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THE RELATION OF NON-HERITABLE FOOD HABITS TO EVOLUTION

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The possibility that the non-heritable behavior of animals can influence the genetic composition of their populations has been suggested in several previous papers (see Cushing, 1941, *a, b, c*). It is the purpose here to consider this possibility further in an attempt to obtain a more precise picture of the way in which animal populations may evolve heritable differences under the guidance of behavioristic traits, the specific expression of which is determined by non-genetic factors. In order that such behavior may affect population genetics it must have its specificity of expression maintained over many generations within the population concerned, passed on by the actions of parents to their young like a tradition. This does not imply a conscious effort on the part of the organisms involved, but only a physiological series of cause and effect relationships consistently maintained between succeeding generations. The effect on population genetics of such behavior would seem most likely to occur through influences on the factors of natural selection and on the exchange of genetic material among populations. Detailed discussions of the relation of these factors to evolution can be found in the recent works of Dobzhansky (1941), Wright (1940), and Mayr (1942).

As the role of acquired mating preferences in birds has already been discussed in relation to non-genetic sexual isolation (Cushing, 1941*b*), it seems appropriate at this time to take up another aspect of bird behavior, that of acquired feeding habits. This type of behavior is such as might seem capable of influencing selection pressure. This especially is true if it can be shown that individuals of similar genetic constitution can acquire different feeding habits and also that opportunities occur for such non-heritable behavior to be perpetuated over many generations under natural conditions.

While it is known that the young of a great variety of species of birds are influenced by their parents to some degree in the food habits they adopt as adults (Thompson, 1923; Nice, 1944), only the raptorial species, the hawks and owls, will be considered here in any detail. This is because relatively more is known regarding these birds in this respect and also because of personal experience and interest in certain aspects of the raptorial habit (Cushing, 1939). As will be reiterated, however, the conclusions reached are such as might well be found to apply to a great variety of birds and to other vertebrate animals.

The most searching analysis of the behavior of raptors to date is that of Sumner (1934), among whose results was the conclusion that young raptors do not show an inherited ability to recognize living animals as prey, but rather must learn to do this. The success of such learning is aided by an inherited curiosity concerned with novel objects which develops into a propensity to follow and take up and handle such objects, especially if in motion. Given this sort of genetic constitution, it follows that a moving animal once seized will sooner or later be given tentative nips, with the eventual discovery that it can be killed and also that it is good to eat. All authorities (to be mentioned later on) support the general thesis that very little repetition is needed to imprint actions involving successful feeding upon a bird and that the bird becomes aware of the possibilities of living prey in a remarkably short time after its initial, successful attack. In spite of this, Sumner's observations indicate clearly that, in the absence of parental or human guidance, the taking of living prey is dependent in the final analysis upon accidental external circumstances and that a young raptor may be very backward in this respect unless presented with the proper set of circumstances. This is a very remarkable conclusion for it implies that the whole array of raptors, and this involves the two independently evolved groups of hawks and owls, are raptors largely because of traditional influences.

Support for Sumner's conclusion is abundantly supplied in the literature on falconry (see Michell, 1900; Russell, 1940; Bond, 1936), from which it can be seen that young hawks are admirably "set" genetically to learn to capture and eat living animals, but that the expression of this "set" through learning is dependent upon external circumstances, quite fortuitous in the case of young hawks regularly fed, but left to their own devices.

It may be argued that hungry hawks will show an inherited ability to kill for themselves even though well fed ones will not. This does not seem probable on the face of it and seems even less so when one considers that falconers find that young hawks need to be fed from one to two times a day in order to prevent serious disabilities arising that would interfere with hunting.

Accepting the point that young raptors must learn that living animals are food, the next step is to consider the extent to which parents are capable of influencing their young to adopt specific feeding habits, for only by such influence can any specific traditions be maintained. A survey of Bent's "Life Histories of North American Birds of Prey" (1937-38) shows that in all species of hawks and owls where any observations have been made on the young after they have begun to fly parents and young remain associated for a considerable time, often well through the summer months. During this interval the young are fed by their parents until they are able to hunt for themselves. As noted above, the evidence from several sources shows that such parental feeding is necessary to the welfare of young hawks and that young hawks otherwise could not survive the relatively long period between leaving the nest and becoming self-sufficient. This point alone, however, throws no light on the possible effects of parental care upon feeding habits, for it has already been shown that young hawks, if allowed liberty and assured of a steady food supply, will often eventually learn to hunt for themselves.

Information on the actual training of the young by the parents is not as extensive as might be desired; nevertheless, its occurrence is indicated by various observations on at least the following species: Marsh Hawk, Red-tailed Hawk, Mexican Goshawk, Golden Eagle, Gray Sea Eagle, Everglade Kite, Bald Eagle, Sparrow Hawk, Great Horned Owl and Burrowing Owl. The observations made range from those showing the parental birds placing the food of the young out of their reach through those that suggest rather elaborate actions, as in the Marsh Hawk where the parents are known to drop the food to the young while both are in flight. Another factor no doubt important to the education of the young is the parents' feeding them less and less well prepared game as they approach the time when they will be able to fly (Bond, 1936). The whole course, as far as observed, seems "designed" to take advantage of the young raptor's instincts of curiosity, play and feeding, and the recognition of living prey comes about more or less naturally as the young develop sufficient ability to follow their parents about for food.

A further contribution to the view that parental association may be important in forming food habits is obtained from the fact that Michell and other falconers advise the use of a "make" hawk (one familiar with the hunting of the prey to be taken) in the instruction of untutored falcons when these are ready for entering at living quarry.

It can be seen that there is a reasonable amount of evidence that the parents of raptors do not merely passively feed their young after leaving the nest, but, through suitable modifications of behavior, also play an active role in aiding them to learn to hunt for themselves. The only evidence known to me that may be construed as refuting this point of view is that relating to the Osprey where two accounts cited by Bent (1937) and Abbott (1911), respectively, state that hand-reared individuals will instinctively begin to fish for themselves when able to fly. However, these statements should be cautiously accepted, especially as the accounts are difficult to interpret critically because the young were probably reared on fish and may well have been responding to an already familiar food.

The next point for consideration is the degree to which the parental guidance that probably occurs in most species of raptors might account for the differences in food preferences and methods of hunting which serve to distinguish these various species. Before proceeding, it is necessary to point out that while there is much apparent interspecific overlapping and intraspecific variation in the food preferences of most hawks and owls, when one considers these preferences in terms of species of animals preyed upon, each species of raptor does have a characteristic way of hunting and an average, generalized type of prey that it hunts. These differences are pronounced enough to be useful for distinguishing the various species; and in some, as the Everglade Kite which preys exclusively on a species of snail, or the bat-catching falcons, the characteristic foraging behavior may be very marked. The important point here is to consider the extent to which tradition could be responsible for the differences observed, and again one can find many helpful data in the field of falconry. After reading such authors as Michell, Russell, Bond and others, one obtains the following information.

All hawks must be "entered" at the type of prey for which they are intended; that is, they must be trained to take living prey of a particular sort rather than just the lure (or, in the case of wild caught adults, the previous prey) to which they have been first accustomed. This transition is most often made by giving them one or two blinded (with head bags) birds resembling the intended game and then flying them at the game itself, selecting only ideal situations for the first few flights. "Long-winged species" of hawks must be re-entered at quarry of an unfamiliar type even though they are adept at killing other forms. Thus, for example, Duck Hawks taken as adults and long used to hunting for themselves before capture, must be entered at crows (a bird rarely taken under natural conditions) before they will pay them any attention. The same hawk must be re-entered at grouse, should it be desired subsequently to hunt such species. Of interest in this respect is Michell's mention of species known to be taken frequently by wild hawks under natural conditions that no falconer has been able to train his tamed hawks to take. Here, as in many other connections, the importance of proper training by man for the development of specific hunting techniques is well emphasized. The question of the influence of training upon the specificity of the hunting habits of "long-winged hawks" is summed up by this quotation from Bond (1936:73): "It appears to be quite difficult for the very limited mind of a young falcon to grasp the fact that a live bird or mammal may be converted into food. The lesson must be learned over again for every species of prey of very different appearance. It is perhaps as a result of this, at any rate I have found it true, that falcons, both wild and trained, are prone to form prey habits, and to confine the food taken to a single species or group as exclusively and as long as may be. When the chosen food gives out, through migration or whatever cause, a new item is selected and followed with the same single-mindedness."

The accipitrine hawks present a somewhat different aspect of the same problem for they are more apt to take anything that flies or runs within a given speed and size group. However, entering must also be done to give these birds the idea of living prey, and specificity also exists for it is recommended that Goshawks intended for such fast and heavy game as grouse or hares be kept to these forms lest they grow lazy and fly only after easier game. Such habits of laziness occur in several connections with respect to hawk training in general, and are exceedingly difficult, if not impossible, to break once formed.

With regard to the technique of hunting, much elaboration could be made of different points in training that show that hawks form relatively set habits of various sorts, but it is sufficient to conclude here that all the evidence suggests that tradition is the dominant factor in determining the specific feeding habits of individual hawks and, therefore, that the prey taken and the way it is taken is determined much more by specific traditions than by specific genetic factors. With this the case, and granting an active role in the teaching of offspring by parents, it seems quite probable that specific parental habits will be acquired by young birds, admitting, of course, that various accidental circumstances could occasionally combine to alter these effects in the later life of the individual.

The conclusion to be reached then is that all evidence so far available favors the contention that the differences in specific food habits of various species of raptors are maintained much more through non-heritable factors passed on by the interaction of parental behavior with that of the offspring than they are through specifically different heritable factors. This cannot be considered proven, but the probabilities are certainly sufficiently in its favor to give it precedence over any alternative explanation. With the most characteristic trait of raptors, that of the taking of living prey for food, apparently not directly maintained by genetic factors, it follows that the genetic complex characteristic of raptors owes its existence to the selection pressure exerted by a non-genetic habit. This follows because of the well-known postulate that unless a character (for example, the talons of raptors) is subjected to a constant selection pressure, it will deteriorate as the population accumulates genes that decrease its efficiency. An obvious corollary to this postulate is that the form of such heritable characters as feet and bills is molded by the kind of selection pressure to which it is subjected. Therefore, the genetic basis of structures relating to the raptorial habit would seem to be in large part determined by the direction in which selection pressure is exerted through the medium of traditional differences in feeding habits.

Still another consideration, however, enters into the picture. It is obvious, for example, that a Goshawk and a Duck Hawk are so different genetically that one could not be conditioned to feed after the fashion of the other. Here, it might be argued, genetic factors exert more influence than non-genetic ones. However, it seems more in keeping with the facts to argue that, given two genetically similar populations with different hunting traditions, selection will build up genetic differences that will eventually restrict further alterations in the specificity of the traditions involved. This argument finds support in the observations of falconers showing that while individuals of any one species do differ in temperament and morphology and that these differences do influence their response to training, the differences seem of much less magnitude than those that can be effected by training.

It has been argued (see Mayr, 1942) that tradition is relatively easy to change and that it does not seem likely that it can be perpetuated long enough to affect the genetic make-up of populations. This may be answered by saying that we need to know more about how often such changes actually occur in nature, that genetic constitution restricts the changes possible, and that it is obvious that several factors most probably need to operate to maintain a tradition consistently over many generations. These would presumably include a sustained food supply of distinctive characteristics and a favorable background of the various factors noted by Wright (1940) as capable of influencing the genetics of wild populations. Such requirements may not be satisfied with any great frequency, yet the different species of hawks are not so numerous as to require a very high frequency for their incipiency. In any event, the role of tradition in evolution should not be so lightly dismissed without better evidence, for such dismissal tends to discourage further attempts to learn the facts of the case.

There is considerable evidence that raptors do acquire aberrant habits in nature; of particular interest is Stager's account (1941) of a small population of Duck Hawks that have regularly plundered a bat cave in New Mexico for many years. Here is a clue as to the possible origin of the species of falcons that are more or less adapted to preying on bats (Allen, 1940). Another interesting case is that of the Everglade Kite which preys exclusively on snails of the species *Pomacea caliginosa*, for here would seem to be an opportunity to study the effects of learning, particularly as Mr. A. Sprunt informs me that the young associate with their parents through the fall and probably also the winter and apparently are "taught" to hunt by their parents.

There is abundant evidence that tradition may play an important role in the food habits of a great variety of birds besides raptors. For instance, many species of flycatchers have been observed to "teach" their young to hunt (Bent, 1942:132, 159, etc.) and many of the seed-eating birds first feed their young on insects and only gradually bring them to a vegetable diet. The observation by Lack (1940) of a bird in the Galapagos Islands that uses a stick held in its bill as a tool to obtain insects, and of Perkins (1912) that the young of the widely divergent Hawaiian finches follow their parents about long after learning to fly are but examples of a great number of cases where it would be dangerous to say without investigation that tradition should not be considered an important evolutionary factor.

Before closing I should like to point out that it is the contention of several authors (most recently Mayr, 1942) that acquired behavior could at best only be effective in species with highly organized nervous systems such as the vertebrates. This is contradicted by the extensive evidence for traditional behavior in insects (see Cushing, 1941*c* for further references) and especially by the remarkable behavior of *Arcella polypora*, a rhizopod protozoan. In this form Reynolds (1924) has found that artificially severed masses of protoplasm readily fuse with individuals raised in the same environment, but shatter into droplets upon contacting individuals raised in another environment. The outcome of such fusions has been experimentally shown to depend not upon genetic differences in the individuals concerned, but upon acquired reactions due to environmental influences (most probably the bacterial flora upon which the *Arcella* feed). A comparable situation also exists among the slime molds, a fact for which I am indebted to Dr. A. Cohen of the California Institute of Technology (see Cohen, 1941, and his reference to Smart, 1935). While it is apparent that acquired behavior in these forms may well rest on a different physiological basis than it does in birds, it still is obvious that much more needs to be known of the nature and basis of acquired behavior in living organisms before one can dismiss its role in evolution either as restricted to the higher vertebrates or as of little significance because of a postulated unstable character. (Should one consider it out of place to compare the behavior of birds, protoza, and the myxomycetes, one can find some argument in a recent paper by Lashley (1938), where a flatworm, *Microstoma*, is held to encompass "all of the major problems of dynamic psychology.")

In closing, I should like to say that no anthropomorphic meaning should be attached to the words teach, tradition, learning, etc., as used here.

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Summary.—This paper points out that available evidence favors the probability that traditional food habits may be sufficiently specific and stable to influence selection pressure and thus the evolution of many species of birds and other animals.

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