Accuracy in bird predation assessment: Camera traps testing the efficacy of plasticine caterpillars as prey models

Accuracy in bird predation assessed by camera traps

Laura Schillé[1,¤], Nattan Plat[1,¤], Luc Barbaro[2], Hervé Jactel[1], Frédéric Raspail[1], Jean-Baptiste Rivoal[1], Bastien Castagneyrol[1,#], Anna Mrazova[1,3,#]

Affiliations
[1]BIOGECO, INRAE, University Bordeaux, Cestas, France
[2]DYNAFOR, University of Toulouse, INRAE, Toulouse, France
[3]Institute of Entomology, Biology Centre of the Czech Academy of Sciences, Ceske Budejovice, Czech Republic
[¤]Laura Schillé and Nattan Plat share the first co-authorship.
[#]Anna Mrazova and Bastien Castagneyrol share the last co-authorship.

Contributions

A.M., L.S., and N.P. developed the original idea. A.M., B.C., L.S., and N.P. developed the methodology. A.M., B.C., H.J., JB.R., L.B., L.S., and N.P. conducted data collection. F.R. implemented the computer code. A.M. and L.S. did the formal analysis and wrote the original draft, and all co-authors provided critical reviews of the manuscript.

Abstract

Sampling methods that are both scientifically rigorous and ethical are cornerstones of any experimental biological research. Since its introduction 30 years ago, the method of using plasticine prey to quantify predation risk has become increasingly popular in the field of biology. However, recent studies have questioned the accuracy of the method, arguing that inaccuracy in inferring evidence of predator bite marks and the artificiality of models may bias the results. Yet, bias *per se* might not be a methodological issue as soon as its statistical distribution in the samples is even, quantifiable, and thus correctable in quantitative

analyses. In this study, we focus on avian predation of lepidopteran larvae models, which represent one of the most widespread predator-prey interactions in various ecosystems worldwide. We compared bird predation on plasticine caterpillar models to that on dead caterpillars of similar size and color, using camera traps and observer posterior assessment to identify biases and quantify actual predation events. Although camera trap analyses revealed that birds respond similarly to plasticine models and dead caterpillars, suggesting no advantage in using dead prey for assessing avian predation, the results of posterior identification of predation marks showed contradictory results, making the interpretation of the results ambiguous. Observer inconsistencies in detecting predation clues on models highlight potential biases, with camera trap data showing these clues do not reliably indicate actual bird predation. Given the uncertainties and shortcomings of technological character revealed, the development of adequate monitoring methods and further research is essential to refine the assessment approach and better understand the biases in using plasticine models.

Keywords: artificial prey; bird predation; camera trap; ecological methods; fake prey; plasticine caterpillar models; real caterpillars

Introduction

The functional role of insectivorous birds in terrestrial ecosystems (1,2) has been the focus of many studies aimed at understanding the predation patterns, feeding behavior, predator control of prey populations and evolutionary ecology (3–6). Traditional methodological approaches to these research topics include direct field observations (7), experimental manipulation in the laboratory (8,9) or in the field (10), and gut or fecal DNA analyses

(11,12). Each of these methods has its own set of limitations regarding standardization, logistics, and ethical considerations such as not sparing living prey or handling captive birds. To address these challenges, the use of artificial prey, particularly those made of plasticine, introduced over 30 years ago by Brodie III (13), has become a valuable tool in bird predation research (14). The method is primarily appreciated for its ability to preserve the bite marks of predators, the identification and quantification of which has been used to infer attacks and predation risk from specific predators.

While plasticine caterpillar models are widely employed as simple, standardized prey models to investigate predation activity in diverse ecosystems (15–17), recent studies have raised concerns regarding their limitations and potential inaccuracies (14,18–20). The main concerns relate to the accuracy of inferences of predator identity and activity from the posterior assessment of putative predation marks on prey models.

Inaccuracy of predator identity - Observers may struggle to attribute a considerable portion of attack marks to a specific predator type, e.g., bird, reptile, or arthropod (18,19). For example, Valdés-Correcher et al. (21) found that up to 24% of predation mark identifications were inaccurate when assessed by untrained scientists using photos of attacked plasticine caterpillar models. This was observed in comparison to evaluations conducted by an expert who had access to the actual plasticine caterpillar models. This result shows that the identification of predator marks often relies on subjective human judgment, which can lead to observer bias. This variability is accentuated by the absence of a standardized training system for observers, thus giving them more certainty in recognizing such marks (18,22; but see Low et al. (23), for examples of predator-type

classified bite mark images), leading to potential discrepancies in interpretations among researchers.

Inaccuracy in determining real predation events among all identified marks - Even though marks were attributed to birds, questions would remain about what one can infer from them. Incidental contact or non-predatory interactions (e.g., by bird claws, attraction of non-predatory animals, or curiosity) with the plasticine caterpillar models can result in marks that are difficult to distinguish from genuine predation attempts, potentially leading to an overestimation of predation rates (24). The misinterpretation of marks can lead to distorted results on predation pressure and misleading conclusions about predator-prey interactions, especially in areas where the attack rate is low (25).

Furthermore, the artificial appearance and texture of plasticine may not adequately simulate the characteristics of real prey, including smell, possibly affecting the behavior of insectivorous birds and thus the validity of predation assessment (19). The literature contains several studies that compared the attack rates on plasticine larvae to those of real larvae, with the latter being quantified based on missing or partially consumed prey items (19,20,24). As opposed to plasticine caterpillar models, the attack rate on living and dead prey has shown comparable results (19), thus justifying not using living prey for ethical reasons (not to glue or pin them alive). By simultaneously studying predation on dead caterpillars versus plasticine models, it becomes possible to compare the response of predators to both types of prey within the same experimental design with the use of passive monitoring methods. This comparative approach makes it possible to test the assumptions on which the plasticine caterpillar model method is biased and to correct it in relation to

observable predation patterns on real dead prey. Quantifying this bias is critical to determining whether plasticine models can reliably mimic real prey, and thus whether the data they provide can reflect an accurate depiction of predation pressure.

Studies comparing predation on both real caterpillars and plasticine models have shown discrepancies, revealing that plasticine models may not be a sufficiently accurate method for assessing predation (19), particularly across large biogeographical ranges (24), varying thermal regimes (26), different seasons of the bird life cycle (20), and for different taxa (19). There appears to be a gap in the literature regarding more detailed analyses that elucidate the origins of the marks found on plasticine models. Moreover, missing plasticine models are usually excluded from the statistical analyses (16,27). Yet, at least part of those missing models can be the result of a predation attempt that was not recorded. On the contrary, studies working with real prey have often assumed that a missing prey was equivalent to a depredated prey (19,20,24), an assumption that may not always hold true. Without direct observation, the reasons behind the disappearance of the prey remain speculative.

To address these methodological uncertainties, and following recommendations from Bateman et al. (18) and Rößler et al. (22), we employed camera traps. As they have been already used to study bird frugivory (28,29), we suggest their application also to experimentally record predation on plasticine models (hereafter “models”) paired with dead caterpillars (hereafter “corpses”) on the experimental trees. We hypothesized that the integration of camera traps could visually confirm predation attempts, providing a direct and unbiased record of predator interactions with the prey. This visual evidence could

enable the differentiation between actual predation marks and those resulting from incidental contact or environmental factors (e.g., rubbing by leaves or branches), therefore increasing the accuracy of predation rate assessment. Ultimately, we believe that the results of this study will help to refine the plasticine caterpillar model method as a tool for ecological research, ensuring that it produces scientifically relevant results.

We used camera traps to quantify predation events on both prey types and possible sources of bias in inferences made from plasticine models. We first assessed bias in the detection of predation clues on plasticine models due to variation among observers (H1). We further hypothesize that observer detection of predation clues leads to an overestimation of predation on plasticine models by attributing unrelated or uncertain marks to actual predation attempts (H2). Taking into account the innate ability of insectivorous birds to recognize suitable prey and the differences in the surface texture of real vs. plasticine caterpillars, we hypothesize that there will be evidence of more predation on corpses than on models, both assessed using camera traps (H3). Finally, we hypothesize that observer detection of predation would lead to an overestimation of the predation on corpses by accounting for missing individuals as a predation event, lacking direct evidence for why the prey disappeared (H4). If we obtain comparable results of the bias between observers and cameras for both models and corpses, and if the test of H3 provides evidence of more predation on corpses than on models, we could conclude that the use of corpses with human post-detection would be a more accurate method than the use of plasticine models with human post-detection.

136 ## Material and Methods

137 ### Study area

138 We carried out this experiment in a pine and oak forest stand of 5ha near Bordeaux, France
139 (44°440N, 00°460W). The climate is oceanic, with 12.8°C average temperature and 870mm
140 annual rainfall. We synchronized the start of the experiment as closely as possible with the
141 breeding period of local insectivorous birds, specifically, when the chicks were in the nest
142 and fed by the parents (starting generally mid-April for resident breeders or early
143 migrants). We choose this timing to quantify bird predation by experienced adults rather
144 than later exploratory predation attempts by young, inexperienced birds. The main
145 insectivorous bird species in the study area were Great Tit (*Parus major*), Eurasian Blue Tit
146 (*Cyanistes caeruleus*), Eurasian Blackcap (*Sylvia Atricapilla*), Common Redstart (*Phoenicurus*
147 *phoenicurus*), Eurasian Blackbird (*Turdus merula*), Western Bonelli's Warbler (*Phylloscopus*
148 *bonelli*), Common Chiffchaff (*Phylloscopus collybita*), Short-toed Treecreeper (*Certhia*
149 *brachydactyla*), Eurasian Nuthatch (*Sitta europaea*), European Robin (*Erithacus rubecula*),
150 Eurasian Wren (*Troglodytes troglodytes*), and Great Spotted Woodpecker (*Dendrocopos*
151 *major*) (30).

152 These bird species have home ranges that vary between 0.3 ha for the Blue Tit (31) and 7.9
153 ha for the Common Chiffchaff (32), the latter value being extreme as compared to most of
154 the insectivorous species (33,34). It is therefore likely that multiple individuals of the same
155 insectivorous bird species defended separate territories in the study area. Together with
156 the fact that we distributed the experiment across the whole forest stand (see below) and
157 that oak trees host a large density of herbivorous insects (N. Plat, A. Mrazova, and L. Schillé

158 personal observation), we doubt that birds learned to avoid corpses and models during the
159 experiment.

160 ## Study design

161 First, we haphazardly selected 12 pedunculate oaks (*Quercus robur*, the dominant
162 broadleaved species of the area) located at least 10m apart from each other. On one branch
163 accessible from the ground of each of these trees, we glued five plasticine models, and on
164 another branch as far as possible from the first one, we glued another set of five corpses of
165 *Operophtera brumata* larvae, previously killed by freezing at -80°C. We use this level of prey
166 density because (i) the natural density of caterpillars was high at this time of the year, and
167 (ii) to optimize the use of camera traps by ensuring an adequate number of statistical
168 replicates. The five caterpillars on each branch were spaced at least 5 cm apart to remain in
169 the focus of camera traps.

170 We used the lepidopteran species *Operophtera brumata* for experimentation, a widespread
171 and often abundant oak-defoliating moth. The caterpillars, whether models or corpses,
172 were directly glued to the branches with two glue drops. We used corpses for ethical
173 reasons, to avoid gluing living caterpillars.

174 We modeled artificial caterpillars with green plasticine (Staedtler brand, model 8421-5),
175 forming 1.5 × 0.3 cm cylindrical shapes and mimicking Lepidopteran larvae. They had the
176 same color as most plasticine models commonly used in studies of predation interactions in
177 ecology (15–17,23,35) and the same size as *Operophtera brumata* dead larvae used as
178 corpses.

Corpses darken when exposed in the field; after 48 hours, their color differs from that of live individuals. We cannot exclude that their smell change too. For these reasons, we exposed fresh models and corpses on a new set of 12 trees every two days. After 16 days, this procedure resulted in a total of 480 model- and 480 corpse- caterpillars installed on 96 oaks.

Predation analysis

We took plasticine models collected in the field to the laboratory in plastic vials. Note that none of the plasticine models disappeared during the experiment. All models were examined by three experienced observers who identified marks of attempted predation by birds using a magnifying glass. The models were considered 'attacked' if they exhibited at least one attack mark on the plasticine surface. Observers carefully reread the bite mark guide published by Low et al. (23) beforehand. These observations were used to evaluate consistency among the observers. In cases of doubt regarding whether a model was attacked or not, the observers discussed and reached a consensus. Hereafter, we refer to the presence of marks reported by human observers' consensus as 'predation clues'.

Predation clues on corpses were directly examined in the field. A missing corpse or one with a missing part was considered attacked, as is generally the case in the literature (19,20,24).

Image analysis

Interactions between predators and corpses as well as models were recorded using camera traps (Brand Ltl Acorn model Ltl-5210M). We installed two camera traps on the trunk of

200 each tree facing the two branches holding models and corpses, respectively. The camera
201 was positioned about 1m from the caterpillars to make it easier to focus (without blurring)
202 (Fig 1). The camera traps were active 24 hours a day for the 14 consecutive days of the
203 experiment. They were set to the highest sensitivity and automatically took bursts of three
204 photos when the passive infrared (PIR) sensors detected motion with a 0.5s trigger speed.
205 At each field visit, we changed the SD cards and checked the batteries to replace them if
206 necessary.

207 We analyzed the images taken by camera traps using the application EcoAssist (36)
208 supporting the MegaDetector learning model (Machine Learning for Wildlife Image
209 Classification, (37)). This learning model automatically detects the presence of animals in
210 images. We used the most conservative detection confidence threshold of 0.01 for the
211 model in the EcoAssist application, as this threshold previously tested showed a 100%
212 success rate (i.e., all birds present in the images were detected). Following this detection
213 process, we carried out a visual examination by an observer of the images. This examination
214 concerned both corpses and plasticine models.

215 Our camera traps were insufficient to monitor all predation events due to the birds' small
216 size and stealthy behavior. Therefore, we defined 'evidence of predatory bird presence' at
217 the branch level as the presence of at least one image showing a foraging bird on the branch
218 (hereafter 'evidence of bird presence'). These images could show individuals in various
219 contexts: birds looking at the camera (Fig 2d and 2e), flying over the target branch (Fig 2a),
220 engaging in foraging activity on the target branch but with natural prey on the bill (Fig 2c

and 2e), foraging on experimental prey (Fig 2f and 2h), standing on the experimental branch (Fig 2b and 2g), or feeding during early morning (Fig 2e).

Subsequently, we statistically compared this evidence of bird presence to the predation clue determined by human observers on the same branch. A branch was categorized as having a predation clue if at least one of its five caterpillars showed a predation clue.

All observed evidence of predator presence, regardless of whether the predator was a bird or not, was also carefully recorded for further discussion. It should be noted, however, that arthropod predators were unlikely to be detected by camera traps. We identified all species associated with the evidence of bird presence.

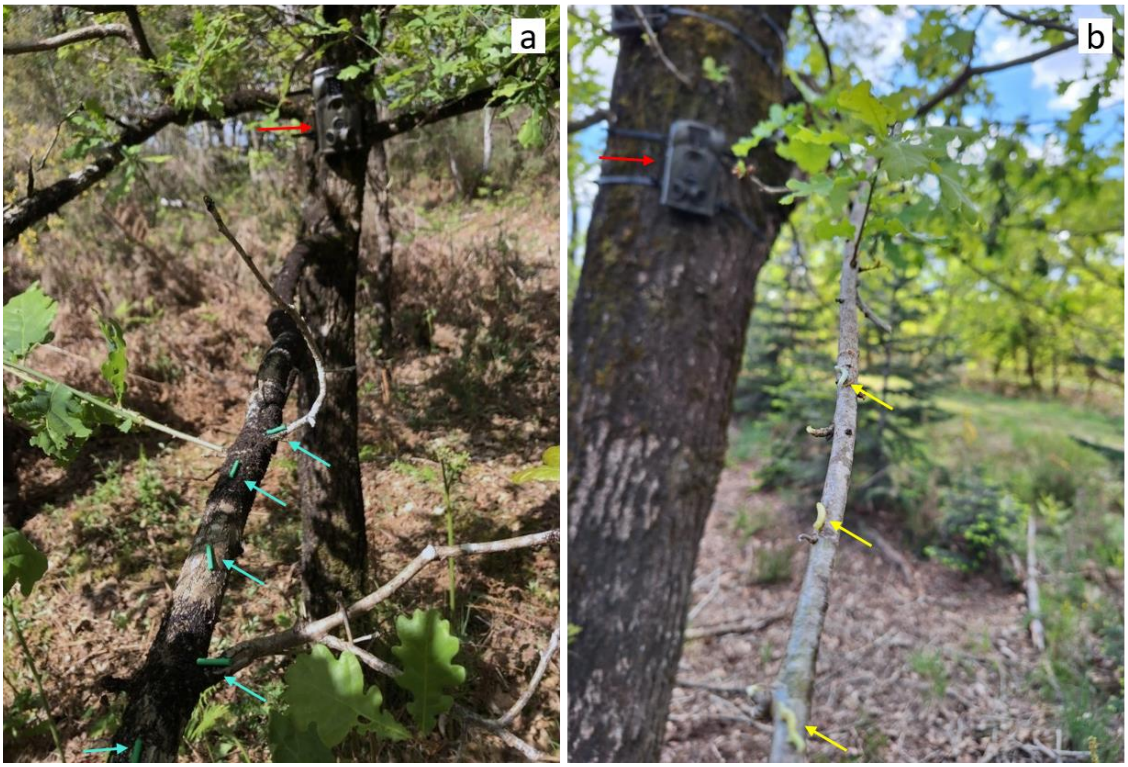

Fig 1. Photographs of the experimental design in the field.

Red arrows point toward the camera traps. Blue and yellow arrows point toward five plasticine models (a) and three corpses (b), respectively.

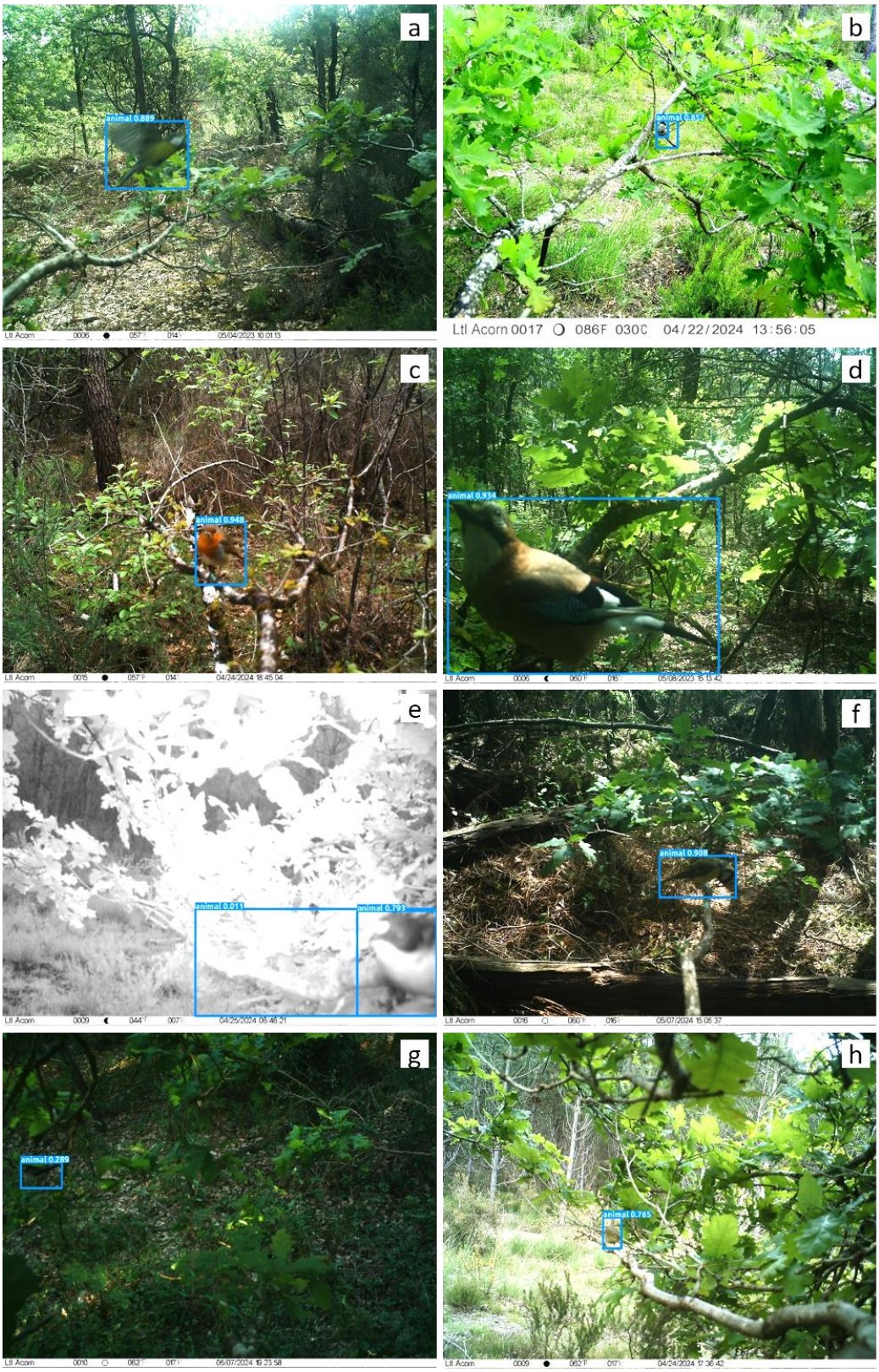

Fig 2. Camera trap photographs of birds taken in various contexts.

*Birds exhibit different behaviors (perched on a branch, actively foraging, flying, etc., see main text). The blue squares correspond to MegaDetector detections with the associated confidence level. The bird species included are: the Great Tit (*Parus major*, Figs 2a and 2f), the Long-tailed Tit (*Aegithalos caudatus*, Figs 2b and 2g), the European Robin (*Erithacus rubecula*, Fig 2c), the Eurasian Jay (*Garrulus glandarius*, Fig 2d), the European Pied Flycatcher (*Ficedula hypoleuca*, Fig 2e), and the Common Chiffchaff (*Phylloscopus collybita*, Fig 2h)*

Statistical analysis

All analyses were performed in R (38). Fig 3 summarizes all the hypotheses tested using the experimental design.

Evaluation of the degree of consistency between observers in the posterior detection of bird predation clues (H1)

We relied on the intra-class correlation coefficient (ICC) to assess the degree of consistency between observers in detecting predation clues on plasticine models. The ICC quantifies the degree of agreement between groups or between observers and is bounded between 0 and 1, where 1 indicates perfect intra-group agreement and 0 indicates no agreement beyond what would be expected by chance. According to Koo and Li (39), an ICC value below 0.50 is considered poor, between 0.50 and 0.75 moderate, between 0.75 and 0.90 good, and above 0.90 excellent. We calculated the ICC using the '*icc*' function of the *irr* package (40), with a two-way random effect model because each plasticine model was evaluated by the same set of three observers.

Comparison between evidence of bird presence assessed by camera traps and predation clues detected by human observers branches with models and corpses (H2 and H4)

We used two generalized linear mixed models (GLMM, *lme4* package; (41)) with a binomial error distribution to evaluate the bias between observer detection of predation clues and evidence of bird presence assessed by camera traps on (i) branches with models (H2) and on (ii) branches with corpses (H4). In both cases, the detection method (predation clues or evidence of bird presence assessed by a camera) was set as a fixed effect, and tree identity nested in temporal permutation was considered a random factor. The model equation was:

$$Y_{ij} = \beta_0 + \beta_1 \times Detection_{Clues,ij} + \gamma_j + \epsilon_{ij}$$

where Y_{ij} is the response variable (one data point per detection method and branch). Y_{ij} could be zero (no predation clue on any model (H2) or corpse (H4) or no evidence of bird presence) or one (at least one model (H2) or corpse (H4) with predation clue or evidence of bird presence). β_0 is the model intercept (i.e., $Detection_{EvidenceBird,ij}$), β_1 the coefficient of the fixed effect of the predation clues detected by the observer (i.e., $Detection_{Clues,ij}$), γ_j the random intercept for tree identity nested in temporal permutation, and ϵ_{ij} the residuals.

Comparison between the evidence of bird presence on corpses versus models both assessed by camera traps (H3)

We used another GLMM with a binomial distribution to assess the predation bias on models compared to corpses. Fixed effect was the type of prey (model or corpse) and random intercepts were tree identity nested in temporal permutation. The model equation was:

$$Y_{ij} = \beta_0 + \beta_1 \times PreyType_{Model,ij} + \gamma_j + \epsilon_{ij}$$

where Y_{ij} is the binomial response variable (presence or absence of evidence of bird presence at the branch level). β_0 is the model intercept (i.e., $PreyType_{Corpse,ij}$), β_1 the coefficient of the fixed effect of the plasticine models (i.e., $PreyType_{Model,ij}$), γ_j the random intercept for tree identity nested in temporal permutation, and ϵ_{ij} the residuals.

For both types of GLMMs, we used the '*nlminbwrap*' optimizer, which facilitated model convergence and provided results comparable to the default optimizer of the *lme4* package. It should be noted that since the two GLMMs we used are binomial with a *logit* link function, an inverse transformation of the coefficients must be applied to estimate it as a percentage of predation.

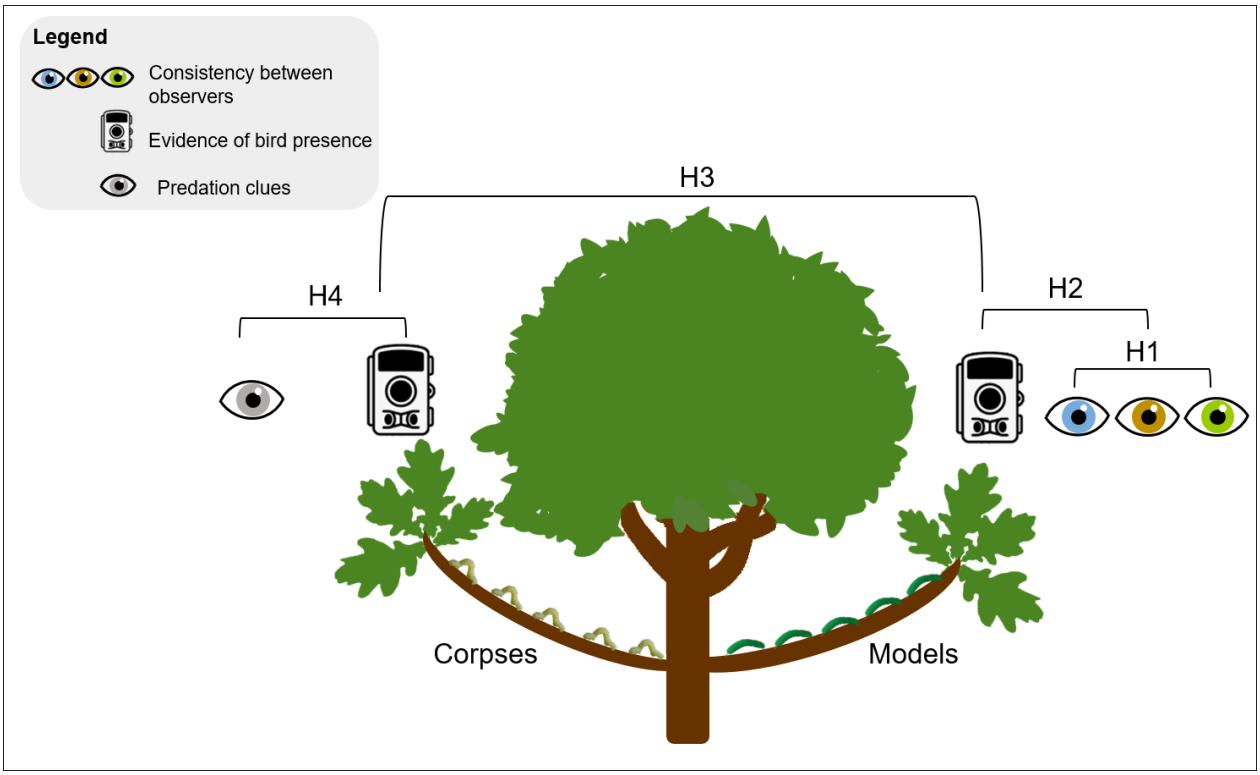

Fig 3. The experimental design testing the four hypotheses.

H1: Evaluation of the degree of consistency between observers in the posterior detection of bird predation clues; H2: Comparison between evidence of bird presence assessed by camera

traps and predation clues detected by human observers branches with models; H3: Comparison between the evidence of bird presence on corpses versus models both assessed by camera traps; H4: Comparison between evidence of bird presence assessed by camera traps and predation clues detected by human observers branches with corpses.

Results

Consistency among observers in the detection of bird predation clues (H1)

Observer A detected ten predation clues on 480 plasticine models, whereas Observer B and Observer C detected only three and four predation clues, respectively. At first, the three of them only agreed on two caterpillars (Fig 4a). The intra-class correlation coefficient (ICC) score was 0.47 (CI 95%: 0.41 - 0.52) indicating a poor agreement between the three observers in their assessments of predation clues on the 480 plasticine models ($F_{(479, 960)} = 3.61$, $P < 0.001$). The three observers therefore re-assessed predation clues to reach a consensus on the attacked vs non-attacked status. The final, consensual status resulting in seven caterpillars with bird predation clues was used in further analyses.

Evidence of bird presence on branches with corpses or models assessed by camera traps (H3)

We obtained 148,157 images from the cameras. The MegaDetector algorithm detected animal presence in 37,495 images (using the lowest detection threshold of 0.01 confidence). After visual evaluation, we ultimately retained only 146 photos showing foraging birds on or around 30 target branches (out of 192). They corresponded to 42 bird individuals belonging to 10 different species (*Aegithalos caudatus*, *Anthus trivialis*,

311 *Phylloscopus collybita*, *Erithacus rubecula*, *Garrulus glandarius*, *Ficedula hypoleuca*, *Cyanistes*
312 *caerulus*, *Parus major*, *Fringilla coelebs*, and *Turdus philomelos*). We also detected other
313 potential predators on certain branches, such as rodents of the genera *Mus* or *Eliomys* and a
314 Red Squirrel (*Sciurus vulgaris*) (see Figs S1m and z, respectively).

315 Evidence of bird presence, defined as the presence on images of a foraging bird on or flying
316 toward a branch, did not differ significantly between branches with plasticine models
317 vs. branches with corpses ($\beta_{1,Corpse} \pm$ SE = -0.5 $\pm$ 0.4, z = -1.3, P = 0.20, Fig 4b). A
318 substantial portion of the variance in bird presence assessment was attributed to random
319 effect (marginal R^2 = 0.019, conditional R^2 = 0.19)

320 Evidence of bird presence vs. predation clues on branches with models (H2) and corpses (H4)

321 We found predation clues on 7 plasticine models (7 branches, Fig 5) and 181 corpses (64
322 branches). Predation clues on branches with plasticine models were associated with the
323 presence of a bird on the same branches in the case of three branches. We observed the
324 presence of birds on 15 branches with no predation clues on models. Predation clues on
325 models were observed on four branches without the presence of birds being detected by
326 camera traps (Fig 4a). We therefore detected significantly more evidence of bird presence
327 than predation clues on branches with plasticine models ($\beta_{1,Evidence} \pm$ SE: 1.3 $\pm$ 0.5, z = 2.4,
328 P < 0.05, Fig 4c). A substantial portion of the variance in predation assessment on branches
329 with plasticine models was attributed to random effect (marginal R^2 = 0.08, conditional R^2 =
330 0.34).

331

Predation clues on branches with corpses were associated with evidence of bird presence on the same branches in 8 cases. In contrast, we observed evidence of bird presence without predation clues on corpses on 4 branches, and predation clues on corpses without the presence of bird being detected on 56 branches (Fig 4a.). There was therefore significantly less evidence of bird presence than predation clues on branches with corpses ($\beta_{1,Evidence} \pm$ SE: -2.7 $\pm$ 0.4, z = -6.8, P < 0.001, Fig 4d.). The random effect accounted for only a small fraction of the variance (marginal R^2 = 0.35, conditional R^2 = 0.38).

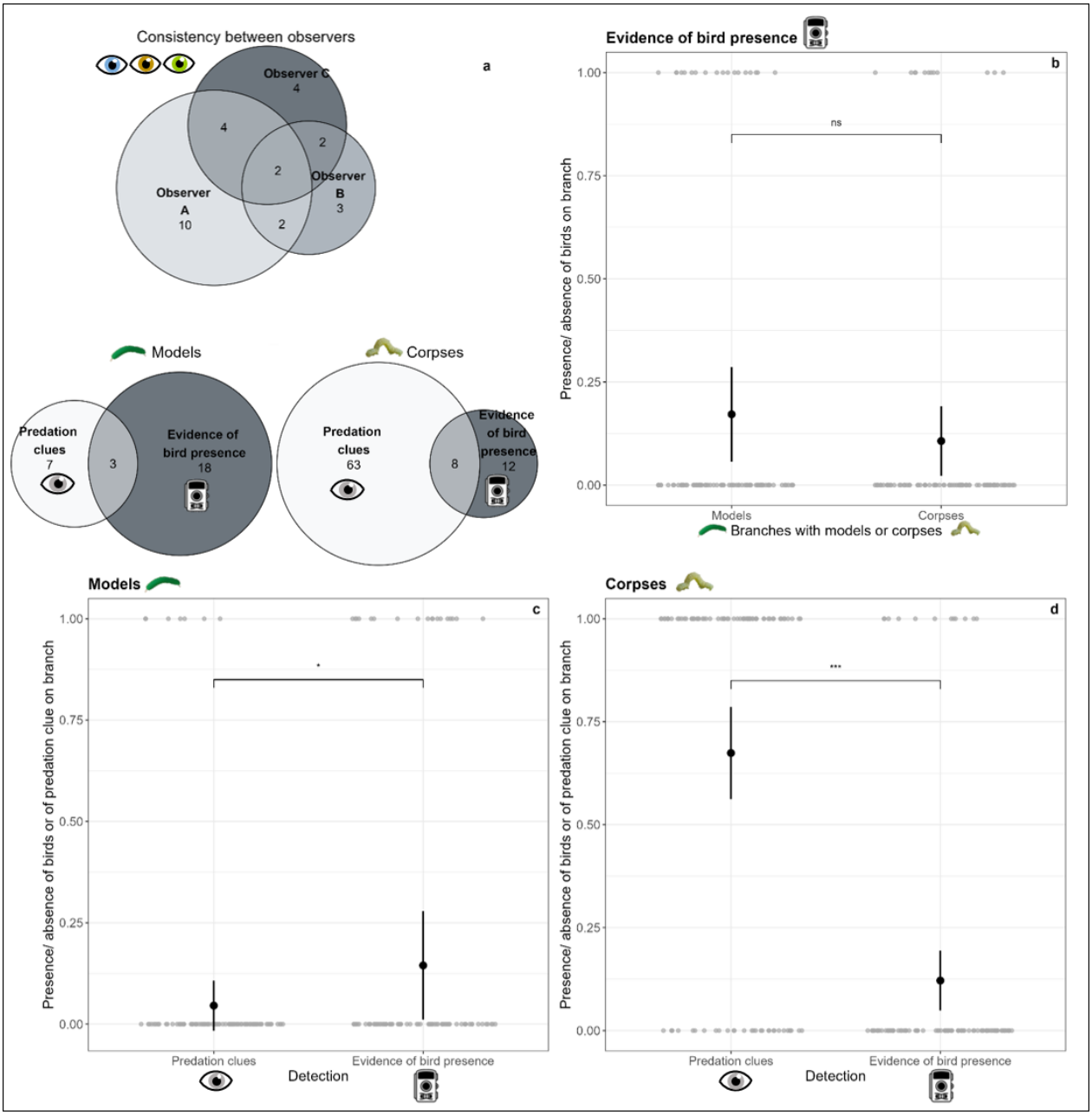

Fig 4. Main results of the study.

Euler diagram of consistency between the three observers (a, upper panel), and Euler diagrams of the number of branches with predation clues and with evidence of bird presence for models and corpses (a, lower right and lower left panels, respectively). Results of the generalized mixed-effects models with binomial distribution for the three hypotheses tested: H2 (c), H3 (b), and H4 (d).

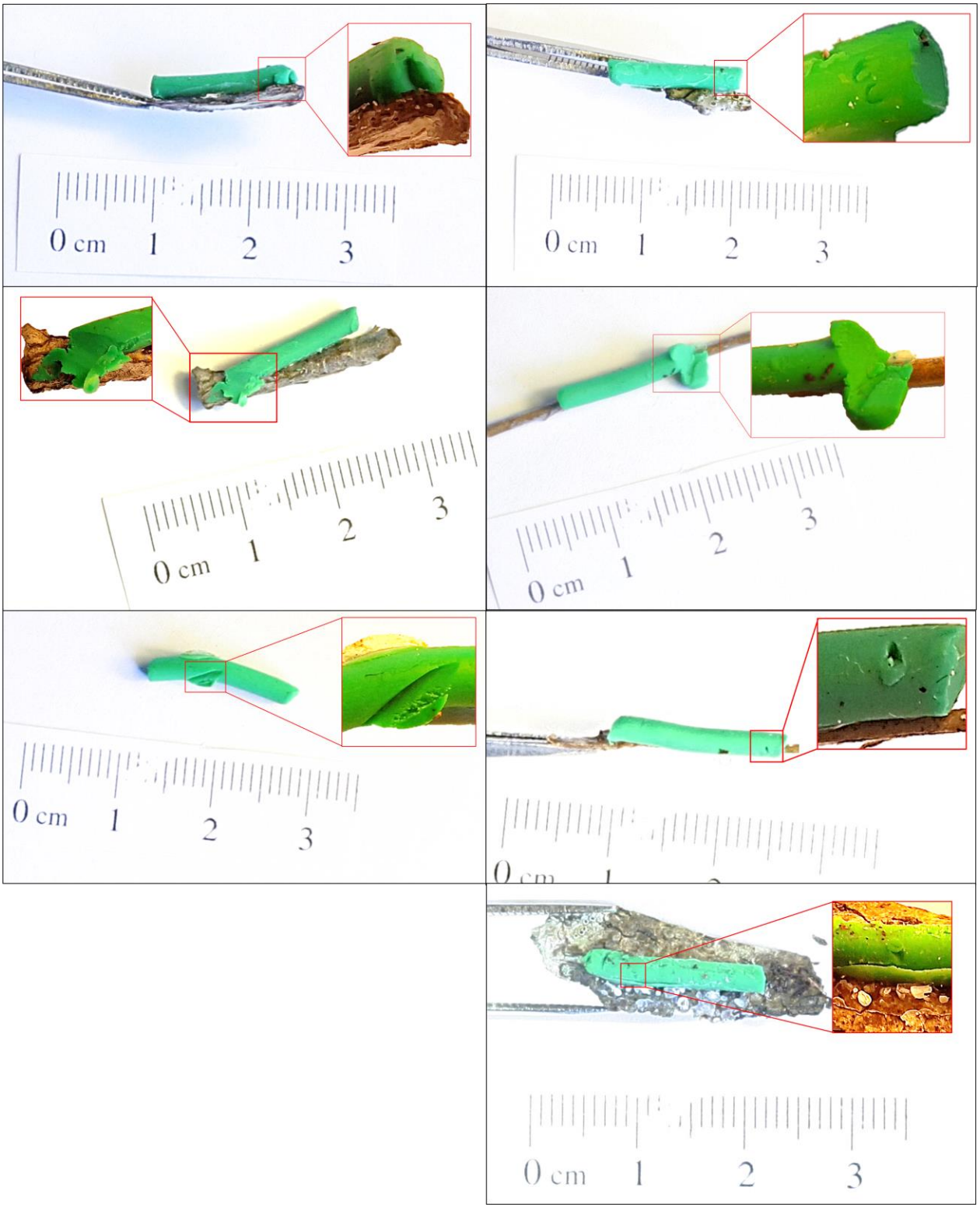

Fig 5. Photographs with mark details.
Seven caterpillars that observers considered to have bird predation clues.

350 ## Discussion

351 ### Lack of consistency in observations of predation clues on plasticine caterpillar models

352 Our study confirms the lack of consistency between observers' evaluation of predation
353 marks on plasticine models. Despite all trained observers re-reading the attack mark guide
354 (23), they did not detect the same number of predation clues. Similar results, even among
355 experienced scientists, were reported by Valdés-Correcher et al. (21) and Castagneyrol et al.
356 (42), using a more robust experimental design. In our case, the lack of consistency among
357 observers may have been aggravated by the small size of plasticine models mimicking
358 *Operophtera brumata* caterpillars (1.5 × 0.3 cm). These models were smaller than the
359 artificial prey commonly used in the scientific literature (3 cm on average across the five
360 following studies (16,17,19,23,24)), resulting in a perception of predation marks that
361 differs from what we typically observed on larger models.

362 To our knowledge, most studies using predation clues on plasticine models rely on a single
363 observer. Information about whether multiple observers could be involved is also rarely
364 provided (e.g., when the primary observer consults one or more colleagues for marks on
365 models that are difficult to assess). Some studies have employed two independent
366 observers evaluating the models by consensus (43,44), which could be a good method to
367 avoid observer bias. It could be also advisable to develop an online standardized training
368 system for identifying bird bill marks on plasticine models, as it is done for insect herbivory
369 (e.g., ZAX herbivory trainer: https://zaxherbivorytrainer.com/(45)). This could
370 complement the comprehensive guide developed by Low et al. (23) and be tailored to

371 different biomes, considering the substantial variations in predator and prey sizes and
372 behaviors.

373 Bird presence assessed by camera traps does not differ between branches with plasticine models
374 and corpses

375 The main result of our study revealed that the evidence of bird presence assessed by
376 camera traps does not significantly differ between experimental branches. Considering that
377 camera traps caught flying birds and birds foraging under poor light conditions (S1 Figure),
378 we assume that the cameras do not miss birds when they are present. Such an outcome
379 would suggest that plasticine models can be used to estimate bird predation, as they offer
380 the additional advantage of overcoming the ethical issues associated with the use of real
381 prey, whether dead or alive. This result differs from our findings regarding the number of
382 predation clues assessed by observers and contradicts other studies that find more bird
383 attacks on real prey compared to plasticine ones (19,20).
384

385 Specifically, we observed a ratio of 7 predation clues on plasticine models to 181 on
386 corpses. Similar to the findings by Zvereva & Kozlov (20), we believe that the corpses were
387 primarily removed and attacked by arthropods as we found ants crawling around 24
388 corpses out of 480, but other predators such as spiders or other arthropods could also be
389 involved. These findings are also in accordance with Nimalrathna et al. (24) who found that
390 the attack rate by vertebrate predators was lower on dead prey than on live prey and
391 plasticine models, while invertebrates predated most on dead prey followed by live prey

392 and plasticine models. Considering our and Nimalrathna et al.'s (24) results, we conclude
393 that our observations of predation on corpses are driven by arthropod consumers.

394 Although tempting to conclude that birds do not distinguish between real and plasticine
395 caterpillars, and thus claim this method reliable, it must be noted that we cannot rely on the
396 (i) posterior evaluation of clues on corpses; and (ii) the evidence of bird presence assessed
397 by camera traps as evidence of predation. Therefore, the evaluation of the plasticine model
398 method is mostly limited by available technology. To our knowledge, there is currently no
399 reliable, affordable technique for accurately identifying birds preying on insects. Camera
400 traps available on the market have motion detection speeds that are too slow for birds or
401 do not allow for fast sequences of pictures or continuous recording. Cameras that do offer
402 continuous recording have other limitations in data storage, power supply, and encoding
403 time. There is thus a need for advanced cameras, that allow us to observe fast behavioral
404 phenomena of relatively small animals, such as foraging birds. These cameras could be
405 used in various fields such as trophic interaction ecology, conservation ecology, and
406 behavioral ecology. Although some initiatives offering prototypes exist (e.g., (46)), the costs
407 are currently still too high to be affordable for scientific purposes.

408 The most limiting trade-off is between the camera performance and energy consumption.
409 For scientific research, we need at least 24 hours of endurance, which is currently not
410 possible for continuous recording. The cameras could therefore operate by capturing a
411 sequence of pictures at intervals of at least 0.5 seconds continuously to maximize the
412 chance of capturing the moment of predation (86,400 pictures/day). At the same time, the
413 batteries must be removable for quick changes in the field. Additionally, the cameras should

414 be affordable, relatively small, light, and waterproof, and finally have programmed a short
415 encoding time.
416

417 ## Predation clues assessed by observers do not correlate with bird presence assessed by camera
418 traps
419

420 Predation clues assessed by observers on plasticine models or corpses did not reflect bird
421 foraging activity as revealed by camera traps. Another study comparing camera traps and
422 posterior detection to assess predation on artificial snakes also revealed that predatory
423 birds were underrepresented in the videos triggered after motion detection compared to
424 the number of predation marks on artificial replicates (47). Moreover, O'Brien & Kinnaird
425 (48) demonstrated in 2008 that camera traps were more suitable for larger birds such as
426 pheasants than for functionally insectivorous birds targeted in our study. We acknowledge
427 that modern camera trap technology has significantly improved since 2008, though, to our
428 knowledge, however, no recent studies specifically address this in the context of bird
429 predation.

430 Contrary to our hypothesis, we found more evidence of bird presence than predation clues
431 on plasticine models suggesting that fake prey underestimates the foraging activity of avian
432 insectivores. Considering the particularly high density of live prey during this time of year
433 (L.S., N.P., A.M. pers. observation), an explanation could be that experienced birds prefer
434 live caterpillars found on the same branch over the models (see also (20)). It is, however,

important to consider the low numbers of both observations (clues vs. evidence) (Fig 4c) implying a weak indicative value.

The glue used to attach the prey sometimes caused such small models to harden, potentially preventing the later detection of predation clues. Finally, we could not exclude curiosity-driven behaviors from some individuals, notably Eurasian jays, who seemed to gaze intently at the camera rather than at the available prey. While we anticipated this curiosity behavior, we expected it to manifest more in predation clues on the models (e.g., such as claw marks). We carefully re-checked models on which no predation clues were initially identified, whereas we obtained evidence of birds foraging on the corresponding branches. The three observers confirmed no predation clue was visible on these models.

We observed more predation clues (181) than presence evidence on corpses (12). As described above, we believe that the effect size is most likely driven by arthropod consumers. This assumption, however, cannot be currently tested as we are not able to distinguish between arthropod and bird clues on corpses and at the same time cannot rely on the evidence of bird presence to be evidence of a genuine predation event. Additionally, we note that photographs from the camera traps revealed potentially predatory rodents on one of the branches with corpses.

Overall, the results discussed here provide only a limited window to the interpretation of whether the use of plasticine models should be regarded as a reliable method. Therefore, we encourage future protocols to explore methods that involve exposing live prey on branches while non-invasively preventing their escape (e.g., applying glue to branch ends) in combination with cameras providing unquestionable evidence of bird predation.

Perspectives

Our study still has not answered the most important question, namely whether plasticine models accurately assess actual predation by birds or not. However, it paves the way for the use of new technologies, such as passive monitoring methods like video surveillance, to obtain real evidence of predation. We, therefore, advocate for their development and use, which will likely refine the widely used plasticine model method in the ecology of trophic interactions.

Taking into account all results and technical difficulties of this study as well as the results of other studies, we summarized the advantages and disadvantages of each method for quantifying bird predation, along with future recommendations in Table 1.

467 ***Table 1**. Advantages, disadvantages, comments, and recommendations for the three methods of assessing bird predation:*

468 *plasticine models, real prey, and cameras. Note that cameras must be used in combination with one of the other two methods. If a*

469 *cell in the third column spans two rows in the first column labeled 'Methods,' it applies to both methods. Literature references*

470 *supporting our arguments are marked in blue.*

Methods	Advantages	Disadvantages	Comments/ recommendations
Plasticine models	- Low-cost - Easy method - Standardized - Ethical - Posterior detection possible	- Artificiality: immobile, too bright color resulting in unnatural contrast with branch; non-natural smell; often oversized regarding the size of the species naturally occurring in the habitat - Inconsistency of human detection	- Most models used are too large compared to native European caterpillars *((14); see S2 Figure)*. Therefore, we recommend adjusting the models' size according to the species likely to be present at study sites. - The vivid green color is not always the most suitable choice for plasticine. We recommend adjusting the color of larvae in a given geography and habitat *(e.g., (49))*. - We recommend several independent observers *(e.g., (43,44))* or an online training system *(on the model of (45))* to mitigate the observer detection bias.
			- It is necessary to consider a realistic density of models concerning the actual abundance of prey in the study area at any given time *(14)*. - Consider exposing the prey (models or real caterpillars) according to the natural behavior of the species they represent (e.g., petioles of

			the leaves, inner space of the rolled leaves, tree trunks, etc.) *(e.g., (15,17,27))*. - Consider the appropriate attachment method regarding the size of the prey, (e.g., the glue may not be the best solution in the case of small prey and could be substituted with pins or double-sided adhesive tape) *(e.g., (15,17,27,50))*.
Real prey	- Really reflects predation	- Expensive and time-consuming rearing - Unethical	- Use live prey to better reflect predation. Develop protocols to utilize live prey without attachment for ethical reasons while preventing their escape from branches *(e.g., (19,20,51)).* - Combination of real prey and cameras.
Camera traps	- Theoretically allows obtaining evidence of predation by birds *(but this study showed that current camera traps do not yet allow this)* - Identification of bird species - Detection of other vertebrate predators - Knowing the exact time of predation	- Expensive *(52)* <u>Currently</u>: - Passive infrared sensors are not suitable for small birds *(48)* - Too slow motion detection speeds for photos and even slower for videos - Only a few photos in burst mode after motion detection decrease the chance of capturing the predation event - Too short video times - Non-existing long-term continuous recording - Low data storage - Short-term power supply	- We strongly encourage programmers and electronicians to use low-cost microcontrollers coupled with small cameras and high-capacity batteries to obtain real evidence of not only bird predation but generally animal behavior under natural conditions. Such a monitoring method could allow us to conduct reproducible experiments on a large geographic scale, in different habitats, and with multiple target larva species to model an overall bias of the plasticine model method.

		- Long encoding time - High power supply *(52)* - Need for artificial intelligence to process thousands of photos *(46)*	

471

Conclusion

Our study sheds new light on the evaluation of the plasticine model method for characterizing bird predation. It confirms the existence of an inter-observer consistency bias in the posterior evaluation of predation marks on these models. It also suggests that predation clues do not accurately reflect the presence of predatory birds as assessed by camera traps, neither on the branches bearing the plasticine models nor on those bearing dead natural caterpillars. As we found no differences in the behavioral responses of birds to artificial prey compared with dead natural ones, we would conclude that using caterpillar corpses did not present particular advantages over using plasticine models for assessing avian predation on folivores. However, taking into account predation clues analyzed by observers showing contradictory results indicates a non-accurate monitoring approach for assessing the reliability of this method. Existing technologies do not yet allow this method to be improved and the use of plasticine to assess bird predation cannot be claimed or refused using currently available techniques. Our study suggests it is necessary to be able to evaluate the inherent biases of using plasticine models in field conditions. To this end, we advocate for the development of more precise monitoring devices and more global initiatives building upon our study, as soon as such a reliable monitoring method can be offered.

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Data availability plan

The R Markdown format will be used to ensure that the statistical analyses are fully reproducible, with the code and data made publicly available (https://recherche.data.gouv.fr/) upon acceptance of the study, following the FAIR principles for scientific data management.

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