

Conspicuous and cryptic morphs of a polytypic poison frog differ in reproductive output because of differences in tadpole performance, not parental effort

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Predation risk can drive life-history evolution in prey, with high adult mortality favouring the prioritization of current over future reproduction. Populations that evolve or adopt different or differently effective strategies to avoid predation, then, should evolve different life-history strategies. We compared reproductive output, under identical captive breeding conditions, of three allopatric morphs of polytypic poison frog (*Oophaga pumilio*) that likely experience different predation risk. We predicted that pairs of a well-defended (conspicuous and highly toxic) morph would prioritize future reproduction, and thus reproduce less often than a poorly defended (cryptic and less toxic) morph, while a cryptic but highly toxic lineage would be intermediate. These predictions were generally met: the conspicuous, toxic morph produced fewer juveniles than the cryptic morphs. However, the results of cross-fostering tadpoles among morphs suggested that these differences arose not from the quality of care parents provided, as predicted by life-history theory, but rather from differences expressed in tadpoles. Moreover, all cross-fostered tadpoles were less successful than tadpoles reared by their own parents, perhaps suggesting that parents discriminate against unrelated tadpoles or that parental care and offspring solicitation behaviours have diverged among populations. These results suggest opportunities for comparative studies exploring the entire complexity of the selective landscapes experienced by these polytypic frogs.

KEY WORDS: cross-fostering, Dendrobatidae, egg feeding, life history, parental care.

INTRODUCTION

Predators can drive the evolution of life-history strategies (Reznick et al. 1990; Keller & Genoud 1997; Candolin 1998; Ghalambor & Martin 2000). When predation on adults is relatively high, adult residual reproductive value is relatively low, and individuals should be selected to prioritize current over future reproduction (Williams 1966;

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Stearns 1992; Williams et al. 2006). This prediction has been tested, and largely supported, by comparing the life histories of prey in predator-present and predator-absent environments, or along a gradient of predator density (e.g., Reznick et al. 1990; Keller & Genoud 1997; Candolin 1998; Ghalambor & Martin 2000). For prey, however, the risk of encountering and falling victim to a predator is not determined solely by predator density. Rather, this risk is shaped by complex interactions among the predator(s), the environment, and the behaviour, physiology and morphology of the prey. Prey responses might evolve, be expressed plastically, or be behaviourally modulated (Lima & Dill 1990; Langerhans 2007). While convergent responses to predators are common (e.g., armour evolution: Reimchen & Nosil 2004), all populations or species will not necessarily respond to predation threats in the same way or as effectively (e.g., Candolin 1998; Herczeg et al. 2009). Even populations of the same species that occupy similar habitats with similar predators might adopt different antipredator strategies and thus face different predation risk and different life-history pressures.

One taxonomically widespread way prey reduce their probability of predator-induced mortality is via chemical defence, a strategy often paired with conspicuous, memorable warning colouration and/or behavioural displays (Ruxton et al. 2004). Such aposematic signals reduce the probability that an individual will be attacked, lowering the costs associated with otherwise risky behaviours like foraging and sexual display (Lima & Dill 1990; Ruxton et al. 2004; Pröhl & Ostrowski 2011). The evolution of aposematism then, results not just in a reduction in predator attacks, but in a change in the relative importance of extrinsic mortality as a selective force, a transition with widespread life-history implications (Williams 1966; Stearns 1992; Williams et al. 2006). Poison frogs (Dendrobatidae) are well-suited for studying the consequences of toxicity, warning signals and the protection they offer. These active, diurnal frogs vary extensively in toxicity, colouration and predation risk (Saporito et al. 2006, 2007, 2012; Rudh et al. 2007; Maan & Cummings 2012; Hegna et al. 2013), with numerous transitions between aposematism and crypsis. Elaborate post-zygotic care is also common in this group (Wells 1977; Beck 1998) and is costly to parents (Dugas et al. 2015), so parental investment patterns should be sensitive to changes in adult mortality and/or the costs of providing care (e.g., foraging, visiting offspring).

A striking example of phenotypic diversification occurs in and around the Bocas del Toro archipelago of Panama, where populations of the strawberry poison frog (*Oophaga pumilio*) display a diversity of colouration that far exceeds colour diversity in the rest of its range. While most populations display the ancestral phenotype of red with blue or black legs, genetically distinct populations in Bocas del Toro display colours spanning the visual spectrum (Siddiqi et al. 2004; Pröhl et al. 2007; Rudh et al. 2007; Brown et al. 2010). Visual modelling suggests that these lineages differ substantially in their conspicuousness to potential predators (Siddiqi et al. 2004; Rudh et al. 2007), and in toxin profiles (Saporito et al. 2006) and toxicity (Maan & Cummings 2012). While few predation studies have been conducted in and around this archipelago, this work is consistent with the assumption that conspicuous red colouration offers protection from predator attack (Hegna et al. 2013). Furthermore, behavioural comparisons among differently coloured lineages suggest that conspicuous populations engage in more risky behaviours, as would be expected if they are better protected against predator attack (Pröhl & Ostrowski 2011; Rudh et al. 2011, 2013; Willink et al. 2013).

To test the prediction that predation risk, along with its behavioural correlates, is associated with life-history strategies, we compared the reproduction of three Bocas del



Fig. 1. — Bocas del Toro *Oophaga pumilio* lineages used in this study, presented in order of the protection against predators conferred by colouration and toxicity. From left to right and most to least protected: Isla Bastimentos (red), Aguacate Peninsula (blue), Isla Popa (green).

Toro *O. pumilio* morphs (Fig. 1) held under identical conditions in captivity. We chose these morphs based on characterizations of visual conspicuousness and chemical defence in the literature. Red frogs from Isla Bastimentos (Tranquilo Bay) are among the most conspicuous and most chemically defended of all *O. pumilio* morphs, while green frogs from Isla Popa are among the least conspicuous and least toxic morphs, and have been classified as ‘cryptic’ using visual modelling exercises (Siddiqi et al. 2004; Saporito et al. 2006; Rudh et al. 2007; Maan & Cummings 2012). Blue frogs from the Aguacate Peninsula have also been classified as cryptic, but are among the most toxic morphs (Siddiqi et al. 2004; Rudh et al. 2007; Brown et al. 2010; Maan & Cummings 2012). Because well-protected morphs should prioritize future reproduction, we predicted that reproductive rate during the study period would be negatively associated with conspicuous colouration and toxicity. Specifically, we predicted that Popa pairs would produce the most offspring in captivity, followed by Aguacate and then Bastimentos pairs. We also cross-fostered tadpoles among populations, allowing us to confirm that any among-lineage differences in reproductive rate truly arose from differences in parental investment.

METHODS

Study species

O. pumilio occurs, often at high density, in lowland forests and disturbed habitats (e.g., banana and cacao plantations) along the Caribbean side of Central America, from Nicaragua to Panama. This small, diurnal, terrestrial frog is territorial and polygamous (Pröhl & Hödl 1999). Following successful courtship, females lay a clutch of ~ 5 eggs in the leaf litter, and males tend the clutch, moistening developing eggs daily. Females transport newly hatched tadpoles to water-filled leaf axils, and then regularly provision developing tadpoles with unfertilized eggs (Weygoldt 1980; Brust 1993; Pröhl & Hödl 1999). During female visits, tadpoles stiffen their tails and vibrate rapidly, a behaviour hypothesized to be analogous to begging in other systems (Weygoldt 1980; Stynoski 2012). Presumably each step of reproduction could be subject to local selection, and thus diverge in isolated populations.

General methods

In February 2008, we captured wild individuals from three populations in the Bocas del Toro archipelago, Panama: (i) red frogs from Tranquilo Bay, Isla Bastimentos: 9°15'8.03"N,

82°8'43.30"W; (ii) green frogs from Punta Laurel, Isla Popa: 9°8'25.98"N, 82°7'39.11"W; and (iii) blue frogs from Shark Hole, Aguacate Peninsula: 9°12'47.13"N, 82°12'49.29"W (Fig. 1). We housed animals at the Bocas del Toro Field Station of the Smithsonian Tropical Research Institute, where, immediately after capture, we paired males and females from the same population in plastic enclosures (37 × 22 × 25 cm). We maintained tanks in ambient conditions and misted them daily. The frogs' diet consisted of wild invertebrates (mostly *Drosophila* spp.) attracted to fruit placed in enclosures, supplemented with vitamin-dusted termites. Each enclosure contained leaf litter and plant material that served as cover and a substrate for egg deposition. For tadpole deposition, we provided bromeliads and four water-filled polyvinyl chloride (PVC) tubes.

We inspected tanks every 2 days for the presence of tadpoles and new juveniles. While we presumably detected all tadpoles deposited in PVC tubes, this was apparently not the case in bromeliads because we occasionally found newly metamorphosed juveniles without previously detecting a tadpole. In such instances, we added a single tadpole to the pair's total; while this probably resulted in underestimation of tadpole production, it should not have done so in a systematic way (the proportion of total metamorphs that we did and not detect as tadpoles did not differ among morphs: $F_{2,40} = 0.9$, $P = 0.402$). In two cases, we found two tadpoles in a single rearing site; we treated these as single events for purposes of this study because nurserymate aggression almost always results in the death of one tadpole (Brust 1990). Whenever pairs from different populations deposited tadpoles on the same census date (i.e., within 2 days), those tadpoles were cross-fostered by swapping PVC tubes between parental enclosures. Regular censuses included the removal and inspection of these tubes, and so this approach created no additional disturbance of parents or tadpoles in the cross-fostering treatment. Foreign tubes were always placed in the same location as the original, and each tadpole was monitored until it died/disappeared or completed metamorphosis. Tadpoles detected in bromeliads were not cross-fostered, as doing so might have introduced substantial handling stress.

Study design and statistical analyses

We tracked the reproduction of 65 *O. pumilio* pairs (Table 1) that were held together 457 ± 108 (mean \pm SD) days (range 90–531 days). Most pairs (35) lasted the duration of the study period (~ 530 days), while others were terminated at the death of one adult or movement to accommodate other research priorities. We compared tadpole and juvenile production among morphs using generalized linear models; specifying a negative binomial error distribution provided better overall model fit (sensu Simpson et al. 2004) than Poisson distributions did. In both tadpole and juvenile models, we included the effect of pair morph and both the linear and quadratic effects of the covariate 'number of days paired'. The quadratic effect accommodates the possibility of a non-linear relationship between pair duration and output in this sample: for example, mortality may be higher (and thus total duration lower) in particularly productive pairs (Dugas et al. 2015). We included cross-fostered offspring in the juvenile totals of rearing pairs; any cross-fostered tadpole that completed metamorphosis represented parental investment, and so including these was more appropriate than excluding them. Cross-fostered tadpoles were less successful overall

Table 1.

Number of *Oophaga pumilio* pairs used in this study, including total number of pairs established, number that produced tadpoles and number that produced juveniles.

Pair lineage	Total pairs	Produced tadpoles	Produced juveniles
Aguacate	22	15	15
Bastimentos	21	15	13
Popa	22	16	16

(see Results) and pairs that produced more tadpoles also had more cross-fostered ($r = 0.70$, $n = 65$, $P < 0.001$). So, our estimate of juvenile production probably underestimates this parameter for very productive pairs, but this bias would be applied equally to pairs from all lineages. Finally, we compared parental rearing success with a model with binomial error structure in which we entered juveniles/tadpoles using the event/trials syntax; this analysis is necessarily restricted to pairs that produced ≥ 1 tadpole. In this model, we included the effect of pair lineage and the number of cross-fostered tadpoles as a covariate (we expected this term to be negatively associated with success: see Results). We also again included the linear and quadratic effects of 'number of days paired'.

To explore how rearing parent and natal parent/tadpole population-of-origin contributed to successful metamorphosis, we considered all tadpoles from the above sample that were reared in artificial rearing sites ($n = 137$). Twenty-seven Aguacate, 17 Bastimentos and 31 Popa tadpoles were reared by their own parents. We swapped nine pairs of tadpoles between Aguacate and Bastimentos parents, 14 pairs of tadpoles between Aguacate and Popa parents, and eight pairs of tadpoles between Bastimentos and Popa parents. Because the primary goal of another concurrent study was to examine mate preferences of cross-fostered offspring, we never cross-fostered tadpoles between pairs from the same lineage. One analytical approach would have been to ask how the main effects of natal parents' lineage, rearing parents' lineage and their interaction predicted successful metamorphosis of individual tadpoles (yes/no). However, a model that included these effects, the covariate of brood size, and the random effects of natal and rearing parent pair did not converge. Regardless, an interaction, while technically possible, would be difficult to interpret in this case given that tadpoles were not cross-fostered within populations. Instead, we used a generalized linear mixed model (binary error distribution, logit link function) in which we included three fixed factors: (i) rearing parents' lineage, (ii) natal parents'/tadpole lineage and (iii) whether a tadpole had been cross-fostered (yes/no). We included rearing and natal parent pair as random effects, and specified a covariance structure of compound symmetry for both. We included the number of tadpoles parents were rearing simultaneously (\sim brood size) as a covariate, including in our estimate any juveniles, presumably reared in bromeliads, that had not been detected as tadpoles but would have been reared during the same time period as the target individual (i.e., emerged up to 45 days later). Because tadpoles in bromeliads may have died before detection, our minimum estimate of brood size, which ranged from 1 to 6, still probably underestimates the number of tadpoles parents were rearing. We used PROC GENMOD and PROC GLIMMIX in SAS v9.2 (SAS Institute, Cary, NC) for all analyses. We used dispersion parameter estimates and visual inspection of residual plots (Simpson et al. 2004) to ensure that we specified an appropriate model.

RESULTS

Nearly identical proportions of pairs from each lineage reproduced in captivity (Table 1). Total tadpole production did not differ significantly among lineages ($\chi^2 = 1.7$, $df = 2$, $P = 0.424$; Fig. 2), and was not associated with the linear ($\chi^2 = 2.8$, $df = 1$, $P = 0.095$) or quadratic ($\chi^2 = 2.3$, $df = 1$, $P = 0.126$) effects of number of days paired (the linear effect remained non-significant after removal of the quadratic: $\chi^2 = 0.7$, $df = 1$, $P = 0.412$). Juvenile production, on the other hand, did differ significantly among lineages ($\chi^2 = 6.3$, $df = 2$, $P = 0.044$; Fig. 2), and was associated with both the linear ($\chi^2 = 8.0$, $df = 1$, $P = 0.005$) and quadratic ($\chi^2 = 8.0$, $df = 1$, $P = 0.005$) effects of number of days paired. Juvenile production was highest in pairs together for intermediate durations. Consistent with these results, among-lineage differences in juveniles/tadpoles were nearly significant ($\chi^2 = 5.3$, $df = 2$, $P = 0.072$; Fig. 2). The number of tadpoles cross-fostered was not significantly associated with juveniles/tadpoles ($\chi^2 = 1.8$, $df = 1$, $P = 0.184$), although the relationship was negative, as expected ($\beta \pm SE = -0.16 \pm 0.12$; intercept = 6.8 ± 6.1). Finally, both the linear and quadratic effects of days paired were significant in this model (linear: $\chi^2 = 5.1$, $df = 1$, $P = 0.023$; quadratic: $\chi^2 = 5.7$, $df = 1$, $P = 0.016$), with success again highest in pairs together for intermediate durations.

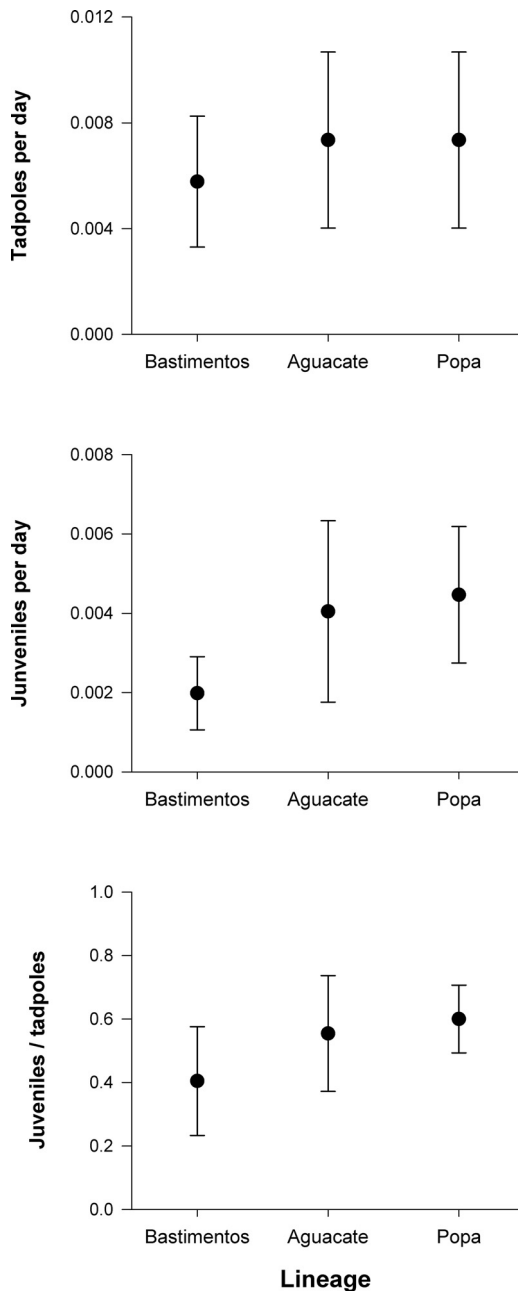


Fig. 2. — Mean (95% confidence intervals) tadpole production per day, juvenile production per day and tadpole success (juveniles/tadpoles) by captive *Oophaga pumilio* pairs from three populations of the Bocas del Toro archipelago, Panama (from most to least protected: Isla Bastimentos; Aguacate Peninsula; Isla Popa).

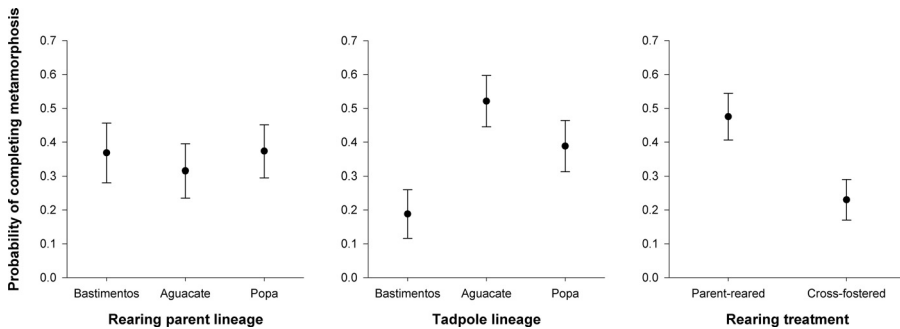


Fig. 3. — Estimated marginal mean (\pm SE) probability of completing metamorphosis by *Oophaga pumilio* tadpoles from three populations in the Bocas del Toro archipelago included in a cross-fostering study (from most to least protected: Isla Bastimentos; Aguacate Peninsula; Isla Popa). We display separately means estimated from a single model containing parent lineage, natal parent/tadpole lineage, whether the tadpole was cross-fostered or not and the linear and quadratic effects of number of days paired.

Bastimentos pairs produced the fewest juveniles and juveniles/tadpole, with Popa pairs producing the most and Aguacate pairs intermediate and quite variable (Fig. 2).

Within the sample of tadpoles we could track (those reared in artificial rearing sites), the likelihood of individual tadpoles completing metamorphosis differed among tadpole lineages ($F_{1,65} = 3.2$, $P = 0.049$; Fig. 3), but did not differ among rearing parent lineages ($F_{2,65} = 0.1$, $P = 0.917$; Fig. 3). Overall, tadpoles that were cross-fostered were less likely to complete metamorphosis than those reared by their own parents ($F_{1,65} = 6.9$, $P = 0.011$; Fig. 3); 37/75 parent-reared tadpoles completed metamorphosis, while 18/62 cross-fostered tadpoles did. The likelihood of a tadpole completing metamorphosis was not associated with the number of tadpoles parents were rearing simultaneously ($F_{1,65} = 0.2$, $P = 0.642$). Natal pair (estimate \pm SE = 0.33 ± 0.46) explained more residual variance than did rearing pair ($< 0.001 \pm 0.85$).

DISCUSSION

Captive breeding of three *O. pumilio* lineages that differ in colouration and toxicity revealed differences in reproductive rate, even when food and rearing sites were not limiting and competitors and predators were absent. At first, these patterns seem consistent with the prediction that the best-protected (i.e., most visually conspicuous and most toxic) lineage, Bastimentos, would invest the least in current reproduction. The cryptic but toxic lineage, Aguacate, was not obviously different from either other lineage, further suggesting that colouration and toxicity might drive life-history divergence. However, these patterns seem unlikely to have been driven by the differences in investment predicted by life-history theory. Cross-fostering of tadpoles among lineages indicated that differences in parental success/output did not result from among-lineage differences in the quantity and/or quality of parental care provided. Instead, Bastimentos tadpoles were less likely to complete metamorphosis than Aguacate or Popa tadpoles, regardless of which parent lineage was rearing them. Proximately, the reduced success of Bastimentos tadpoles could result from

physiological or behavioural tadpole traits that influence the level of care elicited or how it is translated into offspring fitness. One potential explanation is that *Bastimentos* tadpoles have specific nutritional requirements that are not well met in captivity; carotenoids, for example, are critical to *O. pumilio* reproduction (Dugas et al. 2013), and if the intense orange/red colouration in this population is carotenoid-based, tadpoles from this population may be more restricted than the others by the dietary availability of these pigments. A logical next step in testing this hypothesis and assessing the relative importance of physiological and behavioural mechanisms underlying tadpole performance would be to compare the development of tadpoles from different populations when reared in the absence of parents (*sensu* Brust 1990; Stynoski 2012).

Overall, cross-fostered tadpoles were less likely to complete metamorphosis than were tadpoles reared by their own parents. Because we did not conduct within-lineage cross-fostering, this statistical effect includes both (i) any parental rejection caused by cross-fostering *per se*, and (ii) any negative effects of a mismatch between parent and offspring lineage. Active parental rejection of foreign tadpoles might evolve if parents were at risk of caring for unrelated young (cases in Dendrobatidae reviewed by Haase & Pröhl 2002). A field manipulation in Costa Rica, however, demonstrated that females use only the indirect cue of location to identify their tadpoles; *O. pumilio* females continued to provision normally when unrelated tadpoles were experimentally swapped with their own, and ignored their own tadpoles when they were moved to rearing sites only 2 cm away (Stynoski 2009). Dendrobatid parents often use chemical cues when making tadpole deposition decisions (Schulte & Lötters 2014), and such cues could plausibly have mediated any complete or partial parental rejection of cross-fostered tadpoles. Mothers in the current study might have more easily identified unrelated tadpoles if cues have diverged among populations, although the evolution of this parental behaviour would be constrained by variation present in a single population. Because we swapped entire rearing sites (and Stynoski 2009 did not), it is also possible that mothers either detected chemical cues left by natal parents or responded to the lack of their own chemical signature. The high level of obligate post-zygotic maternal investment in this and other dart frogs, together with infrequent maternal presence (i.e., vigilance) and often-fatal aggression between nurserymates (Brust 1990), should set the stage for the evolution of both intra- and inter-specific brood parasitism. Molecular work establishing the genetic relationships between mothers and putative offspring will be critical to understanding the evolution (or lack thereof) of recognition mechanisms in *O. pumilio* and other frogs with parental care.

Reduced tadpole success might also arise from a mismatch between parents and offspring, expressed as behavioural or physiological traits (increased success or an interaction would likewise be consistent with this prediction: Agrawal et al. 2001; Parker et al. 2002; Hager & Johnstone 2003). Lower success of cross-fostered offspring has specifically been predicted to arise when offspring demands (behavioural or physiological) are influenced by and/or tuned to maternal effects on proximate timescales (Hinde et al. 2010). In this experiment, all parents experienced similar breeding conditions, but we can not exclude the possibility of population-specific maternal effects because (i) adults were field-collected and so could have residual effects from wild habitats, and (ii) captive conditions may have differed from natural conditions unequally for the three populations, in effect creating unequal breeding habitats. Population differences in tadpole success and a sensitivity to cross-fostering are both intriguing, and highlight the potential of *O. pumilio* as a model for understanding the evolution of parent-offspring interactions (Weygoldt 1980; Brust 1990, 1993; Stynoski 2012).

Predation risk and sexual selection have both been proposed as mechanisms driving the rapid and dramatic evolution of colour diversity in *O. pumilio* (reviewed by Gehara et al. 2013). Both forces are inextricably linked to life history, and might drive the evolution of reproductive strategies (Reznick et al. 1990; Stearns 1992; Williams et al. 2006). Overall, our results were not consistent with the prediction that better-protected morphs would invest less in current reproduction. However, relatively benign captive conditions could minimize such differences, and these strong a priori predictions should be tested in the wild and in as many populations as possible. Efforts to understand the causes and consequences of colour diversification will benefit from approaches that integrate the full range of differences among lineages, including those expressed in developmental stages that precede reproductive maturity.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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