THE NON-HERITABLE ASPECTS OF FAMILY UNITY IN BIRDS

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Most species of birds are known to form individual family groups in which parents and young remain associated until the group disperses with the maturation of the young. The most striking feature of such family groups is the high degree of specificity that they exhibit, in that each family is maintained as a unit and distinction is made among different families. In many cases this specificity does not appear to be genetically determined, for it is well known that a variety of kinds of birds will hatch and attempt to rear the young of kinds other than their own (see Nice, 1943, for references). Observations of this sort suggest that the genetic factors underlying the behavior patterns involved in the initial formation of family units have in themselves a very low order of specificity and that any specificity which develops is established largely on a non-heritable basis.

In other words, the specific components of the initial formation of family bonds in birds do not seem to have heritable determinants, but appear rather to be established as a result of conditioning or imprinting acting at the time of hatching. Parents and young thus appear to inherit a generalized ability to form a family association, the specific features of which are not inherited.

In this respect such behavior resembles a number of other activities of birds that also owe their specific expression to non-heritable determinants. Such activities are of interest not only for their own sake, but because some of them would seem potentially capable of affecting the genetic composition of the populations in which they occur (Cushing, 1944). In these cases one finds evidence favoring the occurrence of the so-called phenomenon of "organic selection," the existence of which was postulated long ago by Lloyd-Morgan and others, but which has received little attention recently (Cushing, 1941; Huxley, 1942; Gause, 1947).

As the family bond forms the basis for the perpetuation of the other non-heritable behavior patterns noted above, and as little attention has been paid it from an experimental point of view, the present paper presents some experiments designed to test the strength and specificity of the bonds in various families of birds and to establish a basis for later work on the nature of the factors involved. In this paper no more is attempted than a demonstration of the reality of the bond and a rough measure of its strength under disruptive influences.

Although the majority of observations reported was made upon chickens and ducks, the literature cited demonstrates that a variety of other birds also show similar behavior giving some probability to the general applicability of the observations reported here.

The reader should note that we are employing various anthropomorphic terms in preference to coining new words or using relatively clumsy sentences. This is done with full realization that it would be difficult to establish human counterparts to the behavior noted even if these exist. In fact, and to the contrary, it is apparent that the behavior reactions involved, while highly specific, are stereotyped and apparently established at non-conscious levels.

The observations recorded here were made on birds reared in the J. Rulon Miller wildlife area maintained by one of the authors (A. O. Ramsay) on the grounds of the McDonogh School, McDonogh, Maryland. Here it was possible to observe the behavior of several kinds of birds that had been induced to form heterospecific family groups as a result of the hatching of the eggs of one species under the females of another. Table 1 indicates combinations made during two seasons, 1947 and 1948.

Table 1
Composition of Families

No.	Parent	Young	Hatching date
Homospecific			
1	Pekin duck	3 pekin ducklings	May 29, 1947
2	Pekin duck	3 pekin ducklings	June 16, 1947
3	Barred rock hen	12 bantam chicks	May 25, 1947
4	Barred rock hen	10 bantam chicks	May 27, 1947
5	Barred rock hen	25 barred rock chicks	Sept. 20, 1947
Heterospecific			
6	Bantam hen	4 bobwhite quail	June 3, 1947
7	Rhode Island red hen	3 black duck	June 1, 1947
8	Rhode Island red hen	13 mallard	June 7, 1947
9	Rhode Island red hen	3 turkey (game farm)	June 4, 1948
10	Rhode Island red hen	2 turkey (game farm)	June 4, 1948
11	Muscovy duck	1 mallard	May 21, 1948
12	Domestic pigeon pair	1 bobwhite (killed by male at 24 hrs.)	June 15, 1948
Heterogeneous			
13	Barred rock hen	5 muscovy, 2 pekin, 5 barred rock chick	May 24, 1948
14	Bantam hen	1 pheasant, 4 bantam	June 11, 1948
15	Bantam hen	2 mallard, 4 bantam, 1 barred rock	June 10, 1948
16	Mallard hen	2 hybrid (black duck x mallard) 4 mallard	May 14, 1948
17	Mallard hen	3 pekin, 4 mallard, 4 hybrid	May 19, 1948

The usual technique employed was to place eggs of the desired type under broody females confined in wooden nest boxes, each of which opened into enclosed chicken wire runways (2x2x6 ft.) resting on the ground. The families held in these cages were not over twenty feet from each other at the most and could readily see and hear each other as well as some dozen muscovy and pekin ducks and chickens that moved through the area unconfined. In addition, domestic pigeons were rearing young in the same area and chukar partridges and pheasants were present in cages where they could be heard easily. During the second season, two Canada geese and several black and mallard ducks also roamed the area.

There was little doubt that each family unit was well established in the first few days. The young in every case recognized their foster mother, whether of the same or different species, and responded to her behavior. For example, by this time bantam hen 6 was observed to catch flies, call the young bobwhite quail to her, and feed them, which continued until they were able to perform this on their own. In addition, the various species responded to the food and alarm notes of their own mothers and not to those of other individuals.

The families, then, behaved as one might have predicted from a general knowledge of poultry raising practices and from the literature, and even though they were all reared in sight and sound of each other. It seemed desirable, however, to construct some tests upon the relationships involved in order to obtain data regarding the strength of the bond between parent and offspring under varying circumstances.

With this in mind, combinations were made in which two or more family units were placed together in the same enclosure (made by joining two of the runs described above). One such experiment was tried by placing pekin duck 1 and her ducklings in the same enclosure with Rhode Island red 7 that was mothering black ducks. In this case the duck's brood of ducklings was allowed to come to her from their home box about twelve

feet away. This they did readily in response to her calling, answering themselves until they were able to pass through the opening and join their mother in the cage. Once together in the enclosure, the two famlies continued to remain intact in spite of the fact that they were repeatedly stirred up either by us or by their own activities. It was obvious that the ducklings of both species were capable of finding their own parents and that they actively sought them out when removed. In addition, aggressive action on the part of the adult birds, particularly the hen, was observed to add further stability to the family group; for young birds were attacked whenever they approached too closely to the wrong parent. Both parents and young, then, appeared able to distinguish each other under the conditions of the experiment which lasted for an hour.

An additional test of the strength of the parent-young relationship was had when hen 3, fostering bantam chicks, was placed in the same enclosure with the above families 1 and 7 and allowed to call her young to her. There was some fighting between the

Table 2
Families Confined Together

No.	Parent	Age of young in days	Time together in hours	Results
7	Rhode Island red—3 black duck	3	1½	Original groups intact
1	Pekin duck—3 pekin	6		
3	Barred rock hen—12 bantams Added to above groups	9	½	Original groups intact
14	Bantam—1 pheasant, 4 bantam	3	1	Original groups intact
15	Bantam—2 mallard, 4 bantam, 1 barred rock	4		
9	Rhode Island red—3 turkeys	13	1	Original groups intact
13	Barred Rock—5 muscovy, 2 pekin, 5 barred rock chick	23		
9	Rhode Island red—3 turkeys	13	1	Original groups intact
10	Rhode Island red—2 turkeys	13		
9	Rhode Island red—3 turkeys	16	1	Original groups intact
14	Bantam—4 bantam (pheasant dead)	9		
10	Rhode Island red—2 turkeys	16	4	Original groups intact
15	Bantam—4 bantam, 2 mallard, 1 barred rock	10		
13	Barred rock—5 muscovy, 2 pekin, 5 barred rock chick	27	4	Original groups intact
15	Bantam—1 barred rock, 2 mallard, 4 bantam	10		
10	Rhode Island red—2 turkeys	16	18	Original groups intact
13	Barred rock—5 muscovy, 2 pekin, 5 barred rock chick	27		
9	Rhode Island red—3 turkeys	16	17	Original groups intact
15	Bantam—2 mallard, 4 bantam, 1 barred rock	12		
10	Rhode Island red—2 turkeys	18	20	Original groups intact
9	Rhode Island red—3 turkeys	18		
13	Barred Rock—5 muscovy, 2 pekin, 5 barred rock chick	2	11 days	See text
17	Mallard—3 pekin, 4 mallard, 4 hybrid	7		
16	Mallard—2 hybrid, 4 mallard	12		
11	Muscovy—1 mallard	5		

two hens during the ensuing thirty-minute interval which served to completely mix the families several times; but, again, there was no question that both young and parents reacted specifically so as to reform their original units. These observations were confirmed by similar experiments repeated at other times and summarized in table 2.

One of the last to be performed was carried out for considerable time and involved four families including a muscovy (11), barred rock hen (13) and two mallards (16 and 17) as mothers with assorted young ducklings and chicks as noted in table 2. These families were color-banded and confined together in a pen 6x20 feet for eleven days. The hen kept her family intact during the entire period, but the young of the two mallards formed a single family at the end of the first day. This, however, was apparently due to the fact that the two mallard mothers remained inseparably together themselves. In this connection it is notable that these birds were sisters from a family (8) studied the year before. The muscovy kept her single mallard young for three days at which time it joined the large group belonging jointly to the mallards. Relationships persisted like this until the eleventh day when the ducks were released.

At this time it was believed that no original distinctions existed within the large family group formed under the mallards. However, a day after release the single mallard associated with the muscovy rejoined her on the pond to remain until killed by a turtle three days later. This suggests that in an unenclosed area the two mallard families might also have segregated. Unfortunately, this could not be tested, for one mallard and some young were removed to another pond when released.

In addition to the experiments reported above, various attempts were made to incorporate young into groups other than their own. These results are summarized in table 3. While the data presented are not extensive they do show that definite and highly specific barriers to adoption exist which are relatively difficult to overcome. The data also indicate that more extensive work will show that adoption is more apt to occur when the age and general appearance of an introduced bird approximates that of the young in the family with which it is to be united, and in younger rather than older families. It also favors the view that factors of species recognition do not influence the success of adoption at least to an obvious degree. It is hoped that the adoption technique will be of value in studying this point further.

DISCUSSION

A consideration of the above data shows that the heterospecific family groups which can be formed between a variety of species of birds are, in some cases at least, sufficiently stable to maintain themselves even when the families concerned are raised in close contact and subjected to artificial situations designed to disorganize and regroup them. They also confirm the point, in several instances at least, that behavior of both young and adults operates to maintain the family, parental birds resisting the intrusion of foreign young and young birds seeking their own parents. That the relative stability given to families by such interlocking behavior can, of course, be circumvented even in natural conditions, may be seen from the adoption of extraneous young in various species such as bobwhite quail (Stoddard, 1946) and by the communal habits of forms like *Crotophaga* (Davis, 1942) and the California woodpecker (Ritter, 1938).

This work also substantiates the view that in many birds the specificity of the family unit is not primarily established through genetic determinants. However, although a survey of the literature suggests that the same is true for a diversity of species, observations exist to indicate that this is not an invariable situation and that genetic determinants of this specificity will be found to have evolved in some species (see, for example, Lashley, 1915).

Table 3

Adoption Experiments

No.	Adoption family and age of young	Transfer young and age	Family	Time together	Result
3	Barred rock hen—12 bantams, 3 days	Mutual exchange of four chicks between groups		—	Adopted immediately.
4	Barred rock hen—10 bantams, 1 day				
5	Barred rock hen—no young	25 barred rock chicks, 1 day old from hatchery			Adopted immediately.
	25 barred rock chicks, 10 days	19 barred rock chicks, 1 day old		—	Killed four but accepted rest after five days.
	25 barred rock chicks, 21 days	50 Rhode Island Red chicks, 1 day old		24 hrs.	All killed by hen.
1	Pekin—3 pekin ducklings, 10 days	1 mallard, 1 day	8	15 min.	Actively rejected.
	11 days	1 mallard, 2 days	8	15 min.	Actively rejected.
	21 days	1 pekin, 3 days	2	30 min.	Actively rejected.
	21 days	1 chick, 25 days	3	30 min.	Actively rejected.
8	Rhode Island red 13 mallard, 1 day	2 black duck, 6 days	7	—	Accepted at once.
	11 days	1 pekin 20 days	1	30 min.	Actively rejected.
	21 days	1 pekin 12 days	2	30 min.	Actively rejected.
13	Barred rock hen 5 muscovy 2 pekin, 1 day	5 barred rock, 1 day from hatchery		5 days	Actively rejected, then accepted, but even then occasionally pecked by mother.
13	Barred rock hen 2 pekin 5 muscovy 5 barred rock chicks, 28 days	1 barred rock chick, 18 days	15	24 hrs.	Actively rejected.
7	Rhode Island red 3 black duck, 7 days	2 mallard—1 day	8		Accepted at once.

In this regard, however, the possibility should not be overlooked that while genetic factors may not determine the basic specificity of the family bond, they will come to operate secondarily as the family matures. For example, while a pair of domestic pigeons successfully hatched a bobwhite quail in our experiments, the male soon struck and killed it as it ran about the cage. In this case the work of Whitman and others (see Cushing, 1941) showing that many Columbidae will rear and foster the young of pigeons and doves from species other than their own, raises difficulties as to the correct interpretation of the genetic factors underlying the behavior of the male bird. Further work on this point will be necessary, but when one considers that mixed families have been formed between even such extremes as owls and ducklings and chicks (Nice, 1943:241), it would seem that family bonds in birds based upon non-heritable factors are of widespread occurrence.

In conclusion it may be noted that here is a case where a behavior pattern, the establishment of a highly specific bond between parents and young in birds, not only is apparently formed on a non-heritable basis, but also appears to have been so formed during much of the evolution of the group. That genetic factors have not risen more frequently

in spite of the long time involved is striking from an evolutionary view, but is probably due to the fact that it would be a rare circumstance where these would be required. Even if such genetic factors had existed, there would hardly seem to be sufficient selection pressure to prevent their disintegration through random mutation. In this regard it is of interest to note, however, that parasitic birds have used to good advantage the fact that genetic factors for the recogntion of specific young are absent in many birds (see Nice, *loc. cit.*, and the little known paper of Scott, 1904). In this case it is surprising that genetic factors for the recognition of young have not arisen in the host species for the habit of parasitism is sufficiently ancient to be correlated with the evolution of a variety of adaptive characters in parasitic groups (Friedmann, 1929).

SUMMARY

The present paper presents experiments upon heterospecific families of birds showing that such families are united by highly specific bonds, the specificity of which appears to be due to non-heritable factors rather than to genetic ones. Some comments upon the evolutionary relationships of this behavior are presented.

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