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# Effect of prey dorsal colour and pattern on detection by an avian predator

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## Summary

Poisonous prey often show an aposematic colouration consisting of a bright red or yellow base colour sometimes combined with black to warn predators of their unprofitability. Edible prey on the other hand more often choose a cryptic strategy with dull colours blending into the background, such as dark green. In the strawberry poison frog (*Dendrobates pumilio*) in the Bocas del Toro archipelago in Panama however, colours and patterns are highly variable and there are populations of both dull and brightly coloured morphs, some of which have a dorsal pattern consisting of black spots of various sizes. This study compares the detectability of a possibly aposematic bright red colour morph and a possibly cryptic dark green colour morph, as well as two different black patterns, using domestic chickens as predators. The chickens were trained to search for frogs in a photo of the jungle floor shown to them on a computer display, and the correctness of their response and the search time were measured and compared between treatments. The results show that the red frogs were detected significantly faster than the green frogs, and that the presence of a black dorsal pattern also caused the frogs to be detected significantly faster. A black pattern with few, large spots increased detectability slightly more than a black pattern with many, small spots, and this difference was more visible on the green frogs, where a pattern with few, large black spots caused green frogs to be as easily detected as red frogs. These results correspond well with other observations of *D. pumilio*, where black patterns with large spots seem to occur mostly together with bright colours, while the dark green frogs have a small spot pattern or none at all. This together with differences in behaviour and toxicity speak toward different populations of *D. pumilio* having different strategies for predation avoidance, and potentially lower fitness for intermediate hybrids may lead to population divergence and possibly speciation in the future.

## Introduction

In order to escape being eaten by a predator, there are several different strategies a prey could take. One such strategy is being inedible, either by tasting very bad or by being downright poisonous to the predator. However, to avoid being killed by mistake, an inedible prey must be able to signal its unprofitability to the predator. This warning signal often consists of a specific body colouration, and ever since this phenomenon was first described in the end of the 19th century, such a colouration has been termed 'aposematic' (Ruxton et al. 2004). For aposematic signals to be effective they should be easily detectable and memorable to facilitate predator learning (Mappes et al. 2005, Ruxton et al. 2004), and also be distinctive, that is, make aposematic prey look markedly different from edible prey (Merilaita & Ruxton 2007, Ruxton et al. 2004). This manifests itself in aposematic animals having bright colours, and often patterns in contrasting colours (Ruxton et al. 2004).

Another common strategy for prey is being cryptic, which means that instead of signalling to the predator, it is trying to avoid detection altogether. Crypsis is often achieved through a process called background matching, where the prey has a colour and/or pattern that as closely as possible resembles the background against which it is most often seen (Merilaita & Stevens 2011). Crypsis allows the prey to avoid the possible costs of being inedible, such as the synthesis and storage of toxins, but there are often other costs associated with crypsis, for example having to avoid backgrounds that provide a poor match to the body colouration (Ruxton et al. 2004).

Although aposematism and crypsis might seem like opposite strategies, the former promoting bright, strongly contrasting colours and the latter colours that do not contrast against the background, they are not necessarily mutually exclusive. They could both form a part of a continuum of strategies ranging from inedible conspicuous forms to edible non-conspicuous forms (Mappes et al. 2005). A poisonous prey animal may benefit from being cryptic, since this could prevent fatal mistakes where a naïve predator would attack despite the signal (Mappes et al. 2005), and evolving crypsis would also allow a prey to reduce its toxin levels when colonizing an area where necessary components for toxin sequestration are hard to come by (Maan & Cummings 2012). An intermediate strategy that could be advantageous for a poisonous prey is to have a pattern that is cryptic when seen from a distance, but that contains bright spots that function as an aposematic signal close up, something that has been shown to be the case for some butterfly larvae (Bohlin et al. 2008, Tullberg et al. 2005).

A black pattern is commonly seen in aposematically coloured animals. The function of the black parts in this case may be to increase the contrast to the other body colour, which is often yellow or bright red (Stevens & Ruxton 2012). This is however not the only possible reason why a prey animal may have a black pattern. The pattern could for example be a case of disruptive colouration, where the prey has a pattern with contrasting colours that do not follow the body shape, thus making it hard for a predator to distinguish the outline of the body and possibly to even recognize the prey as an animal (Ruxton *et al.* 2004, Stevens & Merilaita 2011). In this case, the pattern would not be aposematic, but rather cryptic, since it makes the prey harder to detect for the predator. A black pattern may also have the dual function discussed above; that is, it might increase the contrast to an aposematic bright colour when seen close up but increase crypsis at a distance (Stevens & Ruxton 2012).

In this study we looked at strawberry poison frogs, *Dendrobates pumilio* (also called *Oophaga pumilio*). As the name suggests this species is toxic, and throughout most of its range in central America it also shows a conspicuous colouration, consisting of a bright red dorsal colour and blue extremities, which is likely to have an aposematic function (Saporito *et al.* 2007). However, in the Bocas del Toro archipelago along the coast of Panama, a large number of different colour morphs have developed on the different islands (see eg. Siddiqi *et al.* 2004). Some of these morphs have darker, seemingly cryptic colours such as green or blue, and some morphs have black patterns of various types. Several hypotheses have been put forward on why these colours and patterns have evolved, for example sexual selection (Summers *et al.* 1999), but one possible explanation is that it is predator pressure that is the driving factor.

To determine which effect the colour and pattern of a prey has, it is necessary to consider the vision system of the predator (Troschianko *et al.* 2011). A bright colour will obviously not be effective if the predator lacks colour vision. Also, a colour that appears dull to us may not necessarily be dull to for example a bird, since birds, having a tetrachromatic vision system with four cone types instead of our trichromatic system (Osorio & Vorobyev 2008), are likely to perceive colours quite differently from how we do. Another important thing to consider when evaluating patterns is the resolving power (spatial acuity) of the predator. What we perceive as a distinct pattern may blur together to a solid colour in the eyes of the predator if their spatial acuity is less than ours (Stevens & Ruxton 2012). Thus, a pattern of red and black that seem conspicuous to us might appear as a solid brown colour that blends in well with the background to the predator.

It is not known what species are the most common predators of poison frogs, but experiments with clay models have shown that birds are the main predators (Hegna *et al.* 2011, Saporito *et al.* 2007). Since the frogs are found on the jungle floor, we made the assumption that their predators are ground-living jungle birds and therefore chose to conduct this study using the domestic chicken (*Gallus gallus domesticus*) as predators. The domestic chicken is an omnivorous species that has also been observed eating frogs in captivity (Løvlie, H., personal comm.) and their ancestor, the red jungle fowl, is a ground-living jungle bird likely to hold an ecological niche similar to that of the actual predators of the strawberry poison frog.

Another advantage of using domestic chicken is that their vision system is better known than most other avian species. We know for example that the domestic chicken has tetrachromatic colour vision, with the maximum sensitivity of the cones at wavelengths of about 418 nm, 455 nm, 507 nm and 569 nm (Bowmaker *et al.* 1997, Osorio *et al.* 1999). From this can be seen that the chicken has a so-called VS (violet sensitive) system of vision, which means that the sensitivity of light in the UV spectrum (below 400 nm) is quite low. Although some bird taxa have independently evolved UV vision through a shift in cone sensitivity (UVS vision), most bird taxa have the ancestral VS form like the domestic chicken, and this system differs little between species (Osorio *et al.* 1999). Since the strawberry poison frog also does not seem to emit light in the UV spectrum (Rudh, A., unpublished data), this aspect can safely be disregarded for this experiment. It is also known that the spatial acuity of the domestic chicken is considerably lower than that of humans (Gover *et al.* 2009), which means that we can expect that a fine-grained pattern with small dots will be harder to distinguish for a chicken than it is for us.

In our experiment, we wanted to test whether two naturally occurring prey colours, a dark green that seems cryptic to us and a bright red that seems conspicuous to us would be cryptic and conspicuous respectively also to a bird predator. We also wanted to test the effect of a black pattern in combination with the two colours and see whether the size of the black spots in the pattern would have any effect on the visibility of the prey.

## Materials and methods

The study was conducted by training chickens to search for and peck at prey in images shown to them on a computer display. The prey consisted of modified photographs of strawberry poison frogs of green or red base colour, with either a black pattern with a few large spots, a black pattern with many small spots or no pattern added, randomly placed in a background photograph of a natural jungle floor. The correctness of the chicken's first response (if it first pecked on the prey or something else) as well as the search time until it found the prey was measured for each trial, and the individual means for both response data and search times were then compared between the different treatments. The trials were carried out in January 2012 at the research station Tovetorp (belonging to the Zoological dept. of Stockholm University) in Södermanland, Sweden.

### *1. The chicken population*

The chickens used were of the old Swedish breed Gammelsvensk dvärghöna, which are bred at the research station. This population, currently about 120 individuals, has been kept at the research station in a free-range setting allowing random mating since the late 1960'ies (Løvlie 2007). Since they have never been selected for productivity, they are likely to be closer to the ancestral red jungle fowl both in genetic make-up and behaviour compared to commercial breeds. These particular birds have previously been used in various experiments related to behaviour and vision, which means both that the birds are used to being handled and that we have some data on their eyesight, for example their temporal resolution (Lisney *et al.* 2011). All birds that had previously participated in colour vision experiments were excluded since their training might affect their motivation to find prey of different colours. We decided to use only hens in this experiment due to them being more quiet and manageable. Hens over 4 years old were excluded to avoid any effect of age-related deterioration in eye-sight. In total, 18 individuals were used in the experiment.

### *2. The frogs*

We prepared two different frog images, both based on real photographs taken in their natural habitat in Panama but modified in Photoshop to have the same size and posture, one showing a frog with a bright reddish orange colour ("red" treatment) and one where the frog had a green base colour with darker extremities ("green" treatment). To these base images, we then applied two different patterns using Adobe Photoshop, one with few, large black spots creating a very coarse-grained pattern ("large" treatment) and the other with many small spots creating a very fine-grained pattern ("small" treatment). Both patterns were based on photos of real frogs but adjusted to have the same amount of black pixels, i.e. coverage percentage. In all, this gave us six different treatments (see Fig. 1 for pictures); red with no pattern (R no), red with large black spots (R large), red with small black spots (R small), green with no pattern (G no), green with large black spots (G large) and green with small black spots (G small). The different frog images were then with the help of a script rotated a random number of degrees and placed in a random position in a background image to create a set of unique images. The background image was always the same and consisted of an actual photograph of the jungle floor taken in the same habitat as the frogs were found, showing a somewhat representative mix of green leaves, brown leaves and bare ground.



Fig. 1. The six different treatments (from left to right); G large, G no, G small, R large, R no and R small.

### 3. Experimental setup

For the experiment we used a 50x60 cm wooden box where the front was open towards a computer display that was attached directly to the box. A large glass window protected the display from damage while allowing the bird full view of the display. The prepared images were shown on this display (a 22 inch Samsung SyncMaster SA 300), which was calibrated with the help of a spectrophotometer so that the difference between the wavelength spectrum of the frog images on the display and the actual wavelength spectrum measured on the live frogs at the time when the photos were taken differed less than 5% when seen by a bird (using the colour receptors of the similar species peacock as reference data). The still image refresh rate of the display was measured with a camera and verified to be above 100 Hz, which is the highest temporal resolution seen by any individual in this population (Lisney *et al.* 2011), meaning that no bird could possibly have been disturbed by flickering of the screen image. The display had a full HD resolution of 1920x1080 pixels, but the height of the box window was limited to give a viewable area of 1920x780 pixels (477x193 mm) to avoid problems for the birds not being able to reach. The frog pictures were 17 mm (68 pixels) long, which is about their natural size.

At the beginning of each trial the hen was put in a smaller net-covered holding box behind the experimental box, and as the trial started a door between the two boxes was lifted up with a string mechanism. The hen was pushed back into the holding box between trials. A food dispenser placed underneath the front window allowed giving a reward, consisting of pieces of boiled spaghetti, to the bird when it showed the desired behaviour. Both the door between the boxes and the food dispenser could be operated remotely, and a video camera placed in the top back corner of the experimental box allowed the experimenter to supervise the trial from behind a curtain out of view of the bird to avoid any possible influence on the bird's behaviour by the experimenter. See Fig. 2 for an overview of the setup.

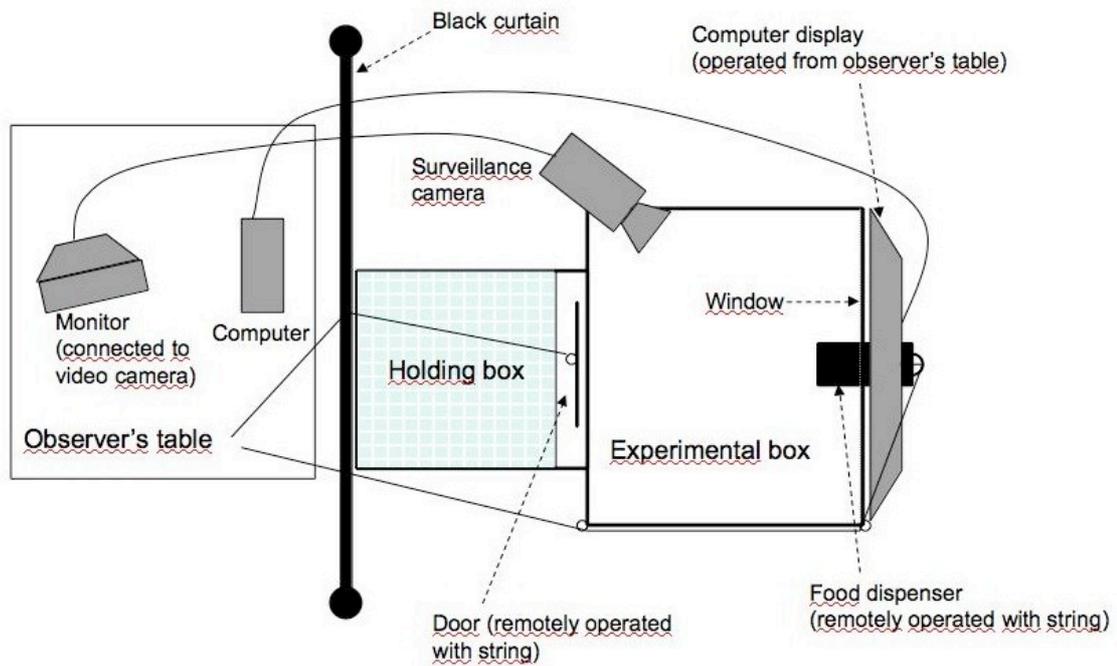


Fig 2. An aerial view of the experimental setup.

#### 4. Training and trial procedures

The birds used in the experiment were kept inside for at least one week before the trials and experienced numerous training sessions to get used to the equipment and learn the task. During training, the hens were first shown pictures of frogs against a white background and rewarded when they pecked at the frog. When the hen was correctly pecking at frog images of all six treatments, the background image was gradually introduced with first 50% higher brightness (causing the background to look whitish and the frog to stand out), and then 25% higher brightness. Not until the hen was able to find at least one frog on the real background with normal brightness were she allowed to start the real trials.

Six trials were made in a row as one session, and during this unique images with the six different treatments were shown in randomised order. All 18 individuals were subjected to 10 sessions on different days. Both the correctness of the initial response, i.e. the first peck at the window, and the search time until the frog was found was measured. To be able to define a "correct response", we showed a circle of 74 mm (300 pixels) in diameter around the frog (corresponding to 5% of the screen area) on the display and drew this circle with a marker on the experimenter's monitor. The circle was then removed from the display before the hen was let into the experimental box, and so visible only to the experimenter. We recorded the initial response as correct when the first peck was within this circle, and as wrong if the hen first pecked anywhere else in the window. The search time was measured as the time from the opening of the door between the boxes until the hen pecked inside the circle, regardless of where the first peck was. In case the hen did not find the frog within 120 seconds, the trial was terminated and the hen was pushed back into the holding box without a reward.

## 5. Data analyses

Our raw data contained 180 sessions with in total 1080 data points. We had to remove 56 data points that were deemed unreliable, due to for example the hen being disturbed during the trial or forgetting the task. Some problems with the time measurements in the beginning forced us to remove another 127 data points for the search time analysis.

The initial response data was converted to numerical values (1 for "correct" and 0 for "wrong"), and a proportion of correct responses was calculated for each individual. We also calculated means per individual for the search time data. We performed two-way ANOVAs on both datasets and analysed them further using the Tukey's HSD post-hoc test.

Since there was a very high individual variation in search time as well as some difference between sessions as most hens had lower search times towards the end of the experiment, we also devised a rank system where the trials within the sessions were ranked, from 1 for the treatment with the shortest search time to 6 for the treatment with the longest search time. For the rank data to be correct all sessions that contained a missing value had to be removed, leaving us with 810 data points (135 complete sessions). The rank data was analysed with a Kruskal-Wallis test, followed by post-hoc pairwise comparisons using Mann-Whitney U tests.

All analyses were conducted in R (R Development Core Team 2012).

## Results

The initial response data (originally 1024 data points) showed a quite high individual variation with the proportion of correct responses ranging from 62.5% to 81.1%. To avoid pseudo-replication we used the proportion of correct responses per individual to compare treatments, giving us  $n=18$  for each treatment. As can be seen in Table 1 as well as Fig. 3, the two treatments G no (green with no pattern) and G small (green with small spots) have clearly lower proportions of correct responses. A two-way ANOVA showed a significant effect both of colour ( $F_{(1, 102)}=18.060$ ,  $p=4.74e-05$ ) and pattern ( $F_{(2, 102)}=7.271$ ,  $p=0.00112$ ), but no significant interaction between the two ( $F_{(2, 102)}=1.914$ ,  $p=0.15278$ ). When comparing the two pattern types (large spots and small spots) post-hoc, a difference bordering on significance was found ( $p=0.076$ ), where the large spot pattern had the higher proportion of correct responses.

For the search time analysis, 867 data points were used. In 61 of these trials, the frog was not found within the two-minute time limit and the search time was consequently set to 120, but these data points were deemed too few to affect the overall distribution of the dataset. The mean search time was 30.5 s, but also here the individual variation was large, with mean search time per individual ranging from 14.6 to 51.8 seconds. We therefore used a mean search time per individual to compare the different treatments (see Fig. 4). The shortest search time, 25.1 s (calculated as mean of individual means), was found for the red frog with large spots, while the longest search time, 43.1 s, was found for the green frog with no pattern (all times shown in Table 1). A two-way ANOVA showed a significant effect of both colour ( $F_{(1, 102)}=10.322$ ,  $p=0.00176$ ) and pattern ( $F_{(1, 102)}=3.950$ ,  $p=0.02227$ ), but no significant interaction between the two ( $F_{(2, 102)}=1.788$ ,  $p=0.17242$ ). The post-hoc analysis showed no significant differences between the two pattern types, although the mean search time for frogs with the large spot pattern was slightly shorter (26.6 s versus 30.5 s for frogs with the small spot pattern).

The rank data used 135 sessions where data for all six treatments was available (810 data points in total), creating a fair ranking from 1 to 6 for all sessions. Since this system removes the problem of individual variation, the data was used without further treatment (see Fig. 5). Like in the previous analyses, the red frog with the large spot pattern (R large) was the easiest to find with a rank of 3.06, while the green frog with no pattern (G no) was the hardest to find with a rank of 4.25 (see Table 1 for all ranks). A Kruskal-Wallis test showed a highly significant effect of treatment ( $\chi^2_{(5,N=810)}=48.3084$ ,  $p=3.073e-09$ ), and the post-hoc tests showed that the treatment G no differed significantly from all red frogs and also from G large ( $p=0.00023$ ) but not from G small, while G small showed significant differences from only R large ( $p=0.00381$ ) and R small ( $p=0.00995$ ). G large did not differ from any of the red frogs, and the red frogs did not differ from each other.

Table 1. Proportion of correct responses, mean search time (both calculated as means of individual means) and mean search time rank for the six different treatments.

Treatment	Proportion correct responses	Mean search time (s)	Mean search time rank
G large	0.74	28.02	3.37
G no	0.54	43.12	4.25
G small	0.65	34.18	3.82
R large	0.81	25.08	3.06
R no	0.74	28.09	3.35
R small	0.74	26.73	3.14

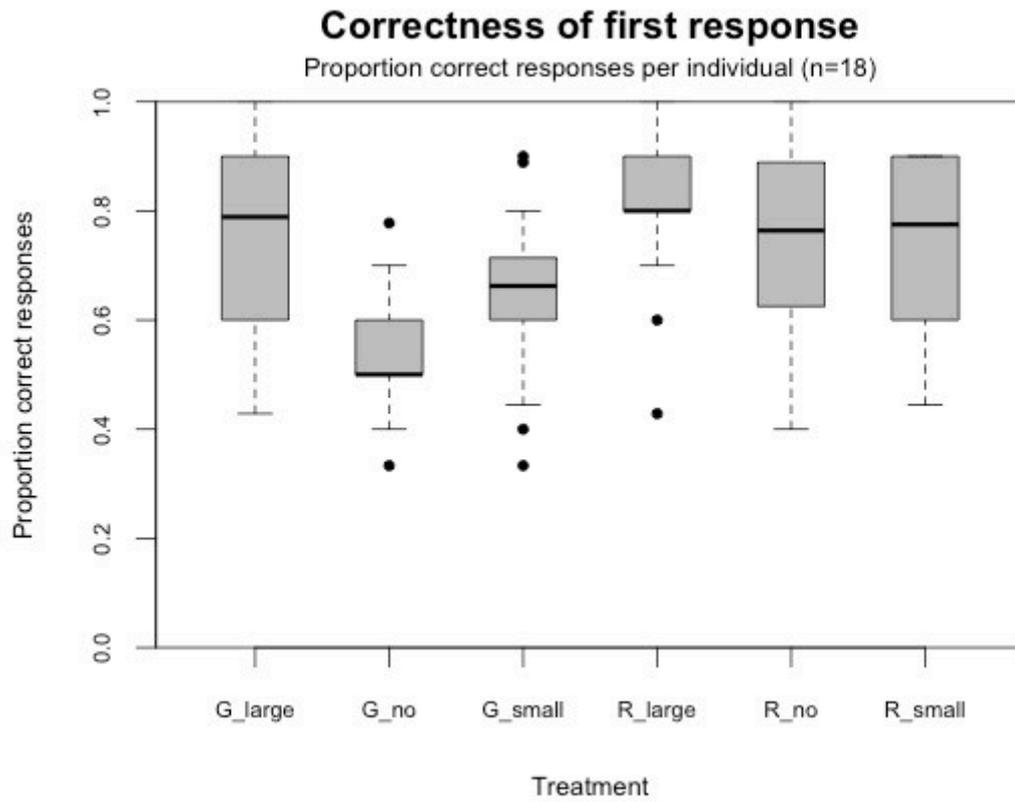


Fig 3. The proportion of correct responses (defined as the first peck on the window being inside the circle around the frog) per individual per treatment.

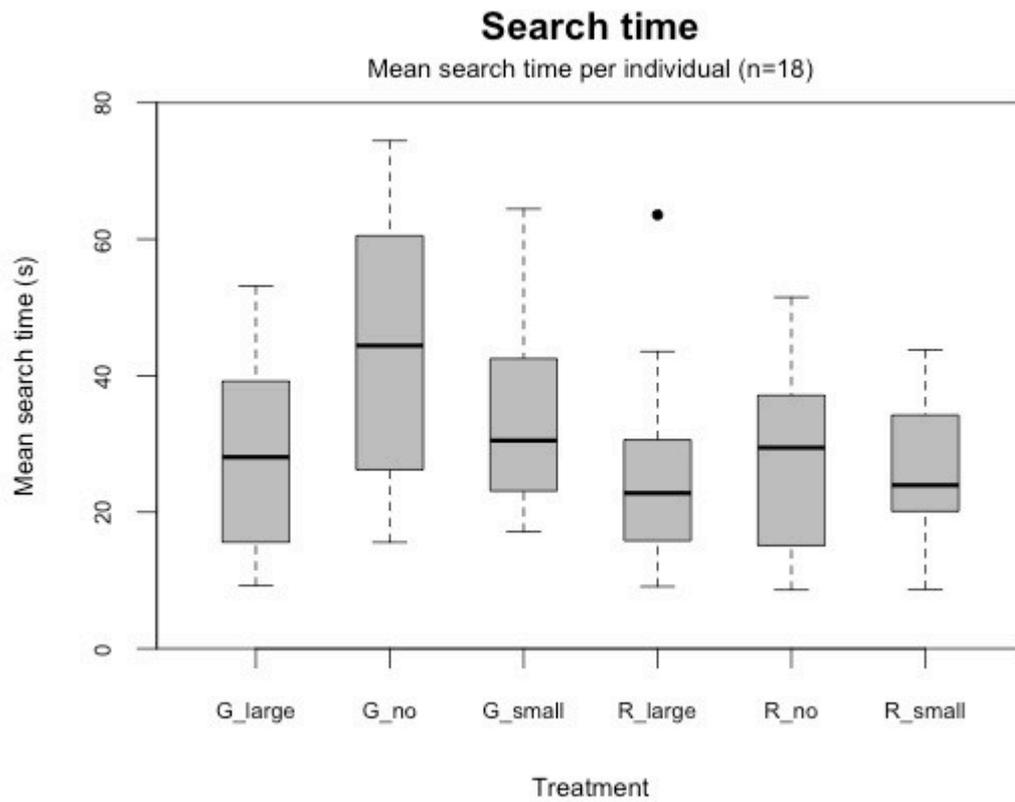


Fig 4. Search time in seconds from the opening of the door to the experimental box to the first peck inside the circle around the frog (max 120 s.) per treatment.

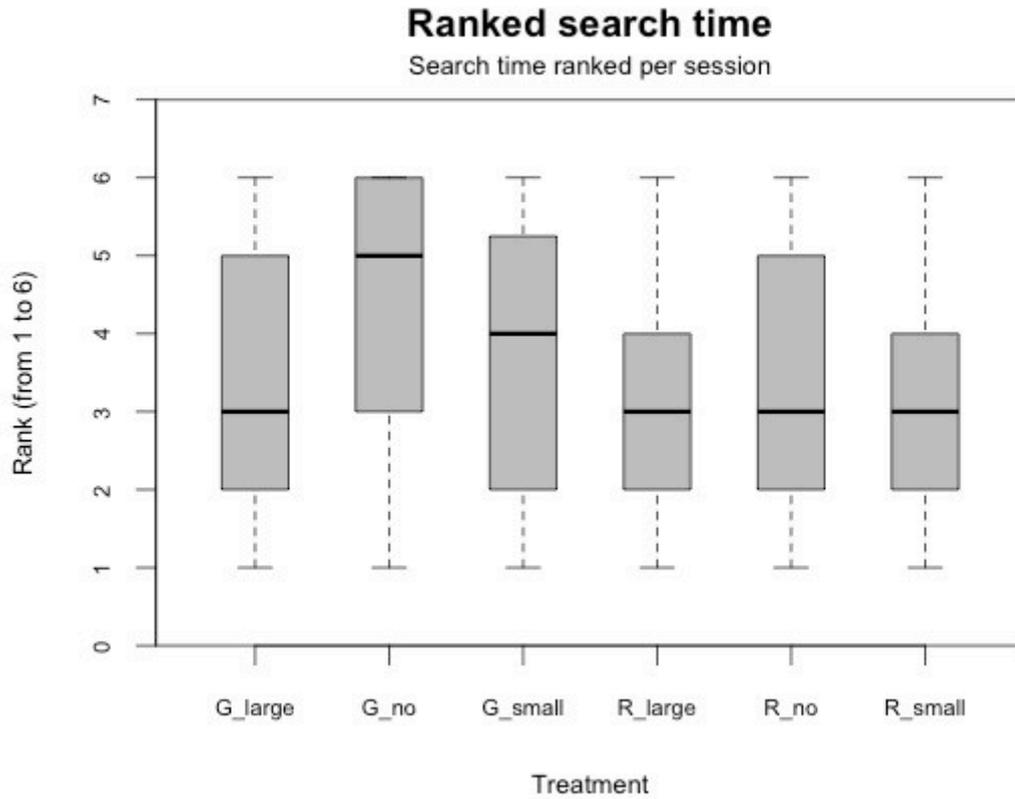


Fig 5. Search time ranked per session (with 1 being the shortest and 6 the longest search time within the session) per treatment.

## Discussion

Our results show that the dark green frogs were harder to find than the bright red frogs for our chicken predators. A black dorsal pattern increased the visibility of the frogs for both colours, and this effect was stronger if the pattern had few but large black spots. The difference between the two colours was both highly significant and expected. That both black patterns would cause the frog to be more easily detected was perhaps less obvious, but from our results we can safely say that the patterns did not work as a disruptive colouration (which would increase crypsis) but instead made the frog more conspicuous to the predator. The difference between the two patterns was not as pronounced, but it remains clear that the pattern with few, large dots had a stronger effect than the pattern with many, small spots, which was in alignment with our predictions.

Behavioural studies of *D. pumilio* have shown that green colour morphs engage in behaviour that increase crypsis (Pröhl & Ostrowski 2011, Rudh et al. 2011). Both these studies show that males in populations with predominantly green colour morphs tend to choose less conspicuous places for mate calling compared to males in populations with red frogs. This correlation between colour and behaviour is a clear indication that green colouration indeed represents a cryptic strategy.

It has also been shown that the toxicity in *D. pumilio* is not only highly variable between populations but is also positively related to the conspicuousness of the dorsal colour to a bird viewer (Maan & Cummings 2012). This also points towards the colour differences being caused by predation pressure rather than for example sexual selection, since a bright colouration must be accompanied with inedibility to be effective as an aposematic signal, while a more cryptic colouration allows for a lower toxicity without it leading to increased predation.

In a somewhat similar study by Hegna *et al.* (2011) that used clay models of red frogs with and without black dots, the conclusion was that a black pattern did not affect predation risk at all. Although this result at first seems like quite the opposite of ours, there is actually no contradiction since Hegna *et al.* used only red frogs and a pattern with small spots. Also in our study, we did not find any significant difference between the red frogs with no pattern and the red frogs with a small spot pattern.

What we found was instead that a pattern with few, large spots made the frog easier to find, to the extent that it would almost totally offset the cryptic effect of the green colour. When considering this, it seems counterintuitive that a frog would have evolved a cryptic colouration and a pattern that makes it more conspicuous at the same time. When looking at the various colour morphs of *D. pumilio* in nature, black patterns with large spots are also almost exclusively found together with bright dorsal colours, i.e. our treatment "green large" does not occur naturally (Rudh, A. pers. comm.).

Cross-breeding experiments have shown that the different populations of *D. pumilio* are able to produce viable offspring, and that the offspring display colours intermediate to those of the parents, while the black patterns seem to be inherited in a dominant fashion (Summers et al. 2004). From this can be inferred that hybrids between brightly coloured frogs with black patterns and dull frogs without patterns are likely to be less fit, and this will probably lead to aposematic and cryptic populations drifting apart to eventually become different species. The aforementioned behavioural differences in preferred mate calling position between cryptic and aposematic populations may act as a prezygotic isolation mechanism speeding up this process.

On a more general note, we can conclude that red seems to be an effective colour when signalling to birds, while dark green seems harder to detect, which is not a very controversial finding. We also found that the colour had a stronger effect than the pattern, which may be an indication of birds using colour as a cue to a higher extent than pattern. For example, a study by Aronsson and Gamberale-Stille (2007) showed that domestic chicken pay more attention to colour than pattern when learning aposematic signals.

The fact that the presence of a black pattern seemed to have little effect on the red frogs while clearly affecting the green frogs might be explained by the black pattern and the red colour having the same effect (i.e. making the frog more conspicuous) and thus leading to a saturation effect in our experiment, where the task would be "too easy" and search time would be decided simply by the moving speed of the hen rather than the time to detection. On the green frogs on the other hand, the black pattern would counteract the cryptic effect of the colour and thus make a noticeable difference. It is therefore quite possible that in an experiment with a larger search area, a black pattern may give an effect also on red frogs.

It is also clear that the size of the black spots in the pattern does make a difference, with blocky, simple patterns increasing visibility more than fine-grained, complex patterns. This makes sense when considering that the purpose of the pattern is to increase the contrast to the surrounding colours. In order to have this function, each spot must be clearly distinguishable and not blur together. We speculated that our small spot pattern might blur together to become a solid colour in the eye of the bird, something that likely did not happen. If that would have been the case, the frogs with the small spot pattern would have become a less bright solid colour and should therefore have been harder to detect than the frogs without a pattern. The reason that this did not happen was probably that this is an effect that is more pronounced at a distance. In our experiment, the hen was allowed to walk all the way up to the picture, which means that she was probably able to distinguish the spots in the pattern despite the weak spatial acuity of the domestic chicken. In a more real situation where the bird would roam over a larger area, this blurring might still come into effect.

It would be desirable to be able to compare black patterns with different internal complexity also when the predator sees the prey at a distance. We initially tried to factor distance into our experiment by showing the picture at different distances from the window of the experimental box, but it turned out to be impossible to train the birds to understand the task with this particular setup. If this problem could be overcome with a different experimental design, we would be able to answer not only if this blurring effect of a fine-grained pattern occurs, but also if the *D. pumilio* colour morphs with bright dorsal colours and a black pattern with small spots could possibly be manifesting an intermediate strategy in between aposematism and crypsis similar to that shown for some butterfly larvae (Bohlin et al. 2008, Tullberg et al. 2005).

## Conclusion

What this study shows is that a dark green prey is harder to detect than a bright red prey to a bird predator (domestic chicken). It also shows that the presence of a black dorsal pattern increases the detectability of the prey, especially if the base colour is dark green. The internal complexity of the black pattern affects how strong this effect is, with a pattern with few, large spots increasing detectability more than a pattern with many, small spots.

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