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RESEARCH PAPER

Sprint speed is unaffected by dietary manipulation in trained male *Anolis carolinensis* lizards

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Abstract

Performance traits are energetically costly, and their expression and use can drive trade-offs with other energetically costly life-history traits. However, different performance traits incur distinct costs and may be sensitive to both resource limitation and to the types of resources that are accrued. Protein is likely to be especially important for supporting burst performance traits such as sprint speed, but the effect of varying diet composition on sprint training in lizards, an emerging model system for exercise training, is unknown. We tested the hypothesis that the response to sprint training is sensitive to both the type and amount of resources in *Anolis carolinensis*. We also measured bite force across all treatments as a control whole-organism performance trait that should be unaffected by locomotor training. Both mass and bite force are reduced by dietary restriction over the course of 9 weeks of sprint training, but sprint speed is unaffected by either training or dietary restriction relative to controls. Furthermore, protein supplementation does not rescue a decline in either mass or bite force in trained, diet-restricted males. These results contrast with those for endurance training, and suggest that sprint speed is more canalized than either endurance or bite force in green anoles.

KEYWORDS

Anolis, diet quality, dietary restriction, exercise, whole-organism performance

1 | INTRODUCTION

Whole-organism performance traits such as running, biting, and flying are key predictors of fitness in a variety of species and contexts (Husak & Fox, 2008; Irschick, Meyers, Husak, & Le Galliard, 2008; Lailvaux & Irschick, 2006; reviewed in Husak, 2015). Under the classic ecomorphological paradigm (sensu Arnold, 1983), such traits are implicitly assumed to be static and invariant over an individual's lifetime. However, the expression and use of such traits are energetically expensive (Garland, 1983; Husak & Lailvaux, 2017); consequently, both performance capacities and the manifestation of other energetically expensive, fitness-related traits are likely to be dependent on the pool of energetic resources acquired from the external environment (Lailvaux & Husak, 2014; Ricklefs & Wikelski, 2002; Zera & Harshman, 2001). This plastic nature of performance means that the expression of performance traits may wax or wane over the course of individual lifetimes according to factors such as predation risk (Braña, 2003; Herrel, Meyers, & Vanhooydonck, 2001; Reznick, Bryant, Roff, Ghalambor, & Ghalambor, 2000; Vanhooydonck & Van Damme, 2003), immune system activation (Zamora-Camacho, Reguera, Rubino-Hispan, & Moreno-Rueda, 2015), mating frequency (Lailvaux, Zajitschek, Dessman, & Brooks, 2011), breeding status (Irschick & Meyers, 2007; Irschick et al., 2006), resource availability (Husak, Ferguson, & Lovern, 2016; Lailvaux, Gilbert, & Edwards, 2012), or age (Careau & Wilson, 2017; Lailvaux, Wilson, & Kasumovic, 2014; Lane, Frankino, Elekonich, & Roberts, 2014; Marck et al., 2016; Sutter et al., 2018) amongst others, as resources are dynamically reallocated to maximize residual reproductive value. However, our understanding of the drivers of this plasticity remains incomplete, especially with regard to factors such as diet quality that are seldom considered in studies of functional and whole-organism performance traits.

Dietary restriction is a powerful technique for exposing investment priorities in life-history traits that are sensitive to resource availability, and key life-history trade-offs can be alleviated, induced, or masked by changing the quantity of resources in the environment (Reznick, Nunney, & Tessier, 2000; Van Noordwijk & Dejong, 1986). However, the expression of life-history traits is also sensitive to diet quality (Simpson & Raubenheimer, 1993). Studies adopting the nutritional geometry framework have shown that altering dietary macronutrient ratios (i.e., ratios of proteins, fats, and carbohydrates) drives changes in the timing, intensity, and duration of the expression of key life-history traits such as sexual advertisement (Maklakov et al., 2008), fecundity (Lee et al., 2008), and longevity (Simpson & Raubenheimer, 1993; Zajitschek, Lailvaux, Dessmann, & Brooks, 2012), independent of total caloric content. Despite the success of the nutritional geometry framework in identifying macronutrient intake targets for many species and traits, these techniques have seldom been applied to performance abilities. Although Lailvaux et al. (2011) found that the very same artificial diets that significantly alter reproductive investment in the Australian black field cricket *Teleogryllus commodus* have no effect on either biting or jumping ability in this same species, similar studies in other animal taxa are lacking.

Manipulations of whole-organism performance capacities in nonmodel organisms have historically proven to be difficult but can be achieved through the application of targeted exercise training regimes (Husak & Lailvaux, 2017). Green anole lizards (*Anolis carolinensis*) have recently emerged as a model system for studying the life-history trade-offs associated with increased investment in locomotor performance. Endurance training in particular, either alone or in conjunction with dietary restriction, increases endurance capacity (Husak, Keith, & Wittry, 2015) but reduces fecundity, immune function (Husak et al., 2016; Husak, Roy, & Lovern, 2017), and survival (Husak & Lailvaux, 2019) relative to untrained controls. Those intraspecific trade-offs are also apparent across species in other lizard groups; for example, phrynosomatid lizards exhibit complex and significant relationships among endurance capacity and components of reproductive life-history (Husak & Lailvaux, 2017). Sprint speed, however, was unrelated to any life-history traits in these same species (Husak & Lailvaux, 2017), suggesting that the costs associated with enhanced endurance are different from those incurred by increasing sprint speed.

If investment in endurance and sprinting activates different physiological pathways and incurs distinct trade-offs, then those pathways may require different substrates for optimal performance increase. In particular, sprint speed should be associated with increased muscularity and power output, requiring higher protein intake (Atherton & Smith, 2012), and indeed sprint-trained green anoles invest more in muscle than endurance-trained animals or controls (Husak, Keith, et al., 2015). Sprint training accomplishes these differential effects at the muscular level by increasing ribosome number and function, whereas endurance training increases mitochondria function, perhaps in an antagonistic manner (Roberts et al., 2018). However, while endurance and sprinting rely on different food substrates to fuel performance, the sensitivity of sprint speed to dietary quantity and quality in green anoles is unknown.

We manipulated both diet quantity and quality to test the hypothesis that the response to sprint speed training is sensitive to diet in male green anoles. Specifically, we tested two explicit predictions of this hypothesis: (a) dietary restriction will reduce sprint speed in both trained and untrained animals; and (b) protein supplementation will rescue sprint speed in diet-restricted, trained individuals. We also measured bite force as a control trait that is known to be susceptible to dietary perturbation (Lailvaux et al., 2012) but that should be unaffected by locomotor training (Husak et al., 2016). Because bite force should also be dependent on protein content, we made the ancillary prediction that bite force will be greater in diet-restricted, protein-supplemented animals than in diet-restricted animals.

2 | METHODS

All procedures were approved by the University of New Orleans Institutional Animal Care Committee (IACUC protocol #15-006). We captured 60 adult male lizards from populations around Orleans Parish in New Orleans, LA in July 2015. Lizards were housed at the University of New Orleans in individual 28.5 × 17.5 × 21 cm plastic terraria with cypress mulch substrate and wooden dowels oriented toward a 75 W incandescent bulb suspended above each cage to allow lizards to bask. We provided each lizard shelf with a Repti-Sun 5.0 UVB 310 40 W Fluorescent Lamp to mimic natural sunlight. Terraria were kept within an animal room maintained at approximately 30°C, 70% relative humidity, with a light:dark cycle of 12:12 hr, and lizards misted daily.

2.1 | Pretreatment measures

Before training, we measured mass, bite force, and sprint speed for each individual using standard methods. Briefly, we measured bite force by inducing lizards to bite down on custom bite plates connected to a Kistler type 9203 force transducer and type 5058a Kistler charge amplifier (Kistler, Winterthur, Switzerland; Herrel, Spithoven, van Damme, & de Vree, 1999; Herrel, Van Damme, Vanhooydonck, & Vree, 2001) in a standardized manner. We measured sprint speed by chasing lizards up a custom racetrack angled at 45° to the horizontal (because anoles often hop on horizontal surfaces) consisting of a 2 m long wooden dowel covered with cork for traction and equipped with paired infrared beams at 0.25 m intervals (SCL Timer; Trackmate Racing, Surrey BC, Canada) which the lizard interrupted as it ran past. Both sprinting and bite force were measured five times per individual on separate days with 1 hr of rest between trials in a room set to 33°C (approximately the optimal performance temperature for this species; Lailvaux & Irschick, 2007) and the maximum values retained for analysis (Losos, Creer, & Schulte, 2002).

2.2 | Diet manipulations and training

Following initial sprint and bite measurements, we allocated lizards randomly to four groups ($n = 15$ per group) and maintained them under treatment conditions for 9 weeks. Control (C) lizards were fed an ad libitum diet of three vitamin powder-dusted crickets three times per week. These lizards were not trained, but were taken out of their cages on training days and briefly handled to simulate handling effects associated with training. Trained animals (T) also received food ad libitum and were trained as in Husak, Keith, et al. (2015) by chasing animals repeatedly down a 2.0-m long, 5-cm dowel three times each week, with each training bout consisting of four runs separated by a 1 hr rest. For the first 3 weeks, we placed the dowel at a 45° angle but increased it to a 55° angle for Weeks 4–6, and a 65° incline for Weeks 7–9. Diet-restricted, trained lizards (D) were under the same training regime but were fed only one vitamin powder-dusted cricket three times per week, which simulates scarce resource availability without compromising lizard health (as in Lailvaux et al., 2012; Husak et al., 2016; Husak, Keith, et al., 2015).

Although manipulations of diet quality for invertebrates and many other animals are achieved using specially prepared diets where the ratios of carbohydrates:fats:proteins are carefully controlled, such artificial diets cannot be used for anoles which typically only accept live prey. Diet-restricted, trained, protein-supplemented lizards (P) were therefore fed, three times per week, one cricket that was gut loaded with whey protein supplement (Muscle Pharm, Burbank, CA). This was done by separating prey crickets from the general cricket population 24 hr before being fed to lizards and replacing their regular food source (Purina Complete Cat Chow) during that time with the protein supplement. To further increase cricket protein content, we dusted protein crickets with protein powder (Naturade 100% Soy Booster; NNC LLC) in addition to the regular vitamin powder immediately before offering them to the lizards. Thus, while we make no claims as to the precise protein content of the protein-supplemented diet, lizards on this diet did ingest more protein over the course of the study than lizards on control or restricted diets.

We did not intend to test for isolated effects of protein supplementation or how protein supplementation with an ad libitum diet would affect performance, but instead to see if protein supplements on a restricted diet would rescue detrimental effects of dietary restriction on sprinting. This makes for an experimental design that is intentionally not fully factorial, as interactions were not of interest in this case.

At the end of 9 weeks, we measured lizards again for mass, bite force, and sprinting (on a track angled at the original 45°) as at the beginning of the study.

2.3 | Statistical analysis

We used R v3.5.1 (R Core Team, 2018) for all analyses. To test the effects of treatment on change in bite force, mass, and sprint speed over the course of the training, we used separate analysis of variances with change between the beginning and end measurements for each trait as dependent variables and treatment as a lone factor. We also included mass at the time of the second measurement as a covariate in the models for bite force and sprint speed to control for body size effects. For mass and bite force we used Tukey's honestly significant difference (HSD) post hoc tests to distinguish among the effects of treatment levels.

3 | RESULTS

We found significant treatment effects on change in mass over the course of the study ($F_{3,54} = 15.88$; $p < .001$; Figure 1a). Lizards on the ad libitum diets (i.e., control and trained animals) maintained similar weights, and change in mass did not differ between these two groups (Tukey's HSD, $p > .99$). However, animals in both the diet-restricted, trained (D) and diet-restricted, trained, protein-supplemented (P) treatments exhibited negative changes in mass that were significantly greater than those of either control (Tukey's HSD: C–D, $p = .01$; C–P, $p < .001$) or trained animals (Tukey's HSD: T–DT, $p = .018$; T–P, $p < .001$). Change in mass was only marginally statistically insignificant between the two diet-restricted groups (Tukey's HSD: D–P, $p = .055$), and indeed protein-supplemented animals lost the most mass over the course of the experiment relative to all other groups.

Change in bite force also differed significantly among treatment groups ($F_{3,52} = 6.46$; $p < .001$; Figure 1b). Trained and control lizards did not significantly differ in their change in bite force over the course of the study (Tukey's HSD: C–T, $p = .88$). Diet-restricted, trained animals (D) did not experience a significantly greater decrease in bite force than controls (Tukey HSD: C–D, $p = .195$), nor did diet-restricted, trained, protein-supplemented (P) lizards (Tukey's HSD: C–P, $p = .118$). However, the bite forces of trained lizards decreased significantly less than that of either the D (Tukey's HSD: T–D, $p = .04$) or P anoles (Tukey's HSD: T–P, $p = .021$). There was no significant difference in change in bite force between the diet-restricted, trained animals and the diet-restricted, trained, protein-supplemented lizards (Tukey's HSD: D–P, $p > .99$).

In contrast to mass and bite force, there was no effect of treatment on change in sprint speed over the course of the study ($F_{3,53} = 0.692$; $p = .56$; Figure 1c). Thus, neither training, diet restriction, nor protein supplementation significantly changed sprint speed relative to control animals.

4 | DISCUSSION

Understanding the factors affecting the expression of whole-organism performance traits is important because performance is part of the integrated organismal phenotype (Ghalambor, Walker, & Reznick, 2003; Lailvaux & Husak, 2014), yet often performance, and other functional traits, are studied as static traits in isolation. Dietary

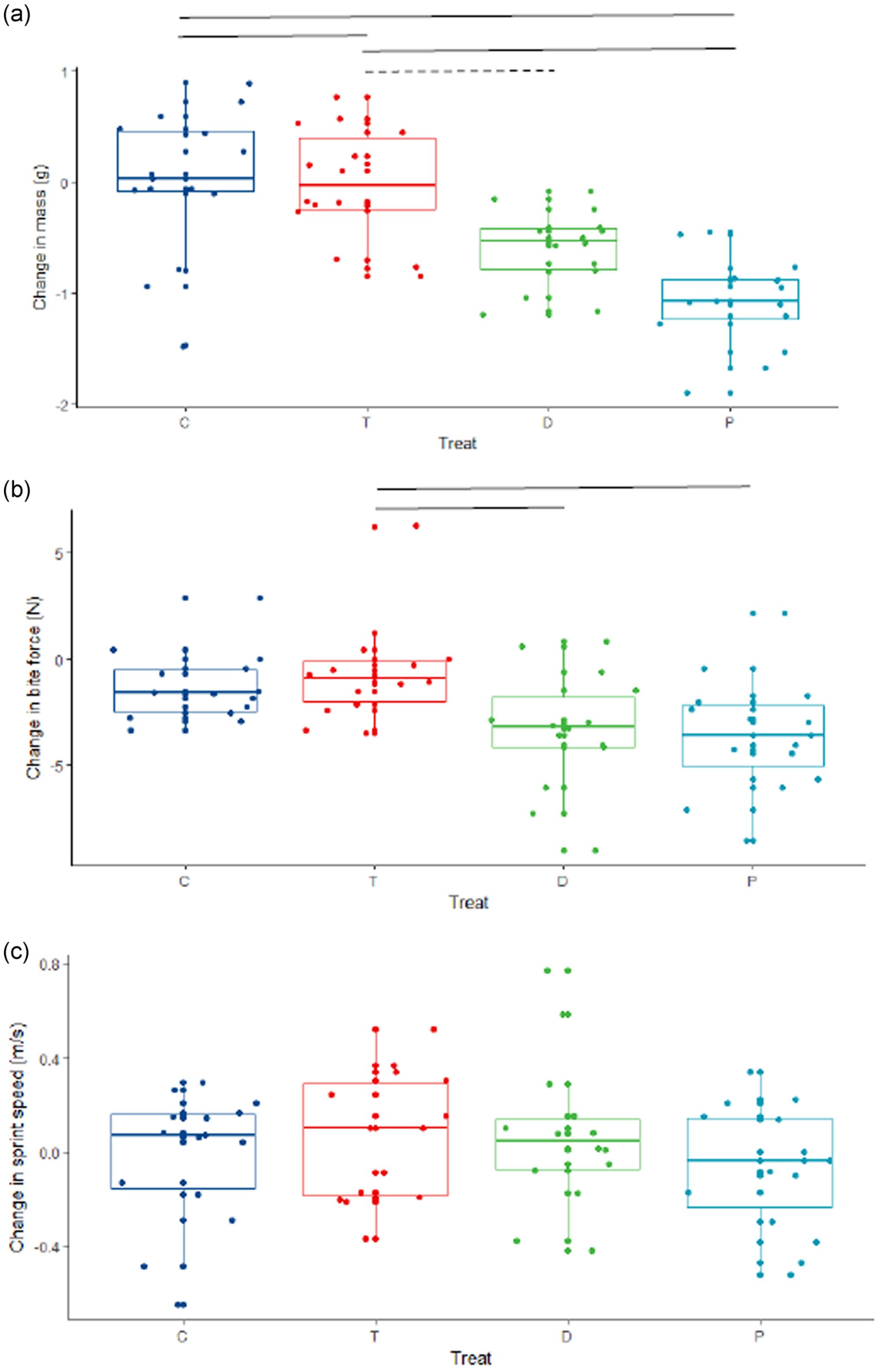

FIGURE 1 Difference between start and end values (raw trait values overlaid onto boxplots) for (a) mass, (b) bite force, and (c) sprint speed for control (dark blue [C]), trained (light blue [T]), diet-restricted, trained (red [D]), and diet-restricted, trained, protein-supplemented (green [P]) green anole males. Treatments affected change in mass ($F_{3,54}$ = 15.88; $p < .001$) and bite force performance ($F_{3,52}$ = 6.46; $p < .001$), but not sprint speed ($F_{3,53}$ = .692; $p < .56$). Both change in sprint speed and change in bite force were modeled with body mass at the time of the second measurement as a covariate. Solid lines above pairs of traits represent significant Tukey's honestly significant difference post hoc test differences of $p < .001$; dashed lines represent differences of $p < .05$ [Color figure can be viewed at wileyonlinelibrary.com]

restriction has previously been shown to affect both heart size and hematocrit (Husak et al., 2016), as well as bite force (Lailvaux et al., 2012) in green anoles. We tested the hypothesis that sprint speed is similarly susceptible to dietary influence, specifically within the context of exercise training.

Our prediction that dietary restriction would result in a negative change in sprint speed over 9 weeks of sprint training was not supported. Sprint-trained, dietary-restricted animals showed a significant decline in mass over the training period (Figure 1a), but this change in mass was not accompanied by any significant change in sprint speed during that time. Dietary restriction regimes strenuous enough to cause significant weight loss should result in decreased investment in energetically costly traits. This lack of a sprint speed decrement is therefore unexpected given the energetic costs of sprint speed production, as well as the putative costs of both building and maintaining the tissues necessary for sprinting (Husak & Lailvaux, 2017; but see Lailvaux, Wang, & Husak, 2018). Although it may seem counterintuitive that sprint-trained lizards were ultimately no faster than untrained animals, this was not entirely unexpected as lizards become acclimated to the sprint training and lose motivation to perform maximally by the end despite evident and significant physiological changes (Husak, Keith, et al., 2015), which does not happen with endurance training. What is most important is that sprint speeds did not decrease significantly compared with controls as a result of either decreased allocation to sprinting or motivation due to poor condition.

Our next predictions that protein supplementation would rescue declines in sprint speed and bite force, were also unsupported. There was no difference between either the sprint speed or bite force of diet-restricted, trained animals, and diet-restricted, trained, protein-supplemented lizards, which means that protein supplementation did not alter or ameliorate the effects of dietary restriction for either measured performance trait (Figure 1b,c). It is unclear why protein supplementation had no effect on performance under such demanding conditions given that both sprint speed and bite force are burst performance traits that are bolstered structurally by muscle and, therefore, likely by protein availability. One possibility is that the protein supplements were not absorbed by the lizards. We used commercial protein supplements of two different types (whey and soy) to avoid potential pitfalls associated with changing only one type of protein. However, because whey is derived from milk, and neither milk nor soy is part of a normal lizard diet, it could be that the lizards are unable to absorb or metabolize either. Yet another possibility is that there could be an upper limit to protein absorption beyond which supplementation has no effect, as is the case in humans (Oben, Kothari, & Anderson, 2008). Such an effect (if it exists in lizards) in conjunction with allometric limitations on food absorption in small animals (Hammond & Diamond, 1994) could have rendered our excess protein supplementation ineffective.

The results of our (admittedly crude) protein treatment notwithstanding, it is notable that sprint speed did not differ between lizards on a restricted diet and those on an ad libitum diet, emphasizing the seeming insensitivity of sprint speed to dietary restriction in *A. carolinensis*. This result is consistent with the ecology of green anoles, which exhibit low movement rates in nature characteristic of organisms that rely more on sprinting than on endurance (Irschick, 2000; Jenssen, Greenberg, & Hovde, 1995) and whose movement rates also are unaffected by sprint training (Husak & Lailvaux, 2019), and also with recent data showing that sprint speed shows significant repeatability in green anoles (Lailvaux, Cespedes, & Houslay, 2019). It is also unlikely that lizards in the diet-restricted groups were able to compensate for compromised sprint speed because of their lower body masses, as sprinting in lizards is not limited by power output (Farley, 1997; see also Irschick, Vanhooydonck, Herrel, & Andronescu, 2003). If sprint speed is important enough to be canalized against environmental perturbation, then it could be less susceptible to both resource limitation and, ultimately, allocation-based life-history trade-offs, as appears to be the case in phrynosomatid lizards (Husak & Lailvaux, 2017). However, this explanation is inconsistent with the results of Zamora-Camacho et al. (2015) who showed that sprint speed is subject to a trade-off with experimentally elevated immune activity in the lacertid lizard *Psammodromus algirus* (see also San-Jose, Huyghe, Schuerch, & Fitze, 2017). The results of our direct manipulation on sprint speed here raise several questions regarding the nature of condition dependence and why specific traits appear to be affected by resource availability in some taxa but not in others.

Our results for bite force offer some potential insight into the apparent trait-specific nature of condition dependence during exercise training. Although sprint speed was invariant across treatments, this was not true of bite force. Indeed, diet-restricted but protein-supplemented, sprint-trained animals exhibited both the greatest loss of mass and the largest decrease in bite force over the course of the experiment, but with no accompanying significant loss of sprint speed (Figure 1a,b). Our results for bite force plasticity match those of both Lailvaux et al. (2012) and Lailvaux et al. (2019) who found clear evidence of plasticity in male bite force in *A. carolinensis*. The lack of similar plasticity in sprint speed is therefore novel and represents scope for understanding the mechanisms whereby certain traits may be shielded against diminished expression associated with reduced resource availability. In contrast with our current results for sprint training, Husak et al. (2016) reported that endurance-trained green anoles had bite force capacities under diet restriction comparable with those on a high-calorie diet. One possible explanation for this discrepancy is that the mechanisms stimulated by exercise training to cause allocation to performance under forced exercise may prevent resources from being shunted away from the performance trait being used, but not from untrained performance traits (Atherton & Smith, 2012; Wilson, 2013; Yan, Okutsu, Akhtar, & Lira, 2011). Endurance and sprinting are supported by different physiological mechanisms: Endurance training reduces standard metabolic rate in green anoles, possibly by increasing mitochondrial efficiency (Lailvaux et al., 2018), whereas sprint training increases protein synthesis in the over-worked skeletal muscle of trained animals (Husak, Keith, et al., 2015). Thus, one might predict trade-offs between power-dependent performance traits (e.g., bite force and sprinting when protein is important for both) when only one is trained, but not necessarily between performance traits with different underlying morphological and physiological underpinnings (e.g., endurance and bite force when protein is more important for one). Indeed, it is worthy of note that the significant differences in bite force in our experiment were only among the trained groups, but not between treatments and controls. This result is consistent with the notion that competition over protein resources driven by forced investment in sprint speed drives a reduction in bite force. Whether our protein supplementation was ineffective or insufficient in ameliorating negative effects of sprint training on bite force is unclear from our current data set, but would be an interesting topic for future study. In particular, studies examining the fate of ingested protein and the degree to which dietary protein is incorporated into the musculature supporting performance under different conditions would be enlightening.

In summary, we found no effect of dietary restriction on sprint speed in green anole lizards when paired with training despite significant decreases in body mass. However, bite force performance decreased due to dietary restriction, and protein supplementation did not rescue it. This suggests that available protein may have been shunted to leg muscles to maintain sprint speed, perhaps due to sprint speed's likely influence on green anole fitness (Calsbeek & Irschick, 2007; Irschick et al., 2005). Our results raise questions regarding the generality of resource-based performance trade-offs, and highlight the importance of considering the roles of plasticity and energetic requirements when studying the links between form and function.

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