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# Bent posture improves the protective value of bird dropping masquerading by caterpillars

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Masquerade describes a defence by animals that have evolved to closely resemble inedible objects such as twigs, stones or bird droppings. Animals that masquerade often match their models in size or shape, and may even adopt specific postures in order to enhance their resemblance, causing predators to misclassify them as their model objects. The caterpillars of some moth species resemble bird droppings, and bend their bodies while resting on branches or leaves. We hypothesized that such bending might enhance the caterpillars' resemblance to real bird droppings. In this study, we tested this hypothesis by pinning artificial caterpillars with green or bird dropping coloration onto tree branches in both straight and bent postures, after which we exposed them to bird predation in the wild. We found that the adoption of a bent posture resulted in a lower attack rate by birds on the artificial caterpillars with the bird dropping coloration, while green caterpillars experienced no benefit from the same treatment. This study is the first experimental demonstration of the protective value of a specific posture in masquerading prey, and highlights the importance of considering an organism's shape and posture in the study of masquerade.
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Most animals are under strong selective pressure to avoid detection and attack by predators, and many of them have evolved antipredator defences in behaviour and morphology (Caro, 2005; Ruxton, Sherratt, & Speed, 2004). Masquerade occurs when an organism closely resembles an inedible object such as a twig, stone or bird dropping (Allen & Cooper, 1985; Edmunds, 1990; Endler, 1981; Skelhorn, Rowland, & Ruxton, 2010). Whereas other types of camouflage, such as background matching and disruptive coloration, prevent predators from detecting prey (Cuthill et al., 2005; Ruxton et al., 2004; Stevens, Cuthill, Windsor, & Walker, 2006), masquerade appears to be an adaptation that reduces the risk of predation by causing predators to misclassify prey as a specific model object (Skelhorn, Rowland, Speed, & Ruxton, 2010). To enhance the protective value, masquerading prey often match model objects in size (Skelhorn, Rowland, Speed, Wert, et al., 2010) and choose appropriate microhabitats to increase their resemblance to models (Skelhorn & Ruxton, 2013).

Masquerading prey may also adopt specific postures that might increase their resemblance to their model objects, but the protective value of this behaviour has never been experimentally demonstrated. The adoption of specific postures has been documented in a variety of masquerading animals, including both vertebrates and invertebrates. For example, round-tailed horned lizards, *Phrynosoma modestum*, flatten their bodies, which may make them look more like stones (Cooper & Sherbrooke, 2012). Twig-mimicking caterpillars hold their bodies rigid on the branches of trees when they rest, which may enhance their resemblance to real twigs (Dockery, Meneely, & Costen, 2009; Wagner, 2005). Caterpillars of some species of moth, such as *Macrauzata maxima*, *Apochima juglansiaria* and *Acronicta alni*, look like bird droppings, and bend their bodies when they are resting on branches or leaves, which may make them look more like real bird droppings (Yasuda, 2010, 2012; Fig. 1).

In this study, we tested the hypothesis that bent posture in the moth caterpillars enhances the protective value of bird dropping masquerade against bird predators. We tested this by pinning artificial caterpillars onto tree branches and exposing them to bird predation in the wild. We examined the attack rate of birds on artificial caterpillars that differed in their posture (bent versus straight) and coloration (bird dropping versus green). If a bent

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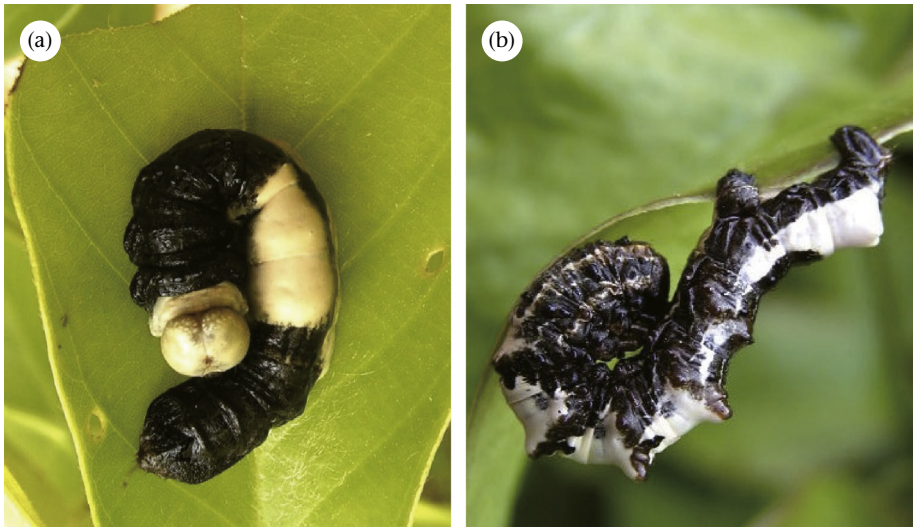


**Figure 1.** Caterpillars of two species of moth, (*a*) *Macrauzata maxima* and (*b*) *Apochima juglansiaria*, which masquerade as bird droppings and bend their bodies while resting. Photos: T. Yamamoto and K. Yamamoto.

posture improves the protective value of resembling bird droppings, the advantage of bending would be greater for caterpillars with bird dropping coloration than for those with green coloration.

## METHODS

### *Artificial Caterpillars*

We made artificial caterpillars from edible pastry, which was a mixture of lard, flour, water and food colouring (see Table A1 for a detailed recipe), by referring to previous studies (e.g. Hossie & Sherratt, 2012, 2013; Rowland, Cuthill, Harvey, Speed, & Ruxton, 2008). For our experiment, we produced four types of artificial caterpillars: (1) bird dropping coloration with a bent posture; (2) bird dropping coloration with a straight posture; (3) green coloration with a bent posture; and (4) green coloration with a straight posture (Fig. 2a).

The size and shape of the artificial caterpillars were modelled on several lepidopteran caterpillars, such as *M. maxima* and *A. juglansiaria* (Fig. 1). The size of the artificial caterpillars was standardized by using a silicon mould (40 mm length and 6 mm diameter). Whereas artificial caterpillars with green coloration were made with green pastry, those with bird dropping coloration were made by alternating blocks of white and black pastry from the anterior end to the posterior end in a 1:2:2:2 (white:-black:white:black) ratio. The pastry caterpillars were made either straight or bent; the latter were made by bending the straight caterpillars such that the anterior end was 5 mm from the posterior end.

### *Prey Presentation*

Experimental trials were conducted at nine sites in Tokyo, Japan. The minimum distance between sites was 2.6 km (Table A2), and the experiment was conducted between 20 September and 16 October 2014. We used cherry trees (*Cerasus* spp.) as the test sites for this experiment because larvae of *A. juglansiaria* (bird dropping masquerading caterpillars) eat their leaves and rest on both leaves and branches. The larvae of this species appear from spring to early summer (Yasuda, 2010), and were not observed during our study

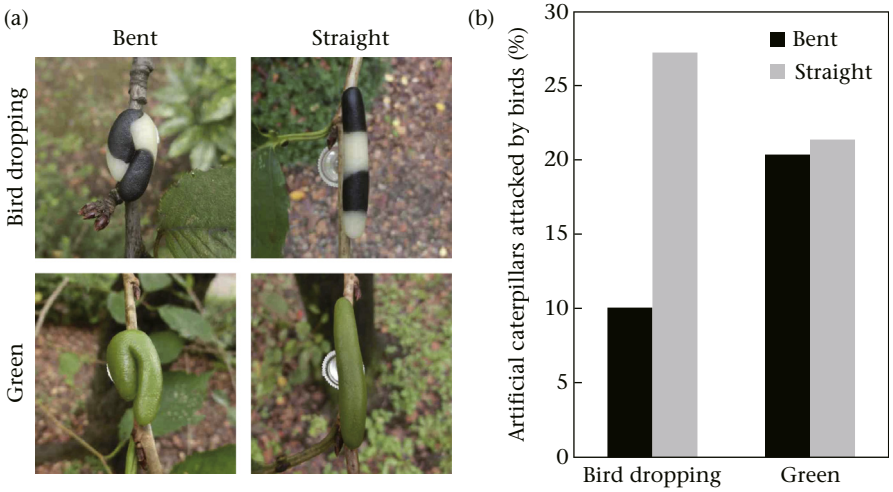


**Figure 2.** Experimental presentations of artificial caterpillars. (a) Artificial caterpillars used in the experiment differ in both colour (bird dropping versus green) and posture (bent versus straight). (b) Percentage of artificial caterpillars attacked by birds ($N = 404$).

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