we still know few for certain. Transcriptomic studies during the course of training will reveal many more details, as will manipulating particular pathways. For example, inactivating myostatin during sprint training could reveal how the regulation of muscle growth impacts reproduction, immunity and growth.

Lots of studies use exercise as a tool, but the phenotypic effects that are measured are often very limited. This is understandable, as most people measure what is relevant to their research question. The consequence is that there is a large database of studies on exercise training effects that have little overlap in phenotypic responses, making formal comparative analyses challenging. We urge researchers, where possible, to measure as many potentially linked phenotypic traits as possible when conducting an exercise study. Additionally, if subjects are euthanized for sampling purposes, use tissues as much as possible or preserve them in a way that could be of use for collaborators or future analysis (e.g. flash freezing and storing at −80°C). Obviously not everything can be measured in every study, but extracting as much information as possible will greatly benefit the community of integrative biologists. While there can be statistical issues with multiple comparisons in such cases, we feel that these probable links will not be discovered unless investigators look for them.

The vast majority of exercise studies focus on endurance and aerobic capacity. This leaves a paucity of knowledge about other types of training. Endurance may not be ecologically relevant for many taxa, so training studies should include consideration of what type of training makes the most sense to the species of interest. We know little about power-based training in humans, much less in other taxa, and human studies are often conducted within very specific experimental contexts, which limits comparisons between humans and other species in particular. Qualitative evaluation of our studies alone show that trade-offs are different between endurance and sprint training, because the molecular response pathways differ, as do the types of changes that happen to enhance performance (e.g. oxygen delivery in endurance training versus muscle hypertrophy in sprint training). Training for three different types of locomotion (endurance, sprinting and exertion) in six-lined racerunner lizards (*Aspidoscelis sexlineata*) resulted in no enhancement in any (O'Connor et al., 2011), but the mechanism for this remains completely unknown.

Finally, a crucial question is how the exercise response is adaptive. Is it advantageous not only in the short term in environments where resources are limited but also in the long term for humans where resources are not limited and trade-offs are unlikely? Using a life-history approach in exercise studies will help us better understand this. If enhanced performance does increase survival in some species, any trade-off with current reproduction should be balanced by increased future reproduction due to the increased survival. Our findings that training-enhanced performance decreases survival in green anole lizards raises many questions about how much enhancement is advantageous and how long the enhancement persists. It is also unclear how much exercise is too much. Presumably selection has shaped a window of responses that are optimal, so why maintain the capacity to respond stronger than necessary? Studies on free-living animals that examine among-individual variation in the response to exercise will help answer this question.

Mechanisms of plasticity are best detected using standardized protocols, but this is challenging in studies of exercise effects, as is evident in human exercise studies (e.g. Pickering and Kiely, 2019). We can make some very general recommendations, such as: (1) have a large sample size, (2) measure performance traits multiple times to ensure maximal responses are recorded, (3) limit resources and make sure animals are in an appropriate energetic state (i.e. not starving), especially for your research question (e.g. should they be in a reproductive state or not?), (4) use a relevant type of exercise for your study species (e.g. do not expect sustained swimming from flounder!) and (5) make exercise regimens challenging but not overly strenuous. This last point will undoubtedly be the most challenging. Empirical data on natural activity of the study species are necessary to determine what an appropriate exercise regimen should be. Even with slightly different methodologies, a comparative dataset of exercise responses and trade-offs will be very helpful in understanding how those responses have evolved and been maintained.

Conclusions

Exercise physiology and life-history theory fit together naturally. Life-history strategies revolve around metabolism, and metabolism is intimately linked to locomotion. Although the exercise response to acute and chronic increased activity appears to be ancient, there appears to be variation in the specific responses across species. What is not known is how and why those differences exist, and how the various costs of exercise fit into energy budgets to affect the integrative phenotype. Furthermore, even though we argue that performance and exercise are important to animal life histories, frankly, it is unknown how relevant laboratory exercise regimes are to free-living animals. More studies on animal activity in nature, as well as on what stimuli increase locomotion, are needed. Nevertheless, the evolutionary maintenance of the exercise response in vertebrates suggests that this form of plasticity is adaptive – we just need to figure out how.

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Competing interests

The authors declare no competing or financial interests.

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References

Adeola, F. and Lailvaux, S. (2023). Bite force, body size, and octopamine mediate mating interactions in the house cricket (*Acheta domesticus*). *J. Evol. Biol.* **36**, 1494-1502. doi:10.1111/jeb.14226

Altizer, S., Bertel, R. and Han, B. A. (2011). Animal migration and infectious disease risk. *Science* **331**, 296-302. doi:10.1126/science.1194694

Anderson, J. F. and Prestwich, K. N. (1985). The physiology of exercise at and above maximal aerobic capacity in a theraphosid (tarantula) spider, *Brachypelma smithi* (FO Pickard-Cambridge). *J. Comp. Physiol. B* **155**, 529-539. doi:10.1007/BF00694442

Areta, J. L. (2023). Physical performance during energy deficiency in humans: an evolutionary perspective. *Comp. Biochem. Physiol. A* **284**, 111473. doi:10.1016/j.cbpa.2023.111473

Arnold, S. J. (1983). Morphology, performance and fitness. *Am. Zool.* **23**, 347-361. doi:10.1093/icb/23.2.347

Arribat, Y., Broskey, N. T., Greggio, C., Alonso, S. C., Kulkarni, S. S., Lagarrigue, S., Carnero, E. A., Besson, C., Cantó, C. and Amati, F. (2019). Distinct patterns of skeletal muscle mitochondria fusion, fission and mitophagy upon duration of exercise training. *Acta Physiol.* **225**, e13179. doi:10.1111/apha.13179

Atherton, P. J. and Smith, K. (2012). Muscle protein synthesis in response to nutrition and exercise. *J. Physiol.* **590**, 1049-1057. doi:10.1113/jphysiol.2011.225003

Baxter-Gilbert, J., Muhlenhaupt, M. and Whiting, M. J. (2017). Comparability and repeatability of three commonly used methods for measuring endurance capacity. *J. Exp. Zool. A* **327**, 583-591. doi:10.1002/jez.2145

Bennett, A. F. (1980). The metabolic foundations of vertebrate behavior. *Bioscience* **30**, 452-456. doi:10.2307/1307946

Bennett, A. F. (1991). The evolution of activity capacity. *J. Exp. Biol.* **160**, 1-23. doi:10.1242/jeb.160.1.1

Bennett, A. F. and Huey, R. B (1990). Studying the evolution of physiological performance. In *Oxford Surveys in Evolutionary Biology* (ed. D.J. Futuyma and J. Antonovics), pp. 251-284. Oxford: Oxford University Press.

Berman, Y. and North, K. N. (2010). A gene for speed: the emerging role of Alpha-Actinin-3 in muscle metabolism. *Physiology* **25**, 250-259. doi:10.1152/physiol.00008.2010

Berwaerts, K., Matthysen, E. and Van Dyck, H. (2008). Take-off flight performance in the butterfly *Pararge aegeria* relative to sex and morphology: a quantitative genetic assessment. *Evolution* **62**, 2525-2533. doi:10.1111/j.1558-5646.2008.00456.x

Boël, M., Romestaing, C., Duchamp, C., Veyrunes, F., Renaud, S., Roussel, D., Voituron, Y. (2020). Improved mitochondrial coupling as a response to high mass-specific metabolic rate in extremely small mammals. *J. Exp. Biol.* **223**, jeb215558. doi:10.1242/jeb.215558

Bouchard, C. (2012). Genomic predictors of trainability. *Exp. Physiol.* **97**, 347-352. doi:10.1113/expphysiol.2011.058735

Bouchard, C., Sarzynski, M. A., Rice, T. K., Kraus, W. E., Church, T. S., Sung, Y. J., Rao, D. C. and Rankinen, T. (2011a). Genomic predictors of the maximal O_2 uptake response to standardized exercise training programs. *J. Appl. Physiol.* **110**, 1160-1170. doi:10.1152/japplphysiol.00973.2010

Bouchard, C., Rankinen, T. and Timmons, J. A. (2011b). Genomics and genetics in the biology of adaptation to exercise. *Compr. Physiol.* **1**, 1603-1648. doi:10.1002/j.2040-4603.2011.tb00367.x

Boutilier, R. G., Ferguson, R. A., Henry, R. P. and Tufts, B. L. (1993). Exhaustive exercise in the sea lamprey (*Petromyzon marinus*): relationship between anaerobic metabolism and intracellular acid–base balance. *J. Exp. Biol.* **178**, 71-88. doi:10.1242/jeb.178.1.71

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphin fish. *Comp. Biochem. Physiol. A* **113**, 3-15. doi:10.1016/0300-9629(95)02064-0

Brill, R. W. and Bushnell, P. G. (1991). Metabolic and cardiac scope of high energy demand teleosts, the tunas. *Can. J. Zool.* **69**, 2002-2009. doi:10.1139/z91-279

Brook, M. S., Wilkinson, D. J., Smith, K. and Atherton, P. J. (2016). The metabolic and temporal basis of muscle hypertrophy in response to resistance exercise. *Eur. J. Sport Sci.* **16**, 633-644. doi:10.1080/17461391.2015.1073362

Brownscombe, J. W., Raby, G. D., Murchie, K. J., Danylchuk, A. J. and Cooke, S. J. (2022). An energetics–performance framework for wild fishes. *J. Fish Biol.* **101**, 4-12. doi:10.1111/jfb.15066

Bubak, A. N., Swallow, J. G., Adeola, F. I. and Lailvaux, S. P. (2022). Maximum performance expression is affected by octopamine and antennae removal in the house cricket, *Acheta domesticus*. *Behav. Ecol.* **33**, 740-744. doi:10.1093/beheco/arac036

Butler, P. J. (1991). Exercise in birds. *J. Exp. Biol.* **160**, 233-262. doi:10.1242/jeb.160.1.233

Butler, P. J. (2016). The physiological basis of bird flight. *Phil. Trans. R. Soc. B* **371**, 20150384. doi:10.1098/rstb.2015.0384

Butler, P. J. and Turner, D. L. (1988). Effect of training on maximal oxygen uptake and aerobic capacity of locomotory muscles in tufted ducks, *Aythya fuligula*. *J. Physiol.* **401**, 347-359. doi:10.1113/jphysiol.1988.sp017166

Careau, V., Thomas, D., Humphries, M. M. and Réale, D. (2008). Energy metabolism and animal personality. *Oikos* **117**, 641-653. doi:10.1111/j.0030-1299.2008.16513.x

Carlson, J. K., Goldman, K. J. and Lowe, C. G (2004). Metabolism, energetic demand and endothermy. In *Biology of Sharks and Their Relatives*, 2nd edn (ed. J. C. Carrier, J. A. Musick and M. R. Heithaus), pp. 203-224. Boca Raton, FL: CRC Press.

Chapman, J. W., Reynolds, D. R. and Wilson, K. (2015). Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. *Ecol. Lett.* **18**, 287-302. doi:10.1111/ele.12407

Chen, C., Nakagawa, S., An, Y., Ito, K., Kitaichi, Y. and Kusumi, I. (2017). The exercise-glucocorticoid paradox: How exercise is beneficial to cognition, mood, and the brain while increasing glucocorticoid levels. *Front. Neuroendocrinol.* **44**, 83-102. doi:10.1016/j.yfrne.2016.12.001

Chessman, B. C. (2019). Effects of temperature and exercise on metabolism of three species of Australian freshwater turtles: implications for responses to climate change. *Aust. J. Zool.* **66**, 317-325. doi:10.1071/ZO18062

Chitre, A. S., Hebda-Bauer, E., Blandino, P., Bimschleger, H., Nguyen, K. M., Maras, P., Li, F., Ozel, A. B., Pan, Y., Polesskaya, O. et al. (2023). Genome-wide association study in a rat model of temperament identifies multiple loci for exploratory locomotion and anxiety-like traits. *Front. Genet.* **13**, 1003074. doi:10.3389/fgene.2022.1003074

Coffey, V. G., Jemiolo, B., Edge, J., Garnham, A. P., Trappe, S. W. and Hawley, J. A. (2009a). Effect of consecutive repeated sprint and resistance exercise bouts on acute adaptive responses in human skeletal muscle. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **297**, R1441-R1451. doi:10.1152/ajpregu.00351.2009

Coffey, V. G., Pilegaard, H., Garnham, A. P., O'Brien, B. J. and Hawley, J. A. (2009b). Consecutive bouts of diverse contractile activity alter acute responses in human skeletal muscle. *J. Appl. Physiol.* **106**, 1187-1197. doi:10.1152/japplphysiol.91221.2008

Costantini, D., Lindecke, O., Pētersons, G. and Voigt, C. C. (2019). Migratory flight imposes oxidative stress in bats. *Curr. Zool.* **65**, 147-153. doi:10.1093/cz/zoy039

Cummings, J. W. (1979). Physiological and biochemical adaptations to training in Rana pipiens. *J. Comp. Physiol.* **134**, 345-350. doi:10.1007/BF00710002

Davison, W. (1997). The effects of exercise training on teleost fish, a review of recent literature. *Comp. Biochem. Physiol. A* **117**, 67-75. doi:10.1016/S0300-9629(96)00284-8

Davison, W. and Herbert, N. A. (2013). Swimming-enhanced growth. In *Swimming Physiology of Fish* (ed. A.P. Palstra and J. V. Planas), pp. 177-202. Heidelberg: Springer.

Deere, J. A. and Chown, S. L. (2006). Testing the beneficial acclimation hypothesis and its alternatives for locomotor performance. *Am. Nat.* **168**, 630-644. doi:10.1086/508026

Dlugosz, E. M., Chappell, M. A., McGillivray, D. G., Syme, D. A. and Garland, T., Jr. (2009). Locomotor trade-offs in mice selectively bred for high voluntary wheel running. *J. Exp. Biol.* **212**, 2612-2618. doi:10.1242/jeb.029058

Dohm, M. R., Hayes, J. P. and Garland, T., Jr. (1996). Quantitative genetics of sprint running speed and swimming endurance in laboratory house mice (*Mus domesticus*). *Evolution* **50**, 1688-1701. doi:10.1111/j.1558-5646.1996.tb03940.x

Dutta, H. (1994). Growth in fishes. *Gerontology* **40**, 97-112. doi:10.1159/000213581

Else, P. L. and Hulbert, A. J. (1981). Comparison of the "mammal machine" and the "reptile machine": energy production. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **240**, R3-R9. doi:10.1152/ajpregu.1981.240.1.R3

Else, P., Turner, N. and Hulbert, A. (2004). The evolution of endothermy: role for membranes and molecular activity. *Physiol. Biochem. Zool.* **77**, 950-958. doi:10.1086/422767

Eme, J., Owerkowicz, T., Gwalthney, J., Blank, J. M., Rourke, B. C. and Hicks, J. W. (2009). Exhaustive exercise training enhances aerobic capacity in American alligator (*Alligator mississippiensis*). *J. Comp. Physiol. B* **179**, 921-931. doi:10.1007/s00360-009-0374-0

Engel, S., Biebach, H. and Visser, G. H. (2006). Metabolic costs of avian flight in relation to flight velocity: a study in Rose Coloured Starlings (*Sturnus roseus*, Linnaeus). *J. Comp. Physiol. B* **176**, 415-427. doi:10.1007/s00360-006-0063-1

Fu, S. J., Dong, Y. W. and Killen, S. S. (2022). Aerobic scope in fishes with different lifestyles and across habitats: trade-offs among hypoxia tolerance, swimming performance and digestion. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **272**, 111277. doi:10.1016/j.cbpa.2022.111277

Full, R. J., Anderson, B. D., Finnerty, C. M. and Feder, M. E. (1988). Exercising with and without lungs: I. The effects of metabolic cost, maximal oxygen transport and body size on terrestrial locomotion in salamander species. *J. Exp. Biol.* **138**, 471-485. doi:10.1242/jeb.138.1.471

Gabillard, J. C., Biga, P. R., Rescan, P. Y. and Seiliez, I. (2013). Revisiting the paradigm of myostatin in vertebrates: insights from fishes. *Gen. Comp. Endocrinol.* **194**, 45-54. doi:10.1016/j.ygcen.2013.08.012

Gaesser, G. A. and Brooks, G. A. (1984). Metabolic bases of excess post-exercise oxygen consumption: a review. *Med. Sci. Sports Exerc.* **16**, 29-43. doi:10.1249/00005768-198401000-00008

Garland, T., Jr. (1984). Physiological correlates of locomotory performance in a lizard: an allometric approach. *Am. J. Physiol.* **247**, R806-R815. doi:10.1152/ajpregu.1984.247.5.R806

Garland, T., Jr and Kelly, S. A. (2006). Phenotypic plasticity and experimental evolution. *J. Exp. Biol.* **209**, 2344-2361. doi:10.1242/jeb.02244

Garland, T. J., Jr and Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological Morphology: Integrative Organismal Biology* (ed. P. C. Wainwright and S. Reilly), pp. 240-302. Chicago: University of Chicago Press.

Garland, T., Jr, Bennett, A. F. and Daniels, C. B. (1990). Heritability of locomotor performance and its correlates in a natural population. *Experientia* **46**, 530-533. doi:10.1007/BF01954257

Garland, T., Jr, Downs, C. J. and Ives, A. R. (2022). Trade-offs (and constraints) in organismal biology. *Physiol. Biochem. Zool.* **95**, 82-112. doi:10.1086/717897

Garland, T., Jr, Else, P. L., Hulbert, A. J. and Tap, P. (1987). Effects of endurance training and captivity on activity metabolism of lizards. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **252**, R450-R456. doi:10.1152/ajpregu.1987.252.3.R450

Gaunt, A. S., Hikida, R. S., Jehl, J. R. and Fenbert, L. (1990). Rapid atrophy and hypertrophy of an avian flight muscle. *Auk* **107**, 649-659. doi:10.2307/4087994

Giacomin, M., Schulte, P. M. and Wood, C. M. (2022). Osmorespiratory compromise in an elasmobranch: oxygen consumption, ventilation and nitrogen metabolism during recovery from exhaustive exercise in dogfish sharks (Squalus suckleyi). *J. Comp. Physiol. B* **192**, 647-657. doi:10.1007/s00360-022-01447-4

Gleeson, T. T. (1979). The effects of training and captivity on the metabolic capacity of the lizard Sceloporus occidentalis. *J. Comp. Physiol.* **129**, 123-128. doi:10.1007/BF00798176

Gleeson, T. T. (1991). Patterns of metabolic recovery from exercise in amphibians and reptiles. *J. Exp. Biol.* **160**, 187-207. doi:10.1242/jeb.160.1.187

Gruber, S. J. and Dickson, K. A. (1997). Effects of endurance training in the leopard shark, *Triakis semifasciata*. *Physiol. Zool.* **70**, 481-492. doi:10.1086/515851

Gu, H. and Barker, J. S. F. (1995). Genetic and phenotypic variation for flight ability in the cactophilic *Drosophila* species, *D. aldrichi* and *D. buzzatii*. *Entomol. Exp. Appl.* **76**, 25-35. doi:10.1111/j.1570-7458.1995.tb01943.x

Halsey, L. G. (2016a). Do animals exercise to keep fit? *J. Anim. Ecol.* **85**, 614-620. doi:10.1111/1365-2656.12488

Halsey, L. G. (2016b). Terrestrial movement energetics: current knowledge and its application to the optimising animal. *J. Exp. Biol.* **219**, 1424-1431. doi:10.1242/jeb.133256

Hanover, A. M., Husak, J. F. and Lovern, M. (2019). Corticosterone in lizard egg yolk is reduced by maternal diet restriction but unaltered by maternal exercise. *Physiol. Biochem. Zool.* **92**, 573-578. doi:10.1086/705708

Hastings, M. H., Herrera, J. J., Guseh, J. S., Atlason, B., Houstis, N. E., Abdul Kadir, A., Sheffield, C., Singh, A. P., Roh, J. D., Day, S. M. et al. (2022). Animal models of exercise from rodents to pythons. *Circ. Res.* **130**, 1994-2014. doi:10.1161/CIRCRESAHA.122.320247

Hawkes, L. A. (2025). Why the superb physiological capacity of birds matters. *J. Exp. Biol.* **228**, jeb247986. doi:10.1242/jeb.247986

He, W., Xia, W., Cao, Z. D. and Fu, S. J. (2013). The effect of prolonged exercise training on swimming performance and the underlying biochemical mechanisms in juvenile common carp (*Cyprinus carpio*). *Comp. Biochem. Physiol. A* **166**, 308-315. doi:10.1016/j.cbpa.2013.07.003

Hedenström, A. (2025). Integrating flight mechanics, energetics and migration ecology in vertebrates. *J. Exp. Biol.* **228** Suppl. 1, jeb248123. doi:10.1242/jeb.248123

Hedrick, M. S., Hancock, T. V. and Hillman, S. S. (2015). Metabolism at the max: how vertebrate organisms respond to physical activity. *Compr. Physiol.* **5**, 1677-1703. doi:10.1002/j.2040-4603.2015.tb00654.x

Heine, K. B. and Hood, W. R. (2020). Mitochondrial behaviour, morphology, and animal performance. *Biol. Rev.* **95**, 730-737. doi:10.1111/brv.12584

Hill, E. W., McGivney, B. A., Gu, J., Whiston, R. and MacHugh, D. E. (2010). A genome-wide SNP-association study confirms a sequence variant (g. 66493737C> T) in the equine myostatin (MSTN) gene as the most powerful predictor of optimum racing distance for Thoroughbred racehorses. *BMC Genomics* **11**, 552. doi:10.1186/1471-2164-11-552

Hillis, D. A. and Garland, T., Jr. (2023). Multiple solutions at the genomic level in response to selective breeding for high locomotor activity. *Genetics* **223**, iyac165. doi:10.1093/genetics/iyac165

Holder, P. E., Wood, C. M., Lawrence, M. J., Clark, T. D., Suski, C. D., Weber, J. M., Danylchuk, A. J. and Cooke, S. J. (2022). Are we any closer to understanding why fish can die after severe exercise? *Fish Fish* **23**, 1400-1417. doi:10.1111/faf.12696

Hoppeler, H., Baum, O., Lurman, G. and Mueller, M. (2011). Molecular mechanisms of muscle plasticity with exercise. *Compr. Physiol.* **1**, 1383-1412. doi:10.1002/j.2040-4603.2011.tb00363.x

Howlett, K., Febbraio, M. and Hargreaves, M. (1999). Glucose production during strenuous exercise in humans: role of epinephrine. *Am. J. Physiol. Endocrinol. Metab.* **276**, E1130-E1135. doi:10.1152/ajpendo.1999.276.6.E1130

Huang, X., Hegazy, A. M. and Zhang, X. (2021). Swimming exercise as potential measure to improve flesh quality of cultivable fish: A review. *Aquac. Res.* **52**, 5978-5989. doi:10.1111/are.15510

Hubal, M. J., Gordish-Dressman, H., Thompson, P. D., Price, T. B., Hoffman, E. P., Angelopoulos, T. J., Gordon, P. M., Moyna, N. M., Pescatello, L. S., Visich, P. S. et al. (2005). Variability in muscle size and strength gain after unilateral resistance training. *Med. Sci. Sports Exerc.* **37**, 964-972. doi:10.1097/00005768-200505001-00881

Huey, R. B., Berrigan, D., Gilchrist, G. W. and Herron, J. C. (1999). Testing the adaptive significance of acclimation: a strong inference approach. *Am. Zool.* **39**, 323-336. doi:10.1093/icb/39.2.323

Husak, J. F. (2015). Measuring selection on physiology in the wild and manipulating phenotypes (in terrestrial non-human vertebrates). *Compr. Physiol.* **6**, 63-85. doi:10.1002/j.2040-4603.2016.tb00670.x

Husak, J. F. and Lailvaux, S. P. (2017). How do we measure the cost of whole-organism performance traits? *Integr. Comp. Biol.* **57**, 333-343. doi:10.1093/icb/icx048

Husak, J. F. and Lailvaux, S. P. (2019). Experimentally enhanced performance decreases survival in nature. *Biol. Lett.* **15**, 20190160. doi:10.1098/rsbl.2019.0160

Husak, J. F. and Lailvaux, S. P. (2022). Conserved and convergent mechanisms underlying performance-life-history trade-offs. *J. Exp. Biol.* **225**, jeb243351. doi:10.1242/jeb.243351

Husak, J. F. and Lailvaux, S. P. (2024). Stable isotopes reveal sex- and context-dependent amino acid routing in green anole lizards (*Anolis carolinensis*). *J. Exp. Biol.* **227**, jeb248024. doi:10.1242/jeb.248024

Husak, J. F., Keith, A. R. and Wittry, B. N. (2015). Making Olympic lizards: the effects of specialised exercise training on lizard performance. *J. Exp. Biol.* **218**, 899-906. doi:10.1242/jeb.114975

Husak, J. F., Ferguson, H. A. and Lovern, M. B. (2016). Tradeoffs among locomotor performance, reproduction, and immunity in lizards. *Funct. Ecol.* **30**, 1665-1674. doi:10.1111/1365-243512653

Husak, J. F., Roy, J. C. and Lovern, M. B. (2017). Exercise training reveals trade-offs between endurance performance and immune function, but does not affect growth, in juvenile lizards. *J. Exp. Biol.* **220**, 1497-1502. doi:10.1242/jeb.153767

Husak, J. F., Rohlf, C. M. and Lailvaux, S. P. (2021). Immune activation affects whole-organism performance in male but not female green anole lizards (*Anolis carolinensis*). *J. Comp. Physiol. B* **191**, 895-905. doi:10.1007/s00360-021-01370-0

Husak, J. F., Sorlin, M. V. and Lailvaux, S. P. (2024). Counting the costs of expensive tissues: mating system, brain size, and IGF-1 affect the ecological costs of transport in mammals. *Front. Ethol.* **3**, 1464308. doi:10.3389/fetho.2024.1464308

Hudson, S. B., Virgin, E. E., Brodie, E. D., Jr and French, S. S. (2021a). Recovery from discrete wound severities in side-blotched lizards (*Uta stansburiana*): implications for energy budget, locomotor performance, and oxidative stress. *J. Comp. Physiol. B* **191**, 531-543. doi:10.1007/s00360-021-01347-z

Hudson, S. B., Virgin, E. E., Kepas, M. E. and French, S. S. (2021b). Energy expenditure across immune challenge severities in a lizard: consequences for innate immunity, locomotor performance and oxidative status. *J. Exp. Biol.* **224**, jeb242608. doi:10.1242/jeb.242608

Irschick, D. J. (2000). Comparative and behavioral analyses of preferred speed: *Anolis* lizards as a model system. *Physiol. Biochem. Zool.* **73**, 428-437. doi:10.1086/317733

Irschick, D. J. and Losos, J. B. (1998). A comparative analysis of the ecological significance of locomotor performance in Caribbean *Anolis* lizards. *Evolution* **52**, 219-226. doi:10.1111/j.1558-5646.1998.tb05155.x

Irschick, D. J., Meyers, J. J., Husak, J. F. and Le Galliard, J. F. (2008). How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evol. Ecol. Res.* **10**, 177-196. doi:10.7275/R58G8HX6

Jenssen, T. A., Greenberg, N. and Hovde, K. A. (1995). Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetol. Monogr.* **9**, 41-62. doi:10.2307/1466995

Johnston, I. A., Bower, N. I. and Macqueen, D. J. (2011). Growth and the regulation of myotomal muscle mass in teleost fish. *J. Exp. Biol.* **214**, 1617-1628. doi:10.1242/jeb.038620

Killen, S. S., Calsbeek, R. and Williams, T. D. (2017). The ecology of exercise: mechanisms underlying individual variation in behavior, activity, and performance: an introduction to symposium. *Integr. Comp. Biol.* **57**, 185-194. doi:10.1093/icb/icx083

Koch, R. E., Buchanan, K. L., Casagrande, S., Crino, O., Dowling, D. K., Hill, G. E., Hood, W. R., McKenzie, M., Mariette, M. M., Noble, D. W. A. et al. (2021). Integrating mitochondrial aerobic metabolism into ecology and evolution. *Tr. Ecol. Evol.* **36**, 321-332. doi:10.1016/j.tree.2020.12.006

Konarzewski, M. and Książek, A. (2013). Determinants of intra-specific variation in basal metabolic rate. *J. Comp. Physiol. B* **183**, 27-41. doi:10.1007/s00360-012-0698-z

Korsmeyer, K. E., Lai, N. C., Shadwick, R. E. and Graham, J. B. (1997). Oxygen transport and cardiovascular responses to exercise in the yellowfin tuna *Thunnus albacares*. *J. Exp. Biol.* **200**, 1987-1997. doi:10.1242/jeb.200.14.1987

Kritchevsky, S. B., Nicklas, B. J., Visser, M., Simonsick, E. M., Newman, A. B., Harris, T. B., Lange, E. M., Penninx, B. W., Goodpaster, B. H., Satterfield, S. et al. (2005). Angiotensin-converting enzyme insertion/deletion genotype, exercise, and physical decline. *JAMA* **294**, 691-698. doi:10.1001/jama.294.6.691

Lailvaux, S. P. and Husak, J. F. (2014). The life history of whole-organism performance. *Q. Rev. Biol.* **89**, 285-318. doi:10.1086/678567

Lailvaux, S. P. and Husak, J. F. (2017). Predicting life-history trade-offs with whole-organism performance. *Integr. Comp. Biol.* **57**, 325-332. doi:10.1093/icb/icx073

Lailvaux, S. P., Hall, M. D. and Brooks, R. C. (2010). Performance is no proxy for genetic quality: trade-offs between locomotion, attractiveness, and life history in crickets. *Ecology* **91**, 1530-1537. doi:10.1890/09-0963.1

Lailvaux, S. P., Gilbert, R. L. and Edwards, J. R. (2012). A performance-based cost to honest signaling in male green anole lizards (*Anolis carolinensis*). *Proc. R. Soc Lond. B* **279**, 2841-2848.

Lailvaux, S. P., Wang, A. Z. and Husak, J. F. (2018). Energetic costs of performance in trained and untrained *Anolis carolinensis* lizards. *J. Exp. Biol.* **221**, jeb176867. doi:10.1242/jeb.176867

Lailvaux, S. P., Cespedes, A. M., Weber, W. D. and Husak, J. F. (2020). Sprint speed is unaffected by dietary manipulation in trained *Anolis carolinensis* lizards. *J. Exp. Zool. A* **333**, 164-170. doi:10.1002/jez.2338

Lee, S. J. (2010). Speed and endurance: you can have it all. *J. Appl. Physiol.* **109**, 621-622. doi:10.1152/japplphysiol.00618.2010

Lieberman, D. E. (2015). Is exercise really medicine? An evolutionary perspective. *Curr. Sports Med. Rep.* **14**, 313-319. doi:10.1249/JSR.0000000000000168

Lorenz, M. W. and Gäde, G. (2009). Hormonal regulation of energy metabolism in insects as a driving force for performance. *Integr. Comp. Biol.* **49**, 380-392. doi:10.1093/icb/icp019

Losos, J. B., Creer, D. A. and Schulte, J. A., II. (2002). Cautionary comments on the measurement of maximum locomotor capabilities. *J. Zool.* **258**, 57-61. doi:10.1017/S0952836902001206

MacKenzie-Shalders, K. L., Byrne, N. M., King, N. A. and Slater, G. J. (2019). Are increases in skeletal muscle mass accompanied by changes to resting metabolic rate in rugby athletes over a pre-season training period? *Eur. J. Sport Sci.* **19**, 885-892. doi:10.1080/17461391.2018.1561951

MacKenzie-Shalders, K., Kelly, J. T., So, D., Coffey, V. G. and Byrne, N. M. (2020). The effect of exercise interventions on resting metabolic rate: a systematic review and meta-analysis. *J. Sports Sci.* **38**, 1635-1649. doi:10.1080/02640414.2020.1754716

Magnoni, L. J., Felip, O., Blasco, J. and Planas, J. V. (2013). Metabolic fuel utilization during swimming: optimizing nutritional requirements for enhanced performance. *Swimming Physiology of Fish* (ed. A. P. Palstra and J.V. Planas), pp. 203-234. Heidelberg: Springer.

Magnuson, J. J. (1978). Locomotion by scombrid fishes: hydromechanics, morphology and behavior. In *Fish Physiology*, Vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 239-313. New York: Academic Press.

Marks, J. R., Beatty, A. E., Schwartz, T. S., Sorlin, M. and Lailvaux, S. P. (2021). Expression of insulin-like growth factors depends on both mass and resource availability in female green anoles (Anolis carolinensis). *J. Exp. Biol.* **224**, jeb242665. doi:10.1242/jeb.242665

Marks, J. R., Beatty, A. E., Husak, J. F., Schwartz, T. S. and Lailvaux, S. P. (2022). Sprint training interacts with body mass to affect hepatic insulin-like growth factor expression in female green anoles (*Anolis carolinensis*). *Gen. Comp. Endocrinol.* **327**, 114067. doi:10.1016/j.ygcen.2022.114067

Marks, J. R., Sorlin, M. and Lailvaux, S. P. (2023). The maternal energetic environment affects both egg and offspring phenotypes in green anole lizards (*Anolis carolinensis*). *Ecol. Evol.* **13**, e9656. doi:10.1002/ece3.9656

Matthews, D. G., Dial, T. R. and Lauder, G. V. (2023). Genes, morphology, performance, and fitness: quantifying organismal performance to understand adaptive evolution. *Integr. Comp. Biol.* **63**, 843-859. doi:10.1093/icb/icad096

McWilliams, S., Carter, W., Cooper-Mullin, C., DeMoranville, K., Frawley, A., Pierce, B. and Skrip, M. (2021). How birds during migration maintain (oxidative) balance. *Front. Ecol. Evol.* **9**, 742642. doi:10.3389/fevo.2021.742642

Mesa, M. G., Bayer, J. M. and Seelye, J. G. (2003). Swimming performance and physiological responses to exhaustive exercise in radio–tagged and untagged Pacific lampreys. *Trans. Am. Fish. Soc.* **132**, 483-492. doi:10.1577/1548-8659(2003)132<0483:SPAPRT>2.0.CO;2

Miller, K. and Camilliere, J. J. (1981). Physical training improves swimming performance of the African clawed frog *Xenopus laevis*. *Herpetologica* **37**, 1-10. https://www.jstor.org/stable/3891789

Minami, N., Li, Y., Guo, Q., Kawamura, T., Mori, N., Nagasaka, M., Ogawa, M., Ito, O., Kurosawa, H., Kanazawa, M. et al. (2007). Effects of angiotensin-converting enzyme inhibitor and exercise training on exercise capacity and skeletal muscle. *J. Hypertens* **25**, 1241-1248. doi:10.1097/HJH.0b013e3280e126bf

Minter, M., Pearson, A., Lim, K. A. S., Wilson, K., Chapman, J. W. and Jones, C. M. (2018). The tethered flight technique as a tool for studying insect life-history strategies association with migration in insects. *Ecol. Entomol.* **43**, 297-411. doi:10.1111/een.12521

Mosher, D. S., Quignon, P., Bustamante, C., Sutter, N. B., Mellersch, C. S., Parker, H. G. and Ostrander, E. A. (2007). A mutation in the myostatin gene increases muscle mass and enhances racing performance in heterozygote dogs. *PLoS ONE* **3**, e79. doi:10.1371/journal.pgen.0030079

Murren, C. J., Auld, J. R., Callahan, H., Ghalambor, C. K., Handelsman, C. A., Heskel, M. A., Kingsolver, J. G., Maclean, H. J., Masel, J., Maughan, H. et al. (2015). Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity* **115**, 293-301. doi:10.1038/hdy.2015.8

O'Connor, J. L., McBrayer, L. D., Higham, T. E., Husak, J. F., Moore, I. T. and Rostal, D. C. (2011). Effects of training and testosterone on muscle fiber types and locomotor performance in male six-lined racerunners (*Aspidoscelis sexlineata*). *Physiol. Biochem. Zool.* **84**, 394-405. doi:10.1086/660850

Ogata, H. Y. and Oku, H. (2000). Effects of water velocity on growth performance of juvenile Japanese flounder Paralichthys olivaceus. *J. World Aquacult. Soc.* **31**, 225-231. doi:10.1111/j.1749-7345.2000.tb00357.x

Okuyama, J., Shiozawa, M. and Shiode, D. (2020). Heart rate and cardiac response to exercise during voluntary dives in captive sea turtles (Cheloniidae). *Biol. Open* **9**, bio049247. doi:10.1242/bio.049247

Orrell, K. S., Congdon, J. D., Jenssen, T. A., Michener, R. H. and Kunz, T. H. (2004). Intersexual differences in energy expenditure of *Anolis carolinensis* lizards during breeding and postbreeding seasons. *Physiol. Biochem. Zool.* **77**, 50-64. doi:10.1086/383497

Owerkowicz, T. and Baudinette, R. V. (2008). Exercise training enhances aerobic capacity in juvenile estuarine crocodiles (*Crocodylus porosus*). *Comp. Biochem. Physiol. A* **150**, 211-216. doi:10.1016/j.cbpa.2008.04.594

Palstra, A. P. and Planas , J. V. (eds). (2013). *Swimming Physiology of Fish*. Heidelberg: Springer.

Palstra, A. P., Schaaf, M. A. and Planas, J. V (2013). Exercise physiology of zebrafish: swimming effects on skeletal and cardiac muscle growth, on the immune system, and the involvement of the stress axis. In *Swimming Physiology of Fish* (ed. A. P. Palstra and J.V. Planas), pp. 323-342. Heidelberg: Springer.

Pie, M. R. and Alvares, L. E. (2006). Evolution of myostatin in vertebrates: is there evidence for positive selection? *Mol. Phylogenet. Evol.* **41**, 730-734. doi:10.1016/j.ympev.2006.05.038

Pickering, C. and Kiely, J. (2019). Do non-responders to exercise exist–and if so, what should we do about them? *Sports Med.* **49**, 1-7. doi:10.1007/s40279-018-01041-1

Pontzer, H. (2018). Energy constraint as a novel mechanism linking exercise and health. *Physiology* **33**, 384-393. doi:10.1152/physiol.00027.2018

Pontzer, H. (2025). The energetics of movement, from exercise to ecology and evolution. *J. Exp. Biol.* **228**, jeb247988. doi:10.1242/jeb.247988

Poole, D. C., Copp, S. W., Colburn, T. D., Craig, J. C., Allen, D. L., Sturek, M., O'Leary, D. S., Zucker, I. H. and Musch, T. I. (2020). Guidelines for animal exercise and training protocols for cardiovascular studies. *Am. J. Physiol. Heart Circ. Physiol.* **318**, H1100-H1138. doi:10.1152/ajpheart.00697.2019

Posthumus, M., Schwellnus, M. P. and Collins, M. (2011). The COL5A1 gene: a novel marker of endurance running performance. *Med. Sci. Sports Exerc.* **43**, 584-589. doi:10.1249/MSS.0b013e3181f34f4d

Powers, S. K., Radak, Z., Ji, L. L. and Jackson, M. (2024). Reactive oxygen species promote endurance exercise-induced adaptations in skeletal muscles. *J. Sport Health Sci.* **13**, 780-792. doi:10.1016/j.jshs.2024.05.001

Price, E. R., Bauchinger, U., Zajac, D. M., Cerasale, D. J., McFarlan, J. T., Gerson, A. R., McWilliams, S. R. and Guglielmo, C. G. (2011). Migration-and exercise-induced changes to flight muscle size in migratory birds and association with IGF1 and myostatin mRNA expression. *J. Exp. Biol.* **214**, 2823-2831. doi:10.1242/jeb.057620

Price, E. R., Bauchinger, U., McWilliams, S. R., Boyles, M. L., Langlois, L. A., Gerson, A. R. and Guglielmo, C. G. (2022). The effects of training, acute exercise and dietary fatty acid composition on muscle lipid oxidative capacity in European starlings. *J. Exp. Biol.* **225**, jeb244433. doi:10.1242/jeb.244433

Randall, D. and Brauner, C. (1991). Effects of environmental factors on exercise in fish. *J. Exp. Biol.* **160**, 113-126. doi:10.1242/jeb.160.1.113

Reardon, K. M., Walton, B. N. and Husak, J. F. (2023). How does mitochondria function contribute to aerobic performance enhancement in lizards? *Front. Physiol.* **14**, 1165313. doi:10.3389/fphys.2023.1165313

Regan, J. C., Froy, H., Walling, C. A., Moatt, J. P. and Nussey, D. H. (2020). Dietary restriction and insulin-like signaling pathways as adaptive plasticity: a synthesis and re-evaluation. *Funct. Ecol.* **34**, 107-128. doi:10.1111/1365-2435.13418

Reznick, D., Nunney, L. and Tessier, A. (2000). Big houses, big cars, superfleas and the costs of reproduction. *Tr. Ecol. Evol.* **15**, 421-425. doi:10.1016/S0169-5347(00)01941-8

Rodgers, B. D. and Garikipati, D. K. (2008). Clinical, agricultural, and evolutionary biology of myostatin: a comparative review. *Endocr. Rev.* **29**, 513-534. doi:10.1210/er.2008-0003

Rodgers, E. M. and Gomez Isaza, D. F. (2024). The growth–promoting effects of exercise in finfish: a systematic review and meta–analysis. *Rev. Aquac.* **16**, 942-953. doi:10.1111/raq.12879

Seipel, K. and Schmid, V. (2005). Evolution of striated muscle: jellyfish and the origin of triploblasty. *Dev. Biol.* **282**, 14-26. doi:10.1016/j.ydbio.2005.03.032

Shirley, M. K., Longman, D. P., Elliott-Sale, K. J., Hackney, A. C., Sale, C. and Dolan, E. (2022). A life history perspective on athletes with low energy availability. *Sports Med.* **52**, 1223-1234. doi:10.1007/s40279-022-01643-w

Sorci, G., Swallow, J. G., Garland, T., Jr and Clobert, J. (1995). Quantitative genetics of locomotor speed and endurance in the lizard *Lacerta vivipera*. *Physiol. Zool*. **68**, 698-720. doi:10.1086/physzool.68.4.30166352

Sorlin, M. V., Marks, J. R. and Lailvaux, S. P. (2022). Endurance training does not affect maximum exertion/distance capacity in *Anolis carolinensis* lizards. *J. Exp. Biol.* **225**, jeb244576. doi:10.1242/jeb.244576

Speakman, J. R. and Selman, C. (2003). Physical activity and resting metabolic rate. *Proc. Nutr. Soc.* **62**, 621-634. doi:10.1079/PNS2003282

Stavres, J., Zeigler, M. P. and Pasternostro Bayles, M. (2018). Six weeks of moderate functional resistance training increases basal metabolic rate in sedentary adult women. *Int. J.Exerc. Sci.* **11**, 32-41. doi:10.70252/FNIK8317

Stearns, S. C. (2000). Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* **87**, 476-486. doi:10.1007/s001140050763

Swallow, J. G., Rhodes, J. S. and Garland, T., Jr. (2005). Phenotypic and evolutionary plasticity of organ masses in response to voluntary exercise in house mice. *Integr. Comp. Biol.* **45**, 426-437. doi:10.1093/icb/45.3.426

Swallow, J. G., Hayes, J. P., Koteja, P. and Garland, T., Jr. (2009). Selection experiments and experimental evolution of performance and physiology. In *Experimental Evolution: Concepts, Methods and Applications of Selection Experiments* (ed. T. Garland and M.R. Rose), pp. 301-351. University of California.

Tomkins, J. L., Radwan, J., Kotiaho, J. S. and Tregenza, T. (2004). Genic capture and resolving the lek paradox. *Trends Ecol. Evol.* **19**, 323-328. doi:10.1016/j.tree.2004.03.029

Treberg, J. R., Munro, D., Jastroch, M., Quijada-Rodriguez, A. R., Kutschke, M. and Wiens, L. (2018). Comparing electron leak in vertebrate muscle mitochondria. *Integr. Comp. Biol.* **58**, 495-505. doi:10.1093/icb/icy095

van Noordwijk, A. J. and de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life-history tactics. *Am. Nat.* **128**, 137-142. doi:10.1086/284547

Wang, A. Z. and Husak, J. F. (2020). Endurance and sprint training affect immune function differently in green anole lizards (*Anolis carolinensis*). *J. Exp. Biol.* **223**, jeb232132. doi:10.1242/jeb.232132

Wang, A. Z., Husak, J. F. and Lovern, M. (2019). Leptin ameliorates the immunity, but not reproduction, trade-off with endurance in lizards. *J. Comp. Physiol. B* **189**, 261-269. doi:10.1007/s00360-019-01202-2

Wegener, G. (1996). Flying insects: model systems in exercise physiology. *Experientia* **52**, 404-412. doi:10.1007/BF01919307

Weibel, E. R., Bacigalupe, L. D., Schmitt, B. and Hoppeler, H. (2004). Allometric scaling of maximal metabolic rate in mammals: muscle aerobic capacity as determinant factor. *Respir. Physiol. Neurobiol.* **140**, 115-132. doi:10.1016/j.resp.2004.01.006

Williams, T. D. and Fowler, M. A. (2015). Individual variation in workload during parental care: can we detect a physiological signature of quality or cost of reproduction? *J. Ornithol.* **156** Suppl. 1, 441-451. doi:10.1007/s10336-015-1213-6

Wood, C. M. and Eom, J. (2021). The osmorespiratory compromise in the fish gill. *Comp. Biochem. Physiol. A* **254**, 110895. doi:10.1016/j.cbpa.2021.110895

Wu, W., Gao, Y. D., Jiang, D. C., Lei, J., R, J. L., Liao, W. B., Deng, C., Wang, Z. Q., Hillis, D. M., Zhang, Y. P. et al. (2022). Genomic adaptations for arboreal locomotion in Asian flying treefrogs. *Proc. Natl. Acad. Sci. USA* **119**, e2116342119. doi:10.1073/pnas.2116342119

Yao, J., Saraf, F., Rathore, V. S., Darkazanli, K., Liu, Y., Korivi, M. and Bhaskar, L. V. K. S. (2025). Importance of selected genetic determinants on endurance performance and physical strength. *Front. Physiol.* **16**, 1568334. doi:10.3389/fphys.2025.1568334

Yap, K. N., Serota, M. W. and Williams, T. D. (2017). The physiology of exercise in free-living vertebrates: what can we learn from current model systems? *Integr. Comp. Biol.* **57**, 195-206. doi:10.1093/icb/icx016

Zamora-Camacho, F. J., Reguera, S., Rubino-Hispan, M. V. and Moreno-Rueda, G. (2015). Eliciting an immune response reduces sprint speed in a lizard. *Behav. Ecol.* **26**, 115-120. doi:10.1093/beheco/aru170

Zhang, Y., Eyster, K., Liu, J. S. and Swanson, D. L. (2015). Cross-training in birds: cold and exercise training produce similar changes in maximal metabolic output, muscle masses and myostatin expression in house sparrows (*Passer domesticus*). *J. Exp. Biol.* **218**, 2190-2200. doi:10.1242/jeb.121822