



Dietary carotenoid supplementation improves the escape performance of the southern corroboree frog



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Nutritional conditions experienced by an individual are known to affect phenotype and performance. In particular, dietary carotenoids influence vertebrate immune function, vision and coloration and have recently been suggested to enhance exercise performance. Despite growing interest in investigating the effect of dietary carotenoids on exercise performance, studies to date have been limited to short-term supplementation during a single life stage. The present study elucidates, for the first time, the effect of long-term carotenoid supplementation during both developmental and adult life stages on the aquatic and terrestrial escape performance of adult southern corroboree frogs, *Pseudophryne corroboree*, testing the predictions of the ‘environmental matching’ and the ‘silver spoon’ hypotheses. Individuals ($N = 24$ per treatment) were exposed to one of four dietary treatments: (1) both developmental and adult life stages were fed a carotenoid-supplemented diet (C–C); (2) developmental life stage, but not adult life stage, was fed a carotenoid-supplemented diet (C–U); (3) adult life stage, but not developmental life stage, was fed a carotenoid-supplemented diet (U–C); (4) both developmental and adult life stages were fed an unsupplemented diet (U–U). There was no effect of dietary carotenoids on swimming speed, hopping speed or righting ability. However, our results do indicate an effect of carotenoid supplementation on both swimming distance and hopping distance. Frogs receiving a carotenoid-supplemented diet during both developmental and adult life stages consistently outperformed other dietary treatments in the distance travelled during aquatic and terrestrial escape trials. Our results do not show support for either the silver spoon or the environmental matching hypothesis, but indicate an overall benefit of exposure to a carotenoid-rich environment across both life stages.

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Environmental conditions experienced by an individual during development can have a lasting impact on adult phenotype and organismal performance, which, in turn, directly affect Darwinian fitness (Butler & McGraw, 2012; Hopwood, Moore, & Royle, 2014; Monaghan, 2008). In particular, nutritional constraints experienced during early development are known to have long-lasting effects on adult phenotype, including morphological, physiological and behavioural traits (e.g. Butler & McGraw, 2012; Goyret, Kelber, Pfaff, & Raguso, 2009; Hopwood et al., 2014; Walker, Stevens, Karadaş, Kilner, & Ewen, 2013). Such examples of developmental plasticity driven by altered developmental environments are widespread. However, what remains poorly understood is how variation in the nutritional conditions experienced during both the developmental and adult life stages interact to influence adult

phenotype and performance (Butler & McGraw, 2012; Dmitriew & Rowe, 2011; Hopwood et al., 2014; Monaghan, 2008).

A number of competing hypotheses exist to describe the way in which developmental and adult environments might interact to affect fitness (reviewed by Monaghan, 2008). However, only two of these hypotheses are commonly recognized in the scientific literature and have been tested empirically. First, the ‘silver spoon’ hypothesis predicts that individuals exposed to superior conditions during development will have a fitness advantage over individuals experiencing poor developmental conditions, irrespective of the quality of their adult environment (Monaghan, 2008). It is argued that individuals experiencing inferior developmental conditions are at a permanent disadvantage due to the developmental constraints imposed by resource limitation (Monaghan, 2008). Second, the ‘environmental matching’ hypothesis predicts that fitness will be highest in individuals in which the adult environment ‘matches’ conditions experienced throughout development. Here, it is predicted that phenotypic traits developed under poor conditions

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become maladaptive in a resource-rich environment through a process of developmental programming (Monaghan, 2008).

Numerous studies have tested these hypotheses in a range of animal models, with the majority of studies focusing on the effects of altered food availability on aspects of reproductive performance (i.e. reproductive rate, offspring number and sexually selected ornamentation; see Barrett, Hunt, Moore, & Moore, 2009; Butler & McGraw, 2012; Descamps, Boutin, Berteaux, McAdam, & Gaillard, 2008; Dmitriew & Rowe, 2011; Taborsky, 2006; Van De Pol, Bruinzeel, Heg, Van Der Jeugd, & Verhulst, 2006; Walker et al., 2013). To date, very little attention has been given to investigating the effects of altered developmental and adult nutrition on behavioural traits (but see Goyret et al., 2009; Hopwood et al., 2014; Raguso, Ojeda-Avila, Desai, Jurkiewicz, & Woods, 2007). A study by Raguso et al. (2007) reported an effect of a carotenoid-enriched larval diet on the time adults spent engaged in feeding and escape behaviour in the tobacco hornworm moth, *Manduca sexta*. The study argued that exposure to dietary carotenoids during the developmental life stage is essential for the production of visual pigments in this species and that differences in feeding behaviour were therefore a direct result of differences in visual sensitivity.

Dietary carotenoids (e.g. β -carotene, lutein and astaxanthin) are known for their ability to influence vertebrate immune function, vision and coloration (reviewed, respectively, by Chew & Park, 2004; Svensson & Wong, 2011; von Lintig, Kiser, Golczak, & Palczewski, 2010). In addition, the effects of short-term supplementation of dietary carotenoids on exercise performance have recently come into focus (Aoi et al., 2003; Blount & Matheson, 2006; Polotow et al., 2014). Carotenoids exhibit an efficient biological antioxidant activity, scavenging exercise-induced reactive oxygen species and limiting oxidative stress, which may play a role in preserving contractile muscle function (Powers, Deruisseau, Quindry, & Hamilton, 2004). The supplementation of carotenoids has been shown to attenuate muscle damage (Aoi et al., 2003), increase the time taken to exhaustion during acute exercise (Ikeuchi, Koyama, Takahashi, & Yazawa, 2006; Polotow et al., 2014) and enhance take-off performance (Blount & Matheson, 2006). Currently, studies quantifying the effects of dietary carotenoid availability on exercise performance have been limited to short-term supplementation (<60 days) at a single life stage (e.g. Aoi et al., 2003; Blount, Metcalfe, Arnold, Surai, & Monaghan, 2006; Ikeuchi et al., 2006; Polotow et al., 2014). The effect of carotenoid availability during both developmental and adult life stages on exercise performance remains to be tested.

Here, we investigated how nutritional conditions experienced during different life stages affect escape performance in adult southern corroboree frogs, *Pseudophryne corroboree*. We manipulated dietary carotenoid availability during development and adulthood and quantified swimming performance, terrestrial escape performance and the ability of frogs to right themselves after being displaced. We tested the silver spoon and environmental matching hypotheses simultaneously for all variables.

METHODS

Study Species

Pseudophryne corroboree is a small (29–33 mm, snout–vent length) stout-bodied toadlet (family: Myobatrachidae) restricted to areas above 1200 m elevation within Kosciuszko National Park in the Snowy Mountains region of New South Wales (Anstis, 2013). The species is characterized by sexually monomorphic bright yellow and black stripes running longitudinally along the dorsal surface (Colefax, 1956). The adaptive significance of this coloration remains unknown, but it is believed to function as an aposematic

signal to visual predators, because the skin of both sexes contains poisonous lipophilic alkaloids (pumiliotoxins and pseudophrynamines; Daly, Spande, & Garraffo, 2005). Locomotion in *P. corroboree* is characteristic of the genus *Pseudophryne*, with the predominate mode of locomotion being a slow to rapid crawl (Colefax, 1956). If *P. corroboree* are disturbed suddenly, they will hop short distances (<15 cm), and swim readily if submerged in water (Colefax, 1956).

Study Animals

Fertilized *P. corroboree* eggs were obtained from a captive colony maintained at Melbourne Zoo, Australia. Eggs were generated from matings between six males and 12 females, resulting in 15–28 discrete male–female pairings depending on whether females partitioned clutches (sequential polyandry). Eggs were held communally surrounded by moist sphagnum moss, *Sphagnum cristatum*, in a plastic container (12 × 17.5 cm and 7 cm high). Embryonic development was suspended for approximately 3 months, by maintaining eggs in a constant-temperature room set to 5 °C. On 19 July 2013, eggs were transported to the University of Wollongong, where they were stimulated to hatch by flooding them with reverse-osmosis (RO) water. On the day of hatching, tadpoles were transferred to individual experimental containers and were fed a basal diet of ground fish flake (75:25 mixture of Sera Flora/Sera Sans; SERA, Heinsberg, Germany) ad libitum thrice weekly until the start of the experiment. Tadpoles were randomly allocated to dietary treatments 12–18 days posthatching and experimental procedures commenced immediately.

Experimental Design

Anuran amphibians provide an ideal model system for investigating the influence of dietary conditions at different life stages on escape performance, owing to their biphasic life cycle, which provides a clear distinction between free-living developmental (tadpole) and adult (postmetamorphic) life stages. To test the influence of dietary carotenoid availability at different life stages on the escape performance of *P. corroboree*, individuals ($N = 24$ per treatment) were randomly assigned to one of four dietary treatments: (1) both developmental and adult life stages were fed a carotenoid-supplemented diet (C–C); (2) developmental life stage, but not adult life stage, was fed a carotenoid-supplemented diet (C–U); (3) adult life stage, but not developmental life stage, was fed a carotenoid-supplemented diet (U–C); (4) both developmental and adult life stages were fed an unsupplemented diet (U–U) (Fig. 1). A summary of the composition of experimental diets is provided in Table 1 and a detailed carotenoid profile is provided in the Appendix (Table A1).

Developmental husbandry and nutrition

Throughout development, tadpoles were housed in individual plastic containers (10 cm diameter and 10.5 cm high) filled with 600 ml of RO water. Thrice weekly all containers received a partial water change (ca. 50% volume) using an automated irrigation system (Aqua Systems, Melbourne, VIC Australia) connected to an RO water system (Sartorius Stedim Biotech, Göttingen, Germany). Excess food and faeces were siphoned from each container once a week using a 30 ml plastic syringe connected to a 15 cm length of aquarium tubing (3 mm, inner diameter). Frogs were held in an artificially illuminated constant-temperature room maintained at 12 °C on an 11.5:12.5 h light:dark cycle, including a 15 min twilight (dim lighting) phase at both dawn and dusk. In addition to overhead room lighting, UV–B light was provided for 1 h/day using fluorescent strip bulbs (Reptisun 10.0 UVB 36" bulb; Pet Pacific,

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