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The relative effects of pace of life-history and habitat characteristics on the evolution of sexual ornaments: A comparative assessment

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Selection may favor greater investment into sexual ornaments when opportunities for future reproduction are limited, for example, under high adult mortality. However, predation, a key driver of mortality, typically selects against elaborate sexual ornaments. Here, we examine the evolution of sexual ornaments in killifishes, which have marked contrasts in life-history strategy among species and inhabit environments that differ in accessibility to aquatic predators. We first assessed if the size of sexual ornaments (unpaired fins) influenced swimming performance. Second, we investigated whether the evolution of larger ornamental fins is driven primarily by the pace of life-history (investment into current vs. future reproduction) or habitat type (a proxy for predation risk). We found that larger fins negatively affected swimming performance. Further, males from species inhabiting ephemeral habitats, with lower predation risk, had larger fins and greater sexual dimorphism in fin size, compared to males from more accessible permanent habitats. We show that enlarged ornamental fins, which impair locomotion, evolve more frequently in environments that are less accessible to predators, without clear associations to life-history strategy. Our results provide a rare link between the evolution of sexual ornaments, effects on locomotion performance, and natural selection on ornament size potentially through habitat differences in predation risk.

KEY WORDS: Fins, killifish, life-history theory, secondary sexual traits, sexual selection.

Life-history theory predicts that selection will favor the evolution of traits that benefit immediate reproductive success when the chances for future reproduction are low (Andersson 1982). A strategy favoring immediate reproductive success is likely advantageous when mortality is high, as any fitness costs associated

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with traits benefiting current reproductive success are unlikely to be realized (Andersson 1994; Kemp 2002). Sexual ornaments are predicted to increase the chances of immediate mating success but at a potential cost to survival and future reproduction (Zahavi 1975; Johnstone 1995; Kotiaho 2001; Kokko et al. 2006; Robinson et al. 2006). The evolution of exaggerated or enlarged sexual ornaments could therefore be more likely when adult mortality is high and the opportunity for future reproductive success is limited (Andersson 1982, 1994). Despite clear theoretical predictions, there is only limited empirical evidence suggesting any coevolution between the size of sexual ornaments and the life-history trade-off between current and future reproduction (Williams 1966; Partridge and Endler 1987).

Predation is a key source of mortality in many natural populations and often drives selection for faster life histories and investment into current reproduction (Gadgil and Bossert 1970; Reznick et al. 1990; Auer et al. 2018). High predation risk also selects for predator avoidance, with sexual ornaments and other conspicuous courtship display traits typically covarying negatively with predation risk (Endler 1980; Basolo and Wagner 2004; Kemp et al. 2009; Pascoal et al. 2014; Heinen-Kay et al. 2015), but with substantial variation in this relationship (Weese et al. 2010; Fowler-Finn and Hebets 2011; Askew 2014; Oufiero et al. 2014). Consequently, in systems where predation selects for faster life-histories there may only be limited coevolution between the size of sexual ornaments and the pace of life-history. Assessing the relative roles that predation risk and life-history strategy have on the occurrence of sexual ornaments may increase our understanding of the mechanisms that promote their evolution. Making such an assessment requires a system where the pace of life-history—at least in part—is driven by mortality from sources other than predation. Here, we use a system of freshwater fishes, the killifishes (Suborder: Aplocheiloidei), which appear to be ideally suited for making a comparative empirical assessment of the effects of the pace of life-history and predation risk on the evolution of ornamental sexual traits.

Several killifish species have independently colonized ephemeral habitats, which can often desiccate during the dry season (Furness et al. 2015). Colonization of ephemeral habitats across much of Africa and South America has been facilitated by the evolution of an annual life-history strategy, embryonic arrest, and desiccation-resistant eggs, which allow populations to persist after adult fish have died (Murphy and Collier 1997; Hrbek and Larson 1999; Furness et al. 2015; Furness 2016). A lower risk of predation in ephemeral habitats has been suggested as a primary explanation for why some aquatic organisms have colonized these harsh habitats (Wilbur 1997). In killifishes, life-history traits broadly display a typical pace-of-life pattern, where rates of growth, development, and reproduction are strongly correlated (Eckerström-Liedholm et al. 2017; Sowersby et al. 2019, 2020, 2021). The correlations among these traits indicate that life-history evolution in killifishes follows a fast-slow life-history continuum, with differential investment in current versus future reproduction strongly associated with inhabiting ephemeral or permanent environments (i.e., an annual or nonannual life-history strategy; Simpson 1979; Genade et al. 2005; Blažek et al. 2013; Berois et al. 2015; Cellerino et al. 2016; Eckerström-Liedholm et al. 2017). Furthermore, annual species that inhabit ephemeral environments and typically exhibit “faster” rates of life-history traits also often have much shorter lifespans (Cellerino et al. 2016).

Precopulatory sexual selection appears to dominate mating competition in killifishes. For example, many species display a degree of sexual dimorphism but with little evidence for parental care or territory defense (Weitzman and Wourms 1967; Thomerson 1974; Haas 1976b; Peters 1986). Precopulatory sexual selection predominately acts on traits that increase attractiveness to mates and the ability to compete with sexual rivals (Buzatto and Firman 2016). In congruence with many other taxa, body size is a key determinant for mate choice in killifishes, with females preferring to associate with larger males (Haas 1976b; Ryan and Keddy-Hector 1992; Passos et al. 2013, 2014). Across killifishes, males in many species have unpaired fins that appear to be exaggerated in size and shape (author pers. obs.). Importantly, fin size is considered to increase mating success in many fishes, via both female choice (Suk and Choe 2002) and male-male competition (Goldberg et al. 2019). In this context, large fin size has been suggested to provide male fish with a metabolically inexpensive strategy of increasing perceived overall size, without investing in the somatic growth of more costly tissues (Basolo 1998; Rosenthal and Evans 1998). Fin displays toward potential rival males does appear to be a general pattern in killifishes (see material and methods) suggesting male-male competition as a mechanism driving the evolution of larger male fins (sensu Goldberg et al. 2019). However, there is also evidence of among-species variation in how male killifishes use their fins during courtship (Passos et al. 2013; Haas 1976a) with males in some species displaying fins toward both females and rival males. Although large ornamental fins may increase mating success, the size and shape of fins also affect hydrodynamics, swimming performance, and energy budgets (Webb; 1975; Beamish 1978; Weihs and Webb 1983; Boisclair et al. 1993). Sexual selection for enlarged and more elaborate fins may therefore impair key aspects of swimming performance, including traits that are known to be highly important for escaping predators (e.g., escape speed and turning radius; Howland 1974; Domenici et al. 1997; Langerhans et al. 2005; Walker et al. 2005).

We hypothesize that the evolution of sexual ornaments will be influenced by the pace of life-history and predation risk. Specifically, we predict that male ornamental fins will be more exaggerated (i.e., larger) in killifish species with faster life-histories that inhabit lower predator risk environments, compared to males from species with slower life-histories living in environments with a higher predation risk. If fin size evolves both due to sexual and natural selection, we further predict that male fin size will be positively associated with increased sexual dimorphism in species inhabiting environments with lower predation risk. To test these predictions, we employ a macroevolutionary comparative framework under a standardized common garden setting, to assess if fin size negatively affects swimming performance and whether enlarged fins are associated with the pace of life-history and/or habitat type (as a proxy for predation risk) across sexes and species.

Material and Methods

Killifishes were housed under standardized laboratory conditions (average 24.3°C, 12-h day:night). To provide shelter and enrichment, aquaria were furnished with gravel substrate, a terracotta pot, a floating string "mop," and commercially available aquatic vegetation. Fish were fed a mixture of newly hatched *Artemia* and commercial frozen red Chironomidae larvae, ad libitum three times daily (once per day during weekends). All individuals used in this study were hatched from eggs under our laboratory conditions. Killifish eggs came from our own population stocks or were sourced directly from dedicated hobbyists.

ASSESSMENT OF SWIMMING PERFORMANCE

We measured two aspects of swimming performance, escape speed and turning performance. Both are important for avoiding predators and are affected by fin hydrodynamics (Langerhans and Reznick 2010). Swimming performance was assessed in an open arena by eliciting responses via a startle stimulus ($N = 259$ individuals, from 19 species; Table S1). We reliably elicited startle stimulus responses by tapping the handle of a small aquarium net, either behind (to initiate an escape response) or in front (to initiate turning) of the focal fish. Swimming performance was recorded at 45 frames per second and escape swimming speed was calculated in a frame-by-frame analysis using ImageJ (Schneider et al. 2012), by tracking the maximal distance (cm) the focal fish covered in five frames, starting from the propulsive stroke of the "C-start" (Odell et al. 2003). Likewise, to calculate turning performance, we measured both the distance (cm) and time (frames) it took for each fish (at the center of mass) to turn 180° in the opposite direction away from the startle stimulus (cm × frames), with higher values indicating slower, wider turning performances.

MEASUREMENTS OF FIN AND BODY AREA

To quantify fin size, we first took standardized photographs of mature killifish that had been raised under common garden laboratory conditions ($N = 28$ species, $N = 227$ individuals, 116 females and 111 males; Table S2). We placed 19 landmarks on each image (tpsDig version 2.31) at characteristic body points to ensure placement was comparable across individuals and species (Figs. S1 and S2). On each image, a scale was set, using a 1-cm measure visible in each photo as a reference. The landmark coordinates were extracted (tpsDig version 2.31) and used to calculate the combined and separate areas of the anal, dorsal, and caudal (tail) fins, as well as the area of the body (without fins) as the areas of polygons. To get a relative measure of fin size, the area of each fin, relative to the body, was estimated as the residuals from a log-log regression of fin area on body area. The model was constructed to obtain relative measures of fin size for each individual and therefore did not contain any additional predictors. Further, the measures described above were intended to quantify the area of the fin(s) and are therefore not informative of putative shape differences. As general shape is potentially important, we also conducted a geometric morphometric analysis incorporating the whole-body outline (including fins); however, this additional analysis yielded largely similar results and is thus not reported here.

We measured fin size on live individuals to obtain high-quality data; however, this approach does place limits on the number of species we could include in our study, potentially reducing statistical power. Therefore, with identical methods we also measured fin size on zootaxa images, which are detailed zoological illustrations of male killifishes from a larger number of species ($N = 74$ species, 41 annual and 33 nonannual; Fig. S3; Table S3; Wildekamp 1993, 2004; Wildekamp and Watters 1995, 1996; Furness et al. 2015). We consider these data as complementary to that obtained from lab reared fish (see the Supporting Information for a comparison between the two datasets), as these illustrations likely depict idealized males (e.g., males in prime condition), with the size of sexual ornaments representing a species maximum rather than a mean phenotype.

EVIDENCE OF SEXUAL SELECTION ACTING ON FIN SIZE

An important feature of our study is the assumption that male fin size is under sexual selection, either via courtship or male-male competition. For the majority of killifishes, there is unfortunately very little information available (in the scientific literature) with regard to whether males display their fins either during courtship and/or male-male competition. To address this knowledge gap, we assessed video recordings ($N = 26$) made by devoted aquarists of male killifish courtship and display behaviors (see the Supporting Information). We observed that in African species ($N = 14$ species), males typically approach females with their fins folded, whereas in South American species ($N = 12$ species) males generally display open fins toward females. Displaying open fins toward rival males appeared to be a common behavior across all species from both continents.

ESTIMATE OF HABITAT TYPE

Within killifishes, there have been several independent evolutionary transitions to living in ephemeral habitats (Furness et al. 2015), via the evolution of eggs that are desiccation resistant and relatively long periods of embryonic diapause. Having eggs capable of entering diapause allows annual species to survive if the ephemeral water body they inhabit seasonally dries up and the adult population dies. These seasonal water bodies are harsh environments to inhabit, but have the advantage of being relatively inaccessible to aquatic predators (Fraser 1995). We could unfortunately not make direct assessments of species-specific predation risk for all species included in our study, as the required high-quality data on predator prevalence are not available for the majority of species. Instead, we relied on the fact that desiccant resistant diapausing eggs are clearly an adaptation to ephemeral habitats (Wourms 1972) and that species lacking this trait are unlikely to prefer or be adapted to survive in those habitats. We evaluated co-occurrence patterns between all species used in our study and other cyprinoid species, as reported in the detailed database Killi-Data (www.killi-data.org). In accordance with Furness et al. (2015), we found that many killifishes, including both species with and without embryonic diapause, frequently co-occur in transitional habitats such as stream margins and floodplains. In these transitional habitats, eggs can be vulnerable to desiccation events, although the adults of some species actively seek other habitats during these drier periods (Wourms 1972; Seghers 1978). We used this information to divide the species into three clear groups based on their habitat use: "permanent specialists," species without eggs capable of diapause that do not co-occur with species that have diapausing eggs; "ephemeral specialists," species with diapausing eggs that do not co-occur with any species without diapausing eggs; and "generalist," species with either diapausing or nondiapausing eggs that co-occur with the counterpart. The aforementioned habitat categories are thus assumed to reflect varying degrees of vulnerability to aquatic predators, where the lowest risk is found in ephemeral specialists and the highest risk in permanent specialists.

ESTIMATING THE PACE OF LIFE-HISTORY

We assessed pace of life-history in killifishes as scores along the dominant eigenvector of a principal component analysis (PCA) of growth rate, time to maturity, and reproductive rate, calculated across 32 species. These traits were measured in previous studies (see details in Sowersby et al. 2019; Eckerström-Liedholm et al. 2017), and the PCA scores were previously described in Eckerström-Liedholm et al. (2019). The dominant eigenvector described 75.4% of the variation in the three measured life-history traits, and thus provides a robust estimate of a species' position along the fast-slow life-history continuum. To accurately compare the relative roles that the pace of life-history and predation risk may have in driving the evolution of sexual ornamentation, both factors are required to contain independent variation. Importantly, our study meets this assumption, as although there is selection toward faster life-histories in ephemeral environments (Sowersby et al. 2019), a substantial amount of the variation in the pace of life-history (45%) is independent from life-history strategy (i.e., the presence/absence of diapausing eggs). Therefore, a large amount of the variation in killifish life-history rates is not explained by adaptations to seasonal environments (Sowersby et al. 2019; Eckerström-Liedholm et al. 2017). This degree of unexplained variation provides us with the opportunity to test the independent effects of both the pace-of-life and predation risk on the evolution of sexual ornaments (Dormann et al. 2013; Morrissey and Ruxton 2018). There is also considerable overlap in habitat use between species at the fast and slow ends of the life-history continuum, providing further evidence that life-history rates are not solely explained by adaptations to seasonal environments.

PHYLOGENY

To control for any potential effects of shared ancestry, which could generate false associations between traits, we used phylogenetically controlled analyses and included species representing four independent evolutionary transitions between an annual and nonannual life-history strategy. Specifically, we controlled for nonindependence of observations due to shared ancestry among species (Felsenstein et al. 1985) by estimating covariance of observations (residuals in our linear models) based on a time-calibrated phylogeny published in Furness et al. (2015). Species in our study that were not included in Furness et al. (2015) were added to the tree according to previously published phylogenies using the add.species.to.genus and bind.tip functions in phytools (Revell et al. 2012) in R (R Core Team 2017). Specifically, we added *Nothobranchius kadleci* alongside its sister species *N. furzeri* (Dorn et al. 2014; Furness et al. 2015). We placed *Ophthamnolebias constanciae*, which was previously included in the genus *Simpsonichthys*, alongside *Ophthamnolebias* [*Simpsonichthys*] *bokermanii* (Pohl et al. 2015). No other members of the genus *Ophthamnolebias* were included in our study, and our placement of *O. constanciae* is further validated by Costa (2006, 2007a). The *Hypsolebias* were also previously included within the *Simpsonichthys* genus but form a well-supported clade in Furness et al. (2015). We added one species, *H. flagellatus*, to this group, next to *S. magnificus* and *S. trilineatus*, which is also supported by Costa (2006, 2007a) and Costa et al. (2012). *Pituna schindleri* and *Scriptaphyosemion cauveti* were added to

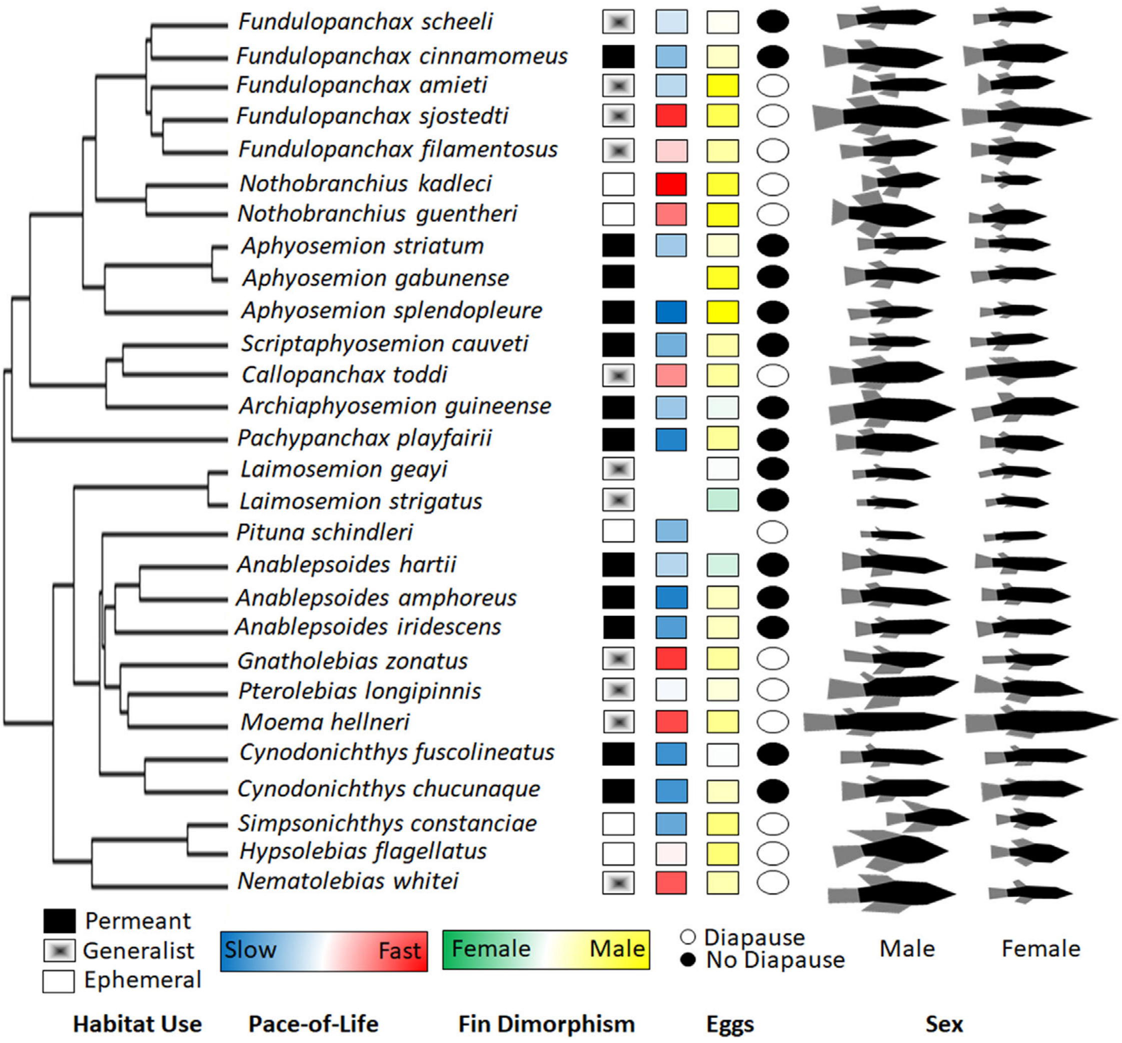

Figure 1. Phylogenetic tree (updated from Furness et al. 2015) of the species used in the study. Black squares represent species that inhabit permanent habitats, partially filled squares represent species that inhabit intermediate (generalsit) habitats, and white squares represent species that inhabit ephemeral habitats. The intensity of red (fast) and blue (slow) color represents the mean pace of measured life-history traits (Sowersby et al. 2019) per species. The intensity of green (female biased) and yellow (male biased) color represents the direction and mean degree of sexual dimorphism per species (maximum 10.6% difference). Black circles represent species that have eggs not capable of entering diapause and white circles represent species that have eggs that are capable of entering diapause. Silhouettes represent mean body and fin size and shape for males and females per species.

their respective monophyletic genera (Costa 2007b; Costa 2011; Furness et al. 2015). The *Moema* are paraphyletic; however, our positioning of *M. hellneri* in this group is valid because the species that breaks monophyly, *Aphyolebias peruensis*, was not included in our study. The resulting phylogeny was pruned and included as a random factor in all Bayesian linear models (see Figs. 1 and S4).

STATISTICAL ANALYSIS

We assessed the costs of ornamental sexual traits on functional ability (i.e., locomotion) by modeling swimming performance (turning performance or escape speed) as a function of either the residuals of total fin area or the area of each individual fin type (i.e., anal, dorsal, and caudal) in separate models. As killifish presumably differ in body shape across species (dorsoventrally), we also included the residuals of a regression of body area on squared body length (as areas scale to the square of a linear measure) as a covariate in all analyses. Furthermore, we tested if swimming performance depended on the pace of life-history, sex, and habitat use, as well as putative interactive effects. Although there are no significant mean body size differences between annual and nonannual killifishes (Eckerström-Liedholm et al. 2017), we acknowledge that performance traits may depend on overall body size. In all analyses, body length was therefore added as a covariate (Johansson et al. 2010), with species and phylogeny included as random effects.

To test which factors influenced fin size in our lab reared fish, we extracted residual fin area from a regression of log10 fin area on log10 body area. We then fit models with residual fin area as a response variable, and the pace of life-history (a continuous variable), habitat use (permanent, ephemeral, or generalist), sex, and their interaction as fixed effects. Phylogeny (Furness et al. 2015; see Fig. 1), species, and the interaction variance of sex and species were added to the models as random effects. The models were run using either residuals of total fin area or the residuals on individual fin area (i.e., the anal, dorsal, or caudal fin; see the Supporting Information for greater detail). As fin size may be linked to body area, there is a risk that any putative relative patterns may be explained by selection on body area, rather than selection on fin area (see Rogell et al. 2020). To account for this potential issue, we also assessed the effect of pace of life-history, habitat use, and sex on body area (independent of fin area). The zootaxa images ($n = 74$ species) were analyzed in congruence with the lab-reared fish, with the exception that we did not include sex or pace of life-history as a fixed effects in these models, as this is a male-only dataset and we only had data on the pace of life-history for less than half the species ($n = 32$ species). As we had a large sample of species represented in the zootaxa images, we also partitioned species variances specific to each habitat type (e.g., the variance across species inhabiting permanent, ephemeral, or intermediate habitats). We did this because any differences among these three variances can reasonably be interpreted as demonstrating that the diversification of sexual ornaments, across species, is dependent on habitat.

All models described were fitted using a Bayesian metropolis-Hastings sampler implemented in the R package 'MCMCglmm' (Hadfield 2010; R Core Team 2017). Parameter-expanded locally noninformative priors were used for all random effects and flat priors were used for the fixed effects, both representing little prior knowledge (as per Hadfield 2010). After a burn-in of 50,000 iterations, every 2000th iteration was saved, generating a total posterior sample of 1000 iterations. Autocorrelations were in the interval between −0.1 and 0.1 for all models, and visual inspection indicated good mixing of the posterior chains, indicating that the models had converged.

Results

FIN SIZE NEGATIVELY AFFECTED SWIMMING PERFORMANCE

As predicted, we found that residual total fin area negatively affected swimming performance in killifishes (specifically turning performance, estimate = 200 [95% CI = 77.7, 359], $P_{\mathrm{MCMC}} = 0.002$; Fig. 2 and Table S4). When focusing on specific fin types, we found that both the residual area of the anal (estimate = 184 [95% CI = 123, 285], $P_{\mathrm{MCMC}} = 0.001$) and the residual area of the dorsal (estimate = 160 [95% CI = 103, 255], $P_{\mathrm{MCMC}} = 0.001$) fins negatively affected turning performance, but not the residual area of the caudal fin (estimate = −153 [95% CI = −288, 52.3], $P_{\mathrm{MCMC}} = 0.182$; Tables S5–S7). In contrast, we did not find any significant effects of the residual area of any fin type on escape speeds ($P_{\mathrm{MCMC}} > 0.05$; Tables S8–S11). When testing if habitat, sex, the pace of life-history, or their interactions affected swimming performance, we found that males overall had a lower turning performance, compared to females (estimate = 192 [95% CI = 131, 250], $P_{\mathrm{MCMC}} = 0.001$; Table S12). A significant second-order interaction between habitat and sex indicated that sex differences in turning performance were smaller in generalist and permanent habitats, compared to ephemeral habitats (estimate generalists = −214 [95% CI = −278, −152], $P_{\mathrm{MCMC}} = 0.001$; estimate permanent specialists = −156 [95% CI = −227, −67], $P_{\mathrm{MCMC}} = 0.001$; Table S12). In addition, we found a significant interaction between sex and the pace of life-history, indicating that in faster-living species, males had a lower turning performance, compared to females (estimate = 37.1 [95% CI = 6.71, 55.2], $P_{\mathrm{MCMC}} = 0.02$; Table S12). However, we found no significant effects (main or interactive) of sex, habitat, or the pace of life-history on escape speed ($P_{\mathrm{MCMC}} > 0.05$; Table S13).

SEXUAL DIMORPHISM IS GREATER IN EPHEMERAL HABITATS

In lab-reared fish, we found that males had significantly larger residual total fin area compared to females, indicative of sexual dimorphism (estimate = 0.274 [95% CI = 0.155, 0.369], $P_{\mathrm{MCMC}} = 0.001$; Table 1 and Fig. 1). Female residual total fin area did not significantly differ across habitats ($P_{\mathrm{MCMC}} > 0.05$; Table 1), but the presence of a significant interaction between sex and habitat indicated that the difference between male and female residual total fin size was larger in ephemeral specialists, compared to both generalists (estimate = −0.158 [95% CI = −0.331, −0.0257] $P_{\mathrm{MCMC}} = 0.026$; Table 1 and Fig. 3) and permanent specialists (estimate = −0.239 [95% CI = −0.454, 0.00268], $P_{\mathrm{MCMC}} = 0.042$; Table 1 and Fig. 3). We did not find any significant main effects of the pace of life-history on residual fin area. However, we did find a significant third-order interaction between the pace of life-history, habitat use, and sex. This interaction indicated that in permanent specialists, there was a significant negative association between pace of life-history and sexual dimorphism in residual total fin area (Table 1 and Fig. 1). This significant third-order interaction depended on the inclusion of one slow-living, permanent habitat specialist species, with relatively large fins (i.e., the effect is dependent on a single species,

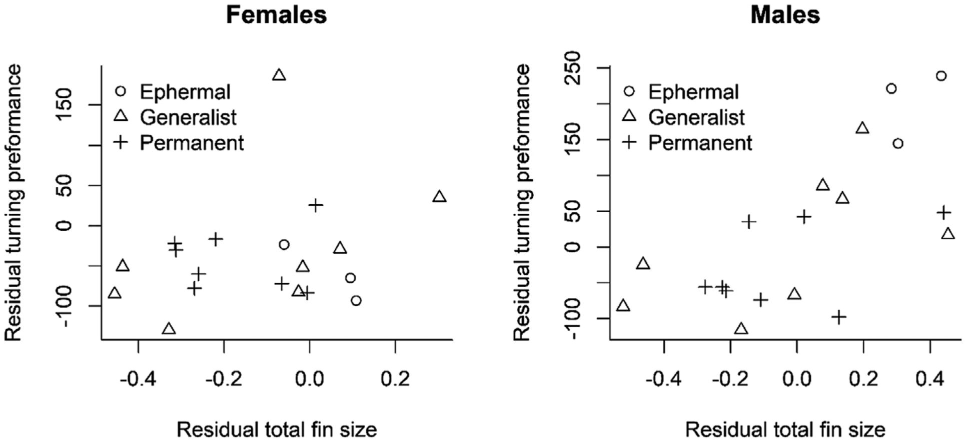

Figure 2. The relationship between residual swimming turning performance and the residuals of total fin area in females (left) and males (right). The area of the fins, relative to body, was estimated as the residuals from a log-log regression of fin area on body area. Each point signifies a species with circle symbols representing species from ephemeral habitats, triangles from generalist habitats, and crosses from permanent habitats. Higher values on the *y*-axis indicate lowered swimming performance.

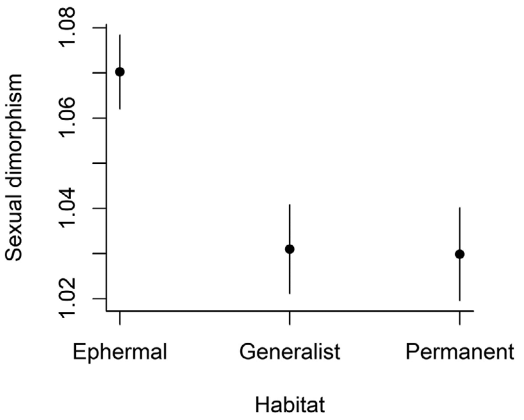

Figure 3. The degree of sexual dimorphism in killifish species in three different habitat types (ephemeral, generalist, and permanent), which differ in levels of predation risk. Male-biased sexual dimorphism increases along the *y*-axis. Sexual dimorphism was calculated from residuals from a regression of log total fin size on log total body area, as the predicted size of male fins (at mean size) / predicted size of female fins (at mean size).

Aphyosemion splendoplure). When this single outlying species was removed, the interaction was no longer significant, thus we do not interpret this result any further. For ease of interpretation, we present the analysis with this species removed. When focusing on specific fin types, we found that the significant interaction between habitat and sex was mainly driven by the types of fins, which also incurred costs on turning performance (i.e., the dorsal and the anal fins, not the caudal fin; Tables S14–S16). Finally, we found that males overall have a larger body area, compared to females (estimate = 0.0755 [95% CI = 0.019, 0.136], $P_{\text{MCMC}} = 0.006$; Table S17).

We found no effect of habitat use on residual total fin area in the larger, male-only dataset (i.e., zootaxa illustrations; $P_{\text{MCMC}} > 0.05$; Table S18). However, we did find that residual dorsal fin area, which lowered swimming performance in lab reared fish, was larger in ephemeral specialists, compared to permanent specialists (estimate = −0.367 [95% CI = −0.66, 0.002], $P_{\text{MCMC}} = 0.04$). In contrast, we found no association between habitat use and the residual area of the anal fin ($P_{\text{MCMC}} > 0.05$; Table S21). When testing whether species variances differed across the three habitat types, we found that separate species variances (for each habitat) improved the fit of the models (delta deviance information criterion (DIC) 5–20, depending on fin type). For residual total fin area and residual dorsal and anal fin area (i.e., the fins that lowered swimming performance), ephemeral specialists had higher among-species variances than generalists, which in turn had higher variances than permanent specialists (Tables S18–S20). The caudal fin, which was not directly related to swimming performance, displayed a different pattern, where generalist species had the highest across-species variance, followed by ephemeral specialists and permanent specialists (Table S21).

Discussion

Using a multispecies killifish system, we found evidence concordant with the evolution of exaggerated sexual ornaments being driven by variation in predation risk among different habitat types. Specifically, we found that species living in ephemeral habitats, which likely have fewer aquatic predators, had larger fins overall and that males of these species had larger fins compared to conspecific females (i.e., greater sexual dimorphism). In contrast to our prediction, we did not find support for any di-

Table 1. **Results of the Bayesian phylogenetic mixed model with the residuals of total fin area (i.e., sum of the areas of the dorsal, anal, and caudal fins) on body area as the response variable, with sex, life-history strategy (continuous variable), habitat use (ephemeral specialist, generalist, or permanent specialist), and their interactions as the predictor variables.**

Parameter	Estimate	Lower CI	Upper CI	P_{MCMC}
(Intercept)	−0.0613	−0.331	0.175	0.474
Sex (Male)	0.274	0.155	0.369	0.001
Pace of Life-History	0.0627	−0.0484	0.228	0.298
Habitat Use (Generalist)	0.123	−0.152	0.452	0.312
Habitat Use (Permanent)	−0.0396	−0.365	0.433	0.97
Sex (Male): Pace of Life-History (PACE)	0.0442	−0.0305	0.0955	0.368
Sex (Male): Habitat Use (Generalist)	−0.158	−0.331	−0.0257	0.026
Sex (Male): Habitat Use (Permanent)	−0.239	−0.454	0.00268	0.042
PACE: Habitat Use (Generalist)	−0.129	−0.325	0.0977	0.22
PACE: Habitat (Permanent)	0.0557	−0.347	0.299	0.952
Sex (Male): PACE: Habitat Use (Generalist)	0.00384	−0.0924	0.117	0.82
Sex (Male): PACE: Habitat Use (Permanent)	−0.0821	−0.26	0.106	0.406
Phylogeny	8.38×10^{-4}	3.59×10^{-8}	0.0733	–
Species	2.67×10^{-4}	9.99×10^{-9}	0.0438	–
Sex: Species	6.41×10^{-6}	4.60×10^{-9}	0.00248	–
Residual Variance	0.0193	0.0171	0.0257	–

The table is structured according to a "contrast treatments" output from R. The "Intercept" represents the mean for female ephemeral specialist species. "Sex (Male)" denotes the difference between females and males of ephemeral specialists. "Pace of Life-History" denotes the slope of the regression of the speed of life-history on fin size for females. "Habitat Use (Generalist)" represents the difference in means for the ephemeral specialists and generalists. "Habitat Use (Permanent)" represents the difference in means for the ephemeral specialist and permanent specialist species. "Sex (Male): Pace-of-Life (PACE)" denotes the difference in slope of the regression of the speed of life-history on fin size between female and males. "Sex (Male): Habitat Use (Generalist)" denotes the difference in fin size between male ephemeral specialists and male generalists. "Sex (Male): Habitat Use (Permanent)" denotes the difference in fin size between male ephemeral specialists and male permanent specialists. "PACE: Habitat Use (Generalist)" denotes the difference in slope of the regression of the speed of life-history on fin size between ephemeral specialists and generalists. "PACE: Habitat (Permanent)" denotes the difference in slope of the regression of speed of life-history on fin size between ephemeral specialists and permanent specialists. "Sex (Male): PACE: Habitat Use (Generalist)" denotes the difference in slope of the regression of speed of life-history on fin size between male ephemeral specialists and males generalists. "Sex (Male): PACE: Habitat Use (Permanent)" denotes the difference in slope of the regression of life-history pace on fin size between male ephemeral specialists and male permanent specialists. Estimate refers to mean parameter estimate from the posterior distribution. Lower and upper CIs represent 95% credible intervals. P_{MCMC} is the Bayesian *P*-value ($\alpha = 0.05$). Adding phylogeny and species as random effects allows us to analyze data at the individual level and provides a proper summary of the within species errors (e.g., the residuals are not confounded by species means). Specifically, "Phylogeny" refers to the variance explained by shared ancestry, whereas "Species" indicates the among-species variance. "Sex: Species" represents the variance explained by sex and species and "Residual Variance" is the variation that remains unexplained by the model (including within species variation). Lower and upper CIs represent 95% credible intervals. The species *Aphyosemion splendopleure* was identified as an outlier and removed from this analysis. All means are based on the mean of the posterior distribution.

rect influence or interactive effect of the pace of life-history on the size of ornamental fins. Overall, our results demonstrate that predation risk likely plays an important role in the evolution of exaggerated ornaments, compared to the pace of life-history.

Exaggerated display traits are predicted to increase the chances of mating success while simultaneously incurring costs to survival (Zahavi 1975; Kotiaho 2001). Despite this robust theoretical prediction, across-taxa, empirical evidence demonstrating the costs of exaggerated secondary sexual traits with respect to locomotion performance has typically remained mixed (Zuk and Kolluru 1998; Jennions et al. 2001; Oufiero and Garland 2007; Baumgartner et al. 2011; Askew 2014; Thavarajah et al. 2016) or even somewhat contradictory (Royle et al. 2006; Johnson et al. 2014). This suggests that the costs associated with secondary sexual traits could in many cases be subtle and difficult to detect (Clark and Dudley 2009). For example, we found a clear negative relationship between swimming performance and the size of ornamental anal and dorsal fins (which alter the height of the overall body profile) but no relationship between swimming performance and the size of the caudal fin (which does not alter the height of the body profile). These differences in the relationship between swimming performance and the size of the anal/dorsal fins and the caudal fin are intuitive when considering how fish move through a dense medium such as water, where the height of body structures will yield a less streamlined body shape leading to increased frictional drag (i.e., affecting the attached flow pattern, sensu Nesteruk et al. 2014). In both terrestrial and aquatic animals, any reduction in locomotion performance attributable to bearing sexual ornaments may hence be determined by the location of the exaggerated trait on the body. In environments with a high risk of predation, selection may favor the evolution of secondary sexual traits that have minimal negative effect on locomotion, resulting in the costs of such traits being difficult to detect. In this context, our results are comparable to studies conducted on swordtail fish (*Xiphophorus* sp.), which have found only a limited negative association between the length of sexually selected sword ornaments, located on the caudal fin, and some aspects of swimming performance (Oufiero et al. 2012, 2014).

Our results indicate that the evolution of large ornamental fins is largely associated with habitat type. Specifically, we found that male killifishes from ephemeral environments had larger anal and dorsal fins, which negatively impacted turning performance, an important trait for predator avoidance (Howland 1974; Domenici et al. 1997). Moreover, the degree of sexual dimorphism in these fins was significantly greater in species living in ephemeral habitats, compared to more permanent habitats. Previous studies on mosquito fish (*Gambusia* spp.) and guppies (*Poecilia reticulata*) have found that predation risk can influence the evolution of exaggerated sexual ornaments (Langerhans et al. 2005) and display traits (Endler 1980; Reznick et al. 1990; Kemp et al. 2009). Our results are in line with these previous studies, as ephemeral habitats are considered to be relatively inaccessible to various aquatic predators and appear to attract fewer piscivorous birds, compared to more permanent water bodies (Werner and McPeek 1994; Fraser 1995; Mamboleo et al. 2012). In killifishes, large ornamental anal and dorsal fins likely increase vulnerability to predators and are selected against when the cost to survival becomes too high in particular environments.

Ephemeral specialist species had larger variances in the size of anal and dorsal fins across species, compared to generalist and permanent specialist species. A valid interpretation of this result is that ephemeral habitats promote the divergence of costly male sexual ornaments, compared to more permanent, higher predation risk habitats. Sexual dimorphism is expected to evolve when the fitness optima of the sexes differ (Cox et al. 2009; Poissant et al. 2010), which in killifishes likely occurs when natural and sexual selections favor different fin sizes. Considering we found that male ornamental fins were most exaggerated in ephemeral environments, which likely have low levels of predation risk, it appears that sexual dimorphism in killifishes is driven by low (yet present) levels of predation (e.g., Reznick and Bryant 2007; Weese et al. 2010). In the context of our study, several wild populations of annual killifishes from highly ephemeral environments do become progressively female biased over time, suggesting sex-specific costs to survival (Reichard et al. 2014; Vrtílek et al. 2018; potentially driven by bird or invertebrate predation, M. Reichard pers. comms.). For instance, wading birds have been observed catching *Nothobranchius* annual killifish in Kenya (L.S. B. Leakey, pers. comms.) and “enormous numbers of avian predators” take fish from ponds near Lake Edward as they seasonally dry up (Curry-Lindahl et al. 1956). Complementing these field observations are experimental findings that show male *Nothobranchius* have a higher risk of being captured by a heron than females (Haas 1976b). That ephemeral habitats have lower abundances of aquatic predators appears quite well supported; however, less is known on the magnitude of avian predation across aquatic habitats. Recher and Recher (1968) describe the chances of fish successfully escaping a bird attack as mainly being determined by postcapture behavior (e.g., body contortions and flexions in the beak) and spines, as opposed to precapture behaviors (e.g., swimming and turning). Therefore, the available evidence suggests that the evolution of ornamental fins may be more limited by aquatic predators, rather than avian predators.

In contrast to our predictions, we found no impact or interactive effect of the pace of life-history on the evolution of enlarged ornamental fins in killifishes. Despite clear theoretical predictions (Andersson 1982, 1994), there has been little empirical evidence demonstrating a link between the pace of life-history and the evolution of sexual ornaments. One exception is found in semelparous salmon species and populations (Salmonidae), which tend to have larger sexual ornaments compared to their ecologically similar, iteroparous relatives (see in Williams 1966). Elsewhere, Kemp (2002) found that male butterflies (*Hypolimnas bolina*) participate in riskier competitive behaviors and accept injury risks as the opportunity for future reproduction declines. In killifishes, a complex interaction between several factors could result in a relatively weak correlation between the pace of life-history and the evolution of sexual ornaments, or potentially the evolution of sexual ornaments has no relationship with the pace of life-history. Alternatively, fin size could instead be developmentally linked to overall body shape, for example, if body depth is under selection to facilitate increased fecundity in fast-living, ephemeral species. However, we found that males have deeper bodies than females, which is indicative of sexual dimorphism resulting from selection acting on males, through mate choice or intrasexual competition, rather than on females through section on fecundity. Interestingly, we did find that fast-living species have overall lowered swimming performances independent of fin size, compared to slow-living species. This effect could be due to trade-offs between swimming performance and life-history traits, such as the high growth and reproductive rates observed in fast-living species (sensu Royle et al. 2006; Lee et al. 2013; Sowersby et al. 2019).

Potential caveats of our study include using habitat type as a proxy for predation risk. We used a proxy because accurately assessing predation levels for the large number of species used in our study ($n = 86$ total) would have been inherently difficult. Our approach is however, comparable to other comparative studies that have also focused on the effects of predation risk by relying on relevant habitat information as proxies (e.g., Stuart-Fox and Ord 2004). We are confident in our use of habitat as a proxy for predation risk, because several species have independently evolved desiccant resistant eggs capable of entering relatively long periods of diapause, which have no other discernible function other than as an adaptation to living in ephemeral habitats. Without such specialized adaptations, other fish species including nonannual killifishes and potential predators are unlikely to successfully occupy habitats that regularly dry out. Therefore, it is an intuitive assumption that killifish capable of embryonic arrest with desiccant resistant eggs (i.e., annual species) that only coexist with other killifish species that have desiccant resistant eggs (i.e., in ephemeral habitats) are less likely to occupy habitats that contain many aquatic predators. Nevertheless, we acknowledge that the use of a proxy will not be as accurate as individual species assessments of predation risk. Abiotic factors, such as water flow regimes and water temperature, may vary across ephemeral and more permanent habitats and could also have an influence on the evolution of ornamental fins.

In killifishes, there is an association between the pace of life-history and habitat type, with faster life-histories typically inhabiting ephemeral environments (Sowersby et al. 2019). However, given the large amount of variation (45%) in killifish life-history rates not explained by adaptations to seasonal environments (Sowersby et al. 2019; Eckerström-Liedholm et al. 2017) we could confidently treat predation risk and the pace of life-history variables as relatively independent, without the risk of collinearity distorting multiple regression models (sensu Dormann et al. 2013; Morrissey and Ruxton 2018). We readily acknowledge that the number of species we included in our analyses of fin size in live fish is relatively small for a comparative study and could therefore have resulted in low statistical power. Yet, our analyses of fin size across a substantially larger male-only dataset of zootaxa illustrations did yield similar results. In particular, the size of the residual dorsal fin area was larger in species from ephemeral habitats compared to those from permanent habitats. Although we did not find a significant link between anal fin size and ephemeral habitats in this larger zootaxa dataset, this is likely due to a large group of non-annual species (family Rivulidae) that appear to have relatively small fins, being absent from the zootaxa dataset.

Conclusion

We demonstrate that exaggerated sexually dimorphic fins that impair locomotive performance are more likely to evolve in ephemeral habitats. This relationship is presumably a consequence of lower predation risk by aquatic predators in these habitats, compared to more permanent habitats. In turn, we found no clear evidence that male ornaments coevolve with the remarkable differences in the pace of life-history that occur across killifishes. Our results highlight the importance of natural selection in shaping the evolution of sexual dimorphism in ornamental traits. Furthermore, we found that the impact different fins have on swimming performance likely depends on their placement on the body, with the size of the posteriorly located caudal fin having no detectable influence on swimming performance. We suggest that the importance of the position of sexual ornaments on the body may have been overlooked and can offer a mechanistic explanation for why previous studies on other taxa have found mixed or contradictory results when investigating the costs of secondary sexual traits.

AUTHOR CONTRIBUTIONS

WS, AGV, and BR conceived the study. All authors contributed to the planning and aims of the study. Data collection was performed by WS, SE-L, JB, SE, and JU. Data analysis was conducted by WS, SE-L, and BR. The first draft of the manuscript was written by WS. All authors contributed to the final version.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

All data has been uploaded to the Dryad Digital Repository (https://doi.org/10.5061/dryad.3j9kd51hf).

LITERATURE CITED

Andersson, M. 1982. Sexual selection, natural selection and quality advertisement. Biol. J. Linn. Soc. 17:375–393.

Andersson, M. B. 1994. Sexual selection. Princeton Univ. Press, Princeton, NJ.

Askew, G. N. 2014. The elaborate plumage in peacocks is not such a drag. J. Exp. Biol. 217:3237–3241.

Auer, S. K., C. A. Dick, N. B. Metcalfe, and D. N. Reznick. 2018. Metabolic rate evolves rapidly and in parallel with the pace of life history. Nat. Commun. 9:14.

Basolo, A. L. 1998. Evolutionary change in a receiver bias: a comparison of female preference functions. Proc. R. Soc. Lond. B Biol. Sci. 265:2223–2228.

Basolo, A. L., and W. E. Wagner. 2004. Covariation between predation risk, body size and fin elaboration in the green swordtail. Biol. J. Linn. Soc. 83:87–100.

Baumgartner, A., S. Coleman, and B. Swanson. 2011. The cost of the sword: escape performance in male swordtails. PLoS ONE 6:e15837.

Beamish, F. 1978. Swimming capacity. Pp. 101–187 in W. S. Hoar and D. J. Randall, eds. Locomotion. Academic Press, Cambridge, MA.

Berois, N., G. García, and R. O. de Sá. 2015. Annual fishes: life history strategy, diversity, and evolution. CRC Press, Boca Raton, FL.

Blažek, R., M. Polačik, and M. Reichard. 2013. Rapid growth, early maturation and short generation time in African annual fishes. EvoDevo 4:24.

Boisclair, D., and M. Tang. 1993. Empirical analysis of the influence of swimming pattern on the net energetic cost of swimming in fishes. J. Fish Biol. 42:169–183. https://doi.org/10.1111/j.1095-8649.1993.tb00319.x.

Buzatto, B. A., and R. C. Firman. 2016. Precopulatory intrasexual competition. (Editors: T. K., Shackelford, V. A. Weekes-Shackelford) Encyclopedia of evolutionary psychological science, Springer International Publishing, Berlin, pp. 6091-6097. https://doi.org/10.1007/978-3-319-16999-6_64-1.

Cellerino, A., D. R. Valenzano, and M. Reichard. 2016. From the bush to the bench: the annual *Nothobranchius* fishes as a new model system in biology. Biol. Rev. 91:511–533.

Clark, C. J., and R. Dudley. 2009. Flight costs of long, sexually selected tails in hummingbirds. Proceedings of the Royal Society of London B: Biological Sciences 276:2109–2115.

Costa, W. J. E. M. 2006. Descriptive morphology and phylogenetic relationships among species of the Neotropical annual killifish genera *Nematolebias* and *Simpsonichthys* (Cyprinodontiformes: Aplocheiloidei: Rivulidae). Neotropical Ichthyology 4:1–26.

———. 2007a. Taxonomic revision of the seasonal South American killifish genus *Simpsonichthys* (Teleostei: Cyprinodontiformes: Aplocheiloidei: Rivulidae). Zootaxa 1669:1–134. https://doi.org/10.11646/zootaxa.1669.1.1.

———. 2007b. Taxonomy of the plesiolebiasine killifish genera *Pituna*, *Plesiolebias* and *Maratecoara* (Teleostei: Cyprinodontifomes: Rivulidae), with descriptions of nine new species. Zootaxa 1410:1–41. https://doi.org/10.5281/zenodo.175565.

———. 2011. Comparative morphology, phylogenetic relationships, and historical biogeography of plesiolebiasine seasonal killifishes (Teleostei: Cyprinodontiformes: Rivulidae). Zoological Journal of the Linnean Society 162:131–148.

Costa, W. J. E. M., P. F. Amorim, and J. L. O. Mattos. 2012. Species delimitation in annual killifishes from the Brazilian Caatinga, the *Hypsolebias flavicaudatus* complex (Cyprinodontiformes: Rivulidae): implications for taxonomy and conservation. Systematics and Biodiversity 10:71-91. https://doi.org/10.1080/14772000.2012.664177.

Cox, R. M., and R. Calsbeek. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution of intralocus sexual conflict. The American Naturalist 173:176–187.

Curry-Lindahl, K. 1956. On the ecology, feeding behaviour and territoriality of the African lungfish, *Protopterus aethiopicus* Heckel. Ark. Zool 9:479-497.

Domenici, P., and R. Blake. 1997. The kinematics and performance of fish fast-start swimming. Journal of Experimental Biology 200:1165–1178.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Dorn, A., Z. Musilová, M. Platzer, K. Reichwald, and A. Cellerino. 2014. The strange case of East African annual fishes: aridification correlates with diversification for a savannah aquatic group? BMC Evolutionary Biology 14:210.

Eckerström-Liedholm, S., W. Sowersby, A. Gonzalez-Voyer, and B. Rogell. 2017. Time-limited environments affect the evolution of egg–body size allometry. Evolution 71:1900–1910.

Eckerström-Liedholm, S., W. Sowersby, S. Morozov, W. van der Bijl, P. K. Rowiński, A. Gonzalez-Voyer, and B. Rogell. 2019. Macroevolutionary evidence suggests trait-dependent coevolution between behavior and life-history. Evolution 73:2312–2323.

Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. Evolution 34:76–91.

Felsenstein, J. 1985. Phylogenies and the comparative method. The American Naturalist 125:1–15.

Fowler-Finn, K., and E. Hebets. 2011. More ornamented males exhibit increased predation risk and antipredatory escapes, but not greater mortality. Eileen Hebets Publications, Lincoln, NE.

Fraser, D. F. 1995. Predation as an agent of population fragmentation in a tropical watershed. Ecology 76:1461–1472.

Furness, A. I. 2016. The evolution of an annual life cycle in killifish: adaptation to ephemeral aquatic environments through embryonic diapause. Biological Reviews of the Cambridge Philosophical Society 91:796–812.

Furness, A. I., D. N. Reznick, M. S. Springer, and R. W. Meredith. 2015. Convergent evolution of alternative developmental trajectories associated with diapause in African and South American killifish. Proceedings of the Royal Society of London B: Biological Sciences 282:20142189.

Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection. The American Naturalist 104:1–24.

Genade, T., M. Benedetti, E. Terzibasi, P. Roncaglia, D. R. Valenzano, A. Cattaneo, and A. Cellerino. 2005. Annual fishes of the genus *Nothobranchius* as a model system for aging research. Aging Cell 4:223–233.

Goldberg, D. L., J. A. Landy, J. Travis, M. S. Springer, and D. N. Reznick. 2019. In love and war: the morphometric and phylogenetic basis of ornamentation, and the evolution of male display behavior, in the livebearer genus *Poecilia*. Evolution 73:360–377.

Haas, R. 1976a. Behavioral biology of the annual killifish, *Nothobranchius guentheri*. Copeia 1976:80–91. https://doi.org/10.2307/144377.

———. 1976b. Sexual selection in *Nothobranchius guentheri* (Pisces: Cyprinodontidae). Evolution 30:614–622. https://doi.org/10.1111/j.1558-5646.1976.tb00938.x.

Hadfield, J. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

Heinen-Kay, J. L., K. E. Morris, N. A. Ryan, S. L. Byerley, R. E. Venezia, M. N. Peterson, and R. B. Langerhans. 2015. A trade-off between natural and sexual selection underlies diversification of a sexual signal. Behavioral Ecology 26:533–542.

Howland, H. C. 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. Journal of Theoretical Biology 47:333–350.

Hrbek, T., and A. Larson. 1999. The evolution of diapause in the killifish family Rivulidae (Atherinomorpha, Cyprinodontiformes): a molecular phylogenetic and biogeographic perspective. Evolution 53:1200–1216.

Jennions, M. D., A. P. Møller, and M. Petrie. 2001. Sexually selected traits and adult survival: a meta-analysis. The Quarterly Review of Biology 76:3–36.

Johansson, F., B. Lederer, and M. I. Lind. 2010. Trait performance correlations across life stages under environmental stress conditions in the common frog, *Rana temporaria*. PLOS ONE 5:e11680.

Johnson, J. B., D. C. Macedo, C. N. Passow, and G. G. Rosenthal. 2014. Sexual ornaments, body morphology, and swimming performance in naturally hybridizing swordtails (Teleostei: Xiphophorus). PLoS ONE 9:e109025.

Johnstone, R. A. 1995. Honest advertisement of multiple qualities using multiple signals. Journal of Theoretical Biology 177:87–94.

Kemp, D. J. 2002. Sexual selection constrained by life history in a butterfly. Proceedings of the Royal Society of London B: Biological Sciences 269:1341–1345.

Kemp, D. J., D. N. Reznick, G. F. Grether, and J. A. Endler. 2009. Predicting the direction of ornament evolution in Trinidadian guppies (*Poecilia reticulata*). Proceedings of the Royal Society B: Biological Sciences 276:4335–4343.

Kokko, H., M. D. Jennions, and R. Brooks. 2006. Unifying and testing models of sexual selection. Annual Review of Ecology, Evolution, and Systematics 37:43–66.

Kotiaho, J. S. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. Biological Reviews 76:365–376.

Langerhans, R. B., C. A. Layman, and T. J. DeWitt. 2005. Male genital size reflects a tradeoff between attracting mates and avoiding predators in two live-bearing fish species. Proceedings of the National Academy of Sciences 102:7618–7623.

Langerhans, R. B., and D. N. Reznick. 2010. Ecology and evolution of swimming performance in fishes: predicting evolution with biomechanics. Pp. 200–248 *in* P. Domenici and B. G. Kapoor, eds. Fish locomotion: an eco-ethological perspective. Taylor & Francis Group, Abingdon, U.K.

Lee, W. S., P. Monaghan, and N. B. Metcalfe. 2013. Experimental demonstration of the growth rate-lifespan trade-off. Proceedings of the Royal Society B: Biological Sciences 280:20122370.

Mamboleo, A. A., H. H. Kilungu, S. R. Moe, G. Soka, and P. K. T. Munishi. 2012. Influence of hydrological fluctuations on vegetation and Avifauna species composition, abundance and diversity in the Bahi Swamp wetlands Central Tanzania. Tanzania J. For. Nat. Conserv. 81:64–86.

Morrissey, M. B., and G. D. Ruxton. 2018. Multiple regression is not multiple regressions: the meaning of multiple regression and the non-problem of collinearity. Philosophy, Theory, and Practice in Biology 10:3. https://doi.org/10.3998/ptpbio.16039257.0010.003.

Murphy, W. J., and G. E. Collier. 1997. A molecular phylogeny for aplocheiloid fishes (Atherinomorpha, Cyprinodontiformes): the role of vicariance and the origins of annualism. Molecular Biology and Evolution 14:790–799.

Nesteruk, I., G. Passoni, and A. Redaelli. 2014. Shape of aquatic animals and their swimming efficiency. Journal of Marine Biology 2014:470715.

Odell, J. P., M. A. Chappell, and K. A. Dickson. 2003. Morphological and enzymatic correlates of aerobic and burst performance in different populations of Trinidadian guppies *Poecilia reticulata*. Journal of Experimental Biology 206:3707–3718.

Oufiero, C. E., and T. Garland. 2007. Evaluating performance costs of sexually selected traits. Functional Ecology 21:676–689. https://doi.org/10.1111/j.1365-2435.2007.01259.x.

Oufiero, C. E., K. Jugo, and T. Garland. 2014. Swimming with a sword: Tail beat kinematics in relation to sword length in *Xiphophorus*. Functional Ecology 28:924–932. https://doi.org/10.1111/1365-2435.12222.

Oufiero, C. E., K. Jugo, P. Tran, and T. Garland. 2012. As the sword grows: individual variation and ontogenetic effects of a sexually selected trait on locomotor performance in *Xiphophorus hellerii*. Physiological and biochemical zoology: PBZ 85:684–693.

Partridge, L., and J. A. Endler. 1987. Life history constraints on sexual selection. Pages 247–264 *in* J. W. Bradbury and M. Andersson, eds. Sexual selection: testing the alternatives. John Wiley & Sons, Ltd, New York.

Pascoal, S., T. Cezard, A. Eik-Nes, K. Gharbi, J. Majewska, E. Payne, M. Ritchie, M. Zuk, and N. W. Bailey. 2014. Rapid convergent evolution in wild crickets. Current Biology 24:1369–1374.

Passos, C., B. Tassino, M. Loureiro, and G. G. Rosenthal. 2013. Intra- and intersexual selection on male body size in the annual killifish *Austrolebias charrua*. Behavioural Processes 96:20–26.

Passos, C., B. Tassino, F. Reyes, and G. G. Rosenthal. 2014. Seasonal variation in female mate choice and operational sex ratio in wild populations of an annual fish, *Austrolebias reicherti*. PLoS ONE 9:e101649.

Peters, R. H. 1986. The ecological implications of body size. Cambridge Univ. Press, Cambridge, U.K.

Pohl, M., F. Milvertz, A. Meyer, and M. Vences. 2015. Multigene phylogeny of cyprinodontiform fishes suggests continental radiations and a rogue taxon position of Pantanodon. Vertebrate Zoology 65:37–44. https://www.semanticscholar.org/paper/Multigene-phylogeny-of-cyprinodontiform-fishes-and-Pohl-Milvertz/6fb0b9a443005fd723d250d5a8f6a4558b87253b.

Poissant, J., A. J. Wilson, and D. W. Coltman. 2010. Sex-specific genetic variance and the evolution of sexual dimorphism: a systematic review of cross-sex genetic correlations. Evolution 64:97–107.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Recher, H. F., and J. A. Recher. 1968. Comments on the escape of prey from avian predators. Ecology 49:560–562. https://doi.org/10.2307/1934125.

Reichard, M., M. Polačik, R. Blažek, and M. Vrtílek. 2014. Female bias in the adult sex ratio of African annual fishes: interspecific differences, seasonal trends and environmental predictors. Evolutionary Ecology 28:1105–1120.

Revell, L. J., D. L. Mahler, P. R. Peres-Neto, and B. D. Redelings. 2012. A new phylogenetic method for identifying exceptional phenotypic diversification. Evolution 66:135–146.

Reznick, D. A., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. Nature 346:357–359.

Reznick, D., and M. Bryant. 2007. Comparative long-term mark-recapture studies of guppies (*Poecilia reticulata*): differences among high and low predation localities in growth and survival. Annales Zoologici Fennici 44:152–160.

Robinson, M. R., J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, L. E. B. Kruuk, and R. Snook. 2006. Live fast, die young: trade-offs between fitness components and sexually antagonistic selection on weaponry in Soay sheep. Evolution 60:2168–2181.

Rogell, B., D. K. Dowling, and A. Husby. 2020. Controlling for body size leads to inferential biases in the biological sciences. Evolution Letters 4:73–82.

Rosenthal, G. G., and C. S. Evans. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. Proceedings of the National Academy of Sciences 95:4431–4436.

Royle, N. J., J. Lindström, and N. B. Metcalfe. 2006. Effect of growth compensation on subsequent physical fitness in green swordtails *Xiphophorus helleri*. Biology Letters 2:39–42.

Ryan, M. J., and A. Keddy-Hector. 1992. Directional patterns of female mate choice and the role of sensory biases. The American Naturalist 139:S4–S35.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods. Comments and Opinion.

Seghers, B. H. 1978. Feeding behavior and terrestrial locomotion in the Cyprinodontid fish, *Rivulus hartii* (Boulenger). Verhandlungen des Internationalen Verein Limnologie 20:2055–2059.

Simpson, B. R. C. 1979. The phenology of annual killifishes. Symposia of the Zoological Society of London 44:243–261.

Sowersby, W., S. Morozov, S. Eckerström-Liedholm, P. Lehmann, P. K. Rowiński, J. Näslund, A. Gonzalez-Voyer, and B. Rogell. 2019. Coevolution between life-history and metabolic rate depends on ontogenetic stage. bioRxiv. https://doi.org/10.1101/705707.

Sowersby, W., A. Gonzalez-Voyer, and B. Rogell. 2020. Sex ratios deviate across killifish species without clear links to life history. Evolutionary Ecology 34:411–426.

Sowersby, W., S. Eckerström-Liedholm, A. Kotrschal, J. Näslund, P. Rowiński, A. Gonzalez-Voyer, and B. Rogell. 2021. Fast life-histories are associated with larger brain size in killifishes. Evolution 75:2286–2298.

Stuart–Fox, D. M., and T. J. Ord. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. Proceedings of the Royal Society of London B: Biological Sciences 271:2249–2255.

Suk, H. Y., and J. C. Choe. 2002. Females prefer males with larger first dorsal fins in the common freshwater goby. Journal of Fish Biology 61:899–914.

Thavarajah, N. K., P. G. Tickle, R. L. Nudds, and J. R. Codd. 2016. The peacock train does not handicap cursorial locomotor performance. Scientific Reports 6:36512.

Thomerson, J. E. 1974. *Pterolebias hoignei*, a new annual Cyprinodontid fish from Venezuela, with a redescription of *Pterolebias zonatus*. Copeia 1974:30–38. https://doi.org/10.2307/144300.

Vrtílek, M., J. Žák, M. Polačik, R. Blažek, and M. Reichard. 2018. Longitudinal demographic study of wild populations of African annual killifish. Scientific Reports 8:4774.

Walker, J. A., C. K. Ghalambor, O. L. Griset, D. McKenny, and D. N. Reznick. 2005. Do faster starts increase the probability of evading predators? Functional Ecology 19:808–815. https://doi.org/10.1111/j.1365-2435.2005.01033.x.

Webb, P. W. 1975. Hydrodynamics and energetics of fish propulsion. Bull. Fish. Res. Board Can. 190:1–156.

Weese, D. J., S. P. Gordon, A. P. Hendry, and M. T. Kinnison. 2010. Spatiotemporal variation in linear natural selection on body color in wild guppies (*Poecilia reticulata*). Evolution 64:1802–1815.

Weihs, D., and P. W. Webb. 1983. Optimization of locomotion. Pages 339–371 *in* P. W. Webb and D. Wiehs, eds. Fish biomechanics. Praeger Press, New York.

Weitzman, S. H., and J. P. Wourms. 1967. South American Cyprinodont fishes allied to *Cynolebias* with the description of a new species of *Austrofundulus* from Venezuela. Copeia 1967:89–100. https://doi.org/10.2307/1442180.

Werner, E. E., and M. A. McPeek. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75:1368–1382.

Wilbur, H. M. 1997. Experimental ecology of food webs: complex systems in temporary ponds. Ecology 78:2279–2302.

Wildekamp, R. H. 1993. A world of killies: atlas of the oviparous cyprinodontiform fishes of the world. Vol. 1. American Killifish Association, Mishawaka, IN.

———. 2004. A world of killies: atlas of the oviparous cyprinodontiform fishes of the world. Vol. 4. American Killifish Association, Mishawaka, IN.

Wildekamp, R. H., and B. R. Watters. 1995. A world of killies: atlas of the oviparous cyprinodontiform fishes of the world. Vol. 2. American Killifish Association, Mishawaka, IN.

———. 1996. A world of killies: atlas of the oviparous cyprinodontiform fishes of the world. Vol. 3. American Killifish Association, Mishawaka, IN.

Williams, G. C. 1966. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton Univ. Press, Princeton, NJ.

Wourms, J. P. 1972. Developmental biology of annual fishes. I. Stages in the normal development of *Austrofundulus myersi* Dahl. The Journal of Experimental Zoology 182:143–167.

Zahavi, A. 1975. Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205–214.

Zuk, M., and G. R. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. The Quarterly Review of Biology 73:415–438.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary Table 1. List of all species and sample sizes used in swimming performance study. Life-history strategy was assessed as per (Furness et al. 2015).

Supplementary Table 2. List of all species and male and female sample sizes used in geometric morphometric analysis conducted on live fish.

SF1. Two examples of the 19 landmark positions (red dots) used to characterize body and fin shape, placed using the software tpsDig (version 2.12, Rohlf 2012).

SF2. The consensus killifish body shape, generated using the software tpsRelw (version 1.46; Rohlf 2010), from 28 species ($N = 229$ images; 118 females and 111 males; 13 annual and 15 nonannual species).

Supplementary Table 3. List of all species used in the study (i.e., from laboratory population and zootaxa illustrations).

SF3. The consensus male killifish body shape, generated using the software tpsRelw (version 1.46; Rohlf 2010), from 74 species ($N = 74$ images; 41 annual and 33 nonannual species).

SF4. Scaled phylogenetic tree used in zootaxa illustration analyses (pruned and updated from Furness et al. 2015).

Supplementary Table 4: Analysis of the effect of total fin size on turning performance.

Supplementary Table 5: Analysis of the effect of anal fin size on turning performance.
Supplementary Table 6: Analysis of the effect of dorsal fin size on turning performance.
Supplementary Table 7: Analysis of the effect of caudal fin size on turning performance.
Supplementary Table 8: Analysis of the effect of the total fin size on escape speed.
Supplementary Table 9: Analysis of the effect of anal fin size on escape speed.
Supplementary Table 10: Analysis of the effect of dorsal fin size on escape speed.
Supplementary Table 11: Analysis of the effect of caudal fin size on escape speed.
Supplementary Table 12: Analysis of turning performance in lab reared fish.
Supplementary Table 13: Analysis of escape speed in lab reared fish.
Supplementary Table 14: Analysis of anal fin area in lab reared fish.
Supplementary Table 15: Analysis of dorsal fin area in lab reared fish.
Supplementary Table 16: Analysis of caudal fin area in lab reared fish.
Supplementary Table 17: Analysis of body area in lab reared fish.
Supplementary Table 18: Analysis of total fin area (size) in zootaxa drawings.
Supplementary Table 19: Analysis of dorsal fin area in zootaxa drawings.
Supplementary Table 20: Analysis of caudal fin area in zootaxa drawings.
Supplementary Table 21: Analysis of anal fin area in zootaxa drawings
Supplementary Table 22. Swimming performance summary statistics.