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Performance Tradeoffs, Ontogenetic Conflict, and Multisport Athletes: How is an Ironman Triathlete Like a Frog?

Ryan Calsbeek[1],[*] and Debora Goedert[*],[†]

*Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA; †CAPES Foundation, Ministry of Education of Brazil, Brasília, DF, Brazil

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[1]E-mail: ryan.calsbeek@dartmouth.edu

Synopsis Life-history theory is a cornerstone of modern evolutionary biology that addresses myriad phenomena ranging from demography and population structure to the evolution of aging and senescence. Trade-offs may arise in a number of contexts, from allocation-based (e.g., egg size vs. egg number) to genomic conflicts (e.g., intralocus sexual conflict in which genes that perform well in males perform poorly in females). Here we test for performance tradeoffs in human athletes. We show that in Ironman triathletes, swimming performance trades off with cycling and running performance. The tradeoff appears to be plastic, in that only highly trained athletes experience the tradeoff. We then investigate whether wood frogs (*Rana sylvatica*) experience similar locomotor performance tradeoffs, to ask whether the divergent environments experienced by tadpoles and frogs leads to *ontogenetic* conflict (tradeoffs over development). We show that although swimming and jumping performance are positively correlated, antagonistic natural selection may still favor alternative adaptive optima in the two life history stages. However, "adaptive decoupling" of the life stages during metamorphosis may resolve ontogenetic conflict and facilitate independent adaptation to both environments. Thus, whereas performance tradeoffs are general in both systems, the unique selective environment of amphibians has favored the evolution of mechanisms to alleviate the costs of those tradeoffs.

The common adage that a "Jack of all trades is the master of none" captures the essence of tradeoffs: specialization comes at a cost. Much of life-history theory is structured around understanding the importance of trade-offs (Roff 1992; Roff and Fairbairn 2007). Trade-offs may arise in a number of contexts, from allocation-based (e.g., egg size vs. egg number; [Sinervo and Licht 1991]) to tradeoffs in performance metrics (e.g., Careau and Wilson 2017), to genomic conflicts (e.g., intralocus sexual conflict in which genes that perform well in males perform poorly in females; Cox and Calsbeek 2009). Trade-offs may also arise ontogenetically, especially in organisms with complex life-histories (Chippindale et al. 2001). Chippindale et al. (2001) showed that whereas fitness variation in *Drosophila* is sexually concordant in juveniles, it becomes sexually antagonistic in adults, a pattern they termed "ontogenetic conflict". Optimizing a single individual for two different life history stages may therefore be constrained by an ontogenetic tradeoff, in which selection on one life-stage impacts the degree to which another life-stage can respond to selection (Sinervo and Calsbeek 2003; Bonduriansky and Rowe 2005; Aguirre et al. 2014).

Both allocation based trade-offs, where resources must be partitioned among various traits (Stearns 1982), and genetic trade-offs (e.g., antagonistic pleiotropy) are widespread, but we know comparatively less about genetic trade-offs at the level of suites of genes or of whole genomes (Rice and Chippindale 2001). Moreover, most of what we know concerning genomic trade-offs is limited to studies of sexual conflict (Cox and Calsbeek 2009). Traits that have a positive genetic correlation between males and females limit the evolution of sexual dimorphism in those traits. The degree to which selection can independently optimize the sexes is

therefore constrained by this sexual conflict. For example, recent studies have demonstrated that high-fitness sires produce sons with high fitness but daughters with low fitness (Chippindale et al. 2001; Fedorka and Mousseau 2004; Pischedda and Chippindale 2006; Foerster et al. 2007) reviewed by Cox and Calsbeek (2009). Alternative alleles that are favored in males and females can impose a fitness cost if females that chose to mate with a given sire are able to produce high fitness progeny of only one sex. This pattern should favor the evolution of mechanisms that can resolve the conflict, such as sexual dimorphism (Lande 1980; Day and Bonduriansky 2004), sex-linkage (Rice and Chippindale 2001), genomic imprinting (Haig 1997; Day and Bonduriansky 2004), or parental control over progeny sex allocation (Cox and Calsbeek 2010).

Sexual conflict is just one of many genetic conflicts that may constrain adaptation however. More generally, genomic conflicts arise when selection favors alternative allelic optima in different types of individuals (Morris et al. 2013) or individuals in different stages of the life history. Given the ubiquity of tradeoffs, the insights gained from studies of sexual conflict should therefore be general to other forms of genomic conflict. Indeed, the "conflict perspective" includes many areas of active study, including ontogenetic shifts in behavior (e.g., sex change in fish), the maintenance of polymorphism within species (e.g., alternative mating strategies), metamorphosis, and sexual dimorphism. As such, ontogenetic conflict is likely to be far more common than currently appreciated.

Anuran metamorphosis represents an extreme case of ontogenetic conflict in which individuals experience at least two divergent body plans: an undulatory-swimming aquatic stage optimized for feeding and growth (i.e., tadpole), and a saltatory terrestrial stage optimized for reproduction (i.e., frog; McDiarmid and Altig 1999). Genetic correlations in traits expressed across the life cycle suggest the possibility of trade-offs between the life stages (Watkins 2001) because natural selection on one life stage can have correlated effects on traits in another life stage (Lande 1983; Lande and Arnold 1983). For example, if swimming speed in tadpoles is genetically correlated with jumping distance in frogs, then selection on tadpole swimming speed could indirectly influence jumping performance in frogs. Genetic correlations may therefore limit the ability of selection to independently optimize different stages of the life history.

Multisport human athletes face similar types of performance tradeoffs. For example, decathletes compete in athletic events with dramatically different morphological optima; running events (e.g., 1500 m) that favor low body mass to maximize speed and endurance tradeoff with throwing events (e.g., javelin) that favor higher body mass and large power output. Likewise, triathletes complete consecutive swimming, cycling, and running events, each of which in isolation favors alternative body plans, technique specialization, and training regimes. In multisport athletes, therefore, tradeoffs may arise due to alternative morphologies favored in different sporting events or may respond plastically to training.

In amphibians, trade-offs could be alleviated if the process of metamorphosis breaks apart the genetic correlations (so-called "adaptive decoupling"; [Moran 1994; Aguirre et al. 2014]). For example, some phenotypes of larvae (i.e., aquatic tadpoles) and adults (terrestrial frogs) are uncorrelated or even negatively correlated (e.g., tadpole size is negatively correlated with frog size; [Emerson 1988; Ficetola and De Bernardi 2006; Johansson et al. 2010]). We know surprisingly little regarding the degree to which trade-offs might be resolved by adaptive-decoupling of genetic correlations (Fellous and Lazzaro 2011), how the action of selection across life-stages could be influenced by these correlations, or to what degree evolutionary change in anurans is impacted by genetic correlations within and between life stages. Here we explore the degree to which tradeoffs constrain the athletic performance in the case of multisport athletes, and optimization of alternative life history stages in the case of amphibians. We begin by describing an investigation of performance tradeoffs in Ironman triathletes, and then build on patterns in this system to compare with patterns observed in an ongoing long-term study of ontogenetic conflict in wood frogs, *Rana sylvatica*.

Performance tradeoffs in multi-sport athletes

The sport of triathlon involves athletes performing consecutive swimming, cycling, and running races. Each of the three sections varies in length depending on the format of the triathlon (e.g., sprint, Olympic, and Iron distances). Iron distance triathlons are among the longest triathlons. In an iron distance triathlon, athletes swim 3.86 km, cycle 180.25 km, and run 42.2 km. Most organized Iron distance events allow 17 h for an official race finish. Here we investigate the role of performance tradeoffs in determining race outcomes in Iron distance triathletes using data from three recent Ironman™ sanctioned triathlons in North America and Hawaii.

We gathered data on swimming, cycling, and running times for every amateur athlete that officially completed (<17 h) Ironman Lake Placid 2016 (Lake

Placid, NY, USA), Ironman Florida 2016 (Panama City beach, FL, USA), and Ironman Hawaii 2015 (Kona, HI, USA) using the publically available records at http://www.ironman.com. We chose these three event venues because whereas the cycling course in Ironman Lake Placid has over 2000 m of elevation gain, the cycling course in Ironman Florida is considerably more flat with only 300 m of elevation gain. Although both Florida and Lake Placid races are open to the general public, most participants at Ironman Hawaii must qualify by finishing near the top of their respective age group in another Ironman event. Thus, Lake Placid heavily emphasizes cycling performance relative to swimming and running, Florida de-emphasizes cycling fitness relative to Lake Placid, and Hawaii represents mostly high performance athletes from other events (nb: owing to its notoriety as the first Ironman, Kona also includes a small number of "celebrity" athletes who enhance television viewership and may or may not be considered "trained"). After gathering the data from each of the three races, we calculated the percent of the finishing time that each athlete spent performing the three sports. We did not include transition times (time spent changing clothing and/or equipment between sports) in any analyses. We created a categorical variable to score whether individuals finished before or after the 10 h mark of each race and used this measure as a proxy for novice versus elite athletes. Because the separate events all sum together to the total race time, relationships based on the percent time spent in each individual discipline may be biased toward negative correlations (the so-called "constant sum constraint"; [Kucera and Malmgren 1998]). We therefore performed a log ratio transformation of the data to (using the natural logarithm of individual discipline times scaled by the geometric mean of the three discipline times) reduce this bias. We present both the raw and the transformed data for comparison.

Results for human performance tradeoffs

Considering all athletes together, the correlation between cycling time and running time was strong and positive ($r^2 = 0.41$, ANOVA $F_{1,6614} = 4677$, $P < 0.0001$) as were the correlations between swimming and cycling times ($r^2 = 0.28$, ANOVA $F_{1,6614} = 2609$, $P < 0.0001$), and swimming and running times ($r^2 = 0.29$, ANOVA $F_{1,6614} = 2826$, $P < 0.0001$). However, at two venues the relationship between swimming time and cycling time changed significantly with training status. At both Ironman Florida and Ironman Hawaii, untrained athletes

showed stronger correlations between swimming and cycling times than did elite athletes, although the difference was only significant at Ironman Hawaii (training status × minutes cycling $F_{1,1977} = 12.37$, $P = 0.004$; Fig. 1A). The difference in relationship between swimming and running performance was qualitatively identical at Ironman Hawaii (training status × minutes running $F_{1,1977} = 6.03$, $P = 0.01$), but these performance measures were not related at either of the other two venues. Finally, this difference in relationship between running and cycling performance was evident at both Hawaii (training status × minutes running $F_{1,1977} = 16.04$, $P < 0.0001$; Fig. 1A) and Lake Placid (training status × minutes running $F_{1,2452} = 11.12$, $P = 0.001$; Fig. 1B), but not Florida (Fig. 1C). These results suggest that for untrained athletes there are generalities in performance across the three disciplines. On average, untrained athletes who perform poorly in one event tend to show low performance in all three events. However, elite athletes, especially those at the world championship event, tend to show more evidence of performance specialization.

Across the three race venues, the percentage of total race time spent cycling was negatively correlated with the percentage of total race time spent running ($r^2 = 0.86$, ANOVA $F_{1,6614} = 4191$, $P < 0.0001$). However, this relationship was weaker for percent time swimming versus percent time cycling ($r^2 = 0.004$, ANOVA $F_{1,6614} = 25.82$, $P < 0.0001$) and for percent time swimming versus percent time running ($r^2 = 0.05$, ANOVA $F_{1,6614} = 364$, $P < 0.0001$). These relationships remained strongly negative after correcting for the constant sum constraint (cycling vs. running $r^2 = 0.19$, $F_{1,6614} = 1575$, $P < 0.0001$; swimming vs. cycling $r^2 = 0.15$, $F_{1,6614} = 1230$, $P < 0.0001$; swimming vs. running $r^2 = 0.42$, $F_{1,6614} = 4878$, $P < 0.0001$). Again, these relationships differed between elite and untrained athletes. The negative relationship between swimming performance and cycling performance was only evident in elite athletes at Ironman Hawaii (training status × % time cycling $F_{1,1977} = 26.59$, $P < 0.0001$; Fig. 1A) and Ironman Florida (training status × % time cycling $F_{1,2175} = 5.84$, $P = 0.02$; Fig. 1C). This relationship did not differ by training status at Ironman Lake Placid ($F_{1,2455} = 0.003$, $P = 0.95$; Fig. 1B). The percentage of total race time spent running and cycling was strongly negatively correlated at all three venues and irrespective of training status ($r^2 = 0.86$, ANOVA $F_{1,6614} = 38,846$, $P < 0.0001$). The percentage of total race time spent swimming and running was weakly and negatively correlated irrespective of training status at all three venues ($r^2 = 0.05$, ANOVA $F_{1,6614} = 364$, $P < 0.0001$). Results remained
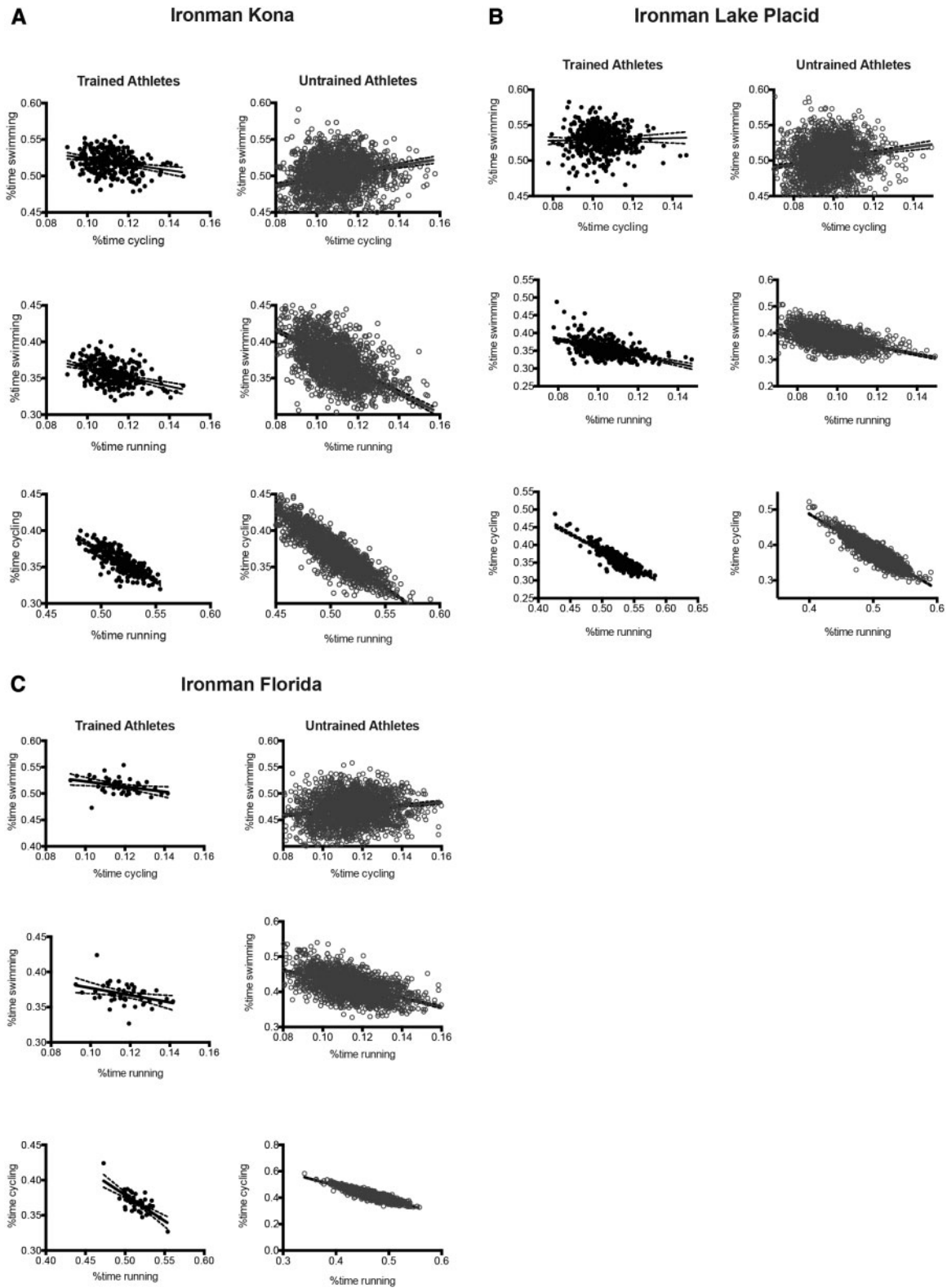
Fig. 1 Correlations between swimming and cycling performance (top row), swimming and running performance (middle row), and cycling and running performance (bottom row) for trained athletes (left column) and untrained athletes (right column) at the Hawaii Ironman world championships event (**A**), Ironman Lake Placid, New York (**B**), and Ironman Florida (**C**). Performance was measured as the percent of total race time allocated to each individual event and does not include any time spent in transition between events. Relationships were similar across all events and in both athlete groups, except that across all race venues examined, elite athletes experience a tradeoff in swimming versus cycling performance that is absent in untrained athletes.

Table 1 The importance of elite versus novice athletic status on performance tradeoffs remained evident after correcting for potential bias owing to the constant sum constraint

Comparison	Venue	df	F-value	P-value
Swimming vs. cycling	Kona	1977	19.14	***
	Florida	2175	6.59	**
	Lake Placid	2455	3.70	*
Swimming vs. running	Kona	1977	7.82	***
	Florida	2175	2.14	NS
	Lake Placid	2455	1.90	NS
Running vs. cycling	Kona	1977	19.14	***
	Florida	2175	6.59	**
	Lake Placid	2455	3.73	*

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Fig. 2 Trained and untrained athletes allocated their race effort differently to the three events within each Ironman. Trained athletes spent significantly more time swimming and cycling (relative to their total race time) compared with untrained athletes, but significantly less time running (relative to their total race time) compared with untrained athletes. Histogram bars shown mean values from all three venues (± 1 SE). Asterisks denote statistically significant ($P < 0.05$) differences. Results from separate venues are shown below the main panel.

qualitatively identical after we corrected for the constant sum constraint (Table 1).

Finally elite athletes distributed their effort across the three disciplines differently compared with novice athletes (Fig. 2). Compared with their novice competitors, elite triathletes tended to spend a greater percentage of their total race-time swimming (average values across all three venues: 10.9% vs. 10.6%) and cycling (53% vs. 49%) and a smaller percentage of their total race time running (35% vs. 39%; for elite vs. novice triathletes, respectively, all $P < 0.0001$; see Fig. 2 panels for separate results by venue).

Performance tradeoffs in amphibians

Wood frogs, *R. sylvatica*, have a broad geographic distribution, ranging from Georgia, north through Canada and into western Alaska (Martof 1970), and are the only amphibian found in north of the Arctic Circle. In the Northeastern USA, wood frogs breed in vernal pools during early spring (e.g., during May at our study sites in New Hampshire and Vermont). Females arrive at pools and lay eggs over the course of a few days soon after ice-melt and eggs hatch after 15–20 days. Larval wood frogs metamorphose after about 60 days and disperse from their natal pools. Larval wood frogs are subject to predation by a variety of aquatic invertebrates (especially dragonfly larvae; *Anax* spp.) as well as by other amphibians, and juvenile frogs face intense predation by garter snakes (*Thamnophis sirtalis*) as well as by small mammals and birds.

We have recently begun building on previous studies on the adaptive decoupling hypothesis by estimating selection coefficients on performance and morphology in different life history stages of wood frogs. During 2015, we measured linear attributes of tadpole
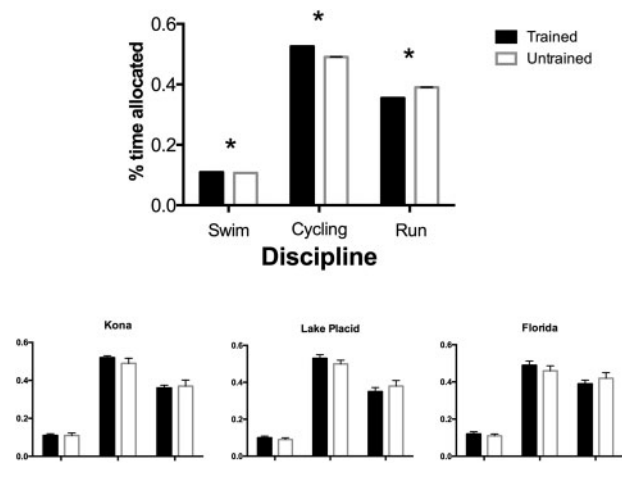
morphology by placing individual tadpoles in a small v-shaped aquarium that constrained mobility while we recorded a digital photograph. Each photograph included a centimeter size standard which was later used to measure body length, tail length, and tail muscle depth from digital photographs. We measured swimming speed by releasing individual tadpoles into a 10 cm × 10 cm aquarium and inducing a C-start (escape swim speed; Calsbeek and Kuchta 2011) by gently touching their tail base with a wooden dowel. Digital video records of swimming trials were analyzed using Image J software to extract maximum swimming speed achieved over a 10 cm distance. Tadpoles were uniquely marked with a four-color combination of elastomer dies (Nauwelaerts et al. 2000) for permanent identification before being released into semi-natural mesocosms to measure viability.

Tadpoles were then released into small wading pools filled to a depth of 15 cm with dechlorinated tap water and 0.5 kg of deciduous leaf litter (Calsbeek and Kuchta 2011). We also released three dragon fly nymphs (*Anax junius*) as tadpole predators. After two weeks, predation trials were ended and surviving individuals were recovered from enclosures. Those individuals that were not recovered were considered to have died.

In 2016, we measured frog body mass (nearest g) using a digital balance, and we measured snout–vent–length (nearest mm) and hind limb length using a handheld metal ruler. We measured jumping

performance of frogs by placing them on the floor of a plexi-glass arena whose walls ensured that frog jumps were in the forward direction. The floor of the arena was graduated in centimeter increments and frogs were motivated to jump by gently tapping their hind quarters. Frogs were held in individual containers of water at 21–23 °C prior to jumping trials. We recorded three successive jumps for each individual. Each frog received a unique toe clipping (one toe per foot, never the fourth toe) for permanent identification and was then released into one of two field enclosures to measure viability.

We released a total of 100 frogs, 50 to each of two semi-natural terrestrial enclosures that were constructed from 2 mm mesh screening and which were erected near one of our study pools. Enclosures were 1 m tall on all sides but were left open at the top, which allowed access by avian predators and small mammals. After two weeks, viability trials were ended and surviving individuals were recovered from enclosures. Those individuals that were not recovered from selection experiments were considered to have died. We estimated the strength of selection on both tadpoles and frogs by assessing the covariance between the survival component of fitness and either swimming or jumping measures of performance (Lande and Arnold 1983; Brodie et al. 1995).

To estimate the degree of phenotypic integration (modularity) in wood frogs, we estimated phenotypic correlations within tadpoles, within frogs, and between tadpoles and frogs that we bred in the laboratory to control genetic relationships. We estimated modularity using Escoufier's RV (Escoufier 1973; Klingenberg 2009). Escoufier's RV is a measure of morphometric modularity in which values close to zero indicate greater phenotypic integration within module (e.g., life history stages) than between modules.

Results

Our preliminary studies indicate that performance tends to be positively correlated across the life history, and that adaptation may therefore be constrained by this ontogenetic conflict. Swimming performance in tadpoles was correlated with jumping performance of those same individuals as frogs (mixed model with full-sib family, maternal ID, and pond of origin as random effects: estimate $= 1.249$, $P = 0.006$; effect size $r = 0.293$, 95% CI: 0.134–0.50; effect size calculated following Nakagawa and Cuthill [2009]; Fig. 3). This correlation was at least partially mediated by the effects of size on performance, as indicated by the reduced strength of the correlation between swimming and jumping performance when performance was analyzed
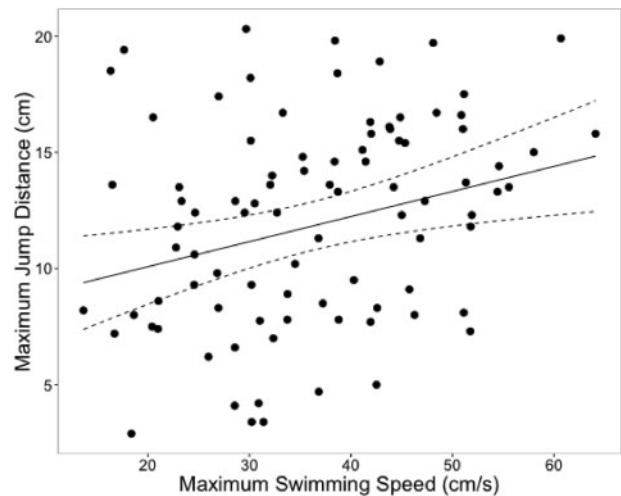

Fig. 3 The correlation between swimming performance of tadpoles and jumping performance of frogs is positive. Data points represent maximum swimming speed and maximum jumping distance for individual wood frogs. Solid line shows the best fit regression and hatched lines show the 95% confidence intervals. Our statistical model included random effects for pond of origin and dam id nested with sire id (see text).

using the residuals from the regressions of swimming speed and jumping performance against body size (estimate $= 0.062$, $P = 0.06$, effect size $r = 0.200$, 95% CI: -0.002 to 0.411). Moreover, tadpoles showed evidence of being highly phenotypically integrated compared with frogs (Escoufier's RV coefficient $= 0.284$, 95% CI: 0.080–0.469; $N = 1480$ iterations; $N = 86$ individuals).

Natural selection acted in opposite directions on tadpole swimming performance and the jumping performance of adult frogs (viability selection favored fast swimming tadpoles ($\beta = 0.32 \pm 0.12$; $P < 0.01$) but favored frogs with shorter jump distances ($\beta = -0.33 \pm 0.13$; $P < 0.01$).

Discussion

I'm so sick of the water

—Michael Phelps

Triathlons are physically, technically, and strategically challenging events. Athletes face numerous challenges ranging from knowledge about pacing to the (related) role of mounting fatigue over the course of the event, to managing individual levels of specialization in each sport. The last of these, specialization, is perhaps most variable for the swimming event. Swimming performance more than either of the other two events depends on learned technique and the cost of poor swimming preparation can be severe. Despite the fact that the swim is the first leg of triathlons, more triathletes die during

the swim than at any other point in the race (Harris et al. 2010). Indeed, far more athletes die during the swim leg of a triathlon than during an open marathon (Redelmeier and Greenwald 2007). The density of water, 800 times that of air, makes the costs of transport while swimming dramatically higher than it is while either cycling or running. Pure swimmers have better coordination in the water and are more efficient swimmers compared with multisport athletes (Seifert et al. 2016). Efficiency gains appear to be more related to drag reduction and moving a greater distance per stroke compared with triathletes (Toussaint 1990), rather than higher stroke frequency or power output.

An alternative explanation for the tradeoff in swimming and cycling/running performance is that an elite swimmer may develop a specialized morphology that is ill-suited to running and/or cycling. For example, an elite swimmer has, on average, higher body mass and body height (Cochrane et al. 2015) compared with an elite runner (Anderson 1996). Similarly, elite cyclists tend to have reduced upper body mass relative to swimmers, owing to both the physiological demands of cycling and the enhanced aerodynamic economy of a narrow profile while cycling (Barry et al. 2015). Morphological data are not available for comparison with the performance data in this study, leaving the relative importance of specialization and morphological differences an open question. Additionally, although much remains to be understood about the molecular and genetic bases of performance, innumerable genes have been linked to power output in humans. For example, variation in the production of alpha-actin-3 and mitochondrial enzymes due to polymorphism in the ACNT3 gene has been associated with tradeoffs between sprinter and endurance phenotypes (reviewed by Berman and North 2010). While the mutant variation of the ACTN3 gene resulting in the endurance phenotype has been shown to be overrepresented in endurance athletes (Vincent et al. 2007), the lack of alpha-actin-3 leads to a trade-off in the muscles' ability to produce powerful contractions at high velocity (Yang et al. 2003). Consequently, while an endurance phenotype leading to increased fatigue resistance could be advantageous for long distance running for example, the sprinter type has been shown to better tolerate high submaximal workloads while cycling, presenting phenotype traits that are related to better cycling performance in the Tour de France (Gomez-Gallego et al. 2009 and references within). This provides a potential molecular basis for running and cycling trade-offs, at least under some race conditions. Interestingly, studies of the ACTN3 polymorphism in Ironman triathlon athletes have found no prevalence of one or the other phenotype (Saunders et al. 2007; Grealy et al. 2015), nor any association of genotype with variation in athlete's race time (Saunders et al. 2007; Grealy et al. 2013), although studies have not considered the potential trade-offs between the individual events within the triathlon competitions.

The negative correlation between cycling performance and running performance is likely the result of triathletes over-taxing themselves during the bicycle portion of the event, and leaving insufficient energetic reserves for the run (Stocker et al. 2013). Prior cycling is known to negatively impact running performance and higher variability in power output while cycling has larger negative impacts on running performance compared with constant power output (Etxebarria et al. 2014). Any learned component of constant power output while cycling is therefore likely to reduce the magnitude of the tradeoff in running and cycling performance. Indeed, elite triathletes experience relatively small reduction in running efficiency after cycling (Cala et al. 2009). This may be partially due to the learned aspect of distributing effort appropriately across the three sports (e.g., elite athletes spend proportionally more time on the bicycle compared with untrained athletes). Multisport athletes also show reduced recruitment of musculature relevant to cycling compared with both novice and elite cyclists who focus training on a single discipline (Chapman et al. 2007), providing further evidence that the tradeoffs described here may respond to training.

Perhaps the most striking pattern to emerge from this study is that the performance variation among novice triathletes is structured differently from that of elites. Whereas a novice athlete generally shows low performance across all three disciplines, data for elite triathletes suggest that tradeoffs are magnified by higher levels of training and performance. This appears to be especially true for swimming performance compared against the other two disciplines. Elite triathletes that are particularly strong cyclists and runners tend to be weak swimmers and vice versa. A portion of this result may be due to the distribution of effort that elite triathletes strategically apportion to each event (elites cycle relatively slower and run relatively faster than novice athletes). However, the dramatic difference in technical requirements to be a proficient swimmer compared with both swimming and cycling is consistent with a real constraint when it comes to optimizing performance across all three disciplines.

Its not easy bein' green

—Kermit the Frog

Metamorphosis has long been viewed as a dangerous period in anuran development (Wassersug 1975; Arnold and Wassersug 1978). Our previous work (Calsbeek and Kuchta 2011) shows that natural selection is particularly intense during metamorphosis since metamorphs are well-suited to neither aquatic nor terrestrial environments. Calsbeek and Kuchta (2011) showed strong stabilizing selection on developmental stage and body proportions, consistent with high mortality at the early tadpole and early metamorph stages. That study provided no information on how traits were correlated between tadpoles and frogs, or how selection acted on frog morphology and performance.

Understanding the potential role of ontogenetic conflict in shaping the evolution of amphibian life histories depends on measuring trait correlations between larval and adult frogs and estimating selection coefficients on performance traits in both life history stages. Trait correlations in the common frog, *Rana temporaria*, were estimated by Johansson et al. (2010) who showed that swimming performance in tadpoles was phenotypically correlated with body shape, and that jumping performance in frogs was phenotypically correlated with body size. They further showed that performance in tadpoles and frogs was not correlated, suggesting that metamorphosis decouples the two life history stages, freeing them to be optimized independently by natural selection (no fitness data were provided in that study). Our preliminary data build on these previous works. Positive correlations in locomotor performance combined with antagonistic selection pressures that favor large trait values in one life stage but smaller trait values in the alternative stage suggest ontogenetic conflict in this system. However, preliminary analyses also indicated strong phenotypic integration among tadpole traits, but apparent decoupling of these trait correlations within the adult frog stage as well as between tadpole and frog stages. Although these studies are in their early stages, our preliminary data suggest that metamorphosis decouples the larval and adult stages similar to the patterns shown in *R. temporaria* (Johansson et al. 2010). If true, then the potential for ontogenetic conflict should be reduced for at least some of the phenotypic traits subject to selection across the life history of wood frogs.

We conclude that human triathletes are not abundantly similar to frogs. While humans show evidence of performance tradeoffs, wood frog locomotor performance seems to be positively correlated across developmental stages. In wood frogs, the locomotor performance tradeoff arises from divergent selective pressures experienced in the different environment of larval and frog stages. Metamorphosis possibly provides a novel means of circumventing the costs of performance tradeoffs in wood frogs in the physiological level, whereas human athletes may have no alternative but to become athletic specialists. Indeed, it is somewhat ironic that as human triathletes achieve more elite athletic ability, they experience greater performance tradeoffs among events. Equally ironic is that the fastest-swimming tadpoles are also the "best" jumping frogs (by human standards), yet natural selection does not favor such "elite frog athletes". The degree to which this impacts adaptation in each life stage will depend on the degree to which phenotypic correlations reported here, reflect the underlying genetic correlations among traits. One additional consideration for future studies should be the importance of individual variation (alluded to in this study) measured at the level of intra-individual variation (Careau and Wilson 2017) for athletes that have competed in multiple Ironman triathlons through time. Such an approach may be better suited to elucidating performance tradeoffs in athletes. Nevertheless it appears that the dramatic ecological differences that are experienced by amphibians with complex life-histories have favored the evolution of metamorphosis to facilitate independent adaptation to aquatic and terrestrial environments in a way that the human selective regime has not.

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