



Adriaenssens, B. (2017) Bold perch live life in the fast lane. *Journal of Animal Ecology*, 86(2), pp. 176-178.

There may be differences between this version and the published version. You are advised to consult the publisher's version if you wish to cite from it.

This is the peer reviewed version of the following article: Adriaenssens, B. (2017) Bold perch live life in the fast lane. *Journal of Animal Ecology*, 86(2), pp. 176-178, which has been published in final form at <http://dx.doi.org/10.1111/1365-2656.12628>. This article may be used for non-commercial purposes in accordance with [Wiley Terms and Conditions for Self-Archiving](#).

<http://eprints.gla.ac.uk/136752/>

Deposited on: 14 February 2017

In Focus

Bold perch live life in the fast lane.

Bart Adriaenssens*

* Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow, Graham Kerr Building, Glasgow G12 8QQ, UK

Email: bart.adriaenssens@glasgow.ac.uk

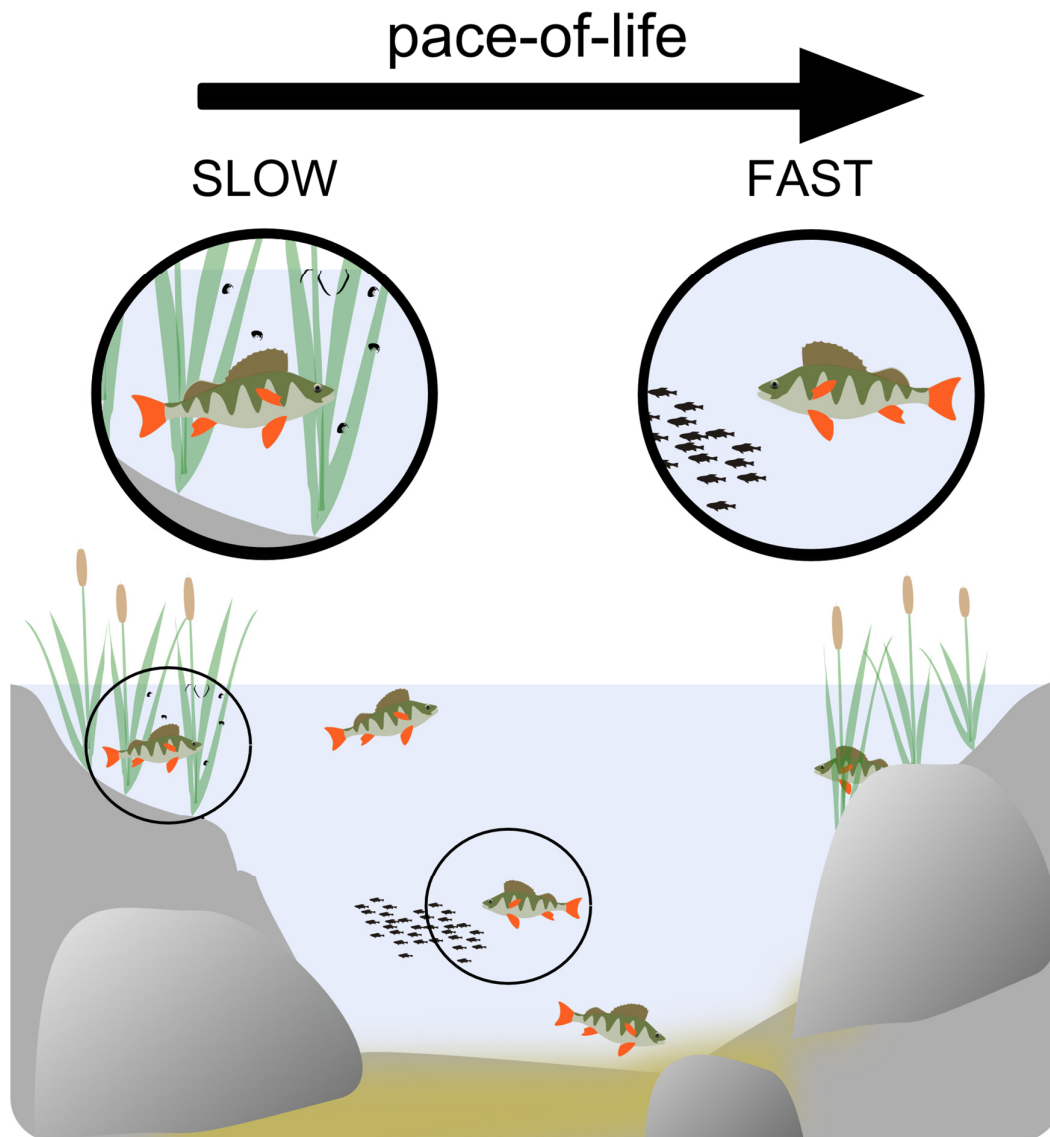


Figure 1. Nakayama and colleagues (2016) studied wild Eurasian perch (*Perca fluviatilis*) and show that: (1) Adult perch growing fast as juveniles moved greater distances and spent more time active. (2) Early maturing individuals with greater reproductive effort became active

more often. And (3) individuals with a high reproductive effort consumed more prey from pelagic (fish) vs. littoral (macroinvertebrates) pathways.

In focus: Nakayama, S., Rapp, T., Arlinghaus, R. (2016) Fast–slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *Journal of Animal Ecology* XX, xxxx–xxxx

The pace-of-life syndrome hypothesis (POLS) suggests that individual behavioural variation co-evolves with life-history variation, causing individuals on a fast life-history trajectory to display more active or bold personalities than individuals following a slow trajectory. In the present study, Nakayama et al. (2016) followed the detailed movement patterns of wild Eurasian perch using acoustic telemetry and studied their relationships with life-history traits inferred from scale samples. Consistent with POLS, individuals with greater reproductive effort changed more often between active and passive behavioural modes. Moreover, individuals growing fast as a juveniles stayed active longer and moved over greater distances when adult. This study shows compelling evidence for covariance between personality and pace-of-life in a natural population.

Natural populations are composed of individuals which markedly differ in behaviour (2009). A surge of recent research examines what causes and maintains such ‘animal personalities’, as well as their ramifications for ecological processes and conservation issues (Sih *et al.* 2012; Killen *et al.* 2016). One hypothesis rapidly gaining popularity in this field provides an adaptive explanation for why seemingly identical individuals display consistently different behaviour. The pace-of-life syndrome hypothesis, POLS in short, postulates that personalities map firmly onto a larger suite of traits, including life-history and physiology (Reale *et al.* 2010). Allocation trade-offs, fundamental to all life-history theory, would then maintain individual differences in life-history as well as behavioural and physiological differences.

In its original form, POLS described how species tend to only display a limited range of possible physiological and life-history trait combinations along a slow-fast continuum (Ricklefs & Wikelski 2002). At the one end of this continuum, long lived, slow growing species with delayed maturation display slow metabolism, high hormonal stress responsivity and more refined immune traits whereas short-lived species occupy the opposite side of this spectrum (Ricklefs & Wikelski 2002; Lee *et al.* 2008). Applying the POLS to population-level behavioural variation, Réale and colleagues argue that individuals prioritizing a fast pace-of-life can achieve similar fitness compared to individuals on a slow pace trajectory but will display more active, bold and aggressive behaviour (Reale *et al.* 2010). This extension of the POLS concept has appealed to many since it elegantly integrates life-history theory with theory of state-dependent behaviour (Houston & McNamara 1999; Wolf *et al.* 2007), and accordingly has inspired many behavioural ecologists to an integrative approach to the study of phenotypic variation.

Whereas tentative evidence exists for the occurrence of positive relationships between behaviour and pace-of-life from studies on captive and domesticated animals, testing this hypothesis under natural conditions has proven to be challenging (Biro & Stamps 2008; Adriaenssens & Johnsson 2009). A partial cause of this lies in the logistic difficulty involved with monitoring behaviour and life-history over suitably long periods in natural populations. This has further been complicated by the notion that behaviours of animals scored in the lab do not always extend to behaviour in the wild upon release (Niemela & Dingemanse 2014).

In this issue, Nakayama and colleagues now provide compelling support for the POLS hypothesis in a population of wild roaming Eurasian perch (*Perca fluviatilis*) (Nakayama, Rapp & Arlinghaus 2016). Eurasian perch are a common freshwater fish throughout most of Europe and northern Asia that actively hunt for small fish and macroinvertebrates in the lakes and rivers they inhabit. Using a sophisticated 3D acoustic telemetry system, Nakayama and colleagues were able to follow the undisturbed behaviour of wild perch in a small lake (~25ha) in Northern Germany. Despite being of same sex (females), similar age (6-9 years) and similar size, differences between individual fish explained between 51 and 66% of observed variance in movement parameters scored during two, separate, 14-day monitoring periods set two months apart. Individuals each had their own typical movement pattern characterized by the distance they navigated, or by how often they switched between active and inactive movement styles. They then used fish scales, much like annual rings in trees, to estimate each fish's prior life-history parameters. This analysis exposed substantial between-individual variation in the speed and timing of life-history events, with individuals growing between 6 to 8cm per year while reaching maturity at either their second or third year.

In agreement with inclusion of behaviour as part of a POLS, they observed individuals with a fast juvenile growth rate to stay active longer and travel greater distances when adult. Early maturing perch with greater reproductive effort also switched more often between active and inactive movement modes. Assuming that active and inactive movement modes overlap with foraging under risk vs. low-risk predator avoidance the authors conclude that overall perch on a fast pace-of-life exhibited more active and less risk-sensitive behaviour. This was also supported by stable isotope analysis, which showed that perch with greater reproductive effort, as well as larger individuals, consumed more prey from pelagic regions of the lake, suggesting riskier foraging behaviour exploiting the open areas in the lake. Lack of cover in these open areas likely makes fish more susceptible to predators such as fish eating birds and larger fish. In the lake studied by Nakayama and colleagues, pike (*Esox lucius*) and European catfish (*Silurus glanis*) are predators posing a realistic threat for perch using open areas (Nakayama *et al.* 2016).

Not all studies have however found similar support for stable positive links between active behaviours and pace-of-life. In fact, over the past years several empirical studies observed patterns that have been difficult to consolidate with the notion of stable positive links between active, aggressive, behaviour and aspects of pace-of-life, leaving the evidence for a broader POLS inconclusive. Numerous studies, for instance, reported negative (Reale *et al.* 2009; Adriaenssens & Johnsson 2011; Debecker *et al.* 2016) or non-linear (Bergeron *et al.* 2013) links between active behaviours and growth or mortality, or associations with directionality contingent on third factors (Heg, Schurch & Rothenberger 2011; Le Galliard *et al.* 2013; Závorka *et al.* 2015; Nicolaus *et al.* 2016). Several of the latter pinpoint variations in conspecific density and resource abundance as key factors determining the direction of links between behaviour and aspects of pace-of-life. In wild great tits (*Parus major*), for instance, fast exploring individuals survived better under low densities, but worse under higher densities in comparison to more slow explorers (Nicolaus *et al.* 2016). Similar results suggest the growth of wild brown trout (*Salmo trutta*) depends on a complex interaction between individual activity and resource abundance (inferred from home range sizes) (Závorka *et al.* 2015). This caused active trout to grow faster than less active individuals when food was abundant but slower when food was scarce (small vs. large home ranges).

It is therefore tempting to suggest that among-study differences in the environmental conditions may also explain some of the variations in strength and sign of correlations between active behaviours and pace-of-life observed in separate studies. This is to some extent supported by work on salmonid fish, where active individuals outgrew inactive individuals in studies in stable, food-rich,

environments, whereas inactive individuals grow at equal or faster speed in environments with less predictable food abundance (summarized in Závorka *et al.* 2015). Considering that the perch studied by Nakayama (2016) occupy a food rich, eutrophic, lake system the results of their study offers further support for this hypothesis.

Together, the variable support for the POLS hypothesis highlights an outstanding need to develop a theoretical framework for covariance patterns between personality and life-history that holds scrutiny under more naturally fluctuating environmental conditions (Adriaenssens & Johnsson 2009). A particular challenge for future work goes to outlining the settings under which we do expect behaviour and POLS to covary, and explaining why and when the relative payoffs of different personalities shift when environments change. Tools allowing long term collection of detailed behavioural data from free-ranging animals, such as those applied by Nakayama *et al.* (2016), will be an invaluable resource in these efforts to gain a better understanding of links between behaviour and life-history.

References

- Adriaenssens, B. & Johnsson, J.I. (2009) Personality and life-history productivity: consistent or variable association? *Trends in Ecology & Evolution*, **24**, 179-180.
- Adriaenssens, B. & Johnsson, J.I. (2011) Shy trout grow faster: exploring links between personality and fitness-related traits in the wild. *Behavioral Ecology*, **22**, 135-143.
- Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009) The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, **77**, 771-783.
- Bergeron, P., Montiglio, P.O., Réale, D., Humphries, M.M., Gimenez, O. & Garant, D. (2013) Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. *Journal of Evolutionary Biology*, **26**, 766-774.
- Biro, P.A. & Stamps, J.A. (2008) Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, **23**, 361-368.
- Debecker, S., Sanmartín-Villar, I., de Guinea-Luengo, M., Cordero-Rivera, A. & Stoks, R. (2016) Integrating the pace-of-life syndrome across species, sexes and individuals: covariation of life history and personality under pesticide exposure. *Journal of Animal Ecology*, **85**, 726-738.
- Heg, D., Schurch, R. & Rothenberger, S. (2011) Behavioral type and growth rate in a cichlid fish. *Behavioral Ecology*, **22**, 1227-1233.
- Houston, A.I. & McNamara, J.M. (1999) *Models of Adaptive Behaviour*. Cambridge University Press, Cambridge, UK.
- Killen, S.S., Adriaenssens, B., Marras, S., Claireaux, G. & Cooke, S.J. (2016) Context-dependency of trait repeatability and its relevance for management and conservation of fish populations. *Conservation Physiology*, **4**, cow007
- Le Galliard, J.-F., Paquet, M., Cisel, M. & Montes-Poloni, L. (2013) Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances. *Functional Ecology*, **27**, 136-144.
- Lee, K.A., Wikelski, M., Robinson, W.D., Robinson, T.R. & Klasing, K.C. (2008) Constitutive immune defences correlate with life-history variables in tropical birds. *Journal of Animal Ecology*, **77**, 356-363.
- Nakayama, S., Laskowski, K.L., Klefoth, T. & Arlinghaus, R. (2016) Between- and within-individual variation in activity increases with water temperature in wild perch. *Behavioral Ecology*, **27**, 1676-1683.
- Nakayama, S., Rapp, T. & Arlinghaus, R. (2016) Fast-slow life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *Journal of Animal Ecology*, n/a-n/a.

- Nicolaus, M., Tinbergen, J.M., Ubels, R., Both, C. & Dingemanse, N.J. (2016) Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, **19**, 478-486.
- Niemela, P.T. & Dingemanse, N.J. (2014) Artificial environments and the study of 'adaptive' personalities. *Trends Ecol Evol*, **29**, 245-247.
- Reale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.O. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **365**, 4051-4063.
- Reale, D., Martin, J., Coltman, D.W., Poissant, J. & Festa-Bianchet, M. (2009) Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, **22**, 1599-1607.
- Ricklefs, R.E. & Wikelski, M. (2002) The physiology/life-history nexus. *Trends in Ecology & Evolution*, **17**, 462-468.
- Sih, A., Cote, J., Evans, M., Fogarty, S. & Pruitt, J. (2012) Ecological implications of behavioural syndromes. *Ecology Letters*, **15**, 278-289.
- Wolf, M., van Doorn, G.S., Leimar, O. & Weissing, F.J. (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581-584.
- Závorka, L., Aldvén, D., Näslund, J., Höjesjö, J. & Johnsson, J.I. (2015) Linking lab activity with growth and movement in the wild: explaining pace-of-life in a trout stream. *Behavioral Ecology*, **26**, 877-884.