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Bird migration and the spread of Crustacea

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Introduction

The passive spread of a high percentage of freshwater organisms is one of the most important requirements in short-lived and insular communities for species to attain and survive - and consequently to balance the lack of a topographical continuity of most inland waters. Unfortunately hardly anything is known about the amounts of seed material typical for any lake into which it is carried, although they must obviously be great, so great in fact that in many cases continental, indeed global "gene pools" of many species are guaranteed, which earlier often led to the belief that with inland water forms it was generally a case, for the most part, of cosmopolitan ones. It should be stressed here that large lakes particularly tend to have a surprising constancy in their range of species and evidently act as filters for species on the mass of seed material which enters, so that only forms peculiar to lakes are assimilated. Conversely, there is a very unsettled state with regard to forms in restricted waters which are subject to fluctuating physiographic conditions.

The causes of passive dissemination - wind, water and animals as well as man - are confirmed by many examples, although there are often more isolated observations to hand than statistically evaluable facts. Until now there are indirect proofs for the three first-mentioned factors, such as the colonisation of numerous newly-formed inland waters or the established facts of cosmopolitan forms in temporary waters, eg. Artemia salina. It has been assumed now for at least a hundered years that, among animals, birds play a prominent role, although also disappointingly few facts are at hand. Hence these data are largely confimed to the description of long-term stages clinging to dead or captive species of birds (ephippia: HUMBERT, DE GUERNE: cited in STEUER 1910, statoblasts of Plumatella, cysts of infusoria, nematode eggs, rotaria eggs: cited THIENEMANN 1950), the spawn of snails and fish, and finally to living animals, such as mussels, ostracods or amphipods (NIETHAMMER 1953, SEGERSTRALE 1954). Doubtless this form of transport by birds has a high, and perhaps for many species an exclusive significance, which cannot be assessed at the present time. Thus there are, compared with dryness, sensitive stages which are very probably threatened by a high drop-out. The passage through the gut must prove favourable for these, and also for other stages, as not improbably it can promote and accelerate germination, as has been shown for Potamogeton seeds (LOHAMMAR 1954 and other examples). While a whole range of data is at hand for plant spores (algae, and also vegetative cells, Chara: PROCTOR 1959, 1962) and seeds, extant data for animals are few. Many experiments on warmth resistance (amongst others MATHIAS 1929a, LOFFLER 1958) and some on acid and pepsin resistance (LOFFLER 1958) indicate the possibility for many long-term stages of a passage through the gut, although up to now only ostracod eggs and protozoa have been cultivated from the excrement of seagulls, while MATHIAS (1937) discusses a passage through the gut at great length, but never observed it with birds, ostensibly because the long-term eggs (Triops, Chirocephalus) which he used were difficult to retrieve in the excrement (MATHIAS 1929). On the other hand, this author has established the passage of Chirocephalus diaphanus through frogs, taking place over a period of one and a half days and without any damage. Also the passage through fish had already been observed earlier, for which STEUER (1910) and TOLLINGER (1911) introduced examples. Thus only KNAUTHE (cit. TOLLINGER 1911) observed the capacity to live of the undigested eggs of Bosmina and Daphnia. In any case these facts already testify towards a damage-free intestinal passage for Anostraca, Cladocera and also, to a limited extent, for Ostracoda. Certainly the passage through birds' intestines has up to now been supported only by the old data of STEUER (1910). Since the greatest significance should be due to it for the spread of inland water organisms, experiments seemed to be indicated above all on the duration also of such passages through the gut. It is then very probable that for forms whose stages in spreading are able to pass through birds' intestines intact or even with benefit to the seed, possess significant selectional advantages (LOFFLER 1963).

Method.

An approcimately two-year-old drake was imprisoned for the duration of the experiment in a sufficiently large (100 x 70 x 80 cm) plastic container, which was easy to wash out and had an outlet. Long-terms stages, such as eggs of Daphnia magna, Triops cancriformis, Artemia salina, Diaptomus spinosus and Cypris pubera were introduced by means of gelatine capsules into the oesophagus, through which either before or during the experiment food, or food and water, were withheld or were both offered. Only artificial food ("Tragger" food) was used for this. The excrement could be washed through the above mentioned outlet of the container into a larger reception vessle, whose contents could then be sorted with the help of a plankton filter (a plastic cylinder with a plankton net). After cleaning with a fine jet of water, the residue was inspected under a binocular (ie. microscope) for eggs and resting stages, and these were transferred into corresponding cultures.

Results.

It should be first of all emphasised that the eggs of Triops and Artemia, as far as they passed undamaged through the digestive tract, also hatched and produced normal animals, which were held up to egg-laying. In the same way Daphnia ephippia succeeded partly in reaching the open with the excrement in good condition. This was to be expected after the pepsin/hydrochloric acid experiments on Daphnia ephippia (24 hrs. in 10% pepsin solution in 1n HC1 at 40°C) (LOFFLER 1958). An acceleration of the time for hatching as opposed to normally treated eggs and resting stages could not be established for the present (about 40 hours for Triops in cultures at 20°C, about 48 hours for Artemia). The percentage of the resting stages and paucity of eggs excreted by the drake (and retrieved) is largely independent of the amount of time spent in the digestive tract, and is on the contraty linked to the size of the resting stages and eggs. Thus at times only 1% of the Daphnia magna ephippia were expelled intact, and 25% were retrieved from the excrement only by way of exception, while the remainder reached the outisde in more or less large fragments. Of the small Cypris eggs, 25% were found in the faeces, and the values for Triops, Diaptomus and Artemia lay at an average of 10%. Doubtless the high mechanical strain through the gizzard is responsible for the loss of the remaining resting stages and eggs, in which the peristaltic action and "grit" (mixture of small stones) possesses an exceptionally destructive power. Just in order to investigate the effect of maximum mechanical stress through the digestive tract, for these experiments a duck was picked out, whose gizzard can produce a pressure of up to 180 mm Hg. (KOLB 1962). In the case of other, more carnivorous duck species, as for example the shovelers there can be taken into account a greater rate of passage for resting stages and eggs through the gizzard. The conditions with definite fish-eaters (Sager sawbills , cormorants) which have very thin-walled gizzards must be still more favourable. Experiments with grit-free ducks were not carried out, since in the first place the grit (up to 10 g. for domestic ducks) is retained for an extraordinarily long time, up to one year (data for domestic hens: MANGOLD 1929, KOLB 1962) and secondly, preference had to be given to natural factors.

In order to learn the mechanism of the gizzard better, 70 red pieces of rubber (about 2-5 mm^3) were guven as food in a gelatime capsule, and during the experiment food and water were offered freely. The complete amount of rubber peices was retrived in the faeces, ground down to the finest material, and no piece succeeded in reaching the open with the above dimensions. Within the first 24 hours about 60 fragments were eliminated, but within a further 24 hours the mass (a long way above 1000) of the finest rubber particles coulb be determined. There then followed an abrupt decrease, until finally another 48 hours later the last particles were observed in the excrement. The experiment shows that obviously pieces of rubber of this size are retained as grit, and that only finer material is carried further in the gut. HEUDE (1962) especially observed such a filter action and sorting function of the stomach, and it is quite likely that Daphnia ephippia had previously been affected by them.

Of critical significance for every form of passive spreading by birds is the duration of the possible transport, which in the case of a passage through the gut is larely determined by the process of digestion. The length of time for the process of digestion and especially for the passage of undigested material depends, in individuals of the same species, on age and sex (FERRANDO and others 1961, HEUDE 1962, MANGOLD 1929), physical condition of the animal (hunger, thirst, vitamon deficiency, etc.) and above all on the composition of the food (especially with plant and grain eaters). It is known that birds have a very rapid process, so that berries can be expelled within 12 minutes by Sylvia atricapilla. This period of time, however, amounts to 4 hrs. with geese (MARSHALL 1960), a time of one and half hours is found for ducks (MATHIAS 1937), and the minimum times for domestic hens are similar (HEUDE 1962, HILLERMAN and others 1953, KAUPP and IVY 1923). The amount of time necessary for the total emptying of the digestive tract from a meal is certainly much longer. A whole day and more have been given for hens and geese (MARSHALL 1960). Liquids on the other hand can pass through in a few minutes (KOLB 1962). Table 1 gives the minimum and maximum times for the passage of the resting stages and eggs under investigation, F signifying an abundance of food, and W an abundance of water during the experiment.

Table 1

	Min. time (in hrs.)	Max. time (in hrs.)
Ephippia (D. magna)	1 (FW)	2 (FW)
Artemia salina	1 (FW), 2·33	2·50 (FW) 5·50. 31·50
Triops cancriformis	1 (FW)	2 (FW)
Diaptomus spinosus	0·75 (FW)	1·75 (FW)
Cypris pubera	2·33 (W)	3 (W)

From these values a quite similar duration emerges for minimum and maximum times with any food and water offered, which on the deprivation of food (from 3-5 hours before the start of the experiment) and deprivation of water (from 3 hours before the start of the experiment) can be significantly increased. Finally in one case several eggs of Artemia salina in good condition were still found in an excretum after 21 hrs. 30 min. Their later expulsion will be further discussed below.

The total duration of the passage through the digestive tract is composed of quite different, protracted stays in the separate sections of the system. In geese the food moistened with saliva slides towards the stomach at about 1·5 cm/s, where it halts in the rudimentary crop, which is no more than a spindle-shaped extension in amongst other geese and ducks. [Delays there]* are scarcely to be expected, but on the contrary are to be anticipated in the proventriculus, which also functions as a retainer in geese and ducks (MANGOLD 1929). Observations where living Paludina were to be found in the crops of ducks which had been shot (THIENEMANN 1950) should previously have shown that food would be thrown up from stomach organs during the death throes. However, only maximum stays of 24 hours have been measured for species of birds with a genuine crop only in exceptional cases (according to the state of the stomach, a short stay or even none has also been observed in the crop, as shown by X-rays). There is no information available on the length of accumulation in the glandular stomach of ducks, and so a short-term stay should be assumed. Quite different time values for the passage of food are known for the gizzard according to the composition of the food and physical condition of the animal, values which in the case of the domestic hen (a laying

* Not in original - added to make sense (ed).

hen, after 18 hours fasting) amount from 0·5 to several minutes, while the complete evacuation demands 2 hrs. 30 min. (HEUDE 1962). In many birds, especially those which take food rich in water, thus including ducks, there exsists an supplementary pylorus stomach, which in case of divers regularly contains feathers and possibly functions as an additional filter (MARSHALL 1960). In the small intestine, with its three sections of duodenum, jejunum and ileum and a total length in ducks of an average 195 cm, the contents are moved forward by peristalsis at several cm/s and finally, after a short stay in the rectal section, are expelled.

The paired caeca leading off at the join of the small and large intestines in many birds are in their histological construction quite similar to the small intestine, but have - especially in geese and ducks - more lymphatic tissue (MARSHALL 1960) and in case of the latter, measure 15-20 cm. (MANGOLD 1929), and according to some observations up to 22 cm. In geese they are longer, and ostensibly present in <u>Fulica</u> in threes (MANGOLD 1929). Their possible functions, namely water absorption, assimilation of non-protein nitrogen, digestion of carbohydrates and proteins, microbial breakdown of cellulose and finally microbial synthesis as well as vitamin synthesis and resorption have only partly, not definitely, been proven (KOLB 1962, MARSHALL 1960). Still less clear at present are the mechanical processes which lead to the filling and emptying of the caeca, which are superfluous to the bird and quite unnecessary. The peristaltic propelling motion of the large intestine, the pumping effect of the caeca and peristalsis of the small intestine are taken into consideration for the filling, the filling pressure and peristalsis of the intestine for evacuation. About 10 intestinal defecations per caeca take place in hend (MANGOLD 1929), wherease the caecal defecations in geese (as some observations have revealed, also with ducks) in contrast to the intestinal ones, present a homogeneous, thick, pasty mass. At any rate a mixing of intestinal and masses into one excrement appears to be possible with ducks. (The green excrements mentioned by Lorenz in 1949 are moreover hardly of caecal origin, but probably arise from discharges of concentrated bile). According to some observations, the evacuation of caecal material in ducks is quite irregular and on the whole often took one day to be expelled, which in comparison with the great activity of defecation (around 50 stools per day) was not expected.

As was now shown, resting stages and eggs of different organisms could also reach the caeca, Thus the above-mentioned <u>Artemia</u> eggs, which were belatedly expelled, are derived from a part of the excrement from the caecum, and probably part of the late-arriving rubber particles can also be explained through storage in the caecum. In order to obtain more light on this subject, domestic ducks (on a poultry farm) were fed with Artemia eggs and were slaughtered after 3 and 7 days respecitvely. In one of the 3-day animals could be found 3 eggs in one caecum, and 1 egg in the other, by which at this stage points of reference for a caecal spreading of many organisms appear to be given. Certainly the precise mechanism for filling and emptying the caeca was only to be clarified through investigation with X-rays, before data, relating to the caecal storage of different eggs and long-term stages, and also on the length of this storage, could be delivered. Thus a great significance for passive spreading is due to this, while ducks are capable, while migrating, of performing at least 480 km distances in a day (SCHÜZ), whereby carriage over more than 1000 km seems to be assured for the above-mentioned Artemia eggs.

With this there arises the question as to what extent not so much the distribution patterns of many species, especially of the better-known crustacea, are determined by bird migration, which certainly, as is accepted today, takes place principally as a "broad front", but is still a case of mass movement along set guidelines. Such guideline effects can be guaranteed to affect water fowl just in arid regions in the form of different inland waters, or through long, southerly-orientated mountain ranges. Since the frequency can be very decisive for the result of passive spreading, such guidelines must be drawn upon for the interpretation of many forms of distribution. Thus the divided distribution of many ecologically tolerant Diaptomus species, which have taken hold of Iran, or the colonial area following the migration over the Andes of Boeckellida, is not comprehensible without bird migration, and difficult to understand apart from guidelines. Here more understanding must be obtained through investigations, particularly on the caeca of aquatic birds shot while on passage.

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Notice

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