Protection by Mimicry—A Problem in Mathematical Zoology

Under the above heading in the *Japan Weekly Mail* of February 3, 1883, we drew attention to what appeared to us an error made by Mr. Alfred R. Wallace in a letter to *Nature* regarding the protection gained by two distinct species of insects from destruction, not by the proportion this saving bears to that of the other species. "On this Mr. Meldola remarks:—"The proportional advantage that either species has after imitation over its former state of existence by the mimic, or calculate the ratio of survivals each would then have had. In the first 1 x 40 to 9 x 80 = 320 per cent. Advantage to B excess of 84 over 20 on 20 = 320 per cent. Ratio 1 to 18 (Müller 1 to 9). 3. A to B as 4 to 1. Dissimilar A loses 20 per cent. ; B, 60 per cent. Remains 80—60. Similar A loses 15 per cent. ; B, 15 per cent. Remains 85—85. Advantage to A excess of 85 over 80 on 80 = 6·25 per cent. Advantage to B excess of 85 over 40 on 40 = 112·5 per cent. Ratio 1 to 18 (Müller 1 to 9). 4. Advantage to A excess of 84 over 80 on 80 = 5 per cent. Advantage to B excess of 84 over 20 on 20 = 320 per cent. Ratio 1 to 16 (Müller 1 to 16). Dr. Müller's squares require to be multiplied by the remains per cent. (taken also inversely) of the two species when dissimilar, to bring out the proper ratio. Thus: 1 to 4 (the squares) in the first example, multiplied by 60 and 80 respectively, give 60 to 320 or 1 to 5·33. In the second 1 x 40 to 9 x 80 = 40 to 720 or 1 to 18. And in the third, 1 x 20 to 16 x 80 = 20 to 1280 or 1 to 64. It will be understood therefore that, whether we reckon the proportionate advantage that each species obtains over its previous state of existence by the mimic, or calculate the ratio of proportionate advantage of mimicry between the two, the comparison has not to be made with the state each would have but had not mimicry taken place, indicated by the proportion of survivors each would then have had. If we ignore this, the comparison is untrue. What we want is the advantage a species which adopts mimicry has over one which fails to do so. So that if we speak of one numerous species A, and two equal non-numerous species B and B', which in particular cases may amount to so much that, while B survives, B' may become exterminated. This is perhaps the simplest way of putting it. It must be remembered, however, that B does no harm to A by being like it; on the contrary, the act of mimicry is of advantage to A over its former state of existence as well as to B; but A being the more numerous the advantage is less. Still after the assimilation neither has an advantage over the other.
Proportionally they suffer from the ravages of the birds equally; the percentage of losses is the same; they are on equal terms. No matter how long they continue the association, neither gains nor loses on the other; though through one being more numerous it loses more individuals, yet equally in proportion with the other. So that, if one is twice as numerous as the other at the time of assimilation, it must always—other conditions being equal—remain twice as numerous.

We now give the mathematical reduction:—

Designation of species ... ... ... A ... ... ... B
(1) Original number ... ... ... $a > b$
(2) No. lost without imitation ... ... ... $e = e$
(3) Remains without imitation $(a - e) ... (b - e)$
(4) No. lost with imitation $\frac{a}{a + b} e$ ... ... ... $\frac{b}{a + b} e$
(5) Remains with imitation $a \left(1 - \frac{e}{a + b}\right)$ ... ... ... $b \left(1 - \frac{e}{a + b}\right)$
(6) Excess of remains due to imitation, or absolute advantage $(3)-(5)$ ... ... ... $\frac{b e}{a + b} \frac{a e}{a + b}$
(7) Ratio of excess to remains without imitation (6) : (3), or proportional advantage $\frac{e}{a + b}, \frac{b}{a - e} \frac{e}{a + b}, \frac{a}{b - e}$
(8) Ratio of proportional advantage of B to propor-
tional advantage of A ... ... ... $\frac{a (a - e)}{b (b - e)}$ or $\frac{a e}{b e}$ $\frac{a}{b}$ $\frac{e}{1 - e}$

From (8) we see that, if $e < b < a$, there is a proportional advantage to both, the mimicry “is twice blessed,” but the proportional advantage to B is greater. If $e$ is zero, there is no advantage to either. If $e = b < a$, the prop. advantage to B is infinite, while that to A is still finite; this is as it ought to be seeing that to B it is a case of “to be or not to be,” of existence with mimicry or extinction without. And in this extreme case it must be evident to every one that the ratio of $a^2 : b^2$, both terms finite, cannot be the ratio of the infinite advantage of B to the finite advantage of A. The greater $e$ the greater are both advantages.

From (9) we see that, if $e$ is small compared to $b$ and $a$, the ratio is nearly $a^2 : b^2$ (Müller's law), but the larger $e$ is the further it deviates from that law, the ratio becoming rapidly greater than $a^2 : b^2$, and approaching infinity as $e$ approaches $b$.

To conclude, we may point out that Müller's law, as given in his own words and quoted above, is incompletely enunciated, and but for the numerical examples, it might lead any one astray as to what the law is. It ought to have the ratio of interpolated between “and” and “the proportional”; then “advantage” and “square” ought both to be plural; “relative” ought to be respective; and, lastly, the fact that the ratio is inverse should be explicitly stated. Finally we enunciate our law. Let there be two species of insects equally distasteful to young birds, and let it be supposed that the birds would destroy the same number of individuals of each before they were educated to avoid them. Then if these insects are thoroughly mixed and become indistinguishable to the birds, a proportionate advantage accrues to each over its former state of existence. These proportionate advantages are inversely in the duplicate ratio of their respective original numbers compounded with the ratio of the respective percentages that would have survived without the mimicry.

This last “ratio compounded” corrects Müller's law, but we still think with Mr. Wallace that the law, even when corrected, has not much bearing on the question that the individual absolute advantages (6) above, together with the probable value of $e$ and the ratio $a : b$ indicated by relative frequency of capture, solve the whole question. In our first paper above mentioned we established formulae for calculating these last-named items, although in a different manner from and quite independent of Müller's law, which we had not then seen.

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