One cost of being gold: selective predation and implications for the maintenance of the Midas cichlid colour polymorphism (Perciformes: Cichlidae)

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In the colour-polymorphic Midas cichlid fish species complex (*Amphilophus citrinellus* spp.), gold morphs occur at much lower frequencies (< 10%) than dark individuals. This might be surprising because gold coloration is dominant and coded for by a single Mendelian locus. Furthermore, gold individuals are considered to be competitively advantaged over dark ones because they grow faster and win aggressive encounters more often compared to dark individuals of equal size. However, one might expect a cost of being gold in terms of natural selection as a result of predation. We tested whether the Jaguar cichlid (*Parachromis managuensis*), a major fish predator of Midas cichlids, preys differentially on colour variants of goldfish (*Carassius auratus auratus*), which were used as a proxy for Midas cichlids because of their similarity in colour. Size-matched pairs of prey fish (gold and dark) were offered to the predator and the time until the fish were attacked was recorded. The gold morph was attacked first more often (approximately 70%) but not faster than the dark morph. This suggests that the predator perceives the gold individual first, and/or that the predator exhibits a preference or higher motivation to attack the gold prey fish. The increased risk of predation of gold prey fish suggests for the Midas cichlid system that being gold may carry significant costs in terms of natural selection as a result of its major piscivorous predator.   © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **111**, 350–358.

ADDITIONAL KEYWORDS: adaptive radiation – *Amphilophus citrinellus* – neotropical species complex – *Parachromis managuensis* – predator–prey experiment.

INTRODUCTION

Predation is a major driver of evolutionary change because it is a ubiquitous agent of natural selection (Darwin, 1859; Mayr, 1963; Endler, 1986; Schluter, 2000). Various evolutionary processes can be induced through predation (Langerhans, 2007), ranging from morphological evolution (Brönmark & Miner, 1992; Reimchen, 1994) and the modification of sexually relevant signals (Stoddard, 1999) to the promotion of ecological divergence (Nosil, 2012).

A number of studies have investigated how visual predation on coloration affects population structure and ecology (Nosil & Crespi, 2006; Langerhans, 2007; Vignieri, Larson & Hoekstra, 2010). Colour-polymorphic populations are comprised of two or more genetically determined colour morphs (Huxley, 1955) and are suitable study objects to infer the maintenance of genetic variation in the wild and its potential involvement in speciation (Gray & McKinnon, 2007; Hugall & Stuart-Fox, 2012). However, colour polymorphisms can be very complex traits (McKinnon & Pierotti, 2010) and the evolutionary dynamics of colour-polymorphic populations exposed to predation are often complex and context-dependent (Allen &

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Greenwood, 1988; Endler & Greenwood, 1988; Bond, 2007). For example, overall prey coloration is often composed of several contributing elements (Kemp, Herberstein & Grether, 2011) and, depending on the predators' visual system and environmental conditions, substantially different evolutionary outcomes are conceivable, ranging from a stable colour polymorphism to the loss of one variety (Gray & McKinnon, 2007; Forsman *et al.*, 2008).

However, although prey conspicuousness can be mitigated through other traits (e.g. behavioural plasticity; Fowler-Finn & Hebets, 2011a, b), conspicuous coloration is often costly and likely to decrease individual survival chances as a result of predation (Kettlewell, 1973; Endler, 1978; Endler, 1980; Godin & McDonough, 2003; Vignieri *et al.*, 2010).

The species-rich family of cichlid fish (Perciformes: Cichlidae) provides plentiful examples for spectacular coloration and colour polymorphisms (Fryer & Iles, 1972). However, few cichlid studies have addressed the consequences of predation on colour polymorphisms (Annett, 1989; Maan *et al.*, 2008; Maan & Sefc, 2013). In the present study, we address the evolutionary consequences of predation on the colour-polymorphic adaptive radiation of Midas cichlid fish (*Amphilophus citrinellus* spp. Günther) from the lakes of Nicaragua (Elmer *et al.*, 2010). Most Midas cichlids are cryptic-greyish coloured (dark) with spotted and barred patterns (Fig. 1) (Barlow, 1976). Interestingly, in several species in this flock of currently 13 described species (Recknagel *et al.*, 2013), a conspicuous orange-golden coloured morph also occurs in both sexes (gold) (Fig. 1) at low frequencies of typically maximally 5–10% (Barlow, 1976). The colour polymorphism in Midas cichlids is determined by Mendelian inheritance that conforms to a two-allele single locus model, with gold being dominant (Henning *et al.*, 2010). All individuals are dark at a young age. During ontogeny, when approximately 100 mm in length (the transition size in our laboratory stock is in the range 30–250 mm), genetically gold individuals start to lose their melanophores and therefore black pigmentation, until underlying orange and red (as a result of xanthophores) pigmentation appears (Barlow, 1976; Dickman, Schliwa & Barlow, 1988). The colour transformation is exclusively genetically determined and not caused by carotenoid-rich diets (Lin *et al.*, 2010). Some intraspecific advantages of being gold have been demonstrated, such as an increased growth rate of golds when being raised with darks, as well as gold morphs dominating dark individuals of equal size (Barlow, 1973; Barlow, 1983). However, given these putative advantages, it remains unclear why gold individuals are rarer in nature (Barlow, 1976) and what role natural selection as a result of predation might play in affecting the relative
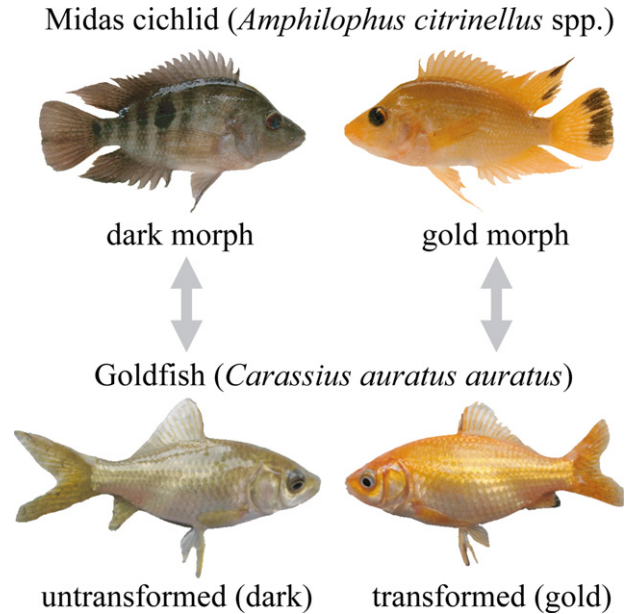

Figure 1. Colour variants of the Midas cichlid and the common goldfish. Top: the common dark Midas cichlid colour morph is depicted on the left and an individual of the rare gold morph is shown on the right. Midas cichlid photographs were provided by Frederico Henning. Bottom: two goldfish of the laboratory strain used in the present study are shown. The photograph on the left depicts a still dark individual, whereas, on the right, an individual is shown after completion of the colour transition into the universally known form. In the present study investigating colour-differential predation by a predatory cichlid, goldfish were used as analogous prey to Midas cichlids.

abundance of the colour morphs. Most crater lakes with Midas cichlids are also inhabited by the large piscivorous Jaguar cichlid (*Parachromis managuensis* Günther), which is a main predator of Midas cichlids (Barlow, 1976; Annett, 1989). Barlow (1976) estimated that an average large Jaguar cichlid (of approximately 300 mm) in the crater lakes would be capable of ingesting Midas cichlids of length 110–120 mm, a finding that we can confirm in our laboratory fish (H. Kusche and A. Meyer, pers. observ.). Consequently, genetically gold Midas cichlids that colour-transform at smaller sizes are likely to be particularly vulnerable to predation by the Jaguar cichlid as a result of their conspicuous coloration. Indeed, laboratory-raised wild-caught broods can sometimes colour-transform even at body lengths of only 30–50 mm, whereas, in nature, such small gold individuals are rarely observed. However, the onset of colour transition is variable and happens usually when the fish are few months old, although some individuals only transform after several years for reasons that remain unknown.

We investigated whether colour-differential predation through the Jaguar cichlid might contribute to the rarity of gold morphs in the wild, despite the reported advantages of being gold (Barlow, 1973; Barlow, 1983). We hypothesized that the dark Midas cichlid morph is suffering relatively less predation pressure by the Jaguar cichlid compared to the conspicuous gold Midas cichlid morph, therefore potentially contributing to the unequal colour morph frequencies in natural populations. The Jaguar cichlid is a gape-limited predator and because a consistent availability of small and size-matching Midas cichlid colour morphs in adequate sample sizes could not be achieved throughout the experimental series, we used colour variants of goldfish (*Carassius auratus auratus* Linnaeus) as alternative prey fish (Fig. 1) to test whether Jaguar cichlids differentially predate on prey fish that differ in coloration. We discuss how these laboratory results may help to interpret the relative abundances of Midas cichlid colour morphs in natural settings.

MATERIAL AND METHODS

EXPERIMENTAL DESIGN

Twelve predators were used in this experiment. Six individuals were descendants of fish from El Salvador that were kept in captivity for multiple generations. Six more individuals were caught in February 2012 in Crater Lake Asososca Managua in Nicaragua, where the Jaguar cichlid co-occurs with both Midas cichlid colour morphs. Experiments were approved by the German Federal Animal Welfare Board (permission number 35-9185.81/G-11/12) and conducted between May 2012 and May 2013 in the animal research facility of the University of Konstanz. Predators were kept individually and were acclimatized for several weeks in standardized tanks (> 200 L) under an artificial light regime (12 h day^{-1}). Each tank had the bottom covered with gravel and was equipped with two halves of a clay pot at the rear wall and a piece of wood in the centre of the tank that served as shelter for the predator. Predators were raised on artificial diets, as well as live fish of various species with different colours and pigmentation patterns, including juvenile Midas cichlids, zebrafish (*Danio rerio* Hamilton, silverish blue-green, horizontal stripes), and various species of poeciliids (*Xiphophorus* spec. and *Poecilia* spec., whose colours ranged from uniformly grey to uniformly red with some intermediate stages and various colour patterns).

Experiments were started when predators readily fed on live fish of approximately 30 mm in total length. The average predator measured approximately 200 mm when the experiment started (the mean total length measured after the experiment series was 202 mm, range 124–286 mm). The predators used in this experiment were of similar size as the average large Jaguar cichlids from our field collections ($N = 10$, mean total length = 236 mm, range 193–320 mm). Goldfish (*C. a. auratus*) were used in these experiments as a substitute for Midas cichlid colour morphs for logistic reasons. Similar to Midas cichlids, goldfish also change colour during ontogeny from an inconspicuous greyish–greenish colour into the well-known and conspicuous gold–orange form. A spectral reflectance analysis showed that the coloration of both ontogenetic stages of goldfish, before and after colour transition, is similar to that of Midas cichlids (Fig. 1; see also Supporting information, Fig. S1). Prey fish were subjected to the predators in size-matched pairs, each consisting of one dark and one gold goldfish.

All predators were routinely fed once a day with fish pellets in the morning and individually tested in the afternoon with simultaneously presented gold and grey prey fish and the time to attack was measured for both prey fish and stopped after 5 min. The first cohort of six predators was tested 20 times each, although one predator (Predator 6) died after the eighth trial. In a second set of predation experiments, a different cohort of predators, consisting of six wild-caught individuals, was tested 12 times each. The trials were recorded by two experimenters. One experimenter attracted the predator towards one front corner of the fish tank, whereas the other experimenter (HK) simultaneously released both prey fish at the same spot into the opposite front corner of the tank. Then time to attack (latency) of both prey fish was measured to the nearest second.

Occasionally, predators were tested more than once per day (twice: $N = 39$; three times: $N = 9$, five times: $N = 1$). Our sample of 180 valid experimental trials excludes 19 trials that were not considered as valid. These trials involved those where the predators view of both prey fish was restricted ($N = 8$) because the predator's focus was still directed towards the area, where the diversionary tactic took place, whereas one or both prey fish managed to hide behind tank equipment. In other trials ($N = 8$), which were also discarded, one or both prey fish instantly escaped upon release and so both prey fish did not stay closely together and the predator could not see them simultaneously. In three trials, the observers could not clearly discriminate which prey fish was attacked first because both fish were devoured almost at the same time.

STATISTICAL ANALYSIS

The data were analyzed in R (R Core Team, 2012) using two complementary ways that require different

methodology and that allow focusing on different aspects of the predators' foraging behaviour: (i) 'choice by prey fish colour' and (ii) 'time to attack depending on prey fish colour, irrespective of the attack order'. In the first type of analysis, a binary logistic regression with a binominal error distribution was used to model the predation event *per se* [response variable: gold prey fish has been attacked first ('1') or not ('0')] under the null hypothesis that both prey fish categories exhibited an equal chance (50%) of being attacked first. We used 'Predator-ID' as a random factor to account for repeated measurements and to test for an overall effect (i.e. independent of the predator). The glmer-function (package 'lme4'; Bates, 2005) was used to fit the models. The sim-function (package 'arm'; Gelman & Hill, 2007) was used for simulation of 5000 values from the posterior distribution of the model parameters. Inference was drawn, based on the 95% credible interval (CrI), the Bayesian analogue to the confidence interval. Conventionally, if zero is not included in the Bayesian 95% CrI, an effect is considered as 'clear' (Amrhein *et al.*, 2012). We also tested for the influence of the prey fish weight ratio as a fixed effect, although this did not reveal any effect of weight on the attack probability (estimate: 0.93; 95% CrI = −0.87 to 2.74). Therefore, prey fish weight was not included in the model. This supports our experimental design that was aimed to exclude the putative effect of prey fish weight on the predators' foraging decisions as much as possible.

In the second line of enquiry, we were interested in whether the time to attack depended on prey fish's colour, irrespective of the order in which prey fish was eaten first. A linear mixed effects model was used to address this question. The nature of censored survival data usually causes an increasing variance with increasing time (Cox & Oakes, 1984) and our experiment does conform to this pattern. To stabilize the variance throughout the time series, a Box-Cox power transformation was applied to the measured attack time using the boxcox-function (package 'MASS'; Venables & Ripley, 2002). In our model, the Box-Cox-transformed time until the predator attacked the prey fish was modelled as a response variable and the colour and the attack-order of the prey fish was set as a fixed effect along with their interaction. Again, aiming at testing for a generalized response pattern, 'Predator-ID' was included as a random effect in the model. The residual analysis revealed that the model assumptions of this model were met adequately (not shown). Bayesian inference was drawn as described above.

We compared the spectral reflectance patterns of Midas cichlid colour morphs and those of goldfish. Measurements were carried out using a spectrometer (QE65000 Scientific-grade Spectrometer; Ocean Optics) for three individuals of each colour morph of Midas cichlid and two individuals each of both colour morphs of goldfish. For each individual, the dorsal flank area was measured three times and the data obtained from these replicates were averaged out in two levels: first by individual and later at the level of colour morph/species.

RESULTS

Throughout the experiment, the number of gold goldfish morphs ($N = 126$) being eaten first exceeded that of dark morphs ($N = 54$) (Table 1). The probability of being gold when attacked first was estimated as 70.05% (95% CrI = 63.13–76.35%). When accounting for 'capture order' (i.e. the fact that in most trials the gold morph was attacked first), the time until an attack took place (latency) did not differ between both prey fish colour categories (model fit of the linear mixed effects model = 0.31 s; range 95% CrI = −1.39 to 2.03 s). Dark morphs were caught slightly (but not significantly) faster by the predator than gold morphs within each category of capture order given the model fit and 95% CrI in parentheses: $gold^{1st}$ = 8.45 s (6.79–10.14 s), $dark^{1st}$ = 8.15 s (6.17–10.11 s), $gold^{2nd}$ = 19.76 s (17.75–21.79 s) and $dark^{2nd}$ = 19.42 s (17.75–21.07 s) (Fig. 2). All twelve predators showed the same attack pattern as inferred

Table 1. Summary of the predation experiment

Predator ID	Trials (*N*)	Dark first (*N*)	Gold first (*N*)
1	20	6	14
2	20	4	16
3	20	5	15
4	20	4	16
5	20	9	11
6	8	2	6
7	12	4	8
8	12	3	9
9	12	4	8
10	12	4	8
11	12	3	9
12	12	6	6

Twelve Jaguar cichlids were tested in standardized 1 : 1 tests with gold and dark goldfish (Fig. 1). Differences in sample sizes were affected by prey fish availability and as a result of predator mortality. The first cohort of six individuals was tested 20 times each, except for Predator 6, which died after the eighth trial. The second cohort consisted of six more specimens and was tested twelve times each.
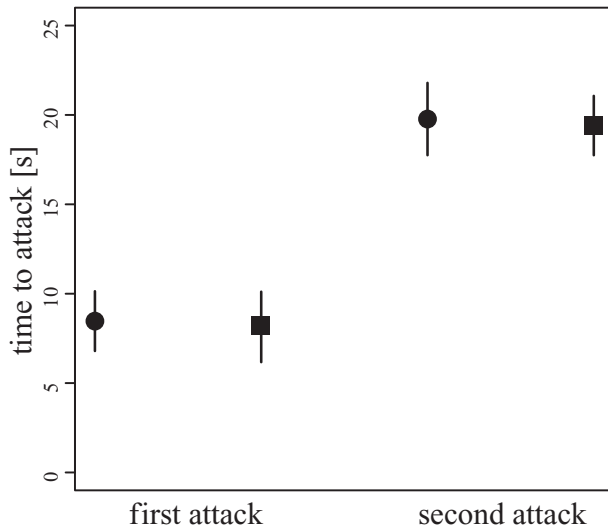
Figure 2. Time to attack, corrected for attack order. The means (dot) along with 95% credible interval (bars) of the posterior model distributions are depicted for the estimated time to attack within each category of attack order (first, second) of both prey fish colour morphs (gold morph = circle; dark morph = square). When attack order was corrected for, the time to attack for both colour morphs was indiscriminant.

from the model, and differed only in their attack latencies (see Supporting information, Fig. S2).

The analysis of spectral reflectance, conducted under the same conditions as the experiments (artificial light conditions; T8-fluorescent lamp), showed that the reflectance properties of colour morphs of either species are quite comparable, suggesting that their colour properties from an observer's (predator's) point of view are quite similar (see Supporting information, Fig. S1). Gold morphs of either species had a clear and pronounced reflectance peak around a wavelength of approximately 610 nm (orange), whereas, in the dark morphs of both species, all wavelengths were rather reflected equally (shades of grey). However, the dark goldfish additionally had a relative increase in reflectance in the greenish section of the light spectrum (λ approximately 550 nm). A similar pattern was observed in the spectral reflectance curves that were corrected for artificial light conditions, similar to those at which the experiment has been conducted. The relative difference in reflectance between the relevant orange peak in the artificial light spectrum (λ approximately 614 nm) and the greenish one (λ approximately 545 nm) is bigger in the gold morph of the Midas cichlid than in the gold goldfish. This indicates that, compared to intraspecific dark morphs, gold goldfish appear 'less orange' than Midas cichlid gold morphs, representing

a slight bias but in a conservative direction. Based on the analysis of opsins, Neotropical cichlids are known to see colour in this spectral range (Weadick *et al.*, 2012).

DISCUSSION

Visual predation can impose discontinuous natural selection pressures within populations based on prey coloration (Nosil & Crespi, 2006; Langerhans, 2007; Vignieri *et al.*, 2010). Understanding how visual predation impacts colour polymorphic populations can yield valuable insights into the study of genetic variation, its maintenance, and its role in mediating diversification (Gray & McKinnon, 2007; Hugall & Stuart-Fox, 2012). However, colour polymorphisms are frequently sex-linked and determined by a complex or unknown genetic architecture (McKinnon & Pierotti, 2010), somewhat impairing the understanding of the associated evolutionary processes. In the present study, we addressed the role of visual predation in a simple colour polymorphic system that is not limited by these constraints: the Midas cichlid species complex. The putative advantages of being gold (Barlow, 1973; McKaye & Barlow, 1976; Barlow, 1983) and the fact that gold Midas cichlids comprise only a small percentage of the adult population (Barlow, 1976) suggest that being gold comes at a cost. Our predation experiment has revealed one such cost, although other potential costs cannot be excluded (e.g. immune deficiency).

The experiments aimed to evaluate the hypothesis that the Jaguar cichlid, a major predator of gold and dark Midas cichlids in nature, shows differential predation for prey fish of different colours. The initial attack bouts were consistently more likely to be directed towards the gold prey fish and, within each category of 'capture order', the time to attack was not different for both prey fish categories when 'capture order' was corrected for. This means that, although gold morphs were likely being attacked first in most cases, once the predator initiated an attack towards one of the prey fish, both categories of prey fish colour were attacked at equal speeds. Under the assumption that both prey fish were simultaneously perceived by the predator, the data are consistent with the hypothesis that the Jaguar cichlid is better able to perceive gold morphs or has a preference towards attacking gold morphs. For the lakes in Nicaragua and the Midas cichlid system, this suggests that gold morphs might experience higher predation rates or at least detection rates by their major natural fish predator compared to dark morphs. We recently conducted a first series of field experiments with Midas cichlid wax models of both colours in Nicaraguan crater lakes and found that piscivorous predators such as

the Jaguar cichlid attack gold fish more frequently, at least in relatively more turbid water (J. Torres-Dowdall, G. Machado-Schiaffino, A. F. Kautt, H. Kusche and A. Meyer, unpubl. data), suggesting that gold morphs would be subjected to stronger selection than the dark individuals by aquatic predators.

Crypsis is a mechanism of predator avoidance and hence survival and its effectiveness depends on the predators' capacity to visually perceive their prey (Endler, 1978; Endler, 1980; Crawley, 2009). Reduced crypsis is possibly the main reason why the gold morphs have been typically attacked first by the predator and why, in natural settings, fewer gold than dark Midas cichlids occur (Barlow, 1976). Midas cichlids prevail within the structured shore benthic habitat mainly consisting of steep rock faces, jumbled boulders, and sunken trees. When disturbed, the fish benefit from this structured habitat in that they can hide behind the rocks and their vertical bars and spots further blur the shape of the fish (Barlow, 1976). Only the dark morph exhibits these patterns that contribute to camouflaging the individual against the background (Barlow, 1976). Background matching might be enhanced as well in the dark morph through the physiological ability to regulate various pigmentation patterns depending on mood and the environment (Barlow, 1976). In the uniformly gold Midas cichlid morph, this is not possible, resulting in an increased conspicuousness, and so golds might be expected to exhibit higher predation rates compared to the dark morph. It has also been reported that even untransformed gold individuals exhibited a slower colour-matching rate than dark individuals (Dickman, Annett & Barlow, 1990), which suggests that, already in early life stages, gold individuals might be particularly vulnerable to predation.

Another aspect that awaits investigation relates to the question of why the genetically determined colour change occurs late in ontogeny in many individuals, when the fish have attained a particular body size. Laboratory-raised Midas cichlids of gold × gold parents (obtained as wild-caught fry) usually transition when approximately 100 mm in length (range 30–250 mm) and, occasionally, even at smaller sizes (H. Kusche and A. Meyer, pers. observ.). However, in the field, among thousands of specimens that we collected during the last 30 years of field work in Nicaragua, we have only rarely seen or collected gold Midas cichlids that are smaller than 100 mm in length. It is likely that this is a result of increased predation on small gold individuals. Various studies on other piscivorous fish predators have demonstrated morphological constraints related to the predator's gape size and prey body size and associated diet consequences (Hambright, 1991; Montaña, Layman & Winemiller, 2011). Therefore,it is also con-

ceivable that the ontogenetic onset of colour transition in Midas cichlid colour morphs might be partly triggered through selection by piscivorous predators and their constraints in feeding ecology (mouth gape size). However, it is still unclear whether the timing of colour transition is a trait that can be selected for.

It should be noted that a previous study on differential predation on Midas cichlid colour morphs has led to a different result (Annett, 1989). That study used the largemouth bass, *Micropterus salmoides*, as a predator (approximately 200–300 mm in length) and found that dark Midas cichlids were proportionally more often devoured (69.2%) than gold morphs (Annett, 1989). The use of different predators might be the main reason for the differences between our and Annett's study. The largemouth bass is a non-native predator, and long-term predation effects (approximately 4–21 days) were addressed in the previous study rather than instantaneous foraging decision-making as investigated in the present study. Also, in the previous study by Annett (1989), the null hypothesis of equal survival probability of both colour morphs is technically met only at the beginning of each trial given the group-wise experimental set up (ten to 27 individuals per colour morph and trial). Moreover, the study by Annett (1989) was conducted against a uniform background simulating the open water column, whereas, in the present study, we aimed to imitate the natural shore habitat from Nicaraguan crater lakes by using a structured fish tank with the bottom covered with gravel and wood. Indeed, Annett (1989) states 'In contrast, piscivores attacking Midas cichlids in aquatic vegetation or in other dark, patterned habitats may be more likely to see the gold morph'.

We assume that the outcome of our laboratory experiment informs on the situation in nature, given the relative rarity of gold morphs of Midas cichlids that are found there and the sympatric occurrence of Jaguar cichlids. However, the Jaguar cichlid is not the only natural predator of Midas cichlids, although it is certainly one of the most abundant (Barlow, 1976). Several species of fish-eating birds are common in Nicaragua. Avian predation through ospreys, kingfishers, cormorants, and herons is perhaps even stronger than that of piscivorous fish at least near the surface (J. Torres-Dowdall, G. Machado-Schiaffino, A. F. Kautt, H. Kusche and A. Meyer, unpubl. data). Preliminary results on bird and fish predation show that various birds of prey readily attack Midas cichlid wax dummies of different coloration and those experiments resulted in a higher attack rate on dark rather than gold models, suggesting that some form of negative-frequency dependent selection contributes to maintain the colour polymorphism

(J. Torres-Dowdall, G. Machado-Schiaffino, A. F. Kautt, H. Kusche and A. Meyer, unpubl. data). However, in our field trials, we find that attacks on gold models increased in correlation with the clarity of the water and, at a visibility of 195 ± 5 cm, Secchi disk readings gold models were attacked more often than dark models. Water clarity is known to vary across seasons and will be lowest during the rainy season when run-off will cloud the water. One might expect that this seasonality with respect to changes in water clarity will also affect predation on the different colour morphs differentially. In summary, the findings obtained in the present study suggest that predation is of great relevance for the maintenance of this conspicuous colour polymorphism at unequal frequencies in this adaptive radiation.

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REFERENCES

Allen JA, Greenwood JJD. 1988. Frequency-dependent selection by predators. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **319:** 485–503.

Amrhein V, Scaar B, Baumann M, Minery N, Binnert J-P, Korner-Nievergelt F. 2012. Estimating adult sex ratios from bird mist netting data. *Methods in Ecology and Evolution* **3:** 713–720.

Annett C. 1989. Differential predation on colour morphs of the Midas cichlid, *Cichlasoma citrinellum*. *Animal Behaviour* **37:** 935–942.

Barlow GW. 1973. Competition between color morphs of the polychromatic Midas cichlid *Cichlasoma citrinellum*. *Science* **179:** 806–807.

Barlow GW. 1976. The Midas cichlid in Nicaragua. In: Thorson TB, ed. *Investigations of the ichthyofauna of Nicaraguan lakes*. Lincoln, NE: School of Life Sciences, University of Nebraska-Lincoln, 333–358.

Barlow GW. 1983. The benefits of being gold: behavioral consequences of polychromatism in the Midas cichlid, *Cichlasoma citrinellum*. *Environmental Biology of Fishes* **8:** 235–247.

Bates D. 2005. Fitting linear mixed models in R. *R news* **5:** 27–30.

Bond AB. 2007. The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annual Review of Ecology Evolution and Systematics* **38:** 489–514.

Brönmark C, Miner JG. 1992. Predator-induced phenotypical change in body morphology in crucian carp. *Science* **258:** 1348–1350.

Cox DR, Oakes D. 1984. *Analysis of survival data*. London: Chapman & Hall.

Crawley M. 2009. *Natural enemies: the population biology of predators, parasites and diseases*. Oxford: Wiley-Blackwell.

Darwin C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: Murray.

Dickman MC, Annett C, Barlow GW. 1990. Unsuspected cryptic polymorphism in the polychromatic Midas cichlid. *Biological Journal of the Linnean Society* **39:** 239–249.

Dickman MC, Schliwa M, Barlow GW. 1988. Melanophore death and disappearance produces color metamorphosis in the polychromatic Midas cichlid (*Cichlasoma citrinellum*). *Cell and Tissue Research* **253:** 9–14.

Elmer KR, Kusche H, Lehtonen TK, Meyer A. 2010. Local variation and parallel evolution: morphological and genetic diversity across a species complex of neotropical crater lake cichlid fishes. *Philosophical Transactions of the Royal Society Series B, Biological Sciences* **365:** 1763–1782.

Endler JA. 1978. A predator's view of animal color patterns. In: Hecht MK, Steere WC, Wallace B, eds. *Evolutionary biology*. New York, NY: Plenum Press, 319–364.

Endler JA. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34:** 76–91.

Endler JA. 1986. *Natural selection in the wild*. Princeton, NJ: Princeton University Press.

Endler JA, Greenwood JJD. 1988. Frequency-dependent predation, crypsis and aposematic coloration. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **319:** 505–523.

Forsman A, Ahnesjö J, Caesar S, Karlsson M. 2008. A model of ecological and evolutionary consequences of color polymorphism. *Ecology* **89:** 34–40.

Fowler-Finn KD, Hebets EA. 2011a. The degree of response to increased predation risk corresponds to male secondary sexual traits. *Behavioral Ecology* **22:** 268–275.

Fowler-Finn KD, Hebets EA. 2011b. More ornamented males exhibit increased predation risk and antipredatory escapes, but not greater mortality. *Ethology* **117:** 102–114.

Fryer G, Iles TD. 1972. *The cichlid fishes of the great lakes of Africa: their biology and evolution*. Edinburgh: Oliver and Boyd.

Gelman A, Hill J. 2007. *Data analysis using regression and multilevel/hierarchical models*. New York, NY: Cambridge University Press.

Godin J-GJ, McDonough HE. 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behavioral Ecology* **14:** 194–200.

Gray SM, McKinnon JS. 2007. Linking color polymorphism maintenance and speciation. *Trends in Ecology & Evolution* **22:** 71–79.

Hambright KD. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* **120:** 500–508.

Henning F, Renz AJ, Fukamachi S, Meyer A. 2010. Genetic, comparative genomic, and expression analyses of the *Mc1r* locus in the polychromatic Midas cichlid fish (Teleostei, Cichlidae *Amphilophus* sp.) species group. *Journal of Molecular Evolution* **70:** 405–412.

Hugall AF, Stuart-Fox D. 2012. Accelerated speciation in colour-polymorphic birds. *Nature* **485:** 631–634.

Huxley J. 1955. Morphism in birds. *Acta International Congress Ornithology XI* **11:** 309–328.

Kemp DJ, Herberstein ME, Grether GF. 2011. Unraveling the true complexity of costly color signaling. *Behavioral Ecology* **23:** 233–236.

Kettlewell B. 1973. *The evolution of melanism*. Oxford: Oxford University Press.

Langerhans RB. 2007. Evolutionary consequences of predation: avoidance, escape, reproduction, and diversification. In: Elewa AMT, ed. *Predation in organisms*. New York, NY: Springer, 177–220.

Lin SM, Nieves-Puigdoller K, Brown AC, McGraw KJ, Clotfelter ED. 2010. Testing the carotenoid trade-off hypothesis in the polychromatic Midas cichlid, *Amphilophus citrinellus. Physiological and Biochemical Zoology* **83:** 333–342.

Maan ME, Eshuis B, Haesler MP, Schneider MV, Van Alphen JJ, Seehausen O. 2008. Color polymorphism and predation in a Lake Victoria cichlid fish. *Copeia* **3:** 621–629.

Maan ME, Sefc KM. 2013. Colour variation in cichlid fish: developmental mechanisms, selective pressures and evolutionary consequences. *Seminars in Cell & Developmental Biology* **24:** 516–528.

Mayr E. 1963. *Animal species and evolution*. Cambridge, MA: Harvard University Press.

McKaye KR, Barlow GW. 1976. Competition between color morphs of the Midas cichlid, *Cichlasoma citrinellum*, Lake Jiloá, Nicaragua. In: Thorson TB, ed. *Investigations of the ichthyofauna of nicaraguan lakes*. Lincoln, NE: School of Life Sciences, University of Nebraska-Lincoln, 465–475.

McKinnon JS, Pierotti ME. 2010. Colour polymorphism and correlated characters: genetic mechanisms and evolution. *Molecular Ecology* **19:** 5101–5125.

Montaña CG, Layman CA, Winemiller KO. 2011. Gape size influences seasonal patterns of piscivore diets in three Neotropical rivers. *Neotropical Ichthyology* **9:** 647–655.

Nosil P. 2012. *Ecological speciation*. Oxford: Oxford University Press.

Nosil P, Crespi BJ. 2006. Experimental evidence that predation promotes divergence in adaptive radiation. *Proceedings of the National Academy of Sciences of the United States of America* **103:** 9090–9095.

R Core Team. 2012. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available at: http://www.R-project.org/

Recknagel H, Kusche H, Elmer KR, Meyer A. 2013. Two new endemic species in the Midas cichlid species complex from Nicaraguan crater lakes: *Amphilophus tolteca* and *Amphilophus viridis* (Perciformes: Cichlidae). *Aqua, International Journal of Ichthyology* **19:** 207–224.

Reimchen TE. 1994. Predators and morphological evolution in threespine stickleback. In: Bell MA, Foster SA, eds. *The evolutionary biology of the threespine stickleback*. New York, NY: Oxford University Press, 240–276.

Schluter D. 2000. *The ecology of adaptive radiation*. Oxford: Oxford University Press.

Stoddard PK. 1999. Predation enhances complexity in the evolution of electric fish signals. *Nature* **400:** 254–256.

Venables WN, Ripley BD. 2002. *Modern applied statistics with S*. New York, NY: Springer.

Vignieri SN, Larson JG, Hoekstra HE. 2010. The selective advantage of crypsis in mice. *Evolution* **64:** 2153–2158.

Weadick CJ, Loew ER, Rodd FH, Chang BS. 2012. Visual pigment molecular evolution in the trinidadian pike cichlid (*Crenicichla frenata*): a less colorful world for neotropical cichlids? *Molecular Biology and Evolution* **29:** 3045–3060.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Spectral reflectance of Midas cichlid and goldfish colour morphs. Depicted are normalized reflectance spectra of Midas cichlids and goldfish colour variants, uncorrected (A) and corrected (B) for the light conditions, under which the experiments were conducted (T8-fluorescent lamp). Although all four groups in (A) have their reflectance peaks at approximately 610 nm, only the orange morphs of either species show a well-defined peak in this orange part of the light spectrum, causing their conspicuous coloration. By contrast, the dark, melanic morphs of either species approach a plateau, indicating that they reflect the light throughout the range of the considered wavelengths ($\lambda = 500–650$ nm) rather uniformly and therefore would appear greyish. In addition, the dark goldfish has a steep increase in reflectance already at approximately 550 nm, rendering

it rather greyish–greenish. In (B), the T8-light-corrected data are shown. T8-light has two characteristic peaks in the greenish and the orange part of the light spectrum (λ of approximately 545 and 614 nm). The relative differences in reflectance between those peaks are indicated by peak height. Similar to the finding shown in (A), the melanic morphs of either species exhibit only very subtle differences in reflectance intensity, as seen under T8-light. Orange morphs of either species exhibited a clearly increased level of relative reflectance at the second characteristic T8-light peak (λ of approximately 614 nm) compared to the first green one (λ of approximately 545 nm, indicated by arrows). The difference in reflectance intensity between the T8-peaks was smaller in the gold goldfish than in the Midas cichlid gold morph, making the gold goldfish a somewhat 'less intense gold' than the Midas cichlid. Photographs of typical gold and dark Midas cichlid morphs and goldfish colour variants are shown for visualization purposes.

Figure S2. Across-predator variance in attack latency. Although all predators conform to the overall trend, there is variation in attack latency among predators. For each of the twelve predators, the means (dot) along with 95% credible interval (bars) of the posterior model distributions are depicted for the estimated time to attack within each category of capture order (first, second) of both prey fish colour morphs (gold morph = circle; dark morph = square). When capture order was corrected for, the time to attack for both colour morphs was indiscriminant. Note the differences in scaling of the ordinate axis.