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Higher Predation Risk for Insect Prey at Low Latitudes and Elevations

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Abstract: Biotic interactions underlie ecosystem structure and function, but predicting interaction outcomes is difficult. We tested the hypothesis that biotic interaction strength increases towards the Equator, using a global experiment with model caterpillars to measure predation risk. Across an 11,660 km latitudinal gradient spanning six continents, we found increasing predation towards the Equator – with a parallel pattern of increasing predation towards lower elevations. Patterns across both latitude and elevation were driven by arthropod predators, with no systematic trend in attack rates by birds or mammals. These matching gradients at global and regional scales suggest coherent drivers of biotic interaction strength, a

finding which needs to be integrated into general theories of herbivory, community organization, and life history evolution.

One Sentence Summary: Attack rates on plasticine caterpillars deployed around the globe reveal consistent patterns in biotic interaction strength.

Main Text: It is widely accepted that species diversity increases towards the tropics (1). This gradient is so ubiquitous that it has been called one of the fundamental laws in ecology (2). However, whether this latitudinal variation in diversity is paralleled by similar gradients in the intensity of biotic interactions, both antagonistic and mutualistic (3–9), remains unclear.

A widespread view is that biotic interactions become increasingly strong at lower latitudes (10–12). However, accumulating evidence (e.g. 7, 8, 13, 14) suggests that when critically examined, this pattern may be weak, absent, or even reversed. Part of this complexity arises because large-scale patterns are usually pieced together from data obtained using a variety of methods and protocols ((e.g. 7, 15, 16), and references therein). Here we use a simple, uniform protocol to quantify ecologically important patterns systematically at a global scale (17, 18). Specifically, we assess predation risk using the attack rate on model caterpillars (Fig. 1) for which the identity of the attacker may be determined (19). This method has been shown to provide accurate estimates of predator activity at individual sites and across local gradients (20, 21). By applying a consistent method at a global level, our study provides a rigorously controlled estimate of latitudinal patterns in predation strength.

Building on general theory (3, 10, 11), we hypothesize that overall biotic interaction strength increases towards the Equator. Many ecological factors that change with latitude also change with elevation, and thus it is important to control for elevational variation when quantifying latitudinal signals in predation rates. Moreover, by testing for congruence between

latitudinal and elevational predation patterns, we can begin to identify candidate mechanisms underlying predation rates.

Regardless of where high predation rates are found, depredation of herbivores is predicted to have broad ecological and evolutionary consequences across trophic levels. Stronger predation on herbivores directly affects the abundance and traits of herbivores (22–24) but also indirectly affects the abundance and traits of plants through trophic cascades (25, 26). Gradients in interaction strength thus provide a foundation for understanding global patterns in ecosystem processes (e.g. herbivory and primary production), ecosystem services (e.g. carbon storage and crop yields), and how long-term environmental change may impact biodiversity.

Predation rates reflect the sum of attacks by several different predator groups, each of which may show a different latitudinal pattern. We expect predation by ectothermic predators such as arthropods to be strongly controlled by local abiotic conditions. Indeed, temperature has been identified as the dominant abiotic factor directly affecting ectothermic insects (27, 28), and in experiments insect performance generally improves with temperature (29). An increase in the intensity of insect-mediated biotic interactions with increasing mean temperature is also supported by the higher folivory rates observed during warmer geological periods (30, 31). Thus, we expect increased attack rates by arthropod predators at low latitude and low elevation. In contrast, endotherms such as insectivorous birds may redistribute themselves through migration in response to local food availability (32). This is expected to homogenize predation rates across latitude and elevation, or elevate predation rates in their higher-latitude breeding grounds.

To test these hypotheses, we systematically measured predation risk by monitoring the fates of 2,879 model caterpillars over 4 to 18 days, resulting in a total of 12,694 caterpillar-days (Table S1). These caterpillars were molded from green plasticine, shaped in the posture of

common generalist caterpillars, and deployed within five plots at each of 31 sites along a latitudinal gradient spanning from 30.4°S to 74.3°N, and an elevation gradient spanning from 0 to 2100 m a.s.l. Whenever an attack was scored, the caterpillar in question was removed without replacement. We used generalized linear mixed-effects models (33) to quantify the effects of latitude and elevation on biotic interaction strength, measured as the probability of a caterpillar being attacked per day exposed (for further validation of this response, see (33)).

Consistent with our predictions, we found that predation rates were highest at the Equator and decreased significantly towards the poles (Fig. 1A; $F_{1,27.8}=10.28$, $P=0.003$). For every 1° latitude away from the Equator, the daily odds of a caterpillar being attacked decreased by 2.7% (odds ratio 0.973, confidence limits 0.959–0.987, Fig. 1A). Thus, at the highest latitude studied (74.3°N; Zackenberg, Greenland), the daily odds of a caterpillar being attacked by a predator were only 13% (odds ratio 0.131, confidence limits 0.046–0.376) of the odds at the Equator. Predation rates also declined with increasing elevation ($F_{1,27.1}=6.35$, $P=0.02$; Fig. 1D), independent of latitude (i.e., no latitude×elevation interaction, $F_{1,27.8}=0.70$, $P=0.41$). For every 100 m moved upwards from sea level, the daily odds of predation decreased by 6.6% (odds ratio 0.934, confidence limits 0.884–0.987). At the highest forested elevation studied (2106 m a.s.l.; Table S1), the daily odds of predation were 24% of those at sea level (odds ratio 0.238, confidence limits 0.074–0.765).

Importantly, higher predation at lower latitudes and elevations was due to more frequent attacks by arthropod predators. The daily odds of a caterpillar suffering an arthropod attack decreased by 3.5% for every 1° latitude moved away from the Equator (odds ratio 0.966, confidence limits 0.947–0.984, $F_{1,25.1}=14.11$, $P<0.001$), as did the odds of feeding marks which could not be attributed to any specific predator group (odds ratio 0.972, confidence limits 0.954–

0.991, $F_{1,24.3}=9.57$, $P=0.005$; Fig. 1C). In contrast, we found no evidence for a gradient in predation by birds or mammals – the frequencies of feeding marks by these predator groups were unrelated to latitude ($F_{1,26.6}=1.20$, $P=0.28$ and $F_{1,28.6}=2.9$, $P=0.10$, respectively). These latitudinal patterns in predation rate were mirrored across elevation: the odds of a caterpillar suffering arthropod attack decreased by 9.6% for every 100 m moved upwards from sea level (odds ratio 0.904, confidence limits 0.839–0.975, $F_{1,26.1}=7.48$, $P=0.01$), whereas the odds of receiving feeding marks not attributable to any specific predator group ($F_{1,21.3}=0.18$, $P=0.68$) or of being attacked by birds ($F_{1,29.3}=1.86$, $P=0.18$) or mammals ($F_{1,25.0}=0.63$, $P=0.44$) were unrelated to elevation (Fig. 1F).

Overall, our study reveals a strong latitudinal signature on biotic interaction strength (i.e., predation rates) across the globe. In doing so, it provides a clear pattern which can be used to inform future efforts in this field (3–7) and to move beyond the obstacle of contradictory evidence from variable methodologies among studies conducted at different subsets of latitude (7, 13). The parallel patterns in predation across elevation (cf. 21) suggest that the ecological factors constraining predation rates are likely to show concordant latitudinal and elevational gradients (34). The clarity of our findings offers a simple lesson: to unmask a global ecological pattern, we may need to apply standardized methods to specific hypotheses determined a priori, rather than combine data derived from different methods a posteriori (cf. 8, 13, 34). This study thus illustrates the power of simple, low-cost, globally-distributed experiments (cf. 17, 18, 35).

We found that global gradients in predation rate were driven by arthropod predators, with no systematic trend in attack rate by birds or mammals. This latitudinal shift in the relative importance of different predator groups has clear implications for understanding evolution, interpreting global patterns of herbivory, and understanding global community organization and

functioning. In terms of arthropod herbivore evolution, much theory has been developed on latitudinal patterns in plant defense against herbivores, suggesting that if plants at lower latitudes suffer high herbivory, they need to evolve stronger defenses (e.g. 10, 11, 15). Our findings motivate an analogous theory for defense deployed by herbivores against their predators. In the tropics, the fraction of model caterpillars attacked per day is notably high (Fig. 1), and attack rates on live prey tend to be even higher (35). Thus, predation in the real world creates a very real selection pressure. This leads to the testable hypothesis that arthropod herbivores in the tropics should be better defended than those at higher latitudes, and that these defenses should target arthropod rather than vertebrate predators (Fig. 1C).

Real herbivores accumulate predation risk over their development time, which may be shortened in warmer climates and thus counteract our predictions for the ecological and evolutionary impact of predation gradients. While a comprehensive assessment goes beyond the current study, we analyzed larval development times from the available literature (Table S2), – finding a much lower latitudinal effect on development times than on predation rates (Table S3). Hence, as a net effect, we expect increased selection pressure on larval herbivores at lower latitudes.

From a plant perspective, the patterns detected in this study suggest increased per capita predation pressure on plant consumers towards the tropics – and strong differences in the relative impacts of different predator groups among different parts of the globe (Fig. 1C). This finding suggests markedly different roles for different predator groups in regulating herbivore abundance and traits across geographic gradients, and potential differences in trophic organization between regions. Whether or not the patterns revealed by the current study translate into patterns in net herbivory is unresolved, particularly considering that our experiments took place in the

understorey whilst most primary production takes place in the canopy layer. While seminal findings suggested latitudinal gradients in herbivory and plant defense (15, 16), recent appraisals of the evidence find less support for these trends (7, 8, 14). Nonetheless, the lack of clear patterns in herbivory may be as much a reflection of variable methods as a true lack of a pattern (7, 13, 15, 16, 36). The current study should stimulate further standardized comparisons of species interactions, facilitating a clearer view of these key biological patterns to enlighten our search for their drivers and consequences.

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Fig. 1. Map of sampling sites with scatter plots showing fates of model caterpillars at different latitudes (A, C) and elevations (D–F). In the map of sampling sites across the globe (B) and across elevations (E), individual sites are shown with symbol size graduated by caterpillar-days, and habitat type identified by the symbol color. For site-specific details, see Table S1. Panels (A) and (D) show the overall fraction of caterpillar models attacked per day (i.e. daily predation rates per model caterpillar) in each habitat type, with the patterns resolved by predator type in panels (C) and (F). Each individual data point reflects the fate of replicate model

caterpillars in one of five sampling plots within a site (horizontal line of data points) (33). Data points are partially transparent and appear darker when overlapping. Curves show values fitted by logistic generalized linear mixed-effects models (33), including only responses for which a significant association with latitude was found (with the orange curve in panels (C) and (F) corresponding to arthropod attack and the gray curve in (C) to unclassifiable attacks. Dotted lines in (A) and (C) represent extrapolation beyond the data range, included to demonstrate symmetry around the equator. Panel (B) also shows a model caterpillar deployed in Northern Finland, showing extensive beak marks typical of a bird attack.

Supplementary Materials:

Materials and Methods

Supplementary Text

Tables S1-S3

Fig S1

References (37-80)



Supplementary Materials for

Higher Predation Risk for Insect Prey at Low Latitudes and Elevations

Tomas Roslin, Bess Hardwick, Vojtech Novotny, William K. Petry, Nigel R. Andrew, Ashley Asmus, Isabel C. Barrio, Yves Basset, Andrea Larissa Boesing, Timothy C. Bonebrake, Erin K. Cameron, Wesley Dáttilo, David A. Donoso, Pavel Drozd, Claudia L. Gray, David S. Hik, Sarah J. Hill, Tapani Hopkins, Shuyin Huang, Bonny Koane, Benita Laird-Hopkins, Liisa Laukkanen, Owen T. Lewis, Sol Milne, Isaiah Mwesige, Akihiro Nakamura, Colleen S. Nell, Elizabeth Nichols, Alena Prokurat, Katerina Sam, Niels M. Schmidt, Alison Slade, Victor Slade, Alžběta Suchanková, Tiit Teder, Saskya van Nouhuys, Vigdis Vandvik, Anita Weissflog, Vital Zhukovich, Eleanor M. Slade.

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Materials and Methods
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Fig S1

Materials and Methods

Study design

The study was implemented as a globally distributed experiment. Using a standardized protocol across sites, we tested the generality, strength and consistency of previously proposed patterns of biotic interaction strength (3–7, 10–12, 36), in this case predation rates. We employed the principle of crowd-sourcing to recruit scientists across latitudes and biomes, using both the internet and personal contacts. To avoid any unintended bias from checking model caterpillars in field conditions and by different individuals, all exposed caterpillars were returned to Finland, where multiple trained people checked the same model caterpillars under standardized conditions before final analyses.

The full original instructions given to participants are available online at <http://www.helsinki.fi/foodwebs/dummycaterpillars/instructions> and at Dryad Digital Repository, doi:XXXX (37). In brief, the experiment was successfully implemented at 31 sites (Fig. 1 of main paper; Table S1). The sites selected were chosen to be subject to minimal disturbance, often being national parks or other protected areas. Participants were instructed to place their study sites in a habitat as close as possible to the climax vegetation type of the region. This resulted in the vast majority of sampling being conducted in forest habitats, with tundra and shrubland sampled in arctic and low-rainfall biomes, respectively (for site-specific habitat, see Fig. 1 of main paper). In seasonal environments, sampling was conducted during the local summer (for exact dates, see Table S1).

Heterogeneity in herbivore appearance, camouflage, and life history all contribute to variation in rates of predation on herbivorous insects (20). Such variation is compounded by mortality from other sources, such as microbes and weather (38). In order to measure the relative risk of predation across sites, we controlled for these other sources of mortality by monitoring attacks on model lepidopteran caterpillars of a standardized appearance (39). In doing so, we adhered to recently-established best practices for this technique (19). All participants were supplied with model caterpillars manufactured by the same team of people using odorless, non-toxic colored plasticine (Lewis Newplast™ in an equal mixture of two colors: green and light green). Model caterpillars resembled undefended, green geometrid larvae. This type of caterpillar was chosen as it represents one of the most abundant groups of Lepidoptera found throughout the world: Geometridae are among the largest families in the animal kingdom, with some 23,000 currently described species (40, 41), including many economically important species (42, 43). The caterpillars were manufactured with a clay gun in the typical size of late-instar geometrid caterpillars (2.5 x 30 mm) and molded into the characteristic looping position of a geometrid (commonly adopted whilst resting). Caterpillars of this type are naturally present in the local fauna of all sampling sites. We note that our model prey may be less attractive to predators guided by movement and olfaction than to those attracted by shape and colour (19, 35, 39). Thus, our focus was explicitly on using a consistent methodology at a global level, thereby gauging interaction intensities at all latitudes and elevations by the same repeatable method (19, 35, 39).

At each study site, 100 caterpillars were distributed among five 3m x 4m plots with 20 caterpillars in each plot. Each caterpillar within a plot was separated by at least 1m, and individual plots were a minimum of 50m apart. To standardize sampling across

sites, caterpillars were glued with Loctite™ Control Superglue onto the upper side of simple, entire leaves on naturally-growing seedlings and/or shrubs not more than 1m above the ground. The selected leaves were neither damaged nor touching the ground. This standardized exposure mimics naturally occurring, exophagous folivorous caterpillars present at each study site, and the standardized distance from the ground allowed comparable access across sites by ground-based predators (e.g. ants) and by bird species foraging on or close to the ground.

To gain maximal replication across latitudes, we structured our sampling around well-defined, discrete work packages, i.e. relatively few revisits, per site. Participants were instructed to check caterpillars a minimum of three times: after 24h, 48h and 96h (4 days) \pm 2 hours from being deployed, with longer exposure times also allowed (see Table S1 for site-specific data). Practical constraints caused a few deviations from this rule: at Huddersfield, data were only available at 72 hours; at Alamala, Tai Po Kau, and Zackenberg data were not available at 24 hours; at Newholme data were not available at 48 hours; and at Kluane Lake data were not available at 96 hours.

Any caterpillar showing signs of attack when checked was removed without replacement, for the purpose of retaining the specific feeding marks for later verification (see below). What this means is that the number of caterpillar-days accumulated in a plot contains information about the predation rate, and is not equivalent to the sampling duration (i.e., the number of days that the experiment was run). To illustrate the difference and its implications, consider a site where the daily risk of predation is 100%. A plot with 20 caterpillars will then accumulate only 20 caterpillar-days regardless of how long the experiment is run. Conversely, a site where the daily predation risk is 0% will accumulate 20 caterpillar-days for every day that the experiment is run. Therefore, this count of individual exposure was used as the denominator for the number of observed attacks in subsequent analyses (see Statistical Analyses, below).

Based on tooth, beak, mandibular or radular marks, all feeding damage on caterpillars was attributed to one of six predator groups: birds (B), lizards (L, of which only a single attack was observed in the full material), mammals (M), arthropods (A), gastropods (i.e. snails or slugs; S), or an unknown predator (U). As additional categories, intact caterpillars were scored as being not attacked (N), whereas caterpillars not retrieved were scored as 'lost' and excluded from analyses. Feeding marks not attributable to any specific predator (i.e. category U) likely consisted mostly of feeding by arthropods and snails, whereas the conspicuous tooth- and beak-marks of birds and mammals are easier to score unambiguously (19).

As the scoring of feeding marks involves a certain element of subjectivity and may vary with observer experience (19), we asked participants to return the caterpillars for separate scoring by an experienced team at the University of Helsinki. We aimed to have at least two experienced people (beyond the person implementing the sampling) scoring each caterpillar independently. This was not always possible, and hence we had two sites scored exclusively by the person implementing the sampling, three sites scored jointly by two experienced people (beyond the person implementing the sampling), in this case delivering a consensus score, 21 sites scored independently by two experienced people (beyond the person implementing the sampling), and six sites scored by three experienced people (beyond the person implementing the sampling). Yet the patterns uncovered were notably robust to the exact details of scoring (compare Fig. S1).

The people conducting the scoring were first trained with pictures of feeding damage and sample caterpillars to arrive at consistent criteria for assigning caterpillars to categories. They then conducted their scoring independently of each other, filling in separate data sheets which were only later combined to form a coherent data set. Given that each caterpillar was stored in a labelled tube (which was necessary to avoid damage or accidental marks occurring on the caterpillar in transit), the scorers typically had access to a truncated version of the site name (but not of the latitude or altitude). Beyond the training caterpillars used to agree on criteria, the scorers were blind to the assessments made by each other on the set under evaluation, and had no systematic knowledge of previous data points derived from other sets. The composition of evaluators also differed among sites. Together, these measures should result in the objective scoring of patterns across sites.

To weigh together individual scorings, we focused on the number of times a given fate was scored, counting each caterpillar-by-fate combination. To avoid inflating the number of observations [degrees of freedom], we divided the counts per fate by the number of people scoring a given caterpillar. Hence, four people each scoring a caterpillar as ‘not attacked’ (N) gave one full count of N, whereas – as the extreme case – four people all scoring the same caterpillar differently including one person assigning it an N would have given it a count of 0.25 for N. For each category A-U, we then summed the resultant scores over the grid, and rounded them to the nearest integer. As caterpillars lost before scoring (i.e. individuals for which the fate was unknown) were omitted from analyses, our final data set consisted of 2,879 caterpillars out of 3,106 initially deployed (after omitting one site; Table S1).

Larval development time

To evaluate how latitudinal patterns in daily attack rates on caterpillars compare to latitudinal gradients in larval development time (see main text), we conducted a literature search for larval development times of Lepidoptera across latitudes. We relied primarily on studies reporting development times for larvae reared outdoors under natural temperature regimes. However, we also included data from a few laboratory rearings in which caterpillars had been kept under fluctuating temperature regimes either closely tracking or realistically simulating local temperature fluctuations. To match the data on development times to our data on attack rates on model caterpillars, we restricted the data set of development times to externally-feeding folivorous species. Thus, species representing other feeding guilds, such as leaf-miners and root-feeders, were excluded. As substrate quality may affect development time, we only included data on individuals reared on their natural host plants, ignoring data for artificial diets. In cases where data were reported separately for two or more treatments (usually different host plant species), we used the shortest development time (indicating a more optimal substrate). As development time is partly a function of insect size, we also extracted data on final body size (pupal mass) for each species. Data reported separately for males and females were averaged for each species.

Overall, we were able to collect relevant data for 30 folivorous species spanning 13 macrolepidopteran families, distributed across a wide latitudinal gradient (0 to 70 degrees absolute latitude; Table S2).

Statistical Analyses

We used generalized linear mixed-effects models to estimate the relationship between predation risk, latitude, and elevation, and to partition local variation among sampling plots within sites from variation among sites at different latitudes. To derive an intuitively-interpretable estimate of the change in predation risk with a change in latitude, we adopted an odds-based approach. Hence, the daily incidence of attack by a given predator group per caterpillar capita was scored as the number of such predation events (see above) out of caterpillar-days accumulating in the plot. Thus, one caterpillar exposed for one day is one trial, and an attack during this day is an event (0/1). The ratio between the two then provides an unbiased estimate of daily attack rates.

This response variable was used because any caterpillar attacked was removed without replacement, and thus the number of caterpillar-days accumulated in a plot contains information about the predation rate, and is not equivalent to the sampling duration (i.e., the number of days that the experiment was run). Because it counts individual exposures, it is the appropriate denominator for the number of observed attacks, yielding daily attack rates per capita (37). Assuming binomially-distributed errors and a logit-link, this response was modelled as a function of the absolute value of latitude, fitting a separate model for each predator group. To estimate the effect of elevation, we included the elevation of the site (meters above sea level; Table S1) as a continuous covariate. To capture local variation between plots, site and plot (nested within site) were included as random effects – thus partitioning variation in attack rates into the contributions of plots within sites and the contributions of latitude. To allow for a change in the effect of elevation across latitudes, we included the interaction between absolute latitude and elevation in preliminary models. As this interaction term was non-significant for all responses ($F_{1,28} \leq 0.4$, $P > 0.4$), it was dropped from the final models, which thus included the main effects of absolute latitude and elevation. Importantly, we note that elevation and latitude varied independently of each other across our study sites (Table S1; Pearson correlation coefficient $r = -0.24$, $n = 31$ sites, $P = 0.20$).

A model formulation alternative to the current one is to model the number of attacks as a function of absolute latitude (and elevation), while including log-transformed caterpillar days as an offset variable (36). Assuming a log-link function and Poisson-distributed errors, this approach will produce results identical to the current one. All models were fitted in SAS for Windows, version 9.4 (SAS Institute Inc., Cary, NC, USA), proc glimmix. Degrees of freedom used for significance tests were derived using the Kenward-Rogers approximation.

To estimate whether and how larval development time decreases towards the Equator, we used the data compiled in Table S2 to relate larval development time to latitude (Table S3). To adjust for a phylogenetic signal in these data, we fitted a modified (see below) PGLS (phylogenetic generalized least squares) model with a Brownian correlation structure (using R packages *nlme* (44) and *ape* (45)). To adjust for a possible size-dependency in growth rates, we included $\log(\text{body weight})$ as a covariate in the analysis (46), and standardized it to allow interpretation of the model intercept.

As species-level phylogeny is still not available for many lepidopteran clades, we had to rely on an available higher-level (family/subfamily) non-ultrametric tree (47) for the PGLS analysis. We assigned all species in our dataset to the lowest taxonomic level

in this phylogeny. By doing this, the 30 species in our dataset were distributed across 17 clades of the tree from (47). We pruned the tree to leave these 17 clades.

The tips of the pruned tree were then replaced with one or several species, corresponding to the number of species in our dataset that belonged to the respective clade. We opted against using zero branch lengths for these added tips, since that would have caused the model errors for species in the same clade to have a correlation of 1 (an unrealistic assumption). Instead, we fitted several models with increasing branch lengths, accounting for the non-ultrametric nature of the tree by setting the variance of model errors proportional to root-to-tip distances for each species. We then determined the optimal branch length by choosing the model with the smallest AIC value. As the AIC values of the models appeared to increase monotonously with increasing branch lengths of the added tips (i.e. the model with the shortest branch lengths had the lowest AIC), species from the same clade were modelled as strongly correlated in the final model.

Model validation

The generalized linear mixed-effects models yielded a very good fit to the data, as shown by a deviance scaling closely with the residual degrees of freedoms (Generalized χ^2/DF close to 1 for all models). Thus, there were no signs of overdispersion.

To verify that our results were independent of variation in caterpillar-days per site, we recreated our data from an explicit, individual-based simulation that mimicked the steps of our sampling design, then analyzed it with our original statistical model (37). We set the number of sites to 1000. We set the coefficient for latitude β_{lat} to 0 (i.e. no latitudinal effect on predation) and simulated three different caterpillar-days scenarios where the correlation between latitude and caterpillar days was (1) strongly positive, (2) null ($r=0$), and (3) strongly negative. For all three scenarios, we successfully recovered the correct estimate of β_{lat} (i.e. zero, equaling no effect; (37)).

We note that the overall analyses presented in the paper concern attack rates over the full course of the experiment, with slightly different exposure times at individual sites. Should attack rates change over time, data derived from caterpillars exposed over different time periods might be incommensurate. To evaluate this scenario, we reran the same analyses as outlined above for data recovered at each visit by the participants after 24h, 48h and 96h (see above). As we recovered similar estimates of predation rates from data on different time periods (Fig. S1), we conclude that predation rates remained constant over time, and that a single model can be fitted to site-specific data recovered over the full course of the experiment.

The fit of the model of larval development time was validated by quantile plots of residuals and Shapiro-Wilk normality tests. Since two species (*Spilosoma luteum* and *Hylesia lineata*) from different latitudes (53.9° and 19.5°, respectively; Table S2) were associated with unusually long development times and thereby with high model residuals, the residuals of the model using full data set significantly deviated from a normal distribution (Shapiro-Wilk normality test $P = 0.03$). Thus, we repeated the analysis with these two outliers omitted. This resulted in normally-distributed residuals (Shapiro-Wilk normality test: $P = 0.29$) but quantitatively similar results (Table S3).

Supplementary Text

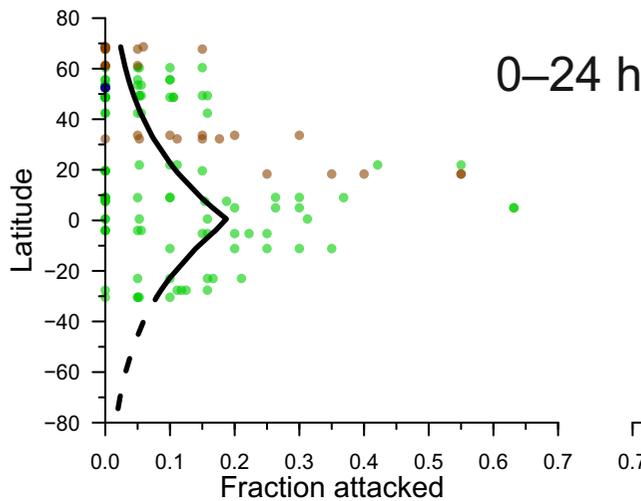
Extended acknowledgements

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Author contributions

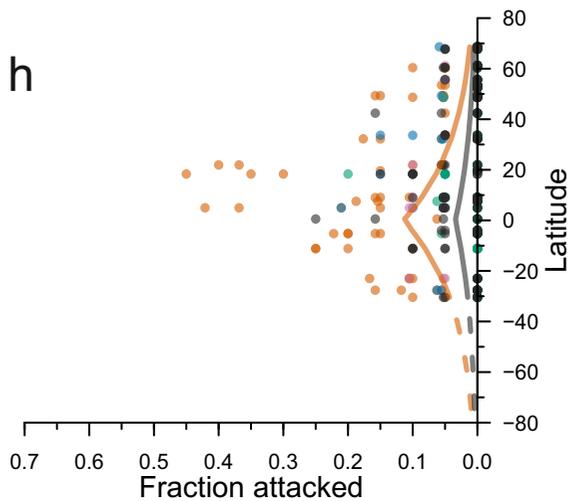
E.S., T.R., and B.H. designed the study, all authors collected and/or contributed data, T.R. and B.H. analyzed the data and wrote a first draft of the paper, W.K.P. contributed substantially to further revisions, illustrations and analyses, and all authors discussed and contributed to the final paper.

$F_{1,27.2}=13.98$
 $P=0.0009$

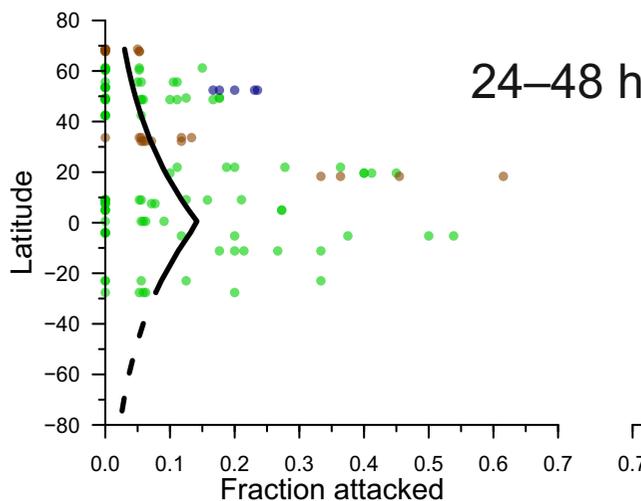


$F_{1,27.7}=10.27$
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$F_{1,24.7}=4.94$
 $P=0.04$

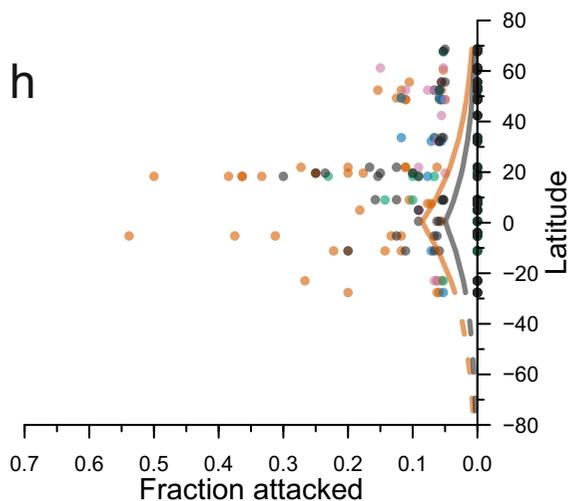


$F_{1,23.6}=4.74$
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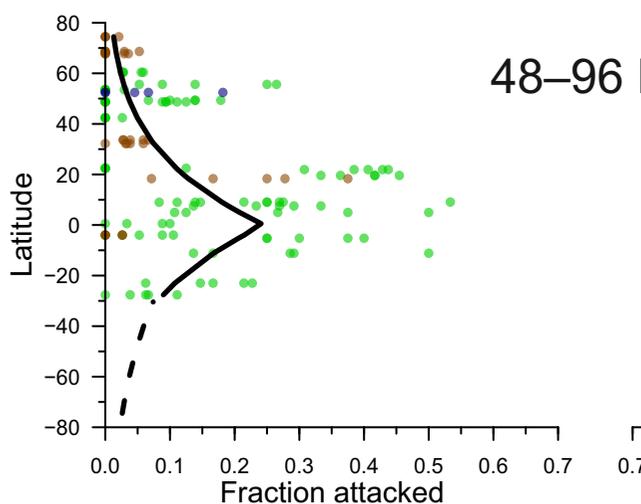


$F_{1,26.0}=5.18$
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$F_{1,30.6}=8.13$
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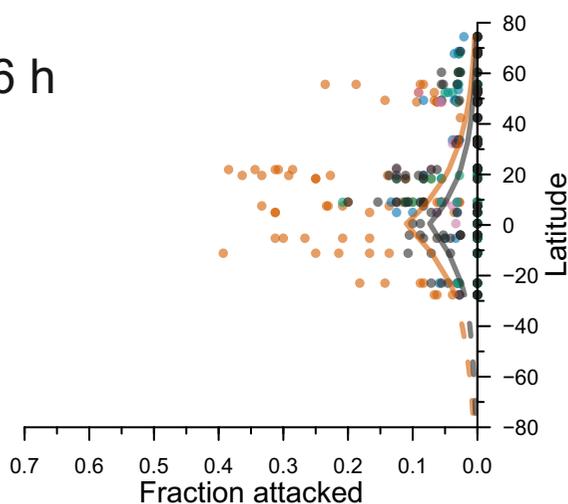


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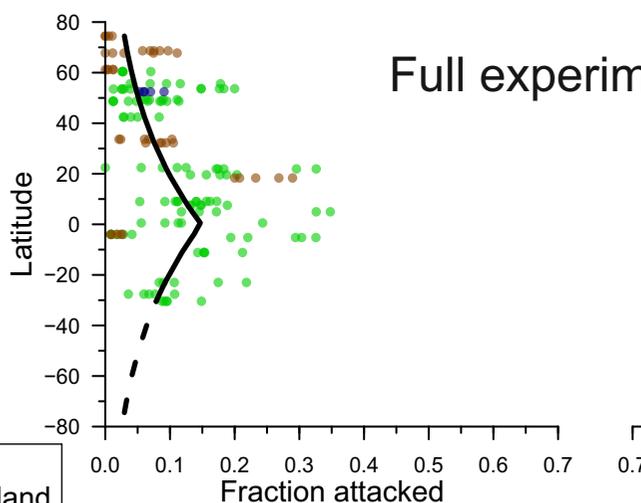


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$F_{1,26.8}=19.21$
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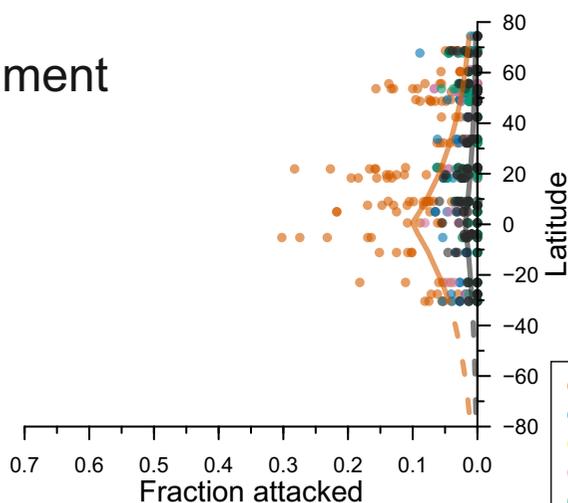


$F_{1,27.8}=10.28$
 $P=0.003$



$F_{1,25.1}=14.11$
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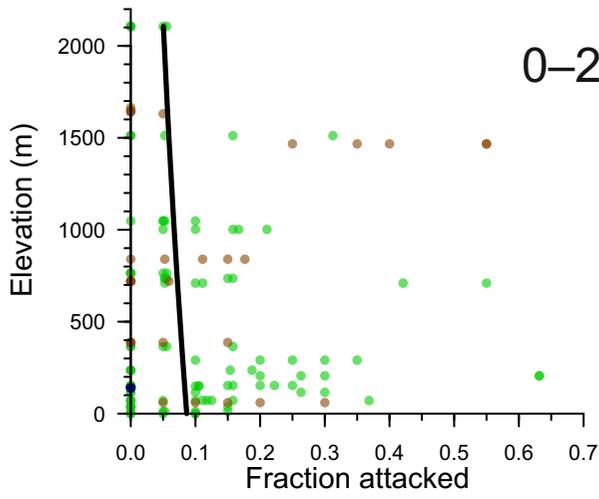
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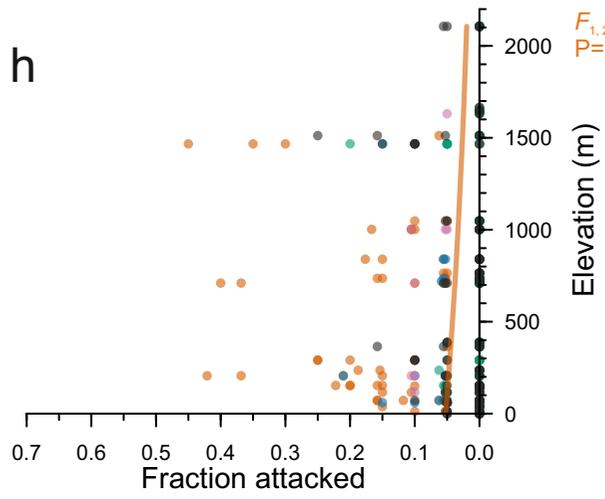
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- Tundra/shrubland
- Wetland

- Arthropods
- Birds
- Lizards
- Mammals
- Gastropods
- Unknown

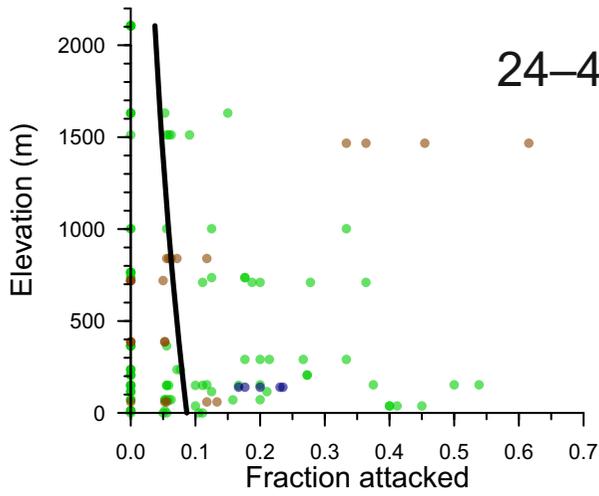
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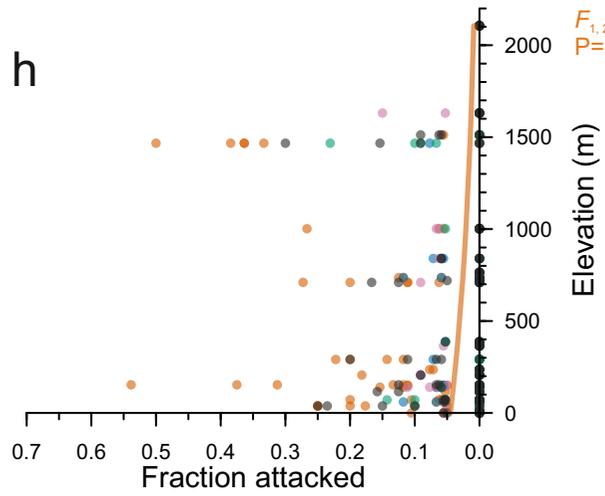
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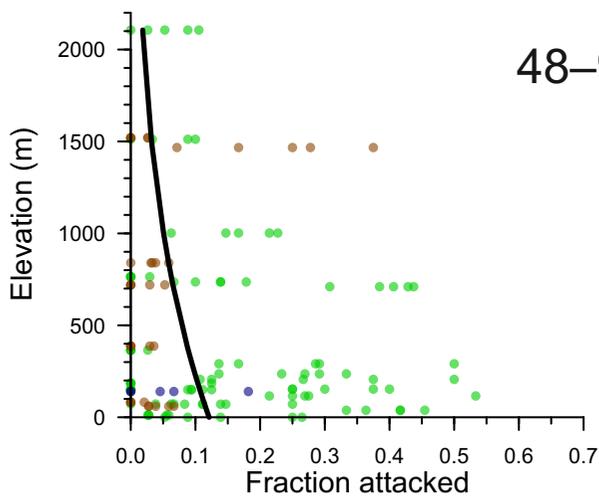
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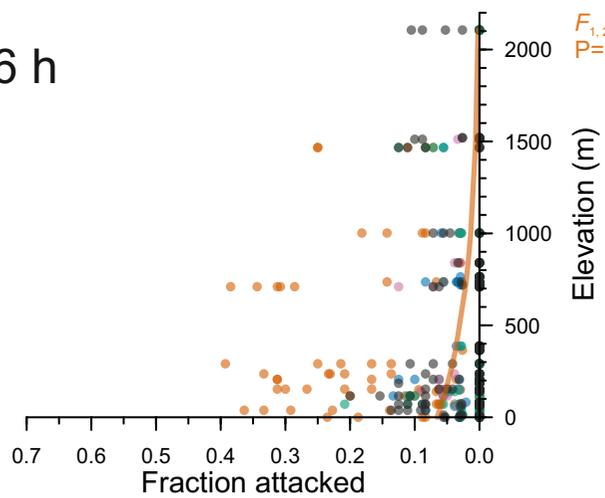
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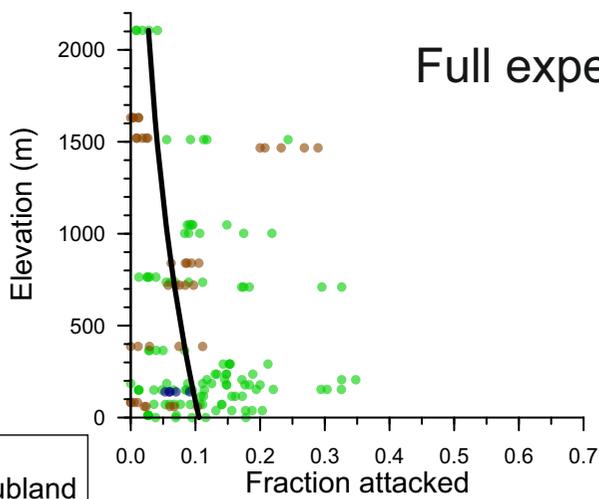
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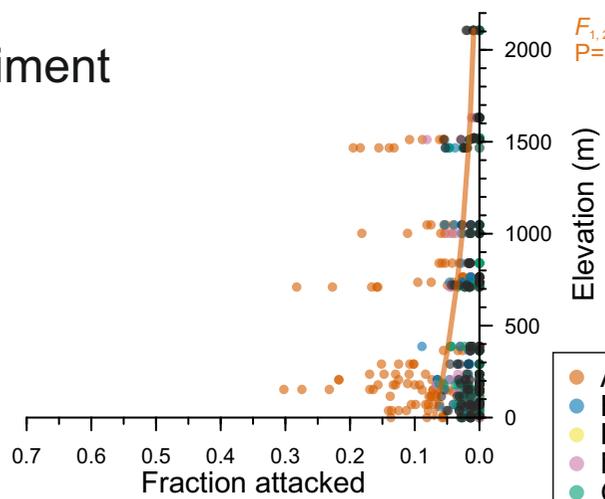
$F_{1,25.7}=6.19$
 $P=0.02$



$F_{1,27.1}=6.35$
 $P=0.02$



$F_{1,26.1}=7.48$
 $P=0.01$



- Forest
- Tundra/shrubland
- Wetland

- Arthropods
- Birds
- Lizards
- Mammals
- Gastropods
- Unknown

Fig. S1.

Fates of model caterpillars at different time periods at different latitudes (p. 8) and elevations (p. 9), demonstrating that attack rates are constant in time and independent of variation in caterpillar-days. Panels on the left show the fraction of caterpillar models attacked per day (i.e. daily predation rates per model caterpillar) during different parts of the experiment (from top to bottom): 0–24h, 24–48h, and 48–96h. The bottom panels show patterns across the full experiment, and are thereby identical to those of Fig. 1 in the main paper. Each individual data point reflects the fate of replicate model caterpillars in one of five sampling plots within a site (horizontal line of data points). Data points are partially transparent and appear darker when overlapping. On the left, habitat types are identified by the symbol color, whereas panels on the right show the same patterns resolved by predator type. Curves show values fitted by logistic generalized linear mixed-effects models, with the orange curves corresponding to arthropod attack and the gray curves to unclassifiable attacks. Dotted lines represent extrapolation beyond the data range, included to demonstrate symmetry around the equator. We note that fates at 24 h, 48h and 96 h (top three panels) were scored in field conditions and by different individuals, whereas for the full experiment, multiple trained people checked the same model caterpillars under standardized, laboratory conditions (bottom panels). Slight variation in the exact set of sites scored at each time step will reflect into additional differences in patterns, and in statistical power (with *F*- and *P*-values reflecting type 3 tests of the estimated fixed effects). Missing at 48-96 hrs are data from sites Huddersfield (latitude 53.6, elevation 178 m.a.s.l.), Newholme (latitude -30.4, elevation 1048 m.a.s.l) and Kluane Lake (latitude 61.2, elevation 1631 m.a.s.l.); missing at 24-48 hrs are Huddersfield, Newholme, Alamala (latitude -4.0, elevation 1520 m.a.s.l.), Tai Po Kau (latitude 22.4, elevation 185 m.a.s.l.) and Zackenberg (latitude 74.5, elevation 82 m.a.s.l.); missing at 0-24 hrs are Huddersfield, Alamala, Tai Po Kau and Zackenberg. Despite these nuances, both patterns and estimates are notably similar across time steps.

Table S1.

Summary of artificial caterpillar monitoring protocols for each study site

Study site	Latitude (decimal degrees)	Longitude (decimal degrees)	Date deployed	End of monitoring	Caterpillar Days	Elevation m a.s.l
Newholme, Australia	-30.4259	151.6426	17.11.2014	21.11.2014	378	1048
Karawatha Forest, Brisbane, Australia	-27.6258	153.0771	22.9.2014	26.9.2014	318	72
Atlantic Forest, São Paulo State, Brazil	-22.9874	-46.0658	16.11.2014	20.11.2014	332	1002
Marcelândia, Mato Grosso, Brazil	-11.1523	-54.5365	8.9.2014	12.9.2014	305	291
Wanang Conservation Area, Papua New Guinea	-5.2263	145.0812	5.12.2014	9.12.2014	276	153
El Colibri, Ecuador	-3.9884	-79.0934	7.8.2014	13.8.2014	546	2106
Alamala, Ecuador	-3.9709	-79.0933	31.7.2014	6.8.2014	574	1520
Kibale National Park, Uganda	0.5547	30.3618	21.9.2014	25.9.2014	243	1512
Danum Valley, Borneo, Malaysia	4.9654	117.7984	13.9.2013	18.9.2013	286	206
Khao Chong, Thailand	7.5430	99.7973	11.11.2014	15.11.2014	274	236
Parque Metropolitano, Panama*	8.9946	-79.5430	18.8.2014	22.8.2014	351	71
El Charco, Panama	9.0841	-79.6634	7.8.2014	11.8.2014	344	116
Tehuacán-Cuicatlán Valley, Mexico	18.3307	-97.4623	4.10.2014	8.10.2014	220	1467
Centro de Investigaciones Costeras La Mancha, Mexico	19.6007	-96.3769	11.8.2014	15.8.2014	325	38
Xishuangbanna, Yunnan, China	21.9192	101.2762	25.8.2015	29.8.2015	283	710
Tai Po Kau, Hong Kong	22.4263	114.1820	22.4.2014	26.4.2014	102	185
Tucson, AZ, USA	32.2233	-111.0969	20.6.2014	24.6.2014	325	840
UC Irvine Ecological Preserve, CA, USA	33.6397	-117.8453	28.4.2015	6.5.2015	616	60
Ithaca, NY, USA	42.4158	-76.5720	12.4.2014	16.4.2014	349	365
Lanzhot 2, Czech Republic	48.6882	16.9424	23.7.2014	29.7.2014	429	150
Lanzhot 1, Czech Republic	48.6891	16.9476	3.5.2014	9.5.2014	411	150
Jezvinec Nature Reserve, Czech Republic	49.3197	13.0675	9.6.2014	13.6.2014	341	736
Zditovo, Belarus	52.4229	25.2615	4.8.2014	22.8.2014	655	140
Cooking Lake-Blackfoot, AB, Canada	53.5031	-112.9428	30.5.2014	3.6.2014	382	764
Huddersfield, UK	53.6363	-1.6970	2.8.2013	7.8.2013	279	178

Vestamager, Denmark	55.6192	12.5406	31.5.2014	4.6.2014	366	0
Turku, Finland	60.4104	22.2697	4.8.2014	9.8.2014	369	12
Kluane Lake, YK, Canada	61.2132	-138.2775	16.7.2014	30.7.2014	1332	1631
Värriö Research Station, Finland	67.7503	29.6113	10.7.2013	16.7.2013	403	387
Toolik Lake, AK, USA	68.6392	-149.5814	23.6.2014	29.6.2014	496	720
Zackenberg, Greenland	74.4667	-20.5667	20.6.2013	28.6.2013	784	82

* One further site, Fort Sherman in Panama, was omitted due to unsuccessful sampling – a high fraction of caterpillars had been reduced to crumbs by an unknown agent (potentially snails), thereby effectively preventing the scoring of remaining feeding marks.

Table S2.

Data used in the analysis of latitudinal trends in larval development times.

Species	Family	Body mass (mg)	Larval development time (days)	Latitude (decimal degrees)	Country	Population	Ref.
<i>Citheronia regalis</i>	Saturniidae	10650.0	39.1	39.1	New Jersey, USA	Cape May Co.	(48)
<i>Anthocharis cardamines</i>	Pieridae	93.4	31.7	54.8	UK	Durham	(49)
<i>Orthosia gothica</i>	Noctuidae	279.7	39.5	60.4	Norway	Bergen	(50)
<i>Pararge aegeria</i>	Nymphalidae	156.9 (51)	42.8	59.2	Sweden	Agesta	(52)
<i>Epirrita autumnata</i>	Geometridae	89.5	37.2	60.2	Finland	Ruissalo	(53)
<i>Epirrita autumnata</i> ¹	Geometridae	53.4	32.8	69.8	Finland	Kevo	(53)
<i>Orgyia vetusta</i>	Lymantriidae	374.8	44.9	38.3	California, USA	Bodega Bay	(54)
<i>Lymantria dispar</i>	Lymantriidae	731.3	49.0	45.5	Quebec, Canada	Mont St. Hilaire	(55)
<i>Hylesia lineata</i>	Saturniidae	751.4	80.9	19.5	Mexico	Santa Rosa NP	(56)
<i>Lymantria dispar</i> ²	Lymantriidae	557.5	52.3	44.7	Michigan, USA	Crawford, Kalkaska County	(57)
<i>Bicyclus anynana</i>	Nymphalidae	194.0	46.0	-11.8	Malawi	Nkhata Bay	(58)
<i>Lasiommata petropolitana</i>	Nymphalidae	152.3	45.1	59.3	Sweden	Stockholm	(59)
<i>Parasemia plantaginis</i>	Arctiidae	212.2	49.1	62	Finland	Jyväskylä	(60)
<i>Utetheisa ornatrix</i>	Arctiidae	190.5	21.1	-22.9	Brazil	Campinas	(61)
<i>Vanessa cardui</i>	Nymphalidae	219.8 (62)	17.6	40.1	Illinois, USA	Savoy	(63)
<i>Acraea acerata</i>	Nymphalidae	89.8	18.7	6.8	Ethiopia	Welayita	(64)
<i>Gonometa postica</i>	Lasiocampidae	5140.0	54.7	0.5	Kenya	Mwingi District, Mumoni	(65)
<i>Papilio polytes</i>	Papilionidae	200.0	14.6	5.4	Malaysia	Penang	(66)
<i>Araschnia levana</i>	Nymphalidae	129.7	30.0	50.0	Germany	Fichtelgebirge	(67)
<i>Doratifera quadriguttata</i>	Limacodidae	346.5	47.1	-33.6	Australia	NSW, Richmond	(68)
<i>Malacosoma disstria</i>	Lasiocampidae	240.2	56.4	46.7	Minnesota, USA	Cloquet	(69)
<i>Eumaeus atala</i>	Lycaenidae	372.5	18.4	29.7	Florida, USA	Gainesville	(70)
<i>Lycaena tityrus</i>	Lycaenidae	132.6	37.5	54.0	Germany	Greifswald	(71)

<i>Lycaena helle</i>	Lycaenidae	62.1	34.0	54.0	Germany	Greifswald	(71)
<i>Melinaea menophilus</i>	Nymphalidae	425.3	13.5	-6.5	Peru	San Martin, Loreto	(72)
<i>Pieris napi</i>	Pieridae	108.7 ³	40.5	39.0	Colorado, USA	Gothic	(73)
<i>Achlya flavicornis</i>	Drepanidae	259.3	65.5	53.9	UK	York	(74)
<i>Spilosoma luteum</i>	Arctiidae	223.7	91.7	53.9	UK	York	(74)
<i>Manduca sexta</i>	Sphingidae	5400.0 (75)	16.5	30.6	Florida, USA	Quincy	(76)
<i>Spilosoma virginica</i>	Arctiidae	271.0	35.0	44.4	Maine, USA	East Bluehill	(77)
<i>Spodoptera litura</i>	Noctuidae	358.0 (78)	19.2	24.0	Taiwan	Wufeng County	(79)
<i>Operophtera brumata</i>	Geometridae	51.5	19.8	60.4	Finland	Turku	(80)

¹ *Epirrita autumnata* is represented by two different data sets - one from Kevo (Northern Finland) and another from Ruissalo (Southern Finland), situated 1044 km apart

² *Lymantria dispar* is represented by two different data sets – one from Quebec (Canada) and one from Michigan (USA), situated 936 km apart

³ Averaged across host plants from a different temperature regime

Table S3.

Best PGLS model of larval development time as a function of absolute latitude and the logarithm of body weight. For the final model, two outliers were omitted (Table A; see text). For comparison, the results of the final model fitted to the full data set are also presented (Table B). The estimated increase in larval development time was 0.36 ± 0.12 (mean \pm SE) days per degree (model including outliers: 0.33 ± 0.18), with an intercept at 22.8 ± 7.1 days at the equator. Thus, the size of the latitudinal effect on daily attack rates (2.7% per degree; see main paper) is larger than the estimated effect on development time, and we conclude that the day-specific pattern in attack rates (main paper) is robust to a potential trend in days spent exposed to attack.

(A)

Effect	Estimate	SE	<i>t</i>	P
Intercept	22.79	7.06	3.23	0.003
Body size	2.43	3.17	0.77	0.45
Latitude	0.36	0.12	2.93	0.007

(B)

Effect	Estimate	SE	<i>t</i>	P
Intercept	25.55	8.07	3.17	0.004
Body size	5.28	3.57	1.48	0.15
Latitude	0.33	0.18	1.80	0.08