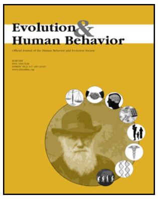
Evolution and Human Behavior 41 (2020) 493–501

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.elsevier.com/locate/ens



Adaptation and plasticity in life-history theory: How to derive predictions.

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ARTICLE INFO

Keywords:
Density dependence
Fast-slow life-history continuum
Hard/soft selection
Individual optimization
Population regulation
Reaction norm
Sexual conflict

ABSTRACT

Why is life paced so differently across as well as within organisms? Can one expect across-species patterns to be repeated within a species too, among individuals? The answer to these questions requires understanding conditions under which reaction norms evolve. We provide an overview of what we believe to be understudied areas of life-history theory, to foster theoretical work and to help deriving predictions for the evolution of human reaction norms. We discuss both why one might expect reaction norms to be aligned with patterns across species, and why that expectation might sometimes fail. It is not impossible for environmental cues to shape life histories in the current generation, but compared with cue-independent genetic adaptation, the adaptive task is now more complex; cues may be unreliable or change in value with time; and parental strategies may differ between situations where offspring have the possibility to disperse to new habitats and situations where environmental conditions remain the same across generations. In that regard, we comment on the value of source-sink theory and on the importance of being specific about the way density regulation affects individual vital rates. We also remind the reader that adaptation does not necessarily optimize population growth rates when conflict between entities (e.g. between the two sexes) is a feature of the adaptive process. All these factors likely play an important role on the evolution of reaction norms, and we argue in favour of their more systematic inclusion in human life-history research.

1. Introduction

Lifespans vary enormously across the tree of life (Jones et al., 2014). We expect humans to usually outlive their pets, and the songbird breeding in one's garden is quite likely to be a different individual from last year's resident; news of ant queens living for decades (Lucas & Keller, 2019) or the Laysan albatross named Wisdom raising a new chick at the age of 68 — at the time of writing, she was still doing this — justifiably surprise us. These examples of life-history variation among organisms can be organised as being part of a fast-slow continuum (for a brief history see Stearns & Rodrigues, 2020), with fast species combining a short lifespan with rapid reproduction and thus a shorter generation time, whereas a typical slow species does the opposite with its long lifespan, low reproductive rate and a long generation time. However, should one have the hope to arrange species along a unidimensional axis, perhaps mediated via body size, the diversity of life histories will soon show that there is more to the question than just a single continuum. Although large-bodied species tend to show longer generation times (Healy et al., 2014) and often produce fewer offspring per reproductive attempt (Jeschke & Kokko, 2009), exceptions are not hard to find: the larger a salmon, the more eggs are laid per female (Einum, Kinnison, & Hendry, 2004), and a similar trend occurs across fish species too (Jeschke & Kokko, 2009). One can certainly imagine a hypothetical alternative where a large salmon lays very few enormous eggs (that then as juveniles outcompete others), but this is not the actual evolutionary outcome.

Broad across-taxa comparisons can reveal some of the potential causalities. A bird can be expected to live longer than a similarly sized mammal, and life history theoreticians have wondered if this might indicate that flying, allowing a partial escape from predation (interpreted as extrinsic mortality), selects for investing in a slower life history. The verbal argument goes like this: the rewards of a more robust body, in the form of late-life reproduction, can only be reaped if the species' ecology permits escaping extrinsic mortality for sufficiently long. It is interesting to note that flight similarly appears to allow bats to outlive other mammals of a similar size (Munshi-South & Wilkinson, 2010; Wilkinson & Adams, 2019), and gliding mammals appear to share some of this lifespan advantage (Holmes & Austad, 1994), though this does not exclude other factors, such as hibernation, from playing a role.

Lifespans also vary within a species, showing between-population variation and within-population patterns. Opposing the above rule between body size and slow life, domestic dog breeds' life expectancy

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https://doi.org/10.1016/j.evolhumbehav.2020.06.007
Received 28 November 2019; Received in revised form 11 June 2020; Accepted 15 June 2020

covaries negatively with body size (O'Neill, Church, McGreevy, Thomson, & Brodbelt, 2013). Sex differences also abound. In mammals, males tend to have shorter lifespans than females, while birds typically show the opposite sex bias in lifespan (Liker & Székely, 2005). While there is evidence that this reflects genetic architecture (the shorter-lived sex being the one that has a reduced sex chromosome, Xirocostas, Everingham, & Moles, 2020), the large number of species varying in sex-specific details of the breeding system allows a more detailed look. It appears that intense competition for mates adversely affects mammalian males (Lukas & Clutton-Brock, 2014), while the variable degree to which males contribute to parenting in birds goes a long way towards explaining the generally higher mortality of avian females (Liker & Székely, 2005).

Given that life-histories vary both between species or populations and within populations, can we expect patterns to align to some extent, or should they differ when measured at different levels? If the former interpretation is valid, then we can expect individuals, not only species, to vary in a pattern akin to a fast-slow continuum. The additional question is whether the relevant causalities also align: do factors expected to be responsible for variation in life-histories among species or populations affect individual life-history in a similar manner (Stearns & Rodrigues, 2020; Zietsch & Sidari, 2020)? Much of the debate relates to whether individuals express genes from the relevant gene pool regardless of their own experiences in life so far, or whether genomes of organisms are also expected to code for so-called *reaction norms*, whereby the same genotype can express different phenotypes according to information they gather about some aspects of their environment.

There is no question that reaction norms exist: e.g., amphibians tend to speed up their development towards metamorphosis when chemical predator cues are added to the water (they thus may mature at smaller adult size, Relyea, 2007; for a taxonomically broad review see Benard, 2004), and birds adjust their parenting based on experimentally induced apparent threat of predation (Ghalambor & Martin, 2001). Reaction norms themselves may be impacted by the life history of the species in question: a response to the same set of experimental conditions can differ between species, depending on factors shaping that species' life history in general. In biogeographic areas argued to favour a slow life history (tropics), bird parents that are given predator cues behave in ways that keeps their own survival as intact as possible while sacrificing (to an extent) the prospects of the current nest, while related species in temperate areas adjust in an opposite manner, favouring the success of the current nest at the expense of their own survival (Ghalambor & Martin, 2001).

However, a verbal description of expected patterns and illuminating examples can only go so far. Formal theory can help resolve whether or not one expects alignment between individual- and population-level patterns to hold. We particularly comment on theory conducted on the evolution of reaction norms: the study of how individuals may adaptively change their phenotype depending on environmental cues (phenotypic plasticity). While not all studies explicitly use reaction norms as a phrase, it is a key underlying theme in adaptive explanations of variation in human life history patterns (Gluckman, Hanson, & Spencer, 2005; Nettle, Frankenhuis, & Rickard, 2013). We start with exposing the problem of inferring adaptations across and within populations. Density regulation of populations also affects life history evolution, and we discuss how this links to the alignment problem. We end with a reminder that models based on the idea that life history traits necessarily maximize population fitness necessarily ignore conflicts between entities. Conflict between individuals is, however, omnipresent in organisms (such as humans) that reproduce sexually, and this makes it incorrect to expect simple maximization principles to hold. In such a case, like in others we review below, formal theory has helped tremendously in predicting adaptations and we here argue for a more systematic use of it in human evolutionary biology.

2. Between- vs within-species patterns: cues and their reliability matter

The between- vs. within-species debate is, in many ways, a nature-nurture debate, where the current gene pool of a species (or population) takes the role of 'nature', and the 'nurture'-related causalities refer to potential adjustments that the organism undertakes to cope with the specific challenges provided by its current environment. Much of the argument is about whether these adjustments are adaptive, especially since life history traits may trade off with others. In a nutshell: (i) Adverse life conditions can lead to early death, (ii) early death is never adaptive per se, but (iii) if the causal pathway to early death involved the organism responding to early adversity cues by investing in more reproduction at the expense of somatic maintenance, then we may be witnessing an adaptive reaction norm in action.

Below, we first discuss conditions under which reaction norms evolve, then move on to examining reasons why they should lead to variation in life-histories among individuals. It is important to note that there can also be non-adaptive variation in life-history, stemming for instance from stochasticity in individual experiences throughout life (e.g. sterility induced by a disease); we leave such topics largely aside as they are discussed in other articles in this special issue (e.g. Del Giudice, 2020).

2.1. An illustrative example: cod maturation reaction norms

To see how reaction norms can arise and be shaped by past selection, consider a well-studied example of cod. Juvenile cod grow without reproducing until they hit a reaction norm that links size and age at maturity. Cod with different growth curves therefore mature at different ages. If food is abundant such that growth is fast, they mature earlier *and* larger than if food is scarce (Fig. 1, from Olsen et al., 2004). Graphically, this means that the reaction norm has a negative slope. But when (and at what size) precisely should a cod mature?

Under 'normal' (non-anthropogenic) conditions, annual survival is higher for larger cod (Olsen et al. 2011), and since reproduction has a negative impact on growth, there is selection to avoid reproducing until a rather large body has been achieved. But if growth is slow due to food limitation, it pays to mature at a smaller body size, to avoid delaying reproduction for too long under mortality risk (Marty, Dieckmann, Rochet, & Ernande, 2011). This explains the negative slope of the reaction norm (Fig. 1). The invention of large-scale fishing equipment that can operate far offshore has completely changed the relationship between size and mortality (Olsen & Moland, 2011): now per capita mortality is highest for the largest cod (mesh size being a major determinant of mortality). The result is a rapid adaptive response, with cod maturing at a smaller-earlier combination of body size and age (Fig. 1). This type of response shows the readiness with which reaction norms evolve. In the cod, anthropogenic selection favoured those with reaction norms that were on the low side of what used to be the norm, and these have spread to become the new norm.

While cod life histories are very different from those of humans, the example highlights a fundamental principle: plastic responses existed in the past as well as today, and in both cases, the fish responds to its own condition (here, growth rate) that may differ from the average member of its population. Adaptive responses of both human and non-human organisms have to be evaluated with respect to the following aspects.

Firstly, for there to be any reason for a population to evolve reaction norms, the lineage has had to consist of a sufficient number of individuals experiencing different conditions during their lives. In the case of cod, there was pre-existing plasticity with respect to the combination of size and age, probably interpretable as the genomes of every single cod already adapted to environmental variation in food availability and related growth trajectories. In the bird case, some birds have lived with strong predator cues, others in safer territories, and this has reliably enough correlated with nest failure rates and/or parental

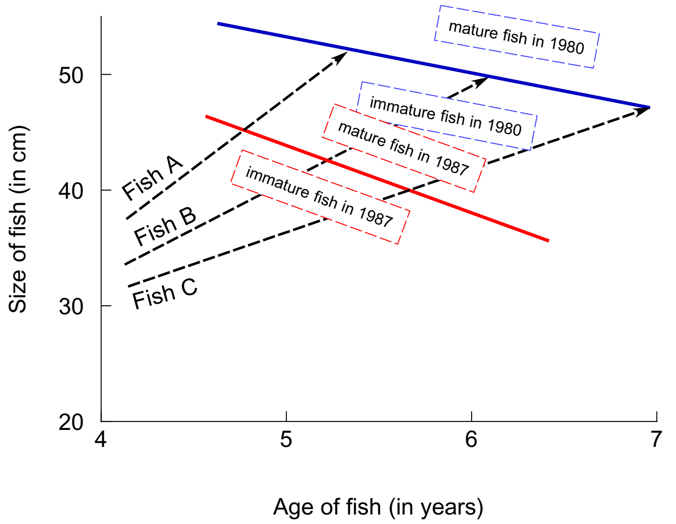

Fig. 1. Maturation reaction norms in cod have changed over time. Each fish (three hypothetical individuals A, B, and C are given) grows until it hits the reaction norm for maturity (negatively sloped lines). The growth trajectories (positively sloped lines) are individual-specific because some fish find more food than others. In the 1980 population, individual A that has reached a length of 48 cm at age 5 would not yet have reached maturity, instead opting to grow a little more until the blue (1980) reaction norm is reached. The same growth trajectory, however, in the 1987 population would already have this fish reach its maturation reaction norm at a smaller size (approximately 45 cm), a little before 5 years of age. The speeding up of the life history can also be seen for fish B and C. As a whole, the population that used to mature at relatively high size and age combination (dark blue line) now does so at a smaller sizes and earlier ages (red line). The evolutionary response is based on two pre-existing expectations: that growth trajectories will differ between individuals (different slopes of the dashed lines), and that slow growers do not benefit from delaying maturation indefinitely (negative slopes of the reaction norms). Adapted from Olsen et al., 2004. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

survival to induce flexibility in parenting depending on current predation risk. Secondly, there has to be a perceivable cue which informs individuals about such environmental variation with enough reliability to warrant adaptive phenotypic change, e.g. birds need to perceive the presence of predators already before they or their eggs are eaten. Below, we discuss specific issues related to cue reliability and environmental variation which we believe are particularly important to consider when studying human life-history.

2.2. *It matters when in life environmental variation occurs*

Plastic responses to changes in the environment may have mild or strong effects on individual fitness, depending on when in life the change occurs. The potential for strong effects appears a priori larger for early plastic responses and associated phenotype change, simply for the reason that phenotypic changes occurring later may occur after some of an individual's reproduction is already in the past (Fawcett & Frankenhuis, 2015; Fischer, van Doorn, Dieckmann, & Taborsky, 2014). A greater benefit of early versus late plasticity is also predicted if it takes time to mount a plastic response (Fischer et al., 2014), or if the cost of plasticity increases with life (e.g. because of developmental constraints; Dufty, Clobert, & Møller, 2002).

The relative benefits of gathering environmental cues may also change throughout life, because individuals' state of knowledge of the current environment may depend on how much they have had time to sample relative to the spatiotemporal scale of variation in the environment itself (Fawcett & Frankenhuis, 2015). The individual's own location may change: e.g. dispersal may make earlier information gathering largely irrelevant. All else being equal, therefore, the individual's estimate of the state of the environment is at its most uncertain after dispersal and should then improve throughout development. In spatiotemporally stable environments, on the other hand, it is adaptive (for non-dispersers) to lose sensitivity to cues rather rapidly (Panchanathan & Frankenhuis, 2016). Overall, this should lead to plasticity occurring early rather than late in an individual's life, over a period coined a “sensitive window” for plasticity.

2.3. *Internal means to assess environmental variation*

Evaluating environmental cues does not have to be a difficult process. Even if it is too difficult for a prey individual to assess the population density of predators, the simple fact that an organism is alive carries information that it probably lives in an above-average environment regarding safety (Ejsmond, Kozlowski, & Ejsmond, 2019). Ontogenetically expressed life history traits may well evolve based on such expectations. The observable fact “I am still alive” may yield a Bayesian computation that one inhabits a relatively safe environment, with the certainty of this conclusion increasing with advancing age. Since all individuals expressing any traits are by default alive, we have a perhaps counterintuitive situation at hand where all individuals shift to a different life history trait value with advancing age, and even if there is no individual variation in how they shift, the situation fully qualifies as an example of an environmental cue (safety) having been detected without actually counting sightings of any predators.

This can also be generalized to any internal cue, such as somatic condition or level of starvation. A mammalian female does not even have to be in a survival-threatening state of starvation for pregnancy rates to drop: in female fin whales, for example, blubber thickness (a measure of recent prey catching success) is a predictor of the pregnancy rate (Williams et al., 2013), and low BMI (body mass index) in otherwise healthy human females associates with menstrual dysfunction (exemplified by ballet dancers, Bacchi, Spiazzi, Zendrini, Bonin, & Moghetti, 2013). The state of own energy reserves is a physiologically readily accessible alternative to using sensory organs to assess of the abundance of food in an organism's current environment. This contrast has also been investigated theoretically: Higginson, Fawcett, Houston, and McNamara (2018) found almost no differences when modelling the relative benefits of using internal or external cues for decisions, suggesting that the use of internal cues could be favoured by selection whenever assessing external cues is more costly, such as when it requires investing in costly sensory organs or extensive sampling.

It appears important to remember that internal states and external conditions can impact life histories directly (e.g. death due to poor condition via, say, susceptibility to infection) and also indirectly (e.g., allocation shifts to, or away from, current reproductive effort). If individuals' internal states have a stronger direct effect than current environmental conditions do, then it makes intuitive sense that internal cues should be favoured over external cues to make allocation decisions. The internal/external distinction may also be important with respect to the temporal scale over which the cue remains reliable. In species characterized by long generation times, as in humans, it has been suggested that developmental responses to cues early in life might not be adaptive because of a high likelihood that the state of the environment changes between cue assessment and the implementation of the life history response (Nettle et al., 2013). Even so, lagged effects might manifest themselves via a different route: if early environmental conditions affect individuals' somatic state leading to long lasting effects on survival, early plasticity based on somatic state (i.e. an internal cue) could be adaptive in humans (Nettle et al., 2013).

2.4. *The role of environmental variation between generations*

The question of the best way to respond to cues is a thorny one not only for the reason that cues and the underlying environmental factor of relevance may vary spatially and/or temporally over an individual's lifetime. Responding to a cue may also create different numbers of offspring and/or change their traits. These offspring will then grow up in a place that may or may not resemble the cue-indicated environment that the parent based its adjustment on. This depends not only on temporal variation in the environment, but also on dispersal.

These thoughts may explain why some models produce patterns that perhaps go against the first intuition. Consider, for example, mothers having to invest in offspring production in the presence of a size-number trade-off: should she produce few offspring well equipped to deal with future challenges, or many tiny ones that will struggle? Classic theory (Lloyd, 1987; Smith & Fretwell, 1974) has been augmented by considerations of cues indicating whether juveniles will develop in good or poor environments (Fischer, Taborsky, & Kokko, 2011), with results that combine intuitive outcomes with some that can appear baffling. Fischer et al.'s model assumes that, in poor environments, only large (high quality) offspring have reasonable chances to survive. Mothers have imperfect information on which type of environment will be experienced by the young. Plasticity is, intuitively, expected to evolve only if the cue is accurate enough, and this expectation is also borne out by the model. Less intuitively, plasticity also evolves more easily if the two environments offspring can experience are not too different. Why? In this situation, both types of environment contribute individuals (and their genes) to future generations, and a fine-tuned response to both is evolutionarily important. If one environment, however, offers very poor prospects, the gene pool of the species as a whole is very little impacted on performance there, and parents do best when they equip all offspring to function well where it matters (in the better of the two environments). Below, in section 2.5, we discuss further examples of this kind.

This type of result generalizes: conditions experienced between parent and offspring can be dramatically different, and even parents currently residing in poor environments may benefit from preparing their offspring for a life in better conditions. Such outcomes are predicted by theory if there is a reasonable chance that some offspring will move to a good habitat, for those offspring will count much more to future generations than their less fortunate siblings. This principle has been called ‘optimism’ favoured by natural selection (McNamara, Trimmer, Eriksson, Marshall, & Houston, 2011). Optimal life-histories in heterogenous environments cannot be inferred from optimization performed for the average environment; expectations must be weighted in favour of the best-performing offspring (Baldini, 2015; Houston & McNamara, 1992; Kawecki & Stearns, 1993). Houston and McNamara (1992) model optimal life-history allocation in reproductive effort of parents in different habitat qualities, assuming that reproductive success is lower in poorer habitats and greater reproductive effort is associated with higher risk of mortality before the next reproductive event. Interestingly, this model predicts divergent reproductive efforts between parents producing offspring which stay in the parental habitat and parents whose offspring disperse — even if dispersal occurs randomly to a poor or good habitat. Compared to parents of non-dispersing offspring, parents of dispersing offspring are also expected to produce more offspring when living in a poor environment and fewer when living in a good environment, dampening the overall difference in optimal phenotype across habitats (Houston & McNamara, 1992). This example emphasizes the fact that optimal strategies derived from models assuming fixed differences in environments between isolated populations (i.e. the non-dispersal case) do not automatically extend to cases where offspring may move between subpopulations, which allows conditions experienced by parents to differ from those impacting their offspring.

2.5. Source-sink population structure: effects on adaptive plasticity

The reason why large differences in habitat productivity act to remove plasticity in both Fischer et al. (2011) and Houston and McNamara (1992) is related to source-sink theories of adaptation (Holt, 1996; Kawecki & Stearns, 1993; Sasaki & de Jong, 1999). By definition, reproduction in a sink habitat falls below the replacement level, and continued existence of a population in sink habitats therefore requires immigration (from sources). Individuals residing in sinks contribute very little to future gene pools no matter how much of a ‘best of a bad job’ they manage to perform there. In such cases, selection will tend to remove plasticity altogether, with phenotypes in each habitat tending towards the optimal phenotype in highly productive habitats (Fischer et al., 2011; Sasaki & de Jong, 1999).

There are at least three different ways that source-sink ideas could apply to humans. One is that it is a mechanism to produce ‘optimism’ in the sense of McNamara et al. (2011), as discussed above. The second context in which sources and sinks apply is that of species range expansion (humans are a well-known example of a species that has performed this at a global scale). If conditions near a species' range edge are difficult to cope with, with a gene pool that is better adapted to conditions at the core of the range, source-sink ideas take the form of genetic swamping: subpopulations trying to establish themselves at the range margin can be so strongly impacted by gene flow from the core that adaptation fails and the species cannot expand any further (the margin of a species range is then a demographic sink, Haldane, 1956, Kirkpatrick & Barton, 1997). This is, however, also counteracted by a positive effect of dispersal, the continued supply of genetic variation to fuel further evolutionary change (Kirkpatrick & Barton, 1997). Humans, obviously, have another compensatory mechanism in place: local challenges can be overcome using cultural evolution — clothing as a way to deal with local climate — but interestingly, this does not appear to have prevented spatial and adaptive genetic differences from arising, e.g. high-altitude Himalayan populations adapting to low oxygen (Arviero et al., 2018), or selection on fatty acid metabolism in Inuits and other first Americans (Amorim et al., 2017). One may hypothesize that the cultural innovations may have been essential for turning a sink region into a potential source in the first place, after which genetic adaptation can take place.

Finally, for a long-lived species, it is interesting to note that sources and sinks not only apply to rich and poor habitats, but also to young and old individual bodies, insofar as they are respectively ‘intact’ and ‘aged’, i.e. damaged in their soma and/or germline. If old parents produce gametes from an ‘aged’ germline (which appears possible for humans, see Monaghan & Metcalfe, 2019 for a review of the mechanisms), this is in principle a similar situation to parents producing offspring in the same habitat they find themselves in. Damaged offspring arising from “aged” gametes may represent a sink (Galipaud & Kokko, 2020), with clear potential for this to impact parental reproductive scheduling (Monaghan & Metcalfe, 2019).

2.6. Consequences for variation in life-histories between versus within populations

So, back to the debate: should within-population patterns be largely aligned with between-species patterns, or not? We suggest a middle ground position here, and present first the argument that speaks in favour of an a priori expectation of alignment. Plastic responses may well resemble species-level adaptations, since they are two different ways to achieve the same goal (Del Giudice, 2020). For example, a species that lives in a temperate zone may benefit from better insulation (a thicker fat layer or more abundant feathers or hair) than its tropical sister species. This should be easy to evolve. Within a species range or a population, then, we can imagine some spatial (microhabitat) or temporal variation, such that some individuals face colder conditions than others, or the same individuals go through seasonal variation in temperature. It then makes good sense to evolve a plastic response: experiencing a lot of cold thickens the fat layer or other forms of insulation (fur). If lifespans are short relative to season length, it may make sense to equip offspring to expect certain weather conditions from the start: in the vole *Microtus pennsylvanicus*, cues of shortening day length triggers a plastic response in mothers, who start producing pups with deeper, longer and denser fur (Lee & Zucker, 1988). This example serves as a reminder that while the way the response is 'coded' in an organism is necessarily different (an entire gene pool of a population vs. all the potential regulatory mechanisms involved in a plastic response), the 'goal' of adaptation is similar, and in many cases achievable too.

The arguments against alignment, then, relate to the complexity of the plastic situation, relative to fixed trait evolution. Cues are of different nature, are unreliable and they can be temporally variable; plasticity can be costly, and its benefits might vary with age; parents and offspring do not always share environments with consequences on local productivity. One resolution is, of course, 'when in doubt, model it', especially since in some cases responses are only expected when the prediction offered by the cue is of a long-term nature, while in other cases the opposite is true (Nettle et al., 2013).

For an example of a situation that at first sight appears simple, but proves complex enough to require formal models to guide intuition in the right direction, consider a male bird who has received some cues that its mate may have been unfaithful. Is this a cue that this particular breeding attempt is an 'unlucky' one for this male, or does this cue imply something permanent about this male — that he is likely to perform below average with respect to paternity in all his breeding attempts? In behavioural ecology, it took a long time to understand the correct order of likely strength of responses. One can expect males to respond more to short-term cues (Kokko, 1999) than to ones with lifelong reliability (Westneat & Sherman, 1993), because strong shifts in investment from offspring survival to that of the (male) parent only pay off when the parent has better prospects in the future than now (i.e., the current reduction in paternity is a non-permanent one). With that knowledge in place, it would at first sight appear tempting to align predictions for an entire species with those for a permanently low-quality male within a species. Since an average male in a species where extra-pair paternity is common across all nests cannot expect much paternity in any of his nesting attempts, is this not perfectly analogous to permanent cues of meagre paternity for a low-quality male in a within-species situation?

The answer is no, instead, when comparing across species, one expects low paternity to be, after all, causally related to low paternal caring effort (Queller, 1997). The reason for this non-alignment from individuals to species is the following: a specific low-quality male can perform consistently below the average of his population, but an average male of a certain species cannot do this. It is mathematically impossible for an average male to sire fewer young than the females are, on average, offering eggs to be fertilized. This means that the male's future production of young remains good, since both extra- and within-pair offspring must count towards it (Queller, 1997). This contrasts with the low-quality male in a within-species comparison, who may perform poorly on both accounts. To sum up, strong responses can be predicted for the very short time scale (cues of a non-permanent reduction in paternity for a given male), and at the opposite end of across-species comparisons (evolved responses to species-wide extra-pair paternity), while reductions that are permanent for a given class of males, while other males maintain high paternity, may create surprisingly little selection for behavioural adjustments.

The take-home message is that when the answer is 'it depends' (which is frequently the case in evolutionary thinking, Barrett, 2015), models would be maximally useful if they explicitly included a range of cue reliability values as well as the spatiotemporal correlation pattern of the environment, relative to the organism's lifespan (which itself may evolve to be longer or shorter, depending on adults' ability to track the changing environment; Nettle et al., 2013, Ratikainen & Kokko, 2019).

3. Back to lifespan: why the fuss about density regulation?

3.1. Population regulation: why does it matter?

If an organism lives in a dangerous environment, can one expect a shift towards a faster life history? If the question is interpreted as a within-species prediction, the answer is complicated for all the reasons above: cue reliability and its spatiotemporal stability influence the answer, together with the chances that offspring disperse to different environments. However, one could take the 'pro-alignment' reasons above (section 2.6) as a baseline, and ask: is the adaptive goal to respond to danger by evolving a faster life history in the first place?

The surprising answer is that even this a priori adaptive goal is debated. Much of the debate involves the choice of the appropriate life history measure (Moorad, Promislow, & Silvertown, 2019). When trying to pick the best life history in the presence of trade-offs, can one compute the success of each potential option based on the expected offspring number it produces (often abbreviated as LRS for lifetime reproductive success, or R_0)? Alternatively, should one consider that well-performing life histories probably produce more than one surviving female offspring for each female of the parental generation, leading to population growth? This distinction matters because if a population is growing, then two competing life histories with the same expected offspring production are not identically competitive, if one manages to place offspring earlier into the growing population than the other. The early-placed offspring form a larger proportion of the current (and thus also the future) gene pool. Specifically, in the absence of any density dependence, the expectation is that a population will grow exponentially. Offspring produced earlier in the life of an individual will themselves, all else being equal, contribute a larger population of descendants to a future gene pool than offspring produced later in life, and the relevant discounting factor is the population growth rate, r.

Exponential growth exists in nature, but we have good reasons to expect it to be transient. Its transiency reflects the fact that unlimited growth leads to impossible population densities very quickly, and ecologists therefore spend much effort understanding mechanisms of density-dependent regulation (Brook & Bradshaw, 2006): population growth slows down if some resource has become depleted or if mortality increases e.g. due to disease. Of course, even an entirely stationary population (in terms of a stable total number of individuals) does not mean that the genotype frequencies remain unchanged: in those cases, should one individual reproduce more than others, this is reflected in a larger R_0 (Mylius & Diekmann, 1995), and predicts that this individual's genes will spread at the expense of others'.

Some populations may spend more of their time in an exponential growth phase, while others might instead remain more or less constant in size over generations. In the former case, 'fast' placement of new individuals into the population (i.e. early reproduction) appears more important than in the latter case. This argument can be formalized, which confirms the intuition that stationarity makes the timing of when exactly an offspring is placed into the population lose its relevance, restoring R_0 – the lifetime production of offspring – as a valid fitness measure (Mylius & Diekmann, 1995). In general, however, the choice of a fitness measure has to be performed carefully (Day & Abrams, 2020), without relying on rules of thumb too much. In the 'general case', populations fluctuate and experience regulation via more than one pathway (disease, breeding site limitations, age-dependent susceptibility to predation, etc.), and the answer is the same as the one that ended the last section: if in doubt, then model the consequences of your favourite assumptions explicitly (e.g. Heino, Metz, & Kaitala, 1997).

But not all is lost in a thick fog of "everything depends on everything, therefore nothing specific can be said". If density-dependence reduces fecundity or (rather equivalently) decreases the survival of neonates, or makes the recruitment of juveniles into the breeding population difficult, then the so-called Williams hypothesis (Williams, 1957) holds. According to this hypothesis, only those species that have a priori low extrinsic mortality are expected to adopt a slow life-history (Abrams, 1993; André & Rousset, 2020; Day and Abrams, 2020). This confirms the intuition we already mentioned in the context of flight: escaping predators (with whatever means) may allow one to reap the benefits of old age, but only if one also has a robust enough body to live up to that age, which is assumed to be more readily achieved through slower life-histories (higher somatic self-maintenance and less reproductive effort). However, if increasing density also (or only) increases adult mortality, the patterns can vary depending on who exactly is at risk to die (Abrams, 1993; André & Rousset, 2020).

3.2. Plastic responses to density regulation

Can individuals be expected to respond adaptively to perceived harshness of the current environment (via an appropriate cue), and if they do so, will the life history adjustments align with those predicted to evolve between isolated populations in different environments? Discussions above provide reasons why the ecological history of a lineage should matter in answering that question (Houston & McNamara, 1992). However, contrary to models for fixed traits evolution, existing models of optimal reaction norms have rarely investigated the role of extrinsic mortality and resulting density effects on individual vital rates. One notable exception is Marty et al. (2011), who modelled the evolution of a reaction norm for the age and size at maturity. The model assumes that individuals disperse at birth to different habitats, which may differ in the conditions they offer for growth (here, of individual bodies rather than population growth), but better habitats may also be riskier to live in. In case of mild positive covariation between mortality and (individual bodies') growth rates, the authors recover the prediction of a negative reaction norm slope between size and age at maturity (as in our Fig. 1), but now with the additional insight that fish A (Fig. 1) is ‘fast’, in the sense of maturing at a young age, not only because it grew fast, but also because it lives in an environment where extrinsic mortality constrains lifespan more than in other habitats on offer for this species. However, this effect may be reversed either if the covariation is negative (such that habitats offering slow growth are safer), or if it remains positive but is much stronger (habitats offering slow growth are also very dangerous). Source-sink theory is again important: the more ‘hopeless' some habitats are, the less performance in them matters for the gene pool as a whole. As a whole, Marty et al. (2011) offer another set of examples for how the effect of environmental harshness can be reversed when considering optimal plastic strategies among individuals, from the expectation of a population evolving a single type of response to a specific environment (see also Baldini, 2015).

Model predictions may also become different if assuming that vital rates are dependent on density at a ‘global’ level (i.e. same population density effects experienced across habitats, as in Marty et al., 2011) or at a more local level (i.e. individuals experience habitat-specific density effects on vital rates). Wright, Bolstad, Araya-Ajoy, and Dingemanse (2018) suggest that, in conjunction with habitat harshness effects, the latter can give rise to adaptive plasticity in life-histories across habitats and consistent individual differences in how fast they live their lives. It would appear fruitful to derive connections between the type of density regulation and optimal reaction norms for other traits than that of age-size at maturity (Marty et al., 2011), including settings where some, but not all, offspring disperse to a different habitat than their natal one.

Should a mother living in a poor environment then equip her young to intense future competition, or not? The answer is likely to depend on the scale of competition and the frequency of dispersal. It seems reasonable to assume that certain aspects of competition occur locally, individuals presumably causing only local depletion of important resources. However, some resources, such as mates, are sometimes fought over at a more global scale. One end of the scale is so-called soft selection (local density regulation), which assumes that each locality offers the same reproductive output regardless of the absolute quality of its inhabitants (Débarre & Gandon, 2011). This option does not penalize individuals for being poor competitors on a global setting; it is sufficient to beat the most local competitors. Hard selection operates under opposite assumptions: all local sites combine at the competition stage to produce a population of competitors, and poorer localities might not achieve any representation in the future gene pool, unless they invest in as good competitors as they can afford, even if this means sacrificing the number of competitors produced and/or the lifespan of the parents. Intriguing as this idea is, not much work has been done in this area. Sasaki & de Jong, 1999 and de Jong & Behera, 2002 touch on some of the ideas, but their populations evolve with discrete generations in a context of local adaptation when there is stabilizing viability selection on a trait with locally varying phenotypic optima. This captures some of the above ideas in terms of differences in productivity across patches but does not directly comment on fast vs. slow life histories (lifespans do not vary when generations are discrete).

4. Do we expect fitness maximization in the first place?

The arguments thus far discussed have been based on selection being able to create an adaptive solution to a problem (of trade-offs, of cue inaccuracy, etc.). A reminder is in place that less than ideal cues for environmental conditions, unpredictable future circumstances, or gene flow from sources to sinks are not the only reason to expect less than ideal performance. Selection also works inefficiently (relative to drift) if effective population sizes are small, but perhaps more strikingly, there are many situations that have nothing to do with drift where evolution, due to conflict between entities, produces something that appears quite incongruous when viewed from the outside. One possible conflict occurs between the sexes (Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008). In an elegant experiment on *Callosobruchus* beetles, it proved rather easy to select for longer (and shorter) lifespan in male beetles. For males, it was detrimental to belong to a selection line where lifespans had evolved upwards, but the opposite was true for female fitness (Berg & Maklakov, 2012). Such genetic antagonism highlights that the two sexes may not achieve their ideal lifespan simply because they acquire their genomes by tapping into the same gene pool. This phenomenon is called intralocus conflict, to describe situations where the value of a phenotypic trait coded for by one locus has different fitness consequences when expressed in different entities (e.g. between sexes). Intralocus conflict is to be distinguished from interlocus conflict, where the conflict occurs over the result of an interaction among entities (e.g. sexes) expressing different traits, presumably coded for by different loci – e.g. male behaviours that harm females, and the female counter-adaptations to them.

In principle, one might expect selection to work on resolving intralocus conflict, so that sexes evolve to express different optima, becoming dimorphic despite sharing a genome. Viewed this way, intralocus conflict is nothing more than the two sexes attempting to solve a sex-specific trade-off problem, and sex-specific expression of genes should do the trick. In reality, however, this can take substantial amounts of time: in *Drosophila*, which can fit tens of generations into a year, there is evidence of genomic constraints preventing resolving this problem for a million years (Ruzicka et al., 2019) — which for flies is many more generations than humans, as *H. sapiens*, have existed.

Indirect evidence for the importance of similar effects in humans is given by the relationship of height on the number of offspring produced when siblings differ in height but also sex (Stulp, Kuijper, Buunk, Pollet, & Verhulst, 2012). Men from shorter sibling pairs have on average fewer children than their sisters, or than other men from taller sibling pairs. The opposite was true for women, suggesting sexually antagonistic selection on genes coding for height in humans. More direct evidence, using a quantitative genetics approach, have shown similar patterns in other groups of modern humans: directional selection was found to favour shorter women, contrary to men who were found to be under stabilizing selection for height (Stearns, Govindaraju, Ewbank, &

Byars, 2012), and at a genomic level, accumulation of allele frequency differences between the sexes on the X chromosome also support the idea of sexually antagonistic selection in humans (Lucotte, Laurent, Heyer, Segurel, & Toupance, 2016).

Recently, it has been argued that a mechanistic understanding of the regulation of growth (specifically the role of estrogen in stopping female bone growth in humans) argues against sexual selection on males to be tall as a potential explanation for human size dimorphism (Dunsworth, 2020). However, estrogen-dependency as a mechanism in no way invalidates a scenario of intralocus conflict where selection favours a larger trait value in males than in females (for any reason, including sexual selection on males). Consider, at any point in an evolutionary lineage, selection acting on males to be tall. This comes with a clear danger that female offspring, now inheriting genes for being tall, are becoming maladapted, perhaps by growing faster and being more resource-hungry compared with the ideal life history. If a mechanism is available that allows females to not follow the male folly of becoming tall (more scientifically put: to avoid expressing phenotypes above the female optimum), then it is entirely logical that estrogen-dependency is put to work in this role, with the end result being height dimorphism that can only be understood by considering selection on both sexes.

Conflict does not necessarily have to be wholly unresolved or wholly resolved. Turning to age at maturity again, intralocus conflict has intriguing consequences for salmon life histories, as there is evidence for a partially resolved conflict because of sex-specific dominance. There is a single locus that is a major determinant of the age at which a salmon migrates back to its river after some time spent growing in the sea (Czorlich, Aykanat, Erkinaro, Orell, & Primmer, 2018). Females spend longer in the sea than males. If both alleles at this locus are ‘early’ or both are ‘late’, the maturation time is pulled in the corresponding direction in both sexes (from the sex-specific average), but heterozygote fish mature late if they are females, and early if they are males. Since fecundity depends very strongly on body size in female fish, it is tempting to conclude that it is more important for female fish to stay longer in the sea.

As already alluded to above, conflict can also occur in interactions between individuals and take more directly observable, behavioural forms (i.e. interlocus conflict). It now ceases to be a requirement that two individuals are influenced by the same genetic variants for their evolved traits to impact each other's fitness. Many organisms (humans included) live in groups, and selection generally does not act on the survival or ‘fitness’ of the entire group. If there is something to be gained by exploiting others, conflict can lead to inefficient resource use, much energy spent in fights (even causing deaths of conspecifics, e.g. Cook, Bean, & Power, 1999, Elias, Botero, Andrade, Mason, & Kasumovic, 2010), and wasteful signalling, all examples of traits that can make perfect sense but only once one realizes that population-wide growth rate is not necessarily maximized when the population exists in a state of tension between cooperation and conflict.

Wastefulness is perfectly exemplified by egg-tossing behaviour in Guira cuckoos. Multiple joint-nesting females lay eggs into a nest, remove each other's eggs in a quest to have more than the fair share of the total ‘cake’ at stake, and numerous eggs are produced and killed before the situation calms down and incubation finally begins; only 26% of eggs laid develop into fledglings (Macedo, 1992). In insects, fascinating levels of conflict impacting lifespans of adults can be shown experimentally: Interacting with males may lead to faster life histories in females (Córdoba-Aguilar, 2009; Macke et al., 2012), and there is remarkable experimental evidence that males that are selected for ‘late’ reproduction appear able to manipulate females to age more slowly than females who interact with ‘early’ males. In guppies, females prefer areas of high predation risk as a means to avoid harassment by males (Croft et al., 2006). There are not many models of conflict as a driver of human life history traits (unless one counts warfare as a life history trait, Bowles, 2009), but female competition for local resources has been argued to select for menopause (Cant & Johnstone, 2008).

5. Conclusion: what about humans?

We have above reviewed factors which we believe to be important to account for when studying variation in life histories within (and across) populations. These include: (i) the ease of information acquisition that is relevant for plastic changes, as well as the spatiotemporal reliability of cues, (ii) individuals potentially moving between ‘sources’ and ‘sinks’, which may refer either to circumstances (e.g. habitats, social groups) they live in, or to their own bodies as a result of ageing, (iii) the shape and nature of density regulation, especially with regard to their local or global effects on vital rates and (iv) intra- or interlocus conflicts and the consequent prediction that evolution can fail, if one thought its goal is fitness maximization. We now call for a better integration of those factors in theoretical and empirical studies of human life histories.

There is a priori no reason to think of human ecology as fundamentally different from that of related, or even somewhat more distant, taxa (despite clear evidence of the sets of literature discussing humans and non-humans having become disconnected over time, Nettle & Frankenhuis, 2019, 2020). Many factors listed above might therefore play a significant role in the evolution of human reaction norms. Humans, however, possess also certain peculiar traits: menopause and a long female post-reproductive lifespan, for instance, is a trait that we share with only a handful other mammal species (Ellis et al., 2018), and there are also opportunities to investigate formally how the more or less unique features of humans impact life-history evolution.

Humans live long lives relative to other great apes, increasing the opportunity for individuals to experience changing environmental conditions (Nettle et al., 2013), especially if ongoing cultural evolution keeps ‘changing the rules’. General models would then predict lifelong plasticity (Ratikainen & Kokko, 2019). Even so, most of phenotypic plasticity seems to occur early in development in humans and other mammals, with early life conditions having been repeatedly shown to affect individual life histories (Ellis, Figueredo, Brumbach, & Schlomer, 2009; Ronget et al., 2017) — to the extent that a recent model of learning, a clearly important way to achieve plasticity in human traits, took this style of age-dependency as given (Deffner & McElreath, 2020). It would be intriguing to link ‘sensitive window’ models with other factors we have above discussed in the context of reaction norms: for example, do we expect longer windows for those who disperse? Note that this question can be expressed in a sex-dependent manner, since human populations show variation between matrilocal and patrilocal systems, thus dispersal is often sex-biased but the direction of the bias varies (Bolnick, Bolnick, & Smith, 2006; Hamilton, Stoneking, & Excoffier, 2005).

Or, can one find significant enough spatiotemporal variation to interpret patterns in a source-sink manner? At the extreme, this would remove all expectations of plasticity due to ‘optimism’ sensu McNamara et al. (2011): ‘even if the current situation is bad, behave as if it was not, since this is the best choice should conditions prove good again, while if they do not, all is lost anyway’. An important line of work in human biology has focused on so-called predictive adaptive responses – defined as adaptive phenotypic changes occurring early in development but with fitness consequences only later in life, usually after puberty – to cues of environmental harshness (Ellis, Figueredo, Brumbach, & Schlomer, 2009; Gluckman, Hanson, & Spencer, 2005). If an individual develops differentially upon receiving such a cue, this effectively means absence of ‘optimism’, perhaps because differences between situations (socially driven, or habitat-dependent) are not, after all, so stark to qualify as a source-sink structure. We remind the reader of Fischer et al. (2011)'s result: modest within-population differences in prospects are best for plasticity.

It is also remarkable how little density regulation of human ecology appears to be discussed in life-history theory applications for this species (but see Baldini, 2015; Bauch, 2008; Deffner & McElreath, 2020; Sng, Neuberg, Varnum, & Kendrick, 2017). Does the rapid human population growth (since the expansion out of Africa) qualify as 'exponential' sufficiently well to mean that density-independent models apply to the human species better than they do to many other mammals? Recent papers discussing life history measures (Baldini, 2015) and individual vs. social learning (Deffner & McElreath, 2020) in a human context both refrain from stating what density dependence patterns best fit the data in our species. Since theory requires one to state age-dependencies too, the question is not an easy one. For example, high infant mortality does not per se say anything about who suffers most (in terms of survival) if the local food supply runs out. In a human population, the physiological (and likely adaptive) response to a famine involves amenorrhea, and should the famine be caused by locally depleted food supply due to density dependence, then one has shifted from exponential growth to fecundity regulation. (Note that we can also imagine many other causes – e.g. wars can lead to famine, but wars are not an automatic outcome of high population density). Simultaneously, food shortage could also selectively remove individuals belonging to frail age classes, either the very young or the very old. Then, again, human life history traits are rather complicated due to menopause (a relatively unique mammalian trait, Field & Bonsall, 2017), and the exact age at death, if long into the post-reproductive period, might matter less than in a mammal where all age classes from maturity onwards participate actively in reproduction (despite grandmother effects, Sear & Mace, 2008).

Still, the question of density regulation during historic, prehistoric and evolutionary times is a highly interesting one, not least because here our species is rather unique. Our population growth and the associated life history responses (e.g. Pelletier et al., 2017) have also cooccurred with range expansions, which can impact not only life history traits (Phillips, Brown, & Shine, 2010) but also neutral genetic variation (gene surfing, Excoffier, Foll, & Petit, 2009). It is also a fiendishly difficult question, since the relationship between wealth and reproductive success flips in women as a population undergoes the demographic transition (Colleran, Jasienska, Nenko, Galbarczyk, & Mace, 2015). Ours is a species where interactions between different processes create a perhaps above-average difficult tangle of causalities to understand with intuition only. Some disentangling is now needed, with help from previous insights and formal modelling.

Acknowledgments

We thank Daniel Nettle and Willem Frankenhuis for inviting us to participate to this special issue, Pau Carazo for discussions, and 3 anonymous reviewers for their constructive comments on earlier versions of this manuscript. Funding was provided by the Swiss National Science Foundation.

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