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ABOUT DISTASTEFULNESS AND MIMICRY: A COMMENT ON PETER SMETACEK'S ARTICLE (J. LEP. SOC., VOL. 60:82–85)

I am writing in response to Smetacek's (2006) conclusion that *Papilio polyctor*, *P. protenor*, and *P. polytes* are distasteful to avian predators and thus chemically defended. Smetacek's experiment on butterflies and wild birds was an immense effort involving years of observations, which I highly appreciate. However, the results presented in his article are interesting and suggestive, not conclusive.

Smetacek's study had limited experimental controls, which compromised reliability of the small dataset. The methods did not fully describe motivational states and prior experiences of the birds, and how these factors were controlled or contributed to the data. These are key aspects of palatability experiments and must be addressed in order to draw conclusions from the predators' behavior. The article mentioned, "The birds at times arrived and devoured everything in sight and at other times ignored everything, including controls, having evidently found sufficient food elsewhere." We do not know how much of the variation in measured palatability was introduced by this lack of control, motivational states of the birds and their prior experience with unpalatable prey.

The author's explanation for persistence of the non-mimetic female form of *P. polytes*—that it persists because it is distasteful—conflicts with earlier data. Ohsaki (1995, not cited in Smetacek 2006) has shown that in nature a much higher percentage of non-mimetic females of *P. polytes* have beak marks on their wings compared to the mimetic females. Ohsaki's data suggests that the non-mimetic female form is palatable and suffers higher rates of predatory attack, whereas the mimetic female form is attacked much less frequently and has a Batesian mimetic advantage. Moreover, the nature of female-limited mimic–non-mimic polymorphism and variation in frequencies of female forms over most of the geographic range of *P. polytes* is in line with theories of Batesian polymorphism, not Müllerian polymorphism. Thus, based on theory and empirical evidence, balanced polymorphism and other traditional explanations (e.g. Turner 1978, and references therein) still seem more satisfactory in explaining the mimic–non-mimic polymorphism in *P. polytes*. Parallel mimic–non-mimic polymorphism in *P. glaucus* and other *Papilio* species is also instructive.

The idea—that a classic Batesian mimic is actually a Müllerian mimic—is intriguing but controlled experiments are required before a definitive conclusion can be reached.

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AUTHOR'S RESPONSE TO TECHNICAL COMMENT

First, all Papilio larvae are believed to be unpalatable, as stated in the Introduction of my paper. On the basis of the data presented, I concluded that *P. polytes*, *polyctor* and *protenor* are also distasteful in the adult stage.

Concerning the misgiving about limited experimental controls compromising the reliability of the small dataset, the normally acceptable ratio is 1:1; this has been exceeded in my experiments as noted in Column 2 of Table 1. As stated, the Papilio species were offered together with the controls. Therefore, it made little difference to the result of the experiments whether the birds arrived hungry or sated. Perusal of the paper will show that the number of times the birds ignored the presentation does not in any way affect the interpretation of data.

With reference to the contention that I have not fully described "motivational states and prior experiences" of the birds and "how they were controlled or contributed to the data", all information that was noteworthy on this subject may be found in the last two paragraphs of the Materials and Methods section. My limited

acquaintance with the wild birds and the language barrier precluded greater familiarity with their "prior experiences" with unpalatable prey. However, it is noted in the paper that only the non-mimetic female form of *polytes* was used in the experiments and on three occasions the wing scales of a *Papilio* were wiped off and the wing shape altered. I trust that these require no further explanation.

As a matter of fact, I cannot recall any palatability experiment where the "key aspects" mentioned by Kunte have been "fully addressed", particularly when using wild birds or else birds caught from the wild.

Concerning Ohsaki (1995), despite the elegant mathematics, I believe that his conclusions are not valid because putative beak marks cannot be construed to be an indicator of palatability, nor of the relative preferences of avian predators. An analogy will clarify my point of view better: during the Second World War, the R.A.F. undertook a survey of bullet and flak damage to all its airplanes as they returned from sorties. Each bullet hole and shrapnel mark was entered on a diagram, with a view to discovering and subsequently strengthening the parts most often damaged. The inherently flawed reasoning became apparent when a junior officer asked, "What about the planes that *didn't* come back?"

Similarly, Ohsaki's discovery that the non-mimetic form of *polytes* had more putative beak marks than the mimetic form in a S.E. Asian forest, cannot be safely interpreted any further. For this reason, I did not rely upon or refer to his paper.

I cannot agree with Kunte that putative beak marks constitute "empirical evidence" of palatability, while actual tasting, eating, rejection, and distress behavior by birds is ignored altogether.

Concerning Batesian mimicry, suffice it to say that as mentioned in the first sentence of the paper, the basic premise is that, of two or more similar looking species, one is palatable and the other is unpalatable. If predators, in this case birds, avoid the "palatable" species, reject it after long examination and even exhibit distress behavior on occasion after eating it, then the species is not entirely palatable and therefore the relationship not Batesian, for while there are varying degrees of distastefulness in Müllerian mimicry relationships, there is no scope for the mimic being even slightly distasteful if the relationship is to be deemed Batesian. All other considerations are secondary. That entirely palatable species exist and the birds in the experiment could distinguish them is evident from the figures presented for controls in Table 1 and the second paragraph of the Results section. Referring to the applicability of theories of Batesian polymorphism, etc. to the distribution of *polytes*, while ignoring its distastefulness is, to my mind, putting the cart before the horse.

With reference to the "small dataset", while 18 specimens of *polytes* are certainly not as many as one could have wished, that one to three of these specimens were offered on 49 occasions should not be ignored, nor the fact that less than half were eaten; on 7 occasions a specimen was rejected after being manipulated for over 5 seconds and distress behavior was observed after a bird ate part of a specimen, as noted in the last paragraph of the Results section. Those readers familiar with feeding birds will agree that rejection after manipulation for 5 seconds or more is a decisive rejection. As observed above, if a species is to be deemed a Batesian mimic, there is no scope for it to be even slightly distasteful. Therefore, I feel entirely justified in treating *polytes* as distasteful and its relationship with *P. aristolochiae* as Müllerian.

Concerning *polyctor* and *protenor*, the distastefulness is so evident that to go on offering specimens will not prove very much more, unless the number of times the presentation was ignored is treated as significant, a course which I believe is not advisable in the present case.

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