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Conspicuous animal signals avoid the cost of predation by being intermittent or novel: confirmation in the wild using hundreds of robotic prey

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Social animals are expected to face a trade-off between producing a signal that is detectable by mates and rivals, but not obvious to predators. This trade-off is fundamental for understanding the design of many animal signals, and is often the lens through which the evolution of alternative communication strategies is viewed. We have a reasonable working knowledge of how conspecifics detect signals under different conditions, but how predators exploit conspicuous communication of prey is complex and hard to predict. We quantified predation on 1566 robotic lizard prey that performed a conspicuous visual display, possessed a conspicuous ornament or remained cryptic. Attacks by free-ranging predators were consistent across two contrasting ecosystems and showed robotic prey that performed a conspicuous display were equally likely to be attacked as those that remained cryptic. Furthermore, predators avoided attacking robotic prey with a fixed, highly visible ornament that was novel at both locations. These data show that it is prey familiarity—not conspicuousness—that determine predation risk. These findings replicated across different predator–prey communities not only reveal how conspicuous signals might evolve in high predation environments, but could help resolve the paradox of aposematism and why some exotic species avoid predation when invading new areas.

1. Introduction

The classic expectation that standing out in the environment increases predation can be traced back to the observation that crypsis appears widespread in nature [1]. Yet many prey species are not cryptic and extravagance seems to be the norm for many animals that rely on conspicuous communication for reproduction [2]. In the latter instance, the general assumption is that social animals simply bear the cost of increased predation in order to communicate effectively with conspecifics. While there are notable cases of conspicuous behaviour and ornamentation being exploited by predators to target prey [3,4], the relationship is often not straightforward [5–7]. For instance, peacocks are iconic symbols of sexual selection [8], and their massive feather trains and loud courtship calls were thought to both attract predators and handicap escape [8,9]. Nonetheless, new evidence suggests peacock locomotion is not impeded by the train [10,11] nor are males disproportionately predated upon in the wild [12]. Communicating animals might also resolve the trade-off between effective signalling and evading predation by using ‘private’ signal channels that are obvious to mates and territorial rivals (but not to predators) [13,14] by reducing signalling

and other conspicuous behaviours when the perceived risk of predation is high [15,16], or by simply relying on signals that are only produced in occasional, brief bouts of communication.

There is also the situation of prey that deliberately disclose their location to predators in order to advertise their unprofitability through highly visible aposematic signals, such as conspicuous warning coloration [17]. The difficulty here is resolving the paradox of how warning signals originate given prey would initially experience increased attack by predators that have yet to associate the signal with unprofitability [1,17,18]. This is equally relevant for reproductive signals, if not more puzzling because socially communicating prey are presumably profitable targets. Various hypotheses have been proposed, including predators learning from others to avoid certain prey types [19,20], or generalization from recognized warning signals to other signals with similar characteristics [21,22]. However, the most credible resolution to this paradox invokes naive predators avoiding novel prey types because of their unknown quality, a phenomenon known as dietary conservatism [1,23]. This would allow a conspicuous signal to initially proliferate to fixation [24] and become associated with unprofitability [25], or allow the improved benefits from effective reproductive signalling to ultimately outweigh the increased risk of predation [26]. Evidence for dietary conservatism has been found in several species—mostly birds [1], but also fish [27] and possibly crabs [28]—but most individuals tested still target novel prey just as frequently as (or more frequently than) familiar prey (e.g. [23,27,28]). Given this background, how novel prey types would fare in natural environments where predator communities are diverse remain unclear. But if dietary conservatism in predators is widespread, it would significantly advance our understanding of how many conspicuous signals got their initial start, both those used in reproduction and warning communication.

With this backdrop, we designed an experiment to test how free-ranging predators make decisions on the choice of prey. The experiment involved quantifying attacks on hundreds of robotic prey mimics deployed throughout a tropical arboreal environment on Borneo and a temperate terrestrial environment in Australia. The contrasting predator–prey communities at these locations provided a test of the extent to which predator decisions can be generalized across diverse and disparate ecosystems [29]. The robotic mimics replicated the morphology and behaviour of a common Southeast Asian agamid lizard, *Draco sumatranus*, in which males perform an elaborate territorial and courtship display centred on the rapid extension of a yellow dewlap (electronic supplementary material, figure S1). At the experimental location on Borneo, these lizards are probably subject to high levels of predation (estimated from attacks on static prey models [30]). In Australia, the robotic lizard mimics were similar in body form and size to several native lizards found at the second experimental location in the NSW Central Tablelands, with the key difference that no lizard in the area had a conspicuously coloured ornament. Three versions of the robotic lizard mimic were deployed (see electronic supplementary material, figure S2): a (i) ‘moving’ dewlap treatment in which the robot performed a population-typical bout of the display during daylight hours (electronic supplementary material, figure S1); a (ii) dewlap ‘always out’ treatment in which the dewlap was fixed

permanently extended; and a (iii) ‘none’ or no dewlap treatment in which the dewlap had been removed. A control was also deployed consisting of a conspicuously coloured plasticine ring that represented a highly visible, non-prey object.

Using these mimics, our aim was to test three alternative hypotheses by which predators locate and attack prey. First, our modelling of predator colour perception showed the artificial dewlap (and controls) should be highly visible to typical avian, mammalian and reptilian predators in both the tropical arboreal environment on Borneo and the temperate terrestrial environment in Australia (electronic supplementary material, figure S3). If predators primarily rely on conspicuous colour to localize prey, the robotic lizard mimic with the dewlap permanently extended should be the most frequently attacked (the ‘conspicuous coloration is costly’ hypothesis; electronic supplementary material, figure S4a). Second, even cryptically coloured prey can become obvious when moving [31], and the types of movements used in the dewlap display of *Draco* are likely to be especially useful for detection by predators [32]. Our computational motion analysis of the dewlap display of robotic lizard mimics (electronic supplementary material, figure S1b) showed it should stand out against the natural background motion of windblown vegetation at both locations (signal-to-noise ratio, 95% confidence range: 1.88–1.96, Borneo; 2.69–2.95, Australia). If predators rely on movement to primarily localize prey, the robotic lizard mimic with the moving dewlap should incur the highest frequency of attack (the ‘conspicuous movement is costly’ hypothesis; electronic supplementary material, figure S4b). For both these hypotheses, the robotic lizard mimic that never extended the dewlap should be the least targeted by predators because it is the least conspicuous of the three (electronic supplementary material, figure S4a,b).

Finally, the robotic lizard mimic with no dewlap and the mimic with the moving dewlap were both familiar prey on Borneo. This was probably the case in Australia as well, given the similar appearance of the mimic to native lizards and that 95% of the time the dewlap was not visible on the robotic mimic with the moving dewlap. By contrast, prey with a dewlap permanently extended was novel at both locations. If dietary conservatism is widespread in predator communities, predators should actively avoid the mimic with the novel phenotype of a permanently extended dewlap (the ‘predator conservatism’ hypothesis; electronic supplementary material, figure S4c).

2. Methods

Extended details on methods are outlined in the electronic supplementary material.

(a) Construction of robotic lizard mimics

The robot was designed to mimic the dewlap display and body morphology of live diurnal male lizards of *D. sumatranus* on the campus of Universiti Malaysia Sarawak at Kota Samarahan, Sarawak, East Malaysia, on Borneo. The artificial dewlap was a close match to the visual appearance of those in life (electronic supplementary material, figure S1a). The robot extended and retracted this dewlap during daylight hours in a population-typical bout of display performed at the population-median display rate (electronic supplementary material, figure S1b). The body of the robotic lizard mimic was made from grey plasticine

(a neutral colour present in most natural backgrounds), cast from a mould of a male lizard equivalent to the average size of male *D. sumatranus* and similar in size and appearance to lizards common at the Australian location. A control was also deployed that consisted of a ring of hot-pink or blue plasticine (which would stand out against most natural backgrounds) grafted to the same housing as used for robotic prey mimics.

(b) Visual colour modelling and computational motion analysis

Reflectance spectra of the predominant background colours around the display perches of male *D. sumatranus* at the Bornean experimental location were taken from the data archive of Klomp *et al.* [30] (as was the dewlap colour of a subset of these lizards shown in electronic supplementary material, figure S1a; habitat data was a representative sample of the substrate within several body lengths of the lizard and any adjacent vegetation that might occur in the immediate background). This was combined with data collected for the artificial dewlap and controls (hot-pink/blue plasticine) and measures of the predominant background colour at the Australian experimental location taken around deployed robots (a representative sample of the substrate within a metre or so of the robot). We used the receptor-noise limited model [33] to estimate the chromatic (colour, ΔS) and achromatic (luminance, ΔL) conspicuousness of stimuli to three representative classes of predator: reptiles, mammals and birds. All visual modelling was conducted using the package ‘pavo’ v. 2.5.0 [34] for R v. 4.0.0 (R Development Core Team, R Foundation for Statistical Computing, Vienna).

For motion analyses, signal-to-noise ratios were based on the average, maximum speed of dewlap display movements divided by the average, maximum speed of environmental motion occurring in visual backgrounds resulting from windblown vegetation. The magnitude of this environmental visual noise is critical for the detection of prey movement by predators (i.e. background visual noise can mask prey movements [35]). Speed was quantified from field-recorded high definition digital video using the Matlab-based ‘Analysis of Image Motion’ program developed by Peters *et al.* [36]. Environmental motion data for the Bornean experimental location were the visual backgrounds of free-ranging territorial male *D. sumatranus* recorded in previous years (these videos were also used to quantify the dewlap speeds, display rates and dewlap area of live lizards shown in electronic supplementary material, figure S1b). Data at the Australian experimental location were the visual backgrounds of robotic mimics (these videos were also used to quantify the speed of dewlap movements and the size of the artificial dewlap of the robotic mimics in electronic supplementary material, figure S1b).

(c) Experimental deployment

The Bornean experiment was conducted on the Universiti Malaysia Sarawak campus, where a large population of arboreal *D. sumatranus* defend territories on trees lining the campus roads. Robotic lizard mimics and controls were secured to trees (electronic supplementary material, figure S5a) at a height within the natural range of perches recorded for territorial male lizards at this location (electronic supplementary material, figure S6). Robotic mimics and controls were initially left undisturbed for 3 days, after which they were inspected for signs of attack on a daily basis until day 5. The Australian experiment was conducted on a private property in the NSW Central Tablelands with a mix of remnant eucalypt woodland and open pasture. Robotic lizard mimics and controls were placed on the ground or low rock outcrops (electronic supplementary material, figure S5b) to match basking locations observed for native lizards

and were inspected daily for signs of attack until day 3. Two colours were used for controls because the colour of the hot-pink controls was observed to progressively fade to resemble raw meat (this did not occur in the Bornean experiment) and was switched with blue plasticine that retained its colour through the experiment.

(d) Assigning predator attack

Impressions left in the plasticine were photographed, irrespective of assumed cause, and labelled with an identification number without reference to treatment. These photographs were used to assign predation several months after the completion of the experiments using a strict protocol outlined in the online Supporting Information. Potential predators of *Draco* lizards observed at the Bornean experimental location included birds, snakes, rats and domestic cats. Several trees on which robotic lizard mimics and controls were deployed were later observed to have large colonies of tree-cutter ant that were extremely aggressive and swarmed when disturbed. This was included as a covariate in all statistical analyses. Potential predators of native lizards observed at the Australian experimental location included birds, terrestrial snakes, monitor lizards, foxes and feral cats. In many cases, the impressions left in plasticine could be easily assigned to a predator or non-predator attack (e.g. electronic supplementary material, figure S7), but some marks were more difficult to discern. Rather than attempt to make subjective categorizations, photographs were manually blinded to treatment and impressions grouped by similarities in appearance. Any group that included impressions left on controls were subsequently removed from the dataset. Of the 106 lizard mimics/controls showing animal markings at the Australian experimental location, 69 were excluded as coming from herbivores (see electronic supplementary material, figure S8) or were otherwise impressions typical of those found on controls.

(e) Statistical analyses

Statistical models corresponding to each of the three hypotheses (see electronic supplementary material, figure S4) were formulated and considered against each other and a null model that assumed the frequency of attack was independent of treatment and control. This was achieved by grouping treatments—dewlap ‘always out’, ‘moving’ or ‘none’—according to the predicted attack under each of the three hypotheses outlined in electronic supplementary material, figure S4. The null model was an intercept-only model, although in the case of the Bornean experiment it retained a binary covariate accounting for the presence or absence of leaf-cutter ants. The four models were fitted as logistic regressions using the base functions of R v. 3.6.3 and evaluated using the sample-size-corrected Akaike information criterion (AIC_c) and its derivative ω . Kaplan–Meier curves were used to visualize the cumulative proportion of robotic lizard mimics and controls attacked over time using the ‘survminer’ package v. 0.4.8 [37].

3. Results

The predator dietary conservatism model was the best-supported explanatory model for the likelihood of attack, irrespective of location (figure 1a). Relative to the control, the odds of attack were greater for the familiar prey types of a robotic lizard mimic with no dewlap and one with a moving dewlap (Borneo: odds ratio (OR) = 3.45, $z = 1.96$, $p = 0.05$; Australia: OR = 2.89, $z = 2.17$, $p = 0.03$; figure 1b,c; electronic supplementary material, table S2). In comparison, attacks on the novel prey type of a robotic lizard mimic

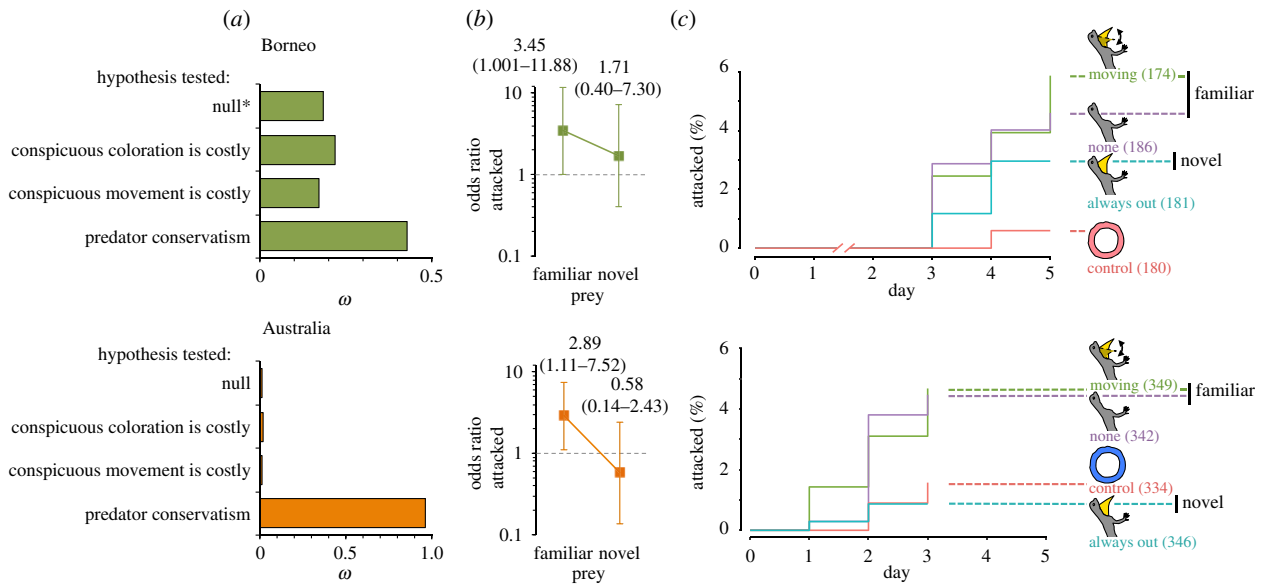


Figure 1. (a) Hypotheses were compared using a conditional probability derivative, ω , of AIC_c that was heavily in favour of the dietary conservatism model. (b) This model was used to estimate the odds ratio (with 95% confidence intervals) of attack relative to controls. (c) The percentage of robotic lizard mimics attacked as a function of time is also shown. The null model applied to Bornean data (indicated by asterisk) included a covariate for leaf-cutter ant colonies found on trees after deployment (and was included in other models applied as well). Data in (c) exclude models on trees with leaf-cutter ant colonies. Sample sizes are given in parentheses. (Online version in colour.)

with a permanently visible dewlap could not be statistically distinguished from control (Borneo: OR = 1.71, $z = 0.72$, $p = 0.47$; Australia: OR = 0.58, $z = -0.75$, $p = 0.45$; figure 1*b,c*; electronic supplementary material, table S2).

Although for the vast majority of time the robotic lizard mimic with the moving dewlap was identical to the mimic with no dewlap, it was still an unusual prey type for Australian predators. To address this directly, we applied a supplementary model to the Australian data only that considered a single linear predictor variable in which robotic lizard mimics were coded by the proportion of time the dewlap was retracted (dewlap ‘always out’ = 0, ‘moving’ = 0.95, or ‘none’ = 1). This model computed a large, positive effect for the odds of attack as a function of the proportion of time the dewlap was not visible (OR = 5.23, $z = 2.65$, $p = 0.008$; electronic supplementary material, table S3), which would be predicted by the predator dietary conservatism hypothesis.

4. Discussion

Social animals are expected to face a trade-off between producing a signal that is detectable by mates and rivals, but not obvious to predators [2,38]. This trade-off is fundamental for understanding the design of many animal signals [4,39], and is often the lens through which the evolution of alternative communication strategies is viewed [13,30]. Given the colour (electronic supplementary material, figure S3) and movement (electronic supplementary material, figure S4*b*) of the dewlap should have been obvious to most predators, the classic paradigm for the evolution of conspicuous reproductive signals [2] would predict these showy males should have incurred an elevated risk of predation [38]. Our findings did not support this and were consistent across two contrasting environments, where predator–prey communities were expected to be diverse in behaviour and ecology. Instead,

the production of an intermittent signal that is only obvious in brief bouts of display appears to be enough to minimize unwanted attention from predators.

Moreover, our data also reveal how ostentatious ornamentation and other elaborate morphologies can evolve despite being permanently visible to predators. First, our study implies dietary conservatism might be widespread in nature. Variation could still exist in the extent to which some predators attack novel prey types, but the reduced predation risk experienced by unfamiliar prey (figure 1) should ultimately facilitate their establishment in the population. This overcomes an acute problem for the validity of the dietary conservatism hypothesis under real-world conditions, in which prey are expected to be targeted by multiple predators [1,24]. Second, there is unlikely to be an upper threshold that novel prey abundance must reach before the dilution of predation risk begins to relax selection against the spread of that prey phenotype [40,41]. This would resolve the paradox of how rare, conspicuous prey escape being disproportionately targeted by predators and avoid extinction [1]. Finally, predators would not have to learn an association between certain prey types and unprofitability, which would solve a central concern of the evolutionary paradox of aposematism [17,40,41]. This, in turn, would explain the diversity in warning signals seen in nature (e.g. colour polymorphism within prey species), where frequency-dependent learning should instead produce widespread convergence on a common warning signal [42] or, at best, a limited set of colour morphs reflecting predator generalization across certain colour types [22].

To be clear, our study cannot conclusively confirm predator conservatism was the cause of the observed differences in attack among prey types. The artificial dewlap was designed to match the yellow dewlap of Bornean lizards in life, and it happens that yellow is a common colour used in aposematic signals [43]. It is conceivable, then, that reduced attacks on the robotic mimic with the dewlap permanently

extended might have resulted from a chance resemblance to an existing (yellow) aposematic signal. Predators can generalize the warning coloration of aposematic prey to other species with similar coloration (that may or may not be similarly defended [21,22]) and it seems likely that a range of (at least putative) aposematic species are present at both experimental locations (e.g. the barred kukri snake *Oligodon signatus* and juvenile olive tree lizard *Dasia olivacea* at the Bornean location, and various soapberry bugs *Leptocoris*, true bugs *Dysdercus* and jewel bugs *Tectocoris* at the Australian location).

Comparison of the data from Australia and Borneo is potentially informative here. If generalization has occurred, it should result in similar levels of avoidance at both locations. By contrast, given the dewlap was entirely novel at the Australian location, the robotic lizard mimic with the dewlap permanently extended should have been 'more novel' for Australian predators than those on Borneo. If predator conservatism indeed explains our findings, this difference in novelty should have resulted in predictable differences in the attack between the two locations. Formal statistical comparison was not possible because of the way experiments were implemented. Qualitatively, however, the data shown in figure 1 suggest attacks on the robotic lizard mimic with the dewlap permanently extended were generally lower in Australia than Borneo, which is more consistent with predator conservatism than generalization.

More broadly, predator dietary conservatism has rarely been considered in the evolution of conspicuous reproductive signals [44], but offers a new perspective on how novel social signals might evolve under current models of sexual selection. Our data suggest the initial evolution of novelty is advantageous in communication because it probably avoids the cost of predation, while also obtaining the added benefits from negative frequency-dependent sexual selection (the 'rare phenotype advantage' [45]), or conveying more reliable cues on condition (e.g. the 'handicap model of sexual selection' [9]), or exploiting previously untapped biases in the psychology or senses of receivers (the 'receiver psychology' [46] and 'sensory drive' [47] models). For selection to operate in this regard, the observed reduction in predation must be maintained for several prey generations. This would be facilitated in predator-prey systems where generation times are skewed towards short-lived prey and long-lived predators (e.g. insects targeted by avian or mammalian predators).

Our experiments have not tested the long-term avoidance of novel prey types by predators, and this remains a final barrier for resolving the aposematic paradox. In particular, neophobia is expected to be common in animals [48] but quickly degrades over time (individuals tend to avoid new foods, at most, for only weeks or months [48]). For this reason, neophobia is a distinct phenomenon to dietary conservatism and is not expected to result in the same selection advantage for prey novelty, but could produce the same

experimental outcome documented here over the short term. Distinguishing dietary conservatism from neophobia would require predation experiments to be repeated regularly for many years.

Alternatively, there are potential 'natural experiments' that could be leveraged to confirm the persistent, long-term effects of dietary conservatism, while examining its ecological implications beyond communication as well. Dietary conservatism seems to explain why predators selectively target native prey over invasive exotics, despite exotic prey being just as profitable and more numerous [49,50]. Tracking the fate of these invading exotic prey could offer a powerful validation of the long-term selection advantage enjoyed by novel prey types in the wild, and extend the relevance of predator dietary conservatism to biological invasions more generally. Community ecology theory would normally predict competitive exclusion of exotics by ecologically similar resident species, and that predation in itself would act as a powerful barrier to the establishment of undefended exotic prey in new areas. Dietary conservatism presents a different outcome in which the balance is skewed in favour of exotic species that are novel or otherwise an unusual variant on a resident prey type. Furthermore, given predators can generalize across prey types [21,22], any exotic invader that happens to exhibit colours or morphology that resemble an aposematic species would similarly be expected to have improved colonization success. Including predator dietary conservatism and generalization in biological invasion theory would provide an additional means of predicting the success of invading species by determining those that are likely to escape predation and become established to the potential detriment of resident species.

Ethics. The work described in this article was approved by the UNSW Animal Care and Ethics Committee under protocol 18/56A. This work was permitted in Sarawak by the State Planning Unit, Sarawak Forest Department (permit no. (159)JHS/NCCD/600-7/2/107).

Data accessibility. All data used in this study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mkkwh70z5> [51].

Authors' contributions. T.J.O.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, visualization, writing-original draft, writing-review and editing; K.B.: data curation, formal analysis, methodology, resources, writing-review and editing; T.E.W.: data curation, formal analysis, methodology, resources, visualization, writing-review and editing; I.D.: resources, writing-review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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