

## ARTICLE

# Predation risk estimated on live and artificial insect prey follows different patterns

 Elena L. Zvereva  | Mikhail V. Kozlov 

Department of Biology, University of Turku, Turku, Finland

**Correspondence**
 Elena L. Zvereva  
 Email: [elezve@utu.fi](mailto:elezve@utu.fi)
**Funding information**

Academy of Finland, Grant/Award Numbers: 311929, 316182

**Handling Editor:** Lee A. Dyer
**Abstract**

Models mimicking prey organisms are increasingly used in ecological studies, including testing fundamental ecological and evolutionary theories. The general consensus is that predation risk estimated on artificial models may not quantitatively correspond to predation pressure on live prey, but it still can be used in various comparisons. We tested whether the use of live and artificial prey reveals the same patterns of variation in predation risk. We exposed live prey (blowfly larvae and puparia) and plasticine models of blowfly puparia in two boreal forest sites, both openly and in ant- and bird-exclusion treatments, and we quantified attacks by both avian and invertebrate predators. Bird attack rates were always higher on live puparia than on their plasticine models, but the magnitude of this difference declined from 8.4-fold in early summer to 2-fold in mid- and late-summer. We attribute these changes to different responses to prey by experienced adult birds that dominate the bird communities in early summer versus explorative juvenile birds that are abundant later in the season. Invertebrate daily predation rates on maggots decreased from 56% in early summer to 28% in late summer, but invertebrate attacks on plasticine models showed no seasonal changes. Overall, invertebrate predation on maggots was 67-fold greater than their predation on models. Observations showed that wood ants did not attack plasticine models and did not leave on them any damage marks. Estimates based on artificial prey indicate a much greater role of bird predation than invertebrate predation, while estimates based on live prey suggest the opposite pattern. Thus, using live and artificial prey may lead to different conclusions about relative importance of different predator groups in a locality. Moreover, for both avian and invertebrate predators, predation risk based on artificial and live prey shows different seasonal changes and may potentially demonstrate different spatial patterns.

**KEYWORDS**

ants, bias, birds, invertebrate predators, live insect prey, plasticine model, predation risk, seasonal changes

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Ecology* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

## INTRODUCTION

Models mimicking prey organisms are increasingly used in ecological research (Howe et al., 2009; Low et al., 2014; Roslin et al., 2017; Rößler et al., 2020). Importantly, the studies employing artificial models of prey organisms frequently test fundamental ecological and evolutionary theories, in particular those related to geographic variation in biotic interactions (Roslin et al., 2017; Zvereva et al., 2019) or to the role of predation in the evolution of prey coloration and other prey traits (Mappes et al., 2014; Rowland et al., 2007).

A generally accepted view is that attack rates on plasticine models, although not reflecting the absolute values of predation risk for a natural prey, allow comparisons between localities or habitats (Howe et al., 2009; Roslin et al., 2017; Tvardikova & Novotny, 2012; Zvereva et al., 2019) and time periods (Drozdová et al., 2013; Khan & Joseph, 2021; Molleman et al., 2016). The predation rates estimated on artificial prey models are generally lower than those estimated on live prey (i.e., the estimates are biased) (Lövei & Ferrante, 2017). However, this bias, thus far, has been implicitly assumed not to vary in space and time and, therefore, is not considered to influence the conclusions of studies that use prey models. Nevertheless, studies directly comparing the spatial and temporal patterns in predation obtained by different methods are scarce and have produced inconsistent conclusions. In some of these studies, plasticine models demonstrated spatial patterns in predation rates that were similar to the patterns revealed by predator exclusion experiments (Low et al., 2016) or detected on natural prey (Zvereva, Zverev, et al., 2020). However, other studies did not find correspondence in the patterns revealed by different methods. For example, bird predation on herbivorous insects estimated using plasticine larvae and in bird exclusion experiments yielded different results in a comparison of predation between forest and tundra habitats (Zverev et al., 2020).

This controversy may be partly explained by the considerable changes that occur in predation during the breeding season (Rommel et al., 2009; Zvereva & Kozlov, 2021). The abundance of foraging birds changes through the season due to fledging of young birds, so do the responses of the bird community to prey characteristics, and particularly coloration, due to changes in the proportions of juvenile birds relative to adult birds (Mappes et al., 2014; Zvereva & Kozlov, 2021). Ant predatory activity and diet preferences also change during the season (Domisch et al., 2009; Drozdová et al., 2013). Consequently, the relative avoidance/acceptance of artificial prey items may also change within the season, leading to temporal variations in the bias imposed by using artificial prey.

Several macroecological studies have discovered a general decrease in predation on insects from low to high latitudes, and this decrease was mostly due to the impact of ectothermic predators (Roslin et al., 2017; Zvereva et al., 2019). This pattern, revealed using plasticine models, emerged due to intensive invertebrate predation in tropical areas and extremely low predation at high latitudes, in particular in boreal forests (Roslin et al., 2017; Zvereva et al., 2019). However, the latter result contradicts numerous studies pinpointing the high ecological importance of ants in boreal forest ecosystems (Domisch et al., 2009), in particular due to their intensive predation on herbivorous insects (Maňák et al., 2013; Punttila et al., 2004). One of the impressive results of ant predation is the occurrence of “green islands” of undamaged plants around nests of *Formica* ants within completely defoliated areas during the outbreaks of geometrid moths in Fennoscandia (Karhu & Neuvonen, 1998). This contradiction led us to hypothesize that studies using plasticine models considerably underestimate ant predation in boreal forests.

One of the advantages of using plasticine models in studies of predation is that these models can be standardized across study areas, thereby avoiding the effect of variable methodologies among studies conducted at different latitudes (Roslin et al., 2017). However, artificial prey lacks many characteristics of live prey (Lövei & Ferrante, 2017), and these differences may influence both the absolute estimates of attack rates by predators and, potentially, the various spatial and temporal patterns in predation. Moreover, different predators use different cues in prey searching and, therefore, may respond differently to plasticine, thus biasing information about the relative importance of various predators in a study area. These suggestions may be tested by comparing attack rates on plasticine insect models and on live insect prey, such as larvae (maggots) and puparia of flies. These insect prey does not naturally occur in tree canopies; nevertheless, as widely accepted in predation studies, the sentinel prey does not have to be real and just a superficial similarity to real prey is often sufficient (Lövei & Ferrante, 2017). In addition, fly larvae and pupae have advantages over natural prey in estimating predation risk. Fly larvae live and pupate within a substrate (such as manure or carrion) and, therefore, do not possess any anti-predatory adaptations. In this respect, the larvae differ from natural local prey, but are similar to plasticine models. When exposed in the tree canopy, both these live prey and plasticine models represent unknown prey for local predators and thus direct comparison between predation risk on live and artificial prey is not affected by predator's experience.

We hypothesize that assessment of predation risk using live or artificial standardized prey may yield different

patterns. In this study, we compared patterns in bird and invertebrate predation on plasticine models and live insect prey in boreal forest sites to test the following predictions: (i) both bird and invertebrate predation rates are greater on live prey than on prey models; (ii) the magnitude of this difference in predation rates depends on predator (birds, ants, other invertebrates), time of the season, and type of live prey (moving larvae and motionless puparia).

## MATERIALS AND METHODS

### Study sites

The experiments were conducted at two sites located 58 km apart in southwestern Finland: one near Kustavi (60°31'58" N, 21°18'08" E) and the other near Turku (60°32'11" N, 22°21'52" E). The sites were managed Scots pine (*Pinus sylvestris*) boreal forests with abundant understorey vegetation dominated by birches (*Betula pendula* and *Betula pubescens*) and rowans (*Sorbus aucuparia*), but differed in composition of potential predators. The insectivorous bird species observed in these sites are listed by Zvereva and Kozlov (2021). The community of arboreal ants in Turku was dominated by *Formica polyctena*, whereas in Kustavi the majority of ants collected on birches belonged to *Lasius platythorax* and *Formica sanguinea*. *Myrmica ruginodis* and *Formica fusca* were recorded in both sites.

### Study design

In our study, we used live larvae (maggots hereafter) and puparia of the blowfly *Calliphora* sp. (Diptera: Calliphoridae) and plasticine models with similar appearance to fly puparia in size, color and shape. Both maggots and puparia have been successfully used in earlier studies of predation (Drozdová et al., 2013; Rimmel & Tammaru, 2009). Maggots, obtained in a local fishing bait shop, were 10–13 mm long. They were divided into two equal parts: one part was placed in a refrigerator (at 4°C) to prevent pupation and the other part was kept at room temperature (22°C) and allowed to pupate. We mixed red and black plasticine (advertised as non-toxic and odorless; Chemical plant “Luch,” Yaroslavl, Russia) in the proportion 4:1 to obtain a color (brown) similar to that of puparia, and we molded models from this plasticine. In earlier studies brown colored caterpillar models yielded the same attack rates by predators as widely used green models (Zvereva et al., 2019; Zvereva, Zverev, et al., 2020). Three individual

models were attached in a line along a stick (about 10 cm long, cut from thin birch branches) using universal glue (Yleisliima; Biltema Suomi Oy, Helsinki, Finland) (Figure 1a). In the same fashion we glued three puparia (Figure 1a). The live and plasticine puparia set in this way mimicked some caterpillar-like prey (Rimmel & Tammaru, 2009).

We conducted four different experiments. Experiment 1 was designed to compare bird and invertebrate predation on three different prey items. For this experiment, at each site, we selected 10 pairs (blocks) of young (2–3 m tall) downy birches (*B. pubescens*). The distance between the paired trees was 1–2 m, and the distance between blocks was about 20 m. One tree in each block was isolated from non-flying invertebrate predators (mostly ants) by applying a ring of non-drying glue (Sticky-Trap, Vilofarm A/S, Hobro, Denmark) at the base of the trunk (ant exclusion hereafter). All ants and other invertebrates were removed by shaking these isolated trees and then manually. We ensured that the branches and foliage of any ant-exclusion plants did not touch other trees to prevent any migration of non-flying invertebrate predators (with possible exception of spiders) from neighboring trees. The second tree in each block remained accessible to ants and other predators (control hereafter).

On each of 20 trees, we placed three kinds of prey items: an open transparent plastic vial (40 mm height and 30 mm diameter) containing three maggots, one stick with three puparia and one stick with three models (Figure 1a). The vial was attached with tape to the tree trunk 80–100 cm above the ground (Figure 1b). Each vial also contained a small stick to ease the movement of predatory invertebrates (we had previously verified that the maggots were incapable of climbing on the stick) (Figure 1b). Sticks with puparia and models were attached with small pieces of wire to birch branches (Figure 1c,d) at 100–150 cm above the ground at the outer part of the crown, so that the distance between them was as far as possible. Experiment 1 was repeated (using the same trees) six times in Kustavi and seven times in Turku from 28 May to 11 September 2021.

For all experiments using vials, care was taken to avoid rainy weather through the time of prey exposure. However, the outcomes of one of July experiments in Turku had to be excluded from data analysis due to unexpected rain, as the maggots escaped from vials when their walls became wet. At 24 h from the start of the experiment, we recorded (i) the number of maggots that had disappeared from each vial; (ii) the number of dead maggots in each vial; (iii) the number of damaged puparia (Figure 1d); and (iv) the presence of attack marks by both invertebrates and birds on each of the three plasticine models (Figure 1c). At 4–7 days from the start of the



**FIGURE 1** (a) Set of experimental baits: stick with three blowfly puparia (upper), stick with three plasticine models of blowfly puparia and vial with three maggots; (b) vial with maggots attached to the tree, with ants attacking these maggots; (c) stick with plasticine models attached to tree branch; the rightmost model bears a bird attack mark; (d) stick with puparia after bird attack; (e) vial with maggots protected from birds (bird exclusion treatment); (f) ants carrying prey from vial in bird exclusion treatment.

experiment, we repeated records on live puparia and plasticine models. Bird and invertebrate attacks were distinguished according to Low et al. (2014).

Experiment 2 was conducted to explore whether birds attacked the maggots exposed in vials. At the beginning of June 2021, at both study sites, we selected 20 young

birches and attached a vial with five maggots to the trunk, as described above. To exclude bird predation, we covered the vials on 10 of these birches with bird netting (Figure 1e,f). The number of maggots that disappeared from vials was recorded at 2 days from the start of the experiment.

Experiment 3 was conducted to compare invertebrate attacks on maggots and puparia. In early June of 2021, we placed two vials (as in experiment 1) on each of 20 birch trees in each of two sites. Half of the trees were isolated from ants by glue rings, as described above. We placed three maggots in one of these vials and three puparia into the other. The number of prey individuals that disappeared from vials was recorded at 4 days from the start of the experiment.

Experiment 4 was designed to facilitate the interpretation of some results of experiments 1–3. On 8 June 2022, in Turku, we explored the behavior of wood ants (*F. polyctena*) during the encounter with four prey types: a live maggot, a live puparium (not attached or attached to a stick), and a plasticine model of a puparium. For this experiment, we slightly modified the method outlined in detail by Zvereva et al. (2016). Each prey item was placed singly on an ant trail at a distance 1–5 m from the nearest mound. Each new item (five items of each kind) was placed no closer than 20 cm to a previous item, in random order. The behavior of the ants was continuously recorded by Elena L. Zvereva until a prey item was attacked and attempts to carry it towards the nest were observed; if no attack occurred, the observation lasted 2 min. We recorded: (i) whether ants came in contact with prey and investigated it; (ii) whether ants attacked prey (bit with mandibulae); (iii) whether ants carried prey away after attacking; (iv) the time from discovery of the prey by the ants to the first attack. After the observations, the puparia and models were investigated for signs of damage.

## Data analysis

Based on earlier studies conducted in or close to our study area (Mappes et al., 2014; Zvereva & Kozlov, 2021), we divided the growing season into three periods corresponding to different stages of the bird breeding season. During the first period (from late May to the third week of June; early summer hereafter), birds construct their nests, lay eggs, and then feed their nestlings, and bird community consists of adult experienced birds. The second period (from the end of June to the end of July; mid-summer hereafter) starts when the juvenile birds leave their nests; the bird population at this time becomes dominated by young naïve birds. During the

third period (August to mid-September; late summer hereafter), the young birds already possess experience in foraging for various natural prey (Mappes et al., 2014) and can no longer be considered naïve.

In all analyses, the individual prey items (maggots, puparia or models) were considered experimental units. This approach, when applied to a group of three closely positioned prey items, parallels the previously used number of beak marks on a single caterpillar-shaped plasticine model, which reflects predation intensity (Zvereva & Kozlov, 2021). Moreover, it allowed us to separate a rejection after probing (i.e., one of three items damaged) from an acceptance after probing (i.e., two or three items damaged). We assessed the daily predation rates as the proportion of prey which disappeared from each vial (maggots) or was attacked (puparia and models) divided by the duration of exposure (in days). The attack rates on models were calculated separately for bird and invertebrate predators.

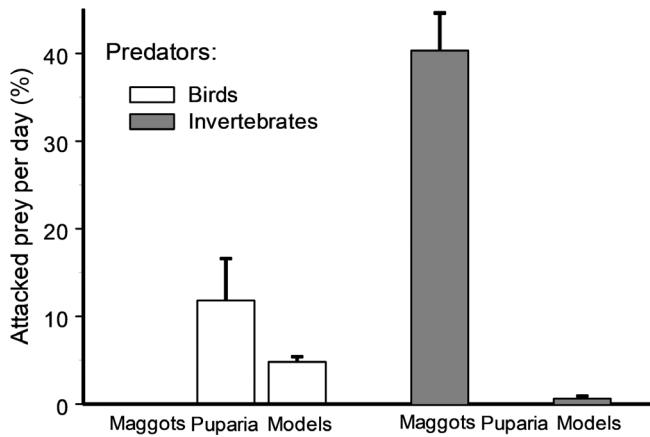
We used a linear mixed model (SAS GLIMMIX procedure, type III tests; SAS Institute, 2009) for the daily predation rates. We considered site (Kustavi or Turku), period (early, mid- and late-summer), treatment (ants or birds excluded or not excluded), bait type (maggots, puparia, models), and their interactions as fixed effects, and 10 blocks nested within each of two sites as a random effect. We facilitated accurate *F* tests of the fixed effects by adjusting the standard errors and denominator degrees of freedom using the latest version of the method by Kenward and Roger (2009). The significance of random effects was explored by a likelihood ratio test (Stroup, 2013), and estimated marginal means were compared by *t*-test (SAS Institute, 2009).

## RESULTS

### Predator attacks on different prey types

Averaged across the entire season, bird attack rates on puparia attached to a stick were 2.5-fold greater than on models (Figure 2; Appendix S1: Table S1). Birds did not attack maggots exposed in vials, as evidenced by similar maggot disappearance rates in the bird exclusion and control treatments (experiment 2:  $F_{1,27} = 0.35$ ,  $p = 0.56$ ).

Invertebrate attack rates were 67 times greater on maggots than on models attached to a stick (Figure 2). Ant exclusion demonstrated that ants contributed 80% to the disappearance of maggots from vials (Figure 3a; Appendix S1: Table S2). Ants removed puparia exposed in vials (experiment 3: Figure 4) but did not damage puparia attached to a stick, as evidenced by similar attack



**FIGURE 2** Daily attack rates of vertebrate (birds) and invertebrate (mostly ants) predators on maggots exposed in vials, puparia attached to sticks and plasticine models of puparia attached to sticks. Values are least square means + SE averaged across all observation dates; data on invertebrate predation are limited to control treatment. The lack of bird predation on maggots is evidenced by bird exclusion (experiment 2); the lack of invertebrate predation on puparia is concluded from ant exclusion (experiment 1).

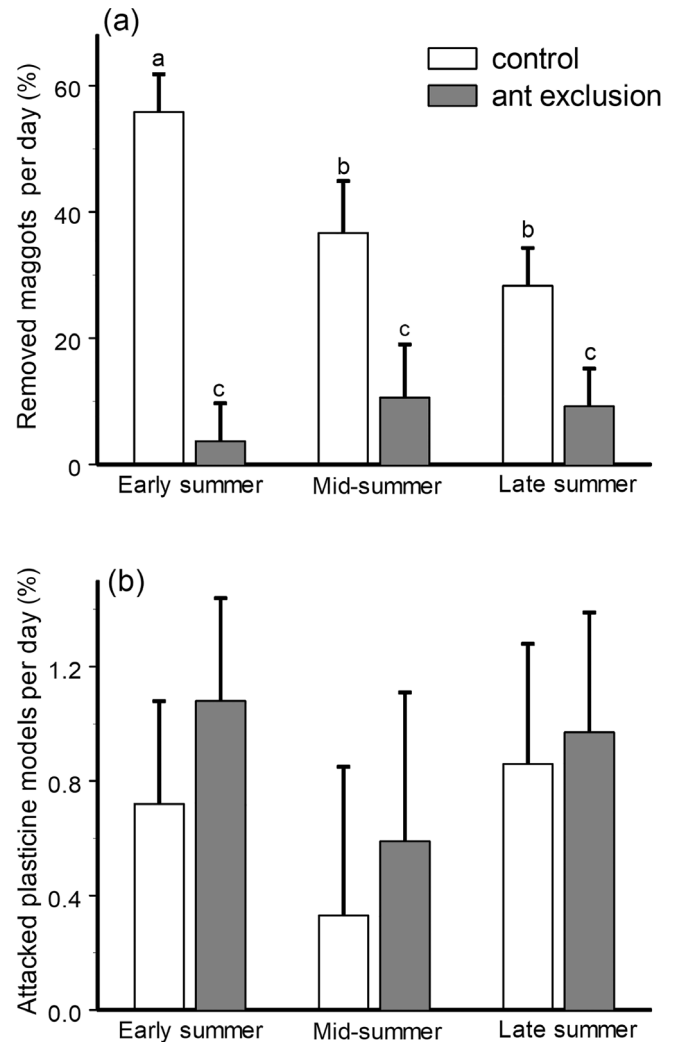
rates on these puparia in the ant exclusion and control treatments (experiment 1:  $F_{1,234.8} = 1.16$ ,  $p = 0.28$ ).

### Bird predation

The daily rates of bird predation varied considerably between sites, between blocks within study sites and between time periods (experiment 1; Appendix S1: Table S1), peaking in mid-summer (Figure 5). Predation rates were higher on live prey (attached puparia) than on plasticine models during the entire season (Figure 5), and the difference in attack rates on these two types of prey changed dramatically during the season. In the early season, daily attack rates were, on average, 8.4-fold higher on live prey than on plasticine prey, but the rates then decreased to 1.8-fold in mid-summer and to 2.1-fold in late summer (Figure 5). As a result, when predation was estimated on live prey, only a 1.5-fold increase was noted from early to mid-summer, while predation estimated on plasticine models showed a 5-fold increase (Figure 5).

### Invertebrate predation

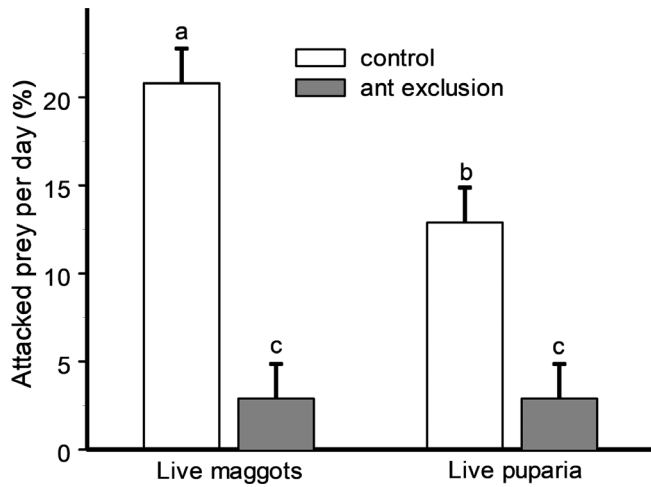
The daily rates of ant predation on maggots did not vary between sites, between blocks within study sites and between time periods (experiment 1; Appendix S1: Table S2). Ant predation in control (ant-accessible) branches was highest in early summer and then declined



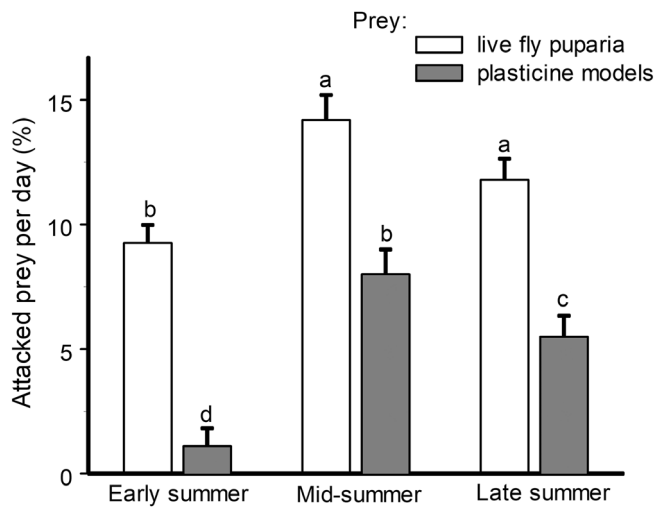
**FIGURE 3** Seasonal variation in daily rates of predation on maggots (a) and invertebrate attacks on plasticine models (b) on trees with allowed ant access (control) and isolated from ants (ant exclusion). Values are least square means + SE. Bars with different letters indicate significant ( $p < 0.05$ ) differences between treatments and time periods ( $t$  test embedded in SAS GLIMMIX procedure). In panel (b), none of the differences are statistically significant. Note the difference in scales between panels (a) and (b).

gradually (Figure 3a). Ant exclusion considerably reduced the disappearance of maggots from the vials (Figure 3a). The daily rates of invertebrate attacks on attached plasticine models were extremely low and did not vary between sites, between blocks within study sites and between time periods (Figure 3b; Appendix S1: Table S3). Moreover, invertebrate predation on plasticine models did not differ between the ant-exclusion and control treatments (Appendix S1: Table S3). In experiment 3, the attack rates on prey exposed in vials were significantly higher for maggots than for puparia (Figure 4; Appendix S1: Table S4).

Observations of wood ant behavior (experiment 4; Appendix S1: Table S5) showed that maggots were



**FIGURE 4** Daily attack rates on moving (maggots) and not moving (puparia) live prey offered in vials on trees with allowed ant access (control) and isolated from ants (ant exclusion). Values are least square means + SE. Bars with different letters indicate significant ( $p < 0.05$ ) differences between treatments and types of prey ( $t$  test embedded in SAS GLIMMIX procedure).



**FIGURE 5** Seasonal variation in bird daily attack rates on live (blowfly puparia) and artificial (plasticine) prey. Values are least square means + SE. Bars with different letters indicate significant ( $p < 0.05$ ) differences between prey types and time periods ( $t$  test embedded in SAS GLIMMIX procedure).

immediately attacked, sometimes by the very first ant that discovered them. Prey movement seemed to stimulate attack and attraction of nestmates. After the first attack, other ants joined and collectively killed a maggot and carried it in the direction of the nest. Puparia not attached to a stick were investigated, but were attacked with a delay (Appendix S1: Table S5); carrying puparia to the nest caused difficulties, as the puparia were frequently dropped. Puparia offered on a stick were

investigated but rarely attacked; no repeated attacks were observed. Plasticine models were carefully investigated with antennae and mouth parts, but were never bitten. No damage was seen on puparia or plasticine models after encounters with ants.

## DISCUSSION

### Bird predation

Birds use visual cues to find their prey, and bird predation is therefore an important factor driving the evolution of prey appearance and behavior (Ruxton et al., 2018). Our plasticine models were similar to the live prey used in our study (fly puparia) in terms of size, shape, color and lack of movements, as well as their position within a tree. Nevertheless, birds avoided attacking our plasticine models even before directly assessing prey suitability by taste, indicating that some other characteristics of these models allow birds to recognize and reject them from a distance.

Birds possess very sophisticated vision systems (Kelber, 2019) and can distinguish even small differences in surface reflectance when searching for prey (Mäntylä et al., 2020). Live and dead organisms, insects in particular, differ in their reflectance spectra (Anderson et al., 2008; Shrestha et al., 2018) and, therefore, can be distinguished visually by birds. In our study sites, birds have never encountered plasticine models used in our experiments. Therefore, we suspect that plasticine shares some spectral characteristics with other inedible objects and that birds avoid plasticine models due to a generalization of visual characteristics, as has been demonstrated in many experiments (e.g., Doktorovová et al., 2019; Svádová et al., 2009). In addition, birds can use olfaction to locate their prey (Amo et al., 2013; Mäntylä et al., 2020) and, therefore, can potentially distinguish live and plasticine prey by smell, without needing to make actual contact. Avoidance of some prey characteristics (e.g., coloration) may be innate (Ruxton et al., 2018). However, birds usually have to learn to avoid unsuitable prey by pecking and rejecting it, and the efficacy of warning coloration or chemical defenses of many insects is based on this avoidance learning (Exnerová et al., 2007; Skelhorn et al., 2016).

The strong (8.4-fold) preference for live prey over plasticine models by birds is observed only in the early season, when the bird community is dominated by experienced adult birds. By contrast, in mid-summer, the live prey are attacked only twice more frequently than plasticine models. This result is in line with earlier findings on seasonal changes in bird preference for differently

colored plasticine models: birds clearly avoided models with warning coloration in the early summer but not in mid-summer (Mappes et al., 2014; Zvereva & Kozlov, 2021). These changes were explained by the naïvety of juvenile birds (which fledge and start feeding independently in mid-summer: Mappes et al., 2014) with respect to different prey items. Moreover, juvenile birds are more explorative than adult birds and, therefore, are less cautious when attacking potential food items (Greenberg & Mettke-Hofmann, 2001). Changes in the avoidance of plasticine models with changes in the level of naïvety of the bird community indicate that the ability of birds to distinguish between edible and inedible objects is not completely innate and has to be learned, independent of whether they base their rejection on visual or olfactory cues. The avoidance of artificial prey slightly increases in late summer, presumably because young birds obtain some experience with prey selection (Mappes et al., 2014) and have begun to recognize and to avoid inedible plasticine models.

## Invertebrate predation

Bird exclusion treatment (experiment 2) indicated that birds did not attack prey in vials, presumably due to avoidance of unknown and/or glossy objects (Waldron et al., 2017) and/or narrow mouth of the vial used. Therefore, disappearance of maggots in vials was attributed to invertebrate predators. Daily attack rates by invertebrate predators on maggots in our boreal forests were very high and approached rates found for invertebrate predation in tropical forests on live wasp larvae (Jeanne, 1979). These high attack rates were observed in both study sites, although their ant communities were dominated by different species. Nevertheless, invertebrate predation rates quantified as attack marks on plasticine models appeared dramatically low compared to attack rates on maggots (67-fold: Figure 2). Similarly, low rates of invertebrate predation on plasticine caterpillars were previously reported from our study sites (Zvereva, Paolucci, et al., 2020) and from other high-latitude sites (Roslin et al., 2017; Zverev et al., 2020; Zvereva et al., 2019).

These low predation rates could not result from the low visibility of attack marks at low temperatures (Muchula et al., 2019), because the summer of 2021 was exceptionally hot in southern Finland, with day temperatures frequently exceeding 25°C. These temperatures should ensure the visibility of even weak marks left by invertebrate predators, had these marks exist.

Similar invertebrate predation on models placed on ant-excluded and control trees indicates that attack marks on our plasticine models were left by invertebrates other

than ants, for example, by predatory bugs, which are abundant in our study sites, and wasps. The lack of attacks by wood ants (*F. polyctena*) on our plasticine models was evident when these models were placed directly on an ant trail, whereas live prey (both maggots and puparia) were attacked and carried away (Appendix S1: Table S5). As a result, the estimates of invertebrate predation rates based on plasticine models do not account for one of the most important groups of invertebrate predators in boreal forests. Some other invertebrate predators were also found not to attack plasticine prey, for example, the ladybird *Harmonia axyridis* (Greenop et al., 2019), beetles of families Staphylinidae and Elateridae, and true bugs of families Geocoridae and Rhyparochromidae (Khan & Joseph, 2021).

Our findings suggest several explanations for the avoidance of plasticine models by ants. First, stronger ant predation on maggots compared to puparia offered in the same way hints at the importance of prey motion. The mobility of prey is known to increase the attack probability by different predators, and particularly ants (Dejean et al., 1999; Witte et al., 2010). The movement of maggots evidently stimulated ant attacks and considerably reduced time to attack compared with motionless puparia (Appendix S1: Table S5). However, these puparia were also attacked by ants (Figure 4; Appendix S1: Table S5), indicating that other signals could also trigger ant attacks.

Second, chemical cues are important for prey recognition by many invertebrate predators (Vet & Dicke, 1992). Studies of ant foraging behavior show that ants analyze prey quality and make decisions about their attack without disturbing the prey (Witte et al., 2010; Zvereva et al., 2016). We observed that ants recognize an inedible item (plasticine model) without needing to bite it. This is explained by ant's extraordinary olfactory sensing abilities (Zhou et al., 2012) and high precision of prey odor discrimination (Binz et al., 2016; Witte et al., 2010).

Third, worker ants, which dominate in boreal forests (e.g., *Formica* spp., *Myrmica* spp.), need only carbohydrates for their own nutrition. They collect insect prey to feed the developing brood and a queen(s) to sustain colony reproduction (Sundström, 1993). Therefore, all the collected insect prey is taken to the nest, and we observed wood ants carrying a maggot away from the vial (Figure 1f). Thus, ants may not be motivated to attack prey that cannot be picked off a surface. This conclusion was supported by our behavioral observations (Appendix S1: Table S5) and by the similar proportion of damages on glued puparia in the control and ant exclusion treatments. An extremely low incidence of ant attacks on fly puparia attached to tree branches was also reported in an earlier study (Rommel & Tammaru, 2009).

The importance for ants of being able to pick up prey is overlooked in most studies of ant predation on sentinel prey, because experimental prey, even when alive, are usually fixed to some surface (e.g., Drozdová et al., 2013; Nimalrathna et al., 2023). We therefore conclude that plasticine models are badly suited for quantifying invertebrate predation because, at least in some habitats, some important groups of predators do not attack plasticine models.

## Sources of biases and their impacts on ecological studies

As expected, both invertebrate and avian predation was always greater on live prey than on plasticine models. However, the present study is the first to demonstrate that the magnitude of the difference in daily predation rates between live and artificial prey strongly depends on the predator type and time of the season. The use of plasticine models, at least in boreal forests, results in greater underestimation of predation risk by invertebrates than by birds, as differences between predation rates on artificial and live prey across the season were, on average, 67-fold for invertebrates and 2.5-fold for birds. Consequently, estimates based on artificial prey show much greater rates of bird predation than invertebrate predation, while estimates based on live prey suggest stronger predation by invertebrates than by birds. Thus, the use of plasticine versus live prey leads to opposite conclusions about the relative roles of different predatory groups with respect to their impact on insects living in tree canopies in our study area.

Our findings suggest that measurements of predation by different groups of predators on the same prey may lead to biased conclusions because different predators use different cues in their prey searches. For invertebrates, discrimination of chemical cues plays the leading role; therefore, some invertebrates may avoid attacking plasticine models due to the wrong olfactory cues emitted by the artificial prey (Lövei & Ferrante, 2017). The latter suggestion is supported by our observations that wood ants encountering plasticine models lose interest to these models after their close investigation (Appendix S1: Table S5). By contrast, birds use mostly visual signals when making decision to attack prey (Ruxton et al., 2018); therefore, birds (especially young ones) may sometimes attack inedible objects resembling live prey, such as plasticine models. Live sentinel prey may also differ in attractiveness for predators depending on the type of bait presentation: birds willingly attack puparia attached to a surface, while ants attack these puparia only when they can easily pick them up. Thus, not only the type of

sentinel prey, but also the way it is offered, is important for adequate quantification of prey mortality due to different predators.

The possibility of determining the predator's identity based on attack marks is often seen as one of the advantages offered by plasticine models (Low et al., 2014; Rößler et al., 2018). This method has been further developed, and more precise identification of attackers has been provided, by amplification and sequencing of mitochondrial DNA left in the bite marks on clay models (Rößler et al., 2020). However, our study shows that important groups of predators, such as some ant species, completely avoid biting plasticine prey after close investigation and, therefore, do not leave any marks on it. Thus, identification based on attack marks on the models is limited to those predators that are non-selective with respect to prey. Consequently, this method of identification will lead to biased conclusions about the composition of the predator community and the relative intensity of their impact on prey.

The difference between adult and juvenile birds in their ability to discriminate inedible objects results in seasonal variations in the magnitude of bias imposed by using plasticine prey on estimates of bird predation. This method underestimates predation risk for live prey by 8.4-fold in early summer but only by about 2-fold in mid- and late-summer. Therefore, the timing of an experiment involving plasticine models may drastically change its conclusions about predation risk for live prey. In particular, our results indicate that studies of evolution in prey coloration using artificial models when bird population consists of both adult and juvenile birds would detect mostly responses of juvenile birds, which actively attack plasticine prey, while adult birds avoid this inedible prey.

Ant predation on live insect prey in our experiment also showed clear changes within the season, in line with other studies conducted in boreal and temperate forests (Domisch et al., 2009; Drozdová et al., 2013). By contrast, invertebrate attacks on plasticine models did not show any seasonal changes. This was mostly because wood ants, one of the most important groups of invertebrate predators in boreal forests, did not attack plasticine models (Appendix S1: Table S5). Thus, the use of models does not reveal the natural temporal patterns in either bird or invertebrate predation pressure on insect herbivores. However, it should be taken into account that live sentinel prey, such as one used in our study, does not possess local antipredatory adaptations and, therefore, may not quantify predation pressure on natural prey community rather reflecting predation risk.

The temporal variation in the differences in predation rates between artificial and live prey, as demonstrated in

our study, could have influenced the results of some previously published studies of high theoretical importance. For example, the lack of a significant latitudinal pattern in bird attacks on plasticine prey in the global study by Roslin et al. (2017), which tested the predictions of the Latitudinal Biotic Interaction Hypothesis (Schemske et al., 2009), may be explained by the different timings of the experiments in relation to bird breeding seasons at different latitudes. Our study has shown that the within-season variation in bird predation, which is especially high on artificial prey, could create noise that would prevent the detection of a pattern existing for natural prey. At the same time, the low number of attack marks left by invertebrates on plasticine models exposed in boreal forests, as revealed by Roslin et al. (2017) and by our study (Figure 2), contrasts with the high pressure of invertebrate predators (primarily ants) on live (moving

and transportable) insect prey. Thus, our comparison of invertebrate attack rates on live prey versus plasticine prey models suggests that the decrease in invertebrate predation with increasing latitude may not be as steep as estimated by Roslin et al. (2017).

## CONCLUSIONS

Concerns about using plasticine models for assessing predation risk, especially for measuring invertebrate predation, have been expressed in several publications (Greenop et al., 2019; Nimalrathna et al., 2023; Vet & Dicke, 1992; Zverev et al., 2020), but our study experimentally demonstrates the limitations and caveats of this method. We have shown (Table 1) that the use of plasticine prey models can lead to wrong conclusions about

**TABLE 1** Overview of experiments and their results.

Experiment no. (s)	Research question	Main findings	For details, see:
1	Do attack rates differ between prey types?	Bird attacks on live prey (puparia) are 2.5-fold greater than on plasticine models. Invertebrate attacks on live prey (maggots) are 67-fold greater than on models.	Figure 2
1	Do seasonal changes in attack rates differ between prey types?	Bird attacks on live prey (puparia) are 8.4-fold greater than on models in early summer and 2-fold greater in mid- and late-summer. Invertebrate attacks on live prey (maggots) decrease 2-fold from early to late summer, but attacks on models do not change within the season.	Figures 3 and 5
1	Does relative importance of bird and invertebrate predation differ between prey types?	Use of models indicates a much greater role of bird predation than of invertebrate predation, while the use of live prey results in the opposite conclusion.	Figure 2 and text
2	Do birds attack maggots offered in vials?	No, presumably because of the narrow mouth of the vial or because of avoidance of an unknown object (vial).	Text
3	Do ants attack puparia offered in vials?	Yes, and ants remove them.	Figure 4
1 and 4	Do ants attack puparia offered on sticks?	Yes, occasionally, but they neither damage nor remove them.	Figure 2, Appendix S1: Table S5
3	Do ants attack maggots and puparia at different rates?	Ants remove puparia from vials at a significantly lower rate than they remove maggots.	Figure 4
1 and 4	Do ants encountering puparia or models leave visible damage on them?	No damage marks are seen on any puparia or models encountered by ants.	Text
4	What are ant behavioral responses to the prey types used in experiments 1–3?	Maggots are immediately attacked, killed and carried away. Puparia offered freely are investigated and then mostly carried away, with some delay. Puparia offered on a stick are investigated, but rarely attacked. Plasticine models are investigated, but never attacked.	Appendix S1: Table S5 and text

predation patterns. First, the predation by wood ants is completely overlooked, resulting in underestimation of the role of invertebrates in overall predation on insect prey in boreal forests. Second, this method provides a biased estimate of seasonal variation in avian predation on insects, dramatically underestimating predation in early summer, and does not reveal seasonal variations in invertebrate predation. Both these biases may considerably influence the outcomes of studies addressing spatial and temporal variations in predation risks. Therefore, we recommend that estimations of predation risk using plasticine prey, and especially the interpretation of the obtained results, should be made with caution, while keeping in mind possible variations in the magnitude of bias imposed by this method.

## ACKNOWLEDGMENTS

The authors were supported by the Academy of Finland (projects 311929 and 316182). We are grateful to P. Puntila for identification of ants, to V. Zverev for help in preparation of illustrations, to T. Klemola for statistical advices, and to K. Sam and to an anonymous reviewer for inspiring comments to an earlier version of the manuscript.



## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Zvereva & Kozlov, 2022) are available from Dryad at <https://doi.org/10.5061/dryad.q573n5tnd>.

## ORCID

Elena L. Zvereva  <https://orcid.org/0000-0003-2934-3421>  
Mikhail V. Kozlov  <https://orcid.org/0000-0002-9500-4244>

## REFERENCES

- Amo, L., J. J. Jansen, N. M. van Dam, M. Dicke, and M. E. Visser. 2013. "Birds Exploit Herbivore-Induced Plant Volatiles to Locate Herbivorous Prey." *Ecology Letters* 16: 1348–55. <https://doi.org/10.1111/ele.12177>.
- Anderson, J., C. Reynolds, D. Ringelberg, J. Edwards, and K. Foley. 2008. "Differentiation of Live-Viable Versus Dead Bacterial Endospores by Calibrated Hyperspectral Reflectance Microscopy." *Journal of Microscopy* 232: 130–6. <https://doi.org/10.1111/j.1365-2818.2008.02074.x>.
- Binz, H., E. F. Kraft, M. H. Entling, and F. Menzel. 2016. "Behavioral Response of a Generalist Predator to Chemotactile Cues of Two Taxonomically Distinct Prey Species." *Chemoecology* 26: 153–62. <https://doi.org/10.1007/s00049-016-0215-z>.
- Dejean, A., B. Schatz, and M. Kenne. 1999. "How a Group Foraging Myrmicine Ant Overwhelms Large Prey Items (Hymenoptera: Formicidae)." *Sociobiology* 34: 407–18.
- Doktorovová, L., A. Exnerová, K. H. Svádová, P. Štys, D. Adamová-Ježová, V. Zverev, M. V. Kozlov, and E. L. Zvereva. 2019. "Differential Bird Responses to Colour Morphs of an Aposematic Leaf Beetle May Affect Variation in Morph Frequencies in Polymorphic Prey Populations." *Evolutionary Biology* 46: 35–46. <https://doi.org/10.1007/s11692-018-9465-8>.
- Domisch, T., L. Finér, S. Neuvonen, P. Niemelä, A. C. Risch, J. Kilpeläinen, M. Ohashi, and M. F. Jurgensen. 2009. "Foraging Activity and Dietary Spectrum of Wood Ants (*Formica rufa* Group) and their Role in Nutrient Fluxes in Boreal Forests." *Ecological Entomology* 34: 369–77. <https://doi.org/10.1111/j.1365-2311.2009.01086.x>.
- Drozdová, M., J. Šipoš, and P. Drozd. 2013. "Key Factors Affecting the Predation Risk on Insects on Leaves in Temperate Floodplain Forest." *European Journal of Entomology* 110: 469–76. <https://doi.org/10.14411/eje.2013.062>.
- Exnerová, A., P. Štys, E. Fuciková, S. Vesela, K. H. Svádová, M. Prokopová, V. Jarošík, R. Fuchs, and E. Landová. 2007. "Avoidance of Aposematic Prey in European Tits (Paridae): Learned or Innate?" *Behavioural Ecology* 18: 148–56. <https://doi.org/10.1093/beheco/arl061>.
- Greenberg, R., and C. Mettke-Hofmann. 2001. "Ecological Aspects of Neophobia and Neophilia in Birds." In *Current Ornithology*, Vol 16, edited by V. Nolan and C. F. Thompson, 119–78. New York: Springer.
- Greenop, A., A. Cecelja, B. A. Woodcock, A. Wilby, S. M. Cook, and R. F. Pywell. 2019. "Two Common Invertebrate Predators Show Varying Predation Responses to Different Types of Sentinel Prey." *Journal of Applied Entomology* 143: 380–6. <https://doi.org/10.1111/jen.12612>.
- Howe, A., G. L. Lövei, and G. Nachman. 2009. "Dummy Caterpillars as a Simple Method to Assess Predation Rates on Invertebrates in a Tropical Agroecosystem." *Entomologia Experimentalis et Applicata* 131: 325–9. <https://doi.org/10.1111/j.1570-7458.2009.00860.x>.
- Jeanne, R. L. 1979. "A Latitudinal Gradient in Rates of Ant Predation." *Ecology* 60: 1211–24. <https://doi.org/10.2307/1936968>.
- Karhu, K. J., and S. Neuvonen. 1998. "Wood Ants and a Geometrid Defoliator of Birch: Predation Outweighs Beneficial Effects through the Host Plant." *Oecologia* 113: 509–16. <https://doi.org/10.1007/s004420050403>.
- Kelber, A. 2019. "Bird Colour Vision - From Cones to Perception." *Current Opinion in Behavioral Sciences* 30: 34–40. <https://doi.org/10.1016/j.cobeha.2019.05.003>.
- Kenward, M. G., and J. H. Roger. 2009. "An Improved Approximation to the Precision of Fixed Effects from Restricted Maximum Likelihood." *Computational Statistics & Data Analysis* 53: 2583–95. <https://doi.org/10.1016/j.csda.2008.12.013>.
- Khan, F. Z. A., and S. V. Joseph. 2021. "Characterization of Impressions Created by Turfgrass Arthropods on Clay Models." *Entomologia Experimentalis et Applicata* 169: 508–18. <https://doi.org/10.1111/eea.13000>.
- Lövei, G. L., and M. Ferrante. 2017. "A Review of the Sentinel Prey Method as a Way of Quantifying Invertebrate Predation under Field Conditions." *Insect Science* 24: 528–42. <https://doi.org/10.1111/1744-7917.12405>.
- Low, P. A., C. McArthur, and D. F. Hochuli. 2016. "It is Safe to Go Out on a Limb: Within-Tree Leaf Age and Location Do Not Alter Predation Risk for Insect Herbivores." *Austral Entomology* 55: 284–90. <https://doi.org/10.1111/aen.12183>.

- Low, P. A., K. Sam, C. McArthur, M. R. C. Posa, and D. F. Hochuli. 2014. "Determining Predator Identity from Attack Marks Left in Model Caterpillars: Guidelines for Best Practice." *Entomologia Experimentalis et Applicata* 152: 120–6. <https://doi.org/10.1111/eea.12207>.
- Maňák, V., H. Nordenhem, N. Björklund, L. Lenoir, and G. Nordlander. 2013. "Ants Protect Conifer Seedlings from Feeding Damage by the Pine Weevil *Hylobius abietis*." *Agricultural and Forest Entomology* 15: 98–105. <https://doi.org/10.1111/j.1461-9563.2012.00597.x>.
- Mäntylä, E., S. Kipper, and M. Hilker. 2020. "Insectivorous Birds Can See and Smell Systemically Herbivore-Induced Pines." *Ecology and Evolution* 10: 9358–70. <https://doi.org/10.1002/ece3.6622>.
- Mappes, J., H. Kokko, K. Ojala, and L. Lindström. 2014. "Seasonal Changes in Predator Community Switch the Direction of Selection for Prey Defences." *Nature Communications* 5: 5016. <https://doi.org/10.1038/ncomms6016>.
- Molleman, F., T. Rimmel, and K. Sam. 2016. "Phenology of Predation on Insects in a Tropical Forest: Temporal Variation in Attack Rate on Dummy Caterpillars." *Biotropica* 48: 229–36. <https://doi.org/10.1111/btp.12268>.
- Muchula, K., G. Xie, and G. M. Gurr. 2019. "Ambient Temperature Affects the Utility of Plasticine Caterpillar Models as a Tool to Measure Activity of Predators across Latitudinal and Elevational Gradients." *Biological Control* 129: 12–7. <https://doi.org/10.1016/j.biocontrol.2018.11.006>.
- Nimalrathna, T. S., I. D. Solina, A. M. Mon, N. Pomoim, S. Bhadra, E. L. Zvereva, K. Sam, and A. Nakamura. 2023. "Estimating Predation Pressure in Ecological Studies: Controlling Bias Imposed by Using Sentinel Plasticine Prey." *Entomologia Experimentalis et Applicata* 171: 56–67.
- Punttila, P., P. Niemelä, and K. Karhu. 2004. "The Impact of Wood Ants (Hymenoptera: Formicidae) on the Structure of Invertebrate Community on Mountain Birch (*Betula pubescens* ssp. *czerepanovii*)." *Annales Zoologici Fennici* 41: 429–46.
- Rimmel, T., and T. Tammaru. 2009. "Size-Dependent Predation Risk in Tree-Feeding Insects with Different Colouration Strategies: A Field Experiment." *Journal of Animal Ecology* 78: 973–80. <https://doi.org/10.1111/j.1365-2656.2009.01566.x>.
- Rimmel, T., T. Tammaru, and M. Magi. 2009. "Seasonal Mortality Trends in Tree-Feeding Insects: A Field Experiment." *Ecological Entomology* 34: 98–106. <https://doi.org/10.1111/j.1365-2311.2008.01044.x>.
- Roslin, T., B. Hardwick, V. Novotny, W. K. Petry, N. R. Andrew, A. Asmus, I. C. Barrio, et al. 2017. "Higher Predation Risk for Insect Prey at Low Latitudes and Elevations." *Science* 356: 742–4. <https://doi.org/10.1126/science.aaj1631>.
- Rößler, D. C., S. Lötters, M. Veith, M. Fugmann, C. Peters, S. Künzel, and H. Krehenwinkel. 2020. "An Amplicon Sequencing Protocol for Attacker Identification from DNA Traces Left on Artificial Prey." *Methods in Ecology and Evolution* 11: 1338–47. <https://doi.org/10.1111/2041-210X.13459>.
- Rößler, D. C., H. Pröhl, and S. Lötters. 2018. "The Future of Clay Model Studies." *BMC Zoology* 3: 6. <https://doi.org/10.1186/s40850-018-0033-6>.
- Rowland, H. M., M. P. Speed, G. D. Ruxton, M. Edmunds, M. Stevens, and I. F. Harvey. 2007. "Countershading Enhances Cryptic Protection: An Experiment with Wild Birds and Artificial Prey." *Animal Behaviour* 74: 1249–58. <https://doi.org/10.1016/j.anbehav.2007.01.030>.
- Ruxton, G. D., W. L. Allen, T. N. Sherratt, and M. P. Speed. 2018. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry*, 2nd ed. Oxford, UK: Oxford University Press.
- SAS Institute. 2009. *SAS/Stat. User's Guide, Version 9.2*. Cary, NC: SAS Institute.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. "Is there a Latitudinal Gradient in the Importance of Biotic Interactions?" *Annual Review of Ecology, Evolution, and Systematics* 40: 245–69.
- Shrestha, S., H. B. Topbjerg, N. K. Ytting, H. Skovgård, and B. Boelt. 2018. "Detection of Live Larvae in Cocoons of *Bathyplectes curculionis* (Hymenoptera: Ichneumonidae) Using Visible/Near-Infrared Multispectral Imaging." *Pest Management Science* 74: 2168–75. <https://doi.org/10.1002/ps.4915>.
- Skelhorn, J., C. G. Halpin, and C. Rowe. 2016. "Learning about Aposematic Prey." *Behavioral Ecology* 27: 955–64. <https://doi.org/10.1093/beheco/arw009>.
- Stroup, W. W. 2013. *Generalized Linear Mixed Models: Modern Concepts, Methods and Applications*. Boca Raton, FL: CRC Press.
- Sundström, L. 1993. "Foraging Responses of *Formica truncorum* (Hymenoptera, Formicidae) Exploiting Stable vs Spatially and Temporally Variable Resources." *Insectes Sociaux* 40: 147–61. <https://doi.org/10.1007/BF01240703>.
- Svádová, K. H., A. Exnerová, P. Štys, E. Landová, J. Valenta, A. Fučíková, and R. Socha. 2009. "Role of Different Colours of Aposematic Insects in Learning, Memory and Generalization of Naive Bird Predators." *Animal Behaviour* 77: 327–36. <https://doi.org/10.1016/j.anbehav.2008.09.034>.
- Tvardikova, K., and V. Novotny. 2012. "Predation on Exposed and Leaf-Rolling Artificial Caterpillars in Tropical Forests of Papua New Guinea." *Journal of Tropical Ecology* 28: 331–41. <https://doi.org/10.1017/S0266467412000235>.
- Vet, L. E. M., and M. Dicke. 1992. "Ecology of Infochemical Use by Natural Enemies in Tritrophic Context." *Annual Review of Entomology* 37: 141–72. <https://doi.org/10.1146/annurev.en.37.010192.001041>.
- Waldron, S. J., J. A. Endler, J. K. Valkonen, A. Honma, S. Dobler, and J. Mappes. 2017. "Experimental Evidence Suggests that Specular Reflectance and Glossy Appearance Help Amplify Warning Signals." *Scientific Reports* 7: 257. <https://doi.org/10.1038/s41598-017-00217-5>.
- Witte, V., D. Schliessmann, and R. Hashim. 2010. "Attack or Call for Help? Rapid Individual Decisions in a Group-Hunting Ant." *Behavioral Ecology* 21: 1040–7. <https://doi.org/10.1093/beheco/arq100>.
- Zhou, X. F., J. D. Slone, A. Rokas, S. L. Berger, J. Liebig, A. Ray, D. Reinberg, and L. J. Zwiebel. 2012. "Phylogenetic and Transcriptomic Analysis of Chemosensory Receptors in a Pair of Divergent Ant Species Reveals Sex-Specific Signatures of Odor Coding." *PLoS Genetics* 8: e1002930. <https://doi.org/10.1371/journal.pgen.1002930>.
- Zverev, V., E. L. Zvereva, and M. V. Kozlov. 2020. "Bird Predation Does Not Explain Spatial Variation in Insect Herbivory in a Forest-Tundra Ecotone." *Polar Biology* 43: 295–304. <https://doi.org/10.1007/s00300-020-02633-2>.

- Zvereva, E. L., B. Castagneyrol, T. Cornelissen, A. Forsman, J. A. Hernandez-Aguero, T. Klemola, L. Paolucci, et al. 2019. "Opposite Latitudinal Patterns for Bird and Arthropod Predation Revealed in Experiments with Differently Colored Artificial Prey." *Ecology and Evolution* 9: 14273–85. <https://doi.org/10.1002/ece3.5862>.
- Zvereva, E. L., and M. V. Kozlov. 2021. "Seasonal Variations in Bird Selection Pressure on Prey Colouration." *Oecologia* 196: 1017–26. <https://doi.org/10.1007/s00442-021-04994-9>.
- Zvereva, E. L., M. V. Kozlov, and N. E. Rank. 2016. "Does Ant Predation Favour Leaf Beetle Specialization on Toxic Host Plants?" *Biological Journal of the Linnean Society* 119: 201–12. <https://doi.org/10.1111/bij.12801>.
- Zvereva, E. L., L. N. Paolucci, and M. V. Kozlov. 2020. "Top-Down Factors Contribute to Differences in Insect Herbivory between Saplings and Mature Trees in Boreal and Tropical Forests." *Oecologia* 193: 167–76. <https://doi.org/10.1007/s00442-020-04659-z>.
- Zvereva, E. L., V. Zverev, and M. V. Kozlov. 2020. "Predation and Parasitism on Herbivorous Insects Change in Opposite

Directions in a Latitudinal Gradient Crossing a Boreal Forest Zone." *Journal of Animal Ecology* 89: 2946–57. <https://doi.org/10.1111/1365-2656.13350>.

Zvereva, E. L., and M. V. Kozlov. 2022. "Data from 'Predation Risk Estimated on Live and Artificial Insect Prey Follows Different patterns'." Dryad, Dataset. <https://doi.org/10.5061/dryad.q573n5tnd>.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Zvereva, Elena L., and Mikhail V. Kozlov. 2023. "Predation Risk Estimated on Live and Artificial Insect Prey Follows Different Patterns." *Ecology* e3943. <https://doi.org/10.1002/ecy.3943>