SPECIATION OR IRRUPTION: THE SIGNIFICANCE OF THE DARWIN FINCHES†

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Criticism is made of the conventional use of the Darwin finches in teaching. An alternative, 'irruption', theory is presented, to explain the occurrence of the finches in the Galapagos Islands. This postulates that all the species we know today arrived in the archipelago as a mass irruptive migration movement from the north-east. The theory is explained by reference to the European crossbills. In a discussion of the educational role of the theory, it is suggested that we need to make more effort to encourage the creative and critical faculties in advanced work in schools and at undergraduate level. The occasional presentation of alternative theories, and the discussion of their evaluation, are recommended as means to achieving these aims.

1. Introduction

The Darwin finches of the Galapagos Islands are well known to most teachers and students of advanced biology courses at schools and colleges. It is suggested, however, that our use of the Darwin finches in teaching is unsatisfactory; they are usually presented as part of the 'evidence' for Darwinist evolution theory, but this is merely in the sense that the theory can 'explain' or be used to describe the facts. It is not evidence in a strict hypothetico-deductive sense, which must involve the comparison of observations with predictions from the theory.

In paradigm cases of this kind, one is frequently met with the query: 'But what other explanation could there be?' Such a comment is a symptom of bad teaching, since when students are presented with data so closely tied to a single interpretation, they are hardly able to view the interpretation or theory in a critical spirit. In fact my principal contention is that we do not pay sufficient attention to awakening habits of criticism and creative thinking in our students. A different treatment of the Darwin finches could give us, however, a useful basis for pursuing these aims, and the one recommended here involves the comparison of different explanations for the data.

Much has been written on the Darwin finches (Geospizinae), of which there are 13 species in the Galapagos archipelago and a fourteenth on Cocos Island. All the previous studies on the Galapagos species argue or assume that speciation has occurred within the archipelago. However, the next section of this article presents a radically different theory which denies that speciation occurred in the archipelago. Because the theory is easy to understand and makes such a clear contrast with the Darwinian interpretation, it should form the basis for interesting and valuable teaching situations. These are discussed in the final section of the article.

2. The Irruption Theory

One of the main variables studied in the interspecific variation of the Geospizinae is the number of species on each island, or the insular species abundance. Various factors accounting for this have been proposed: island area, diversity of habitats, isolation from the nearest island, distance from the centre of the archipelago, altitude, richness of the flora, interference by man, interspecific competition, and so on. Though mentioned in passing by Hamilton and Rubinoff[1] (p. 390), the 'target surface' of islands seems not to have been considered seriously for the Galapagos Islands. It is proposed here that the islands do function as targets for immigrants, and that this is the principal factor determining the number of species of Geospizinae on most of the islands.

More particularly it is suggested that the Geospizinae arrived as the species we know today, in an irruptive migration movement on one or more occasions. It is supposed that the flocks approached the archipelago from a constant direction, and that if they crossed a coastline they landed on that island and did not continue in flight to reach another island beyond. Birds flying within sight of an island, however, might be expected to change direction towards it, though under the influence of strong winds the attempt to land on the island might only succeed if they were passing fairly close on a straight course. Moreover a high island would be seen earlier than a low one, and so a border zone directly related to the height of the island and extending the effective width of the island should be added. For each island, a value has been calculated for its 'target width', which for islands fully exposed to the direction of the birds' approach is the width of the island viewed from that direction, with the addition of the border at each extremity. Some islands, however, are 'shadowed' by others from the migration front, and then the 'target width' is calculated only for their 'unshadowed portions'. Finally it is assumed that islands close together could freely exchange bird species by subsequent dispersal.

Given this simple model, it should be possible to find values for the direction of the birds' approach, width of border zone for each increment of altitude, and maximum distance apart of two islands considered to be able to exchange bird species freely, to show a relation between insular species abundance and island 'target width'. For calculation of the values presented in Table 1, it has been assumed that the direction of the migration was 234 degrees, the border zone is 1 km for every 250 m of altitude, and islands up to 15 km apart could freely exchange bird species. The four islands concerned in this last category are Baltra (about 1 km from Santa

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Table I. Geospizine species abundance and derivation of $\log_{10}$ target width for Galapagos islands.

Island[a]	Target Abbre-viation	Log_{10} Border km[b]	Geospizine width km[c]	target width	species abundance[d]
Baltra (South Seymour)	Ba	—	8.0	0.90	8
Barrington	Bn	1.0	11.5	1.06	7
Culpepper	Cu	0.7	3.4	0.53	2 or 3
Duncan	Du	1.8	4.8	0.68	8
Fernandina (Narborough)	Fe	0.6	0	—	10
Floreana Charles	Fl	2.6	19.7	1.29	9
Hood	Ho	0.8	14.1	1.15	4*
Isabela (Albemarle)	Is	6.7	39.8	1.60	11
James	Ja	3.6	37.2	1.57	10
Jervis	Je	1.5	0	—	8
Marchena (Bindloe)	Ma	1.4	15.8	1.20	7
Pinta (Abingdon)	Pi	3.1	19.2	1.28	9
San Cristobal (Chatham)	Sl	2.9	23.3	1.37	8
Santa Cruz (Indefatigable)	Sz	3.5	36.0	1.56	10
Tower	To	0.3	5.6	0.75	4
Wenman	We	1.0	5.0	0.70	6*

[a] Names used are those given in Harris[3], with alternative English names in parentheses.
[b] Calculated at 1 km per 250 m altitude, using altitudes in Table 6 of Bowman[4] (p. 12); to nearest 0.1 km.
[c] See text for method of calculation.
[d] From Table 2 of Harris[3] omitting species thought by Harris to be stragglers. Figure for Baltra from Table 7 Bowman[4] (p. 20).
*See, however, the Note Added in Reprinting.

Cruz), Fernandina (3 km from Isabela), Jervis (8 km from James), and Duncan (11.5 km from Santa Cruz), and it is assumed that these small islands gained most or all of their species from their much larger neighbours.

Figure 1 shows the construction made to arrive at values for the 'target widths'. The map used was that in Swarth[2] at a scale of 1:10⁶. The values for species abundance were taken from Harris[3] (table 2), omitting species thought by him to be stragglers. Table 1 gives, for each of the 16 main islands, the abbreviations used in Figs 1 and 2, the width of the border, the 'target width' calculated for a 234-degree approach, the logarithm of the 'target width', and the species abundance. Baltra, close to the coast of Santa Cruz, is not given an altitude in Bowman's[4] table, and it is assumed to be negligible.

Figure 2 shows the relation between species abundance and $\log_{10}$ 'target width' for all islands except the four islands nearer than 15 km to a larger neighbour. The fact that ten of the 12 islands in Fig. 2 fall into a narrow zone (which predicts at most two values of species abundance for any 'target width') suggests a close relation between 'target width' and species abundance. Harris[3] gives '2 or 3' for the species abundance on Culpepper, and both values fall into the zone, as does that for Baltra and Santa Cruz if these are considered as a single island.

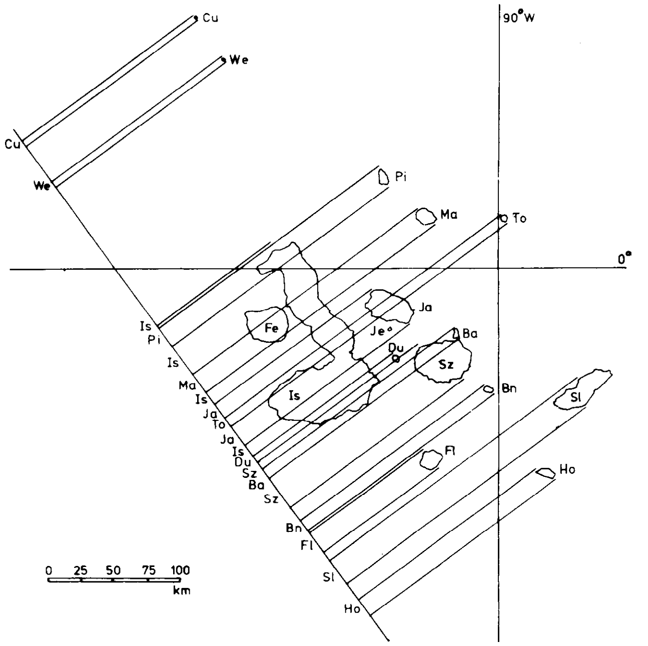

Figure 1. The construction made on a map of the Galapagos archipelago to determine target widths for a 234° approach. the figure merely shows the principle, and is not accurate to scale.

The exceptions are Wenman, with one more species than the maximum predicted in Fig. 2, and Hood with three fewer than the minimum predicted. No explanation is offered in the case of Wenman, other than to point out that the 'target width' merely allows one to postulate the most probable value(s) for species abundance, and some deviations are expected in a large enough sample. Hood, however, appears to be a real exception, especially considering that it is probably the best place in the archipelago to see migrants today.[5]

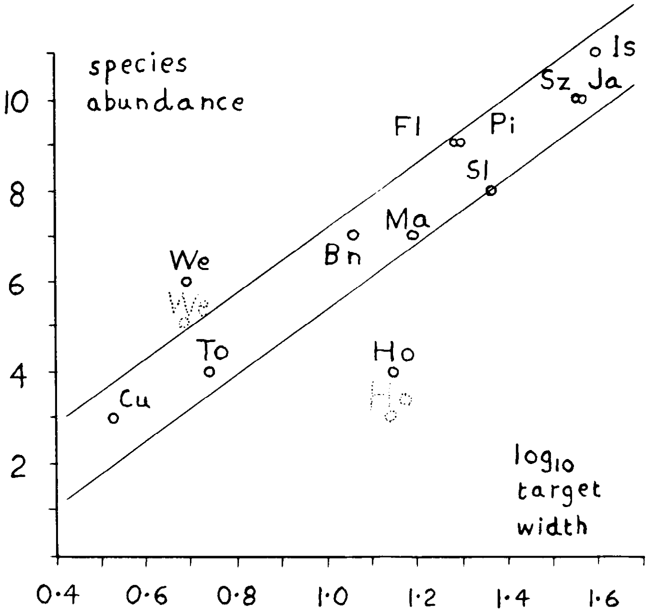

Figure 2. Relation between insular species abundance of Geospizinae and $\log_{10}$ target width of Galapagos islands, determined for a 234° approach. The two dotted entries show the amendments suggested in the Note Added in Reprinting.

The most acceptable explanation may lie in the poor range of habitats on the island; only one of the four vegetation zones found on some other islands is encountered on Hood.[6]

3. Darwin Finches and Crossbills

The development of the irruption theory owes much to the analogy between the Geospizinae and the crossbills, *Loxia*, an analogy which can probably be carried further than hitherto. Within each group, *(a)* the plumage of the different species is fairly uniform, *(b)* a proportion of the males breed in juvenile plumage rather than fully differentiated male plumage, *(c)* the interspecific variation in body weight is not great, *(d)* the bill morphology is the main distinction between the species, and *(e)* there is a correlation between preferred food and bill morphology. This is illustrated for the crossbills in Fig. 3. The migration behaviour of crossbills is of particular interest in the context of the irruption theory, and an account is given by Newton[7] who has reviewed the migration behaviour of the European finches. Finches which normally have a food supply (often herb seeds) which is dependable from year to year tend to have a fairly steady breeding population in any given area from one year to the next. They also tend to have rather circumscribed migration behaviour, with fixed breeding and wintering areas, and regular migration routes. The irruptive species, on the other hand, have more widely fluctuating breeding populations in a given area, and when they migrate they often spread over extensive and varied areas (i.e., they irrupt). They frequently do not return to the same breeding areas two years running. The fundamental reason behind this appears to be the species' dependence, for part of the year at least, on tree seeds. Unlike many herbs, some of the important trees do not produce a constant crop of seeds in any one area; heavy crops may only occur once every few years. The interval between good crops may be longer the further north in Europe the trees are growing. However, while there may be a poor crop in one area, there may be a good crop in other distant areas. The fluctuating populations and erratic direction of movements are probably related to this unreliability of the food supply. Species of irruptive finches are the crossbills, Siskin, Northern Bullfinch, Mealy and Lesser Redpolls, Pine Grosbeak, and Brambling.[8]

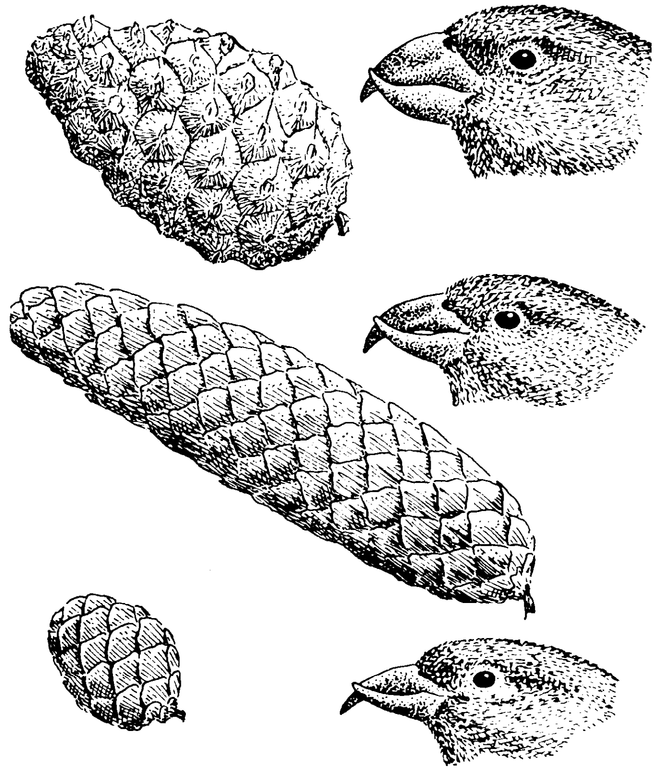

Figure 3. The heads of the three crossbill species, and the main cones eaten: top, Parrot Crossbill *Loxia pytyopsittacus* and pine; centre, Common Crossbill *L. curvirostra* and spruce; bottom, Two-barred Crossbill *L. leucoptera* and larch. After Newton, Reference 7, p. 109.

The crossbills are somewhat different from the other irruptive finches, perhaps because they rely on tree seeds for the whole year, and not just a part of it. Crossbill's migratory behaviour is correspondingly peculiar. While most finches which migrate do so twice a year, crossbills in Europe (but not in North America) migrate only once; and even then, they may migrate only in some years, remaining where they are in others. These movements take place in mid-Summer, when one crop of spruce has finished and before the next is ready. In most years when crossbills move, they do so in various directions, from an area of failing food supply to another which is, or promises to be, better.

However, in exceptional years, crossbills indulge in a longer and more directed migration which may result in the birds invading far distant areas in great numbers. In these years, they tend to move predominantly in one direction, and to cover vast distances, up to 4000 km, often passing right through good feeding areas where normally they would stop. The stimuli which set off this mass movement seem to be high population density and a relatively poor seed crop. The birds can be seen to be unusually restive before setting off, and if this restiveness is communicated from one species of crossbill to another, it may explain why the different species tend to irrupt simultaneously; in addition, the food species of the different crossbills tend to crop in phase[9,10].

In the irruption theory, the Geospizinae are supposed to have had the same migratory behavior as the crossbills, and this would account for the simultaneous mass movement of different species of Darwin finches over the great distances necessary to bring them to the Galapagos from mainland America. One might ask, at this point, why they did not migrate back to their normal home range in a subsequent year, as generally happens with crossbills (though some permanent colonies have been established, in England for instance, as a result of irruptions). One possibility is that the colonizers found themselves in an environment with climate and food species different from those of their home range; it is likely that the conditions causing eruption (movement away from the area), in particular high population density and failing food supply owing to

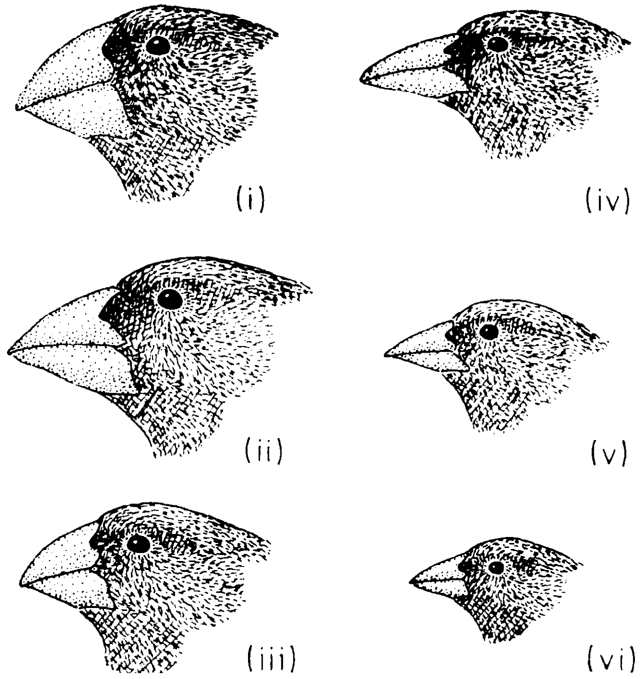

Figure 4. Darwin finches, heads of six species of the genus *Geospiza:* (i) *G. magnirostris;* (ii) *G. conirostris;* (iii) *G. fortis;* (iv) *G. scandens;* (v) *G. difficilis;* (vi) *G. fuliginosa.*

periodicity in cropping of the relevant seeds, never occur on the Galapagos Islands. The irruption theory also supposes that all populations of geospizine finches have become extinct on the American continent; since this is generally believed to have happened for a number of other animal groups, the irruption theory poses no special difficulties in this respect.

4. The Educational Role of Alternative Theories

The following discussion refers to the general use of alternative theories in biology teaching. While the irruption and evolution theories of the Darwin finches are recommended as suitable material, other theories are available, such as those of Dr H. Hillman in electron microscopy,[11] and Dr B. E. C. Bank's interpretation of ATP.[12] Discussions on the latter topic are available on tape from Audio Learning Ltd, Sarda House, 183-189 Queensway, London W2 5HL.

Comparison of alternative theories may be used to achieve two aims—the encouragement of creative thinking, and of a critical attitude. It is assumed that these are desirable in a biologist, especially one doing research. The mere presentation of alternatives may help in both aims, and so might a second method, the discussion of the evaluation of theories, for which alternatives are useful but not essential. The aims are distinct, and the methods are distinct, but in practice these distinctions will often be difficult to make out. The kinds of teaching procedure recommended here need only be practised once or twice during an advance school or elementary university course, but during these sessions a number of important ideas can be conveyed to students who might otherwise not come across them.

One use of alternative theories has special relevance to stimulating students' creative imagination. This involves the dramatic presentation of a radical alternative at the end of a course on a generally accepted theory. Thus an extended treatment of evolutionism might be concluded with a brief but convincing account of the irruption theory, so that students experience a kind of 'intellectual shock'. All too often facts and ideas are absorbed uncritically and complacently, and shaking students out of this passive attitude, and leaving them guessing once in a while, could heighten their alertness and stimulate interest. For this to be effective, the radical alternative should be unfamiliar to the students.

Following such a presentation, or instead of it, alternative theories may be compared in a discussion of how theories in science are evaluated. By 'evaluation' is meant the process leading to a theory's acceptance or rejection, or to some comparable attitude towards its. Generally this will involve the scientist deciding whether it is true of false, or more or less likely to be one or the other. Occasionally, however, evaluation may involve rejection on other grounds, of which an example is given shortly. There may be many methods of evaluation, but a short selection of four will now be considered as an aid to conducting a discussion.

1. Most fashionable at present is the hypothetico-deductive approach. For this to be applicable, one must be able to make predictions from the theory in order to compare them with observations. Non-correspondence of prediction and observation leads to rejection of the theory, while if they correspond one may provisionally accept it. Undoubtedly some biological theories can yield predictions, and so can be evaluated hypothetico-deductively. However it will generally be found that theories in the history of life, such as evolutionism, do not yield predictions, though they may yield expectations based on 'reasonable' assumptions which nevertheless cannot be observed. Such expectations are not legitimately to used in place of predictions (which are derived by deduction from observations and the theory) in hypothetico-deductive evaluation. The status of Darwin's theory in this respect has been discussed by Harper.[13] Use of evolution and irruption theories in considering this method of evaluation might therefore lead to interesting and suprising conclusions, in particular that the method cannot be used for either theory.
2. Irrespective of observations, a theory may be evaluated by examining its logical consistency. Thus if a contradiction is found in the theory, it is a sound reason for rejecting it; though failure to find inconsistency cannot be regarded as a reason for acceptance. This inconsistency method has recently been used by Greenwood.[14]
3. Another method may be called credibility evaluation. An example is seen in the rejection of Newton's theory of gravitation by some 17th-century Cartesian who could not believe that forces causing motion can act at a distance, without contact of bodies. For them the theory of gravitation was 'beyond belief'. More specifically we can say that a theory is

evaluated by credibility when it is rejected either because it is thought to be incredible, or because it cannot be imagined. This might be a legitimate method for someone whose imagination and open-mindedness corresponds with all that is possible. However, most of us are less talented, and then the evaluation will tend to be determined by the poverty of our imagination or our adherence to other scientific or metaphysical theories. In the case of the irruption theory, the example of the crossbills may be used (legitimately) to assist students to understand the theory; but in addition, some students may find it easier to believe the theory about Darwin's finches as a result of learning about the crossbills. If so, they might well be using credibility evaluation.

4. Related to the last method is evaluation in accordance with the rules of scientific hypothesis-formation. A number of early 19th-century theories in biogeography would, if proposed today, be generally dismissed because the supernatural is invoked to explain species' creation. Today, supernatural causes are rejected, either because they conflict with a more scientific method or, perhaps more often, because they conflict with scientists' metaphysical belief in the non-occurrence of miracles. The latter case would be an example of credibility evaluation, but the former is quite a different method relating to scientific convention. One's attitude to the former is presumably related to one's opinion on whether operation of the convention (the refusal to recognize supernatural causes) can be guaranteed not to eliminate true theories. Another rule of hypothesis formation is perhaps Occam's razor, and this might be relevant to the Darwinian and irruption theories.

Not all the points made here about these methods will be universally agreed, but it is hoped they will be found useful in discussion. The four methods have been mentioned because they are all in common use. Biology students should be made aware of them, and they should also be encouraged to have opinions on their legitimacy. The author's opinions are that methods (1) and (2) are legitimate; (4) is legitimate so long as it is realized that it rests on a convention which might in fact exclude true theories; and (3) is entirely disreputable.

It is suggested that the comparison of evolution and irruption theories is a good basis for a discussion of the concept of evaluation, and this in turn will help students cultivate a critical approach to science. As a further aid, the following practical measures are suggested as ways a scientist might set about evaluating the irruption theory; how these relate to the four methods discussed above raises questions for further consideration. The theory might be approached through *(a)* the compatibility of the supposed irruption with local climatic conditions; *(b)* the probable origin of other groups of Galapagos species; *(c)* the acceptability of the values assumed for the other variables in the model, in relation to migrating passerines' observed behaviour on approaching islands; *(d)* the applicability of the model to other groups of species in other archipelagos; *(e)* checking whether the geospizine faunas of the four small islands are subsets of their larger neighbour; and *(f)* the fossil record.

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Note Added in Reprinting

Since the original publication of this article, the author has seen Lack's *Island Biology*,[15] in which Lack considers that there is inadequate evidence for past breeding of *Geospiza fortis* on Hood and *G. fuliginosa* on Wenman. If this is accepted, the insular species abundance of Hood and Wenman should be reduced to three and five respectively. This would remove the anomalous status of Wenman, but enhance that of Hood.

References

[1] Hamilton, T.H., and I. Rubinoff, 1963. Isolation, endemism, and multiplication of species in the Darwin finches. *Evolution* 17 (4): 388-403.

[2] Swarth, H.S., 1931. The avifauna of the Galapagos Islands. California Academy of Science.

[3] Harris, M.P., 1973. The Galapagos avifauna. *Condor* 75, 265-278.

[4] Bowman, R.I., 1961. Morphological differentiation and adaption in the Galapagos finches. University of California Press.

[5] Harris, M.P., 1974. A field guide to birds of the Galapagos. Collins, London. P. 45.

[6] Reference 4, p. 12.

[7] Newton, I., 1972. Finches. Collins, London.

[8] *Ibid.*, pp. 219-225.

[9] Ibid., pp. 229-239.

[10] Baker, R.R., 1978. The evolutionary ecology of animal migration. Hodder and Stoughton, London.

[11] Hillman, H., and P. Sartory, 1977. The unit membrane, the endoplasmic reticulum, and the nuclear pores are artifacts. *Perception* 6, 667-673.

[12] Banks, B.E.C., 1970. A misapplication of chemistry in biology. *School Science Review* 52 (179): 286-297.

[13] Harper, G.H., 1977. Darwinism and indoctrination. *School Science Review* 59 (207): 258-268.

[14] Greenwood, J.J.D., 1979, 1979. Alternatives to evolution by natural selection. *School Science Review* 61 (214): 161-163.

[15] Lack, D., 1976. Island biology. Blackwell Scientific Publications, Oxford.

[16] Lack, D., 1974. Darwin's finches: an essay on the general biological theory of evolution. 1961 ed., Harper and Row, New York.