

Rapid growth and large body size in annual fish populations are compromised by density-dependent regulation

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Abstract

We tested the effect of population density on maximum body size in three sympatric species of annual killifishes *Nothobranchius* spp. from African ephemeral pools. We found a clear negative effect of population density on body size, limiting their capacity for extremely fast development and rapid growth. This suggests that density-dependent population regulation and the ephemeral character of their habitat impose contrasting selective pressures on the life history of annual killifishes.

KEYWORDS

Nothobranchius, plasticity, population regulation, somatic growth, sympatry, temporary habitat

Body size is a crucial phenotypic trait for individual survival and reproductive success (Blanckenhorn, 2000). In males, large body size indicates better condition, enables possession of superior territories and ultimately leads to larger male mating preference by females (Jennions *et al.*, 2001). In females, body size is positively associated with fecundity (Fleming, 1996; Monroe *et al.*, 2015) and in animals with asymptotic growth (such as fishes), fecundity increases disproportionately with body length (Barneche *et al.*, 2018). While larger body size and the ability to reach it quickly, is advantageous in many contexts, rapid growth is costly (Dmitriew, 2011). High investment into rapid growth is associated with late-life decreases in fecundity and survival (Hector & Nakagawa, 2012; Lee *et al.*, 2013).

Temporary habitats select for rapid growth (Daňko *et al.*, 2017). Temporary environments favour individuals that develop rapidly and reproduce before the conditions deteriorate. In addition, the long-term costs of rapid growth and development are not necessarily experienced in a temporary habitat, as environmental conditions often deteriorate before these costs are expressed.

Selection for large body size and rapid development interferes with the force of density-dependent regulation at the population level (Lorenzen & Enberg, 2002). A low population density with high availability of resources selects for individuals that rapidly exploit resources and consequently grow fast and have high reproductive success (fast life history). In contrast, high population density with

intensive competition for resources favours individuals that utilise resources effectively despite growing more slowly and producing offspring at a lower rate (slow life history) (Reznick *et al.*, 2002). Thus, while at low population density selection for fast life history is intensified, high population density may impose constraints on rapid growth.

Killifishes (Cyprinodontiformes) from Africa and the neotropics have repeatedly evolved the ability to exploit ephemeral freshwater pools that develop during the rainy season (Furness *et al.*, 2015). Their life cycle is adapted to the transient nature of their habitat, with a rapid adult phase and long-term survival of desiccation-resistant eggs stored in the dry substratum. The length of the active life phase varies among species and regions, but is always constrained by annual desiccation and typically lasts <6 months (Reichard, 2015), with a high variability in the duration of the season (García *et al.*, 2018). Population densities vary greatly even among adjacent populations (Lané *et al.*, 2016; Volcan *et al.*, 2019; Vrtílek *et al.*, 2018a) with embryonic survival success during the dry phase, or conditions in the previous wet phase as the potential drivers. Despite the causes of inter-population variation in density are largely unknown, density-dependent population effects strongly interact with selection for fast life history.

Here, we tested whether population density constrains rapid growth in annual killifishes. Using longitudinal data from six natural sites with African annual killifishes, we compared peak population density with maximum body size. We used the turquoise killifish, *Nothobranchius furzeri* Jubb 1971, a well-studied species in life-history

evolution research (Cellerino *et al.*, 2016) and its coexisting sympatric species, *Nothobranchius orthonotus* (Peters, 1844) and *Nothobranchius pienaari* Shidlovskiy, Watters & Wildekamp, 2010 (Dorn *et al.*, 2014; Reichard *et al.*, 2009, 2017a). *Nothobranchius furzeri* exhibits particularly rapid life history. Fish hatch after the pools fill with rainwater (Polačik *et al.*, 2011) and grow rapidly to reach sexual maturity in as few as 2 weeks (Vrtílek *et al.*, 2018b), following a daily production of 20–120 eggs. The life history of the other two species is very similar (Blažek *et al.*, 2017; Vrtílek *et al.*, 2018a).

Nothobranchius spp. are income breeders with an immediate conversion of resources into current reproductive effort (Vrtílek & Reichard, 2015). They feed on a wide range of planktonic and benthic invertebrates whose availability severely decreases at high killifish density (Polačik *et al.*, 2014; Polačik & Reichard, 2010). Sexual dimorphism in colouration, morphology and body size is pronounced, with males being the larger sex. The growth of annual killifishes is particularly plastic and continues after sexual maturity when resources are available (Vrtílek & Reichard, 2015). Cross-sectional sampling of natural populations usually shows large body size differences

among populations and relatively low intra-population variation (Vrtílek & Reichard, 2016), indirectly suggesting the effect of local conditions.

We measured total length (L_T ; from tip of the mouth to the distal point of caudal fin) of *Nothobranchius* fish from six sites in southern Mozambique. The pools represented typical *Nothobranchius* habitats in the region and were visited over their entire adult-phase lifetime. Full details on the sampled sites are provided in Vrtílek *et al.* (2018a). The sites contained either only *N. furzeri* population (2 sites, Ch1 (22° 16' 33" S, 32° 53' 54" E) and LS5 (24° 24' 59" S, 32° 46' 30" E)), *N. furzeri* together with *N. orthonotus* (2 sites, Ch2 (22° 30' 28" S, 32° 34' 54" E) and LS2 (24° 18' 15" S, 32° 36' 55" E)) or *N. furzeri* with *N. orthonotus* and *N. pienaari* (2 sites, Ch3 (22° 33' 17" S, 32° 43' 38" E) and LS1 (24° 11' 40" S, 32° 22' 45" E)). Community complexity and species combinations were limited due to nested pattern of community assembly (Reichard *et al.*, 2017a). Fish were sampled during each visit of the site (3–6 visits per site, median interval 11 days; Figure 1) using a seine net (2.7 m long, 0.7 m deep, 4 mm mesh size). Standardised catch per unit effort (CPUE) consisted of five seine-net

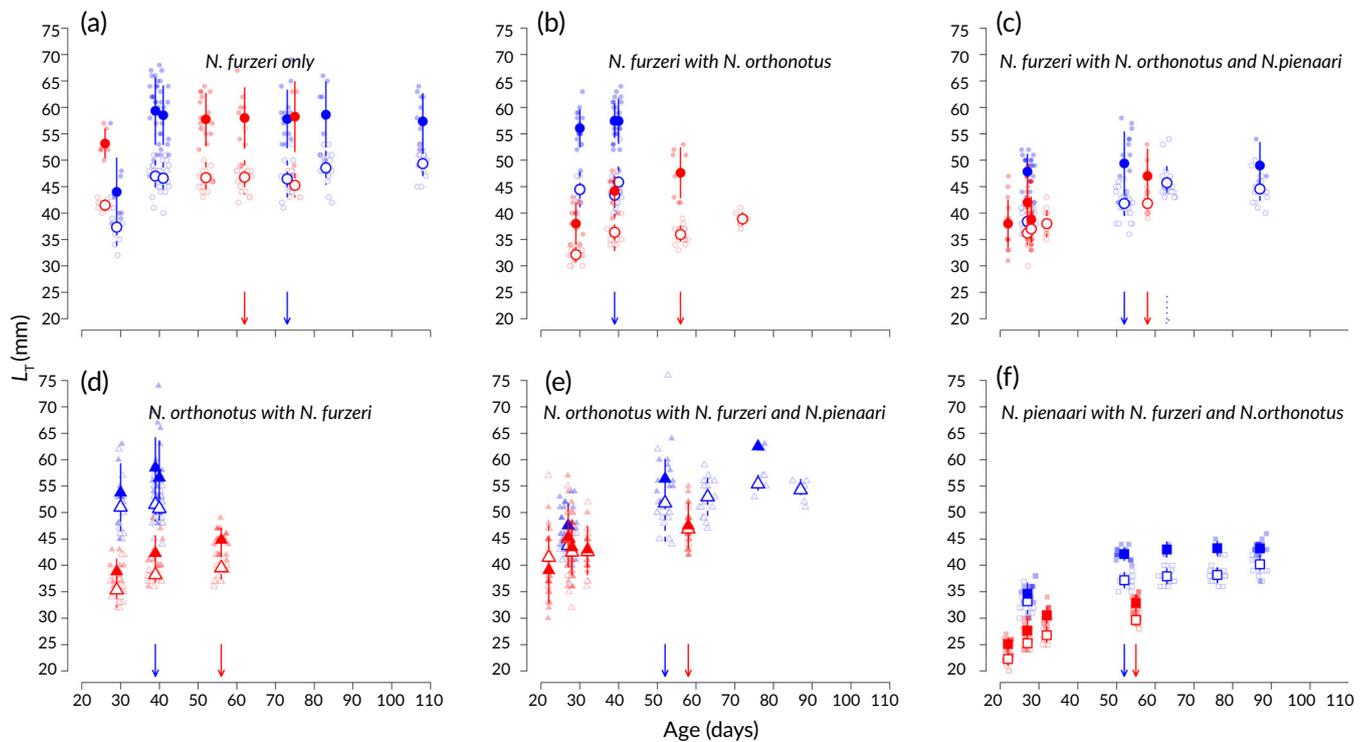


FIGURE 1 Seasonal dynamics in total length (L_T) structure in populations of three sympatric *Nothobranchius* species: (a)–(c) *N. furzeri* (—●—) Ch1 males, (—○—) Ch1 females, (—●—) LS5 males, and (—○—) LS5 females; (—●—) Ch3 males, (—○—) Ch3 females, (—●—) Ch2 males, and (—○—) Ch2 females; (—●—) LS2 males, (—○—) LS2 females, (—●—) LS1 males, and (—○—) LS1 females; (d), (e) *N. orthonotus* and (f) *N. pienaari*. Each panel shows a pair of populations with the same species community (*N. furzeri* only, *N. furzeri* with *N. orthonotus* or all three species) (—▲—) Ch3 males, (—△—) Ch3 females, (—▲—) Ch2 males, and (—△—) Ch2 females; (—▲—) LS2 males, (—△—) LS2 females, (—▲—) LS1 males, and (—△—) LS1 females; (—■—) LS2 males, (—□—) LS2 females, (—■—) LS1 males, and (—□—) LS1 females. Colour differentiates populations according to their maximum density: ■, the higher density population of the pair; □, the lower density population of the pair. Small symbols represent measured values, large symbols indicate sample means (\pm SD), closed symbols and solid lines represent male values, open symbols with dashed lines are for females. ↓, The age when data for the analysis of the effect of population density on maximum body size were collected (Table 1, Figure 2). Location of populations: CH1, 22° 16' 33" S, 32° 53' 54" E; CH2, 22° 30' 28" S, 32° 34' 54" E; CH3, 22° 33' 17" S, 32° 43' 38" E; LS1, 24° 11' 40" S, 32° 22' 45" E; LS2, 24° 18' 15" S, 32° 36' 55" E; LS5, 24° 24' 59" S, 32° 46' 30" E

hauls (5 m long) that covered all habitats in the pool. Fewer hauls were completed when the pool was too small to avoid repeated sampling of the same area. CPUE reflects population density because it directly assesses the number of individuals per unit area. A random sample of 15 individuals of each sex from each species was measured on-site on each occasion using a plastic sheet with a ruler. After measurements were taken, fish were released back into the pool.

Fish age was estimated from otoliths. *Nothobranchius* spp. hatch synchronously and the population is typically represented by a single age cohort (Polačik *et al.*, 2011; Reichard *et al.*, 2017b). During the first sampling at each site, we took a subsample of three individuals (mixed sex) per species per site, euthanized them in clove oil and stored them in 96% ethanol. Otoliths were dissected, polished and the number of daily increments was read by a commercial facility (Barcelona Otolith Reading Services, Spain; borsbarcelona@gmail.com). We estimated hatching date as the number of daily increments subtracted from the date of fish collection. To provide a population-level estimate of age, where different ages were recorded (maximum of 3 days difference), we used the earliest estimated hatching date (Vrtílek *et al.*, 2018a). Otolith samples were not available for site Ch3 so the hatching date was estimated by reading otoliths from the adjacent sites (Ch1 and Ch2). Hatching in *Nothobranchius* is triggered by pool inundation and we directly observed that these three pools were filled at the same time.

To test the effect of population density on maximum body length L_{Tmax} , we used values from the sampling dates when population-level L_T approached its maximum, corresponding to an age of 52–73 days in all pools except Ch3 (Figure 1). In Ch3 (with *N. furzeri* and *N. orthonotus*), the last sample was collected at the age of 39 days, just before the pool desiccated (Vrtílek *et al.*, 2018a). Given that Ch3 was a low-density site where we predicted larger L_T , any failure of fish to reach maximum L_T before habitat desiccation would have resulted in more conservative estimates in our analysis. Estimates of population density were based on maximum relative fish density (CPUE). Maximum CPUE was typically recorded during the first visit to the site (five of the six sites) and density steadily declined throughout the season (Vrtílek *et al.*, 2018a). The only exception was Ch3 where the pool desiccated earlier and relative population density increased (Vrtílek *et al.*, 2018a). Our use of maximum CPUE for population density estimates therefore corresponds to the period where it has the strongest effect on L_T as fish growth is most intense early in life (Quince *et al.*, 2008). Thus, CPUE represents a biologically relevant estimate, because lower growth early in life was not compensated by a longer growth period (Figure 1).

We fitted species-specific generalised least-squares models (GLS) with L_{Tmax} as the dependent variable and population density as a continuous explanatory variable in interaction with sex to test for different effects of population density on growth in females and males. We corrected for non-independence of the measurements from the same population by defining compound-symmetry correlation structure using population identity (Pekár & Brabec, 2016). We tested whether heteroscedasticity correction was necessary using the Akaike information criterion. To validate our results, we ranked

populations according to their density. Fitting the models with ranked density resulted in a qualitatively equivalent outcome to the original analysis. We present the outcomes of the more biologically meaningful models with numeric density estimates. All analyses were performed using R software 3.5.1 (www.r-project.org) and package nlme 3.1-137 (Pinheiro *et al.*, 2018).

Population density was strongly negatively associated with L_{Tmax} in all species (Table 1 and Figure 2). Males were consistently larger than females (Table 1 and Figure 2), but the stronger effect of population density on male body size was pronounced only in *N. pienaar* (GLS: density \times sex interaction: $F_{1,55} = 6.00$, $P < 0.05$). In *N. furzeri* ($F_{1,157} = 0.04$, $P > 0.05$) and *N. orthonotus* ($F_{1,110} = 0.03$, $P > 0.05$), no interaction between sex and population density was found.

In annual killifishes, selection for rapid growth and large body size is very strong in both sexes. Fish must reproduce before their habitat desiccates, resulting in sexual maturation in as few as 14 days (Vrtílek *et al.*, 2018b). Female fecundity is strongly correlated to body mass (Blažek *et al.*, 2017; Vrtílek & Reichard, 2015) while male hierarchy is contingent upon variation in body size (Polačik & Reichard, 2009). Here, we demonstrate that the selection for rapid growth and large body size imposed by habitat seasonality and reproductive strategy is severely compromised by density-dependent regulation at the population level.

Resource competition often governs density-dependent regulation and life-history evolution in fish (Bassar *et al.*, 2013). For example, high-density populations of Trinidadian guppies *Poecilia reticulata* Peters 1859 have evolved divergent life-history strategies from low-density populations. Stream sections that contain predatory fish sustain low-density *P. reticulata* populations, where survivors benefit from high *per capita* food availability compared with predator-free high-density populations (Bassar *et al.*, 2010). Predators thus indirectly select for a fast-living phenotype, expressed in rapid maturation and growth and high fecundity (Reznick, 1982). Under this scenario, natural selection favours individuals that are able to take advantage of the abundant resources associated with rapid growth (Sæther *et al.*, 2016).

In annual killifishes, population density does not appear to be regulated by predation, or at least, predation is not predictable. Various predators coexist with *Nothobranchius* spp., including piscivorous birds, lungfish and large predatory hemipterans, but with no geographic pattern (Reichard *et al.*, 2014). Instead, annual killifish population density is probably determined by particular local conditions that vary from year to year. Pool volume (a function of the amount of precipitation) and hatching success (based on the egg bank in the dry sediment) vary stochastically among years, limiting any directional density-dependent selection. Our long-term data suggest that population density varies considerably among years, at least in some populations (M.R., unpubl. data), making it implausible to suppose directional and stable selection pressure.

Life-history evolution in annual killifishes is contingent upon a strong aridity gradient, with a contrast in the duration of the aquatic phase between coastal wet and inland dry regions (Terzibaszi Tozzini *et al.*, 2013). A previous experimental study contrasted populations of

	Estimate	SE	t-value ^a	P	ρ
<i>N. furzeri</i> (n = 161)					
Females	47.817	0.922	51.838	<0.001	0.064
Males	57.441	0.939	13.963	<0.001	
Density	-0.257	0.039	-6.557	<0.001	
<i>N. orthonotus</i> (n = 114)					
Females	56.472	0.827	68.317	<0.001	0.013
Males	60.394	0.881	5.734	<0.001	
Density	-0.372	0.028	-13.267	<0.001	
<i>N. pianaari</i> ^b (n = 59)					
Females	41.250	0.557	74.089	<0.001	0
Males	47.138	0.588	7.268	<0.001	
Density in females	-0.415	0.027	-15.206	<0.001	
Density in males	-0.095	0.039	-2.449	0.018 ^c	

ρ , The value for the population intra-class correlation in each species' model (i.e., the variance explained by population density divided by the total variance).

^aNote that the t-values for males represent the contrast between the sexes, while t-values for females represent the statistical significance for their body size to be different from zero.

^bOnly two populations of *N. pianaari* were tested.

^cThe estimate and test statistic for the effect of density on male body size represents the difference from the effect of density in females, not the overall density effect in males.

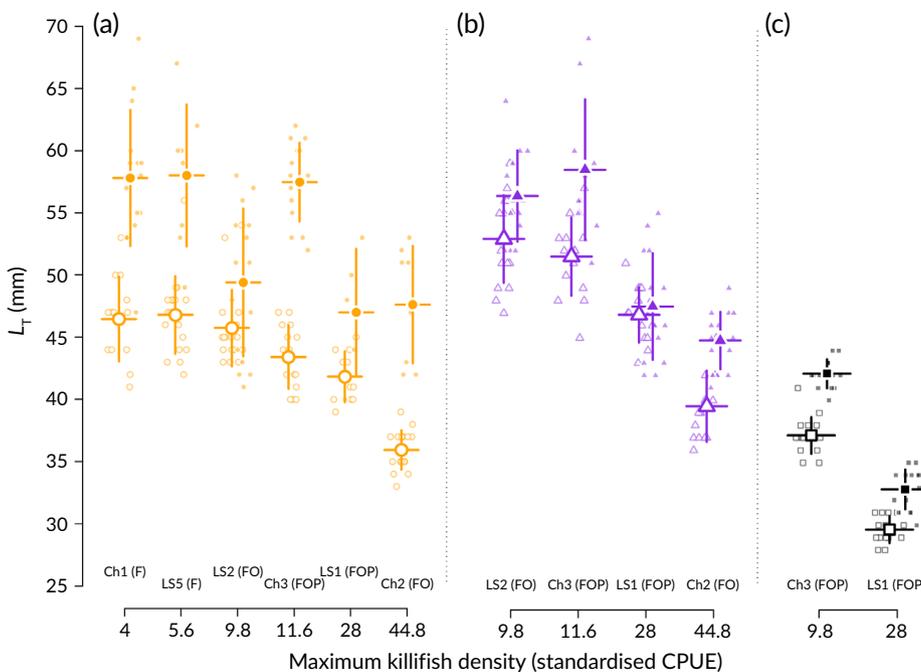


FIGURE 2 The effect of population density on female (open symbols) and male (closed symbols) total length (L_T) in (a) *Nothobranchius furzeri*, (—●—) males, and (—○—) Females (b) *Nothobranchius orthonotus* and (c) *Nothobranchius pianaari*. Large symbols, mean (\pm SD); small symbols, measured values. Species community structure is abbreviated next to the site names: F, *N. furzeri* only; FO, community of coexisting *N. furzeri* and *N. orthonotus*; FOP, community with all three species, *N. furzeri*, *N. orthonotus* and *N. pianaari*. n.b. The maximum recorded population density was analysed on a continuous scale but was ranked for graphical display. Location of populations: CH1, 22° 16' 33" S, 32° 53' 54" E; CH2, 22° 30' 28" S, 32° 34' 54" E; Ch3, 22° 33' 17" S, 32° 43' 38" E; LS1, 24° 11' 40" S, 32° 22' 45" E; LS2, 24° 18' 15" S, 32° 36' 55" E; LS5, 24° 24' 59" S, 32° 46' 30" E

annual fishes from dry and wet regions in a common laboratory environment and predicted more rapid life history in populations from dry region. However, no difference in the rate of juvenile growth, sexual maturation or maximum size was found between dry- and wet region populations, despite corroboration of the predicted difference in lifespan and functional aging rate (Blažek *et al.*, 2017). Here, we show that realised growth rate in natural populations is strongly contingent upon local population density, apparently overriding potential directional selection for rapid development across environmental gradient.

Rapid development and early maturation are predicted to impair further somatic growth (Quince *et al.*, 2008). In the present study, fish exhibited all the external signs of sexual maturity from the first sampling but sustained growth throughout the monitoring period. In the wild, juvenile growth of *Nothobranchius* spp. was much greater (at least 35 mm at the age of 30 days even in high density populations of *N. furzeri*) than in the laboratory (L_S ; standard length of 20 mm at the age of 30 days (Vrtílek & Reichard, 2015) and L_T 30 mm at maturity after 32 days (Blažek *et al.*, 2017)). In the laboratory, the growth

rate of adult fish rapidly adjusted to the amount of food at the age of 2 months and individuals were capable of rapid compensatory growth (Vrtílek & Reichard, 2015). The present study suggests that the capacity for compensatory growth pertains to natural populations. Adult mean L_T increased by approximately 30% since maturity in both sexes in all three species, as population density decreased steadily over the course of the season (Vrtílek *et al.*, 2018a). The sustained growth was especially apparent in fish from higher density populations.

In addition to population density, community complexity may affect fish growth (Fox, 1994). We acknowledge that the distribution of population densities in our study was entirely collinear with community complexity, with the highest population densities in the most complex killifish communities (three coexisting species) and the lowest population densities in single-species communities. Whether there is a functional link at the habitat level between sustenance of dense populations and rich communities is unclear (Reichard *et al.*, 2017a), but examining the species-specific slopes of the density effect on the maximum body size suggests that *N. furzeri* (present in all communities) is the species with growth rate least affected by population density while *N. pienaar* was the most affected and inhabited exclusively the most complex communities. This link has to be taken with extreme caution due to the limited number of replicated communities, though it may provide an explanation for annual killifish community assembly and the relative rareness of certain species. While we have not studied the mechanistic causes of density-dependent growth regulation, we note that *Nothobranchius* killifish are aggressive. Increased aggression and the associated stress response may have contributed to growth limitation in addition to the indirect effect of competition for food.

Ephemeral habitats impose strong selection for rapid development (Dańko *et al.*, 2017) but directional selection is rarely apparent in the wild because of variation in local conditions and phenotypic plasticity (Pujol *et al.*, 2018). Realised somatic growth in temporary habitats is regulated by population density while the evolution of growth rate is mainly shaped by trade-offs between current and future reproductive effort. Indeed, annual killifishes exhibit great phenotypic plasticity (Cellerino *et al.*, 2016), adjusting their growth to the prevailing ecological conditions both in the wild and the laboratory with very limited evidence so far for local adaptation.

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AUTHOR CONTRIBUTIONS

M.R. conceived and designed the study, M.V., J.Ž., M.R., M.P. and R.B. collected the data, M.V. analysed data and drafted manuscript, all authors revised and approved the final version of the manuscript.

ETHICAL STATEMENT

All fieldwork was carried out in accordance with legal regulations of Mozambique (collection licence: ADNAP-170/7.10/16). The research procedures were approved by the ethical committee of the Institute of Vertebrate Biology, Czech Academy of Sciences.

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REFERENCES

- Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science*, *360*, 642–645.
- Bassar, R. D., López-Sepulcre, A., Reznick, D. N., & Travis, J. (2013). Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories. *The American Naturalist*, *181*, 25–38.
- Bassar, R. D., López-Sepulcre, A., Walsh, M. R., Turcotte, M. M., Torres-Mejia, M., & Reznick, D. N. (2010). Bridging the gap between ecology and evolution: Integrating density regulation and life-history evolution. *Annals of the New York Academy of Sciences*, *1206*, 17–34.
- Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *Quarterly Review of Biology*, *75*, 385–407.
- Blažek, R., Poláčik, M., Kačer, P., Cellerino, A., Řežucha, R., Methling, C., *et al.* (2017). Repeated intraspecific divergence in lifespan and ageing of African annual fishes along an aridity gradient. *Evolution*, *71*, 386–402.
- Cellerino, A., Valenzano, D. R., & Reichard, M. (2016). From the bush to the bench: The annual *Nothobranchius* fishes as a new model system in biology. *Biological Reviews*, *91*, 511–533.
- Dańko, M. J., Burger, O., & Kozłowski, J. (2017). Density-dependence interacts with extrinsic mortality in shaping life histories. *PLoS One*, *12*, 1–18.
- Dmitriev, C. M. (2011). The evolution of growth trajectories: What limits growth rate? *Biological Reviews of the Cambridge Philosophical Society*, *86*, 97–116.
- Dorn, A., Musilová, Z., Platzer, M., Reichwald, K., & Cellerino, A. (2014). The strange case of east African annual fish: Aridification correlates with diversification for a savannah aquatic group? *BMC Evolutionary Biology*, *14*, 1–13.
- Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries*, *6*, 379–416.
- Fox, M. G. (1994). Growth, density and interspecific influences on pumpkinseed sunfish life histories. *Ecology*, *75*, 1157–1171.
- Furness, A. I., Reznick, D. N., Springer, M. S., & Meredith, R. W. (2015). Convergent evolution of alternative developmental trajectories associated with diapause in African and South American killifish. *Proceedings of the Royal Society B*, *282*, 20142189.
- García, D., Loureiro, M., Machín, E., & Reichard, M. (2018). Phenology of three coexisting annual fish species: Seasonal patterns in hatching dates. *Hydrobiologia*, *809*, 323–337.
- Hector, K. L., & Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up growth in diverse taxa. *Journal of Animal Ecology*, *81*, 583–593.

- Jennions, M. D., Møller, A. P., & Petrie, M. (2001). Sexually selected traits and adult survival: A meta-analysis. *The Quarterly Review of Biology*, 76, 3–36.
- Lanés, L. E. K., Godoy, R. S., Maltchik, L., Poláčik, M., Blažek, R., Vrtílek, M., & Reichard, M. (2016). Seasonal dynamics in community structure, abundance, body size and sex ratio in two species of Neotropical annual fishes. *Journal of Fish Biology*, 89, 2345–2364.
- Lee, W.-S., Monaghan, P., & Metcalfe, N. B. (2013). Experimental demonstration of the growth rate - lifespan trade-off. *Proceedings of the Royal Society B*, 280, 1–8.
- Lorenzen, K., & Enberg, K. (2002). Density-dependent growth as a key mechanism in the regulation of fish populations: Evidence from among-population comparisons. *Proceedings of the Royal Society B*, 269, 49–54.
- Monroe, M. J., South, S. H., & Alonzo, S. H. (2015). The evolution of fecundity is associated with female body size but not female-biased sexual size dimorphism among frogs. *Journal of Evolutionary Biology*, 28, 1793–1803.
- Pekár, S., & Brabec, M. (2016). Marginal models via GLS: A convenient yet neglected tool for the analysis of correlated data in the behavioural sciences. *Ethology*, 122, 621–631.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2018). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-137. Retrieved from <https://CRAN.R-project.org/package=nlme>
- Poláčik, M., Donner, M. T., & Reichard, M. (2011). Age structure of annual *Nothobranchius* fishes in Mozambique: Is there a hatching synchrony? *Journal of Fish Biology*, 78, 796–809.
- Poláčik, M., Harrod, C., Blažek, R., & Reichard, M. (2014). Trophic niche partitioning in communities of African annual fish: Evidence from stable isotopes. *Hydrobiologia*, 721, 99–106.
- Poláčik, M., & Reichard, M. (2009). Indirect fitness benefits are not related to male dominance in a killifish. *Behavioral Ecology and Sociobiology*, 63, 1427–1435.
- Poláčik, M., & Reichard, M. (2010). Diet overlap among three sympatric African annual killifish species *Nothobranchius* spp. from Mozambique. *Journal of Fish Biology*, 77, 754–768.
- Pujol, B., Blanchet, S., Charmantier, A., Danchin, E., Facon, B., Marrot, P., Roux, F., Scotti, I., Teplitsky, C., Thomson, C. E., & Winney, I. (2018). The missing response to selection in the wild. *Trends in Ecology & Evolution*, 33, 337–346.
- Quince, C., Abrams, P. A., Shuter, B. J., & Lester, N. P. (2008). Biphasic growth in fish I: Theoretical foundations. *Journal of Theoretical Biology*, 254, 197–206.
- Reichard, M. (2015). The evolutionary ecology of African annual fishes. In N. Berois, G. García, & R. O. de Sá (Eds.), *Annual fishes: Life history, diversity and evolution* (pp. 133–158). Boca Raton, FL: CRC Press.
- Reichard, M., Blažek, R., Poláčik, M., & Vrtílek, M. (2017b). Hatching date variability in wild populations of four coexisting species of African annual fishes. *Developmental Dynamics*, 246, 827–837.
- Reichard, M., Janáč, M., Poláčik, M., Blažek, R., & Vrtílek, M. (2017a). Community assembly in *Nothobranchius* annual fishes: Nested patterns, environmental niche and biogeographic history. *Ecology and Evolution*, 7, 2294–2306.
- Reichard, M., Poláčik, M., Blažek, R., & Vrtílek, M. (2014). Female bias in the adult sex ratio of African annual fishes: Interspecific differences, seasonal trends and environmental predictors. *Evolutionary Ecology*, 28, 1105–1120.
- Reichard, M., Poláčik, M., & Sedláček, O. (2009). Distribution, colour polymorphism and habitat use of the African killifish *Nothobranchius furzeri*, the vertebrate with the shortest life span. *Journal of Fish Biology*, 74, 198–212.
- Reznick, D. N. (1982). The impact of predation on life history evolution in Trinidadian guppies: Genetic basis of observed life history patterns. *Evolution*, 36, 1236–1250.
- Reznick, D. N., Bryant, M. J., & Bashey, F. (2002). r- and K-selection revisited: The role of population regulation in life-history evolution. *Ecology*, 83, 1509–1520.
- Sæther, B.-E., Visser, M. E., Grøtan, V., & Engen, S. (2016). Evidence for r- and K-selection in a wild bird population: A reciprocal link between ecology and evolution. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152411.
- Terzibasí Tozzini, E., Dorn, A., Ng'oma, E., Poláčik, M., Blažek, R., Reichwald, K., ... Cellerino, A. (2013). Parallel evolution of senescence in annual fishes in response to extrinsic mortality. *BMC Evolutionary Biology*, 13, 77.
- Volcan, M. V., Gonçalves, A. C., & Guadagnin, D. L. (2019). Body size and population dynamics of annual fishes from temporary wetlands in Southern Brazil. *Hydrobiologia*, 827, 367–378.
- Vrtílek, M., & Reichard, M. (2015). Highly plastic resource allocation to growth and reproduction in females of an African annual fish. *Ecology of Freshwater Fish*, 24, 616–628.
- Vrtílek, M., & Reichard, M. (2016). Female fecundity traits in wild populations of African annual fish: The role of the aridity gradient. *Ecology and Evolution*, 6, 5921–5931.
- Vrtílek, M., Žák, J., Poláčik, M., Blažek, R., & Reichard, M. (2018a). Longitudinal demographic study of wild populations of African annual killifish. *Scientific Reports*, 8, 4774.
- Vrtílek, M., Žák, J., Pšenička, M., & Reichard, M. (2018b). Extremely rapid maturation of a wild African annual fish. *Current Biology*, 28, R822–R824.

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