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The role of rare morph advantage and conspicuousness in the stable gold-dark colour polymorphism of a crater lake Midas cichlid fish

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Abstract

1. Genetically based stable colour polymorphisms provide a unique opportunity to study the evolutionary processes that preserve genetic variability in the wild. Different mechanisms are proposed to promote the stability of polymorphisms, but only few empirical examples have been documented, resulting in an incomplete understanding of these mechanisms.

2. A remarkable genetically determined stable colour polymorphism is found in the Nicaraguan Midas cichlid species complex (*Amphilophus* cf. *citrinellus*). All Midas cichlids start their life with a dark-grey coloration (dark morph), but individuals carrying the dominant "gold" allele (*c*. 10%) lose their melanophores later in life, revealing the underlying orange coloration (gold morph). How this polymorphism is maintained remains unclear. Two main hypotheses have been proposed, both suggesting differential predation upon colour morphs as the proximate mechanism. One predicts that the conspicuous gold morph is more likely to be preyed upon, but this disadvantage is balanced by their competitive dominance over the dark morph. The second hypothesis suggests a rare morph advantage where the rarer gold morph experiences less predation. Empirical evidence for either of these mechanisms is still circumstantial and inconclusive.

3. We conducted two field experiments in a Nicaraguan crater lake using wax models simulating both morphs to determine predation pressure upon Midas cichlid colour morphs. First, we tested the interaction of coloration and depth on attack rate. Second, we tested the interaction of fish size and coloration. We contrasted the pattern of attacks from these experiments to the predicted predation patterns from the hypotheses proposed to explain the colour polymorphism's stability.

4. Large models imitating colour morphs were attacked at similar rates irrespectively of their position in the water column. Yet, attacks upon small models resembling juveniles were directed mainly towards dark models. This resulted in a significant size-by-colour interaction.

5. We suggest that gold Midas cichlids experience a rare morph advantage as juveniles when individuals of this morph are extremely uncommon. But this effect is

reduced or disappears among adults, where gold individuals are relatively more common. Thus, the interaction of rare morph advantage and conspicuousness, rather than either of those factors alone, is a likely mechanism resulting in the stability of the colour polymorphism in Midas cichlids.

1 | INTRODUCTION

The maintenance of genetically based colour polymorphisms in nature is an interesting phenomenon and remains one of the major unresolved issues in ecology and evolution (Ford, 1945; Huxley, 1955; Mitchell-Olds, Willis, & Goldstein, 2007). A stable colour polymorphism is defined as the presence of two or more genetically determined colour morphs within a given population, the frequency of the rarest being too high to be explained solely by mutation (Ford, 1945; Huxley, 1955). Theory predicts that this genetic variation should be lost, either by drift if the variation is neutral, or due to the fixation of the morph with the highest fitness (Lande, 1975; Turelli & Barton, 2004). Different mechanisms have been postulated to explain the maintenance of colour polymorphisms (Gray & McKinnon, 2007), including heterosis (e.g. Tuttle, 2003), divergent selection (e.g. Nokelainen, Valkonen, Lindstedt, & Mappes, 2014; Rosenblum, 2006) and frequency-dependent selection (e.g. Olendorf et al., 2006). Often, the proximate mechanism involved in the maintenance of colour polymorphisms is differential predation pressure on different morphs (Bond, 2007).

Predators play a fundamental ecological role in the maintenance of interspecific (Paine, 1966; Ray, Redford, Steneck, & Berger, 2005) and intraspecific diversity (Bond, 2007). Yet, the specific mechanisms by which diversity is maintained by predation are far from simple and often are context dependent (Chesson, 2000). Predators may promote the stability of polymorphisms if different predators prey selectively upon different morphs (Losey, Ives, Harmon, Ballantine, & Brown, 1997; Nokelainen et al., 2014). Colour polymorphisms can also be associated with disruptive selection, and often predation plays an important role counterbalancing other selection pressures (Gray & McKinnon, 2007; Maan et al., 2008). Another way in which predation can lead to stable colour polymorphisms is negative frequency-dependent predation, often referred as apostatic selection (Merilaita, 2006; Punzalan, Rodd, & Hughes, 2005). It results when predators focus on the most abundant prey morph, overlooking those that are rare (Allen, 1988; Bond, 2007; Punzalan et al., 2005; Tinbergen, 1960); and empirical studies have shown that this is a plausible mechanism for maintaining genetic polymorphisms (e.g. Bond & Kamil, 1998; McKillup & McKillup, 2008; Olendorf et al., 2006; Takahashi & Kawata, 2013). All the above-mentioned mechanisms are commonly invoked to explain the stability of polymorphisms, but empirical examples are still scant, resulting in a still incomplete understanding of the maintenance of colour polymorphisms in the wild (Gray & McKinnon, 2007).

A remarkable stable colour polymorphism is found in the Midas cichlid fish species complex (*Amphilophus* cf. *citrinellus* Günther) of Nicaraguan lakes. Several species in this complex are polymorphic in terms of coloration, presenting mainly two morphs: "dark" (sometimes called "normal" as in polymorphic populations 90%–95% of the individuals have this coloration) and "gold" (Barlow, 1976). This polymorphism is inherited as a Mendelian trait, where the allele determining a gold phenotype is dominant (Henning, Renz, Fukamachi, & Meyer, 2010). All Midas cichlids start their life as melanic, dark-coloured fish, but at a size of 60 mm standard length or larger, genetically gold-coloured individuals begin to lose their melanophores, which are replaced by yellow/orange xanthophores (Dickman, Schliwa, & Barlow, 1988; Henning, Jones, Franchini, & Meyer, 2013). Thus, the proportion of gold individuals in a population varies among fish size classes. Gold Midas cichlids are extremely rare when small (less than one every 1,000) but significantly increase in frequency among adult fish (to about one in every 10 or 20 fish; Barlow, 1983; Torres-Dowdall, Machado-Schiaffino, Kautt, Kusche, & Meyer, 2014; A.M., pers. obs.).

Based on historical records, the low frequency of the gold morph in Midas cichlids is relatively constant across polymorphic populations and through time (Barlow, 1983; Elmer, Lehtonen, & Meyer, 2009; Wilson, Noack-Kuhnmann, & Meyer, 2000). Differential predation upon the two colour morphs has been proposed to play an important role for their coexistence (Barlow, 1983; McKaye, 1980; McKaye & Barlow, 1976) and empirical studies have confirmed that gold and dark morphs of Midas cichlids are not exposed to the same selection pressures due to predation (Annett, 1989; Kusche & Meyer, 2014; Torres-Dowdall et al., 2014). Several hypotheses have been proposed that differ in the relative importance of different types of predators (Barlow, 1983; McKaye, 1980; McKaye & Barlow, 1976), the distribution of predation risk across different water depths (McKaye, 1980) and the importance of predation across different size classes (Barlow, 1983). However, all of them can be grouped into two main categories depending on which morph is predicted to experience a higher predation risk.

On the one hand, Midas cichlids of the gold morph are predicted to suffer higher predation pressure than dark morphs as they are visually more conspicuous, at least to the human eye (Barlow, 1983; McKaye, 1980; McKaye & Barlow, 1976). Some support comes from

a laboratory experiment testing prey colour preference in the Jaguar cichlid (*Parachromis managuensis*), one of the most common predatory fish of Midas cichlids in the wild. Jaguar cichlids preferentially attack gold individuals first when it is offered a gold and a dark-bronze individual of the common goldfish (*Carassius auratus*; Kusche & Meyer, 2014). Nonetheless, other types of piscivorous predators do not preferentially attack gold Midas cichlids (Annett, 1989; Torres-Dowdall et al., 2014). Given that it is unknown which predators are the most important for the population dynamics of Midas cichlid populations, only limited inferences can be derived from these empirical studies.

On the other hand, if predators in the system form search images of their prey (Allen, 1988; Bond, 2007; Punzalan et al., 2005; Tinbergen, 1960), then the rarer morph, in this case, gold Midas cichlids are predicted to experience an overall lower predation rate. This rare morph advantage is an alternative mechanism by which the colour polymorphism in Midas cichlids can be maintained in the wild (Barlow, 1983; Torres-Dowdall et al., 2014). Yet, under a rare morph advantage, it would be expected that the gold morph increases in frequency to similar levels of the dark morph, which is not what is observed in polymorphic populations of Midas cichlids (Barlow, 1983). It is possible that the Midas cichlid polymorphism is maintained by an interaction between rare morph advantage and differences in detection probability of both morphs, in which conspicuous individuals are preyed upon more frequently unless they are very rare in the population (Bond & Kamil, 1998; Franks & Oxford, 2009). The expected outcome of this process is that the relative abundance of prey morphs is skewed towards the morph with the lowest detection probability (Bond & Kamil, 1998; Franks & Oxford, 2009). This possibility has not been tested in the Midas cichlid system yet.

The goal of our study was to determine how morph conspicuousness, relative abundance and their interaction affect predation on Midas cichlids. We measured predation risk by conducting field experiments using coloured wax dummy models simulating gold and dark individuals. We specifically tested: (i) what are the main predators of Midas cichlids? (ii) How does predation vary with depth? (iii) How does predation pressure change with Midas cichlid size? and (iv) how do these three factors affect the relative predation pressure on gold and dark morphs of Midas cichlids? If predators attack Midas cichlids based on conspicuousness, we expect wax models simulating the gold morph to be the target of most attacks, independently of model size and position in the water column. If Midas cichlids' predators attack preferentially the most abundant morph, then the model simulating the dark morph should receive the most attacks independently of model size and position in the water column. To test for an interaction between conspicuousness and relative abundance, we took advantage of the natural variation in the relative frequency of dark and gold fish across size classes. If both the relative abundance of morphs and their differences in detection probability affect predation pressure, we would expect a size-by-colour interaction with dark individuals being proportionally over-predated when small, but predation rates upon gold individuals should rapidly increase with fish size. This is expected because small gold individuals are extremely rare, but their relative abundance increases among bigger size classes.

2 | MATERIALS AND METHODS

2.1 | Study system

This study was conducted in the Crater Lake Asososca Managua, Nicaragua (12°09′N, 86°16′W). Asososca Managua is an extremely young (1245 ± 125 years old) and small (0.74 km^2) crater lake and with a maximum depth of 104 m (Kautt, Machado-Schiaffino, Torres-Dowdall, & Meyer, 2016; Pardo, Avellán, Macías, Scolamacchia, & Rodríguez, 2008). Access to the lake for the general public has been restricted for over 50 years, which has preserved the lowland tropical forest vegetation and also prevented hunting and fishing activities, resulting in the maintenance of terrestrial and aquatic fauna diversity (Martínez-Sánchez, Maes, van den Berghe, Morales, & Castañeda, 2001). The lake has relatively clear water due to its oligotrophic and oligomictic nature (Avilés-García & Peña-Martínez, 2000), and water clarity remained approximately constant throughout the duration of this study (Secchi disk measurements, mean = 4000 ± 400 mm).

There are only four species of fish known from Asososca Managua: *Atherinella sardina* (Atherinidae), *Gobiomorus dormitor* (Eleotridae), *P. managuensis* and *Amphilophus tolteca* (Cichlidae). *Amphilophus tolteca*, a newly described member of the Midas cichlid species complex, is endemic to this lake and has a characteristic dark coloration and elongated body shape (Kautt et al., 2016; Recknagel, Kusche, Elmer, & Meyer, 2013). As other, but not all, species in the Midas cichlid species complex, the *A. tolteca* population is polymorphic in terms of coloration, with the amelanic gold morph representing only about 7% of the total population (Torres-Dowdall et al., 2014).

The Jaguar cichlid (*P. managuensis*) and the bigmouth sleeper (*G. dormitor*) are piscivorous fish that often prey upon Midas cichlids. Bigmouth sleepers are commonly observed preying upon small sized cichlids, including larvae or juveniles. Although bigmouth sleeper fish found in crater lakes are of a medium size (mean standard length ± SD = 160.29 ± 15.68 mm, gape height ± SD = 16.60 ± 2.45 mm, n = 9), there has been reports of fish large enough to be a danger to adult Midas cichlids (standard length >250 mm; Barlow, 1976; Nordlie, 2012). This predatory species rests on the substrate in open areas and strikes prey from large distances (Winemiller & Ponwith, 1998). The Jaguar cichlid can attain very large sizes under laboratory conditions, allowing them to consume medium to large size adult Midas cichlids (mean standard length ± SD = 268.26 ± 35.87 mm, gape height ± SD = 44.58 ± 4.83 mm, n = 6, J.T.D., pers. obs.). In the wild, Jaguar cichlids are commonly smaller but in some cases, they do reach large sizes (mean standard length ± SD = 190.77 ± 37.39 mm, n = 79, J.T.D., pers. obs.). Previous reports have suggested that Jaguar cichlids could consume prey that are up to 38% of their standard length, suggesting that the largest fish could prey upon adult Midas cichlids (*c.* 113 mm standard length; Barlow, 1976). This piscivorous fish is a rover predator, commonly found in the littoral zone of the lakes where it cruises and explosively attacks close by prey (J.T.D., pers. obs.). Additionally, the American crocodile (*Crocodylus acutus*) and an aquatic turtle (probably *Kinosternon scorpioides* and/or *Chelydra serpentina*) inhabit Asososca Managua (J.T.D., pers. obs.).

We conducted a short bird survey to evaluate the diversity and abundance of potential avian predators. The results of this survey are presented in the Supporting Information online (Figure S1). A short video illustrating the underwater environment of Crater Lake Asososca Managua, including observations of gold and dark Midas cichlids and a Jaguar cichlid is presented in the Supporting Information online (Video S1).

2.2 | Wax model design

We placed realistic wax models of the two different colour morphs of *A. tolteca* in its natural habitat and studied attack marks (as a proxy for predation rate) left by different predators. These models were produced following previously described protocols (Rowland, 1979; Torres-Dowdall et al., 2014; Figure 1). In brief, silicone moulds of different sizes were made from *A. tolteca* specimens (euthanized with an overdose of MS222 and preserved in ethanol 75%). We produced three moulds of the larger size and one mould of each of the smaller size (see below for size description). Liquid wax was poured into the moulds to produce the models. We coloured wax with standard orange pigment to produce "gold-morph" models and with ground charcoal to produce the dark models (2 g of pigment per 100 ml of melted wax was used). Photos and spectral reflectance of the wax models are presented in the Supporting Information online (Figure S2).

Models were placed in the Crater Lake Asosoca Managua following Torres-Dowdall et al. (2014) with certain modifications (see description of the two experiments below). In short, we suspended individually numbered models in the water column 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. We used grey pipes because they were inconspicuous, at least to the human eye, against the water column background and they were not visible from the water surface. Pipes were randomly distributed in different positions along the lake, with a minimum distance from the shore of 5 m, but attached to littoral vegetation (e.g. tree branches and bushes), assuring that there were enough perches for avian predators. 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, and thus aerial predators would potentially see the models floating in the water column. On the other hand, aquatic predators would have to detect models against either the water column, sky or against the underwater walls of the crater lake, depending on the position of the predator itself.

2.3 | Experiment 1: Effect of colour and depth on predation

The aim of our first experiment was to test if predation pressure on Midas cichlids varies with depth, and moreover, if the relative predation on the colour morphs changes in relation to depth. For this experiment, we used dark- and gold-coloured models of 120 mm length, which is approximately the average size for *A. tolteca* adults (mean standard length = 118 ± 13 mm, Recknagel et al., 2013). We placed the wax models in 20 floating units; each composed of a pair of models (one gold and one dark) positioned 150 mm below the water surface, and a second pair 3 m below the water surface (Figure 1a). This depth was chosen because Midas cichlids are very abundant at this depth (Dittmann et al., 2012; but depth distribution is unknown in Asososca Managua), and some of the piscivorous bird species found in the lake can dive at least this deep (Quintana, Yorio, Lisnizer, Gatto, & Soria, 2004). Floating experimental units were randomly distributed in different positions along the shore of the lake. We checked all models for marks of attacks every third day over 12 sampling events, for a total of 960 observations (12 sampling events × 20 floating units × 4
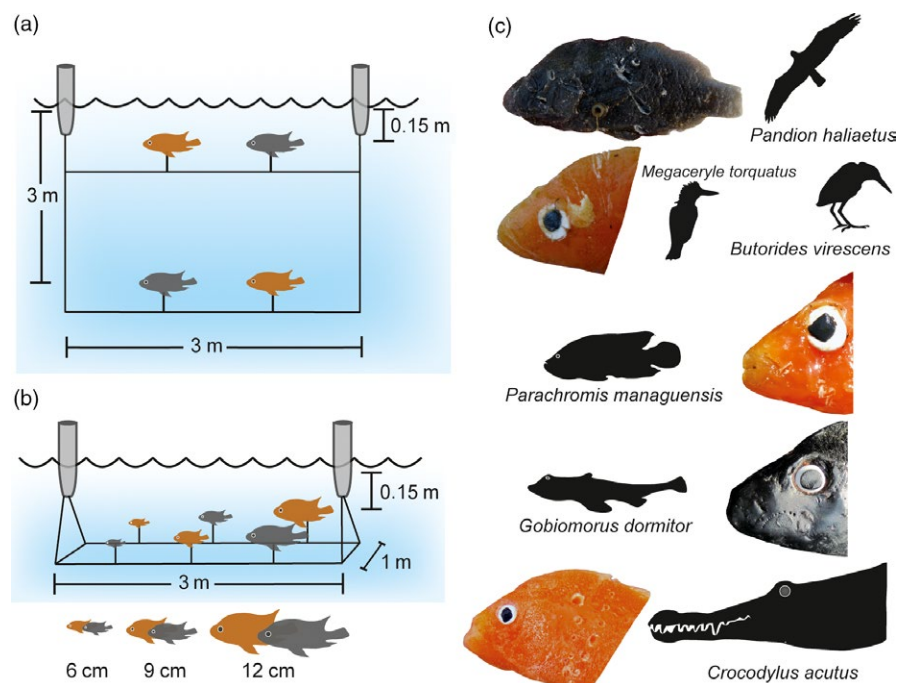

FIGURE 1 Experimental set-ups of wax models to test Midas cichlid fish predation risk. (a) We set models at the surface and 3 m deep to test how predation risk changes with depth (experiment 1). (b) We used three different sizes of models to determine how predation changes with prey size (experiment 2). (c) Fish and birds attacked most of the models of Midas cichlids

wax models). Attacks were identified in the field based on teeth or beak impressions left on the wax models and assigned to four predator categories: bird, fish, crocodile and turtle following Torres-Dowdall et al. (2014; Figure 1c). Some attacks (n = 7) were the probable result of intraspecific aggression rather than predation attempts and were therefore excluded from our analyses to avoid bias. Intraspecific aggression is often directed towards the sides and caudal peduncle of the fish (J.T.D., pers. obs.), and therefore could be distinguished from predatory attacks that are mainly directed towards the head of the fish (Torres-Dowdall et al., 2014). Every attacked model was collected, photographed, numbered and replaced by a new unmarked model. Missing models (n = 13) were also immediately replaced with new ones to ensure consistent presentation to predators, but missing models were not considered as attacks in our analyses.

2.4 | Experiment 2: Effect of colour and size on predation

For our second experiment, we created different silicone moulds representing fish of small, medium and large size (Figure 1b). The largest size class (120 mm) matches the most common size of fish of either colour morphs found in Asososca Managua (Recknagel et al., 2013), the intermediate models (90 mm) represent a common size at which several genetically gold Midas cichlid transform, and the smallest models (60 mm) represents a stage at which gold individuals occur very rarely (Torres-Dowdall et al., 2014; Henning F, Meyer A, unpublished; J.T.D., pers. obs.). Thus, the smaller size used is an approximation to the earliest size at which transformed Midas cichlids can be observed in the wild. We placed pairs (gold and dark) of models of the three different sizes on a floating unit (Figure 1b) and replicated it for a total of ten units.

All fish models were placed at 150 mm depth, which exposes models to both, bird and fish predator (see Results). We checked the models every third day for signs of attacks and repeated it on six occasions for a total of 360 observations (6 sampling events × 10 floating units × 6 wax models). As described before, missing models (n = 4) were rapidly replaced, but were not considered as attacks in our analyses.

2.5 | Statistical analyses

We analysed predator attacks using generalized linear mixed models (glmer) with binomial error distribution as implemented in package lme4 in R (Bates, D., Maechler, M., Bolker, B., & Walker, S., 2015a, Bates, D., Maechler, M., Bolker, B.M., & Walker, S., 2015b). Colour, depth in the water column (in experiment 1), model size (in experiment 2) and their interactions were treated as predictor variables, floating unit as a random intercept, and presence or absence of attacks was included as the response variable. The significance of individual predictor variables was tested using likelihood ratio tests (LRT) that compare the likelihood of a model including the term of interest to that of a reduced model lacking that term (Pinheiro & Bates, 2009). LRT were computed as implemented in package lme4 in R (Bates et al., 2015a,b). In all cases, the model of interest was also compared to a null model including only the random intercepts. LRT are presented in the text and the estimates and standard errors of the fixed effects in Table 1. These analyses were performed including all pooled attacks, and then repeated separately for avian and fish attacks. None of the wax model placed at 3 m of depth was attacked by birds. Therefore, when analysing birds' attacks in experiment 1, we only included colour as a predictor variable.

When considering only fish' attacks at different sizes (i.e. experiment 2), none were directed towards large, dark models. The lack of

TABLE 1 Estimates and standard errors for factors affecting the probability of models being attacked by all predators, only by piscivorous birds and only by piscivorous fish. The effects on the probability of being attack of wax model colour (i.e. gold or dark), depth at which wax models were placed (i.e. 150 mm or 3 m) and wax model size (i.e. 60 mm, 90 mm or 120 mm) were tested using generalized linear mixed models with binomial error distribution. Experiment 1 tests the effects of wax model colour, position in the water column and their interaction. Experiment 2 tests the effects of colour and size of the models and their interaction

	All attacks			Avian attacks[a]			Fish attacks		
	Estimate (SE)	z	p	Estimate (SE)	z	p	Estimate (SE)	z	p
Experiment 1									
Intercept	−1.775 (0.195)	−9.08	<.001	−2.842 (0.285)	−9.96	<.001	−2.349 (0.237)	−9.91	<2e−16
Colour$_{gold}$	0.094 (0.256)	0.37	.714	−0.650 (0.478)	−1.36	.174	0.435 (0.300)	1.45	.147
Depth$_{3m}$	0.210 (0.251)	0.84	.403	–	–	–	0.670 (0.290)	2.31	.021
Colour$_{gold}$ × Depth$_{3m}$	−0.024 (0.351)	−0.07	.945	–	–	–	−0.362 (0.390)	−0.93	.353
Experiment 2									
Intercept	−2.642 (0.520)	−5.08	<.001	−3.297 (0.834)	−3.95	<.001	−4.094 (1.008)	−4.06	<.001
Colour$_{gold}$	0.442 (0.673)	0.66	.511	−0.327 (0.814)	−0.40	.688	1.438 (1.133)	1.27	.205
Size$_{medium}$	1.297 (0.611)	2.12	.034	−1.433 (1.154)	−1.24	.214	2.729 (1.059)	2.58	.010
Size$_{small}$	3.720 (0.601)	6.19	<.001	0.732 (0.691)	1.06	.289	4.787 (1.045)	4.58	<.001
Colour$_{gold}$ × Size$_{medium}$	−0.709 (0.824)	−0.86	.390	0.256 (1.656)	0.15	.877	−1.702 (1.228)	−1.38	.166
Colour$_{gold}$ × Size$_{small}$	−1.828 (0.783)	−2.33	.020	−1.130 (1.179)	−0.96	.338	−2.467 (1.195)	−2.06	.039

[a]No attacks by birds were observed at 3 m of depth.

observations in one of the factor levels may cause problems with the estimation of standard error of model parameters, especially when interactions between predictor variables are included in the model (Agresti, 1996; Suchower & Copenhaver, 1997). This was the case when testing for the interaction between model size and colour in the probability of being attacked by piscivorous fish, but not when considering only the additive effects of these two predictor variables (Table S1). In these cases, the presence of the interaction can still be tested with a LRT comparing models with and without the interaction. A model including the interaction between colour and size received significant more support than a model only including the additive effect of these two variables (glmer: $\chi^2 = 8.09$, $df = 2$, $p = .0175$). Thus, in order to obtain meaningful estimates and standard errors for the full model, we added one positive value (i.e. an attack) to all the factor levels and reran the models (Agresti, 1996; Suchower & Copenhaver, 1997).

3 | RESULTS

In both field predation experiments, we found clear marks of attack from different predator types, predominantly from fish and birds. From a total of 1,320 observations in the two experiments, we observed attack marks on 261 occasions. When considering all the attacks from both experiments, independently of the size or the depth at which wax models were placed, fish attacked them significantly more frequently (16.3%) than birds (2.9%; $\chi^2 = 134.93$, $df = 1$, $p < .0001$). This difference was maintained even when considering only models positioned at the surface (fish: 16.3%, birds: 4.6%, $\chi^2 = 60.95$, $df = 1$, $p < .0001$). Below, we present the results for the two experiments as well as for fish and birds' attacks separately.

3.1 | Experiment 1: Effect of colour and depth on predation

The number of attacks on gold and dark models of *A. tolteca* positioned at two depths in the water column was noted (Figure 1a). Out of 960 exposed models, 160 showed marks of attacks (*c.* 17%). Of these, 130 models were attacked by fish, 21 by birds, 7 by turtles and 1 by a crocodile. When all the attacks were analysed together, we found that a model including the effects of wax model colour and depth did not explain the variation on attack rate better than the null model including only the random intercepts (glmer: $\chi^2 = 1.49$, $df = 3$, $p = .68$, Table 1, Figure 2). However, we found significant differences in the pattern of attack when analysing birds and fish separately.

When considering models attacked by birds, we found 20 attacks on models placed at the surface, but no attacks on models at 3 m depth (Figure 2). The model considering the effect of colour did not explain variation better than the null model including only the random intercepts (glmer: $\chi^2 = 1.93$, $df = 1$, $p = .16$, Table 1).

Piscivorous fish attacked models at both positions in the water column, but models located at deeper waters more often (glmer: $\chi^2 = 6.09$, $df = 1$, $p = .0136$, Table 1, Figure 2). Of the models attacked by fish, 60% were at 3 m depth and 40% were at the surface. Piscivorous fish
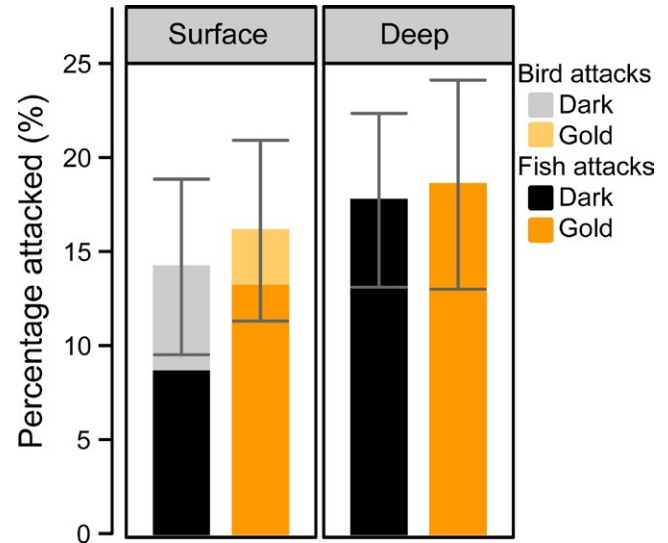

FIGURE 2 Cumulative percentage of attacked wax models when positioned at two different depths (experiment 1). Gold and dark wax models simulating Midas cichlid fish were attacked at an equal rate, both, when positioned at the surface or 3 m deep in the water column. Piscivorous birds attacked exclusively models at the surface and fish attacked models at both levels, but preferentially in the deep. Error bars depict variation on the cumulative percentage of attack models across sampling events (95% confidence interval)

attacked models of both colours at a similar rate (glmer: $\chi^2 = 1.36$, $df = 1$, $p = .24$), and independently of the depth at which they were placed (colour-by-depth interaction: glmer: $\chi^2 = 0.87$, $df = 1$, $p = .35$).

3.2 | Experiment 2: Effect of colour and size on predation

The number of attacks on gold and dark models of *A. tolteca* of three different sizes was quantified (Figure 1b). The attack rate was high, with 101 attacks out of 356 exposed models (*c.* 28% attack rate, four models were lost; Figure 3). When considering all attacks, there was a significant effect of model size on the likelihood of being attacked by predators (glmer: $\chi^2 = 83.59$, $df = 1$, $p < .0001$, Table 1), with most of the attacks being directed towards small models (*c.* 68%), medium size models receiving fewer attacks (*c.* 22%) and large models were attacked the least (*c.* 10%, Figure 3). Overall, there was support for differential predation between colour morphs (glmer: $\chi^2 = 6.79$, $df = 1$, $p = .0092$); but this effect was driven by differential attack upon the small size models (interaction between model size and colour: glmer: $\chi^2 = 6.83$, $df = 2$, $p = .0328$, Table 1, Figure 3). Among the small size class, dark models were attacked more often than gold models (glmer: $\chi^2 = 12.86$, $df = 1$, $p = .0003$), but no differences between colour morphs were found in the medium (glmer: $\chi^2 = 0.40$, $df = 1$, $p = .52$) or in the large (glmer: $\chi^2 = 0.44$, $df = 1$, $p = .51$, Figure 3) size classes.

When analysing the data by predator type, we found that birds only attacked 18 models (*c.* 5% attack rate) and fish attacked 86 models (*c.* 24% attack rate; three models were attacked both by birds and fish). The number of attacks by birds was too small to detect any statistical
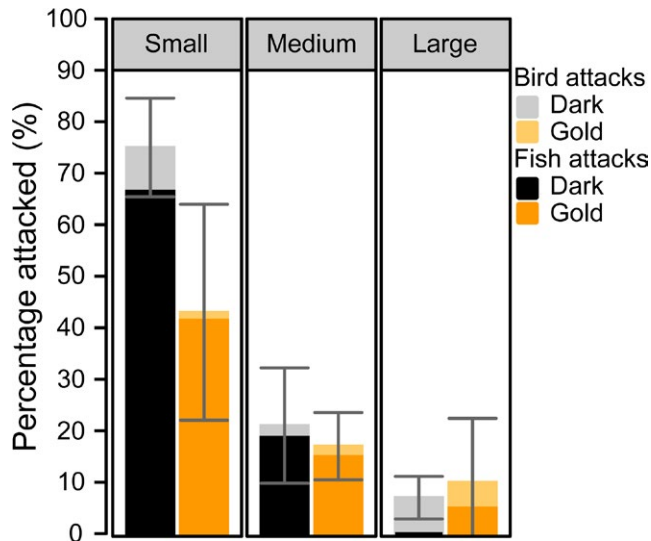
FIGURE 3 Cumulative percentage of attacked gold and dark wax models of three different sizes (experiment 2). Small, dark models were attacked the most when compared to small, gold models. No difference in the percentage of gold and dark models is observed in the bigger size classes, resulting in a significant colour-by-size interaction. Error bars depict variation on the cumulative percentage of attack models across sampling events (95% confidence interval)

effects of colour, size or their interaction and the full model did not explain the observed variation on attack rate better than the null model including only the random intercepts (glmer: $\chi^2 = 9.17$, $df = 5$, $p = .102$, Table 1, Figure 3). On the other hand, piscivorous fish differentially attacked models based on size (glmer: $\chi^2 = 89.67$, $df = 2$, $p <.0001$, Table 1), with most of the attacks on small models (c. 73% of the attacks), less attacks upon medium-sized models (c. 23% of the attacks) and almost no attacks on large-sized models (c. 4% of the attacks, Figure 3). Piscivorous fish preferentially attacked dark models (glmer: $\chi^2 = 3.95$, $df = 1$, $p = .0470$), but this effect was driven by attacks upon the smaller size class (interaction between model size and colour: glmer: $\chi^2 = 6.01$, $df = 2$, $p = .0496$, Table 1, Figure 3). Among the small size class, piscivorous fish attacked dark models more often than gold models (glmer: $\chi^2 = 7.74$, $df = 1$, $p = .0054$) but no differences between colour morphs were found in the medium size class (glmer: $\chi^2 = 0.41$, $df = 1$, $p = .52$). Among the large size class, there were only three attacks on gold models and no attacks on dark ones (Figure 3).

4 | DISCUSSION

Conducting field experiments using coloured wax models as dummies, we found that predation pressure upon a Midas cichlid species from a clear water crater lake is contingent on the identity of the predator and the size and colour morph of the prey. Piscivorous fish were found to be the most important predator of this Midas cichlid species, attacking preferentially smaller, dark-coloured models. Yet, the preference for dark models disappeared in medium and large size classes. Thus, the role of predation in the maintenance of the colour

polymorphism seen in Midas cichlids might be more complex than originally proposed under the assumption of gold individuals being more conspicuous (Annett, 1989; Barlow, 1976; Kusche & Meyer, 2014; McKaye, 1980; McKaye & Barlow, 1976; Torres-Dowdall et al., 2014). Our study highlights the importance of validating in the field preconceptions about the relative conspicuousness of prey morphs and its relation to predation risk.

The earliest considerations of predation as a key driver of the maintenance of Midas cichlids colour polymorphism proposed that gold Midas cichlids should be more noticeable to visually oriented predators and thus the target of more predatory attacks (Barlow, 1976; McKaye, 1980; McKaye & Barlow, 1973, 1976). This disadvantage of being gold might compensate for the competitive advantage that gold individuals have over dark ones (Barlow, 1973; Barlow & Ballin, 1976; Barlow & Wallach, 1976; Lehtonen, 2014; McKaye & Barlow, 1976). In particular, visually oriented piscivorous birds were predicted to be the main predators of Midas cichlids and that they would preferentially attack individuals of the conspicuous gold morph in shallow waters (McKaye, 1980). This hypothesis provided an adaptive explanation for why gold-coloured individuals tend to breed at greater depths than dark-coloured individuals (McKaye & Barlow, 1976), as by nesting deeper they could escape intense bird predation (McKaye, 1980). Piscivorous birds are known to be the top predators in several freshwater ecosystems (Steinmetz, Kohler, & Soluk, 2003) and to attack morphs of polymorphic species differentially based on coloration (Maan et al., 2008); thus, this was a likely mechanism involved in the maintenance of Midas cichlid colour polymorphism. However, our results suggest that in Asososca Managua piscivorous fish are more important predators of Midas cichlids than piscivorous birds. We found that fish attacked our models six times more frequently than birds, and still two times more frequently when considering only models positioned at the surface of the water (Figure 2). The attack rate by birds was lower in this study (2.2%) than previously found in this system (7.3% in Torres-Dowdall et al., 2014), which might be explained by seasonal changes in bird assembly. Asososca Managua has a rich avian community that includes several migratory piscivorous species (Figure S1), and seasonal variation in predation pressure due to the migration of predators has the potential to promote biodiversity (Bauer & Hoye, 2014; Mappes, Kokko, Ojala, & Lindström, 2014). Nonetheless, even when piscivorous birds are at their peak of abundance in the crater lakes, they do not preferentially prey on gold individuals of this Midas cichlid species (Torres-Dowdall et al., 2014). Hence, since piscivorous birds are not the main predators of Midas cichlids and they do not preferentially prey on individuals of the gold morph; avian predation is an unlikely mechanism to contribute to the maintenance of the colour polymorphism in Midas cichlids. However, it will be necessary to validate the generality of this finding in other Midas cichlid species.

Another factor known to affect predation risk is microhabitat selection (Swain, Benoît, & Hammill, 2015). It was hypothesized that the depth of Midas cichlids in the water column could influence both overall predation pressure and relative predation on the gold and dark individuals (McKaye, 1980; Torres-Dowdall et al., 2014). This could be due to either a change in the identity of predators (e.g. from birds to

piscivorous fish), or because changes in light conditions might result in reduced differences in the detection probability of both colour morphs (Kirk, 2010). We found a strong effect of depth on the identity of the predator. Birds (judging from the beak marks, different species of heron and kingfishers) exclusively attacked models positioned at the surface. This result reinforces our previous conclusion that birds would have only a limited impact on Midas cichlids populations given that these fish are widely distributed in the water column (Dittmann et al., 2012; McKaye & Barlow, 1976). On the other hand, piscivorous fish attacked models at both depth levels, but preferentially attacked those located deeper in the water column, possibly trying to avoid being preyed upon themselves by avian predators. Yet, the overall attack rates on models positioned at the surface or 3 m deep were rather similar, suggesting that predation pressure is relatively constant across these depths (Figure 2). Moreover, the attack rate on gold and dark models was the same irrespective of depth (Figure 2). A caveat to this interpretation is that our design only covered the first 3 m of the water column. In Asososca Managua, average breeding depth of Midas cichlids is unknown, but in other crater lakes they are known to breed in much deeper waters (Elmer et al., 2009; McKaye & Barlow, 1976). Nonetheless, our results from Asososca Managua suggest that in shallow waters predators do not preferentially attack gold Midas cichlids.

We found that predators attacked models of the smallest size more eagerly and often ignored larger models in the vicinity. This result is not surprising given that most of the piscivorous fish in the system are expected to be gape-limited (Barlow, 1976, 1983; also see *Study system* above). More interestingly, we found a significant size-by-colour interaction effect on attack rate on models. Within the models that were attacked, the percentage of attacks upon gold models was only *c*. 36% among the smallest models, but rose to *c*. 45% among medium size ones, and reached *c*. 60% of the attacks upon the largest models (although not significantly different from random; Figure 3). This pattern of attacks is expected under rare morph advantage with difference in prey conspicuousness (Bond & Kamil, 1998; Franks & Oxford, 2009). In nature, gold individuals of the size of our smallest models are extremely rare (less than one in a 1,000), as most genetically gold individuals have not yet transformed; hence, this is the size class at which frequency-dependent effects are expected to be most significant. However, in bigger size classes, the proportion of gold individuals increases as more genetically gold fish transform, so the strength of the rare morph advantage should rapidly weaken and conspicuous individuals should become a common target of predatory attacks. Apostatic selection with difference in detection probability among morphs is then a plausible mechanism to explain both, the size-by-colour pattern of predation observed in our study, and the long-term stability of Midas cichlids colour polymorphisms with the more conspicuous gold morph being rare in all populations. Yet, as manipulation of the relative abundance of gold and dark fish in the wild is not feasible, it remains an open question if by increasing the frequency of the gold morph they would become the main target of attacks as it would be predicted by apostatic selection.

Prey detection by visually oriented predators in the wild is most likely influenced by background matching ability. Dark, melanic Midas cichlids are known to match the background by changing luminance

and pattern of body coloration from spotted, to barred, to completely dark (Barlow, 1976; Dickman, Annett, & Barlow, 1990; Sowersby, Lehtonen, & Wong, 2015). Once transformed, gold Midas cichlids lose their melanophores and therefore the ability to change body coloration. In our study, we only simulated the extreme phenotypes: the amelanic gold phenotype and the melanic, completely dark phenotype. Thus, it is possible that our experiments overestimated predation on the melanic, dark morph. If background matching ability results in melanic individuals being extremely cryptic, then apostatic selection might become less plausible as an explanation for the maintenance of the Midas cichlids colour polymorphism. Future studies incorporating variation on wax models simulating the different patterns of melanic Midas cichlids (i.e. spotted and barred colour patterns) might help to determine the generality of our results.

Predation has been hypothesized to play a major role in the stability of the Midas cichlids' colour polymorphism, yet several aspects of predation were poorly understood in this system. Our results suggest that clarifying the role of predation will require a better knowledge of the piscivorous fish inhabiting Nicaraguan lakes (i.e. *P. managuensis*, *P. dovii*, and *G. dormitor*), as these seem to represent the most important predators of Midas cichlid fish. It should also be noted that adult Midas cichlids often prey on smaller Midas cichlids. Moreover, we suggest that the interaction of rare morph advantage and difference in detection probability between dark and gold morphs, rather than either of those factors alone, is a likely mechanism resulting in the stability of the Midas cichlids colour polymorphism. Increased survival of small, gold Midas cichlids might have important implications for the maintenance of the colour polymorphism because very few Midas cichlids reach adulthood and surviving the juvenile stage is of major importance, as indicated by the strong difference seen in attack risk among size classes (Figure 3). Additionally, there appear to be a dosage effect of the gold allele and homozygote gold transform earlier than heterozygotes (Henning F, Meyer A, unpublished). Therefore, if predation is lower in small, gold fish, then homozygote gold might have enhanced survival compared to heterozygotes or homozygote dark. Yet, still remains unclear how background matching (Dickman et al., 1990; Sowersby et al., 2015) and changes in environmental conditions (e.g. seasonal changes in water clarity due to algae blooms or bank erosion during wet season; Torres-Dowdall et al., 2014) affect the visual detection of prey, and aquatic and avian predators might respond differently to these factors.

The maintenance and the relative abundance of different colour morphs within populations likely depend on the interaction of multiple factors (e.g. Gray & McKinnon, 2007; Lattanzio & Miles, 2014). Assortative mating (Barlow, 1976; Elmer et al., 2009; McKaye & Barlow, 1976) and ecological differentiation between morphs (Klingenberg, Barluenga, & Meyer, 2003; Kusche, Elmer, & Meyer, 2015; Meyer, 1990) might also contribute to the maintenance of colour polymorphism in Midas cichlids. Disentangling these factors might be challenging, especially if the goal is to understand how colour polymorphisms persist in the wild. Field experiments that take advantage of the natural variation in morph relative abundances, and simultaneously consider different factors are likely to further our understanding of this problem. By taking such an approach, we were able to contrast predictions from

several hypotheses postulated to explain the maintenance of Midas cichlids colour polymorphism against data collected under natural conditions, which allowed us to reject some of those hypotheses and to refine the focus of future research in the system.

AUTHORS' CONTRIBUTIONS

J.T.D., G.M.S. and A.M. conceived the ideas and designed the methodology; J.T.D., J.G.B., G.M.S and A.M collected the data; J.T.D. and J.G.B. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data from the full experiment available from the Dryad Digital Repository https://doi.org/10.5061/dryad.9gv03 (Torres-Dowdall, Golcher-Benavides, Machado-Schiaffino, & Meyer, 2017).

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