


Visual illusions in predator–prey interactions: birds find moving patterned prey harder to catch

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Abstract Several antipredator strategies are related to prey colouration. Some colour patterns can create visual illusions during movement (such as motion dazzle), making it difficult for a predator to capture moving prey successfully. Experimental evidence about motion dazzle, however, is still very scarce and comes only from studies using human predators capturing moving prey items in computer games. We tested a motion dazzle effect using for the first time natural predators (wild great tits, *Parus major*). We used artificial prey items bearing three different colour patterns: uniform brown (control), black with elongated yellow pattern and black with interrupted yellow pattern. The last two resembled colour patterns of the aposematic, polymorphic dart-poison frog *Dendrobates tinctorius*. We specifically tested whether an elongated colour pattern could create visual illusions when combined with straight movement. Our results, however, do not support this hypothesis. We found no differences in the number of successful attacks towards prey items with different patterns (elongated/interrupted) moving linearly. Nevertheless, both prey types were significantly more difficult to catch compared to the uniform brown prey, indicating that both colour patterns could provide some benefit for a moving individual. Surprisingly, no effect of background (complex vs. plain) was found. This is the first

experiment with moving prey showing that some colour patterns can affect avian predators' ability to capture moving prey, but the mechanisms lowering the capture rate are still poorly understood.

Keywords Aposematism · Colour polymorphism · Motion dazzle · Predator–prey interactions · Visual illusions

Introduction

Animal colouration has several different functions and the potential to affect an individual's fitness significantly (Cott 1940). One important role of colouration is predator avoidance. Among the various antipredator strategies related to prey colouration, aposematism and camouflage are probably the most studied (Poulton 1890; Cott 1940; Ruxton et al. 2004). Aposematic species advertise their unprofitability (e.g. toxicity) with warning signals (Poulton 1890), so that predators learn to avoid them. These signals are often conspicuous and brightly coloured. Camouflaged species, on the other hand, rely on colouration that makes them hard to detect or recognize by predators (Cott 1940), thereby reducing the chance of being attacked. In addition to these effects, which are thought to work when animals are still, it has been suggested that colouration could have a different function when an individual is moving (Thayer 1909; Stevens 2007; Kelley and Kelley 2014). Because detection by predators is often likely during movement (Sih 1984), it would be beneficial for prey to have colour patterns that hinder capture once detected. Some patterns are thought to protect moving individuals by creating visual illusions, effects that may alter the perception of the viewer (Kelley and Kelley 2014). Such illusions may, for example,

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make it difficult for a predator to judge the speed and direction of prey with certain markings (Stevens 2007; Kelley and Kelley 2014), a phenomenon called motion dazzle. These markings include bars, stripes and zigzag patterns, which are all common in the animal kingdom (Cott 1940), indicating that the motion dazzle effect could potentially work in a variety of species.

Some observational studies have found a correlation between animal escape behaviour, or type of movement, and colour patterns (Jackson et al. 1976; Pough 1976; Brodie 1992; Allen et al. 2013; Rojas et al. 2014). For example, Jackson et al. (1976) examined the colour patterns and behaviour of several snake species in northern Mexico and found that those with striped patterns, as well as uniformly coloured species, were likely to rely on fleeing as their antipredator strategy. Species with blotched or spotted patterns, in contrast, rely on the disruptive elements of their colouration to avoid detection by predators in the first place. In a more recent study, Allen et al. (2013) found the same association of longitudinal stripes and rapid escape speed in Australian and North American snakes. Jackson et al. (1976) suggested that uniform and striped patterns are suitable for a rapid escape as a primary defence because these patterns could generate the illusion of immobility in an individual moving rapidly. They concluded that this phenomenon occurs because these patterns do not have any reference points that allow an observer to detect forward movement (Jackson et al. 1976). Therefore, these patterns could elevate the threshold velocity for movement recognition and confuse predators. This idea obtained support when Brodie (1989) found that colour pattern and antipredator behaviour were genetically correlated in colour polymorphic, nonaposematic garter snakes (*Thamnophis ordinoides*). Again, individuals with striped patterns relied on direct flight, whereas individuals with unmarked, spotted or broken patterns showed more cryptic behaviour, changing direction during flight. Both combinations seemed to increase the survival of individuals (Brodie 1992), and therefore, Brodie suggested that correlational selection could be the mechanism favouring them.

Although there are several studies about motion dazzle (e.g. Jackson et al. 1976; Pough 1976; Brodie 1992), most of them have provided only correlational evidence of an association between colour patterns and behaviour. All the experimental studies to date have used games with humans as predators, trying to catch computer-generated moving prey with different colour patterns (Stevens et al. 2008, 2011; Scott-Samuel et al. 2011; von Helversen et al. 2013; Hughes et al. 2014). These studies have provided some evidence of motion dazzle, showing that high-contrast patterns (e.g. bands, stripes and zigzag patterns) are more difficult to capture compared to conspicuous uniform colouration (Stevens et al. 2008, 2011). In contrast, von

Helversen et al. (2013) found that longitudinally and vertically striped objects were actually captured more easily compared to objects with uniform colouration.

Motion dazzle, however, has never been tested experimentally with any predators other than humans. There are many between-species differences in visual systems (Cuthill et al. 2000; Stevens 2007; Kelley and Kelley 2014), and visual illusions could be perceived in different ways across species (Nakamura et al. 2006; Pepperberg et al. 2008; Watanabe et al. 2011, 2013). Knowing that birds are capable of detecting movement and recognize objects in motion (Dittrich and Lea 2001), we tested for the first time how avian predators respond to possible visual illusions by using wild great tits (*Parus major*). Birds are an important predator group for many species in different taxa (e.g. Niskanen and Mappes 2005; Noonan and Comeault 2009; Nokelainen et al. 2014), and therefore, an experiment with bird predators may provide relevant information about how motion dazzle works in nature.

To make the situation more realistic, we used colour patterns that exist in nature. Previous studies with humans and computer games (Stevens et al. 2008, 2011; Scott-Samuel et al. 2011; von Helversen et al. 2013) have all used simplified black and white patterns, for example, longitudinal and vertical stripes. However, to avoid any direct interference from the birds' previous experience, we chose patterns that came from an organism they could not have encountered before, the aposematic poison frog *Dendrobates tinctorius* (Fig. 1). *Dendrobates tinctorius* has yellow and black dorsal colour patterns that vary significantly within (Rojas and Endler 2013) and among populations (Wollenberg et al. 2008). It is diurnal and field experiments with plasticine models suggest that it may suffer attacks from birds (Noonan and Comeault 2009). In a previous study, Rojas et al. (2014) found a connection between colour pattern geometry and movement type of

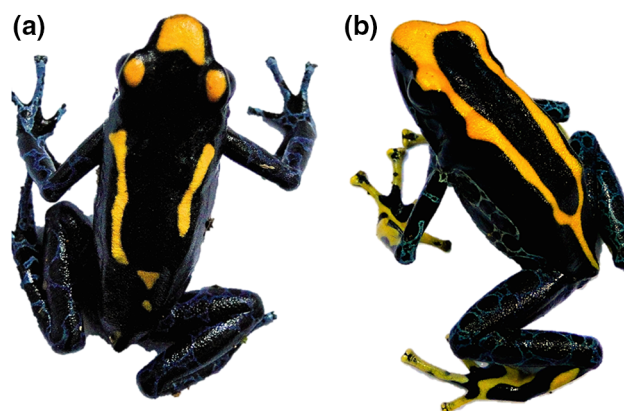


Fig. 1 Typical colour patterns of *Dendrobates tinctorius*: an individual with an interrupted yellow pattern (a) and an individual with an elongated yellow pattern (b)

frog individuals. Individuals with more elongated colour patterns showed directional movement with higher linear speed, over longer segments in their trajectories, compared to individuals with more interruptions in their yellow patches, which changed direction unpredictably and moved at lower linear speed and over shorter segments.

Rojas et al. (2014) suggested that the observed combinations of certain colour patterns and behaviours could benefit individuals by making them less vulnerable to predation. They propose that individuals with more elongated yellow patterns (Fig. 1b) could benefit from directional and fast movement because this combination could create the illusion of immobility or reduced speed. Frogs with interrupted patterns (Fig. 1a), on the other hand, would benefit from random and slow movement, given that interrupted patterns could be visually disruptive (Cott 1940; Stevens 2007), and together with a slower movement could help to avoid motion-oriented predators (Hatle and Faragher 1998; Hatle et al. 2002). Thus, different colour patterns of *D. tinctorius* could be efficient against predators when combined with a specific type of movement (Rojas et al. 2014), and this might enable different colour morphs to remain in the same population.

The field study by Rojas et al. (2014), however, provided only correlational evidence and did not look at predator response to these colour patterns and movement combinations. The aim of our study was to test experimentally how these combinations work against avian predators. We used great tits, which have been used as a model for bird perception of signals for decades, as predators. Notably, these birds are naïve to the patterns used, which was essential for our experiment. Therefore, possible differences in the capture success between different prey patterns should be detected. It is important to clarify that the purpose of our experiment was not to study how easily great tits would prey on dyeing poison frogs. Specifically, our aim was to determine whether linearly moving prey with elongated colour patterns is more difficult to catch by predators than prey with interrupted or uniform colour patterns. We tested this by placing a great tit in an experimental cage and moving prey items bearing different patterns (uniform brown, elongated and interrupted) linearly across the cage floor, recording the number of successful attacks. Our hypothesis was that prey with an elongated pattern would experience the least number of successful attacks because this pattern could create a motion dazzle effect, making it more difficult for birds to direct their attack. If so, individuals with more elongated patterns would benefit from moving directionally, which could help explaining the differences in the behaviour of frog individuals observed in the field (Rojas et al. 2014). In addition, we also used two different backgrounds: plain and leaf litter, and hypothesized that prey items would be more

difficult to capture in a more complex background. Therefore, we predicted a lower number of successful attacks with a leaf-litter background.

Materials and methods

Predators

We used wild-caught great tits as predators. Birds were caught from a feeding site and kept in captivity for approximately 5 days. They were housed individually in plywood cages with a daily light period of 11 h, fed on sunflower seeds, peanuts and tallow, and provided with fresh water ad libitum. The sex and age of each individual were recorded, and after the experiment, all birds were ringed for identification purposes before being released at the capture site. Altogether, we used 30 birds (15 males, 15 females).

The experiment was conducted at Konnevesi Research Station in Central Finland from October to December 2013. Wild birds were used with permission from the Central Finland Centre for Economic Development, Transport and Environment and licence from the National Animal Experiment Board, and used according to the ASAB guidelines for the treatment of animals in behavioural research and teaching.

Prey items and experimental cage

Artificial prey items consisted of two 17-mm-long, oval-shaped pieces of paper, glued together and holding a small piece of mealworm (*Tenebrio molitor*) in the middle. Each prey item had one of three possible colour patterns (shown in Fig. 2): a uniform brown (control), and two other resembling colour patterns of *D. tinctorius*, an elongated pattern and an interrupted one. The brown prey item was chosen as a control in order to compare the attack success between conspicuous frog patterns and camouflaged, unicoloured prey items. The same colour tones were used for the yellow and black of the patterned prey, so that both of them were equally different from the brown control prey, regardless of their colour distribution in the great tit's tetrahedral vision space.

The experiment was conducted in a 76 × 60 × 77 cm size plywood cage. The cage was illuminated with a light bulb, and it had two perches at a height of 64 cm. Birds were observed through a one-way glass in the front wall. Prey items moved in a straight line across the cage using a motor-driven belt that circulated under the cage floor. A screw was attached to the belt, and a 5-mm-wide slit on the cage floor allowed the screw to move from one side of the cage to the opposite. In that way, birds were able to see the

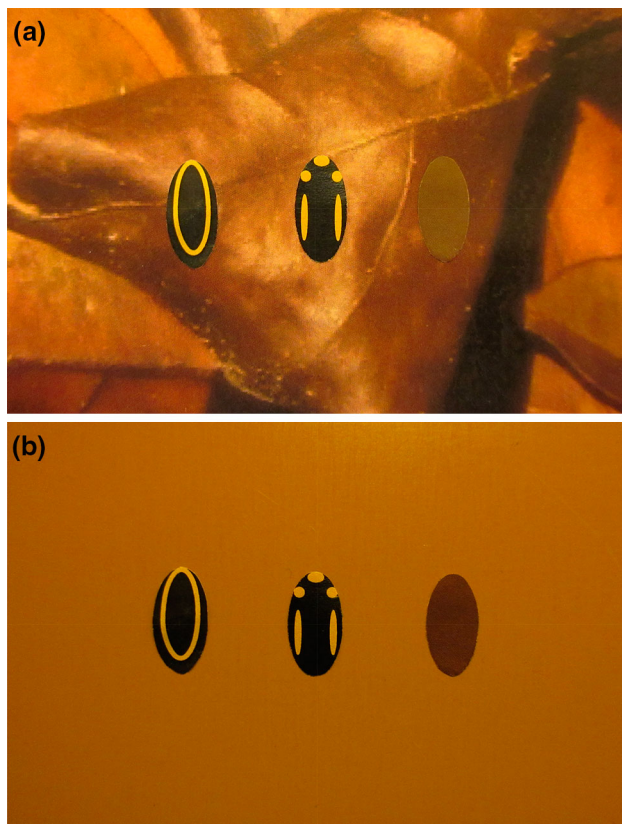


Fig. 2 Three different patterns used during the experiments, striped (*left*); interrupted (*middle*); and uniform (*right*), against (a) leaf litter and (b) plain background

prey items only while the screw they were attached to moved linearly across the cage floor.

We did the experiment with two different backgrounds. The light brown floor of the cage was used as a plain background, whereas the other background resembled leaf litter, which is the natural background of *D. tinctorius*. This was done by taping coloured leaf-litter patterned sheets of paper on the cage floor (Fig. 2).

Bird training

Before the experiment, birds were trained in their home cages to consume artificial prey items that were still. This was done in order to familiarize the birds with the different colour patterns to be used in the experiment, and to motivate them to attack these prey when moving. The purpose of the training was also to make sure that birds associated all prey patterns with palatable food, so that after the training, they did not have biases towards any of the prey items. This was important because we wanted to test the capture success and any hesitation to attack could have lowered the capture rate and affected the results.

In order to identify a possible innate preference or aversion towards any of the patterns, we recorded the order

in which 10 birds ate the different prey items during the training. This was done by offering each bird all three prey items (uniform brown, elongated and interrupted) at the same time, and recording both the order in which birds ate them and the time until they started to eat. For every bird, this was repeated five times so that every bird ate 15 prey items altogether (five of each prey type) during the preference test. The 20 birds that were not used in this preference test were equally trained with 15 prey items. Therefore, all birds used in the actual experiment had the same training, which would ensure the association of the three patterns with a (palatable) reward.

Once birds were familiarized with prey items, one bird at a time was placed in the experimental cage. We waited for birds to habituate to the cage and let the motor run without prey items so that the birds also got used to the noise. Birds were trained to attack moving prey items by offering them a piece of mealworm moving slowly across the cage. Each bird was presented at least four slow-moving mealworm pieces. If the bird kept hesitating to attack after those four trials, more training was done. After the training, birds were food-deprived for 45 min to ensure their motivation to attack during the experiment.

Experimental design

We tested 15 birds with a plain background, and the other 15 with a leaf-litter background. Birds were assigned to each background treatment randomly, but we checked that there were no biases in age or sex between the two groups. All birds were trained with the actual background they had during the experiment.

The experiment consisted of five trials in each of which birds were presented with all three different prey types in a randomized order. Prey moved across the cage with a speed of 16 cm/s. This speed was chosen based on preliminary observations, so that it was not too easy for the birds but also not unrealistically high. The direction of the movement was changed randomly between different prey items, such that sometimes prey came from the left side of the cage and sometimes from the right side.

We let the prey item run across the cage until the bird attacked. Birds were considered to attack when they clearly tried to peck the moving prey item. If the attack was successful, we let the bird eat the prey, but if the bird did not manage to catch the prey item in the first attempt, we stopped the motor and replaced it with the next prey type. So, if the bird did not attack the prey within the first 20 rounds (i.e. belt cycles), we gave it a 10-min break (waiting for the bird to be more motivated), after which the same prey item was offered again, continuing for as long as it took for the bird to attack. In many instances, the birds approached the prey but did not try to hit it. However, we

did not count that as an attack and waited until the bird actually tried to hit the prey item. This means that *all* the unsuccessful attacks were *truly* unsuccessful, and there were thus no “unrealized” attacks.

In the course of each trial, we had a 3-min break between different prey items (i.e. after each attack). During these 3 min, we let the motor run before offering the next prey, but stopped it a few times at random intervals to prevent the birds from associating these pauses with the appearance of food. We also had a 10-min break between the trials to make sure that the bird was motivated to attack. During the breaks, we let the motor run without prey items so that the birds did not associate the motor sound with food. All trials were recorded with a video camera (Canon Legria HF R37).

During the experiment, we counted the number of rounds it took for a bird to attack each prey item and classified each attack as successful (a bird captured the prey item) or unsuccessful (a bird attacked but did not capture the prey item). Afterwards, we measured from the videos how long it took for a bird to start the attack after the prey item was exposed. We also checked whether the attack was unsuccessful because birds failed to hit the prey, or because they did not manage to detach it from the screw.

Statistical analyses

We used a generalized linear mixed model (GLMM) with binomial error distribution to analyse the differences in the number of successful attacks between different prey types. We used the success of attack (0/1) as a binary response variable, and pattern (elongated/interrupted/control), trial number (1–5), background (plain/litter) and order (the order in which prey items were presented to a bird within a trial) as explanatory variables. In addition, we used bird identity (ID) as a random factor in the model. We started the model selection with the model that included also sex and age of the bird and interactions between pattern and trial and pattern and background. However, these terms were nonsignificant, and dropping them out from the model did not reduce the fit of our model significantly (Table 1).

The differences in the time before birds started their attack were analysed using a mixed-effects Cox model. The time before attack started was used as response variable and pattern, trial number, background, order and attack success were explanatory variables. Again, bird ID was entered as a random factor. Interactions between pattern and background, and pattern and trial were included in the first model, but interaction between pattern and trial was removed from the final model because it did not change model fit significantly (Table 2).

A mixed-effects Cox model was used also to test for possible avoidance or preference towards the different prey

Table 1 Comparisons of GLMMs explaining attack success on prey items

Model	Model df	AIC	χ^2	df	<i>P</i>
a	22	496.58			
b	14	487.03	0.124	8	0.597
c	12	487.73	4.701	2	0.095
d	11	485.86	6.448	1	0.725

Model a included explanatory variables pattern + background + trial + order + sex + pattern:background; model b, pattern + background + trial + order + sex + pattern:background; model c, pattern + background + trial + order + sex; and model d, pattern + background + trial + order. Bird ID was included as a random factor in each model

Table 2 Mixed-effects Cox model explaining the time before birds started their attack in the experiment

Source	Coefficient	<i>Z</i>	<i>P</i>
Interrupted	−0.3735	−1.39	0.160
Striped	0.0348	0.13	0.900
Plain background	−0.0236	−0.17	0.860
Trial 2	−0.3241	−1.21	0.230
Trial 3	−0.1215	−0.45	0.650
Trial 4	−0.10119	−0.38	0.710
Trial 5	−0.2908	−1.07	0.290
Order 2	−0.077	−0.64	0.520
Order 3	0.0909	0.75	0.450
Successful attack	0.1949	1.63	0.100
Interrupted: trial 2	0.6770	1.79	0.074
Striped: trial 2	0.2171	0.58	0.560
Interrupted: trial 3	0.3161	0.84	0.400
Striped: trial 3	0.0773	0.21	0.840
Interrupted: trial 4	0.3065	0.81	0.420
Striped: trial 4	−0.0148	−0.04	0.970
Interrupted: trial 5	0.5626	1.48	0.140
Striped: trial 5	0.4491	1.19	0.230

Time before attack is used as a response variable. Prey pattern, background type, trial number, order in which prey items were presented to birds within a trial, attack success and interaction between prey pattern type and trial were fixed factors, and bird ID a random factor. The reference level is the control pattern with leaf-litter background in the first trial, when control prey item is the first one to be presented within this trial (order 1) and attack is unsuccessful

types during the training session (i.e. before the actual experiment). The order in which prey items were consumed was used as a response variable, pattern as an explanatory variable and bird ID as a random factor. The differences in time before birds ate prey items during the training were analysed similarly, using now time before eating as a response variable. All statistical analyses were done with the software R 3.0.2, using packages *lme4* and *coxme*.

Results

Overall, birds captured 66 % of the moving prey items successfully. In most of the cases, the unsuccessful attacks were directed behind the prey, i.e. birds jumped behind the prey trying to hit it but were unable to reach it (see supplementary material for videos of a successful and an unsuccessful attack). Control (uniform brown) prey items were captured significantly more often than elongated and interrupted ones (Table 3; Fig. 3). There was no significant difference in the success of attack between elongated and interrupted prey (estimate = -0.002 , $Z = -0.007$, $P = 0.994$). For all patterns, the percentage of successful attacks was higher in the last trials (Table 1), showing the clear learning curves during the experiment (Fig. 4). The background and the order in which prey items were presented within a trial did not have a significant effect on the success of attack (Table 3).

The time before birds started their attack did not differ significantly between prey items with elongated and interrupted patterns (coefficient = 0.37 , $Z = 1.53$, $P = 0.13$) or between control prey items and either of these patterns (Table 4). Also, background, trial number, order in which prey items were presented within a trial or the success of attack did not have a significant effect on the time before birds started the attack (Table 4).

During training, the birds did not seem to avoid or prefer either elongated pattern ($Z = -1.12$, $P = 0.26$) or interrupted pattern ($Z = -1.00$, $P = 0.32$) compared to the control. Also, there were no differences in the preferences between these two different patterns ($Z = -0.13$, $P = 0.90$). Similarly, the time before birds ate the prey

Table 3 GLMM explaining the attack success in the experiment

Source	Estimate	Z	P
Intercept	-0.2985	-0.652	0.5143
Interrupted	-0.8498	-2.815	0.0049
Elongated	-0.8517	-2.822	0.0048
Plain background	0.7775	1.651	0.0988
Trial 2	0.5264	1.535	0.1247
Trial 3	1.6446	4.472	<0.0001
Trial 4	1.8701	4.955	<0.0001
Trial 5	2.8971	6.480	<0.0001
Order 2	-0.0883	-0.302	0.7624
Order 3	0.2693	0.915	0.3602

Attack success was included as a response variable and prey pattern, background type, trial number and order in which prey items were presented to birds within a trial were fixed factors. In addition, bird ID was included in the model as a random factor. Intercept gives the estimate for the control pattern with leaf-litter background in the first trial, when prey item is the first one to be presented within this trial (order 1)

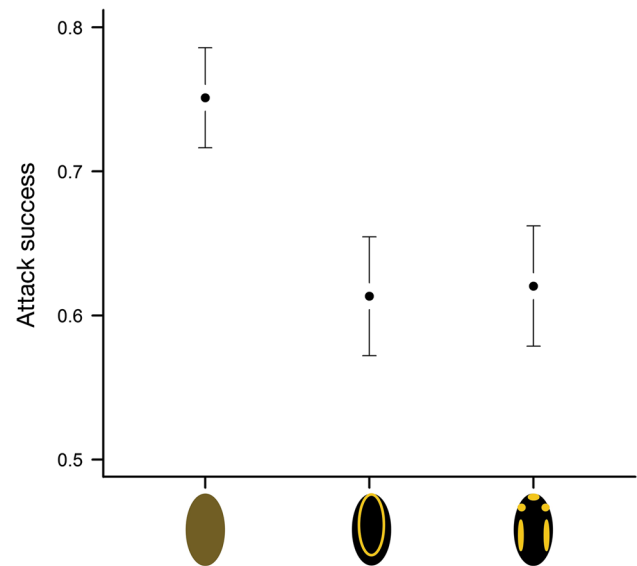


Fig. 3 Overall attack success and its 95 % confidence interval for different prey types: uniform (left), striped (middle) and interrupted (right)

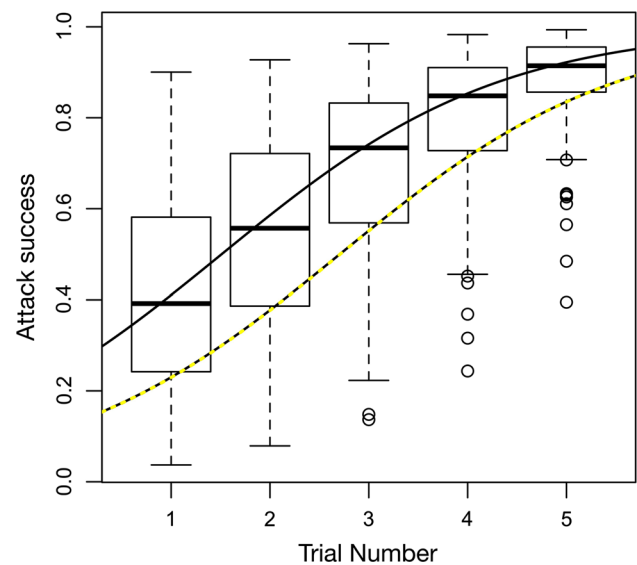


Fig. 4 Attack success in different trials during the experiment. The solid line represents the learning curve for uniformly coloured (brown) prey. The dotted lines (yellow and blue) represent the learning curve for prey items with striped and interrupted patterns. These two curves overlap because of undistinguishable differences in bird response (colour figure online)

items during training did not differ between control and elongated ($Z = 0.75$, $P = 0.46$), control and interrupted ($Z = -0.04$, $P = 0.97$) or elongated and interrupted ($Z = 0.71$, $P = 0.48$) prey items, suggesting no pre-existing biases in favour or against any of the patterns considered in the study.

Table 4 Comparisons of mixed-effects Cox models explaining delay before the birds started their attacks on prey items

Model	Model df	AIC	χ^2	df	<i>P</i>
a	21	−15.66			
b	19	−17.04	5.379	2	0.068
c	11	−6.11	5.074	8	0.750

Model a included explanatory variables pattern + background + trial + order + success + pattern:background + trial:pattern; model b, pattern + background + trial + order + success + trial:pattern; and model c, pattern + background + trial + order + success. Bird ID was included as a random factor in each model

Discussion

Our study shows that some colour patterns can benefit moving prey by lowering the rate of successful attacks. We found that it was easier for birds to capture a uniformly coloured prey item compared to prey with striped or interrupted yellow colour patterns. However, in contrast to our predictions, there was no difference in the capture rate between these two different pattern types.

This is the first time that a motion dazzle effect has been tested with avian predators. Previous studies with human predators and computer-generated prey items have shown that although a camouflaged grey item was most difficult to capture, different high-contrast patterns (e.g. bands, stripes and zigzag patterns) also lowered the capture rate compared to uniform conspicuous colouration (Stevens et al. 2008, 2011). This is consistent with our results that also found uniformly coloured prey items to be easiest to capture, even though the unicoloured prey items in our experiment were not conspicuous. On the other hand, a recent study showed opposite results, finding that human predators captured longitudinally and vertically striped objects more often than objects with uniform colouration (von Helversen et al. 2013). The authors suggest that this result might be explained by how the prey in their experiment was captured by the predators (humans, in this case). Participants were asked to “attack” only once the prey had reached a specific zone of the screen, as opposed to a natural situation where predators would chase the prey, finding it difficult to hit it due to their dazzle patterns. The differences between the studies using human predators, thus, could arise from different experimental designs, but also from differences between the visual systems of humans and birds (Nakamura et al. 2006). Birds may have, for example, higher temporal and spatial acuity (Jarvis et al. 2002). Therefore, experiments with birds are needed when testing the effect of the colouration of moving prey against avian predators.

We did not find any difference in the attack success towards striped versus interrupted colour patterns.

Although birds have shown to be able to recognise different objects in motion (Dittrich and Lea 2001) and to discriminate among prey with similar patterns (Dittrich et al. 1993; Green et al. 1999), it has been suggested that predators find difficult to follow the movement of prey with striped patterns (Jackson et al. 1976). This is most likely because striped patterns in motion do not have any reference points on which a predator could focus. Thus, we expected birds to find prey with elongated patterns more difficult to capture; our results, however, do not support this motion dazzle hypothesis. Instead, both interrupted and striped patterns were captured less, suggesting that any kind of nonuniform pattern could protect an individual from predators during movement. Our experiment, though, does not reveal the mechanisms that made these patterns more difficult to capture. About half of the times, the attack was unsuccessful because birds failed to hit the moving prey object, which may indicate difficulties in the accurate estimation of speed. There is some evidence (Scott-Samuel et al. 2011; von Helversen et al. 2013) that targets with patterns could be perceived to move either faster or slower compared to plain objects, which could make it more difficult to hit them. Scott-Samuel et al. (2011) showed that objects with zigzag or check patterns were perceived to move slower than objects with plain patterns, although this difference was found only when patterns had a high contrast against their background and objects were moving at high speed. In contrast, von Helversen et al. (2013) found that longitudinally and vertically striped objects were actually perceived to move faster than unicoloured objects. These studies, however, presented prey with repeated patterns (bars, stripes, etc.) on computer screens, which was not the case in our study.

On several occasions, birds hit the moving prey item, but the attack was unsuccessful because they did not manage to detach it from the screw to where it was attached. This could mean that the pattern made it more difficult for the bird to perceive the shape of the prey object and thus direct the attack and grab it successfully, i.e. the object may have benefited from a disruptive effect (Stevens and Merilaita 2009). Of course, it is also possible that prey colouration (uniform brown vs. black and yellow patterns) could cause the observed differences in the attack success. The two colour patterns used in our experiment both resembled aposematic frogs, which could evoke in the birds an innate hesitation to grab them. However, birds never had a chance to associate these patterns with anything unpalatable, and even though they might have some innate aversion to these colour combinations (Schuler and Hesse 1985; Lindström et al. 1999), they had been trained to associate the three types of prey with a palatable reward. Moreover, the preference test during the training showed that birds did not seem to avoid or prefer any of the prey

types. Furthermore, the time before birds started their attack did not differ between prey objects, indicating that birds did not hesitate more to attack prey with warning signals. Thus, aposematism does not seem to explain the observed differences in the attack success.

Surprisingly, the background did not affect the attack success or the time delay before birds started their attack. We predicted that the more complex leaf-litter background would have made prey capture more difficult. This was found in a computer game experiment (Stevens et al. 2008), which showed that human predators missed more prey items when the background was more heterogeneous. In addition, it has been shown that background can affect the perceived speed of a target (Blakemore and Snowden 2000). However, birds in our experiment seemed to capture prey items equally well in both backgrounds. It is possible that yellow warning signals made patterned prey items easy to detect even on a more heterogeneous background. On the other hand, the leaf-litter background did not provide better concealment even for the uniform brown prey items, so it seems that movement made all prey items easily detectable regardless of the background.

Birds learned to capture prey items better throughout the experiment, and the success of attack increased towards the last trials. Many previous studies have shown that great tits are able to learn relatively complex tasks (e.g. Lyytinen et al. 2004), so the improvement in attack success with time was not surprising. There were clear learning curves for all prey types (Fig. 4), showing that experienced birds captured also both patterns more easily in the last trials. This suggests that colour patterns could be most effective against naïve predators and that predators might be able to improve their capture success with experience. On the other hand, our study design was simplified compared to real situations in nature. Although we changed the direction of the movement randomly, such that sometimes prey items were moving from right to left and sometimes from left to right, prey was always crossing the front part of the cage, moving in a straight line and at constant speed. This probably made it easy for the birds to learn to predict prey movement and increase their capture rate. In more realistic situations, prey trajectory would not be that predictable. Also, when moving through the vegetation, prey might not be clearly visible all the time, making it more difficult for a predator to follow them.

In our experiment, prey items moved at a speed of 16 cm/s, but it is not known how high speed must be for visual illusions to occur. It is possible that prey movement was not fast enough to cause a motion dazzle effect, and this could explain why there were no differences in the attack success between elongated and interrupted patterns. In an experiment with humans (Stevens et al. 2008), all prey items were harder to catch at fast (20 cm/s) than at

slow speed (15 cm/s), but there was no interaction between the speed and the prey type. This means that same prey types were most difficult to capture in both speeds, and thus, the occurrence of motion dazzle did not seem to depend on the speed. When considering *D. tinctorius* individuals, the speed that we used was probably in the upper limit of their moving ability and higher speed may not be realistic for the frogs. The previous field study with the species (Rojas et al. 2014) showed that frogs with elongated patterns moved directionally, at a speed of 1.14 cm/s, whereas frogs with more interrupted patterns moved slower, 0.31 cm/s. However, these are only the average speeds over each segment, including brief pauses during movement, so the maximum speed of the frogs is higher. Moreover, frogs can do long jumps when escaping predators, and it is this fast movement that could potentially cause visual illusions and confuse predators. Therefore, instead of considering only the average linear speed, also the speed of movement bursts should be taken into account when studying motion dazzle in animals (Rojas et al. 2014).

We did not find any evidence that prey with striped patterns benefitted more from the linear movement compared to prey with more interrupted patterns; hence, the hypothesis that visual illusions could explain the observed connection between colour pattern and movement type in *D. tinctorius* was not supported. Rojas et al. (2014) suggested that motion dazzle could be one possible explanation for linear movement to be advantageous for individuals with more elongated patterns. However, our study did not provide any evidence that the fitness of frog individuals would depend on the combination of their movement and colour pattern. Instead, the results of our experiment suggest that both elongated and interrupted colour patterns are equally difficult to capture, and in that sense, the fitness of both colour morphs is the same. This may allow both of them to coexist in the same population, but does not explain the observed differences in their movement.

Overall, our study provided the first experimental evidence that colour patterns can affect the ability of birds to capture moving prey items. All previous studies have used human predators, but because visual processing is different between different species (Stevens 2007; Kelley and Kelley 2014), it is important to get information on how other predators perceive visual illusions. Our results showed that patterned prey, regardless of the pattern type, is more difficult to catch compared to prey with uniform colouration. This supports the idea that instead of some specific markings, many different patterns have the potential create visual illusions. There are still relatively few studies that have investigated the function of colour patterns during movement and therefore this provides a promising area for further research.

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Conflict of interest None.

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