Differential predation on the two colour morphs of Nicaraguan Crater lake Midas cichlid fish: implications for the maintenance of its gold-dark polymorphism

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Predation can play an important role in the evolution and maintenance of prey colour polymorphisms. Several factors are known to affect predator choice, including the prey's relative abundance and conspicuousness. In polymorphic prey species, predators often target the most common or most visible morphs. To test if predator choice can explain why in Midas cichlid fish the more visible (gold) morph is also more rare than the inconspicuous dark morph, we conducted predation experiments using two differently coloured wax models in Nicaraguan crater lakes. Contrary to expectations, we observed an overall higher attack rate on the much more abundant, yet less conspicuous dark models, and propose frequency-dependent predation as a potential explanation for this result. Interestingly, the attack rate differed between different types of predators. While avian predators were biased towards the abundant and less colourful dark morphs, fish predators did not show a strong bias. However, the relative attack rate of fish predators seemed to vary with the clarity of the water, as attack rates on gold models went up as water clarity decreased. The relative differential predation rates on different morphs might impact the relative abundance of both colour morphs and thus explain the maintenance of the colour polymorphism.

ADDITIONAL KEYWORDS: *Amphilophus citrinellus – Amphilophus tolteca –* apostatic selection – polychromatism.

INTRODUCTION

Colour polymorphisms, i.e. the presence of two or more genetically determined colour morphs within a given population, are a widespread phenomenon in nature (Gray & McKinnon, 2007). Body coloration influences several aspects of the life of organisms, affecting fitness through its effect on inter- and intraspecific interactions (Andersson, 1994; Ruxton, Sherratt & Speed, 2004). Because of the strong relationship between colour and fitness, colour polymorphisms make an interesting case for the study of the evolution of traits under selection. Furthermore, the long-term stability of genetically determined colour polymorphisms is intriguing, because genetic variation is expected to decrease in traits under selection (Turelli & Barton, 2004; Gray & McKinnon, 2007). The maintenance of polymorphisms can be explained by a balance between different selection pressures or evolutionary forces (e.g. Rosenblum, 2006), or by frequency-dependent selection (Allen, 1988; Sinervo, Svensson & Comendant, 2000; Olendorf *et al.*, 2006).

Predation is a powerful agent of selection, driving phenotypic evolution (Reznick & Endler, 1982; Abrams & Rowe, 1996; Langerhans, 2007), and affecting the diversity and abundance of prey (Paine, 1966; Bond, 2007). In particular, predators can have a strong impact on prey variation in terms of coloration

(Bond, 2007). Conspicuousness of prey depends on how well their body coloration matches the background coloration of the environment where they live, and prey types that are easier to detect by visually orientated predators are expected to suffer fitness consequences (Endler, 1978). Differential survival of colour morphs would be expected to promote the evolution of crypsis, which often, but not always, is concomitant with the elimination of the more conspicuous morphs from the population (Bond & Kamil, 2002; Maan *et al*., 2008; Vignieri, Larson & Hoekstra, 2010). Industrial melanism in the peppered moth (*Biston betularia*), the long-term variation in the proportion of dark and light morphs associated with changes in the bark colour of trees, offers a classical example for the role of predation on colour polymorphism dynamics (Cook, 2003, but see Riley, 2013). Visually orientated birds predate on moths roosting on trees, and the light morph suffered higher predation when the proportion of sooty, darkened trees increased; and vice versa for dark moths on lighter trees (Cook *et al*., 2012).

Several factors can counteract the negative effects of differential predation upon morphs, promoting the maintenance of diversity. For example, morphs of polymorphic species often differ in other factors besides coloration or conspicuousness that also affect a predator's choice, including the morph's relative abundance. Several mechanisms, including search image formation (Tinbergen, 1960), neophobia (Barnett, 1958) and dietary conservatisms (Maples, Roper & Harper, 1998), can result in a pattern in which predators focus on the most abundant prey morph, overlooking those that are rare (Allen, 1988). This form of negative frequency-dependent selection is considered to be a powerful explanation for the conservation of stable colour polymorphism in nature (Allen, 1988; Olendorf *et al*., 2006). Yet another factor that influences the probability of maintenance of polymorphisms is competition between morphs. For example, trade-offs between competitive ability and risk of predation in different prey species or morphs can increase the probability of the long-term coexistence of different morphs within a population (Lively, 1986; Chase *et al*., 2002).

An interesting system to study colour polymorphisms is the Neotropical Midas cichlid fish species complex (*Amphilophus* spp.). Many of the 13 species of Midas cichlids that have been described so far are polymorphic in terms of coloration. Most individuals of Midas cichlids are dark, but in almost all populations up to 5–10% of the individuals show a gold phenotype (Barlow, 1976, 1983; Henning *et al*., 2010), and this proportion has been maintained relatively constant through time (Barlow, 1976, 1983; Wilson, Noack-Kuhnmann & Meyer, 2000; Elmer, Lehtonen &

Meyer, 2009). The gold–dark polymorphism in Midas cichlid fish is determined by a single Mendelian locus, in which the gold allele is dominant over the dark allele (Henning *et al*., 2010). All Midas cichlid start their life as melanic, dark fish; but fish carrying the gold allele lose their melanophores during ontogeny, revealing the underlying yellow/orange xanthophores (Dickman, Schliwa & Barlow, 1988; Henning *et al*., 2013; Fig. 1A, B). Both sexes can express the gold phenotype, and there is evidence for assortative mating, which at least in one population of Midas cichlids has led to genetic differentiation among morphs (Elmer *et al*., 2009).

Laboratory-based behavioural studies suggest that gold fish have a dominance advantage over dark fish in competition for breeding sites (Barlow, 1983), and that gold fish grow faster than equally sized dark fish when sharing a common tank (Barlow, 1973, 1983). Yet why gold fish are less abundant in the field and why the polymorphism appears to be stable in nature remains unknown. Differential predation on colour morphs has been proposed to play a role in maintaining this polymorphism (Barlow, 1983; Annett, 1989; Kusche & Meyer, 2014). The reasoning behind this hypothesis is that gold Midas cichlids are visually more conspicuous than the dark morph, which has a coloration pattern that matches better the environmental background (Barlow, 1976). However, experiments conducted under laboratory conditions have yielded somehow contradicting results. Using enclosures in swimming pools with a uniform background simulating the open water column, Annett (1989) found that gold Midas cichlids were preyed upon less often than the dark morph by the largemouth bass (*Micropterus salmoides*), a predator that is not found in Nicaraguan crater lakes. By contrast, Kusche & Meyer (2014) tested the preference of the Jaguar cichlid (*Parachromis managuensis*), a common predator of Midas cichlids in the field, using gold and grey morphs of the goldfish (*Carassius autatus*) as a proxy for gold and dark morphs of the Midas cichlids. When both colour morphs were offered at the same time against a background of gravel and wood, simulating the benthic habitat of Midas cichlids, the Jaguar cichlid attacked the gold fish first, supporting the hypothesis that gold Midas cichlids are more conspicuous and might therefore suffer a higher predation rate than dark fish. Taken together, these studies suggest that the Midas cichlid colour morphs experience differential predation rate, but which morph is preyed upon more heavily probably depends on the predator under study and the visual conditions under which the experiment is conducted. Thus, the contribution of predation in the maintenance of the Midas cichlid gold morph at a low frequency in the wild remains speculative.
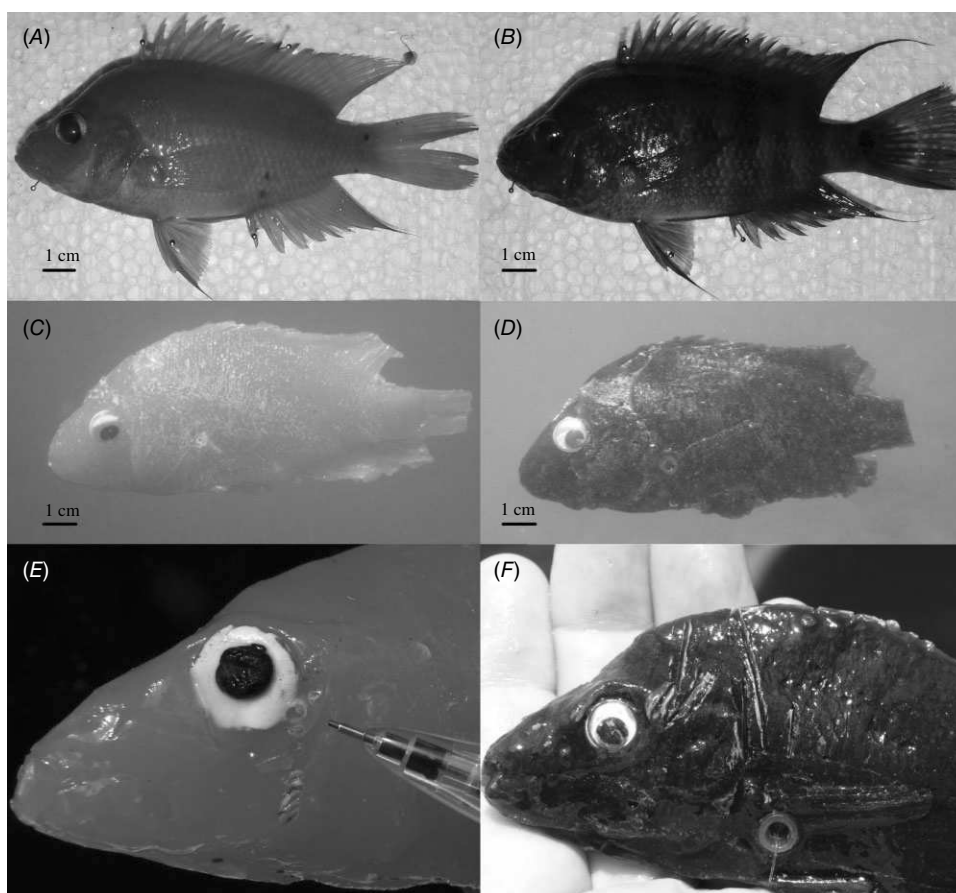
Figure 1. Gold (A) and dark (B) Midas cichlid morphs and the models that resemble them closely (C, D). Both, fish (E) and avian (F) predators attacked the wax models leaving distinctive marks.

In the present study, we conducted a predation experiment in a crater lake in Nicaragua, using wax models that simulated dark and gold Midas fish (Fig. 1C, D). Wax is an ideal material to test predation, as it is easy to modify shape and can be dyed with different colours. It is positively buoyant and attack marks by fish and bird predators are recorded in the wax making it possible to identify even the type of the specific predator. Our specific questions were: (a) Do models simulating gold fish experience a higher attack rate than models simulating dark fish? (b) Do different predators (i.e. piscivorous fishes and birds) have similar rates of attack on gold and dark models? Furthermore, we replicated our predation experiment, but at a smaller scale, in another crater lake in Nicaragua to determine the generality of our results.

MATERIAL AND METHODS

STUDY AREA AND RELATIVE ABUNDANCE OF GOLD–DARK MORPHS

This study was conducted in March 2013, in the crater lake Asososca Managua, Nicaragua. The water is relatively clear in this crater lake, although natural but irregular changes of visibility occur as a consequence of changes in algae biomass associated with the oligomictic nature of this lake (Avilés-García & Peña-Martinéz, 2000). Our study coincided with one such event, resulting in a significant decrease in visibility in the lake from 415 ± 5 cm (Secchi disk measurement) at the beginning of the study to 195 ± 5 cm at the end (Fig. 2).

We determined the relative abundance of gold and dark fish in the lake using linear transects following Dittmann *et al*. (2012), with the difference that we counted fish at one depth only (average of 7 m). Seven line transects were covered by two SCUBA divers, swimming side by side, both recording the number of dark and gold fish observed. The length of transects was determined by distance covered during 10 min of diving, which varied depending on visibility and number of fish in each transect. The total number of gold and dark fish observed by each diver was averaged to determine the proportion of gold fish. Variation between observers in the proportion of gold and dark fish was low (Table S1).
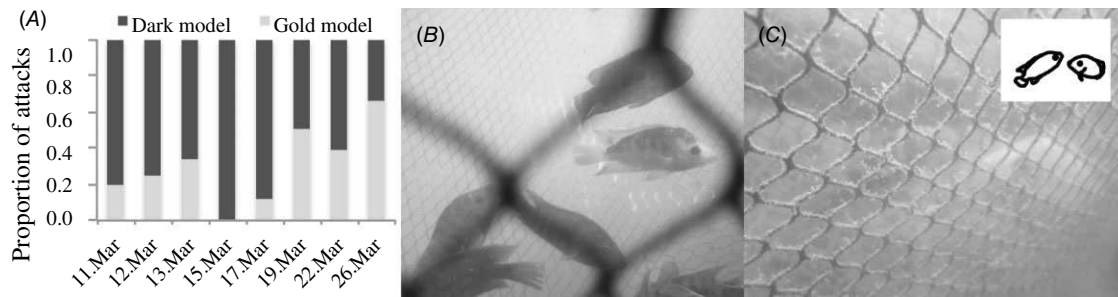
Figure 2. The proportion of attacks per day on the gold morph increased with time (A). This was correlated with algae blooming that reduced the visibility on the lake; (B) March 8; (C) March 27. The insert in C specifies the location of the dark and gold fish in the photo. Note that the gold fish in B is in transition (a period that last approximately 2 weeks), and it has not lost all its melanophores.

PREDATION EXPERIMENT USING WAX MODELS

We used preserved 12-cm (standard length) Midas cichlids as templates for silicone moulds, in which liquefied coloured wax that closely resembles both colour morphs was poured to make the models (Fig. 1C, D). We suspended individually numbered models at about 15 cm below the water surface by attaching them with monofilament to 3-m-long, 15-mm-diameter, grey PVC pipes that were floating at about 1 m depth below the models. This position in the water column was selected to maximize the probability that both aerial and aquatic predators would attack the models. Furthermore, Midas cichlids are commonly seen close to the surface of the water, foraging on resources that fall into the lake (personal observations, Fig. S1). We used grey pipes because they were inconspicuous against the water column background and they were not visible from the water surface. Pipes were randomly distributed in different positions along the lake, but with a minimum distance to the shore of 5 m. Because Asososca Managua is a crater lake, its shores are very steep, above and below the water line. The bottom of the lake was not visible where the models were placed, an thus aerial predators would see the models floating in the water column. Aquatic predators would have to detect the models against a distant background of a mix between the sky and terrestrial vegetation. On each pipe we attached two models separated by 1 m each, in one of the following combinations: gold–gold, gold–dark and dark–dark. Sixty-four wax models were placed in the water every day and checked for predator attacks on eight different occasions (466 observations, some data was lost due to missing pipes or models). When a model was attacked, it was photographed, and we determined the type of predator that attacked it, and replaced the damaged model with a new one. Multiple attacks on the same model were counted as one attack.

We analysed predator attacks using a nominal logistic regression analysis (JMP10), considering colour, date, colour of the neighbouring model, and their interactions as predictor variables. We created a set of candidate models by starting with the full model and then removed terms until all combinations were analysed, including a null model (intercept only). We used Akaike's information criterion adjusted for small sample size to evaluate the relative importance of competing candidate models when contrasted against data, and report a subset of those with at least 0.125 of Akaike weight of the top model (Burnham & Anderson, 2002). We determined the importance of the different factors by model averaging (Burnham & Anderson, 2002). These analyses were performed including all pooled attacks, and then repeated separately for avian and fish attacks.

In an attempt to test the generality of our results, we conducted a similar experiment, but at a smaller scale, in a second crater lake, Asososca León (Elmer *et al.*, 2010). The gold morph is present in this lake, but its relative abundance is very low (< 1%, our personal observations). We used 20 wax models, 10 dark and 10 gold, in 10 PVC pipes holding one gold and one dark model each. We deployed the models for around 18 h, setting them before sunset and collecting them the next day before noon. Models were then checked for traces of attacks and photographed.

RESULTS

RELATIVE ABUNDANCE OF GOLD–DARK MORPHS IN ASOSOSCA MANAGUA

On average, the proportion of the gold morph in the Asososca Managua Midas cichlid fish population was 0.071 (min = 0, max = 0.111, SD = 0.036, $N = 7$). This value was influenced by one transect in which no gold fish were observed, but eliminating this value only slightly increased the mean proportion of the gold morph (0.082 ± 0.019 SD). There were no significant differences in the proportion of morphs observed by each diver ($P = 0.5$).

Table 1. Confidence set of candidate models for the probability of attack upon gold and dark wax models

Response variable	Model	K	AICc	ΔAICc	w_i
All attacks	C + D + C*D	6	390.396	0.000	0.331
	C + D + C*D + N	7	391.187	0.791	0.223
	C + N + D + C*N + C*D	8	392.427	2.031	0.120
	C + N + D + N*D + C*D	8	392.454	2.058	0.118
	C + N + D + C*N + N*D + C*D	9	390.396	0.000	0.331
Fish attacks only	C + D + C*D	6	226.920	0.000	0.358
	C + D + C*D + N	7	227.848	0.928	0.225
	C + N + D + C*N + C*D	8	229.343	2.423	0.107
	C + N + D + N*D + C*D	8	229.779	2.859	0.086
	D	4	230.856	3.936	0.050
	C + N + D + C*N + N*D + C*D	9	230.898	3.978	0.049
Avian attacks only	C	4	201.193	0.000	0.357
	C + D	5	202.919	1.726	0.151
	C + N	5	203.201	2.008	0.131
	FULL	10	204.627	3.434	0.064
	C + D + C*D	6	204.705	3.512	0.062
	C + D + N	6	204.945	3.752	0.055
	C + N + C*N	6	205.202	4.009	0.048

AIC$_C$, Akaike's information criterion adjusted for small sample size; C, model colour; D, date; K, number of parameters; N, colour of closest model; w_i, Akaike weight.

Table 2. Model-averaged parameter estimates, their unconditional standard errors (SE) and 95% confidence intervals (95% CI) for a composite model determining the probability of attack upon gold and dark wax models

Response variable	Parameter	Estimate	SE	95% CI Lower	95% CI Upper	Cumulative w_i
All attacks	C	0.417	0.151	0.121	0.713	0.991
	D	−8.808E-07	3.613E-07	−1.589E-06	−1.726E-07	0.988
	N	0.117	0.126	−0.130	0.364	0.641
	C*D	−7.749E-07	3.206E-07	−1.403E-06	−1.466E-07	0.908
Fish attacks only	C	0.099	0.209	−0.311	0.508	0.920
	D	−1.386**E**-06	4.864E-07	−2.339E-06	4.327E-07	0.997
	N	0.119	0.160	−0.193	0.432	0.568
	C*D	−1.098E-06	4.898E-06	−2.058E-06	−1.376E-07	0.843
Avian attacks only	C	0.791	0.250	0.301	1.281	0.999
	D	1.424E-07	3.956E-07	−6.331E-07	9.178E-07	0.463
	N	0.013	0.139	−0.259	0.285	0.430
	C*D	3.877E-08	2.609E-07	−4.725E-07	5.501E-07	0.179

C, model colour; D, date; N, colour of closest model; w_i, Akaike weight.

PREDATION EXPERIMENT USING WAX MODELS

We observed the traces of at least 73 attacks on the models (≈ 16% attack rate; Fig. 1E, F): 34 by piscivorous birds (ospreys, kingfishers, cormorants and several species of egrets were seen in the area); 35 by piscivorous fish (*Parachromis managuensis* and *Gobimorus dormitor* inhabit the lake); three by both fish and avian predators; and six for which predator type was not identified. Overall, dark models were attacked more frequently than gold ones (odds ratio: 2.35, $P = 0.0025$; Tables 1, 2). However, there was a significant change in the proportion of attacks upon each colour-model throughout the course of the experiment, with the attacks upon the gold models increasing towards the end of the experiment (Table 2, Fig. 2).

Analysing avian and fish attacks separately reveals that these two types of predators are responsible for the different effects on the overall model (Table 2). Avian predators mainly drove the differential attack rate on dark over gold models (odds ratio: 5.40, $P < 0.0001$), and colour was the only significant factor in the model (Table 2). Conversely, fish predators did not show an overall preference for either colour model (odds ratio: 0.80, $P = 0.61$), but were responsible for the temporal change of relative attack frequency on dark versus gold models (Table 2). Most attacks by fish on gold models occurred at the end of the experiment (13 out of 19 in last two days of observation), whereas most attacks on dark models were before that (12 out of 16). This change in the colour model attack rate by fish coincided with a naturally occurring reduction of visibility due to an algae bloom (Fig. 2).

Similar results were obtained in our smaller experiment in Asososca León. Of 20 models (10:10 dark/gold) deployed for 18 h, four dark (three by birds, one by fish), but no gold models were attacked.

DISCUSSION

Our experiments showed that predation is not selectively neutral with regard to the colour polymorphism in Midas cichlids. Yet, we find no support for the hypothesis that the more conspicuous, gold morph suffers a proportionally higher predation pressure than the more cryptic, but also much more abundant dark morph in this species. Previous research on Midas cichlids suggested that gold fish have a competition advantage over the more abundant dark fish (Barlow, 1973, 1983; McKaye & Barlow, 1976). Nonetheless, in nature gold individuals constitute only a small percentage of the population (Barlow, 1983). For example, we found that around 7% of the fish are gold in Asososca Managua, and this is one of the crater lakes with a relatively high proportion of gold fish (our pers. observ.; Barlow, 1973). It has been hypothesized that the competitive benefits of being gold might be counteracted by the costs of being relatively more conspicuous, thus suffering a higher predation rate. This balance between predation and competition was proposed to explain the apparent stability of dark fish being 10–20 times more common than gold individuals (Barlow, 1983; Kusche & Meyer, 2014). Based on our results and the results of previous studies (Kusche & Meyer, 2014), it would appear that the relative predation pressure upon the gold and dark colour morphs depends on the type of predator and the environmental condition, such as water clarity, affecting predator–prey interactions.

Predators that differ in their foraging preference can have different or even opposite effects on prey polymorphisms (Losey *et al*., 1997; McKillup & McKillup, 2008). For example, the few experiments conducted on predation upon Midas cichlid colour morphs showed that the identity of the predator affects the predation rate upon each colour morph (Annett, 1989; Kusche & Meyer, 2014). Besides predatory fish, Midas cichlids are also preyed upon by piscivorous birds, and therefore we designed our experiment to maximize the chances that models could be attacked both by avian and by fish predators. This would allow testing if the rate of attack on alternative colour morphs depended on the type of predator. Indeed, we found that avian and fish predators attacked Midas cichlid colour morphs differently. Avian predators had a strong preference for dark models, whereas fish predators did not show any colour bias. This result suggests caution when making generalizations about the consequences of predation on prey diversity if information on abundance and impact of different predators is not available. For example, water depth might be a relevant factor in the maintenance of the colour polymorphism in Midas cichlids if the relative impact of predators changes along this axis, as it is likely to do. This could be due to changes in the relative impact of birds versus fish predators at different water depth, or due to changes in the relative abundances of colour morphs in Midas cichlids along the water column as the gold morph is more common at greater depths (McKaye & Barlow, 1976; Elmer *et al*., 2009; Dittmann *et al*., 2012), although Midas cichlids of both morphs are commonly seen foraging at the surface of the water (see Supporting Information). Understanding the role of water depth on predation rate was beyond the scope of the present study, but future research should focus on this and other issues to better understand the interaction of predation and colour polymorphism in Midas cichlid fishes.

Our results also underline the importance of the visual environment, supporting the idea that conspicuousness is not absolute but depends on the surrounding conditions (Endler, 1978; Kekäläinen *et al*., 2010). This could reconcile our results with those of Kusche & Meyer (2014). They found that the Jaguar cichlid, the most common fish predator of Midas cichlids, attacked first gold-coloured goldfish over grey-coloured ones, which suggests that under their laboratory conditions gold-coloured fish where more conspicuous for this predator. We observed a marked reduction in the visibility of the lake during our study, and a correlated increase in the proportion of predatory fish attacks on gold models (Fig. 2). It appeared that as visibility in the lake decreased, gold fish became relatively more conspicuous, and therefore the main target of attack by predatory fish. A similar mechanism has been proposed as an explanation for

the positive correlation between water clarity and the relative abundance of the more conspicuous blotched morph found in several polychromatic species of Lake Victoria haplochromine cichlids (Seehausen & Bouton, 1996; Maan *et al.*, 2008). This mechanism would be in agreement with theoretical models suggesting that the stability of polymorphisms is dependent on the degree of difference in conspicuousness among morphs (Merilaita, 2006).

One question that arises from our findings is why the dark morph is preyed upon more often than the more conspicuous gold morph. Furthermore, if gold fish have a competitive advantage over dark fish (Barlow, 1973, 1983; McKaye & Barlow, 1976) and they are preyed upon less often than dark fish, then why do they constitute only a small fraction of the population? One potential interpretation of our results is that differential predation on colour morphs might be driven by the interaction of the relative abundances of the morphs and their difference in conspicuousness rather than just the difference in conspicuousness as had been hypothesized earlier (Barlow, 1983; Annett, 1989; Kusche & Meyer, 2014). The fact that predators overattacked the model simulating the most abundant, although less conspicuous, morph is in agreement with predictions of negative frequency-dependent selection (Allen, 1988; Bond, 2007). Because the dark model is always the most abundant morph in nature, we cannot test in the field the prediction that the dark morph would be overlooked if the gold morph was the most abundant. However, our smaller scale experiment in Asososca León confirmed our finding that the dark model is preyed upon more often. The fact that none of the gold models was attacked in Asososca León, where the gold morph is very rare (< 1%), would be in agreement with this hypothesis. Moreover, empirical studies (Bond & Kamil, 1998) and theoretical models (Franks & Oxford, 2009) suggest that the interaction of relative abundance and difference in conspicuousness might result in a stable polymorphism with the most conspicuous morph being rare, as seen in Midas cichlids.

In our study, we assume that for Midas cichlids natural predators, gold fish are more conspicuous against the environmental background coloration than dark fish, as is the case for the human eye. Two characteristics of the visual system of the predators support this assumption. First, like humans, fish and birds have trichromatic vision (tetrachromatic in some species), using three different types of photopigments with peak sensitivities at different regions of the light spectrum allowing them to see colours (Bowmaker, 1998; Hart, 2001; Carleton, 2009). Second, long-wave-sensitive visual pigments present both in avian (Hart, 2001) and in fish predators (Carleton, 2009) have peaks of maximal absorbance

that overlap with the peak of maximum reflectance of gold fish (560–640 nm; Kusche & Meyer, 2014). Thus, we consider that our assumption that gold fish are conspicuous is well founded. A second assumption of our design is that behavioural differences between gold and dark fish do not affect predation rate, at least not to the same degree as colour. Behavioural differences between prey morphs are known to affect detectability and therefore can influence predation rate on different morphs (Maan *et al.*, 2008; Isaac & Gregory, 2013). Laboratory behavioural studies suggest that gold fish are dominant over dark fish (Barlow, 1973, 1983), which could imply behavioural differences between morphs. It is currently unknown if morphs behave differently in nature, and if true, whether that would affect the rate of predation. Further studies are needed to determine the effect of behaviour on Midas cichlids predation risk.

The potential role of negative-frequency dependence on the maintenance of the colour polymorphism in Midas cichlids needs to be further tested, but our study provides a crucial step toward understanding the role of predation in this system by demonstrating that predation is not selectively neutral with regard to colour, that different predators impact colour morphs differently and that difference in conspicuousness between morphs depends on water clarity.

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