



Long-term effects of early nutrition and environmental matching on developmental and personality traits in zebra finches



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Developmental plasticity is a key feature of many organisms and individuals can benefit from early programming to optimize their phenotypes for the expected environmental conditions. However, environmental conditions may sometimes change unexpectedly. Mismatches between early and adult life, for example, can have important repercussions for adult phenotypes, potentially leading to better performance under matched than mismatched conditions as predicted by the predictive adaptive response hypothesis. We conducted a long-term experimental manipulation of dietary conditions in a population of zebra finches, *Taeniopygia guttata*. Broods were exposed to two early nutritional treatments until independence and we used a split-brood design to independently manipulate nutritional conditions after independence to create matched and mismatched nutritional environments in later life. Developmental trajectories of all individuals were followed for more than 5 years and we scored behavioural responses in trials in a special environment and while interacting with a special object three times during adult life. Overall, we found no evidence for early programming affecting morphology. Tarsus and wing length were exclusively influenced by the early nutrition. Body weight showed lasting effects of the early treatment and independent effects of nutritional condition during adulthood, but no effects of environmental matching or mismatching. Special-object trials showed effects of the adult nutritional treatment while environmental matching affected hopping activity in special environments. These behavioural responses showed substantial long-term individual stability over a 3-month period and were only marginally smaller when measured over a period of more than 4 years. Interestingly, survival of individuals from low-quality early nutritional condition was higher compared with high-quality early condition individuals, which became evident only after years of survival monitoring. Beyond the nutritional treatment itself, we found sizable brood identity effects that slowly but steadily declined with age, indicating a significant but decaying effect of natural variation in parental provisioning on adult phenotypes.

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Phenotypic plasticity, the ability to modify the phenotype in response to environmental conditions, is a key feature of many organisms and an important component of phenotypic evolution (Bateson & Gluckman, 2011; West-Eberhard, 2003). Depending on whether phenotypic changes are reversible within an individual's lifetime, phenotypic plasticity can be categorized into reversible phenotypic flexibility or irreversible developmental plasticity (Piersma & Drent, 2003; West-Eberhard, 2003). While unlimited

phenotypic flexibility seems ideal for optimizing phenotypes, there are often costs or constraints that limit the ability to change phenotypes reversibly (Piersma & Drent, 2003; West-Eberhard, 2003). This can make developmental plasticity more efficient for producing optimal phenotypes when the environment during early life is a sufficiently good predictor for conditions experienced later in life (Hanson & Gluckman, 2014). Individuals can thus be primed by the early environment and adjust their phenotypes adaptively. Such developmental priming may have adverse effects, however, if environmental conditions change unexpectedly (Monaghan, 2008). A key question is therefore when, how and why phenotypes are susceptible to early priming (DeWitt, Sih, & Wilson, 1998).

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A critical period for environmental priming is the growth phase during early ontogeny (Holveck & Riebel, 2009; Lindström, 1999; Naguib, Nemitz, & Gil, 2006), because important developmental decisions are made at this life stage. In species with determinate growth, this includes the size of the body and the relative proportions of its different components (Buchanan, Leitner, Spencer, Goldsmith, & Catchpole, 2004). Individuals may respond to poor initial conditions with compensatory growth, but compensation itself may invoke costs and trade-offs affecting other traits (Metcalf & Monaghan, 2001), for example in physiology and metabolism (Crisuolo, Monaghan, Nasir, & Metcalfe, 2008). Ultimately, behaviour can also be permanently influenced by the early environment. Developmental plasticity can thereby contribute to the emergence of stable individual differences in behaviour ('animal personality') that have their own downstream consequences for individual performance (Réale, Reader, Sol, McDougall, & Dingemanse, 2007).

Early nutritional conditions may match or mismatch nutritional conditions during later life due to environmental changes and/or dispersal to environments varying spatially or temporally. The predictive adaptive response (PAR) hypothesis predicts that developmental trajectories are adaptively optimized to exploit the predictability of environmental conditions (e.g. Gluckman, Hanson, & Spencer, 2005; Hanson & Gluckman, 2014). Unexpected changes, however, might then have pathological consequences, in extreme cases leading to poor performance under apparently favourable adult conditions (Monaghan, 2008). A notable example of an apparently failed predictive adaptive response is type II diabetes and the metabolic syndrome in humans, which have a particularly high prevalence in cohorts of people that have experienced poor early conditions followed by substantially improved conditions later in life (e.g. Fall, 2001; Ravelli et al., 1998). It has been hypothesized that organisms that were metabolically primed to poor nutritional conditions develop a 'thrifty phenotype' that only performs well if nutritional conditions remain poor, but becomes pathological if conditions are better than anticipated (Hales & Barker, 1992, 2001). An environmental mismatch between early and late environmental conditions therefore exposes the putative predictive adaptive response.

Unfortunately, long-term studies under experimentally matched and mismatched juvenile and adult environments are largely lacking for vertebrates (Bertram & Hanson, 2001). We hence experimentally addressed this issue by testing the effects of the early and late environment for individual phenotypes over more than 5 years in an avian model species, the zebra finch, *Taeniopygia guttata*. By experimental dietary manipulation, we created matches and mismatches between early and late environmental conditions with a switch at nutritional independence from parental provisioning. We manipulated early dietary conditions at the brood level and subsequently used a split-brood design when manipulating nutritional conditions for the entire life span after independence from parental care. We focused on a skeletal trait (tarsus length) that is largely determined during early life and is linked to fitness in the zebra finch (e.g. Bolund, Schielzeth, & Forstmeier, 2011), as well as on wing length, body weight and exploratory behaviour, which can respond plastically throughout life, to a certain extent, and which are all also fitness relevant (e.g. Carere, Drent, Koolhaas, & Groothuis, 2005; van Oers, Drent, de Jong, & van Noordwijk, 2004; Stamps & Groothuis, 2010; Tinbergen & Boerlijst, 1990). Our analysis is based on more than 5 years of data collection.

Zebra finches are distributed over most of the Australian continent across different climate zones (Zann, 1996), without evidence for significant genetic population structure (Balakrishnan & Edwards, 2009). In some areas, they are exposed to seasonal changes (Zann & Straw, 1984), while in others environmental

changes are highly variable (e.g. Morton & Davies, 1983). Although both the frequency and amplitude of the variability in relation to individual life span is imperfectly known, we believe that zebra finches are a suitable study system, because they naturally live under highly variable environmental conditions (Immelmann, 1965; Zann, 1996). We used a captive population of zebra finches that is comparatively little affected by domestication and has, until recently, been indistinguishable from native wild zebra finches in Australia with a panel of microsatellites (Forstmeier, Segelbacher, Mueller, & Kempenaers, 2007). We hence expected less adaptation to ad libitum food conditions in aviaries than in most domesticated populations which have lived in captivity for many decades (Tschirren, Rutstein, Postma, Mariette, & Griffith, 2009).

Zebra finches have been used to study long-term effects of early rearing conditions, but so far studies have either addressed (mis) matches between the nestling and fledging phase (Crisuolo et al., 2008; Honarmand, Goymann, & Naguib, 2010; Krause, Honarmand, Wetzel, & Naguib, 2009), or between the juvenile phase (nestling and fledgling phase) and the second month of life (immature phase) (Kriengwatana et al., 2014). No study has yet upheld the nutritional manipulation throughout the entire lifetime and it is therefore impossible to address long-term effects of developmental (mis)priming. Our study aimed to experimentally fill this gap and test for the relative importance of early conditions and the magnitude of (mis)matching effects on morphology and behaviour. Specifically, we tested for effects on tarsus length, wing length, body weight and body condition, latency to feed and hopping activity in a special-environment and in special-object trials, weight loss under mild stress and life span.

We predicted that structural body size would be largely shaped by the early environment; hence individuals under good nutritional conditions should attain larger sizes. Wing length, however, may be more phenotypically flexible and individuals may be able to compensate for a bad start during subsequent moults. Thus, for wing length, it seems possible that effects of a favourable environment early or late in life are complementary but not additive (Scharf, Braf, Ifrach, Rosenstein, & Subach, 2015), giving rise to a case where only individuals under low early and low late nutrition grow shorter wings. We expected body weight and condition to be most flexible and most prone to a predictive adaptive response with individuals under matched conditions reaching highest condition. Furthermore, we tested the extent to which both the early and current environment, as well as their interaction, affect traits of an animal personality phenotype. We predicted individuals in poor conditions to take greater risks in a mildly stressful situation and to lose most weight when exposed to food deprivation. Finally, we expected, based on the predictive adaptive response hypothesis, that individuals in matched environments would be longest lived.

METHODS

Subjects and Housing

We used zebra finches of wild Australian origin that have been bred at Bielefeld University for about 10–11 generations (referred to as 'Bielefeld-AUS' in Forstmeier et al., 2007). Pairs were randomly formed in 2010, ensuring that partners were unrelated to at least the grandparent level, and were allowed to breed in cages (83 × 30 cm and 40 cm high) equipped with wooden nestboxes (15 × 15 cm and 15 cm high). Coconut fibres and hay were provided as nesting material. During pair formation and incubation, all pairs received a high-quality diet as described below.

First broods were alternately assigned to either early high-quality or early low-quality nutritional treatments (see below). Pairs were allowed to rear second broods that were raised under

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