PREDATION AVOIDANCE

Global selection on insect antipredator coloration

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Natural selection has repeatedly led to the evolution of two alternative antipredator color strategies—camouflage to avoid detection and aposematism to advertise unprofitability—but we lack understanding of how ecological context favors one strategy over the other. We conducted a globally replicated predation experiment at 21 sites on six continents to test how predator community, prey community, and visual environment influenced the predation risk of 15,018 artificial paper "moth" prey with cryptic or warning coloration. Results indicated that aposematic strategies fare better in environments with low predation intensity, whereas camouflage strategies are advantaged when other camouflaged prey species are rare and when light levels are low. This study demonstrates how multiple mechanisms shape antipredator strategies, helping to explain the evolution and global distribution of camouflaged and aposematic animals.

Predation is one of the most pervasive agents of natural selection and has led to two antipredator color strategies distributed globally: camouflage, which decreases the chance of prey being detected by predators, and aposematism, in which prey advertise unprofitability to predators with conspicuous warning signals. The coexistence of these strategies demonstrates that each can be successful in different circumstances. A large body of theory describes how ecological variables such as predation intensity and illumination conditions are expected to favor one strategy over another, but this remains largely untested (Fig. 1) (*1*–*4*). Evaluating the action of multiple variables requires experimental replication across a range of ecological conditions. To address this, we conducted a global-scale naturalistic experiment investigating the relative role of the main ecological variables proposed to drive the evolution and global diversity of antipredator color strategies.

Camouflage functions by reducing the probability of detection and/or recognition through coloration and patterning that reduce the signal-to-noise ratio between prey and background (*5*). Warning colors tend to be highly salient to capitalize on predator cognitive biases for signals that are easy to detect, recognize, and remember (*1*, *6*). Aposematic species display warning color as an honest indicator of defenses, whereas Batesian mimics have warning coloration but lack defenses. Although some organisms can be perceived as alternately camouflaged or warning colored at different viewing distances (*7*) or by adopting different postures (*8*), warning coloration and camouflage are generally considered alternative antipredator strategies. Camouflage and warning coloration are present in most groups of animals (*3*), with warning coloration being the rarer strategy [for example, estimated 15.1% of Finnish caterpillars (*9*), 8% of adult Lepidoptera (*10*), 8.2% of amphibians (*11*), and 2.7% of birds (*12*)].

We conducted a globally distributed field predation experiment in which we provided wild avian predators in 21 woods and forests across six continents with 15,018 paper "moth" artificial prey targets (~720 per location) (table S1). These targets were printed with a cryptic bark-like brown color, typical orange-black warning coloration (*6*, *13*, *14*), or similarly conspicuous (*15*) but atypical turquoise-black warning coloration (Fig. 2 and table S2). The inclusion of atypical warning-colored prey tested whether orange-black coloration is successful because it is conspicuous or because there is signal generalization of the orange-black colors of Lepidoptera in prey communities (*16*). Targets were pinned to trees with a mealworm reward (*17*), and we monitored which were consumed (Fig. 2, table S3, and movies S1 and S2). We used palatable mealworms because attack rates on defended prey are extremely low; this was confirmed with a supporting experiment in which the prey were made unpalatable by injecting mealworms with quinine (fig. S1) (*17*). How predators may learn about novel defended (aposematic) prey was inferred from initial predation risk and the rate of change in predation on undefended prey in the context of prior literature (*17*, *18*).

We tested key theoretical predictions in relation to predator community, prey community, visual environment, and latitude (Fig. 1 and table S4) by measuring predation on the three color treatments across eight daylong trials. Latitude is often invoked as an indirect driver of antipredator color strategy because theory suggests that the intensity of biotic interactions between plants and herbivores in the tropics promotes the evolution of plant defenses and therefore the availability of toxins for herbivores to acquire (*19*–*21*), which should facilitate the evolution of aposematic strategies at low latitudes (*4*). In terms of predator community, when predation intensity is high, initial selection against new prey with typical warning coloration is predicted to be strong because uneducated predators are pushed by competition to sample conspicuous, potentially defended prey (*2*, *22*–*24*). Predator dietary niches are also proposed as critical, with insectivore specialists being potentially better than generalist species at overcoming the defenses of aposematic prey and/or finding cryptic prey, favoring either cryptic or aposematic strategies (*25*–*27*). The relative abundance of prey color strategies in the community is considered important because familiarity with cryptic prey can mean predators more actively search for cryptic prey, leading to greater attack rates (*28*), whereas aposematic strategies are expected to be more successful as they become more common and share the cost of educating predators (*29*, *30*). In addition, the role of the visual environment was investigated because increased ambient illumination and prey salience are thought to advantage warning signals by making them easier to learn but disadvantage cryptic prey by making them easier to find (*31*).

Two valid statistical models comparing predation on treatments were identified by deriving a directed acyclic graph (DAG) (*32*) to avoid confounders and conditioning on posttreatment variables and colliders (figs. S2 and S3). Inferences were further supported by individual treatment analyses of predictors of target predation risk.

Overall, 3247 diurnal putative avian attacks were observed (21.6% of targets). Predation risk increased through the 8-day experiment 1.2 times per day on average, whereas in the unpalatable prey experiment, predation risk decreased over time (fig. S1). There was no overall "best" strategy—the protective value of each target type depended on ecological context, with predation intensity, local illumination, and the ratio of warning-colored prey in the community having the largest

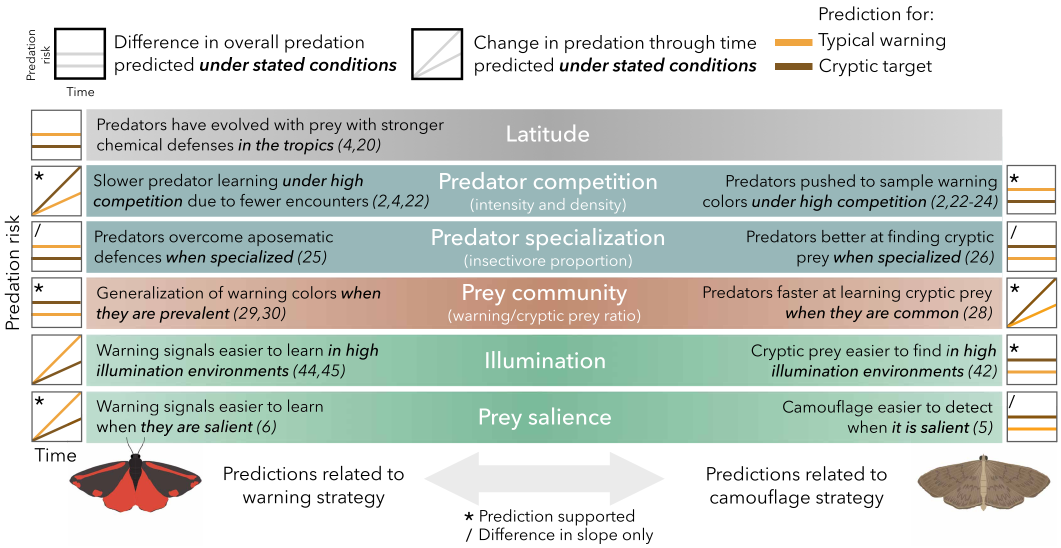

Fig. 1. Summary of potential ecological variables affecting predation on camouflaged and undefended and defended typical warning-colored (aposematic) prey. Ecological variables are in white text. Main predictions are summarized in black text, and visualization of predictions is presented in plots, corresponding to changes in either overall predation or learning speed (slope difference). Within plots, brown lines indicate camouflage, and orange lines indicate typical warning color. Predictions supported by this study are indicated with an asterisk. Lepidoptera images: left, *Tyria jacobaeae*; right, *Patania ruralis*. [Credit: iStock.com/jph9362 (left) and iStock.com/ViniSouza128 (right)]

significant effects. This included significant differences between the atypical and typical warning-colored targets, demonstrating that they conveyed different information to predators despite their similar conspicuousness.

Latitude is not linked to antipredator color strategy

Predation at the start of the experiment was slightly greater at low latitudes relative to high latitudes, but this difference decreased throughout the experiment, and predation was overall no greater in locations closer to the equator (fig. S4 and table S5) (*33*). We did not observe the predicted lower predation on warning-colored prey at lower latitudes. This challenges the idea that the geographic distribution of antipredator color strategies reflects simple latitudinal shifts in attack rates on the basis of toxin availability (*4*, *20*). Climatic seasonality also had no effect on predation risk (*9*, *17*, *34*).

Predation intensity has the strongest effect on antipredator color strategy selection

Predation intensity at each location was measured by quantifying the background level of predation on mealworms without paper targets (Fig. 2B), whereas predator density (predators per square kilometer) and diversity (Shannon index) were measured with standardized bird surveys (fig. S5) (*17*). We found that in sites with high predation intensity, predation risk of the typical warning-colored treatment was up to 50% greater than that of the other treatments at the start of the experiment (Fig. 3, A and B; figs. S6 to S9; and table S6). This was the largest effect in our experiment and suggests an increased willingness of predators to sample typical warning-colored prey in competitive predator communities (*24*), supporting theoretical predictions (*2*).

Predator encounter rates could determine how higher sampling of novel warning-colored prey affects long-term survival (*2*). If many predators are responsible for predation, per-predator encounter rates decrease, slowing predator learning about the relationship between warning color and defense (*2*, *4*, *22*). This idea is supported by our results: In locations with high predation intensity, predation risk increased throughout the experiment at a slower rate for the typical warning-colored treatment as compared with the cryptic and atypical warning-colored treatments (Fig. 3A). However, predator density and diversity had no effect on predation on treatments (figs. S7, S10, and S11), which suggests that the slower increase in predation on typical warning signals in environments with high predation intensity is not solely due to different individuals sampling prey and learning slowly. The more

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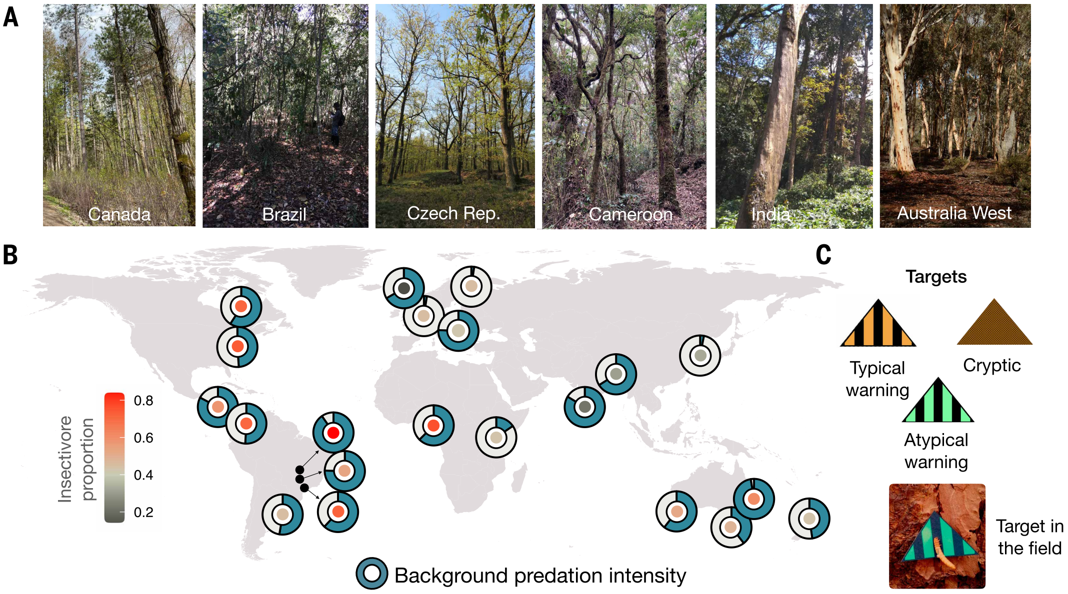

Fig. 2. Distribution of experiment across the globe and artificial targets used. (**A**) Artificial prey were exposed to avian predation in temperate and tropical woods and forests. (**B**) Global distribution of 21 locations. Icons show proportion of insectivorous predators in the inner circle and background predation intensity (percentage consumed in mealworm-only experiment) in the outer circle. (**C**) Three treatments used and an example of the artificial prey used.

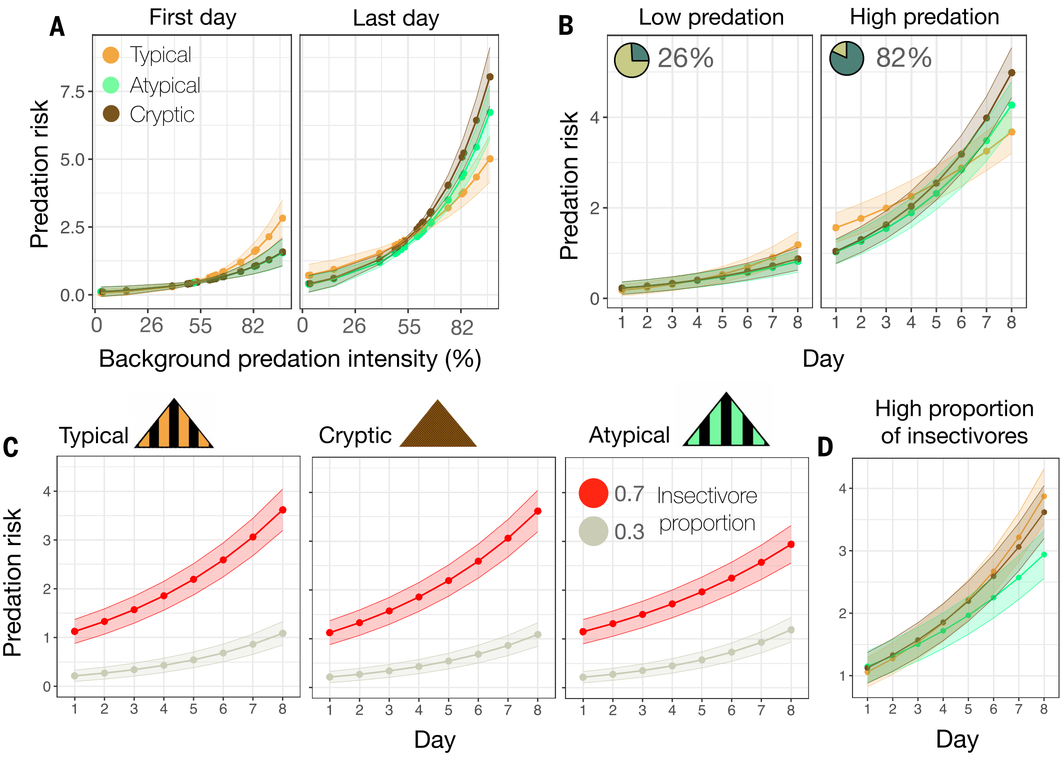

Fig. 3. Predator community and predation risk, measured as the predicted hazard ratio estimated from the Cox mixed model (exponentiated coefficients). Predation risk values represent the risk of predation when the reference level (typical warning color) of the treatment variable has a baseline risk of 1. (**A**) Predation on treatments on the first and last day in environments with increasing background predation intensity (measured from the mealworm-only experiment). (**B**) Predation on treatments in environments with low (26%, mean – SD) and high (82%, mean + SD) background predation intensity. (**C**) Predation on treatments in locations with high and low levels of insectivore proportions. (**D**) Predation on treatments in conditions with high insectivore proportion (0.7). All predictions correspond to models in which all other covariables (except for the one of interest) were kept at mean values.

rapid increase in predation on the cryptic and atypical warning treatments likely reflects predators learning more quickly that prey unlikely to be defended are acceptable when competing for resources (*35*). On the basis of the pattern of high initial predation but slow learning for the typical warning-colored treatment, we infer that new defended aposematic prey would have low fitness in environments with high predation intensity because they would be sampled at a high rate by uneducated predators (*24*) that do not then encounter the novel prey frequently enough to learn the relationship between color and defense (*18*, *36*, *37*). By contrast, the relative advantage of camouflage strategies decreases as predators gain experience with the local prey community.

To investigate the role of predator dietary niches on predation risk, the proportion of insectivores was estimated by combining bird survey results with dietary niche data (*38*) for avian species recorded at each location (Fig. 2B and table S7). We found that as the proportion of insectivorous predators (those that consume at least 60% insect prey) increased, predation risk increased faster for cryptic and typical warning treatments than for the atypical warning treatment (Fig. 3C, figs. S10 and S11, and table S8). Insectivorous predators may have traits, such as the ability to form search images, that help them find cryptic prey (*28*). Likewise, insectivorous predators may be better able to learn the defense status of typical warning-colored prey because of its familiarity or perceptual features such as high contrast, color stability, and distinctiveness (*6, 13, 14, 39*), which would favor aposematic (defended) prey with typical warning signals. Alternatively, insectivorous predators may be more neophobic (*40*) and slower to overcome wariness of atypical signals; however, this hypothesis was not supported by the similar predicted predation risk of all treatments at the start of the experiment (Fig. 3, C and D).

Prey community has frequency-dependent effects

The influence of the antipredator color strategy used by prey in the community was investigated by using global biodiversity records to score the color of 2586 lepidopteran species found in study locations (Fig. 4A, fig. S12, and table S2). Typical warning color was generally more common at lower latitudes (Fig. 4B). Locations where prey with typical warning colors were more common had slightly lower (~20%) risk of predation on typical warning-colored targets relative to other treatments toward the start of the experiment (Fig. 4, C and D). This supports the idea that familiarity with warning signals decreases predation risk through signal generalization (*29*, *30*). Similarly, atypical warning targets were attacked more often at the start of the experiment relative to typical warning targets in communities where typical warning signals were common (Fig. 4C). Abundant typical warning signals may drive predators to sample unfamiliar, potentially defended prey to find enough food (*4*, *41*). These results highlight constraints on the establishment of atypical warning signals and help explain the similarities in the form of warning signals and evolution of mimetic species complexes (*29*, *30*).

Predation risk of the cryptic treatment increased more rapidly through the experiment when camouflaged prey were more prevalent in the prey community, supporting theoretical predictions (Fig. 4D, figs. S6 and S7, and table S6). High abundance of cryptic prey may reduce the protective value of crypsis, for example, if predators use search images to improve detection of camouflaged prey (*28*).

Visual environment affects camouflage strategies more than aposematic strategies

We investigated the visual environment by collecting 9152 images of targets (mean, 435 per location) throughout the experiment and modeling images as they would be perceived by an avian predator, to measure ambient illumination and prey salience against the background (figs. S13 and S14) (*14*, *17*). Crypsis had lower protective value in high-illumination locations (Fig. 5, A and B; figs. S6 and S7; and table S6), possibly because these areas are less densely forested, improving sight lines and increasing encounter rates, or because spatial and chromatic contrasts are easier to resolve in bright light (*42*). Local illumination had little effect on predation risk of the typical warning-colored treatment, and the target-level analysis found that although higher illumination increased predation on all treatments, this effect was slightly weaker for the typical warning treatment (table S9). Predation on the cryptic and atypical warning color treatments increased more rapidly throughout the experiment in low-illumination locations compared with the typical warning color treatment (Fig. 5A). This supports the hypothesis that camouflage strategies decline in performance once predators learn what to search for in low-light environments because these lack dynamic shadows that alter the appearance of camouflage prey (*43*). Contrary to expectations, typical warning signals were not easier to learn in high-illumination environments (Fig. 5A) (*44*, *45*). Overall, this suggests that camouflage strategies trade off lower probability of detection with increased ease of learning in low-illumination environments, whereas the performance of typical warning coloration is consistent irrespective of light environment.

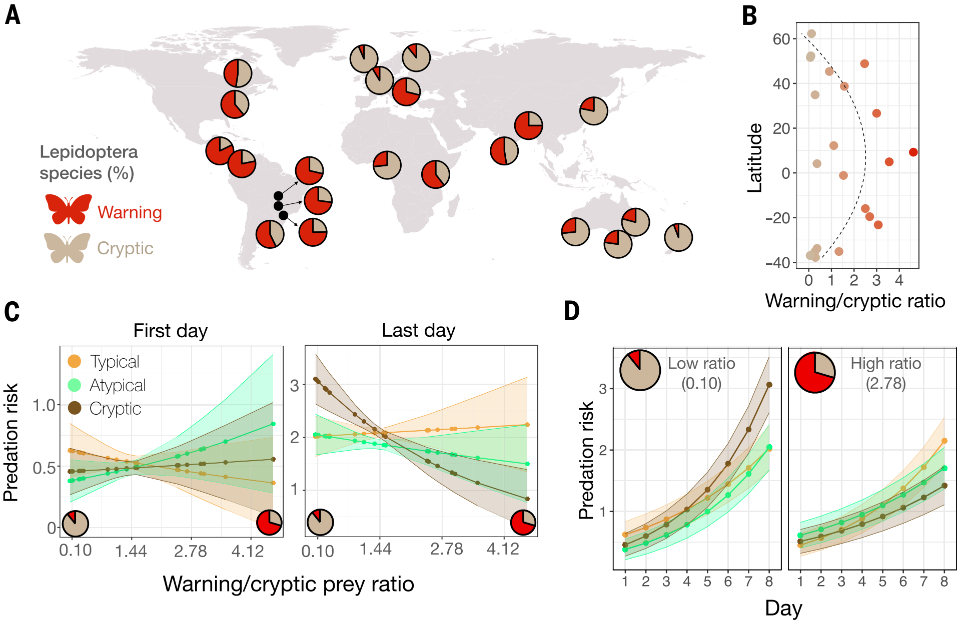

Fig. 4. Effects of prey community on predation risk. (**A**) Global distribution of lepidopteran community coloration estimated from species recorded at each location and classified as either typical warning color, cryptic, or "other." (**B**) Latitudinal distribution of typical warning coloration prevalence relative to cryptic coloration. (**C**) Predation on treatments in communities with varying warning/cryptic prey ratio. (**D**) Effect of warning/cryptic prey ratio on predation risk during the first and last days of the experiment. All predictions correspond to models in which all other covariables (except for the one of interest) are kept at mean values.

Background appearance varied across locations because of the tree community's bark color, the types and abundances of

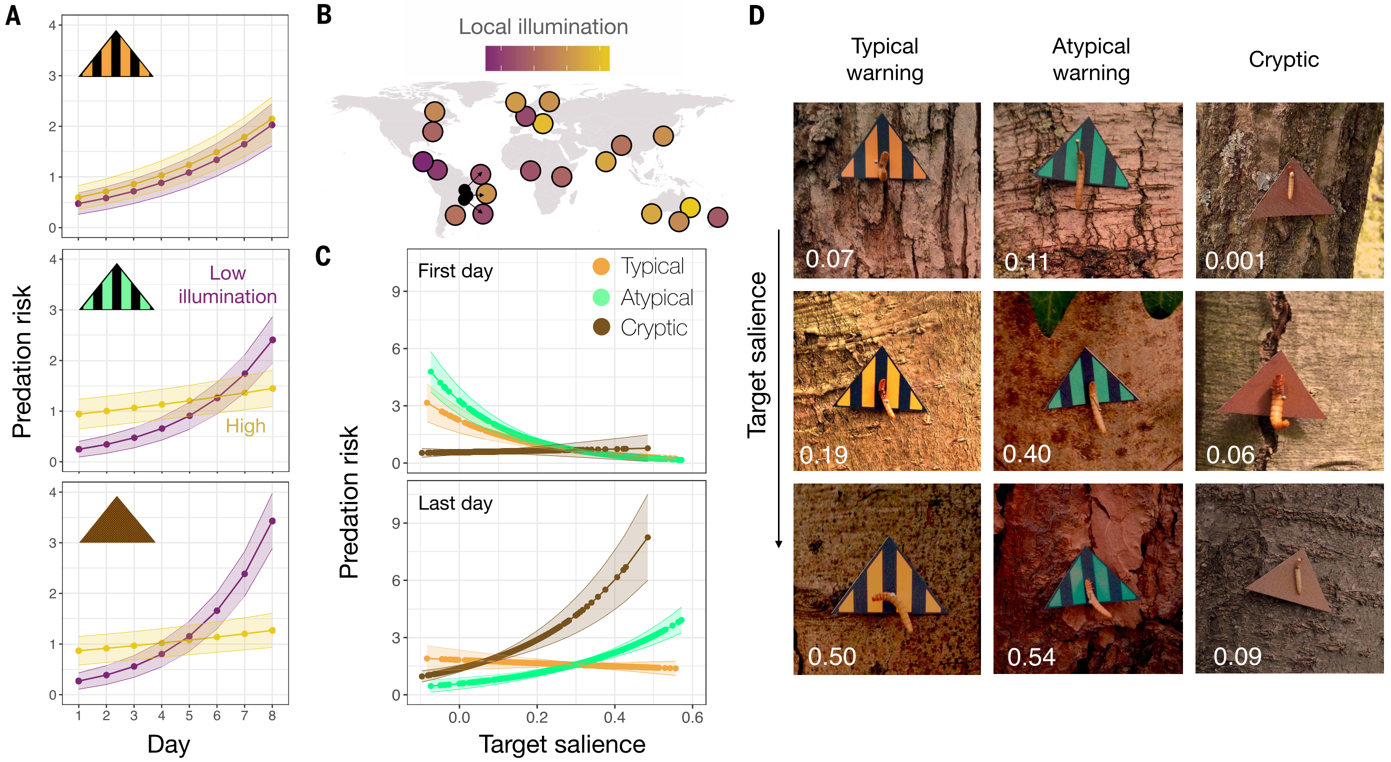

Fig. 5. Effect of visual environment on predation risk. (**A**) Variation in predicted risk through experiment days, for low-illumination locations (mean – SE) and high-illumination locations (mean + SE). Lines indicate predicted values of risk for each target type, estimated from the main model. (**B**) Global distribution of local illumination levels. (**C**) Effect of target salience on predation risk when all covariables are kept at mean values, for the first and the last day ($n = 2908$ targets). (**D**) Examples of targets and backgrounds with different salience values. These were calculated from standardized photographs and indicate the distance in color, luminance, and edge orientation between background and target, considering light environment (*47*).

mosses and lichens, weather, and time of day (Fig. 5D). Unexpectedly, salience and predation of cryptic targets initially had no overall relationship (table S9), but more salient cryptic targets tended to have greater predation risk as the experiment progressed, indicating the importance of camouflage quality for resisting predator learning (*35*). Risk of predation for both warning-colored treatments decreased with increasing salience (Fig. 5C), as predicted if warning color is more effective when signals are easy to detect, recognize, and remember (*6*). The effect of salience on atypical warning-colored prey reversed throughout the experiment (Fig. 5C and table S9), with increased salience protecting turquoise-black prey early in the experiment but becoming a liability once predators had an opportunity to learn that prey were undefended. This was not the case for the typical warning color, indicating that this has a protective effect independent of target-background salience (*6*). As expected, the effects of visual environment decreased when nocturnal predation events were analyzed (fig. S15 and table S11) (*17*).

Conclusions

Our study identified how a complex suite of ecological variables influences the success of crypsis versus warning coloration under natural conditions in terrestrial forest ecosystems across the globe. We found that camouflage effectiveness is highly context dependent. High predator competition initially protects novel cryptic prey but leads to relatively greater predation over time. The success of cryptic strategies also declines when cryptic prey are common, which is consistent with predators learning to search for these prey (*28*), and although low illumination improves camouflage initially, this advantage erodes as predator performance improves.

By contrast, warning coloration is generally less sensitive to ecological context but not immune: Predator competition increases initial predation risk and slows learning of the association between warning colors and defense, likely undermining aposematic strategies. Atypical warning colors are also disadvantaged where typical warning-colored prey are common (*1*). Although warning-colored prey are more frequent at lower latitudes, this is not a consequence of simple latitudinal shifts in attack rates (*4*); instead, it emerges from multiple interacting ecological variables associated with latitude.

The results of our large-scale field experiment refine current theory on the evolutionary ecology of antipredator strategies, such as the importance of frequency-dependent selection (*3*), complementing and extending previous laboratory-based findings (*41*, *46*). Our experiment's ability to compare the importance of multiple ecological variables concludes that predator competition is most critical to the success of camouflage and warning color strategies. One direction for future studies is to investigate this effect through methods to establish the contributions of individual predators to prey survival. Other priorities include testing how ecological predictors influence predator responses to defended prey and assessing variation in predator generalization across communities. Our findings suggest a hypothesis that camouflage, although widespread, may be a less stable defense that is more vulnerable to ecological and anthropogenic change. This predicts that predation outcomes should be more variable for individuals and populations pursuing camouflage strategies compared with warning coloration and that camouflage should be gained and lost more frequently than warning coloration at macroevolutionary scales. Last, our study demonstrates how globally distributed experiments can be key to uncovering complex ecological explanations for the evolution of biological traits.

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ACKNOWLEDGMENTS

We thank S. Anderson, M. Araya-Salas, R. Andara Vieira de Arimatea, J. Borges, H. Evans, J. Evans, K. Evans, L. Evans, S. Filho, S. Glaberman, S. de Graaf, S. Hoobler, M. Labuta, S. Yeonhee Lee, M. Lurgi, J. Makar, I. Konstantinov Malinov, B. Margetts, E. Mlamba, B. van Pinxteren, L. Pointeaux, M. Polido, K. Rankin, M. Gonçalves Santos, M. L. Gonçalves Santos, G. Gonzaga da Silva, H. Toppinen, V. L. Vaherto, B. C. Pinheiro do Valle, T. Wallenius, C. León, M. Watts, and M. Yonatan for assistance with fieldwork. We also thank D. Stuart-Fox and J. Higham for providing feedback on previous versions of this manuscript. We thank Fundación Elsa Shaw de Pearson (Argentina), Campbell Park Nature Reserve (Australia East), Manningham Council (Australia South), Wilga State Forest (Australia West), Reserva Ecológica do IBGE (Brazil Brasilia), Reserva Biológica da Serra do Japi (Brazil Serra do Japi), RPPN Vale Encantado (Brazil Uberaba), Mount Cameroon National Park (Cameroon), National Capital Commission (Canada), Reserva Paraíso Andino (Colombia), Refugio Nacional de Vida Silvestre Hacienda Barú (Costa Rica), Environmental Department of Municipality of Prague and Podyjí National Park (Czech Republic), Buxa Tiger Reserve (India), Brackenhurst Retreat and Conference Centre (Kenya), The Gemeente Amsterdam (Netherlands), Waitākere Ranges Regional Park (New Zealand), Fountainhead Regional Park and D. Deem (USA), and Swansea City Council (Wales) for access to field sites. **Funding:** This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (to R.R.C. and F.D.-L.); Melbourne Postdoctoral Fellowship through University of Melbourne (to A.M.F.); National Research Foundation of Korea (RS-2024-00333709 to C.K.); Creative-Pioneering Researchers Program through Seoul National University (to C.K.); Australian Research Council Future Fellowship (FT180100491 to J.Ke.); Research Grant from NCBS-TIFR, India (to K.K.); National Council for Scientific and Technological Development - CNPq (proc.142299/2020-0 to V.M.L.); Agencia Nacional para la Promoción Científica y Tecnológica (PICT 2018-03622 to M.C.D.M.); Australian Research Council DECRA (DE200100500 to I.M.); Junior Research Fellowship, UGC-CSIR, Government of India (to A. Pal and A. Paul); Maria Zambrano Fellowship—NextGeneration EU (to O.P.); Max Planck Society (to H.M.R. and R.J.B.); Universidad del Rosario BigGrant (IV-FGD005 to C.S.); Natural Sciences and Engineering Research Council of Canada (to T.N.S. and K.L.-H.); Natural Environment Research Council Independent research fellowship (NE/P018084/1 to J.T.); Czech Science Foundation (19-09323S to A.E., 21-17125S to T.A., and 24-11498S K.D.); Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; proc. 312847/2022-0 to R.G.-F.); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (to R.G.-F.); and Institutional Research Support Grant of the Charles University (SVV 260686/2023 to K.D.). **Ethics:** Ethical approval was granted by University of Melbourne Faculty of Science Animal Ethics Committee (1915093.1) (Australia East and South), University of Western Australia Animal Ethics Committee (RA/3/100/1733) (Australia West), UFTM Animal Ethics Committee (23085.009118/2021-49) and ICMBio (80470) (Bazil Sera do Japi and Brazil Uberaba), Reserva Ecológica do IBGE (017 PAPD) (Brazil, Brasilia), Ministry of the Environment of the Czech Republic (MZP /2019/630/1082) (Czech Republic), Carleton University Animal Care Committee (protocol 115569) (Canada), University of Auckland Animal Ethics Committee (2903) (New Zealand), Mokpo National University IACUC committee (MNU-IACUC-2021-013) (South Korea), George Mason University IACUC (1743276) (USA), Swansea University AWERB (26413_271120125406_1) (Wales). In Argentina, Colombia, Costa Rica, Finland, India, Kenya, Cameroon and the Netherlands, formal ethical approval was not required. Permissions to run the experiment were granted by the Province of Buenos Aires (Disp OPDS 48/2019) (Argentina), Faculty of Natural Sciences, Universidad del Rosario (Colombia), Escuela de Ciencias Biológicas, Universidad Nacional (UNA-PPAA-AVAL-303-2021) (Costa Rica), University of Jyväskylä (Finland), NCBS Animal Ethics Committee (India), National Museums of Kenya (Kenya), Ministry of Research and Innovation and Ministry of Forestry and Fauna (00125/MINRESI/B00/C00/C10/C12 and 2530/PRBS/MINFOF/SETAT/SG/DFAP/SDVEF/SC/NGY) (Cameroon), and the Gemeente Amsterdam (Netherlands). **Author contributions:** Conceptualization: I.M. , W.L.A. Methodology: I.M., A.E., K.D., O.P., T.N.S., J.M., H.M.R., J.T., W.L.A. 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Writing – original draft: I.M., A.E., K.D., O.P., W.L.A. Writing – review & editing: I.M., A.E., K.D., O.P., T.N.S., T.A., S.B., R.J.B., E.B.-S., K.E.C., Y.C., C.E., A.M.F., C.K., J.Ke., K.K., J.M., O.N., J.C.R., H.M.R., C.S., J.T., K.D.L.U., S.-S.W., W.L.A. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** Raw datasets and code used for analyses and figures are available in Dryad (*48*). This research was funded in whole or in part by Natural Environment Research Council (NE/P018084/1), a cOAlition S organization. The author will make the Author Accepted Manuscript (AAM) version available under a CC BY public copyright license.

SUPPLEMENTARY MATERIALS

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Materials and Methods; Supplementary Text; Figs. S1 to S15; Tables S1 to S11;
References (*49*–*80*); MDAR Reproducibility Checklist; Movies S1 and S2

Submitted 10 September 2024; accepted 14 July 2025

10.1126/science.adr7368