

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

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1 Accuracy in bird predation assessment: Camera traps testing the

² efficacy of plasticine caterpillars as prey models

³ Accuracy in bird predation assessed by camera traps

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 13
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14 **Contributions**

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

19 Abstract

- 20 Sampling methods that are both scientifically rigorous and ethical are cornerstones of any
- 21 experimental biological research. Since its introduction 30 years ago, the method of using
- 22 plasticine prey to quantify predation risk has become increasingly popular in the field of
- 23 biology. However, recent studies have questioned the accuracy of the method, arguing that
- 24 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
- 26 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 27 28 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 29 caterpillars of similar size and color, using camera traps and observer posterior assessment 30 31 to identify biases and quantify actual predation events. Although camera trap analyses revealed that birds respond similarly to plasticine models and dead caterpillars, suggesting 32 33 no advantage in using dead prey for assessing avian predation, the results of posterior identification of predation marks showed contradictory results, making the interpretation 34 of the results ambiguous. Observer inconsistencies in detecting predation clues on models 35 highlight potential biases, with camera trap data showing these clues do not reliably 36 indicate actual bird predation. Given the uncertainties and shortcomings of technological 37 character revealed, the development of adequate monitoring methods and further research 38 is essential to refine the assessment approach and better understand the biases in using 39 plasticine models. 40

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

43 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

49	(11,12). Each of these methods has its own set of limitations regarding standardization,
50	logistics, and ethical considerations such as not sparing living prey or handling captive
51	birds. To address these challenges, the use of artificial prey, particularly those made of
52	plasticine, introduced over 30 years ago by Brodie III (13), has become a valuable tool in
53	bird predation research (14). The method is primarily appreciated for its ability to preserve
54	the bite marks of predators, the identification and quantification of which has been used to
55	infer attacks and predation risk from specific predators.
56	While plasticine caterpillar models are widely employed as simple, standardized prey
57	models to investigate predation activity in diverse ecosystems (15–17), recent studies have
58	raised concerns regarding their limitations and potential inaccuracies (14,18–20). The main
59	concerns relate to the accuracy of inferences of predator identity and activity from the
60	posterior assessment of putative predation marks on prey models.
61	Inaccuracy of predator identity - Observers may struggle to attribute a considerable
62	portion of attack marks to a specific predator type, e.g., bird, reptile, or arthropod (18,19).
63	For example, Valdés-Correcher et al. (21) found that up to 24% of predation mark
64	identifications were inaccurate when assessed by untrained scientists using photos of
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05	attacked plasticine caterpillar models. This was observed in comparison to evaluations
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66 67 68 69	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

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

Inaccuracy in determining real predation events among all identified marks - Even 73 though marks were attributed to birds, questions would remain about what one can infer 74 from them. Incidental contact or non-predatory interactions (e.g., by bird claws, attraction 75 of non-predatory animals, or curiosity) with the plasticine caterpillar models can result in 76 marks that are difficult to distinguish from genuine predation attempts, potentially leading 77 to an overestimation of predation rates (24). The misinterpretation of marks can lead to 78 79 distorted results on predation pressure and misleading conclusions about predator-prey interactions, especially in areas where the attack rate is low (25). 80

Furthermore, the artificial appearance and texture of plasticine may not adequately 81 simulate the characteristics of real prey, including smell, possibly affecting the behavior of 82 83 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 84 larvae, with the latter being quantified based on missing or partially consumed prey items 85 (19.20.24). As opposed to plasticine caterpillar models, the attack rate on living and dead 86 prev has shown comparable results (19), thus justifying not using living prev for ethical 87 reasons (not to glue or pin them alive). By simultaneously studying predation on dead 88 caterpillars versus plasticine models, it becomes possible to compare the response of 89 predators to both types of prey within the same experimental design with the use of passive 90 91 monitoring methods. This comparative approach makes it possible to test the assumptions 92 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 96 discrepancies, revealing that plasticine models may not be a sufficiently accurate method 97 for assessing predation (19), particularly across large biogeographical ranges (24), varying 98 thermal regimes (26), different seasons of the bird life cycle (20), and for different taxa 99 (19). There appears to be a gap in the literature regarding more detailed analyses that 100 101 elucidate the origins of the marks found on plasticine models. Moreover, missing plasticine 102 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 103 104 contrary, studies working with real prev have often assumed that a missing prev was equivalent to a depredated prey (19,20,24), an assumption that may not always hold true. 105 Without direct observation, the reasons behind the disappearance of the prev remain 106 speculative. 107

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 120 of bias in inferences made from plasticine models. We first assessed bias in the detection of 121 predation clues on plasticine models due to variation among observers (H1). We further 122 123 hypothesize that observer detection of predation clues leads to an overestimation of predation on plasticine models by attributing unrelated or uncertain marks to actual 124 predation attempts (H2). Taking into account the innate ability of insectivorous birds to 125 recognize suitable prey and the differences in the surface texture of real vs. plasticine 126 caterpillars, we hypothesize that there will be evidence of more predation on corpses than 127 on models, both assessed using camera traps (H3). Finally, we hypothesize that observer 128 detection of predation would lead to an overestimation of the predation on corpses by 129 accounting for missing individuals as a predation event, lacking direct evidence for why the 130 prey disappeared (H4). If we obtain comparable results of the bias between observers and 131 cameras for both models and corpses, and if the test of H3 provides evidence of more 132 predation on corpses than on models, we could conclude that the use of corpses with 133 human post-detection would be a more accurate method than the use of plasticine models 134 with human post-detection. 135

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).

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

personal observation), we doubt that birds learned to avoid corpses and models during theexperiment.

160 Study design

First, we haphazardly selected 12 pedunculate oaks (*Ouercus robur*, the dominant 161 broadleaved species of the area) located at least 10m apart from each other. On one branch 162 accessible from the ground of each of these trees, we glued five plasticine models, and on 163 another branch as far as possible from the first one, we glued another set of five corpses of 164 *Operophtera brumata* larvae, previously killed by freezing at -80°C. We use this level of prev 165 166 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 replicates. The five caterpillars on each branch were spaced at least 5 cm apart to remain in 168 the focus of camera traps. 169 We used the lepidopteran species *Operophtera brumata* for experimentation, a widespread 170

and often abundant oak-defoliating moth. The caterpillars, whether models or corpses,

were directly glued to the branches with two glue drops. We used corpses for ethical

173 reasons, to avoid gluing living caterpillars.

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

184 Predation analysis

We took plasticine models collected in the field to the laboratory in plastic vials. Note that 185 none of the plasticine models disappeared during the experiment. All models were 186 examined by three experienced observers who identified marks of attempted predation by 187 birds using a magnifying glass. The models were considered 'attacked' if they exhibited at 188 least one attack mark on the plasticine surface. Observers carefully reread the bite mark 189 guide published by Low et al. (23) beforehand. These observations were used to evaluate 190 consistency among the observers. In cases of doubt regarding whether a model was 191 attacked or not, the observers discussed and reached a consensus. Hereafter, we refer to 192 the presence of marks reported by human observers' consensus as 'predation clues'. 193 194 Predation clues on corpses were directly examined in the field. A missing corpse or one 195 with a missing part was considered attacked, as is generally the case in the literature

196 (19,20,24).

197 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

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

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

Our camera traps were insufficient to monitor all predation events due to the birds' small size and stealthy behavior. Therefore, we defined 'evidence of predatory bird presence' at the branch level as the presence of at least one image showing a foraging bird on the branch (hereafter 'evidence of bird presence'). These images could show individuals in various contexts: birds looking at the camera (Fig 2d and 2e), flying over the target branch (Fig 2a), 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).
- 223 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
- 225 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
- 228 arthropod predators were unlikely to be detected by camera traps. We identified all species
- associated with the evidence of bird presence.



- 230
- Fig 1. Photographs of the experimental design in the field.
- Red arrows point toward the camera traps. Blue and yellow arrows point toward five
- 233 plasticine models (a) and three corpses (b), respectively.





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

236 Birds exhibit different behaviors (perched on a branch, actively foraging, flying, etc., see main

- 237 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
- 240 *2c), the Eurasian Jay (Garrulus glandarius, Fig 2d), the European Pied Flycatcher (*Ficedula
- hypoleuca, *Fig 2e*), and the Common Chiffchaff (Phylloscopus collybita, *Fig 2h*)

242 Statistical analysis

- All analyses were performed in R (38). Fig 3 summarizes all the hypotheses tested using the
- 244 experimental design.
- 245 Evaluation of the degree of consistency between observers in the posterior detection of bird
- 246 predation clues (H1)

We relied on the intra-class correlation coefficient (ICC) to assess the degree of consistency 247 248 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 249 1, where 1 indicates perfect intra-group agreement and 0 indicates no agreement beyond 250 what would be expected by chance. According to Koo and Li (39), an ICC value below 0.50 is 251 252 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 253 254 two-way random effect model because each plasticine model was evaluated by the same set of three observers. 255

256 *Comparison between evidence of bird presence assessed by camera traps and predation clues*

257 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:

264

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

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.

271 *Comparison between the evidence of bird presence on corpses versus models both assessed by*

272 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:

276
$$Y_{ij} = \beta_0 + \beta_1 \times PreyType_{Model,ij} + \gamma_j + \epsilon_{ij}$$

277	where Y_{ij} is the binomial response variable (presence or absence of evidence of bird
278	presence at the branch level). β_0 is the model intercept (i.e., $PreyType_{Corpse,ij}$), β_1 the
279	coefficient of the fixed effect of the plasticine models (i.e., $PreyType_{Model,ij}$), γ_j the random
280	intercept for tree identity nested in temporal permutation, and ϵ_{ij} the residuals.
281	For both types of GLMMs, we used the ' <i>nlminbwrap</i> ' optimizer, which facilitated model
282	convergence and provided results comparable to the default optimizer of the <i>lme4</i> package.
283	It should be noted that since the two GLMMs we used are binomial with a <i>logit</i> link function,
284	an inverse transformation of the coefficients must be applied to estimate it as a percentage
285	of predation.



286

287 Fig 3. The experimental design testing the four hypotheses.

288 H1: Evaluation of the degree of consistency between observers in the posterior detection of

289 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:

291 *Comparison between the evidence of bird presence on corpses versus models both assessed by*

292 camera traps; H4: Comparison between evidence of bird presence assessed by camera traps

and predation clues detected by human observers branches with corpses.

294

295 Results

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

297 Observer A detected ten predation clues on 480 plasticine models, whereas Observer B and

298 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

301 observers in their assessments of predation clues on the 480 plasticine models ($F_{(479, 960)}$ =

302 3.61, P < 0.001). The three observers therefore re-assessed predation clues to reach a

303 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.

305 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
- 308 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
- 310 individuals belonging to 10 different species (*Aegithalos caudatus, Anthus trivialis,*

311Phylloscopus collybita, Erithacus rubecula, Garrulus glandarius, Ficedula hypoleuca, Cyanistes312caerulus, Parus major, Fringilla coelebs, and Turdus philomelos). We also detected other313potential predators on certain branches, such as rodents of the genera Mus or Eliomys and a314Red Squirrel (Sciurus vulgaris) (see Figs S1m and z, respectively).315Evidence of bird presence, defined as the presence on images of a foraging bird on or flying316toward a branch, did not differ significantly between branches with plasticine models317vs. branches with corpses ($\beta_{1,Corpse} \pm SE = -0.5 \pm 0.4$, z = -1.3, P = 0.20, Fig 4b). A

substantial portion of the variance in bird presence assessment was attributed to random

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

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



339

340 Fig 4. Main results of the study.



345 H2 (c), H3 (b), and H4 (d).



346

- 347 *Fig 5. Photographs with mark details.*
- 348 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

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

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

different biomes, considering the substantial variations in predator and prey sizes andbehaviors.

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

384

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

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

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

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

- be affordable, relatively small, light, and waterproof, and finally have programmed a shortencoding time.
- 416

417 Predation clues assessed by observers do not correlate with bird presence assessed by camera

- 418 traps
- 419

Predation clues assessed by observers on plasticine models or corpses did not reflect bird 420 foraging activity as revealed by camera traps. Another study comparing camera traps and 421 posterior detection to assess predation on artificial snakes also revealed that predatory 422 birds were underrepresented in the videos triggered after motion detection compared to 423 424 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 that modern camera trap technology has significantly improved since 2008, though, to our 427 428 knowledge, however, no recent studies specifically address this in the context of bird predation. 429

Contrary to our hypothesis, we found more evidence of bird presence than predation clues
on plasticine models suggesting that fake prey underestimates the foraging activity of avian
insectivores. Considering the particularly high density of live prey during this time of year
(L.S., N.P., A.M. pers. observation), an explanation could be that experienced birds prefer
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 437 preventing the later detection of predation clues. Finally, we could not exclude curiosity-438 driven behaviors from some individuals, notably Eurasian jays, who seemed to gaze intently 439 at the camera rather than at the available prey. While we anticipated this curiosity 440 behavior, we expected it to manifest more in predation clues on the models (e.g., such as 441 claw marks). We carefully re-checked models on which no predation clues were initially 442 443 identified, whereas we obtained evidence of birds foraging on the corresponding branches. The three observers confirmed no predation clue was visible on these models. 444 We observed more predation clues (181) than presence evidence on corpses (12). As 445 described above, we believe that the effect size is most likely driven by arthropod 446 447 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 448 on the evidence of bird presence to be evidence of a genuine predation event. Additionally, 449 we note that photographs from the camera traps revealed potentially predatory rodents on 450 one of the branches with corpses. 451

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.

457 Perspectives

458	Our study still has not answered the most important question, namely whether plasticine
459	models accurately assess actual predation by birds or not. However, it paves the way for the
460	use of new technologies, such as passive monitoring methods like video surveillance, to
461	obtain real evidence of predation. We, therefore, advocate for their development and use,
462	which will likely refine the widely used plasticine model method in the ecology of trophic
463	interactions.
464	Taking into account all results and technical difficulties of this study as well as the results of

465 other studies, we summarized the advantages and disadvantages of each method for

466 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

Real prey	- Really reflects predation	 Expensive and time-consuming rearing Unethical 	-	the leaves, inner space of the rolled leaves, tree trunks, etc.) <i>(e.g., (15,17,27))</i> . 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) <i>(e.g., (15,17,27,50))</i> .
			-	Use live prey to better reflect predation. Develop protocols to utilize live prey without attachment for ethical reasons while preventing their escape from branches (<i>e.g.</i> , (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) 	

472 Conclusion

Our study sheds new light on the evaluation of the plasticine model method for 473 474 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 475 predation clues do not accurately reflect the presence of predatory birds as assessed by 476 camera traps, neither on the branches bearing the plasticine models nor on those bearing 477 dead natural caterpillars. As we found no differences in the behavioral responses of birds to 478 artificial prev compared with dead natural ones, we would conclude that using caterpillar 479 corpses did not present particular advantages over using plasticine models for assessing 480 avian predation on folivores. However, taking into account predation clues analyzed by 481 observers showing contradictory results indicates a non-accurate monitoring approach for 482 assessing the reliability of this method. Existing technologies do not yet allow this method 483 to be improved and the use of plasticine to assess bird predation cannot be claimed or 484 refused using currently available techniques. Our study suggests it is necessary to be able to 485 evaluate the inherent biases of using plasticine models in field conditions. To this end, we 486 advocate for the development of more precise monitoring devices and more global 487 initiatives building upon our study, as soon as such a reliable monitoring method can be 488 offered. 489

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500	

501 Data availability plan

The R Markdown format will be used to ensure that the statistical analyses are fully 502 reproducible, with the code and data made publicly available 503 (https://recherche.data.gouv.fr/) upon acceptance of the study, following the FAIR 504 principles for scientific data management. 505

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