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Behavioural mimicry among poison frogs diverges during close-range encounters with predators

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Abstract

Aposematic species signal their unpalatability to potential predators with recognizable, and frequently conspicuous, colour patterns. These visual signals are often also associated with bold behaviour and a reduced propensity to escape from approaching predators. Bold behaviours may act as an aversive signal and allow defended prey to avoid the energetic/opportunity costs that arise from fleeing predators. For Batesian mimics, non-defended species which replicate the colours of defended models, behavioural mimicry may also improve mimic fidelity and reduce energetic/opportunity costs. However, as predators may test the honesty of aposematic signals through sampling behaviour, Batesian mimics can be at high risk during close-range interactions with predators. This raises the question of whether/when Batesian mimics should deviate from behavioural mimicry and initiate more extensive escape behaviour. Here, we exposed the chemically defended poison frog *Ameerega bilinguis* and its (non-toxic) Batesian mimic *Allobates zaparo* to a simulated predator encounter. We predicted *Al. zaparo* would escape to a greater distance and in a more erratic manner than *Am. bilinguis*. Yet, contrary to our predictions, *Al. zaparo* did not flee far from predators. It was, however, more likely to initiate escape prior to physical contact from the predator. We suggest that bold behaviour coupled with pre-emptive movement allows *Al. zaparo* to retain the benefits of behavioural mimicry while reducing the likelihood that predators will test signal honesty. Our data highlight that when examining the evolution of mimicry, we must consider both morphological and behavioural traits, as well as how risk to the prey may change how they behave throughout the predation sequence.

Keywords: aposematism, Batesian mimicry, behavioural mimicry, escape behaviour, predation sequence, poison frogs

Introduction

Aposematism is often characterized by bright conspicuous colours which warn potential predators that an animal is unprofitable as prey (Skelhorn et al., 2016; Stevens & Ruxton, 2012). However, aposematic phenotypes also extend beyond morphology and into behaviour (Mappes et al., 2005; Tan et al., 2024). Defended species are generally associated with bold and predictable movements, as well as a reduced propensity to flee from approaching predators (Dowdy & Conner, 2019; Mappes et al., 2005; Tan et al., 2024). This sets aposematic species apart from undefended, or cryptic, species which often exhibit reduced movement to limit detection risk but rapid escape once approached by a potential threat (Broom & Ruxton, 2005; Ioannou & Krause, 2009; Stevens & Ruxton, 2019; Tan et al., 2024).

The distinction between aposematic and cryptic behaviour may be understood through examining how the risk associated with predator interactions differs at each stage of the predation sequence (Bateman et al., 2014; Broom et al., 2010; Endler, 1991). To successfully hunt, a predator must (1) encounter, (2) detect/identify, (3) pursue, (4) capture/subdue, (5) handle, and then (6) consume their prey (Bateman et al., 2014; Endler, 1991). At each step of the sequence, predators are faced with decisions about prey profitability that will dictate whether they continue their hunt (Kikuchi et al., 2023; Skelhorn et al., 2016). In response, prey have evolved many different defensive strategies which may prevent, or disrupt, each of these different stages (Cuthill, 2019; Kikuchi et al., 2023; Lima & Dill, 1990). For example, cryptic colours reduce *detection* (Cuthill, 2019) whereas aposematic colours warn predators against initiating *pursuit*, *capture*, or *consumption* (Mappes et al., 2005; Stevens & Ruxton, 2012). When camouflage fails to prevent *detection*, undefended species may then institute escape behaviours that help evade *capture* (Broom & Ruxton, 2005; Ioannou & Krause, 2009). Whereas if aposematic signals are ignored, chemically defended prey may then rely on their defensive toxics to reduce the likelihood of *consumption* (Caro & Ruxton, 2019; Sherratt & Stefan, 2024; Winters et al., 2021).

In Batesian mimicry, an undefended species displays the colours of an aposematic "model" to take advantage of the avoidance behaviours predators show towards defended species (Bates, 1862; Kikuchi & Pfennig, 2013). However, mimicry is not limited just to morphology, and replicating the behaviour of their models can also be an important

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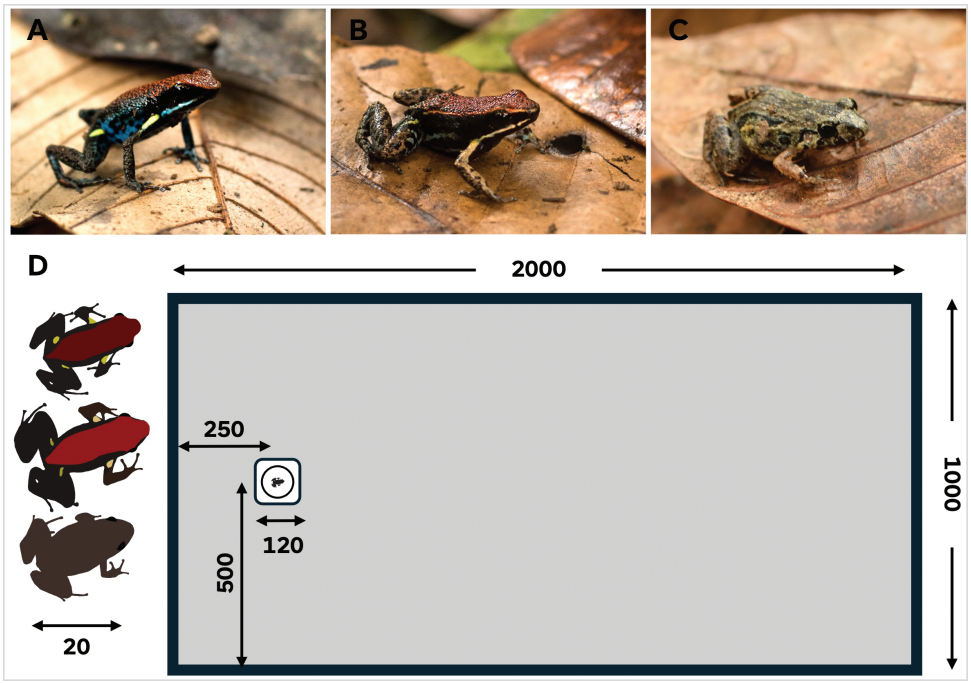

Figure 1. The study system and experimental setup. Top: The three species from left to right: (A) *Ameerega bilinguis* (toxic model), (B) *Allobates zaparo* (non-toxic Batesian mimic), and (C) *Adenomera hylaedactyla* (cryptic). Bottom: (D) The experimental arena (dimensions in mm) showing frog placement at the beginning of each trial. Frog illustrations were drawn to scale from top to bottom: *Am. bilinguis* (mean SVL = 22.51 mm), *Al. zaparo* (mean SVL = 26.92 mm), and *Ad. hylaedactyla* (mean SVL = 23.34 mm).

component of the mimetic strategy (Page et al., 2024; Srygley, 1999; Tan et al., 2024). In both aposematic and mimetic species, bold behaviour, such as slow and predictable movements, may be selected for if it can itself act as a signal to predators or draw attention to morphological signals like colour (Dowdy & Conner, 2019; Klank et al., 2024; Page et al., 2024). Conversely, escape behaviour may be lost if it is no longer necessary for survival or would impart opportunity or energetic costs (Dowdy & Conner, 2019; Higginson & Ruxton, 2010; Klank et al., 2024; Speed et al., 2010).

The risk posed by predators may, however, differ between models and mimics at different stages throughout the predation sequence. Mimicry can reduce the likelihood of *pursuit*, but during close-range interactions, predators may test the honesty of aposematic signals (Gamberale-Stille & Guilford, 2004; Skelhorn & Rowe, 2006b). Here, through "taste-rejection" or "go slow" behaviours, predators cautiously handle seemingly defended prey in order to assess toxin levels before selectively consuming those found to be palatable (Barnett et al., 2007; Guilford, 1994; Holen, 2013; Skelhorn & Rowe, 2006a2006c). Consequently, unlike their defended models, Batesian mimics cannot rely on deterring predators via secondary defences, and therefore their risk of consumption will increase greatly where visual signals are ignored (Gamberale-Stille & Guilford, 2004; He et al., 2022). As such, mimics may benefit from reducing the likelihood of predator encounters, either prior to *detection* through incorporating camouflage into their signals or during *pursuit* with (non-mimetic) escape behaviours that reduce the likelihood of *capture* (Kikuchi & Pfennig, 2013; Kikuchi et al., 2023; McEwen et al., 2024; Stevens, 2007). However, many questions remain in our understanding of how mimic behaviour may change throughout the predation sequence, or where on the predation sequence Batesian mimics may be expected to replicate or to deviate from the behaviour of their defended models.

Poison frogs (Dendrobatidae) are a classic example of aposematism with conspicuous colours, slow and bold movements, and reduced escape behaviour evolving alongside the sequestration of potent alkaloid toxins (Cooper Jr et al., 2009b; Klank et al., 2024; Maan & Cummings, 2012; Pröhl & Ostrowski, 2011; Santos et al., 2003). Aposematic dendrobatids are both more likely to be active prior to disturbance and less likely to quickly flee when approached by a predator than sympatric species, which are non-toxic and cryptically coloured (e.g., *Craugastor* spp. Craugastoridae) (Blanchette et al., 2017; Cooper Jr et al., 2009a, 2009b; Gray et al., 2023; Ozel & Stynoski, 2011). Indeed, these bold movements may themselves also act to enhance the warning signal and reduce predation rates beyond that conveyed by the same colours on static frogs (Paluh et al., 2014; Saporito et al., 2007).

Allobates zaparo (Aromobatidae) is a non-toxic frog that is a Batesian mimic of the chemically defended poison frog *Ameerega bilinguis* (Dendrobatidae) (Darst & Cummings, 2006; Darst et al., 2005, 2006; McEwen et al., 2024). The two species are similar in appearance, with both exhibiting a dark red dorsum and yellow spots at the base of the limbs (Figure 1A–C) (Darst & Cummings, 2006; Darst et al., 2006; McEwen et al., 2024). As such, avian predators experienced with the colours and toxins of *Am. bilinguis* avoid attacking both species (Darst & Cummings, 2006). However, as a Batesian mimic, *Al. zaparo* is still at risk from predators which ignore the signal (Barnett et al., 2007; Sherratt et al., 2004). To avoid these encounters, *Al. zaparo* may benefit from reducing the likelihood of *detection* or *capture* through morphological or behavioural strategies that deviate from perfect mimicry (Kikuchi & Pfennig, 2013; McEwen et al., 2024). In a previous study,

we found that both species can use defensive postures to reduce detectability, but no evidence that the dorsal colours of the undefended *Al. zaparo* were more cryptic than those of the defended *Am. bilinguis* (McEwen et al., 2024). Yet, it remains to be seen whether the post-detection behaviour of *Al. zaparo* is aligned with that of *Am. bilinguis*, or instead deviates from mimicry and towards more effective escape behaviours that are more reminiscent of non-defended species.

Here, we tested the hypothesis that a Batesian mimic, *Al. zaparo*, would be more cautious than its defended model, *Am. bilinguis*, during close-range interactions with predators. To test this hypothesis, we compared the escape behaviour of *Al. zaparo*, *Am. bilinguis*, and the sympatric, cryptically coloured and non-toxic species, *Adenomera hylaedactyla* (Leptodactylidae), during a simulated predator encounter.

Firstly, in line with previous work contrasting the behaviour of aposematic and cryptic frogs (Blanchette et al., 2017; Cooper Jr et al., 2009a, 2009b; Gray et al., 2023; Ozel & Stynoski, 2011), we predicted that the chemically defended *Am. bilinguis* would exhibit reduced escape behaviour and more predictable movement than the non-toxic *Ad. hylaedactyla*. Specifically, we predicted that *Am. bilinguis* would perform fewer jumps, travel a shorter distance, stop more quickly, and move in a more linear trajectory than would *Ad. hylaedactyla*. Secondly, when considering mimicry, we predicted that *Al. zaparo* would mimic *Am. bilinguis* during the early, largely visual, stages of the predation sequence (Darst & Cummings, 2006; Darst et al., 2005; McEwen et al., 2024). Whereas, in the latter stages, where a predator has ignored the visual signal and may test the honesty of any chemical defence directly, *Al. zaparo* would travel further, move more erratically, and be more likely to move prior to physical contact from the "predator" than *Am. bilinguis*.

Materials and methods

In June 2019, we captured 20 individuals from each of three different species of terrestrial frog at the Iyarina Forest Reserve, Provincia de Napo, Ecuador (Anderson et al., 2021; McEwen et al., 2024): the chemically defended poison frog *Ameerega bilinguis* (Dendrobatidae), the Batesian mimic *Allobates zaparo* (Aromobatidae), and the cryptically coloured *Adenomera hylaedactyla* (Leptodactylidae) (Figure 1A–C). The three species are sympatric and exposed to the same predators, sharing the same terrestrial microhabitat (leaf litter), activity patterns (diurnal), and size (mean snout-vent length ± SD) from our sample: *Am. bilinguis* (22.51 ± 1.63), *Al. zaparo* (26.92 ± 1.84), *Ad. hylaedactyla* (23.34 ± 2.74) (Caldwell, 1996; Darst et al., 2005; McEwen et al., 2024; Toledo et al., 2007).

Frogs were encountered along non-linear transects through the forest. Once captured, each frog was individually housed in a plastic container (10 cm diameter × 10 cm height) that contained soil and leaf litter (~3 cm depth) collected from the same location as the frogs. Frogs were fed to satiation with live termites once per day and were kept at the ambient temperature, humidity, and photoperiod (Anderson et al., 2021; McEwen et al., 2024). Frogs were allowed to acclimatize to their enclosure for a minimum of 24 hr and began the experiment between two and five days post-capture. Each frog was released at the original site of capture within seven days (Anderson et al., 2021; McEwen et al., 2024).

Behavioural trials took place outside, under natural daylight conditions, within an enclosed rectangular arena (~200 cm × ~100 cm) atop an area of soil where the leaf litter had been removed (Figure 1D). Each trial was filmed from directly above with the camera positioned ~140 cm above the centre of the arena. Each recording was captured at 23.98 frames per second and 720p HD resolution (1280 × 720 pixels), using a Fujifilm X-T10 CSC digital camera with an XC 16-50 mm F3.5-5.6 OIS II lens (Fujifilm Holdings Corp., Tokyo, Japan). Methods were approved by the McMaster University Animal Research Ethics Board, Canada (AREB 18-05-20) and the Ministerio del Ambiente, Ecuador (permit 014-2019-IC-FLO-DNB/MA).

We used a repeated measures design, with each frog completing four experiment sessions over two consecutive days, one each morning (10:00 a.m.–12:00 p.m.) and one each afternoon (04:00 p.m.–06:00 p.m.). At the beginning of each experimental session, a frog was placed on a 120 × 120 mm starting pad 250 mm from one edge of the arena (Figure 1D). The frog was covered by a transparent plastic dome (75 mm diameter) and was allowed to acclimatize until it had stopped moving for 5 s. Once the frog was settled, the starting pad was rotated so that the frog was facing forwards into the arena. The dome was then removed, and the frog was slowly approached from behind by the experimenter (BLM). The experimenter (BLM) attempted to gently touch the frog, slightly posterior to the sacral hump, with a short (200 mm) wooden stick. A stick was used to minimize physical contact between the frog and the researcher. Once physical contact was made, or the frog started moving unprompted, the experimenter retreated until the frog stopped moving or, if the frog did not move after being touched, for 2 s. The frog was then approached four more times in the same manner, with a 2 s interval between each, for a total of five "predator" approaches within each of the four experimental sessions.

We analysed the videos to quantify several different metrics of the duration (1–3), linearity (4), and initiation (5) of escape behaviour: (1) the total number of jumps (total jumps), (2) the total distance travelled in mm (escape distance, see Supplementary Material for distance scaled to body length), (3) the time spent moving in seconds (escape time), (4) the angle of each jump in degrees (jump angle & escape trajectory, see below), and (5) the proportion of the five "predator" approaches that resulted in movement prior to physical contact from the "predator" (pre-emptive jumps).

We recorded variables 1–4 using the R package PATHTRACKR v1.2.3 (Harmer & Thomas, 2019). As the frog did not always contrast strongly with the soil background, automated motion tracking was not possible, and landmark locations were instead recorded manually. Each video was converted to greyscale and split into still images at a frequency of 16 frames per second (~0.0625 s intervals) using the open-source software *FFmpeg* (Tomar, 2006). Using the manual-track function in PATHTRACKR, for each image, we manually clicked on the frog to record the pixel coordinates of its location across time. To identify jumps, we first passed the coordinate data through a 5-frame moving median filter and computed the smoothed frame-to-frame velocity. Jumps were recorded as beginning when the offset in the frog's location between adjacent frames first exceeded a threshold of 5 pixels (~0.75 mm) and ending when frame displacement first dipped below this threshold. We then used the video frame

Table 1. Results from the analysis of escape behaviour, main effects, and pairwise contrasts between species extracted from the generalized linear mixed effects models.

	Number of jumps	Distance (mm)	Time (s)	Pre-emptive jumps
Main effect	$\chi^2 = 8.63$, *d.f.* = 2, $p = 0.013$	$\chi^2 = 25.25$, *d.f.* = 2, $p < 0.001$	$\chi^2 = 29.52$, *d.f.* = 2, $p < 0.001$	$\chi^2 = 50.60$, *d.f.* = 2, $p < 0.001$
Am. bilinguis vs *Ad. hylaedactyla*	$z = -2.96$, $p = 0.009$	$z = -4.50$, $p < 0.001$	$z = -1.73$, $p = 0.194$	$z = 1.96$, $p = 0.124$
Al. zaparo vs *Am. bilinguis*	$z = 0.81$, $p = 0.697$	$z = -0.46$, $p = 0.892$	$z = -4.14$, $p < 0.001$	$z = 6.42$, $p < 0.001$
Al. zaparo vs *Ad. hylaedactyla*	$z = 2.15$, $p = 0.080$	$z = -5.25$, $p < 0.001$	$z = -5.87$, $p < 0.001$	$z = 8.18$, $p < 0.001$
Relationship between species	ABI $\underset{=}{\overset{\leq}{\underset{\text{AZA}}{}}}$ AHY	(ABI = AZA) < AHY	AZA < (ABI = AHY)	(ABI = AHY) < AZA

Note. Species codes: *Am. bilinguis* (ABI—toxic model), *Al. zaparo* (AZA—Batesian mimic), and *Ad. hylaedactyla* (AHY—cryptic).

rate and scale to calculate the distance travelled, time spent moving, and angle of displacement for each jump.

For variable 5, we hand-scored the number of pre-emptive movements using the open-source video playback software *VLC media player* v. 3.0.8 (VideoLAN, Paris, France). During video scoring the frogs were too small for diagnostic features to be accurately determined and the experimenter (BLM) was blind to species identity.

We performed a series of generalized linear mixed effects models, with different error distributions depending on the data, to analyse the number of jumps (Poisson), distance travelled (log-transformed, Gaussian), escape time (log transformed, Gaussian), and the proportion of pre-emptive jumps (Binomial). Each model included the fixed effect of *species* and the random intercepts of *frog ID* and *session number*, and we checked model assumptions using R package DHARMa v.0.4.6 (Hartig, 2022). To fit model assumptions, we used functions *lmer* or *glmer* from R package lme4 v.1.1.34 (Bates et al., 2015) to analyse the number of jumps (total jumps) and escape time, and function *glmmTMB* from R package glmmTMB v.1.1.8 (Brooks et al., 2017) to analyse the distance travelled (escape distance) and number of pre-emptive jumps. We then conducted pairwise comparisons between the three species and adjusted *p*-values accordingly, using R package multcomp v.1.4.25 (Hothorn et al., 2008).

We analysed jump angle (converted from degrees to radians between 0 and 2π) with Bayesian circular mixed effects models (function *bpnme*) from R package bpnreg v.2.0.3 (Cremers, 2024). We first examined the absolute angle of each jump between 0° and 180° by converting negative degrees to positive prior to converting degrees to radians. We then analysed overall escape trajectory between −180° and 180° by allowing jumps to the left (negative angles) and to the right (positive angles) to cancel each other out. Our models included the fixed effect of *species* and the random intercept of *frog ID*, with 5,000 iterations and a burn-in of 1,000. We interpreted statistical significance as instances where the 95% credible intervals of two species did not overlap.

Results

We found a significant effect of species on the number of jumps (total jumps), the total distance travelled (escape distance), the time spent moving (escape time), and the proportion of jumps that occurred before physical contact (pre-emptive jumps). We therefore performed pairwise comparisons between each of the three species (ABI = *Am. bilinguis*, AZA = *Al. zaparo*, AHY = *Ad. hylaedactyla*; Table 1; Figure 2A–D; Supplementary Material). In line with predictions regarding aposematic and cryptic behaviour, we found that although there was no difference in the time spent moving (escape time: ABI = AHY), the toxic *Am. bilinguis* performed fewer jumps (total jumps: ABI < AHY) and moved a shorter distance (escape distance: ABI < AHY) than did the cryptic *Ad. hylaedactyla*.

When compared to *Am. bilinguis*, the mimetic *Al. zaparo* was not statistically different from its toxic model in either the number of jumps (total jumps: AZA = ABI) or the distance travelled (escape distance: AZA = ABI). When compared to the cryptic *Ad. hylaedactyla*, *Al. zaparo* travelled a shorter distance (escape distance: AZA < AHY) and although any difference in the number of jumps was not statistically significant, the effect was marginal and tended towards *Al. zaparo* performing fewer jumps than *Ad. hylaedactyla* (total jumps: AZA ≤ AHY, $p = 0.080$). The mimetic *Al. zaparo*, did however, spend the shortest amount of time moving (escape time: AZA < (ABI = AHY)) and was the most likely to move prior to physical contact from the "predator" (pre-emptive jumps: (ABI = AHY) < AZA), with there being no difference between the aposematic *Am. bilinguis* and cryptic *Ad. hylaedactyla* in both cases.

When analysing both jump angle and escape trajectory, we found that models including *species* as a fixed effect better fit the data than did the null models (Table 2). When analysing jump angle, 0°–180°, we found that the 95% credible intervals for each species did not overlap (ABI < AZA < AHY, Figure 2E–G, and K). The toxic *Am. bilinguis* had the smallest directional change between jumps (~30°), the mimetic *Al. zaparo* was intermediate (~40°), and the cryptic *Ad. hylaedactyla* had the largest jump angle (~50°). Conversely, when analysing overall escape trajectories, −180° to 180°, the 95% credible intervals of each species did overlap. As such, there was no evidence to suggest the three frog species differed in the direction of travel (ABI = AZA = AHY; Table 2; Figure 2H–J, and L). Moreover, the credible intervals of *Al. zaparo* and *Ad. hylaedactyla* overlapped with zero, and those of

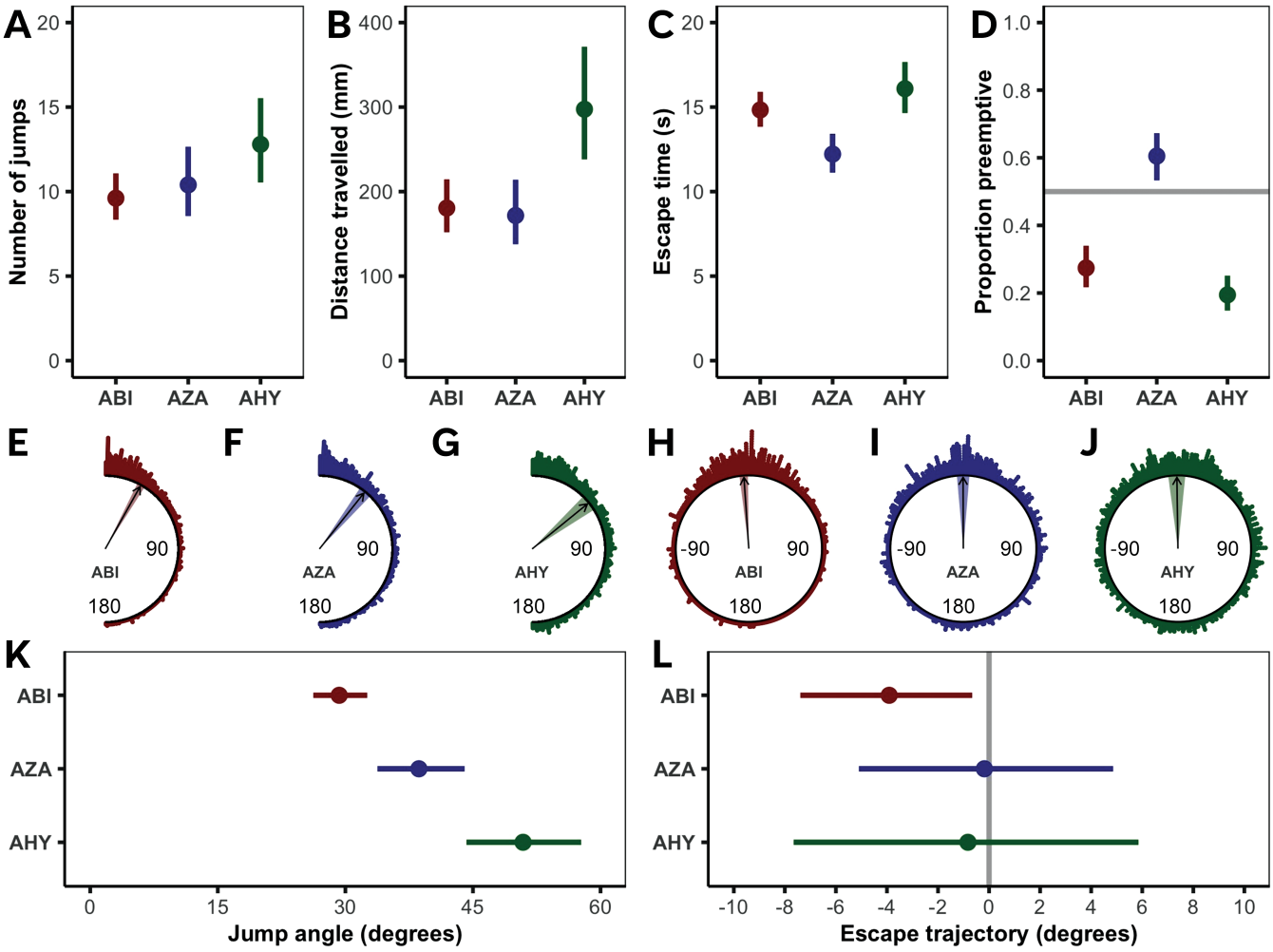

Figure 2. Escape behaviour results. Species codes: *Am. bilinguis* (ABI, red—toxic model), *Al. zaparo* (AZA, blue—Batesian mimic), and *Ad. hylaedactyla* (AHY, green—cryptic). Top: Means ± 95% CI from generalized linear mixed effect models for (A) the number of jumps (total jumps), (B) the distance travelled (escape distance, mm), (C) the time spent moving (escape time, s), and (D) the proportion of "predator" approaches that resulted in a pre-emptive jump (pre-emptive jumps, the grey line indicates a 50:50 threshold). Middle: Raw circular data for jump angle (0°–180°: (E) *Am. bilinguis*, (F) *Al. zaparo*, and (G) *Ad. hylaedactyla*) and escape trajectory (−180° to 180°: (H) *Am. bilinguis*, (I) *Al. zaparo*, and (J) *Ad. hylaedactyla*). Circular histograms show the raw data and the shaded arrows show the circular means ± 95% CI from the Bayesian circular mixed effects models. Bottom: Means ± 95% CI from Bayesian circular mixed effects models (replotted from (E)–(J)) for (K) jump angle and (L) the overall escape trajectory (the grey line indicates a forward trajectory of 0°).

Table 2. Circular mean, mode, and 95% credible intervals for absolute jump angle (0°–180°) and escape trajectory (−180° to 180°) in degrees extracted from the Bayesian circular mixed effects models.

	Jump angle (0°–180°)				Escape trajectory (−180° to 180°)			
	Mean	Mode	Lower CI	Upper CI	Mean	Mode	Lower CI	Upper CI
Am. bilinguis	29.27	29.18	26.23	32.57	−3.91	−3.70	−7.39	−0.66
Al. zaparo	38.65	37.97	33.78	44.01	−0.18	0.76	−5.10	4.86
Ad. hylaedactyla	50.89	50.70	44.24	57.72	−0.83	−1.16	−7.66	5.85
Relationship between species	ABI < AZA < AHY				ABI = AZA = AHY			

Model fit	DIC	DIC.alt	WAIC1	WAIC2	DIC	DIC.alt	WAIC1	WAIC2
Null model	6,188	**6,218**	6,225	6,230	7,683	**7,721**	7,696	7,698
Full model	**6,180**	6,231	**6,214**	**6,217**	**7,672**	7,739	**7,685**	**7,687**

Note. Model fit metrics: lower values (bold) indicate a better fit to the data. Species codes: *Am. bilinguis* (ABI—toxic model), *Al. zaparo* (AZA—Batesian mimic), and *Ad. hylaedactyla* (AHY—cryptic).

Am. bilinguis were very close to zero (within 0.66°). Taken together, therefore, despite differences in jump angle, on average over a sequence of jumps, all three species moved in an almost straight line opposing the approaching "predator".

Discussion

Aposematic colours are generally associated with bold movements and reduced escape behaviour, whereas cryptic species are usually shy and more likely to flee (Mappes et al., 2005; Stevens & Ruxton, 2019; Tan et al., 2024). Here, we found that the aposematic poison frog, *Am. bilinguis,* and the non-toxic, cryptically coloured, *Ad. hylaedactyla,* broadly conform to these two predictions. When approached by a simulated predator, *Am. bilinguis* performed fewer jumps, travelled a shorter distance, and moved in a more linear (less erratic) trajectory than did *Ad. hylaedactyla*.

Batesian mimics display the conspicuous colours of aposematic species but lack the secondary defences that allow their defended models to survive close-range interactions with predators (Bates, 1862; Gamberale-Stille et al., 2009; Kikuchi & Pfennig, 2013). As such, we predicted that *Al. zaparo* would deviate from behavioural mimicry and flee from an approaching predator in a manner similar to that of *Ad. hylaedactyla*. Contrary to this prediction, we found that *Al. zaparo* was largely bold in behaviour, moving a similar distance to *Am. bilinguis* that was shorter than *Ad. hylaedactyla*, and abandoning escape behaviours more quickly than either of the other two species. However, *Al. zaparo* did deviate from behavioural mimicry in the number of jumps performed and in jump angle, where it was intermediate between the aposematic and cryptic species. Yet, *Al. zaparo* was the most likely to initiate its escape behaviour before physical contact was made by the approaching predator.

Taken together, we can describe three different behavioural paradigms. The toxic *Am. bilinguis* moves relatively slowly and predictably, but frequently waits until a predator has ignored the aposematic signal and made physical contact before initiating its escape. Whereas the non-toxic *Ad. hylaedactyla* relies on crypsis, remaining stationary until camouflage is broken, and then rapidly and erratically fleeing to a greater distance. The mimetic *Al. zaparo*, meanwhile, largely mimics the bold behaviour of *Am. bilinguis*, but frequently starts its escape before a predator can make physical contact.

When compared to their defended models, Batesian mimics are constrained by two main factors: (1) mimics are less likely to survive close encounters with predators because the (dis) honesty of their signals can be tested directly (i.e., through smell or taste) and (2) mimicry is frequency dependent such that if mimics are more abundant than their models, predators may no longer associate the signal with unprofitability (Finkbeiner et al., 2018; Gamberale-Stille & Guilford, 2004; He et al., 2022; Kikuchi & Pfennig, 2013; Sherratt & Stefan, 2024; Stevens, 2007). As these constraints arise from predators being able to test the honesty of an aposematic signal, rather than the presence of mimics per se, they may be mitigated by mimics reducing the frequency of direct predator interactions relative to their models (Kikuchi & Pfennig, 2013; Sherratt & Stefan, 2024; Stevens, 2007). Previous studies suggest that *Al. zaparo* is a good morphological mimic and no more cryptic than *Am. bilinguis* (Darst & Cummings, 2006; Darst et al., 2006; McEwen et al., 2024). Here, we find that when faced with an approaching predator *Al. zaparo* also mimics the bold movements of *Am. bilinguis*. Contrary to our prediction, therefore, *Al. zaparo* did not flee from predators in a manner more closely resembling that of the similarly undefended, but cryptic, *Ad. hylaedactyla*. Instead, *Al. zaparo* seems to mitigate the costs of its salient signal by deviating from behavioural mimicry as the predator approaches. In this manner it appears to largely maintain the visual signals and bold behaviour of *Am. bilinguis,* but in a way that results in predators being less able to test the honesty of the signal.

Poison frogs of the sister families Dendrobatidae and Aromobatidae, including *Am. bilinguis* and *Al. zaparo,* respectively, often defend territories and attract mates using conspicuous visual and acoustic signals (Pašukonis et al., 2013; Ringler et al., 2012; Rojas, 2017; Santos et al., 2003, 2014). The greater risk of detection that results from salient signalling and the energetic and opportunity costs associated with prolonged escape behaviour have both been suggested to drive the evolution of toxin sequestration and aposematism (Speed et al., 2010). As predators associate both colour and bold behaviour with toxicity, poison frogs can spend more time on conspicuous feeding, breeding, and combative behaviours (Carvajal-Castro et al., 2021; Dugas et al., 2015; Pröhl & Ostrowski, 2011; Santos et al., 2014; Willink et al., 2013). For *Al. zaparo*, which lacks chemical defences, morphological, and behavioural mimicry may play a similar role. Behavioural mimicry may increase the efficacy of aversive signalling, while the need for conspicuous signals and to maintain territory ownership may simultaneously reduce the utility of both camouflage and extended escape behaviour.

It is also important to note that while convergent escape behaviours have likely evolved in concert with morphological mimicry, *Am. bilinguis* and *Al. zaparo* are more closely related to each other than to *Ad. hylaedactyla*. It is therefore possible that these behaviours are a conserved synapomorphy shared among poison frogs, rather than traits which have evolved directly due to selection for mimicry. Future studies are therefore needed to examine defensive behaviours more broadly across conspicuously and cryptically coloured poison frog lineages.

In this study, we have identified how behavioural traits may differ between an aposematic frog and its Batesian mimic during key moments of the predation sequence. However, these species exist in a wider ecological context where search, pursuit, and escape behaviours are complicated by habitat heterogeneity, the presence of multiple predator species, and multiple mimetic species. Firstly, although these frogs will frequently remain motionless until touched during close-range interactions with predators, more work is needed to examine the distance at which escape behaviour may begin when a predator is spotted from afar (i.e., the flight initiation distance (Broom & Ruxton, 2005; Ydenberg & Dill, 1986)). Then, once detected, a frog will need to transverse through the three-dimensional structure of the leaf litter where it will not always be visible to the predator. Full, partial, or transient occlusion, either when static or during motion, may disrupt the observer's ability to accurately detect or track moving prey (Cuthill et al., 2019). Especially as poison frogs may utilize both salient signalling and camouflage (McEwen et al., 2024), direct their escape towards hidden refuges (Cooper Jr, 2016; Pröhl & Ostrowski, 2011), and employ high contrast flash marks which may help disrupt effective tracking (Loeffler-Henry et al., 2018, 2023; Murali, 2018; Murali & Kodandaramaiah, 2020). Moreover, behavioural differences

between model and mimic may confuse predators (Loeffler-Henry & Sherratt, 2021), flash marks may be more effective if prey begin their escape early (Loeffler-Henry et al., 2021), and different escape behaviours may be necessary for predators which differ in their primary approach angle, sensory modality, perceptual acuity, or susceptibility to frog toxins (Endler & Mappes, 2004; McEwen et al., 2024; Stevens, 2007). Future work is needed to explore the efficacy of escape behaviour given the role viewing angle, intermittent or deimatic flash marks, and transient occlusion may play in a predator's ability to track and capture moving frogs.

The evolution of both aposematism and Batesian mimicry represents a complex set of evolutionary and ecological trade-offs between the competing benefits of salient warning signals versus the low predator encounter rate afforded by cryptic colours and behaviour (Kikuchi et al., 2023; Postema et al., 2022). Batesian mimics benefit from resembling their defended models, but the risks associated with predator encounters may vary throughout the predation sequence (Kikuchi & Pfennig, 2013; Kikuchi et al., 2023; Stevens, 2007). Consequently, as such trade-offs may differ between model and mimic, it may at times be an advantage for mimics to diverge from perfect resemblance of their models (Kikuchi & Pfennig, 2013; McEwen et al., 2024; Stevens, 2007). Here, we find that although *Al. zaparo* is a good morphological mimic (Darst & Cummings, 2006; Darst et al., 2005; McEwen et al., 2024), and does share some behavioural traits with *Am. bilinguis*, it deviates from exact behavioural mimicry during close-range interactions with predators. Yet, *Al. zaparo* also does not conform to the stereotypical behaviour of non-toxic frogs. Taking these data together, we suggest that this behavioural flexibility allows mimetic frogs to achieve high mimic fidelity while simultaneously avoiding high-risk physical interactions with predators. These results highlight the importance of more comprehensively examining the morphological and behavioural context when attempting to understand the evolution of mimicry, including multiple anti-predator strategies, and how the risk of predation changes throughout the predation sequence.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

Raw data and analysis code are available in the Dryad data repository at [https://doi.org/10.5061/dryad.bnzs7h4m8].

Author contributions

James Barnett (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Funding acquisition [equal], Investigation [lead], Methodology [lead], Project administration [lead], Resources [equal], Software [equal], Supervision [equal], Validation [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead]), Brendan McEwen (Conceptualization [lead], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [lead], Methodology [lead], Project administration [equal], Writing—review & editing [equal]), Isaac Kinley (Data curation [equal], Formal analysis [equal], Software [equal], Validation [equal], Writing—review & editing [equal]), Hannah Anderson (Conceptualization [equal], Investigation [equal], Writing—review & editing [equal]), and Justin Yeager (Conceptualization [equal], Funding acquisition [equal], Methodology [equal], Project administration [lead], Resources [lead], Supervision [lead], Validation [equal], Writing—original draft [equal], Writing—review & editing [equal])

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Conflicts of interest

None declared.

Ethical statement

This work was approved by the McMaster University Animal Research Ethics Board, Canada (AREB 18-05-20) and the Ministerio del Ambiente, Ecuador (permit 014-2019-IC-FLO-DNB/MA).

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