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E. B. Poulton

Adaptations which hinder or prevent Inbreeding in Insects.

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Adaptations which hinder or prevent Inbreeding in Insects.

Professor E. B. Poulton, F. R. S., Oxford, England.

My attention was first directed to the importance of this subject by a series of breeding experiments, carried on since 1917, upon the abundant British Geometrid moth *Abraxas grossulariata* L. The injurious effect of inbreeding became obvious in the third generation and in only a single family was it possible to obtain a few moths of the fifth [1]). The fatal effect manifested itself in all stages. The larvae often died when fully formed in the egg, and those which hatched died at various periods. The pupae, too, often failed to produce living moths. One of the most marked effects of inbreeding is a slower rate of growth and development, often leading to surprising results. Thus a larva of the second inbred generation, which hatched in July 1921, was only about half-grown when it was exhibited to the Entomological Society of London on 18th October 1922! It had been observed feeding on that day and was still alive on 28th November, but died a week later [2]). Another interesting effect commonly seen in the pupae of inbred *A. grossulariata* is the substitution of a probably ancestral reddish brown tint for the characteristic intense black which, with the bright yellow bands, gives the well-known wasp-like appearance.

Many years before these experiments were undertaken, the remarkable all-female families of *Acraea encedon* L., bred by W. A. Lamborn in the Lagos district, together with other families in which males predominated, led to the hypothesis of an adaptation for the promotion of crossbreeding [3]). But it was the suddenly realised interpretation of the puzzling behaviour of a Saturniid moth, observed forty years earlier, which led me to think that adaptations to prevent inbreeding are probably widespread among insects.

In 1887 I was anxious to observe the larval stages of the European Emperor Moth, *Aglia tau* L., and had obtained a number of pupae, fully expecting that the moths, of which the males are well known to "assemble", would pair freely and that plenty of fertile eggs would be laid. To my astonishment only a single pairing was obtained, while many males and females, emerging in the same cage at nearly the same time, died without taking any notice of one another. The solution is, I believe, that active

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[1]) The late Arthur Bacot, who had great experience in breeding Lepidoptera, once told me that he had never succeeded in rearing a fifth generation of inbred moths.

[2]) *Proc. Ent. Soc. Lond.*, 1922, pp. lxxvi, xcv.

[3]) *Ibid.*, 1911, pp. liv, lv; *Linn. Soc. Lond., Journ. Zool.*, Vol. XXXII, Sept. 1914, p. 391.

flight is necessary for the males before they become susceptible to the scent of the virgin females, but active flight under normal conditions would carry them far away from the females of their own family. Were it otherwise, their remarkable powers would lead directly to inbreeding; for the females of "assembling" males are heavy, sluggish insects and lay their eggs in a limited space [1]).

During the past months many examples of this and other adaptations for the same end have occurred to me or have been suggested by the kindness of friends. A brief account of these will, it is hoped, induce others to look for further evidence which I am convinced exists on a very large scale. The adaptations may be classified under the following barriers against inbreeding: — Time, Space, and Physiological.

A. **Time Barriers.**

Emergence of sexes in the same family at different times: — The commonly observed emergence of males before any of the other sex have appeared has been regarded as an adaptation to ensure full and free competition for the females, but it also tends to encourage cross-breeding in the same manner as the delayed male susceptibility of other species. The early emergence of the males results in their dispersal, taking them away from the females of their own families [2]). In some insects the barrier of time appears to be complete, and inbreeding entirely prevented. Thus E. Lindner [3]), when rearing *Cnethocampa pityocampa* Schiff., in captivity, has found that the females emerge in July of one year and the males in July of the following year; also that in captivity the females of *Saturnia pavonia* L. and *spini* Schiff. stay over an extra winter far more rarely than the males. Dr. V. G. L. van Someren [4]) has shewn that there is great inequality in the sexes of the families reared from the eggs laid by females of *Acraea esebria* Hew., sometimes males, sometimes females preponderating. There was, however, practical equality (46 ♂♂ to 45 ♀♀) in the largest family, with a great excess of males among the earlier emergences and of females among the later, and indications of the same kind of sequence in some of the smaller families. Such an alternation of sex predominance in successive waves of emergence would, of course, tend to hinder inbreeding. In examples such as these, however, the difference of time, combined with the power of flight, would lead directly to the barrier of space.

Dr. J. W. Munro [5]) has brought forward evidence which suggests that the males of the Sawfly, *Lophyrus pini* L., may emerge some considerable time before the females of the same brood.

[1]) *Proc. Ent. Soc. Lond.*, Vol. 11, 1927, pp. 75—82.

[2]) The emergence of male insects before their females have appeared is utilised by certain Orchids for securing cross-pollination. The flowers attract the males by a rough resemblance to the females, and probably, even more effectually, by a scent like that of the female. An abstract of the work of Pouyanne and Godfery on this subject is given in *Proc. Ent. Soc. Lond.*, 1927, Vol. 11, pp. 31—33. Mrs. Coleman has recently shewn that the male of an Ichneumonid, *Lissopimpla semipunctata* Kirby, is thus utilised by an Australian Orchid: *The Victorian Naturalist*, xliv, p. 20, May 1927.

[3]) *Zeitschr. f. wiss. Insektenbiol.*, 9, 1913, pp. 379, 380.

[4]) *Proc. Ent. Soc. Lond.*, Vol. 11, 1927, pp. 5—10.

[5]) *Ibid., vol. III*, 1928, p. 34.

Mr. J. V. Pearman, who has had much experience with the British *Psocidae*, kindly informs me that "in several species there is a marked difference in the rate of embryonic development within eggs of the same batch laid by a single female, some of the eggs hatching within a month and the others not until nearly six months later." He has, however, as yet no evidence bearing on the proportion of the sexes in the earlier and later hatchings.

B. Space Barriers.

(1) The winged sexual forms of social and some gregarious insects: — The flight of the sexual forms from the nest or community not only leads to the founding of new societies, but also tends to prevent their development from an inbred stock. In many species the worker ants of the nests over a wide area, by driving off their winged males and females in separate waves, and in response to some climatic stimulus, on the same days, create a mixed swarm in which the chances against inbreeding are very high. The care in keeping the sexes separate in the nest was forcibly brought to my notice when observing a small nest of *Iridomyrmex emeryi* Crawley, in the Blue Mountains, N. S. W. All the winged females crowded the floor of a low chamber, while all the winged males were hanging as densely packed from the ceiling [1]). Although the Social Hymenoptera supply the most obvious instances of cross-breeding promoted by dispersal, similar facts are conspicuous in the Aphides and other communal Homoptera. In the *Psocidae*, too, Mr. Pearman tells me that "migration and dispersal of the colony may take place before any oviposition (and possibly pairing), although sometimes there is oviposition (and possibly pairing) before the colony scatters."

The creation, by dispersal, of a space barrier against inbreeding naturally suggests concentration for the promotion of cross-breeding, a good example being the adaptive instinct which leads sexually mature insects to seek high points in the landscape, where the scattered males and females from many parts of a wide area can meet [2]). Or again, there is the gregarious instinct in migration which leads "to the streaming of large populations, and not of small batches of individuals, from an area of high pressure" [3]), thus ensuring that a new colony if established will not be inbred.

(2) Families of one sex or with the sexes numerically unequal: — Families of these kinds are probably common in Lepidoptera, especially in the species with gregarious larvae where inbreeding would be especially likely to occur. The first example known to me was observed by the late Dr. W. Hatchett Jackson in the companies of *Vanessa io* L., which were found to be "principally, but not entirely, of one or of the other sex" [4]). Lamborn's families of *Acraea encedon* have been already quoted, but it is necessary to draw attention to his important evidence that there are in this species two strains of females, both requiring fertilization, but one producing all-female offspring, the other mixed sexes

[1]) *Entom. Monthly Mag.*, 3rd Ser. Vol. VIII, May 1922, p. 124.
[2]) *Proc. Ent. Soc. Lond.*, 1904, pp. xxiii—xxvi.
[3]) *Trans. Ent. Soc. Lond.*, 1902, p. 464. See also Prof. Vernon L. Kellogg in *Proc. Ent. Soc. Lond.*, 1904, p. xxii.
[4]) *Trans. Linn. Soc. Lond.*, 2nd Ser., Zool., Vol. V. Mem. 4, 1890, p. 156.

often with a preponderance of males. Similar evidence for the existence of all-female-producing and mixed-sex-producing strains of *Hypolimnas bolina* has been recently obtained by H. W. Simmonds in Fiji[1]). Dr. V. G. L. van Someren has bred a great preponderance of females (66 ♀♀ to 22 ♂♂) from the ova of *Acraea rangatana* Eltr., collected from the food-plant[2]). In the *Pierinae*, Miss M. E. Fountaine bred 32 females of *Mylothris spica* Möschl., from a batch of ova found on a leaf[3]), and Lamborn has recorded evidence which suggests that a preponderance of males may be produced by *Mylothris rubricosta* Mab[4]). Among the moths, Prof. J. W. Heslop Harrison, F. R. S., has observed families with preponderant females among the *Geometridae*[5]).

Dr. J. W. Munro, D. Sc.[6]), has observed that batches of cocoons of an undetermined *Bracon*, from individual larvae of the weevil *Hylobius abietis* L., "yielded only one sex, now male, now female." The females of this *Bracon* observed in his laboratory always paired, and he has no reason to suppose that the parents of the unisexual families were parthenogenetic. He has also observed that only females of the weevil *Strophosomus coryli* F. were to be taken in spring, the males appearing in June. He suggests that there is a preponderance of female broods in the late summer and that these over-winter and account for the predominance of this sex in spring.

Dr. J. G. Myers[7]) has brought forward many additional records. Omitting on the present occasion consideration of all-male and all-female parasitic Hymenoptera, the following two examples are quoted from the Diptera: — (1) An Indian *Chrysomyia (Calliphoridae)* in which Prof. T. Bainbrigge Fletcher[8]) found that "under the same climatic conditions in captivity one female will produce only males, whilst another will produce females"; (2) the great predominance of females found by R. R. Parker[9]) among the various species of flies which emerged from one privy-vault in Montana. Dr. Myers thinks it likely that the great disproportion may indicate broods of one sex, and he points out that in carrion-feeding species "such tremendous numbers sometimes emerge from one small carcase which has been 'blown' by comparatively few female flies, that were the offspring in the usual nearly equal proportions of the sexes, the closest in-breeding would tend to result".

The interesting results obtained by Dr. E. Hindle[10]) in families of Lice *(Pediculus humanus)*, which were all-male, all-female, predominant male, or predominant female, are probably adaptations to prevent inbreed-

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[1]) *Proc. Ent. Soc. Lond.*, Vol. III, 1928, p. 43, Mr. Simmonds's final conclusion, after a prolonged series of experiments, was announced at the meeting of June 6, 1928.
[2]) *Ibid.*, Vol. II, 1927, p. 9.
[3]) *Ibid.*, Vol. II, 1927, p. 75; III, 1928, p. 18.
[4]) *Ibid.*, 1923, pp. xcii—xciv.
[5]) *Ibid.*, Vol. III, 1928, p. 18.
[6]) *Ibid.*, Vol. III, 1928, p. 33.
[7]) *Proc. Ent. Soc. Lond.*, Vol. III, 1928, p. 41.
[8]) *Scientific Repts. Agric. Res. Inst. Pusa* (1916—1917), Calcutta, p. 91—102.
[9]) *Ent. News*, Philadelphia, xxix, pp. 145—146.
[10]) *Parasitology*, Vol. 9, 1916—17, p. 259.

ing; for the late A. Bacot[1]) hat shewn that the habits of these insects are such as to expose the species to this danger.

(3) Flight necessary for the male before developing susceptibility to the scent of the virgin female. — Many examples of delayed susceptibility in the males of "Assembling" moths are quoted in the Proc. Ent. Soc. London for October 1927[2]), where numerous observations, kindly placed at my disposal by experienced naturalists, are brought forward, together with a discussion of Fabre's charming writings on the subject. The experience of others, referred to in this little paper, was confirmed by Mr. J. A. Simes[3]), who in 1926 observed that males and females of *Saturnia pavonia* L. (= *carpini* Schiff.), emerging in the same cage, refused to pair. He had been led by this to conclude "that a period of flight on the part of the male was essential to pairing". Dr. G. V. Bull[4]) has supported this opinion by his observation that a bred male *S. pavonia* paired after dashing himself about in the cage; and Dr. Eltringham[5]), in the paper referred to, has brought forward more complete and convincing evidence of the same kind in *Lasiocampa quercus* L. Prof. Heslop Harrison[6]) has also observed the unwillingness of bred Saturniid moths of many species to pair, although all "assemble" freely in nature; also once with *Orgyia antiqua* L., and *Parasemia plantaginis* Hübn.

C. Physiological Barriers.

It is possible that infertility of the first pairings between closely related sexes, and the prepotency of more distant crosses when two successive pairings have occurred, may play a part in the prevention of inbreeding, but specially directed observations on a large scale are required. The following note by the late Dr. T. A. Chapman[7]), F. R. S., bears upon the first of these suggestions, and probably upon the second. He found that the males and females of a large brood of *Acronycta strigosa* F. paired readily and frequently together, but no eggs were laid. He then got some captured males, which paired with equal readiness with the bred females, and as a result obtained plenty of fertile eggs.

It is possible that preferential mating may co-operate with these principles. Thus Mr. Pearman informs me that the males of *Psocidae* "pay court to the females, and the latter appear to exercise choice in their selection of partners. I have observed on many occasions among captive individuals reluctance by the females to pair with males of their own blood."

Dr. J. W. Munro[8]) has also recorded that males of the Blowfly *Calliphora erythrocephala* Mg. do not normally pair with females of the same brood, but wait for later emerging females. He calls attention to the

[1]) *Parasitology*, vol. 9, 1916—17, pp. 228, 232, 233, 335, 256.
[2]) *Proc. Ent. Soc. Lond.*, Vol. 11, 1927, pp. 75—82.
[3]) *Ibid.*, Vol. 11, 1927, p. 82.
[4]) *Ibid.*, Vol. 111, 1928, p. 37.
[5]) *Ibid.*, Vol. 11, 1927, p. 76.
[6]) *Ibid.*, Vol. 111, 1928, p. 19.
[7]) *Ibid.*, 1903 (1904), p. cxi, note.
[8]) *Proc. Ent. Soc. Lond.*, Vol. III, 1928, p. 34.

"By inter-breeding the favourable variations arising in one direction are combined with others arising in different directions; by the kaleidoscopic changes produced by inter-breeding more varied results are presented for selection, and the beneficial qualities arising in one part of the mass may quickly become the heritage of the whole [1]). By inter-breeding excessive spontaneous variation is checked, and the whole community of the species advances surely and with stability into adjustment with the progressive changes of the environment."

[1]) The rapidity with which variations can be passed on over considerable areas is seen in the rapid spread southward of the dark form *doubledayaria* Mill. of *Amphidasys betularia* L., after its sudden predominance in the northern manufacturing districts. This variety, entirely unknown in the Oxford and Reading districts in my boyhood, is now quite common. The appearance of single examples of the *dorippus* Klug form of *Danaida chrysippus* L. in South Africa and Ceylon is to be reasonably explained by transference through inter-breeding from more northern localities in East Africa and the West Coast of India.