Title: Global selection on insect antipredator coloration.

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Abstract:

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 predation risk of 15,018 artificial paper 'moth' prey with cryptic or warning coloration. Results indicated that aposematic strategies fare better in low predation intensity environments while 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 explain the evolution and global distribution of camouflaged and aposematic animals.

Main Text:

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, where 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 using 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, while Batesian mimics possess 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 (e.g., estimated 15.1% of Finnish caterpillars (*9*), 8% of adult Lepidoptera (*10*), 8.2% of amphibians (*11*), 2.7% of birds (*12*)).

We conducted a globally distributed field predation experiment where 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 either 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, table S2). Including 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, supplementary movies S1&S2). We used palatable mealworms because attack rates on defended prey are extremely low; this was confirmed by a supporting experiment where the prey were made unpalatable by injecting mealworms with quinine (*17*) (Fig. S1). How predators may learn about novel defended (aposematic) prey is 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, table S4) by measuring predation on the three color treatments across eight, day-long 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 novel prey with typical warning coloration is predicted to be strong because uneducated predators are pushed via 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 as familiarity with cryptic prey can mean predators more actively search for cryptic prey leading to higher 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*). Finally, 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 post-treatment variables and colliders (Fig. S2&3). Inferences were further supported by individual treatment analyses of predictors of target predation risk.

Overall, 3,247 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, while 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 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 higher at low latitudes relative to high latitudes, but this difference decreased throughout the experiment and predation was overall no higher in locations closer to the equator (table S5, Fig. S4) (*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 based on 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) while predator density (predators/km^2) and diversity (Shannon index) were measured via standardized bird surveys (*17*) (Fig. S5). We found that in high-predation-intensity sites, predation risk of the typical warning colored treatment was up to 50% higher than the other treatments at the start of the experiment (Fig. 3A&B, Fig. S6-10, 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 high predation intensity locations, predation risk increased throughout the experiment at a slower rate for the typical warning colored treatment compared to the cryptic and atypical warning-colored treatments (Fig. 3A). Predator density and diversity had no effect on predation on treatments (Fig. S7, 10&11), however, suggesting that the slower increase in predation on typical warning signals in high predation intensity environments is not solely due to different individuals sampling prey and learning slowly. The more 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*). Based on the pattern of high initial predation but slow learning for the typical warning colored treatment, we infer that novel defended aposematic prey would have low fitness in high predation intensity environments 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*). In 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, 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, Fig. S10&11, table S8). It is possible that insectivorous predators possess 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 due to 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. 3C&D).

Prey community has frequency dependent effects

The influence of the antipredator color strategy employed by prey in the community was investigated by scoring the color of 2,586 lepidopteran species found in study locations using global biodiversity records (Fig. 4A, Fig. S12, table S2). Typical warning color was generally more common at lower latitudes (Fig. 4B). In locations where prey with typical warning colors were more common there was slightly lower (ca. 20%) risk of predation on typical warning colored targets relative to other treatments towards the start of the experiment (Fig. 4C&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 in order 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, Fig. S6&7, table S8). High abundance of cryptic prey may reduce the protective value of crypsis, for example, if predators utilize 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 9,152 images of targets (mean: 435 per location) throughout the experiment and modelling images as they would be perceived by an avian predator to measure ambient illumination and prey salience against the background (*14*, *17*) (Fig. S13&14, table S10). Crypsis had lower protective value in high illumination locations (Fig. 5A&B, Fig. S6&7, 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 while 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 to 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 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.

Background appearance varied across locations due to the tree community's bark color, the types and abundances of mosses and lichens, weather and time of day (Fig. 5D). Unexpectedly, there was no overall relationship between salience and predation of cryptic targets initially (table S9) but more salient cryptic targets had higher 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, 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 (*17*) (Fig. S15, table S11).

Conclusion

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 higher predation over time. The success of cryptic strategies also declines when cryptic prey are common, consistent with predators learning to search for these prey (*28*), and while low illumination improves camouflage initially, this advantage erodes as predator performance improves.

In 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 lab-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 using 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 new hypothesis that camouflage, while widespread, may be a less stable defense which 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 to warning coloration, and that camouflage should be gained and lost more frequently than warning coloration at macroevolutionary scales. Finally, our study demonstrates how globally distributed experiments can be key to uncovering complex ecological explanations for the evolution of biological traits.

References

1. J. Mappes, N. Marples, J. A. Endler, The complex business of survival by aposematism. *Trends Ecol. Evol.* **20**, 598–603 (2005).
2. M. Puurtinen, V. Kaitala, Conditions for the spread of conspicuous warning signals: a numerical model with novel insights. *Evolution (N. Y).* **60**, 2246–2256 (2006).
3. G. D. Ruxton, W. L. Allen, T. N. Sherratt, M. P. Speed, *Avoiding Attack: The Evolutionary*

Ecology of Crypsis, Mimicry and Warning Signals (Oxford University Press, Oxford, ed. 2nd, 2018).

4. D. W. Kikuchi, M. E. Herberstein, M. Barfield, R. D. Holt, J. Mappes, Why aren't warning signals everywhere? On the prevalence of aposematism and mimicry in communities. *Biol. Rev.* **96**, 2446–2460 (2021).
5. S. Merilaita, N. E. Scott-Samuel, I. C. Cuthill, How camouflage works. *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 15–16 (2017).
6. M. Stevens, G. D. Ruxton, Linking the evolution and form of warning coloration in nature. *Proc. R. Soc. B Biol. Sci.* **279**, 417–426 (2012).
7. J. B. Barnett, I. C. Cuthill, N. E. Scott-Samuel, Distance-dependent pattern blending can camouflage salient aposematic signals. *Proc. R. Soc. B Biol. Sci.* **284**, 20170128 (2017).
8. C. Kang, H.-J. Cho, S.-I. Lee, P. G. Jablonski, Post-attack aposematic display in prey facilitates predator avoidance learning. *Front. Ecol. Evol.* **4** (2016).
9. J. Mappes, H. Kokko, K. Ojala, L. Lindström, Seasonal changes in predator community switch the direction of selection for prey defences. *Nat. Commun.* **5**, 5016 (2014).
10. Y. Kim, Y. Hwang, S. Bae, T. N. Sherratt, J. An, S.-W. W. Choi, J. C. Miller, C. Kang, Prey with hidden colour defences benefit from their similarity to aposematic signals. *Proc. R. Soc. B Biol. Sci.* **287**, 20201894 (2020).
11. K. Loeffler-Henry, C. Kang, T. N. Sherratt, Evolutionary transitions from camouflage to aposematism: Hidden signals play a pivotal role. *Science (80-.).* **379**, 1136–1140 (2023).
12. Z. Emberts, J. J. Wiens, Why are animals conspicuously colored? Evolution of sexual versus warning signals in land vertebrates. *Evolution (N. Y).*, doi: 10.1111/evo.14636 (2022).
13. L. M. Arenas, J. Troscianko, M. Stevens, Color contrast and stability as key elements for effective warning signals. *Front. Ecol. Evol.* **2**, 25 (2014).
14. O. Penacchio, C. G. Halpin, I. C. Cuthill, P. G. Lovell, M. Wheelwright, J. Skelhorn, C. Rowe, J. M. Harris, A computational neuroscience framework for quantifying warning signals. *Methods Ecol. Evol.* **15**, 103–116 (2024).
15. M. Vorobyev, D. Osorio, Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. London. Ser. B Biol. Sci.* **265**, 351–358 (1998).
16. K. V. Pegram, R. L. Rutowski, Relative effectiveness of blue and orange warning colours in the contexts of innate avoidance, learning and generalization. *Anim. Behav.* **92**, 1–8 (2014).
17. See supplementary materials and methods.
18. J. Skelhorn, C. G. Halpin, C. Rowe, Learning about aposematic prey. *Behav. Ecol.* **27**, 955–964 (2016).
19. D. N. Anstett, K. A. Nunes, C. Baskett, P. M. Kotanen, Sources of controversy surrounding latitudinal patterns in herbivory and defense. *Trends Ecol. Evol.* **31**, 789–802 (2016).
20. D. W. Schemske, G. G. Mittelbach, H. V. Cornell, J. M. Sobel, K. Roy, Is there a latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.* **40**, 245–269 (2009).
21. H. Hillebrand, On the generality of the latitudinal diversity gradient. *Am. Nat.* **163**, 192–211 (2004).

22. S. T. Aluthwattha, R. D. Harrison, K. B. Ranawana, C. Xu, R. Lai, J. Chen, Does spatial variation in predation pressure modulate selection for aposematism? *Ecol. Evol.* **7**, 7560–7572 (2017).

23. D. W. Kikuchi, M. Barfield, M. E. Herberstein, J. Mappes, R. D. Holt, The effect of predator population dynamics on Batesian mimicry complexes. *Am. Nat.* **199**, 406–419 (2022).

24. K. McMahon, N. M. Marples, L. G. Spurgin, H. M. Rowland, B. C. Sheldon, J. A. Firth, Social network centrality predicts dietary decisions in a wild bird population. *iScience* **27**, 109581 (2024).

25. J. A. Endler, J. Mappes, Predator mixes and the conspicuousness of aposematic signals. *Am. Nat.* **163**, 532–547 (2004).

26. J. A. M. M. Galloway, S. D. Green, M. Stevens, L. A. Kelley, Finding a signal hidden among noise: how can predators overcome camouflage strategies? *Philos. Trans. R. Soc. B Biol. Sci.* **375**, 20190478 (2020).

27. E. L. Zvereva, M. V. Kozlov, The costs and effectiveness of chemical defenses in herbivorous insects: a meta-analysis. *Ecol. Monogr.* **86**, 107–124 (2016).

28. A. B. Bond, A. C. Kamil, Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *Proc. Natl. Acad. Sci.* **103**, 3214 (2006).

29. D. W. Kikuchi, A. Dornhaus, V. Gopeechund, T. N. Sherratt, Signal categorization by foraging animals depends on ecological diversity. *Elife* **8** (2019).

30. C.-Y. Kuo, Resolving the paradox of local warning signal diversity with predator learning. *bioRxiv*, doi: 10.1101/2023.05.04.539348 (2023).

31. J. A. Endler, The color of light in forests and its implications. *Ecol. Monogr.* **63**, 2–27 (1993).

32. Z. M. Laubach, E. J. Murray, K. L. Hoke, R. J. Safran, W. Perng, A biologist's guide to model selection and causal inference. *Proc. R. Soc. B Biol. Sci.* **288**, 20202815 (2021).

33. A. L. Hargreaves, Geographic Gradients in Species Interactions: From Latitudinal Patterns to Ecological Mechanisms. *Annu. Rev. Ecol. Evol. Syst.* **55**, 369–393 (2024).

34. E. L. Zvereva, M. V. Kozlov, Seasonal variations in bird selection pressure on prey colouration. *Oecologia* **196**, 1017–1026 (2021).

35. J. Skelhorn, C. Rowe, Cognition and the evolution of camouflage. *Proc. R. Soc. B* **283**, 20152890 (2016).

36. M. Chouteau, M. Arias, M. Joron, Warning signals are under positive frequency-dependent selection in nature. *Proc. Natl. Acad. Sci.* **113**, 2164–2169 (2016).

37. C. A. Barnett, J. Skelhorn, M. Bateson, C. Rowe, Educated predators make strategic decisions to eat defended prey according to their toxin content. *Behav. Ecol.* **23**, 418–424 (2012).

38. H. Wilman, J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, W. Jetz, EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027 (2014).

39. P. Chai, Field observations and feeding experiments on the responses of rufous-tailed jacamars (Galbula ruficauda) to free-flying butterflies in a tropical rainforest. *Biol. J. Linn. Soc.* **29**, 161–189 (1986).

40. R. Greenberg, The role of neophobia in determining the degree of foraging specialization

in some migrant warblers. *Am. Nat.* **122**, 444–453 (1983).

41. L. Lindström, R. V. Alatalo, A. Lyytinen, J. Mappes, Strong antiapostatic selection against novel rare aposematic prey. *Proc. Natl. Acad. Sci.* **98**, 9181–9184 (2001).
42. A. Kelber, C. Yovanovich, P. Olsson, Thresholds and noise limitations of colour vision in dim light. *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 20160065 (2017).
43. I. C. Cuthill, S. R. Matchette, N. E. Scott-Samuel, Camouflage in a dynamic world. *Curr. Opin. Behav. Sci.* **30**, 109–115 (2019).
44. B. Rojas, P. Rautiala, J. Mappes, Differential detectability of polymorphic warning signals under varying light environments. *Behav. Processes* **109**, 164–172 (2014).
45. O. Nokelainen, F. de Moraes Rezende, J. K. Valkonen, J. Mappes, Context-dependent coloration of prey and predator decision making in contrasting light environments. *Behav. Ecol.* **33**, 77–86 (2022).
46. M. Stevens, J. Mappes, S.-L. Sandre, The effect of predator appetite, prey warning coloration and luminance on predator foraging decisions. *Behaviour* **147**, 1121–1143 (2010).
47. Dryad: Data for “Global selection on insect antipredator coloration.” https://datadryad.org/stash/share/AV0qpuTvirZmPU7NnWGKYkN3o42sfyPMILK6bVeyu8I.
48. T. W. Pike, Quantifying camouflage and conspicuousness using visual salience. *Methods Ecol. Evol.* **9**, 1883–1895 (2018).
49. I. C. Cuthill, M. Stevens, J. Sheppard, T. Maddocks, C. A. Párraga, T. S. Troscianko, Disruptive coloration and background pattern matching. *Nature* **434**, 72–74 (2005).
50. M. Stevens, E. Hopkins, W. Hinde, A. Adcock, Y. Connolly, T. S. Troscianko, I. C. Cuthill, Field experiments on the effectiveness of ‘eyespots’ as predator deterrents. *Anim. Behav.* **74**, 1215–1227 (2007).
51. Z. W. Rowe, D. J. D. Austin, N. Chippington, W. Flynn, F. Starkey, E. J. Wightman, N. E. Scott-Samuel, I. C. Cuthill, Background complexity can mitigate poor camouflage. *Proc. R. Soc. B Biol. Sci.* **288** (2021).
52. R. He, E. Pagani-Núñez, E. Goodale, C. R. A. Barnett, Avian predators taste reject mimetic prey in relation to their signal reliability. *Sci. Rep.* **12**, 2334 (2022).
53. E. L. Zvereva, B. Adroit, T. Andersson, C. R. A. Barnett, S. Branco, B. Castagneyrol, G. M. Chiarenza, W. Dáttilo, E. Del-Val, J. Filip, J. Griffith, A. L. Hargreaves, J. A. Hernández-Agüero, I. L. H. Silva, Y. Hong, G. Kietzka, P. Klimeš, M. Koistinen, O. Y. Kruglova, S. Kumpula, P. Lopezosa, M. March-Salas, R. J. Marquis, Y. M. Marusik, A. T. Moles, A. Muola, M. Murkwe, A. Nakamura, C. Olson, E. Pagani-Núñez, A. Popova, O. Rahn, A. Reshchikov, A. Rodriguez-Campbell, S. Rytkönen, K. Sam, A. Sounapoglou, R. Tropek, C. Wenda, G. Xu, Y. Zeng, M. Zolotarev, N. A. Zubrii, V. Zverev, M. V. Kozlov, Predation on live and artificial insect prey shows different global latitudinal patterns. *Glob. Ecol. Biogeogr.* **33** (2024).
54. C. R. A. Barnett, M. Ringhofer, T. N. Suzuki, Differences in predatory behavior among three bird species when attacking chemically defended and undefended prey. *J. Ethol.* **39**, 29–37 (2021).
55. A. Exnerová, E. Landová, P. Štys, R. Fuchs, M. Prokopová, P. Cehláriková, Reactions of passerine birds to aposematic and non-aposematic firebugs (Pyrrhocoris apterus ; Heteroptera). *Biol. J. Linn. Soc.* **78**, 517–525 (2003).

56. J. Carroll, T. N. Sherratt, A direct comparison of the effectiveness of two anti-predator strategies under field conditions. *J. Zool.* **291**, 279–285 (2013).

57. J. Troscianko, M. Stevens, Image calibration and analysis toolbox – a free software suite for objectively measuring reflectance, colour and pattern. *Methods Ecol. Evol.* **6**, 1320–1331 (2015).

58. C. A. Schneider, W. S. Rasband, K. W. Eliceiri, NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671–675 (2012).

59. R. Maia, C. M. Eliason, P.-P. Bitton, S. M. Doucet, M. D. Shawkey, pavo: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.* **4**, 906–913 (2013).

60. S. E. Newson, K. L. Evans, D. G. Noble, J. J. D. Greenwood, K. J. Gaston, Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *J. Appl. Ecol.* **45**, 1330–1338 (2008).

61. J. Marin, G. Rapacciuolo, G. C. Costa, C. H. Graham, T. M. Brooks, B. E. Young, V. C. Radeloff, J. E. Behm, M. R. Helmus, S. B. Hedges, Evolutionary time drives global tetrapod diversity. *Proc. R. Soc. B Biol. Sci.* **285**, 20172378 (2018).

62. S. Sahney, M. J. Benton, P. A. Ferry, Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. *Biol. Lett.* **6**, 544–547 (2010).

63. S. A. Fabricant, A. Exnerová, D. Ježová, P. Štys, Scared by shiny? The value of iridescence in aposematic signalling of the hibiscus harlequin bug. *Anim. Behav.* **90**, 315–325 (2014).

64. S. Chamberlain, D. Oldoni, J. Waller, rgbif: interface to the global biodiversity information facility API. (2022). https://doi.org/10.5281/zenodo.6023735.

65. D. N. Karger, S. Lange, C. Hari, C. P. O. Reyer, O. Conrad, N. E. Zimmermann, K. Frieler, CHELSA-W5E5: daily 1 km meteorological forcing data for climate impact studies. *Earth Syst. Sci. Data* **15**, 2445–2464 (2023).

66. W. J. Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux, vegan: Community Ecology Package. R package version 2.6-2 (2024). https://github.com/vegandevs/vegan.

67. J. Del Hoyo, A. Elliott, J. Sargatal, *Handbook of the Birds of the World* (Lynx edicions Barcelona, 1992).

68. A. L. Pigot, C. Sheard, E. T. Miller, T. P. Bregman, B. G. Freeman, U. Roll, N. Seddon, C. H. Trisos, B. C. Weeks, J. A. Tobias, Macroevolutionary convergence connects morphological form to ecological function in birds. *Nat. Ecol. Evol.* **4**, 230–239 (2020).

69. Y. Toda, M.-C. Ko, Q. Liang, E. T. Miller, A. Rico-Guevara, T. Nakagita, A. Sakakibara, K. Uemura, T. Sackton, T. Hayakawa, S. Y. W. Sin, Y. Ishimaru, T. Misaka, P. Oteiza, J. Crall, S. V. Edwards, W. Buttemer, S. Matsumura, M. W. Baldwin, Early origin of sweet perception in the songbird radiation. *Science (80-.).* **373**, 226–231 (2021).

70. T. M. Inc., *MATLAB Release 2022a.* (Natick, Massachusetts, USA, 2022).

71. L. Itti, C. Koch, Feature combination strategies for saliency-based visual attention systems. *J. Electron. Imaging* **10**, 161–169 (2001).

72. T. M. Therneau, Mixed effect Cox models. (2022). http://ftp.edu.ee/pub/cran/web/packages/coxme/vignettes/coxme.pdf.

73. T. M. Therneau, T. Lumley, Package ‘survival.’ *R Top Doc* **128**, 112 (2020).

74. S. Arif, M. D. B. Massey, Reducing bias in experimental ecology through directed acyclic graphs. *Ecol. Evol.* **13** (2023).

75. T. Poisot, J. D. Bever, A. Nemri, P. H. Thrall, M. E. Hochberg, A conceptual framework for the evolution of ecological specialisation. *Ecol. Lett.* **14**, 841–851 (2011).

76. T. D. Mize, Best practices for estimating, interpreting, and presenting nonlinear interaction effects. *Sociol. Sci.* **6**, 81–117 (2019).

77. M. N. Scholer, M. Strimas-Mackey, J. E. Jankowski, A meta-analysis of global avian survival across species and latitude. *Ecol. Lett.* **23**, 1537–1549 (2020).

78. K. Rönkä, C. De Pasqual, J. Mappes, S. Gordon, B. Rojas, Colour alone matters: no predator generalization among morphs of an aposematic moth. *Anim. Behav.* **135**, 153–163 (2018).

79. B. Kazemi, G. Gamberale-Stille, B. S. Tullberg, O. Leimar, Stimulus salience as an explanation for imperfect mimicry. *Curr. Biol.* **24**, 965–969 (2014).

80. L. P. Brower, L. S. Fink, A natural toxic defense system: Cardenolides in butterflies versus birds. *Ann. N. Y. Acad. Sci.* **443**, 171–188 (1985).

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Ethics:

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Data and materials availability:

Raw datasets and code used for analyses and figures are available in Dryad (*47*)

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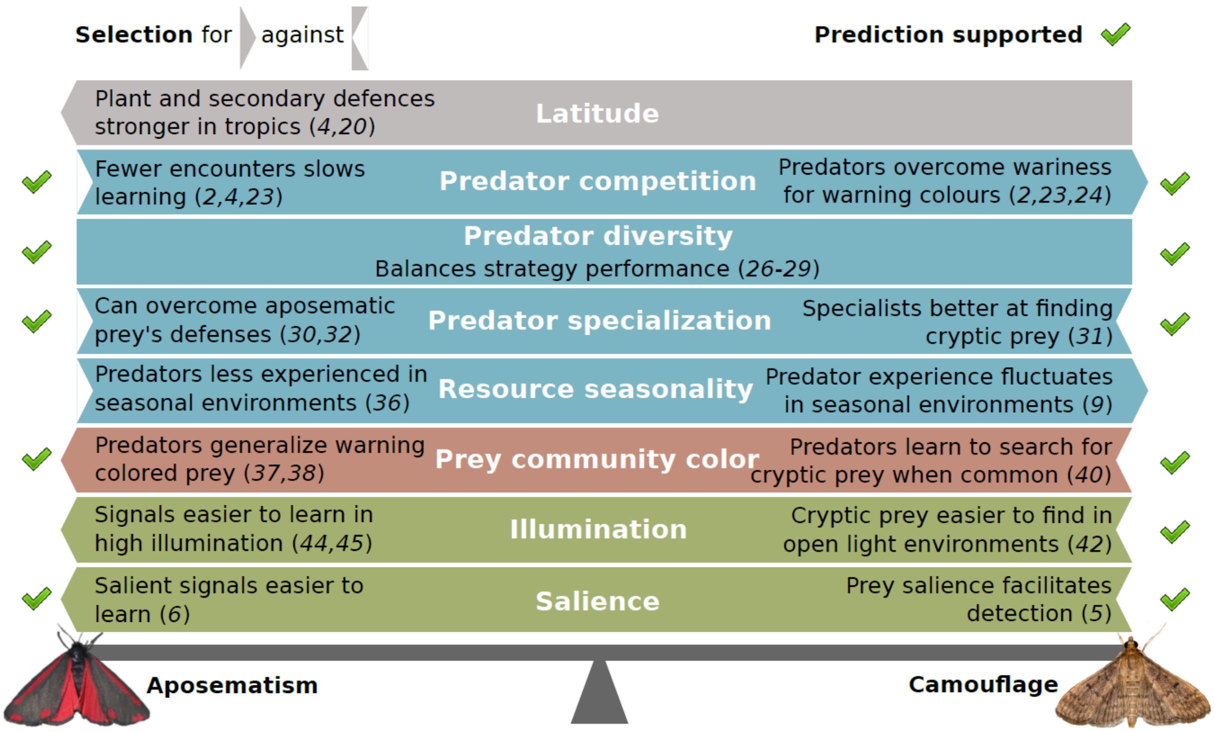

Figure 1. Summary of potential ecological variables (white text) affecting predation on camouflaged and undefended and defended typical warning colored (aposematic) prey. Main predictions summarized in black text, and visualization of predictions presented in plots, corresponding to changes in either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

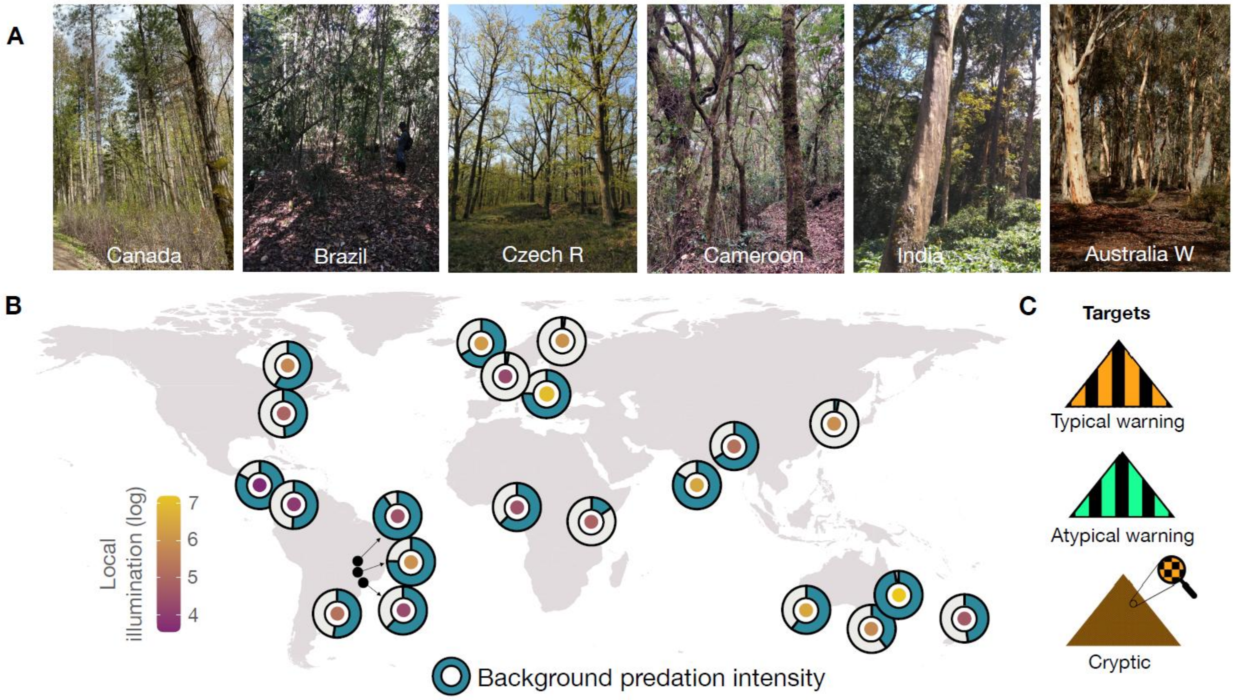

Figure 2. (A) Artificial prey were exposed to avian predation in temperate and tropical woods and forests. **(B)** Global distribution of 21 locations. Icons show proportion of insectivorous predators in the inner circle and background predation intensity (% consumed in mealworm only experiment) in the outer circle. **(C)** The three treatments employed, and an example of the artificial prey used.

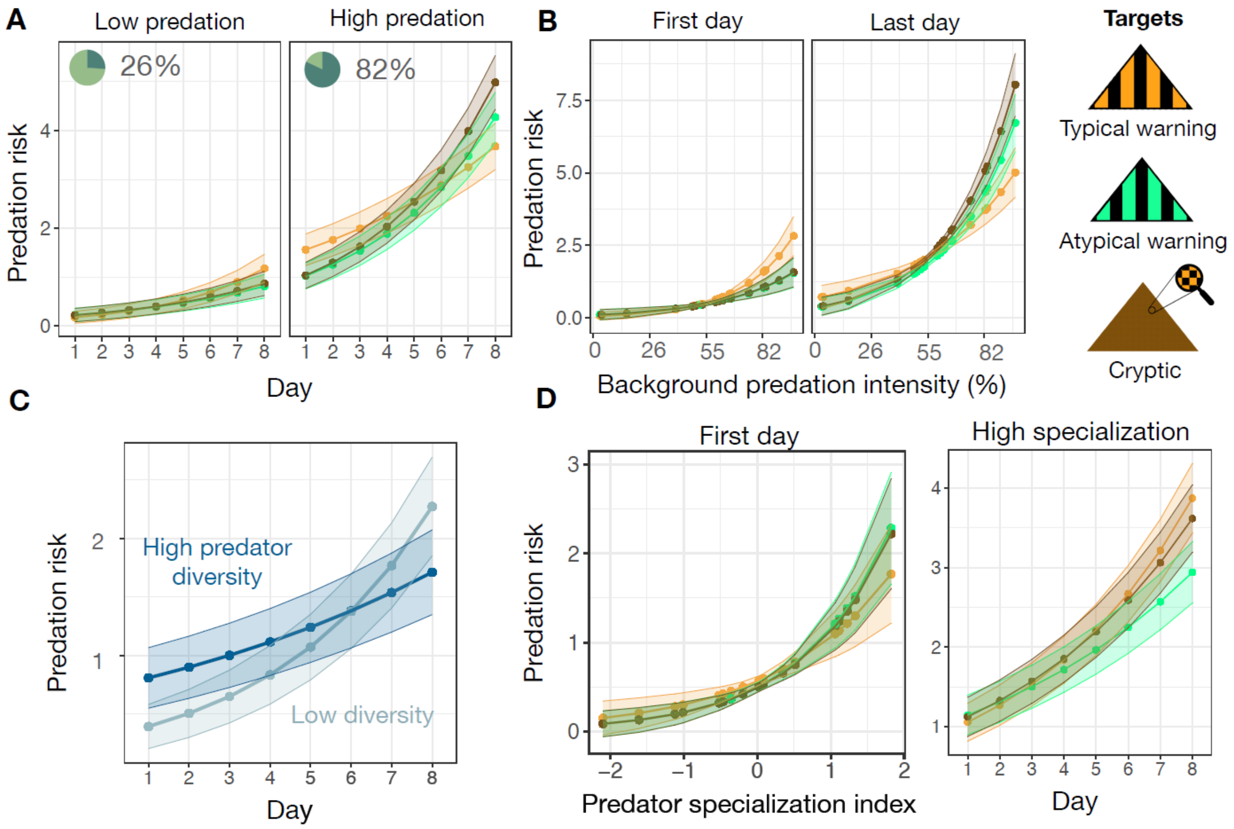

Figure 3. Predator community and predation risk, measured as the predicted hazard ratio estimated from the Cox mixed model (exponentiated coefficients). Predation risk values represent the risk of predation when the reference level (typical warning color) of the treatment variable has a baseline risk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

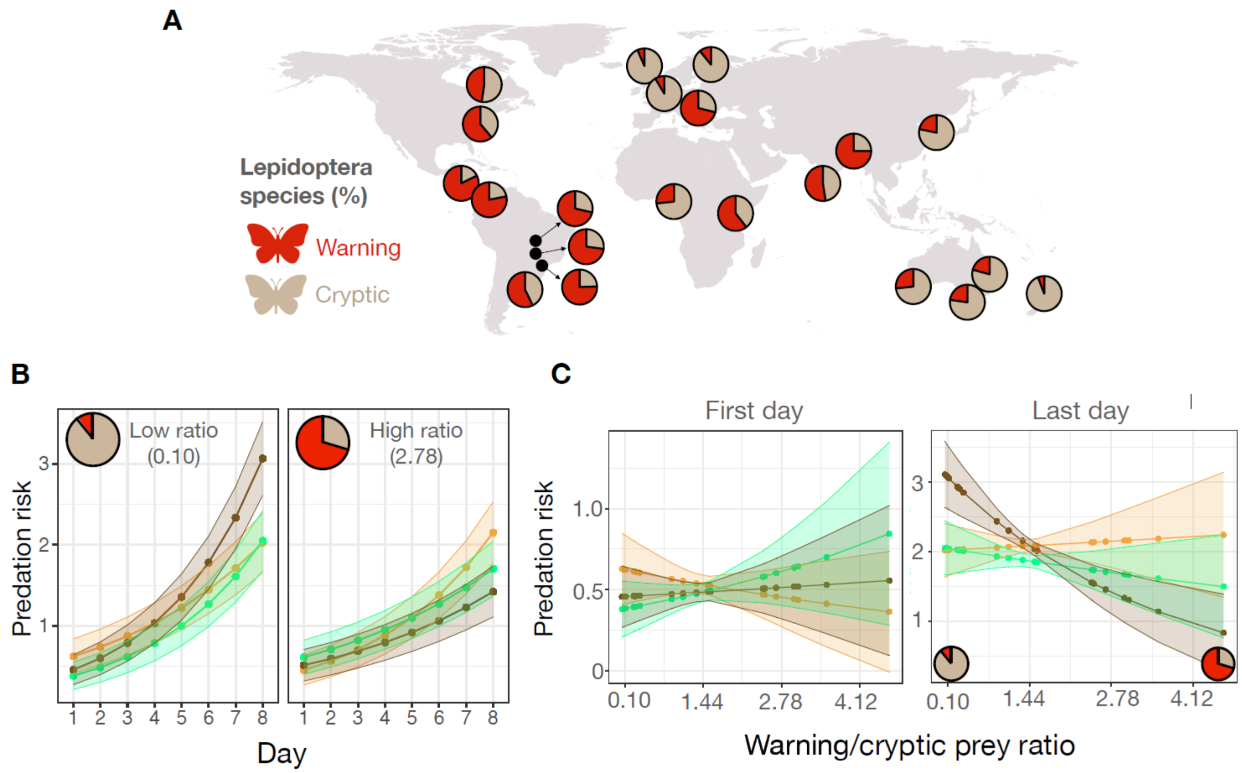

Figure 4. Effects of prey community on predation risk. **(A)** Global distribution of lepidopteran community coloration estimated from species recorded at each location and classified as either typical warning color, cryptic or 'other' (not shown). **(B)** Latitudinal distribution of typical warning 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 where all other covariables (except for the one of interest) are kept at mean values.

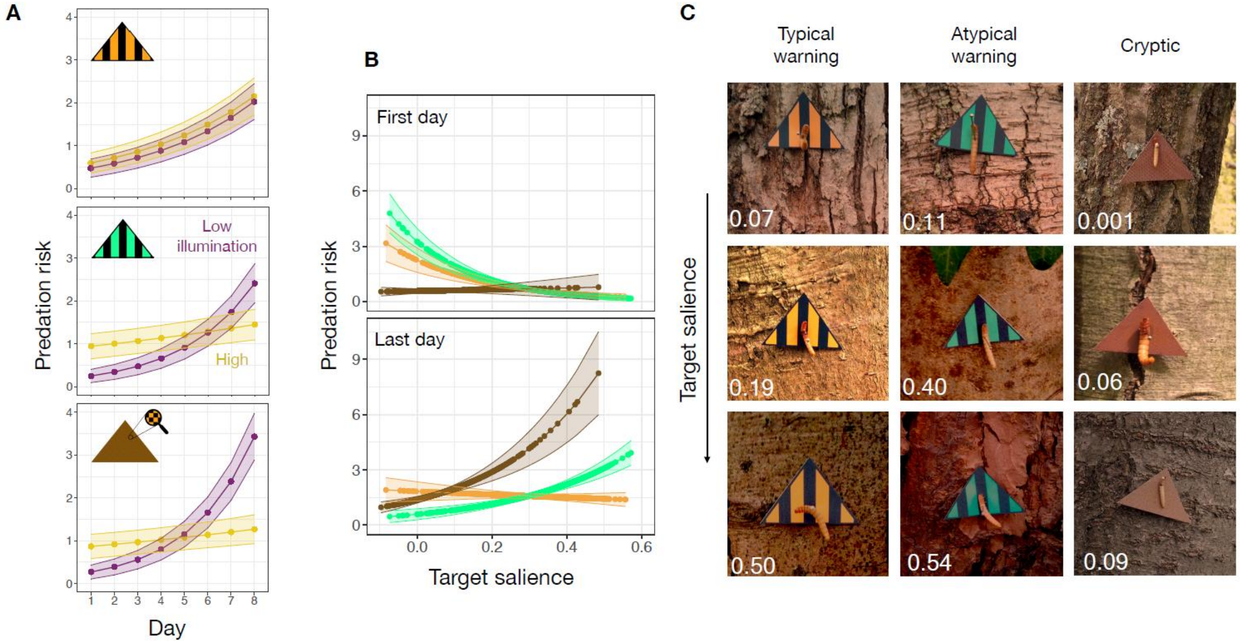

Figure 5. Effect of visual environment on predation risk. **(A)** Variation in predicted risk through experiment days, for low illumination locations (mean - SE) and high illumination locations (mean + SE). Lines represent predicted values of risk for each target type, estimated from the main model. **(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 = 2,908 targets). **(D)** Examples of targets and backgrounds with different salience values. These were calculated from standardized photographs and represent the distance in color, luminance, and edge orientation between background and target, considering light environment (*48*).

Supplementary Materials for

Global selection on insect antipredator coloration.

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Materials and Methods

1. Experimental design

The globally distributed experiment was initiated by WLA and IM at the June 2019 Antipredator Colouration Meeting (University of Exeter, UK). Following the workshop, at which six location leads were present (WLA, IM, AE, HMR, ON, EB-S), a further 9 location leads were recruited through academic networks, with the goal of including multiple experimental locations on each continent. The experimental design and protocol were created through a collaborative process among network members between June 2019 and March 2020.

We used a standard and well-established field predation paradigm where triangular paper 'moths' printed with different color patterns and attached to a mealworm prey are exposed to free-living predators in natural conditions (*49*–*51*). Mealworms and other undefended insect larvae are used in field experiments targeting avian predators in various habitats (*33*, *49*, *52*, *53*) since they are readily consumed by birds with different foraging strategies (*54*, *55*), although their usage might exclude some specialized predators, particularly those catching prey in flight (*39*). We deployed three treatments: 1.) typical warning color pattern consisting of orange and black stripes surrounded by a black border, 2.) atypical warning color pattern that was identically patterned and equally conspicuous (see Target design) but with the orange replaced by a turquoise color atypical of warning coloration, and 3.) a cryptic pattern consisting of a fine orange and black checkerboard with the same average color and lightness as the typical warning treatment, but having a brown appearance (Fig. 2). To ensure all predators globally would be required to make similar generalizations about the warning treatments' potential defenses, the warning color pattern was designed to have some general features typical of many aposematic lepidopteran species found globally, but not closely mimic any specific species. Based on effect sizes of previous experiments using this paradigm (*49*–*51*), anticipated predator learning rates (*56*), and how many targets could be placed and checked by experimenters in the time available, at each location 720 targets (240 per treatment, 90 per day) were tested.

To test experimental hypotheses, avian predation rates on treatments were analyzed with respect to multiple experimental variables, summarized in table S4.

2. Target design

Targets were designed using Inkscape (Inkscape Project 2020) and printed on Toughprint waterproof Inkjet paper (Memory Map Ltd) using a color-calibrated Canon Pro-100S printer and Canon inks. To find 1.) treatment colors that produced typical and atypical warning colored targets that differed in color but were equally conspicuous to avian predators relative to the cryptic color, and 2.) typical warning colored and cryptic treatments that had the same average color and lightness, but differed in internal contrast and overall conspicuousness, we printed a selection of colors and measured these in avian color space. Specifically, photos of color swatches were taken using a Samsung NX1000 camera that had UV filters removed and Nikkor EL 80mm lens. Two images were taken, one through a Baader UV/IR-Cut filter to record reflectance between 420 and

685 nm, and a second through a Baader U-Filter to record reflectance between 320 and 380 nm. These images were aligned and transformed to blue tit (*Cyanistes caeruleus*) photoreceptor quantal catches using functions within the MicaToolbox (*57*) for ImageJ (*58*). Blue tits were chosen as they have visual systems typical of small passerine birds that are the most abundant avian predators in many woods and forests globally (see avian survey). Color contrasts between patch colors were calculated using the coldist function in the R package pavo (*59*), which implements the Receptor Noise Limited model (*15*) for estimating color and lightness contrast as just noticeable differences (JNDs). The default 1:2:2:4 cone densities and 0.1 Weber fraction were used. We then selected swatch colors that best fulfilled criteria, finding orange and turquoise colors that differed less than 2 JNDs in their color (5.30 vs 6.98) and lightness (8.78 vs 9.60) contrast with the cryptic color, and the average color and lightness of the warning and cryptic treatments being less than 2 JNDs (0.56). Similar overall lightness also meant each treatment had similar thermal absorption, so any effect of target temperature on predation is considered unlikely to bias our results. The selected targets were batch printed, with the color of each sheet checked visually, and every 10th sheet photographed and measured to ensure it was within 1 JND of the target color in avian color space. Targets, along with a smartphone camera (Cubot Quest Lite with Sony 13 MP camera and f/2.0 aperture lens), 26 mm dressmaking pins and two 18% gray reflectance standards were shipped to location leads.

3. Experimental procedure:

3.1 Overview

The experiment at each location consisted of a reconnaissance visit to establish the transect, a first survey of the avian community along the transect, tree selection and tape banding of 180 trees, then the eight experimental days, followed by a 'mealworm only' test of the background predation intensity, and finally a second survey of the avian community. To standardize predator learning opportunities between locations while allowing for logistical, personnel and weather challenges, the eight experimental days had to be completed within 12 calendar days.

3.2. Location and transect selection

The experiments took place in managed and unmanaged woodlands, forests, and scrublands. Formal parkland, plantations, and other intensively managed areas were excluded. At each location a single approximately 2 km non-linear transect with sufficient suitable trees (see 3.3 tree selection), and low foot traffic (estimated fewer than two persons an hour) was established. Location leads obtained necessary permissions to run experiments at each site.

All experiments were standardized to the onset of the peak breeding season at each location: the time of year when the proportion of uneducated fledglings in the avian predator community is lowest. In the southern hemisphere temperate zones, experiments ran in September and October 2020 and 2021 and in the northern hemisphere temperate zones experiments ran between March and June in 2020 and 2021. As peak breeding seasons in tropical zones are generally less pronounced, location leads used local records and expertise to identify the onset of the peak breeding season. Tropical zone experiments took place between January 2021 and April 2022.

3.2 Bird survey

A standardized bird survey based on the British Trust for Ornithology Breeding Bird Survey protocol (*60*) was conducted in each location to quantify avian communities. The survey consisted of two transect walks by 1–4 observers at each location as an attempt to identify and record all unique individuals on both sides of the transect, noting whether the identification was based on visual and/or acoustic cues. The first survey took place as close as possible before experimental days, and the second as close as possible after the experimental days, while avoiding days on which weather was atypical. Detections further than an estimated 50 m away were not recorded. Birds that could not be identified to species were recorded as unique unknown types. Weather, observers present and start and finish times were also noted.

To account for differences in surveying experience and ability between locations, each team self-assessed whether their observers were either 1.) experienced local birdwatchers confident that they detected almost all birds (10/21 teams), 2.) experienced local birdwatchers but likely missed a few possible detections (4/21), 3.) familiar with local avifauna but not expert, and likely missed several detections (7/21), or 4.) familiar with common species only and likely missed some detections (0/21).

3.3. Tree selection

Up to 10 m either side of the transect, 180 trees suitable for placing targets were identified. Criteria were trunks at least 10 cm in diameter, with areas of bark free from moss and lichen; absence of arboreal ant nests; distance at least 5 m from another selected tree; and approximately even distribution along the transect. To reduce the risk of predation by terrestrial ants, a loop of gray duct tape was tightly wound around the trunk approximately 30 cm off the ground to create a continuous barrier. If selected trees had a highly ridged or non-circular shape, coir fiber was used underneath the tape to seal the barrier. Each tree was labeled 1–180 on the band using a permanent marker to enable random selection of trees in each experimental day and the location of each numbered tree was mapped to aid in relocation of trees and targets.

3.4. Experimental days

In each of the eight experimental days, 90 targets were placed on a random selection of the 180 trees and predation was observed over 22 hours. To prepare for each day, 30 targets from each treatment were labeled on the back with day number 1–8 and target number 1–30. Thirty minutes prior to the placement on each day, ca. 120 living mealworms (*Tenebrio molitor* larvae) were removed from refrigeration and pinned through the thorax from the ventral side to a piece of corrugated card or foam and transported in a storage container to the experiment location. Live mealworms were used following preliminary testing that found dead mealworms decomposed over 22 hours in warm and humid locations, which may have affected palatability, whereas living mealworms had 92% survival over the experimental period. The lengths of a random sample of

10 mealworms were measured to the nearest mm to check whether mealworm size influenced avian predation rates.

A random number generator was used to select 90/180 trees to place targets on each day. Pinning of targets to selected trees began approximately 2 hours after sunrise. At a selected tree, a location to place the target on the trunk or a main branch was chosen by an experimenter. Suitable locations were 1–1.6 m above the ground with an immediate background of bark. All sides of the tree were used, and locations on trees were chosen independently between days. Once chosen, a target was drawn at random from a well-mixed bag containing all the targets for the day. The target number was noted by the corresponding tree number on the map, and the target was firmly pinned to the tree with a mealworm attached in front of it positioned ‘head-up’ to approximate a typical posture of a resting moth body.

Target predation was checked three times. The first check began about 30 minutes before solar noon on the day the target was deployed, the second about 60 minutes before sunset, and the final one at sunrise the next morning. Analyses were performed both including and excluding night-time predation. Start time was recorded and each check took ca. 1 hour. Avian predation was recorded if the whole or large part of the mealworm was removed with no other traces left at the target. Targets predated by non-avian predators were censored (recorded as 0, a non-event of avian predation), recording predator type if possible in the categories ‘Formicidae’ (if present in the immediate vicinity of the target at the time of a check), ‘Arachnida’ (if a hollow mealworm exoskeleton trace was found), ‘Gastropoda’ (if there was a mucus trail around the target), ‘Vespoidea’ (if wasps were present at the target), ‘Other Arthropoda’ (when low counts of predation were accompanied by signs of activity of arthropod groups including cockroaches, isopods, millipedes, crickets, true bugs and earwigs), and ‘Mammalia’ if predation by rodents was suggested by bite marks on the target. As all predators large enough to take whole mealworms (e.g. lizards, mammals, frogs, as well as birds) are known to use color vision to find prey, any potential for misidentifying avian predation is unlikely to affect inferences about how visual environment or prey community color affects predation on treatments. As the background predation intensity measure comes from the same experimental paradigm, and seasonality affects recruitment of all tetrapod classes, these relationships are also unlikely to be affected. Tests of predator density, predator diversity and insectivore proportion may be impacted if predator type is misidentified, requiring some caution in interpretation, although evidence suggests the variables are spatially correlated across tetrapod classes (*61*, *62*). Furthermore, we note that while birds were frequently observed in the vicinity of targets (Movies S1 & 2), other tetrapods were rarely observed. If a target could not be found at a check it was searched for on the floor around the tree. If found and the mealworm was missing avian predation was recorded. If the mealworm was present it was replaced. If the target could not be found it was recorded as ‘Lost’ and censored. Altogether 177 targets were lost, with a median of five per location. Any targets with the mealworm remaining at the sunrise check were recorded as censored and removed. After each day the condition of the tape barrier was checked and replaced if necessary.

3.5 Target photography

Each day, 6/30 randomly selected targets from each treatment were photographed adjacent to an 18% gray card when initially placed and then again at each checkpoint until predation had occurred.

Photos were taken using a CUBOT Quest Lite smartphone with 13 Mp camera holding the 18% gray card at arm's length, oriented in the same plane, approximately 5 cm away, and in the same light as the target (direct vs. indirect), avoiding self-cast shadows on the target, standard or the immediate background. In general, the automatic exposure settings resulted in a well-exposed image, but if the image was overexposed a second image was taken on a shorter exposure.

3.6 Background predation intensity

Directly after completion of the 8 experimental days, a ninth 'mealworm only' experiment was conducted to measure background predation intensity. The same experimental procedure was followed, except that 90 mealworms were pinned without an accompanying paper target to the random sample of the experimental trees. Background predation intensity was recorded as the proportion of mealworms consumed using the same criteria for target predation as the main experiment.

3.7 Unpalatable prey experiment

Since all prey in the main experiment were palatable, we wanted to investigate the relationship between how quickly the predators overcome the wariness for undefended prey and how quickly they would learn about prey unpalatability if the prey were defended. We investigated this relationship by running a second experiment where the prey in all three treatments were defended (unpalatable).

We made the mealworms unpalatable by injecting them with 0.01 ml of 6% chloroquine phosphate solution shortly prior to the target placement. This chloroquine concentration makes the mealworms aversive to birds (*63*). To inject the mealworms with chloroquine, we used a hypodermic syringe inserted through the intersegmental membrane before the last abdominal segment. We tested in the lab without predators that the survival of quinine-injected mealworms during the 22-hour period did not differ from the survival of untreated mealworms.

Except for the prey unpalatability, the experimental protocol was identical to the main experiment. The unpalatable prey experiment took place in the Czech Republic (50.0755° N, 14.4378° E) in April 2020 at a different location but in the same type of habitat (temperate oak forest) as the main experiment conducted in the same country. Results are presented in Fig. S1.

4. Lepidopteran survey

For analysis of prey communities, occurrence data from the GBIF database (www.gbif.org) were extracted using the occ_data function from R package rgbif (*64*). Lepidoptera (butterfly and moth) occurrences identified at the species level were obtained from a 3 km radius around the transect starting point for each location. To prevent the warning/cryptic prey ratio being biased due to a small number of records, if this resulted in fewer than 50 unique species per location, the radius was expanded in 0.001 km increments until the minimal number of 50 species was reached.

The coloration of unique lepidopteran species was classified as either ‘typical warning’, ‘atypical warning’, ‘warning with both typical and atypical coloration’, ‘cryptic’, or ‘other’, based on photographs showing the head, thorax, abdomen, and spread wings obtained through the Google Image Search. In polymorphic species with geographically distinct color morphs, the locally occurring morph was classified. If more than one color morph occurred in the location, then the species was classified in the “more conspicuous” category (warning > other > cryptic).

The following morphotypes were classified as ‘typical warning’: a) Lepidopterans with at least 10% of the body area on at least one side (ventral/dorsal) colored conspicuously bright orange/yellow/red. b) Lepidopterans with at least 10% of the body area on at least one side (ventral/dorsal) colored conspicuously white or pale orange/yellow/red in combination with contrasting dark brown or black markings, where both the black/dark and the conspicuous pale/white colors covered at least 10% of one side (ventral/dorsal) of the body. In disputable cases, the proportion of colored areas were measured manually using ImageJ.

The following morphotypes were classified as ‘cryptic’: a) Lichen-mimicking lepidopterans; b) Inconspicuous lepidopterans with both ventral and dorsal sides dimly colored brown/gray/green/yellow/lavender/white; never completely white. Red/yellow/orange coloration absent or covering maximum 2% of the body area, not occurring next to black/dark brown colors and not forming any conspicuous pattern.

The following morphotypes were classified as ‘atypical warning’: a) Lepidopterans with at least 10% of the body area on at least one side (ventral/dorsal) colored conspicuously bright blue/green/blue-violet. b) Lepidopterans with at least 10% of the body area on at least one side (ventral/dorsal) pale blue/green colored or with conspicuous blue/green iridescence, in combination with contrasting dark brown or black markings, where both the black/dark and the pale blue/pale green/iridescent area covered at least 10% of one side (ventral/dorsal) of the body. Lepidopterans with blue or green hidden warning signals were classified as 'other' coloration type.

Morphotypes that passed criteria for both ‘typical warning’ and ‘atypical warning’ were classified as ‘warning with both typical and atypical coloration’.

All remaining lepidopterans were classified as ‘other’, mostly consisting of species that were neither cryptic, nor typical warning color. Additionally, this category also contained mimics of hymenopterans and T-moths (Pterophoridae) due to their peculiar morphology, and inconspicuous lepidopterans with warning signals restricted to their hind wings and/or body that were not visible in their typical resting posture, since they fulfill criteria of cryptic coloration in their resting posture but can expose warning coloration when encountered by a predator. Due to their peculiarity or ambiguous appearance, the lepidopterans classified as ‘other’ were excluded from further analyses.

To check the assumption that typical warning coloration was more common than atypical warning coloration, the typical warning/atypical warning prey ratio was calculated as the number of ‘typical warning’ species divided by the number of ‘atypical warning’ species for each location. Consequently, the typical warning/cryptic prey ratio variable was calculated for each location as the number of lepidopteran species classified as ‘typical warning’ and ‘warning with both typical and atypical coloration’, divided by the number of species classified as ‘cryptic’.

All classifications were initially made by KD, with the classification results checked by IM, AE and WA and with disputable cases discussed until consensus was reached. A summary is presented in table S2 and examples of species for each coloration category are given in Fig. S12.

5. Predator community

The results of the bird survey (section 3.2) were used to calculate predator density, predator diversity, and insectivore proportion. Climatic seasonality was calculated using the CHELSA-W5E5 dataset (*65*).

Following the British Trust for Ornithology Breeding Bird Survey protocol (*60*), we calculated the species abundances for each location as total numbers of birds of each species detected along the transect. The maximum number of the two surveys was taken as the measure of species abundance.

Since the location survey reports contained all avian species recorded along the transect irrespective of whether they were relevant to the target predation, the next step in the data analysis was to filter out the species that were unlikely to be responsible for the predation of experimental targets (such as aerial hawkers or strictly frugivorous specialists). We based this on the species foraging characteristics included in the Elton Traits database (*38*). We excluded the species with no invertebrates in their diet, the species that (despite having invertebrates in the diet) are unlikely to be predators of experimental targets due to specific foraging behavior and/or substrate: aerial hawkers (swifts, nightjars, bee-eaters, swallows), raptors, owls, large ground-foraging birds (tinamous, rails, gallinaceous birds), water birds (ducks, herons, ibises, cormorants), and specialized frugi-, nectari-, and granivorous taxa (pigeons, parrots, toucans, hornbills, hummingbirds). This way, 113 species from the original bird survey list were filtered out across all locations.

The resulting dataset consists of at least partly insectivorous species (most of them having over 20% of invertebrates in their diet according to the Elton Traits database (*38*)) that forage in the understory as well as on the ground and in trees. From these data, we calculated avian predator density as the total number of birds recorded at each location standardized to 1 km of the transect length and the Shannon diversity index using the R package ‘vegan 2.6-2’ (*66*). The insectivore proportion at each location was calculated as the proportion of individuals belonging to avian species having at least 60% of their annual diet consisting of invertebrates according to the Elton Traits database (*38*). This criterion corresponds to the species classification into five main dietary categories used by Wilman et al. (*38*) and differentiates the avian species that are more specialized on invertebrate diet from dietary generalists and species specialized on other dietary sources (such as seeds or nectar) with only a small fraction of their diet consisting of invertebrates. It does not capture the narrow dietary specialization to a few individual prey types that has been proposed to be more common in the tropics for some taxonomic groups (*20*), but is extremely rare in birds at the species level (*67*). A similar approach to trophic niche classification has recently been used in studies focused on ecology and evolution of avian foraging traits on a global scale (*68*, *69*). Results of the bird survey are presented in table S7. We present correlations between this and other variables in Fig. S3.

Climatic seasonality could be linked to resource abundance and either continuous or seasonal abundance of naive predators (e.g. fledglings). To estimate climatic seasonality at each location we extracted climatic information using climatic raster layers derived from the CHELSA algorithm (*65*), which provides estimates at a resolution of 30 arc sec. We used the function raster and chose the bioclimatic variable of the coefficient of variation in temperature across months. Higher values indicate higher seasonality in temperature and lower values indicate more stable conditions through the year. This variable was highly correlated with latitude (r = 0.80).

6. Image analysis

The images of targets from each location were sorted into a standard directory structure and analyzed in Matlab (*70*).

First each image was checked by an observer (WA, HB, or MV) and if necessary one of the following flags recorded: ‘Standard close to target’; ‘Image blurred’; ‘No target’; ‘No standard’; ‘Standard in different light to target’; ‘Accidental photo’; ‘Other’. The observer then clicked on the three corners of the target and dragged a box around part of the standard that was estimated by the observer to be under the same illumination as the target (i.e., avoiding shadows on the standard if the target was in direct light). The observer then confirmed that they were satisfied with the selected areas before moving on to the next image. The image coordinates of the target and standard, along with the camera EXIF information and any flags, were recorded.

Each image was then processed automatically as follows. To estimate the relative radiometric intensity (illumination) falling on the target, we computed the amount of light reflected by the selected area of the standard. To this end, we first averaged the values of its G-channel (avGrey). Illumination was then computed as:

$$illumination = avGray * F^2/(IT * ISO)$$

where *F* is the F-number of the camera, IT is the image exposure time, and ISO is the ISO sensitivity.

We calculated local illumination as the average of illumination values across targets at their noon photo, within each location. The noon photo offered a good approximation to general light values due to vegetation density, weather and other characteristics across locations. We also calculated the local variation in illumination at each location, which corresponds to the coefficient of variation in light through the day for a target. Larger values refer to locations where illumination on targets varied more throughout the day. To compute the target saliency with respect to the background, we first defined its immediate background as a square of side 2.5 times the horizontal span of the target on the image and centered on the target. The RGB values of the resulting image were then converted to relative quantum catches following a standard procedure (*57*): first, the RGB values were linearized following a linearization process computed using eight measurements of Spectralon (Labsphere Inc., North Sutton, NH) standards with reflectance varying between 2% and 99%. The linearized images were then converted to relative quantum catches using polynomials to fit the sensitivities of the blue tit (*Cyanistes caeruleus*).

The saliency of the target in each image was computed using Pike's algorithm to quantify conspicuousness (*48*) based on models of saliency-based visual attention (*71*). The algorithm considers the response of the different classes of cones of a species and its luminance channel (double cones) to build three saliency maps based on center-surround operations: a luminance map, which enhances luminance values that differ from their neighboring values; an orientation map, which enhances edge orientations that differ from their neighboring orientations; and a color map, which enhances the values of cone-opponent channels that differ from their neighboring values. We adapted Pike's algorithm to accommodate three opponent channels LM (i.e., L-M), LS, and MS for the blue tit. The luminance, orientation, and color saliency maps were then combined to form a single saliency map with all weights equal to one. The adopted measure of saliency was extracted by computing the distance between the histogram of saliency values for the image restricted to the triangular target and the histogram of the immediate background, i.e., all the pixels in the square neighborhood but the ones in the triangular target. We therefore obtained a single number for each image representing the saliency of the target in the image to a model passerine predator.

7. Data Analysis

To test which variables could predict predation risk across locations we fitted Mixed Effects Cox proportional hazards models using the R package coxme (*72*, *73*). Given the high number of potential predictor variables and their potential associations, to guide the structure of our models we first derived a global Directed Acyclic Graph (DAG; *32*) which allowed us to visualize potential confounding paths and biases and design statistical models that can lead to valid causal inference. DAGs are diagrams that display the causal relationships between sets of variables and can be used to select which sets of predictors should be included or excluded in regression models, to avoid confounding associations or overcontrolling (*74*). WLA, IM, TNS, OP, AE, and KD discussed and decided on potential associations among variables and their direction. The potential links established in the global DAG were guided by biological principles, theory and expert knowledge (as it is recommended), rather than statistical links, and they were established before performing any formal analyses. Most links were clear, though we note a link between predator diversity and insectivore proportion was not included as theory on this only proposes highly specific specialization may be related to diversity via niche occupancy (*75*), rather than the overall degree of specialization to invertebrate prey, which is the variable we investigate in this study. We report the global DAG in Fig. S2, which includes all locality-level predictors. A separate statistical analysis was done at the target level, using information from the photos taken. These models are described in section 8.5.

After establishing potential associations between all predictors, we divided our analyses into two main models. This was done because estimating effects for all variables in the same model would cause biasing paths between some variables. The first model included as predictors of avian attacks all predictors but only those in italics could be estimated with confidence without causing biasing paths (i.e. be set as exposure variables, see Fig. S2&6): *Treatment*, *day number*, *location illumination*, *location variation in illumination*, *ratio of warning/cryptic prey*, predator density, predator diversity, insectivore proportion*, background predation intensity*, and *seasonality*. These variables are only weakly correlated, with the maximum correlation value of $r^2 = 0.34$ (Fig. S3). This corresponds to the link between predator diversity and warning/cryptic prey ratio, and, as explained below, the effect of these two variables was not estimated from the same model.

The model structure described above includes all our predictors, however, the effect of insectivore proportion, predator diversity, and predator density cannot be accurately estimated from the model above (only controlled for). Hence, we built a second model that included all the predictors from the above list except for the warning/cryptic prey ratio and the background predation intensity (Fig. S2&10). This is because insectivore proportion and predator density are likely to affect both target predation rates and presence of aposematic prey (or background predation intensity), creating biasing paths in the models if these predator community predictors are set as exposure variables.

For the two models described above we used as the response variable the survival object, which is a combination of two variables: the time lapsed until each check in minutes, and whether the event was an attack (1) or whether it was censored (0) due to survival or due to the target being taken by a non-avian predator such as an ant or spider (as described above). We also added the location variable as random term. By adding the specific times the checks were done in each location, we accounted for the amount of time that the targets were exposed to predation. For the main models we also censored all targets that were predated overnight, since 19% of all attacks on prey remaining at the sunset check were consumed by the sunrise check. Given there was little light available for visual foraging between these checks, overnight predation was unlikely to be due to visual predators and its inclusion in main models could heavily bias results. We present a separate analysis of overnight predation on each treatment to test the assumption of visual diurnal predation.

Using the function coxme, we used the basic model structure described above and added interactions for those terms that theoretical predictions suggested could have a conditional effect on predation rate. For example, we expected that the effect of local illumination on predation risk might depend on the color treatment and the moment at which the experiment occurred. This implied adding a three–way interaction of local illumination × day × treatment. The structure of the full models is presented in figure S2B&C. Most hypotheses were focused on the learning speed and the differences across treatments, so we added interaction with day and treatment for all our predictors, except for local variation in illumination, given we did not expect this to differently affect treatments or vary through the days. We also added location as a random term, scaled all variables to facilitate model convergence and comparison of effect sizes, and log transformed illumination due to its wide range of variation. To further test how different ecological predictors affected predation of each treatment, we used models with the same structure as described above but analysed data separately for each treatment. These models tested specifically whether variable X had an independent effect on either treatment.

We report the Cox regression coefficient, the hazard value (exp(coef)), the Z statistic and the p-value for each predictor. We used a forest plot of the hazard (relative risk) to visualize the effect sizes and their significance. For all plots in the main text we used the predict_coxme function developed by Johan Junkka (https://github.com/junkka/ehahelper) which estimates predicted risk values from a Cox model with random factors, based on the hazard ratio. Using this custom-made function was necessary because the available *predict* function for cox models does not incorporate random factors. For all plots we predicted values for the mean -1SD and the mean +1SD. For all these plots only the variable of interest was allowed to vary with all other variables in the model kept at mean values, as recommended (*76*).

Supplementary Text

Seasonality relationships

The constant presence of naive predators in non-seasonal environments may increase attack rates on novel warning colored prey. We ran all our experiments before the breeding season but also examined predation in relation to seasonality, given non-seasonal locations can have constant presence of naive predators (*9*). In less seasonal environments, because recruitment is less temporally pronounced, the constant presence of naive predators may hinder the evolution of warning colored prey (*9*). Alternatively, longer average lifespans in less seasonal environments may make predator communities on average better educated (*77*), favoring the evolution of warning colors. Our experiment, however, did not support either hypothesis, finding little evidence for any effect of seasonality on the protective value of crypsis or warning coloration (table S6).

Unpalatable prey experiment

We compared the change in predation risk over experiment days between the unpalatable and the palatable experiments, for each prey type (Fig. S1). For the palatable prey we assumed this to represent the speed at which predators overcome wariness and learn prey are palatable, while for the unpalatable experiment this represents the speed at which predators learn avoidance. We do not report statistical results from these models because the processes in each experiment are opposite (increase in predation vs decrease in predation), and therefore are strongly expected to lead to significant differences in the slope of the relationship. Instead, we focus on interpreting the magnitudes and directions of the slopes between experiments.

Our results, as expected, show that predation risk remained the same or decreased through the days when defended prey had either typical or atypical warning color. This supports previous findings showing that contrasting color patterns are memorable and facilitate learning of avoidance (*6*). In the case of the cryptic treatment, we found that despite it being chemically defended, attacks increased through days. This aligns with the expectation that predation risk would increase rapidly for undefended prey, especially when they are conspicuous, and that this is mirrored in predation risk for defended prey, which is reduced especially for the two conspicuous treatments. This demonstrates that the results of the main experiment using undefended prey can be confidently extrapolated to consider how predator community, prey community, and visual environment are likely to affect defended prey.

Predator Community

Altogether, we recorded 3,143 individuals belonging to 466 avian species across all locations. Individual locations varied in both the number of individuals (median = 127, min. = 36, max. = 365) and the number of species (median = 27, min. = 12, max. = 98).

The dataset of at least partly insectivorous birds used in the predation data analysis contained 2,590 individuals belonging to 353 species, with the number of individuals (median = 121, min. = 33, max. = 291) and species (median = 24, min. = 10, max. = 66) highly variable across locations. This dataset included Passeriformes (312 species), Piciformes (30 species), Cuculiformes (5 species). Coraciiformes (4 species), Bucerotiformes (1 species), and Trogoniformes (1 species). The complete list of all species recorded at each location, numbers of individuals, and species classification as (1) potential target predators, and (2) insectivorous specialists are included in the supplementary dataset.

The avian predator density varied from 17 (Canada) to 146 (Brazil, Serra do Japi), the values of the Shannon diversity index ranged from 1.622 (Canada) to 3.541 (Brazil, Serra do Japi), and the insectivore proportion varied from 0.131 (Wales) to 0.848 (Brazil, Brasília). The location values for all predator community variables are included in table S7.

Neither predator density (predators/km^2) or predator diversity (Shannon index) impacted predation on treatments. However, overall predation risk in high diversity environments was initially high but increased slowly compared to low diversity environments (Fig. S4B).

Since the location teams differed in the level of bird surveying experience, we tested for the effect of the self-assessed bird-identification skills on the predator community variables used in the predation data analysis by comparing highly experienced teams (self-assessment score 1; 10 locations) with less experienced teams (self-assessment score 2 and 3; 11 locations). Team experience affected reported predator density (two-sample Welch t-test: $t = 3.526$, $df = 13$, $p = 0.004$), but there was no evidence it affected the values of the Shannon diversity index ($t = 1.839$, $df = 18$, $p = 0.082$) or the insectivore proportion ($t = 0.283$, $df = 17$, $p = 0.780$). The number of team members participating in the survey was not related to any of the predator community variables ($r < 0.2$ for all variables, Fig S3B).

To evaluate the impact of bird surveying experience on our main results, we re-calculated the two predator community variables that varied significantly (or close to) depending on experience: predator density and diversity. We calculated the difference between the averages of the expert category (score 1) and the less expert teams (scores 2 and 3) for each of the variables (density and diversity) and added that mean difference value to the indices for locations with level 2 and level 3 of experience. This resulted in an increase in metrics for 11 populations, while data for 10 locations remained unchanged, given these were already locations with experts. Using these new variables, we re-run our main model with the same structure explained before. We find that using these two re-calculated variables that consider experience level leads to qualitatively and quantitatively similar results (Fig. S9&11).

Lepidopteran survey results

In total, we obtained GBIF records of 2586 unique lepidopteran species. Number of species per location varied from the set minimum of 50 species (Kenya, USA, Brazil Brasilia, India Buxa, Colombia) up to a maximum of 593 species (Netherlands), with a median of 70 species. In eight locations, the minimal radius size (3 km) returned less than 50 unique species. Increasing the radius size until at least 50 species were returned resulted in a median increased radius of 8.73 km (min. = 3.93 km, max. 90.01 km). Overall, 36% of records were of butterflies and 64% moths, minimizing potential for any biases generated by the dominance of either taxon.

To check the assumption that typical warning coloration was more common than atypical warning coloration, the typical warning/atypical warning prey ratio was calculated as the number of 'typical warning' species divided by the number of 'atypical warning' species for each location. Lepidopterans with 'both typical and atypical warning colors', as well as 'cryptic' and 'other' lepidopterans, were excluded from this calculation. In three localities (Cameroon, New Zealand, Wales), no 'atypical warning' species were present. In the remaining localities, the typical warning/atypical warning ratio ranged from 1.73 (India Buxa) to 22 (Netherlands), with a median of 8.17. Thus, the assumption was met across all locations.

Furthermore, we calculated the typical warning/cryptic prey ratio variable as the number of lepidopteran species classified as 'typical warning' and 'warning with both typical and atypical coloration', divided by the number of species classified as 'cryptic'. The typical warning/cryptic ratio varied between locations (median = 1.10, min. = 0.06, max. = 4.63). It was the highest in Costa Rica, Colombia and Brazil Serra do Japi, and lowest in New Zealand, Wales and the Netherlands. Additionally, the proportion of "other" lepidopterans also varied between locations (median = 14%, min. = 2%, max. = 26%). Species counts of lepidopterans for each location are provided in table S2.

Image analysis results

The effect of illumination was significant for all targets, and targets that were in locations with higher illumination had a higher predation risk. The effect of salience, however, varied depending on the day and the type of prey, as described in the main text (Fig. 5).

Our dataset also showed that there were no differences in illumination across the targets and that cryptic targets had lower levels of salience compared to typical orange and atypical turquoise warning colored targets (β = -0.24, t-value = -58.758, $p < 0.001$; Fig. S13), which were equally salient (β = 0.003, t-value = 0.811, p = 0.459). This indicates that any difference in the rate of learning of the typical and atypical warning colored treatments cannot be attributed to increased salience, which has explained faster learning of orange/red warning colors in previous studies (*78*, *79*).

We also analyzed how levels of illumination and salience varied through the day, for targets with at least two photographs (n=2,422). In support of previous findings (Arenas et al. 2014), we found higher variation in salience through the day for cryptic targets while warning signals were more stable (β = 1.68, t-value = 29.76, $p < 0.001$; Fig. S14). We found no variation across targets in levels of variation in illumination through the day (β cryptic = -0.029, t-value cryptic = -1.825, β atypical warning color = –0.01, t-value = -1.183, p=0.18).

Mealworm size

The mean mealworm size was 22.82 mm with a standard deviation between locations of 2.75 mm. We found a weak association between mealworm size and background predation intensity, such that larger mealworms were predated more in the 'mealworm only' day (p = 0.024), but this link was driven by a single location where slightly larger than average mealworms were used and predation intensity was high. Once this location was removed there was no link between mealworm size and background predation intensity ($\beta = 0.04$, $T = 1.78$, $p = 0.091$). The results of main models remained unchanged if mealworm size was included in the model as covariate, and this variable had no effect on predation risk in the main model.

Nocturnal predation results

To explore the effects of including nocturnal predation in our analysis, we ran the same main model as presented in the main text but instead of censoring nocturnal attacks, we considered them as predation. The model results are similar, but when including night-time predation there is a decreased effect of the visual environment variables (local variation in illumination and local illumination, Fig. S15, table S11). This is expected given that non-visual predators are likely to account for a higher proportion of night-time predation, for which light environment would be irrelevant. Differences in diurnal and nocturnal visual environments and visual predator communities could also contribute differences in predation on treatments, but this would require further investigation.

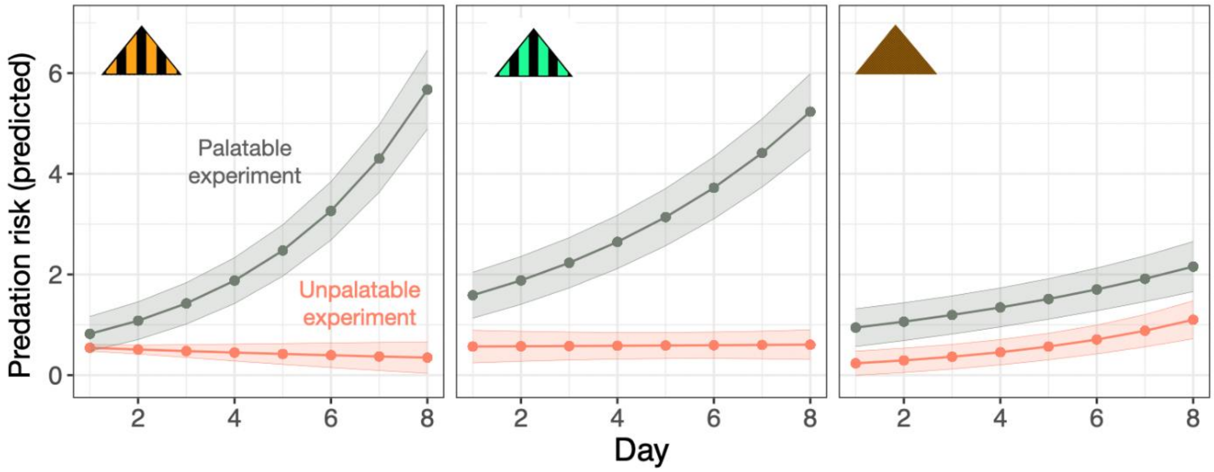
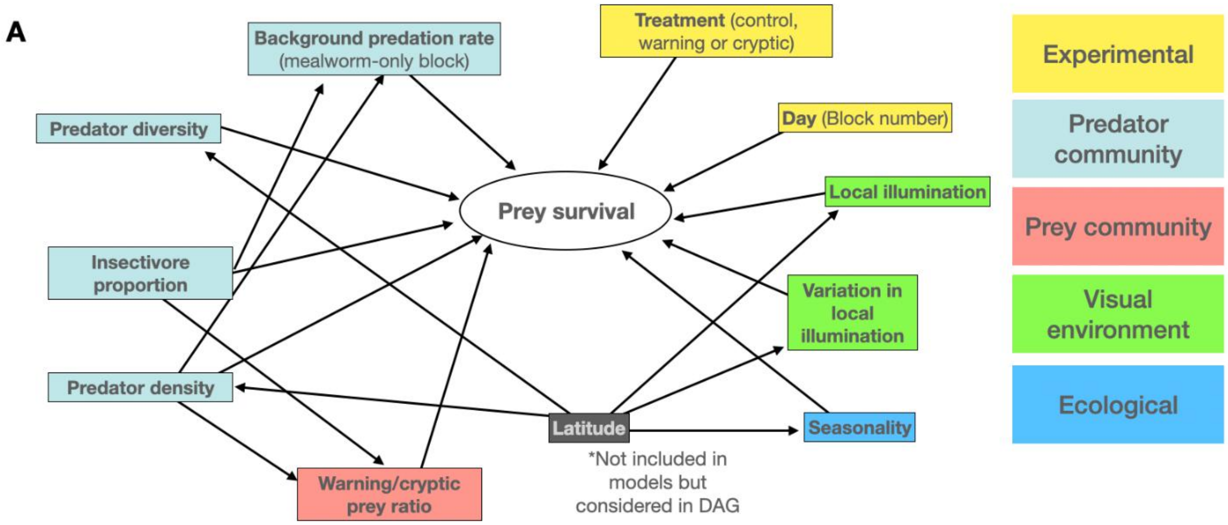


Figure S1. Results of unpalatable predation experiment in comparison with experiment with undefended prey in Czech Republic. For the unpalatable experiment (red line) predation risk was similar at the beginning of the experiment across experiments and targets but decreased or remained unchanged for prey with typical or atypical warning color. For cryptic prey, predation risk increased through the experiment, despite prey being defended.



B

Full model predictors (DAG 1)

Predation intensity x Day x Treatment
Predator diversity x Day x Treatment
Insectivore proportion x Day x Treatment
Predator density x Day x Treatment
Warning/cryptic ratio x Day x Treatment
Local illumination x Day x Treatment
Variation in local illumination
Seasonality x Day x Treatment

C

Reduced model predictors (DAG 2)

~~Predation intensity x Day x Treatment~~
Predator diversity x Day x Treatment
Insectivore proportion x Day x Treatment
Predator density x Day x Treatment
~~Warning/cryptic ratio x Day x Treatment~~
Local illumination x Day x Treatment
Variation in local illumination
Seasonality x Day x Treatment

Figure S2. Global directed acyclic graph (DAG) for Cox regression models. **(A)** We explored which variables could be included in the same model without leading to biasing paths and confounding effects. Because latitude is potentially related to many other predictors, we considered it in our DAG but excluded it from the main models. **(B)** Final set of predictors used in main Cox regression model (results in table S6). **(C)** Second set of predictors used for model (results in table S8).

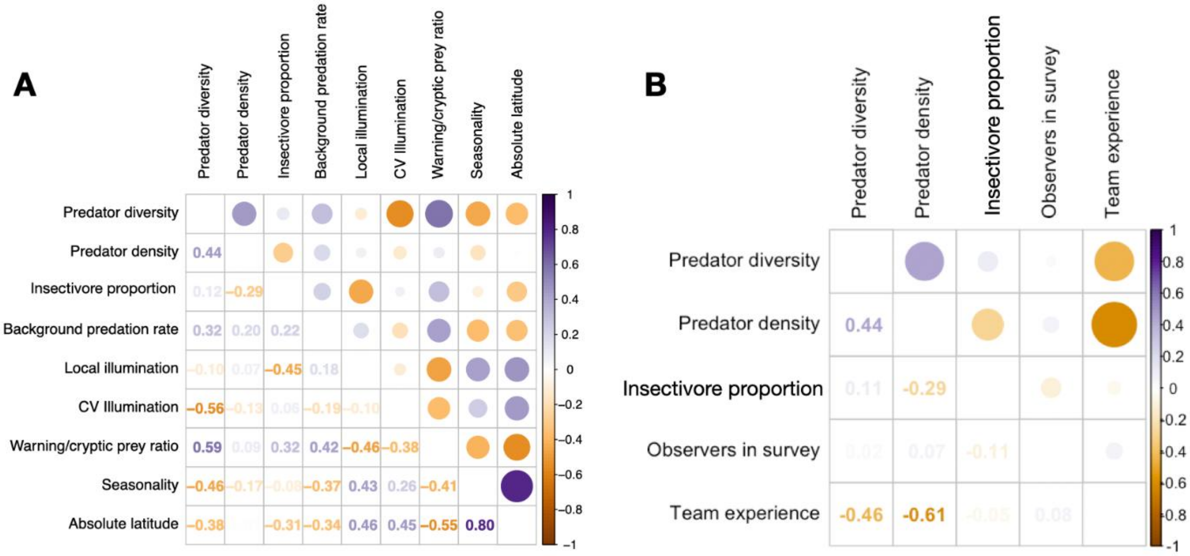


Figure S3. (**A)** Correlation coefficient (r) between predictor variables included in model plus latitude. (**B)** Correlations (r) between predator community variables and level of experience and numbers of observers in bird surveys.

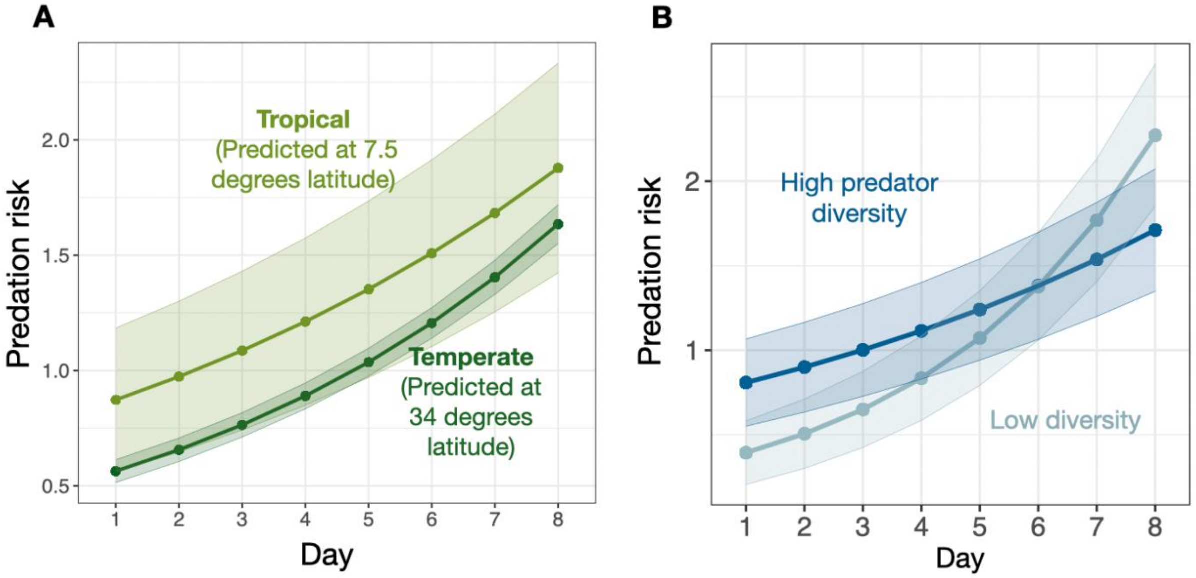


Figure S4. (A) Differences in predicted predation risk using one sample tropical and one sample temperate location (mean latitude + and - SD) according to a reduced model for prediction that included only latitude and experimental day. Treatment was not included because it had no effect on the model. Predicted values for tropical regions have larger confidence intervals because there are fewer locations compared to temperate regions. **(B)** Increase in predation rate through the experiment for locations with high and low predator diversity, as calculated from Shannon Diversity Index.

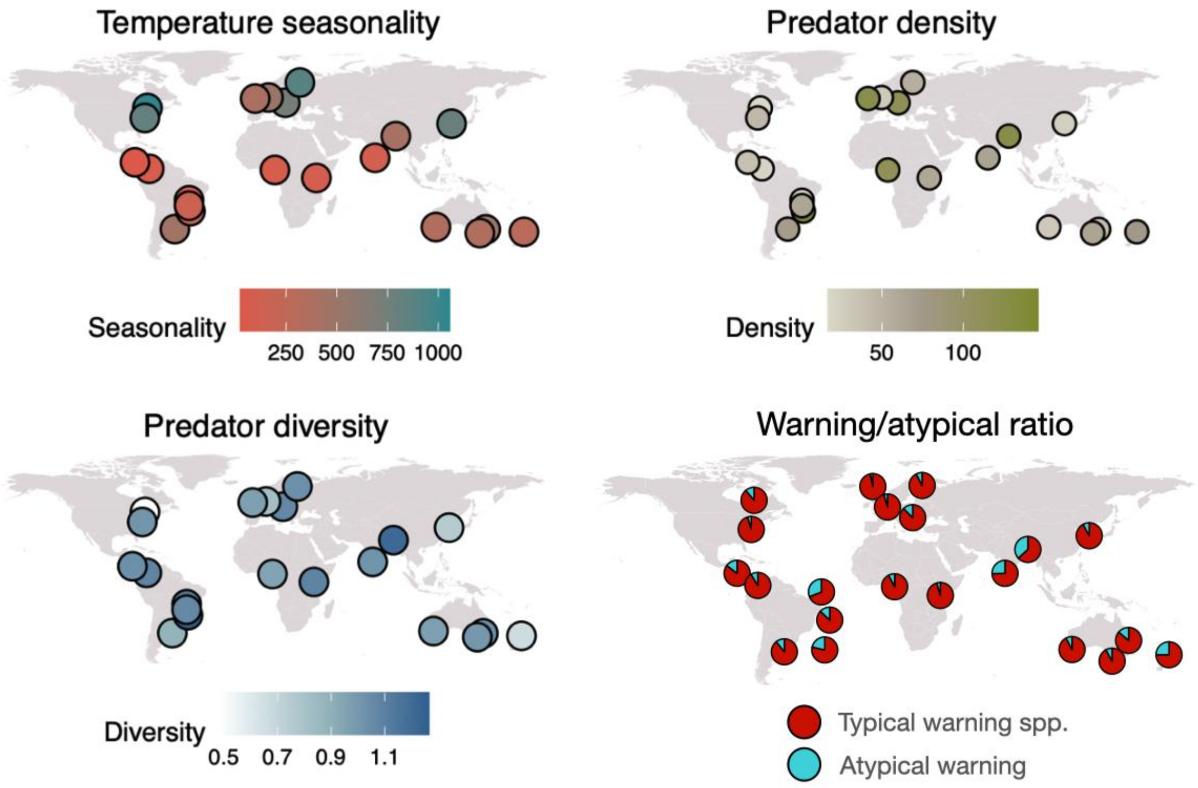


Figure S5. Global variation in predictor variables not presented in main figures.

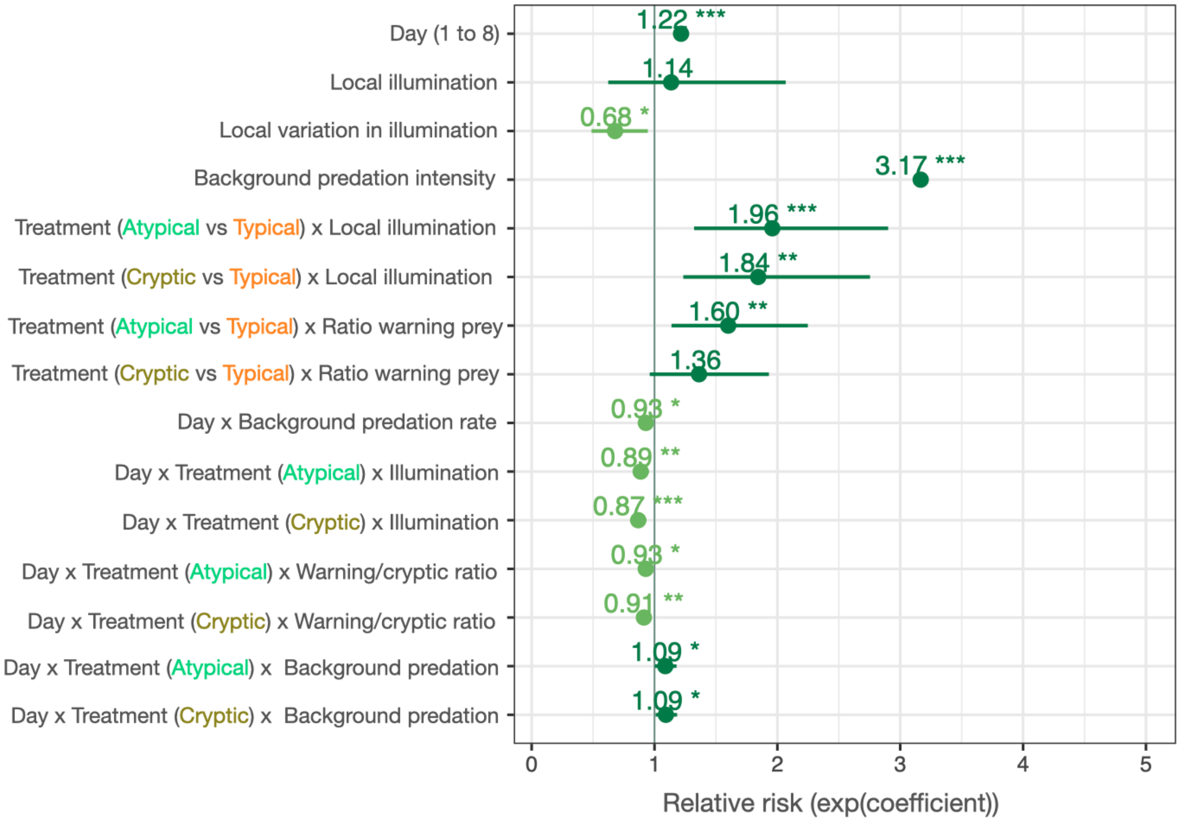


Figure S6. Results for model constructed following global DAG. Forest plot shows only variables for which estimates were reliable according to the DAG design and that included significant results. Variables not present were not significant or could not be estimated accurately from this model and are estimated in Fig. S10, full results in table S6. Higher relative risk represents higher risk of predation. If not specified due to space, level of comparison for treatment was always the typical warning color. Error bar for background predation intensity not presented because it reached relative risk values beyond 5. Asterisks represent significance of p-values, * < 0.05, ** < 0.01, *** < 0.001.

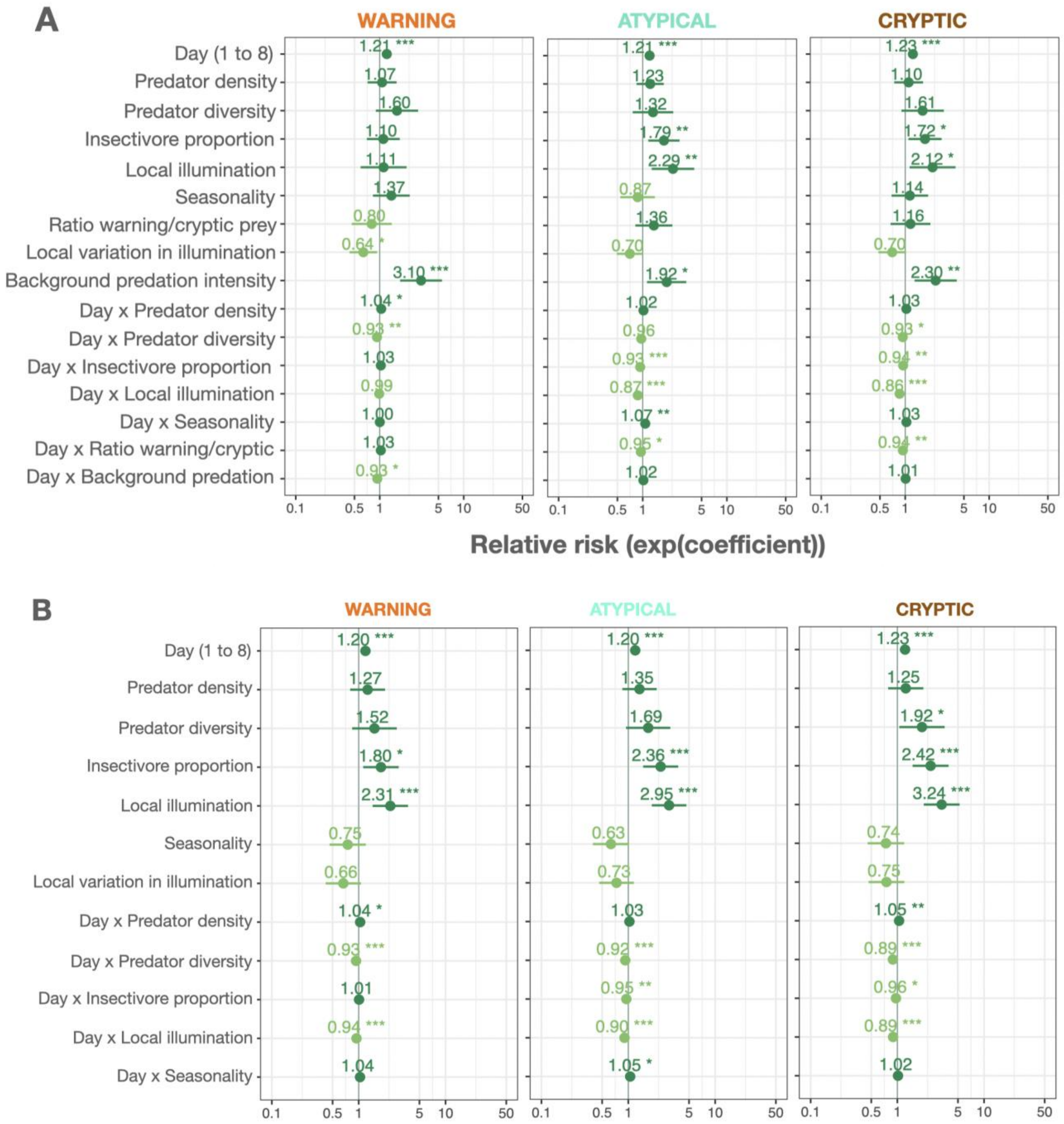
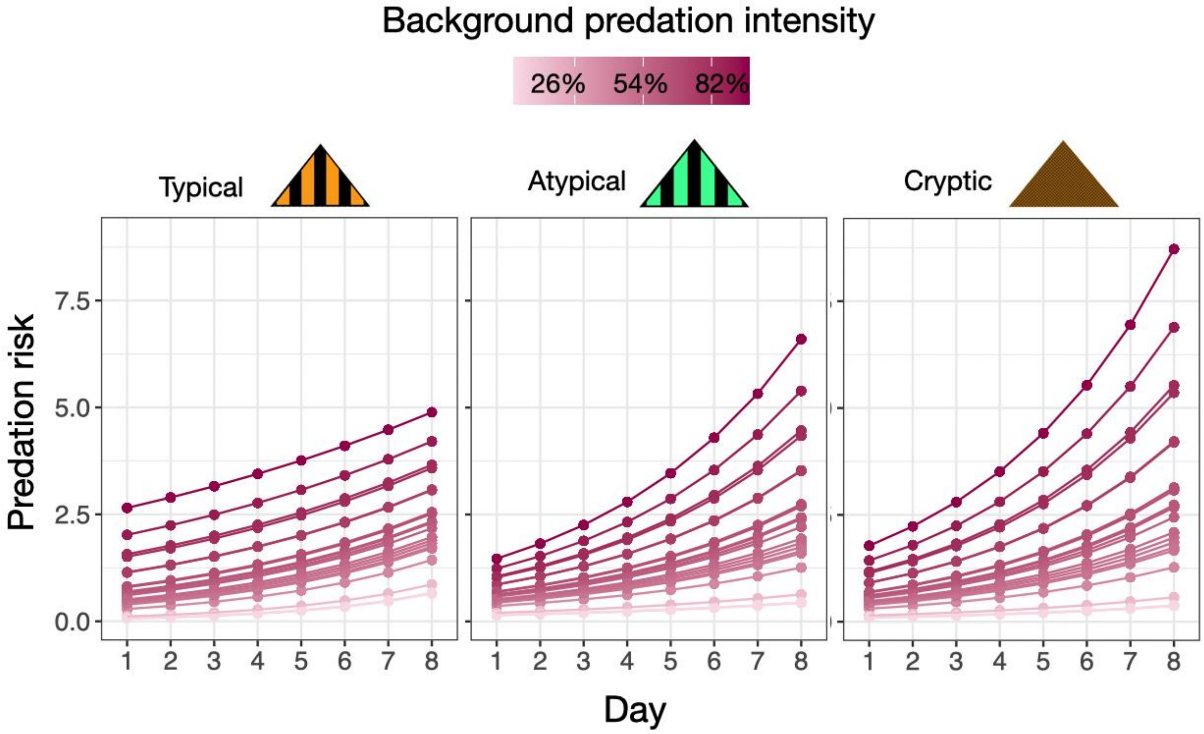


Figure S7. Results for the global model separating the analysis by treatment, for the main model (global DAG with all variables) and the second model. **(A)** As seen in the main results, background predation intensity has a larger effect on predation risk of prey with typical warning colors compared to atypical warning colors or cryptic colors. Illumination does not affect typical warning colored prey, but higher illumination significantly increases predation risk for atypical warning and cryptic targets. The effect of prevalence of alternate typical warning prey depends on the block number, but in general has a stronger effect on atypical and cryptic targets. **(B)** The effect of insectivore proportion is stronger for atypical and cryptic targets, and it is consistent for typical targets through the experiment but increases for atypical and cryptic targets. Asterisks represent significance of p-values, * < 0.05, ** < 0.01, *** < 0.001.



1240 **Figure S8.** Effect of background predation intensity on each treatment, when using predictions from independent models for each type of target (Fig. S7). At the beginning of the experiment, predation intensity has the largest effect on the typical warning colored treatment, with risk of predation being the highest in communities with high predation intensity.

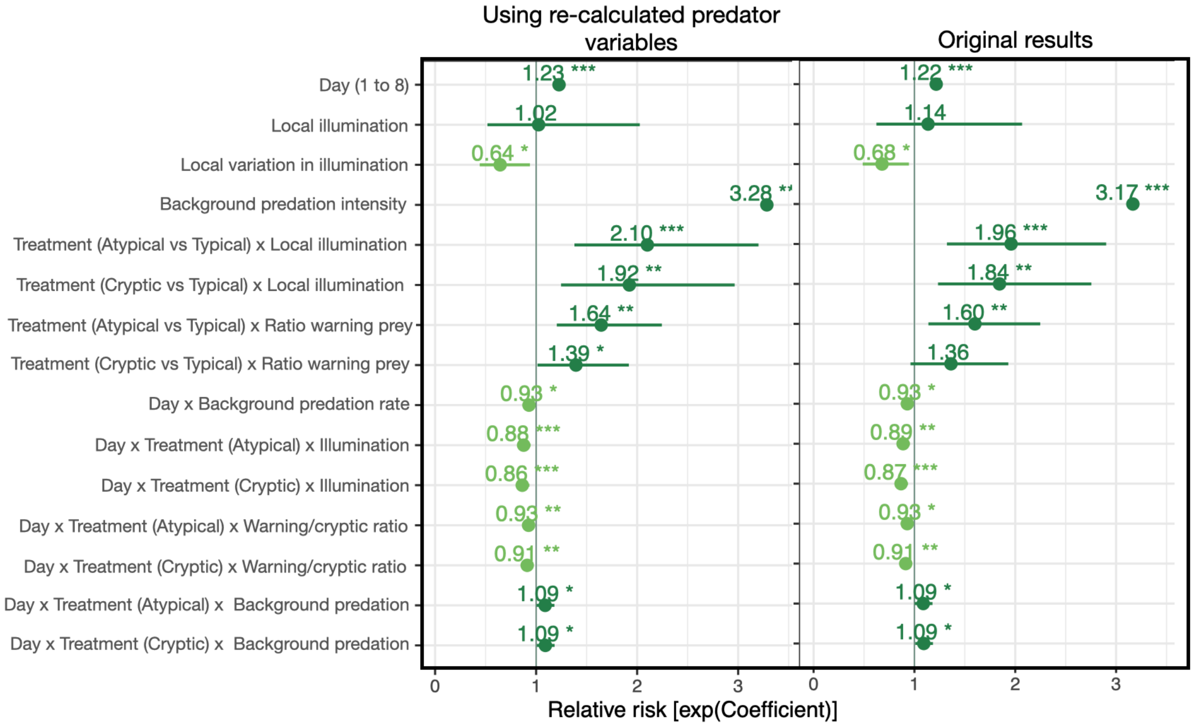


Figure S9. Results for model constructed following the global DAG but using re-calculated measures of predator density and diversity that take into account surveyor experience. The forest plot shows only variables for which estimates were reliable according to the DAG design and that included significant results. Variables not present were not significant. Higher relative risk values represent higher risk of predation. Results remain relatively unchanged when compared to the main model presented in the manuscript (on the right side of the graph).

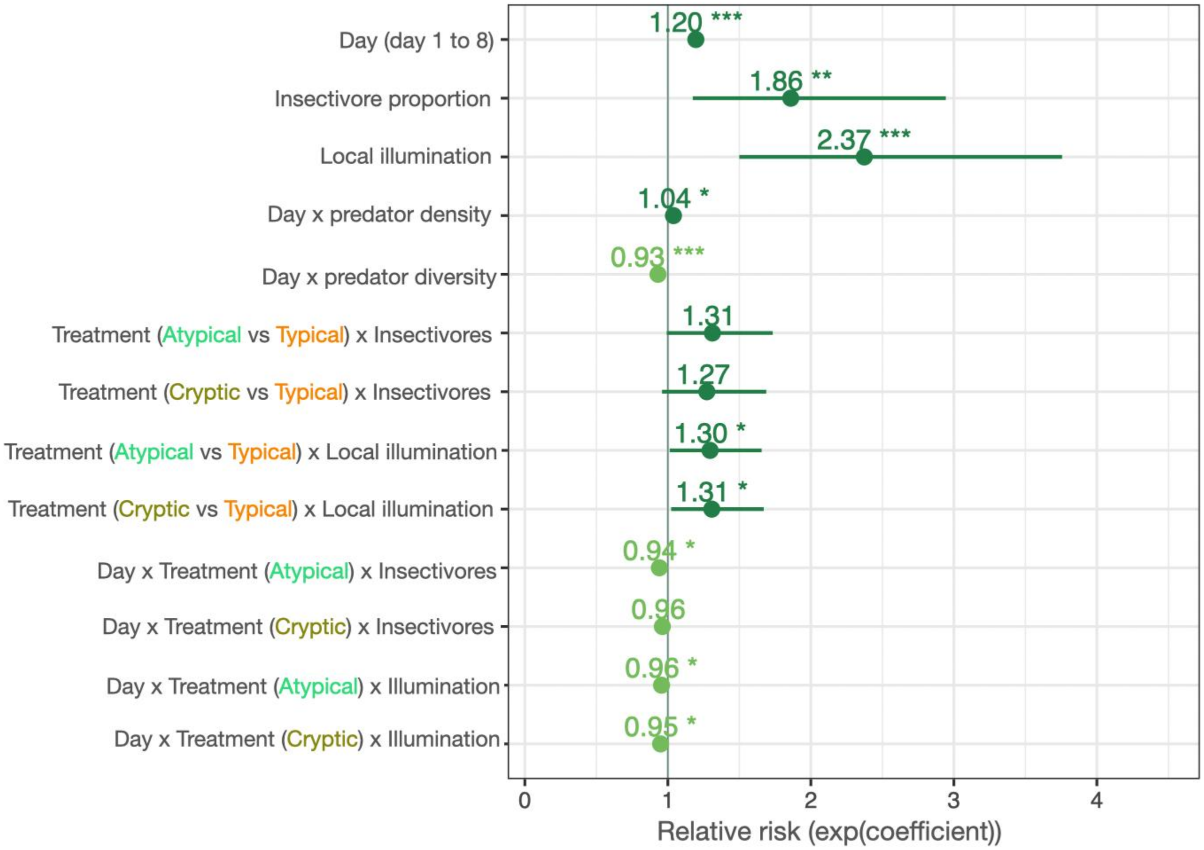


Figure S10. Results for the second model constructed following the global DAG, removing two variables 1255 from the full model that led to biasing paths. Forest plot shows only variables for which estimates were reliable according to the DAG design and that included significant results. Variables not present were not significant, full results in table S8. Higher relative risk represents higher risk of predation. If not specified, level of comparison for treatment was always the typical warning color.

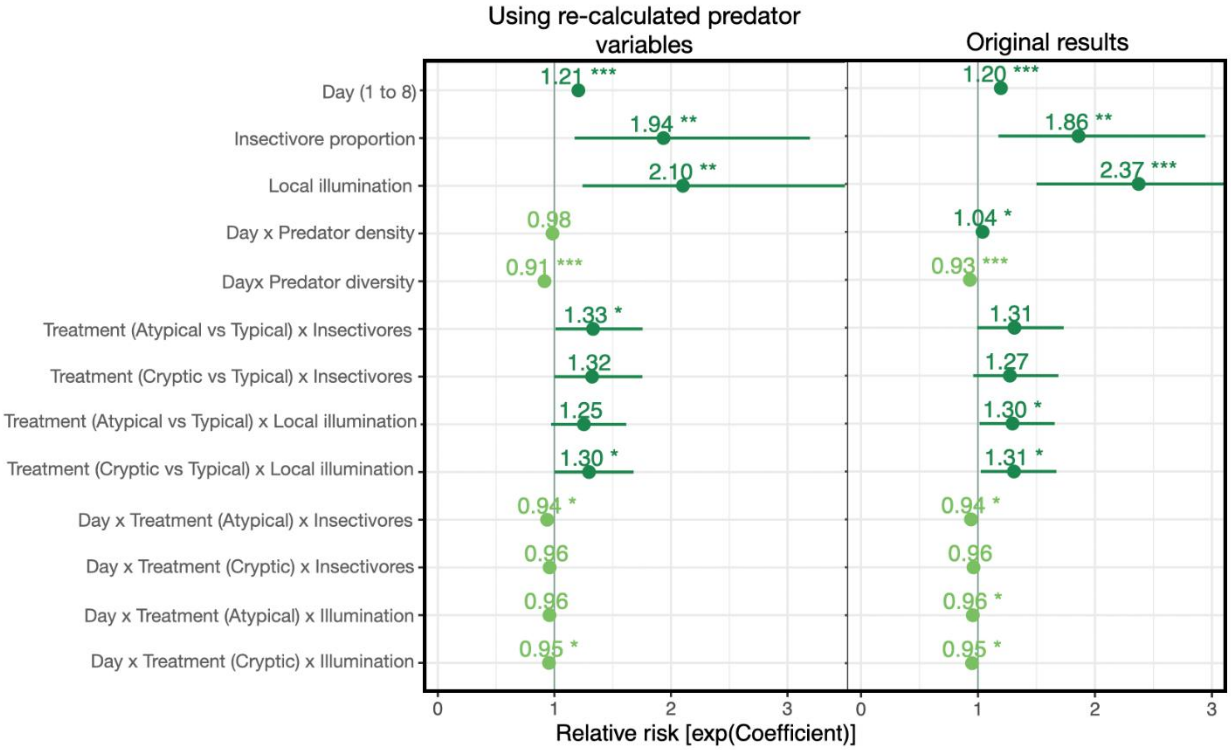


Figure S11. Results for model constructed following second DAG structure but using re-calculated measures of predator density and diversity that take into account surveyor experience. Forest plot shows only variables for which estimates were reliable according to the DAG design and that included significant results. Variables not present were not significant. Higher relative risk values represent higher risk of predation. Results remain similar relative to the main model presented in the manuscript (on the right side of the graph).

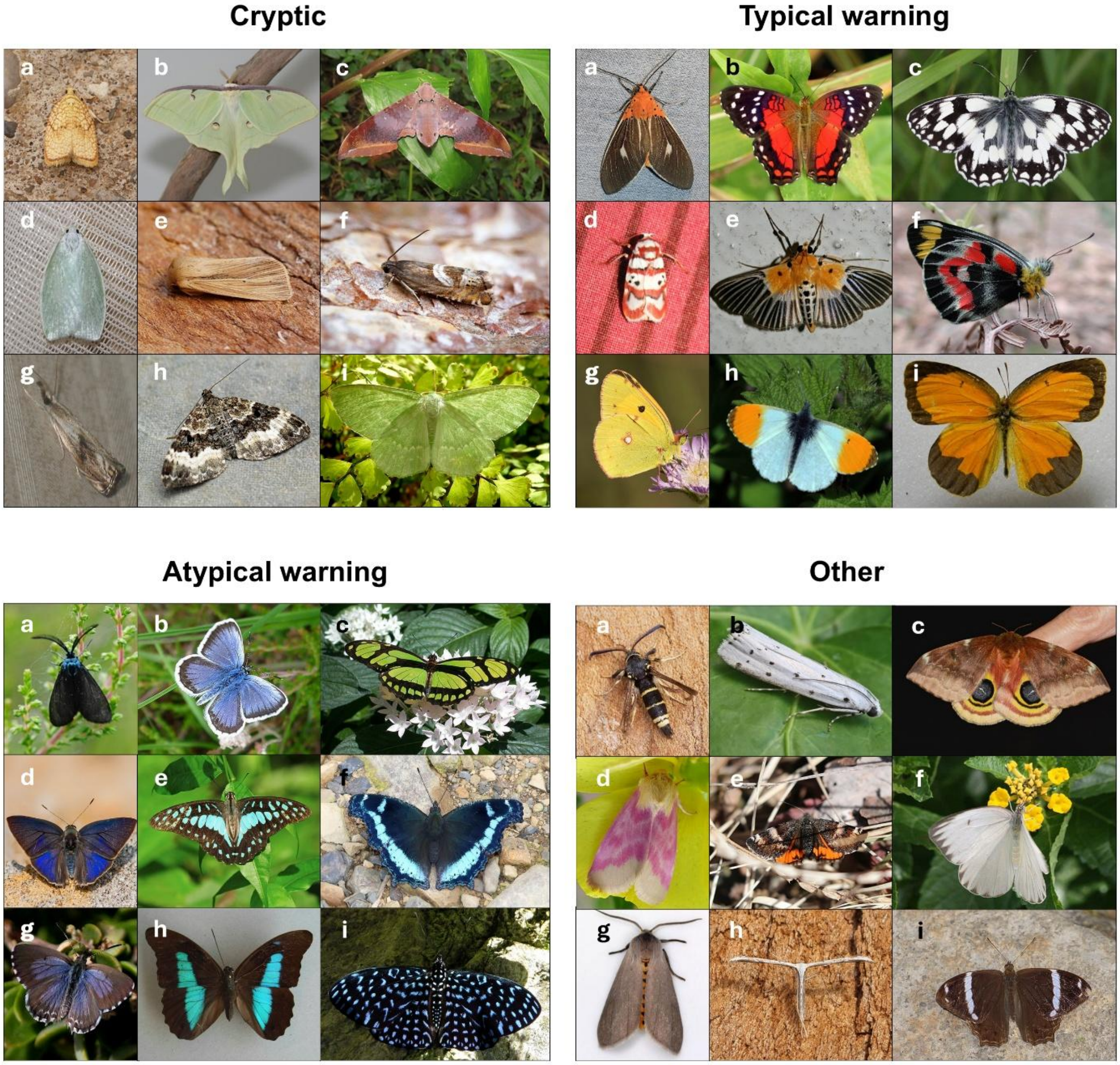


Figure S12. Examples of lepidopteran species that met the criteria for each color category.

Cryptic: a) *Acleris forsskaleana* by Ben Sale (CC BY 2.0), b) *Actias luna* by Megan McCarthy (CC BY 3.0), c) *Ambulyx moorei* by Vinayaray (CC BY-SA 4.0), d) *Nymphostola galactina by* Possums' End (CC BY 4.0), e) *Mythimna impura* by Ben Sale (CC BY 2.0), f) *Graptolita jungiella* by Ben Sale (CC BY 2.0), g) *Catoptria verellus* by Ilia Ustyantsev (CC BY-SA 2.0), h) *Epirrhoe alternata* by Ben Sale (CC BY 2.0), i) *Geometra papilionaria* by Gailhampshire (CC BY 2.0).

Typical warning: a) *Asota producta* by Yaklovlev Alexey (CC BY-SA 2.0), b) *Anartia amathea* by Charles J. Sharp (CC BY-SA 4.0), c) *Melanargia galathea* by Charles J. Sharp (CC BY-SA 4.0), d) *Cyana peregrina* by Praveenp (CC BY-SA 4.0), e) *Nevrina procopia* by Yakovlev Alexey (CC BY-SA 2.0), f) *Delias harpalice by* Neil Hamilton (CC BY-SA 3.0), g) *Abaeis nicippe* by Julio A Genaro (copyright-free), h) *Colias croceus* by Zeinel Cebeci (CC BY-SA 4.0), i) *Anthocharis cardamines by* Charles J Sharp (CC BY SA 3.0).

Atypical warning: a) *Rhagades pruni* by Rick Geling (CC BY 3.0), b) *Plebejus argus* by Gailhampshire (CC BY 2.0), c) *Philaethria dido* by Cyndy Sims Parr (CC BY-SA 2.0), d) *Rapala manea* by Anitava Roy (CC BY-SA 4.0) , e) *Graphium doson* by Tamaghna Sengupta (CC BY-SA 3.0), f) *Kaniska canace* by Atanu Bose Photography (CC BY-SA 4.0), g) *Theclinesthes serpentata* by Geoffrey Cox (CC BY 4.0), h) *Prepona pylenes* by Notafly (CC BY-SA 3.0), i) *Hamadryas arete* by Carlos Zikan (CC BY-SA 4.0).

Other: a) *Paranthrene tabaniformis* by Ben Sale (CC BY 2.0), b) *Myelois circumvoluta* by © Entomart, c) *Automeris io* by Andy Reago and Chrissy McClarren (CC BY 2.0), d) *Schinia florida* by Christian Grenier (CC0 1.0), e) *Archiearis infans* by Rob Foster (CC BY 4.0), f) *Ascia monuste* by Anne Toal (CC BY 2.0), g) *Euchaetes egle* by Patrick Coin (CC BY-SA 2.5), h) *Emmelina monodactyla* by Ben Sale (CC BY 2.0), i) *Lethe confusa* by Subhendukhan (CC BY-SA 4.0).

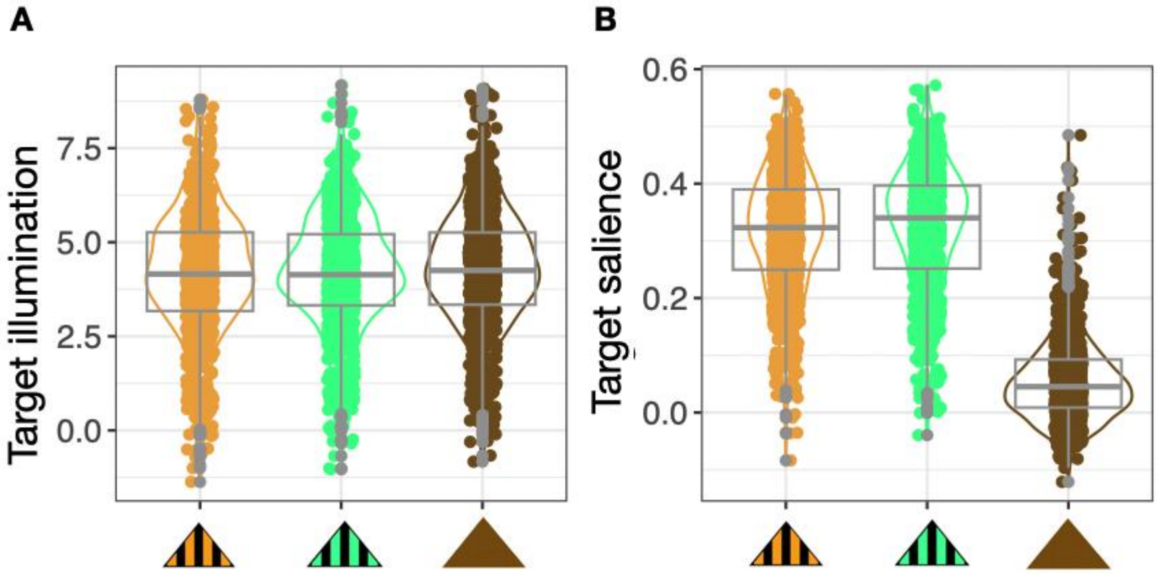


Figure S13. Variation in **(A)** target illumination and **(B)** salience for the three targets across all locations. There were no differences in the illumination environment of where each treatment was placed, but cryptic targets were less salient.

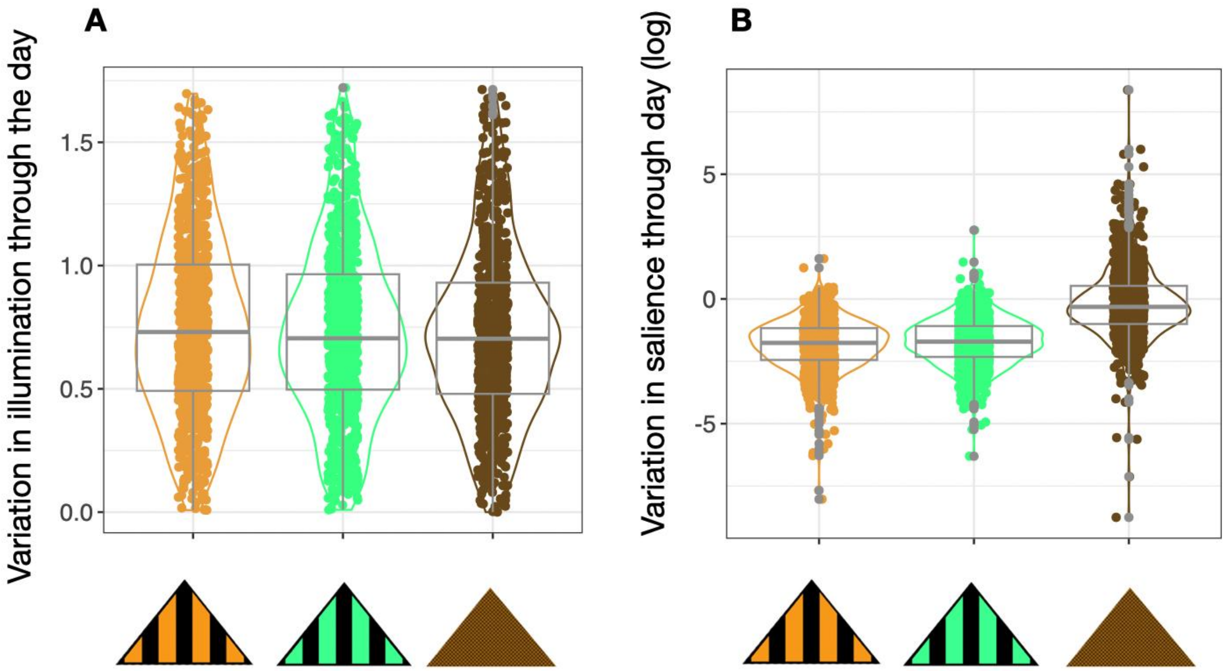


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Figure S14. Distribution of diurnal variation in **(A)** illumination and **(B)** salience. The salience of the cryptic treatment was more affected by diurnal variation in lighting.

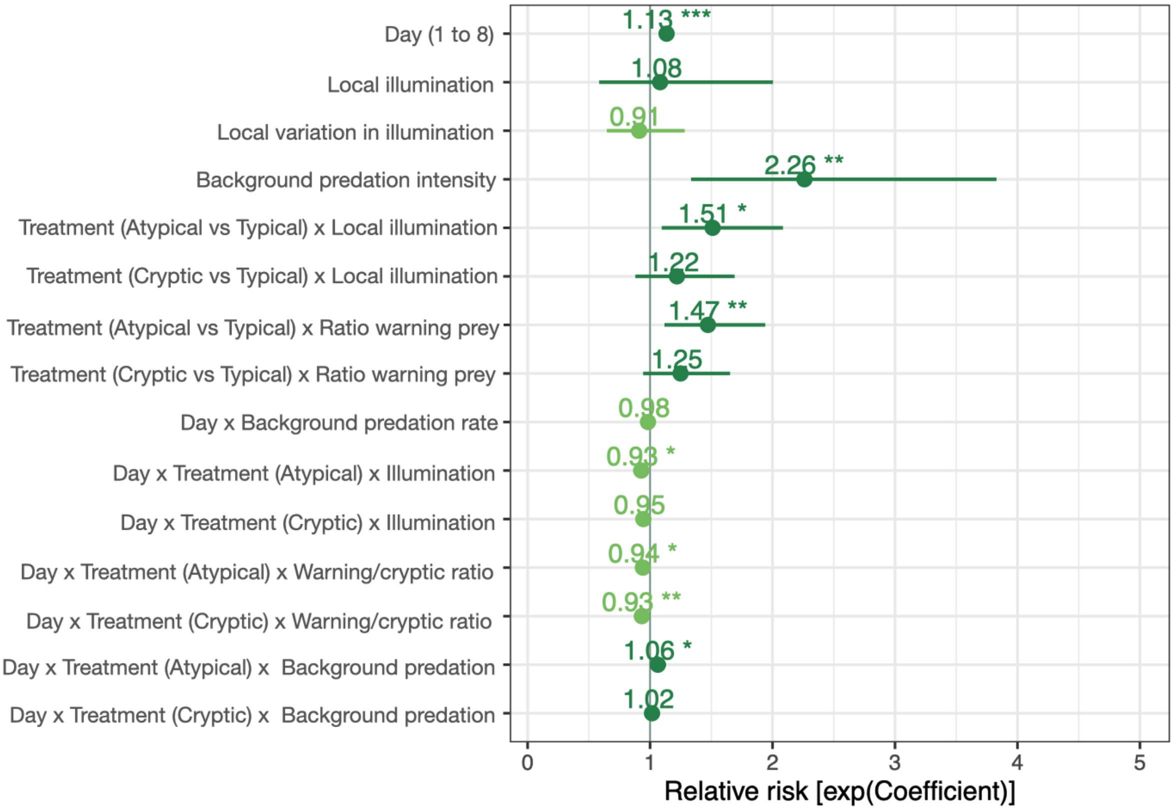

Figure S15. Results for model constructed following global DAG but without censoring night time attacks. 1310 For comparison, this forest plot shows only variables for which estimates were reliable according to the DAG design and that included significant results for the main model in the manuscript, without night attacks. Higher X values represent higher risk of predation.

Table S1. Experimental locations and timings.

Site Name	Latitude	Longitude	Start date	End date
Reserva Natural El Destino, Partido de Magdalena, Buenos Aires Province	-35.1441	-57.3733	17/09/2021	25/09/2021
Campbell Park Woodland, Australian Capital Territory	-35.2791	149.1756	26/09/2020	7/10/2020
100 Acres Reserve, Park Orchards, Victoria	-37.775	145.2252	22/09/2021	2/10/2021
Wilga State Forest, Western Australia	-33.7637	116.0686	28/09/2020	5/10/2020
Reserva Ecológica do IBGE	-15.9321	-47.8846	23/07/2021	31/07/2021
Serra do Japi, Jundiaí, State of São Paulo	-23.2313	-46.966	8/1/2022	17/01/2022
Vale Encantado Uberaba, State of Minas Gerais	-19.5504	-47.8998	12/10/2021	22/10/2021
Mount Cameroon National Park, Buea	4.1417	9.1171	23/01/2022	31/01/2022
NCC Greenbelt, Ottawa, Ontario	45.3389	-75.6126	11/5/2021	19/05/2021
Reserva Paraíso Andino-La vega Cundinamarca	4.9494	-74.3704	21/01/2021	29/01/2021
Refugio Nacional de Vida Silvestre Hacienda Barú, Puntarenas	9.2599	-83.8735	11/1/2021	19/01/2021
Podyjí National Park, Znojmo	48.827	16.0098	26/04/2021	4/5/2021
Laajavuori, Jyväskylä	62.2616	25.6933	8/6/2020	17/06/2020
Rajabhatkhawa, Buxa Tiger Reserve, West Bengal	26.6503	89.4406	21/11/2021	29/11/2021
Honey Valley, Kodagu, Karnataka	12.219	75.6562	21/10/2021	30/10/2021
Brackenhurst Conference Centre, Limuru	-1.1236	36.6756	25/03/2022	4/2/2022
Het Amsterdam Bos, Amstelveen	52.3159	4.8252	27/05/2021	6/6/2021
Waitakere Ranges Regional Park, Auckland	-36.9181	174.5407	15/11/2021	27/11/2021
Pyeongbawi, Jeollanam-do	34.9098	126.4451	17/04/2021	25/04/2021
Fountainhead Regional Park, Virginia	38.7179	-77.3162	5/5/2021	16/05/2021
Clyne Valley Country Park, Swansea	51.6142	-4.0158	8/3/2021	18/03/2021

Table S2. Species counts and ratios of lepidopteran coloration for each location. The typical warning/cryptic species ratio was calculated as the number of lepidopteran species classified as ‘typical warning’ and ‘warning with both typical and atypical coloration’, divided by the number of species classified as ‘cryptic’. The typical warning/atypical warning species ratio was calculated as the number of ‘typical warning’ species divided by the number of ‘atypical warning’ species for each location, while species with ‘both typical and atypical warning coloration’ were excluded from this calculation.

Location	Radius (km)	Number of cryptic species	Number of typical warning species	Number of atypical warning species	Number of warning species that have both typical and atypical color	Number of other species	Total number of species	Typical warning /cryptic species ratio	Typical warning/ atypical warning species ratio
Argentina	3	21	25	3	3	18	70	1.33	8.33
Australia East	3	205	50	8	4	31	298	0.26	6.25
Australia South	3	122	35	3	1	16	177	0.30	11.67
Australia West	23.5	33	12	1	0	8	54	0.36	12
Brazil Brasilia	7.2	10	20	9	5	6	50	2.50	2.22
Brazil Serra do Japi	3	42	110	30	19	28	229	3.07	3.67
Brazil Uberaba	90	13	27	4	8	9	61	2.69	6.75
Cameroon	7.4	33	12	0	0	6	51	0.36	-
Canada	3	44	40	5	0	23	112	0.91	8
Colombia	6.6	9	21	2	11	7	50	3.56	10.5
Costa Rica	3	8	29	5	8	14	64	4.63	5.8
Czech Republic	3	15	35	5	2	13	70	2.47	7
Finland	3	426	49	4	3	48	530	0.12	12.25
India Buxa	10	8	19	11	5	7	50	3.00	1.73
India Honey Valley	3	48	44	15	9	23	139	1.10	2.93
Kenya	12.9	15	21	1	2	11	50	1.53	21
Netherlands	3	481	44	2	1	65	593	0.09	22
New Zealand	3	49	3	0	0	1	53	0.06	-
South Korea	3	129	35	3	1	29	197	0.28	11.67
USA	3.9	14	21	1	1	13	50	1.57	21
Wales	3	443	30	0	1	59	533	0.07	-

Table S3. Total number of attacks and proportion per target treatment at each location.

Location	Typical	Atypical	Cryptic	Prop. Typical	Prop. Atypical	Prop. Cryptic	Total Attacks
Argentina	55	55	53	0.34	0.34	0.33	163
Australia East	105	102	105	0.34	0.33	0.34	312
Australia South	22	18	21	0.36	0.30	0.34	61
Australia West	99	96	88	0.35	0.34	0.31	283
Brazil Brasilia	75	86	73	0.32	0.37	0.31	234
Brazil Serra do Japi	53	52	58	0.33	0.32	0.36	163
Brazil Uberaba	63	64	61	0.34	0.34	0.32	188
Cameroon	97	92	68	0.38	0.36	0.26	257
Canada	27	23	20	0.39	0.33	0.29	70
Colombia	30	24	23	0.39	0.31	0.30	77
Costa Rica	71	79	78	0.31	0.35	0.34	228
Czech Republic	98	130	150	0.26	0.34	0.40	378
Finland	17	19	10	0.37	0.41	0.22	46
India Buxa	47	56	57	0.29	0.35	0.36	160
India Honey Valley	19	13	15	0.40	0.28	0.32	47
Kenya	5	8	14	0.19	0.30	0.52	27
Netherlands	3	3	3	0.33	0.33	0.33	9
New Zealand	12	8	11	0.39	0.26	0.35	31
South Korea	8	15	9	0.25	0.47	0.28	32
USA	83	83	74	0.35	0.35	0.31	240
Wales	83	82	76	0.34	0.34	0.32	241

Table S4. Summary of experimental variables measured, and predictions tested. Numbers in square brackets denote the section of the Materials and Methods reporting variable data collection.

Variable	Description	Units/levels	Key predictions
Predation risk	Estimated hazard ratio based on the parametrized model, also referred in some instances as “attack rate”. Predation risk values in plots represent the risk of predation where the reference level (typical warning target) of the treatment variable is given a baseline risk of 1.	Relative risk, from 0 to 8 in our models.	
Treatment	Target color pattern.	Typical warning Atypical warning Cryptic	Cryptic advantage as crypsis is the more common strategy globally (*9*, *10*).
Day	Day of experiment.	Ordinal 1:8	Predation on undefended prey to increase over time (overcoming wariness, learning).
Background predation intensity [3.6]	Proportion of mealworms taken during the ‘mealworm-only’ experiment.	0.023 to 0.97	Disadvantage for warning color due to predator competition/hunger eliminating novel potentially defended morphs (*2*).
Predator density [5]	Abundance of birds per km.	17 to 146 individuals	Advantage for undefended warning color as greater density reduces per-predator encounters, slowing population learning (*2*).
Predator diversity [5]	Shannon diversity index.	1.621 to 3.540	
Insectivore proportion [5]	Proportion of birds with at least 60% of invertebrates in diet (Wilman et al. 2014).	0.13 to 0.85	Disadvantage for undefended warning color as insectivorous predators are more able to overcome assumed defenses (*25*, *27*, *80*).
Seasonality [5]	Variation in temperature across months. Extracted from Bioclim (BIO4).	235 to 10,560 (dimensionless CV)	1.) Advantage for undefended warning color with increased seasonality, as fewer naive predators present (*9*, *34*). 2.) Advantage for warning colored prey in less seasonal tropical environments, as longer lifespans make predators on average more educated (*77*).
Warning/ cryptic prey ratio [4]	Ratio of the percentage of lepidopteran species recorded at each location classified as typical warning colored divided by the percentage of cryptic species.	0.061 to 4.624	1.) Undefended typical warning prey advantaged when typical warning signals are abundant due to generalization (*29*, *30*). 2.) Undefended warning prey disadvantaged when warning signals are common due to foraging need (*4*, *41*). 3.) Cryptic prey disadvantaged when cryptic

			prey are common due to predator performance (e.g. search images) (*28*).
Target illumination [6]	Illumination on target estimated from photographic standard measurements.	Relative radiometric intensity	1.) Warning colored prey advantaged relative to cryptic prey in high illumination as strategy is more effective with reduced visual noise (*42*). 2.) Camouflage prey decline in performance rapidly in low light environments because they lack dynamic shadows (*43*). 3.) Undefended warning prey decline in performance rapidly in bright environments as signals easier to learn (*44*, *45*)
Location illumination [6]	Mean target illumination for noon photos at each location.	Relative radiometric intensity 3.532 to 7.284	
Target salience [6]	Salience of target against the background bark, estimated from photographs.	-0.121 to 0.571	Attack rates on cryptic prey increases with increasing target salience while attack rates on warning colored prey should decrease with increasing target salience.

Table S5. Model results for link between latitude (absolute value) and predation of targets. Treatment is not included in the model presented below because it did not have a significant effect ($p > 0.1$). Model presented below was used for predictions in plot S6.

Predictor	β	exp(β)	se(β)	z	p-value
Latitude (absolute value)	-0.018	0.098	0.014	-1.22	0.220
Day (1 to 8)	0.097	1.102	0.016	5.88	< 0.001
Latitude x Day	0.002	1.001	0.0004	3.23	0.001

Table S6. Results for global DAG. Significant parameters highlighted in blue (those that could be reliably estimated from the model when treated as exposure variables).

Predictor	β	exp(β)	se(β)	z	p-value
Treatment (atypical vs typical warning)	-0.09	0.91	0.15	-0.63	0.53
Treatment (cryptic vs typical warning)	-0.11	0.90	0.14	-0.74	0.46
Day (block number 1 to 8)	**0.20**	**1.22**	**0.02**	**11.05**	**< 0.001**
Predator density	0.07	1.07	0.19	0.36	0.72
Predator diversity (Shannon diversity index)	0.49	1.63	0.28	1.74	0.08
Insectivore proportion	0.12	1.13	0.22	0.54	0.59
Mean local illumination (log)	0.13	1.14	0.31	0.41	0.68
Seasonality in temperature	0.28	1.33	0.25	1.16	0.25
Warning/cryptic prey ratio	-0.19	0.83	0.27	-0.70	0.48
Variation in local illumination	**-0.39**	**0.68**	**0.17**	**-2.29**	**0.02**
Background predation rate	**1.15**	**3.17**	**0.28**	**4.13**	**< 0.001**
Treatment (atypical vs typical warning) x Day	0.00	1.00	0.03	-0.10	0.92
Treatment (cryptic vs typical warning) x Day	0.01	1.01	0.02	0.53	0.59
Treatment (atypical vs typical warning) x predator density	0.13	1.14	0.13	0.97	0.33
Treatment (cryptic vs typical warning) x predator density	0.02	1.02	0.13	0.16	0.87
Day x Predator density	0.04	1.04	0.02	2.46	0.01
Treatment (atypical vs typical warning) x predator diversity	-0.12	0.88	0.22	-0.56	0.58
Treatment (cryptic vs typical warning) x predator diversity	-0.01	0.99	0.23	-0.03	0.98
Day x Predator diversity	-0.08	0.93	0.03	-2.86	< 0.001
Treatment (atypical vs typical warning) x insectivore proportion	0.47	1.60	0.16	2.90	< 0.001
Treatment (cryptic vs typical warning) x insectivore proportion	0.41	1.51	0.16	2.50	0.01
Day x insectivore proportion	0.03	1.03	0.02	1.42	0.15
Treatment (atypical vs typical warning) x local illumination	**0.67**	**1.96**	**0.20**	**3.35**	**< 0.001**
Treatment (cryptic vs typical warning) x local illumination	**0.61**	**1.84**	**0.20**	**2.99**	**< 0.001**
Day x local illumination	-0.01	0.99	0.03	-0.47	0.64
Treatment (atypical vs typical warning) x seasonality	-0.29	0.75	0.18	-1.59	0.11
Treatment (cryptic vs typical warning) x seasonality	-0.21	0.81	0.18	-1.15	0.25
Day x Seasonality	0.00	1.00	0.02	-0.04	0.97
Treatment (atypical vs typical warning) x warning/cryptic prey ratio	**0.47**	**1.60**	**0.17**	**2.71**	**0.01**

Treatment (cryptic vs typical warning) x warning/cryptic prey ratio	0.31	1.36	0.18	1.74	0.08
Day x warning/cryptic prey ratio	0.03	1.03	0.02	1.21	0.23
Treatment (atypical vs typical warning) x background predation rate	-0.41	0.66	0.23	-1.79	0.07
Treatment (cryptic vs typical warning) x background predation rate	-0.40	0.67	0.23	-1.77	0.08
Day x background predation rate	**-0.07**	**0.93**	**0.03**	**-2.52**	**0.01**
Treatment (atypical vs typical warning) x Day x density	-0.02	0.98	0.02	-0.88	0.38
Treatment (cryptic vs typical warning) x Day x density	-0.01	0.99	0.02	-0.37	0.71
Treatment (atypical vs typical warning) x Day x diversity	0.03	1.03	0.04	0.73	0.47
Treatment (cryptic vs typical warning) x Day x diversity	0.01	1.01	0.04	0.17	0.86
Treatment (atypical vs typical warning) x Day x insectivore proportion	-0.10	0.91	0.03	-3.39	< 0.001
Treatment (cryptic vs typical warning) x Day x insectivore proportion	-0.08	0.92	0.03	-2.86	< 0.001
Treatment (atypical vs typical warning) x Day x local illumination	**-0.12**	**0.89**	**0.04**	**-3.23**	**< 0.001**
Treatment (cryptic vs typical warning) x Day x local illumination	**-0.14**	**0.87**	**0.04**	**-3.75**	**< 0.001**
Treatment (atypical vs typical warning) x Day x seasonality	0.06	1.06	0.03	1.86	0.06
Treatment (cryptic vs typical warning) x Day x seasonality	0.04	1.04	0.03	1.23	0.22
Treatment (atypical vs typical warning) x Day x warning/cryptic prey ratio	**-0.07**	**0.93**	**0.03**	**-2.34**	**0.02**
Treatment (cryptic vs typical warning) x Day x warning/cryptic prey ratio	**-0.09**	**0.91**	**0.03**	**-2.78**	**0.01**
Treatment (atypical vs typical warning) x Day x background predation rate	**0.08**	**1.09**	**0.04**	**2.04**	**0.04**
Treatment (cryptic vs typical warning) x Day x background predation rate	**0.09**	**1.09**	**0.04**	**2.16**	**0.03**

Table S7. Predator community metrics for each location. Predator density (abundance of birds per km), predator diversity (Shannon diversity index), insectivore proportion (proportion of individuals belonging to species with at least 60% of invertebrates in diet; Wilman et al. 2014), number of observers, and team bird-survey experience (self-assessment score; 1 – most experienced, 3 – least experienced).

Location	Transect length (km)	Predator density	Predator diversity	Insectivore proportion	Number of observers	Team experience
Argentina	2.0	72	2.433	0.455	2	2
Australia East	1.8	40	2.824	0.608	2	3
Australia South	2.0	64	2.721	0.477	4	3
Australia West	2.0	30	2.624	0.517	1	3
Brazil Brasilia	1.6	21	3.103	0.848	1	1
Brazil Serra do Japi	2.0	146	3.540	0.722	2	1
Brazil Uberaba	2.3	63	2.900	0.528	2	1
Cameroon	1.8	112	2.588	0.761	1	1
Canada	2.0	17	1.622	0.706	3	3
Colombia	2.1	21	2.955	0.711	2	2
Costa Rica	2.2	37	2.817	0.582	2	2
Czech Republic	2.0	114	2.913	0.417	1	1
Finland	1.7	54	2.808	0.446	1	1
India Buxa	1.8	124	3.363	0.307	3	1
India Honey Valley	2.2	65	2.763	0.217	2	3
Kenya	2.0	61	2.968	0.430	4	1
Netherlands	2.0	29	2.277	0.448	2	3
New Zealand	2.0	75	1.941	0.427	2	1
South Korea	2.0	25	2.131	0.327	1	3
USA	1.8	45	2.747	0.738	4	2
Wales	1.8	123	2.628	0.131	3	1

Table S8. Results for second global DAG. Significant parameters highlighted in blue (those that could be reliably estimated from the model when treated as exposure variables).

Predictor	β	exp(β)	se(β)	z	p-value
Treatment (atypical vs typical warning)	-0.14	0.87	0.13	-1.04	0.30
Treatment (cryptic vs typical warning)	-0.16	0.85	0.13	-1.23	0.22
Day (block number 1 to 8)	**0.18**	**1.20**	**0.02**	**11.30**	**< 0.001**
Predator density	0.25	1.28	0.23	1.08	0.28
Predator diversity (Shannon diversity index)	0.43	1.54	0.29	1.47	0.14
Insectivore proportion	**0.62**	**1.86**	**0.23**	**2.65**	**0.01**
Mean local illumination (log)	0.86	2.37	0.23	3.69	< 0.001
Seasonality in temperature	-0.34	0.71	0.24	-1.41	0.16
Variation in local illumination	-0.35	0.71	0.22	-1.57	0.12
Treatment (atypical vs typical warning) x Day	0.01	1.01	0.02	0.45	0.65
Treatment (cryptic vs typical warning) x Day	0.02	1.02	0.02	0.91	0.36
Treatment (atypical vs typical warning) x predator density	0.07	1.07	0.13	0.52	0.60
Treatment (cryptic vs typical warning) x predator density	-0.04	0.96	0.13	-0.31	0.76
Day x Predator density	**0.04**	**1.04**	**0.02**	**2.41**	**0.02**
Treatment (atypical vs typical warning) x predator diversity	0.17	1.19	0.18	0.95	0.34
Treatment (cryptic vs typical warning) x predator diversity	0.14	1.16	0.18	0.80	0.42
Day x Predator diversity	**-0.07**	**0.93**	**0.02**	**-3.37**	**< 0.001**
Treatment (atypical vs typical warning) x insectivore proportion	0.27	1.31	0.14	1.90	0.06
Treatment (cryptic vs typical warning) x insectivore proportion	0.24	1.27	0.14	1.67	0.10
Day x insectivore proportion	0.01	1.01	0.02	0.39	0.70
Treatment (atypical vs typical warning) x local illumination	**0.26**	**1.30**	**0.13**	**2.06**	**0.04**
Treatment (cryptic vs typical warning) x local illumination	**0.27**	**1.31**	**0.13**	**2.14**	**0.03**
Day x local illumination	**-0.06**	**0.94**	**0.02**	**-3.69**	**< 0.001**
Treatment (atypical vs typical warning) x seasonality	-0.03	0.97	0.15	-0.22	0.82
Treatment (cryptic vs typical warning) x seasonality	0.00	1.00	0.15	0.03	0.98
Day x Seasonality	0.03	1.03	0.02	1.81	0.07
Treatment (atypical vs typical warning) x Day x density	-0.01	0.99	0.02	-0.53	0.60
Treatment (cryptic vs typical warning) x Day x density	0.01	1.01	0.02	0.55	0.58
Treatment (atypical vs typical warning) x Day x diversity	-0.02	0.99	0.03	-0.49	0.62

Treatment (cryptic vs typical warning) x Day x diversity	-0.05	0.95	0.03	-1.53	0.12
Treatment (atypical vs typical warning) x Day x insectivore proportion	**-0.06**	**0.94**	**0.02**	**-2.47**	**0.01**
Treatment (cryptic vs typical warning) x Day x insectivore proportion	-0.04	0.96	0.02	-1.57	0.12
Treatment (atypical vs typical warning) x Day x local illumination	**-0.05**	**0.96**	**0.02**	**-2.02**	**0.04**
Treatment (cryptic vs typical warning) x Day x local illumination	**-0.05**	**0.95**	**0.02**	**-2.33**	**0.02**
Treatment (atypical vs typical warning) x Day x seasonality	0.01	1.01	0.03	0.48	0.63
Treatment (cryptic vs typical warning) x Day x seasonality	-0.01	0.99	0.03	-0.48	0.63

Table S9. Results of independent models testing the effects of salience and illumination on target predation.

For Cryptic targets (n=971)	**β**	**exp(β)**	**se(β)**	**z**	**p-value**
Target illumination (log)	0.61	1.83	0.05	11.50	< 0.001
Day	0.13	1.14	0.04	2.99	0.003
Target salience	0.21	1.24	2.23	0.10	0.92
Target salience × Day	0.44	1.55	0.43	1.01	0.31
For Typical warning colored targets (n=960)					
Target illumination (log)	0.61	1.84	0.06	10.47	< 0.001
Day	-0.03	0.97	0.10	-0.31	0.76
Target salience	-4.64	0.01	1.68	-2.76	0.006
Target salience × Day	0.52	1.68	0.30	1.73	0.08
For Atypical warning colored targets (n=977)					
Target illumination (log)	0.72	2.05	0.06	11.98	< 0.001
Day	-0.25	0.78	0.09	-2.67	0.008
Target salience	-6.46	0.002	1.48	-4.36	< 0.001
Target salience × Day	1.22	3.40	0.28	4.33	< 0.001

Table S10. Results of association between target-level salience (response) and illumination (predictor) values for each type of target, while using location as a random factor in a generalized linear mixed model. The negative association between salience and illumination at the target level is likely due to the presence of 3-D relief creating high-contrast shadows in the background but not the flat 2D target in high illumination conditions.

For Cryptic targets (n=971)	**β**	**se(β)**	**t-value**	**p**
Target illumination (log)	-0.008	0.001	-5.19	< 0.001
For Typical warning colored targets (n=960)				
Target illumination (log)	-0.004	0.002	-1.94	0.051
For Atypical warning colored targets (n=977)				
Target illumination (log)	-0.005	0.002	-1.99	0.046

Table S11. Model results for first DAG model when night attacks were not excluded.

Predictor	**β**	**exp(β)**	**se(β)**	**z**	**p-value**
Treatment (atypical vs typical warning)	-0.01	0.99	0.10	-0.09	0.93
Treatment (cryptic vs typical warning)	0.00	1.00	0.10	-0.01	0.99
Day (block number 1 to 8)	**0.13**	**1.13**	**0.01**	**10.10**	**< 0.001**
Predator density	0.20	1.23	0.19	1.06	0.29
Predator diversity (Shannon diversity index)	-0.19	0.82	0.27	-0.73	0.47
Insectivore proportion	-0.07	0.94	0.22	-0.30	0.77
Mean local illumination (log)	0.08	1.08	0.31	0.25	0.80
Seasonality in temperature	-0.22	0.80	0.25	-0.91	0.37
Warning/cryptic prey ratio	0.07	1.07	0.28	0.24	0.81
Variation in local illumination	-0.09	0.91	0.17	-0.53	0.59
Background predation rate	**0.82**	**2.26**	**0.27**	**3.03**	**< 0.001**
Treatment (atypical vs typical warning) x Day	-0.02	0.98	0.02	-1.13	0.26
Treatment (cryptic vs typical warning) x Day	-0.01	0.99	0.02	-0.59	0.56
Treatment (atypical vs typical warning) x predator density	0.13	1.13	0.10	1.20	0.23
Treatment (cryptic vs typical warning) x predator density	0.00	1.00	0.10	0.00	1.00
Day x Predator density	0.02	1.02	0.01	1.52	0.13
Treatment (atypical vs typical warning) x predator diversity	-0.25	0.78	0.15	-1.63	0.10
Treatment (cryptic vs typical warning) x predator diversity	-0.15	0.86	0.15	-0.99	0.32
Day x Predator diversity	-0.02	0.98	0.02	-0.79	0.43
Treatment (atypical vs typical warning) x Insectivore Proportion	**0.31**	**1.36**	**0.12**	**2.50**	**0.01**
Treatment (cryptic vs typical warning) x Insectivore Proportion	0.18	1.19	0.12	1.44	0.15
Day x Insectivore proportion	0.04	1.04	0.02	2.26	0.02
Treatment (atypical vs typical warning) x local illumination	**0.41**	**1.51**	**0.16**	**2.51**	**0.01**
Treatment (cryptic vs typical warning) x local illumination	0.20	1.22	0.17	1.19	0.23
Day x local illumination	-0.02	0.98	0.02	-0.90	0.37
Treatment (atypical vs typical warning) x seasonality	-0.15	0.86	0.15	-1.02	0.31
Treatment (cryptic vs typical warning) x seasonality	-0.09	0.92	0.15	-0.59	0.56
Day x Seasonality	0.04	1.04	0.02	1.90	0.06
Treatment (atypical vs typical warning) x warning/cryptic prey ratio	**0.39**	**1.47**	**0.14**	**2.75**	**0.01**
Treatment (cryptic vs typical warning) x warning/cryptic prey ratio	0.22	1.25	0.14	1.55	0.12
Day x warning/cryptic prey ratio	0.00	1.00	0.02	0.15	0.88
Treatment (atypical vs typical warning) x background predation rate	-0.21	0.81	0.17	-1.26	0.21

Treatment (cryptic vs typical warning) x background predation rate	0.02	1.02	0.16	0.14	0.89
Day x background predation rate	-0.02	0.98	0.02	-0.81	0.42
Treatment (atypical vs typical warning) x Day x density	-0.01	0.99	0.02	-0.66	0.51
Treatment (cryptic vs typical warning) x Day x density	0.00	1.00	0.02	0.01	0.99
Treatment (atypical vs typical warning) x Day x diversity	0.03	1.04	0.03	1.28	0.20
Treatment (cryptic vs typical warning) x Day x diversity	0.03	1.03	0.03	1.21	0.22
Treatment (atypical vs typical warning) x Day x insectivore proportion	-0.07	0.94	0.02	-2.83	0.00
Treatment (cryptic vs typical warning) x Day x insectivore proportion	-0.04	0.96	0.02	-1.68	0.09
Treatment (atypical vs typical warning) x Day x local illumination	**-0.08**	**0.93**	**0.03**	**-2.41**	**0.02**
Treatment (cryptic vs typical warning) x Day x local illumination	-0.06	0.94	0.03	-1.79	0.07
Treatment (atypical vs typical warning) x Day x seasonality	0.04	1.04	0.03	1.41	0.16
Treatment (cryptic vs typical warning) x Day x seasonality	0.01	1.01	0.03	0.39	0.70
Treatment (atypical vs typical warning) x Day x warning/cryptic prey ratio	**-0.06**	**0.94**	**0.03**	**-2.30**	**0.02**
Treatment (cryptic vs typical warning) x Day x warning/cryptic prey ratio	**-0.07**	**0.93**	**0.03**	**-2.60**	**0.01**
Treatment (atypical vs typical warning) x Day x background predation rate	**0.06**	**1.06**	**0.03**	**1.98**	**0.05**
Treatment (cryptic vs typical warning) x Day x background predation rate	0.02	1.02	0.03	0.52	0.61

Movie S1. A marsh tit *Poecile palustris* visiting an already predated typical warning colored target. Wales, UK.

Movie S2. A nuthatch *Sitta europaea* predating a camouflage target. Czech Republic.