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 of distasteful nature assimilating in appearance when subject to the attacks of young and inexperienced birds. The article was sent to Mr. Wallace, who by letter, and in an article in NATURE, vol. xxvii. p. 481, without hesitation, acknowledged the correction, saying that he had misstated Dr. Müller's proposition. He then gives Dr. Müller's own words, which are :—"If both species are equally common, then both will derive the same benefit from their resemblance—each will save half the number of victims which it has to furnish to the inexperience of its foes. But if one species is commoner than the other, then the benefit is unequally divided, and the *proportional advantage* for each of the two species which arises from their resemblance is *as the square* of their relative numbers." This alters the question altogether. Mr. Wallace had stated it, through an oversight, quite otherwise. He said :—"The number of individuals sacrificed is divided between them in the proportion of the square of their respective numbers." Such was what we took objection to; and we showed that it was not according to the squares, but to the simple numbers.

Mr. Wallace carries out his article, which is accompanied by one by Mr. Meldola (p. 482), to show by examples how it is that, notwithstanding the *loss* is in direct ratio to the numbers of each species, the proportional *saving* through resemblance is inversely as the squares; and he further says :—"The advantage will be measured solely by the fraction of *its own numbers* saved from destruction, not by the proportion this saving bears to that of the other species." On this Mr. Meldola remarks :—"The fact that these numbers stand to one another in the ratio of" the squares, "is a mathematical necessity from which I do not see how we can escape." Now even if this latter statement were strictly correct, we fail to see how it affects Mr. Wallace's statement. We shall show, however, that it is not correct but only an approximation when the number eaten by the birds is a small percentage, for as this becomes greater the ratio of proportional advantages increases considerably above that of the squares.

The proportional advantage that either species has after imitation over its former state (before imitation), appears to be according to the fraction of its original number remaining. Because while in its former state, should it lose one half its number, it would have one-half left, while if it after imitation lost only one-fourth, it would have three-fourths remaining; a clear advantage of one-fourth over one-half, or 50 per cent. This, however, is not a simple case for an example when we come to consider the relative numbers of the two species; we will therefore put it thus :—A has double the number of B. Supposing that when dissimilar A loses 30 per cent. then B loses 60 per cent. But after assimilation both lose in the same proportion, namely, 20 per cent. A has consequently an advantage, over its former state, of 10, and similarly B of 40. But in the former state the remainder of A not lost was 70 per cent., while that of B was 40 per cent., so that A's real advantage is 10 on 70 or 14·2857 per cent., and B's 40 on 40, or 100 per cent. These two numbers do not bear Dr. Müller's ratio of 1 to 4 (the squares of the numbers) but a greater, namely, $1 \text{ to } 7 = 1^2 \times 40 \text{ to } 2^2 \times 70$.

The following examples will illustrate the increasing ratio :—

1. A to B as 2 to 1.

If when dissimilar A loses 20 per cent. then B loses 40 per cent., the remains being for A, 80 per cent. ; for B, 60 per cent. When similar each loses $13\frac{1}{3}$ per cent., leaving remains of $86\frac{2}{3}$ per cent.

The advantage to A therefore is the excess of $86\frac{2}{3}$ over 80 on 80 = 8·33 per cent., and the advantage to B is the excess of $86\frac{2}{3}$ over 60 on 60 = 44·44 per cent. These advantages compared to each other are as 1 to 5·33 (according to Dr. Müller 1 to 4).

2. A to B as 3 to 1.

Dissimilar A loses 20 per cent. ; B, 60 per cent. Remains 80—40.

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).

3. A to B as 4 to 1.

Dissimilar A loses 20 per cent. ; B, 80 per cent. Remains 80—20.

Similar A loses 16 per cent. ; B, 16 per cent. Remains 84—84.

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 64 (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 ratios. 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 1×40 to $9 \times 80 = 40$ to 720 or 1 to 18. And in the third, 1×20 to $16 \times 80 = 20$ 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 to be made with the state each would have been in 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′ ; if B mimics A, while B′ mimics no species, B receives protection, and thus has an advantage over 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 mimicking 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)	$\frac{be}{a+b}$		$\frac{ae}{a+b}$
(8) Ratio of excess to remains without imitation (6) : (3), or *proportional advantage*	$\frac{e}{a+b} \cdot \frac{b}{a-e}$		$\frac{e}{a+b} \cdot \frac{a}{b-e}$
(9) Ratio of proportional advantage of B to proportional advantage of A	$\frac{a(a-e)}{b(b-e)}$ or $\frac{a^2}{b^2} \frac{1 - \frac{e}{a}}{1 - \frac{e}{b}}$		

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 undistinguishable 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 formulæ 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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