THE COMPANION IN THE BIRD'S WORLD

BY KONRAD Z. LORENZ

Introductory Note

WHEN Dr. Lorenz's paper on the 'Kumpan'[1] was published in 1935, it seemed to be such an original and important contribution to our knowledge of the instincts and behavior of birds, that I was anxious to have a summary of its theses and conclusions appear in the pages of 'The Auk'. Knowing that Dr. Lorenz was conversant with English, I wrote to him, asking if he would consent to prepare such an account of his own work, and he replied that he would be pleased to do so if given sufficient time.

Dr. Lorenz's paper was delayed in reaching me from various causes. He found difficulty in summarizing a work which consisted in so large a measure of observational detail, and accordingly has stressed those subjects of the most theoretical importance; and he added: "I shall not refrain from using some new observations, and the results of experiments which have come to my knowledge since the publication of my paper." My function has been mainly editorial; and although it has seemed best to condense some parts of the author's manuscript, I trust that its value has not been impaired.

The doctrine of 'releasers,' herein set forth,—or devices for the production of stimuli, which serve as the 'keys' to 'unlock' or release those 'innate perceptory patterns,' characteristic of the species and the individual, and which result in instinctive reactions,—seems at last to offer a sound and satisfying explanation of that riddle so long embodied in 'the secondary sexual characters of birds,' and one which I believe that Darwin, when struggling with his 'Theory of Sexual Selection,' would have welcomed with open arms.—FRANCIS H. HERRICK.

THE CONCEPTION OF THE "RELEASER"

IF WE observe a man performing a number of separate actions, each of which has for its object the same thing and which, taken together and considered as a functional unit, serve an end of definite survival value to the man himself, we shall not hesitate to infer two things: first, that the man, in performing these actions, is conscious of their goal and that it is this very goal that constitutes the purpose of all his movements; second, that in performing the several actions of the sequence, he is constantly aware of the identity of the object toward which they are directed. On seeing a similar series of actions executed by some animal, we are prone to come to the same conclusions, but both would be totally erroneous in case we should have to do with a series of purely instinctive acts.

Much serious harm has been done by confounding the biological end, or survival value of instinctive action, with the purpose pursued by the animal as a subject. I cannot go into the details of my argument against this widely spread error, but for the purposes of this paper, suffice it to say that

---

[1] 'Der Kumpan in der Umwelt des Vogels (Der Artgenosse als auslösendes Moment sozialer Verhaltungsweisen)' [The Companion in the Bird's World; the fellow-member of the species as a releasing factor of social behavior.] Journ. f. Ornith., vol. 83, pt. 2–3, 1935.

I consider instinctive action as 'desired reflex action', meaning that instinctive action, while in no way purposive in itself and quite as rigid as any other reflex as to the coordination of movements, yet in its very 'going off' constitutes the purpose of all truly purposive or appetitive behavior ever met with in animals. Being appeted, sought or desired, is the one point in which instinctive action differs from all other reflex actions. The common reflexes, like unused machines, may lie idle indefinitely, as if waiting for adequate stimulation, without in any way inciting the animal to search for such stimulation by purposive behavior, as it certainly does in case of the instinctive reactions.

It is the second of the assumptions mentioned that concerns us more closely; namely, that the animal, in consistently treating one definite object to a series of separate actions, must throughout its acting, be aware of the identity of this object. Man, in striving to conquer his environment and to master the problems which it puts before him by connecting cause and effect, is confronted with the absolute necessity of conceiving every object he encounters as a permanent unit which remains identical throughout the changes of space and time. Not so the animal, more especially the lower animal, that does not master its environment by insight or learning but is innately adapted to it by possessing highly differentiated instinctive powers of response. The lower animal very rarely 'solves problems' as an individual, and whenever it does so, this is only in an abysmally simple way. As a rule, a lower organism either has solved a problem as a species by evolving instinctive ways of reacting that fit every single one of the emergencies that normally occur, or its fails miserably when confronted with a problem for which it does not possess any suitable instinctive responses. Since the innate coordinations of movement that we call instinctive actions are not adapted to any goal or end anyhow, it suffices that every one of them be released, much as in reflexes, by a simple combination of stimuli, if only this combination is sufficiently characteristic of the biologically 'right' situation; that is, of the one situation in which the performance of the innately coordinated movements attains its full survival value. If an instinctive action is directed toward a particular object, its successful performance is independent of the animal's perceiving this object as a 'thing', that is, as a permanent unit in space and time as we would perceive it. All that is needed on the part of the animal is the disposition to respond with just that reaction to certain stimuli characteristic of its particular object. The sea-urchin (*Sphaerechinus*) possesses a very complicated reaction of combined defense and flight, which is of survival value exclusively as a means of escaping the sea-urchin's chief enemy, the starfish (*Asterias*). The whole of this highly differentiated sequence of single acts is released by a single chemical stimulus emanating from the mucus covering the ambulacral tentacles of the starfish. Another good example is that of the biting reaction of the common tick (*Ixodes*). The tick will bite, or try to bite, any object possessing the two characters of (1) smelling of butyric acid and (2) having a temperature of approximately 37 degrees centigrade. The releasing of comparatively complicated sets of reactions through a very simple combination of stimuli, is characteristic of the greater part of all purely instinctive reactions and by no means exclusively of those of lower animals. The Jackdaw (*Coloeus monedula*) possesses a very interesting reaction of defending any fellow-member of the species in the grip of some bird or animal of prey. For a long time I have been familiar with the fact that my tame but free-living Jackdaws would furiously attack me if I gripped one of them in my hand, but I was very much astonished when I inadvertently elicited exactly the same response by carrying a wet, black bathing-suit in my hand. Subsequent experiments showed that anything glistening black and dangling, carried by any living creature would release the very same reaction in the Jackdaws. Even Jackdaws themselves were subject to attack from their fellows when they happened to carry nesting material possessing the characteristics just mentioned. In a bird that readily recognizes and discriminates fellow-members of the flock, it is rather surprising that the process of releasing the social defending reaction so closely resembles that which elicits the responses of lower organisms as already noticed.

An instinctive reaction of survival value, when directed exclusively to a particular object, may be released as if through a surprisingly small choice among the large number of stimuli normally emanating from the object. In this circumstance, the reactions of the highest vertebrates do not differ from those of ticks, sea-urchins and the like. The receptory part of the animal's reaction responds to a small but characteristic combination of stimuli, very much in the way in which a highly selective wireless receiving-station is attuned to a particular wave-length. This perceptory correlate to a very definite combination of stimuli has been termed by William McDougall the 'innate perceptory inlet.' Without knowing this author's terminology, I used the term 'angeborenes Auslöse-Schema' in German which, respecting the priority of McDougall's term, I shall compromise by translating 'innate perceptory pattern.'

It is an old but fitting metaphor to liken the releasing set of stimuli to the *key*, and the innate perceptory pattern to the *lock* of the instinctive reaction. Even more appropriate, is the simile of a combination lock that cannot be opened except by a definite series of manipulations which, by reason of their general improbability, it is practically impossible to find by chance. The relation of the particular form of the lock to the key that fits it, or of any innate perceptory pattern to the set of stimuli to which it responds, is ever a compromise between greatest possible simplicity and greatest possible general improbability. The improbability of the innate perceptory pattern is to guard the instinctive reaction from being released by chance through other than the biologically 'right' influences. Surprisingly simple though the innate perceptory patterns are in the three cases cited as examples, they are evidently efficient enough, when natural conditions are taken for granted, to prevent the 'erroneous' unlocking of the reaction. It is extremely unlikely that in its natural state the tick is ever misled by its innate perceptory pattern to bite or to try to bite any object that is of no use to it as a potential host. Nor will it often occur in wild life that a Jackdaw erroneously defends a black bathing-suit instead of a fellow Jackdaw caught in the grip of some animal of prey. The species in these cases need not reckon with the experimenting human, cleverly imitating the key to the instinctive reaction's lock. But certainly there are instances in which the very simplicity of innate perceptory patterns may offer an opportunity to entrap animals by artificially supplying key stimuli that release certain definite actions, as the pike is caught by means of a piece of tin that is drawn through the water, and supplies the quickly moving silvery reflections which normally release the preying reactions in this fish.

If an instinctive action has for its object any other thing than a fellow-member of the species as, for instance, the natural prey, nesting materials and the like, it is quite clear that the choice of stimuli, effected by means of the innate perceptory pattern, can include only such as are inherently characteristic of the object. All that the evolution of the species can do, is to adapt the innate perceptory patterns as closely as possible to the preexistent sets of key stimuli. The complication, and with it the highest general improbability of opening the lock, that is, releasing the reaction, cannot exceed a certain predetermined boundary drawn by the kind and number of potential key-stimuli emanating from the object. This constitutes a considerable limitation to the scope of object-treatment by purely instinctive reactions. There is, however, one special case where this limitation does not exist and this is whenever the object of instinctive action is represented by a fellow-member of the species. In this case not only the receptory patterns may be specialized to receive predetermined stimuli, but the issuing of stimuli may be adapted to the special needs of releasing social reactions. Not only the receiving, but also the issuing of stimuli is within the range of influence of such factors as may govern the evolution of a species. The pike, to put it very crudely, is not in a position to attach any special characteristics to the minnow which mark it as adequate prey and thus prevent the pike from snapping at other things; but the Blue Titmouse may, evolutionally speaking, attach bright yellow marks to the corners of the mouth of the young, or a circle of white feathers around its cloaca, and develop two corresponding innate perceptory patterns, one of them releasing the feeding reaction on the opening of the young bird's mouth, the other one starting the reaction of carrying away excretory sacs on the unfolding of the circlet, if white, at the posterior end of the baby bird. The innate perceptory pattern need not, in this case, compromise between simplicity and lock-like general improbability, because the key-stimuli corresponding to it, being sent out by a contrivance especially evolved for that end, may be very simple and yet of an unsurpassable general improbability. The layman, on seeing the glowing color design of a male Golden Pheasant's plumage, the striking blue and red pattern of a young Hawfinch's mouth or the curious 'dance' movements executed by Mallard drakes on occasion of their communal display, is often heard to remark on the 'incredibility' of these phenomena, thereby correctly acknowledging their extreme general improbability.

The means evolved for the sending out of key-stimuli may lie in a bodily character, as a special color design or structure, or in an instinctive action, such as posturing, 'dance' movements and the like. In most cases they are to be found in both, that is, in some instinctive acts which display color schemes or structures that were evolved exclusively for this end. All such devices for the issuing of releasing stimuli, I have termed *releasers* (*Auslöser*), regardless of whether the releasing factor be optical or acoustical, whether an act, a structure or a color.

The essential general improbability of all releasers is brought about in a way characteristic and very similar even where they have been evolved independently in very different forms of animal life. Throughout the universe it is order that is improbable while disorder, chaos, entropy or whatever one chooses to call it, is what we should expect from the laws of probability. I do not think it too far-fetched an explanation to suppose that the striking orderliness and regularity which so strongly appeals to our sense of beauty in the coloring, the notes and the display movements of so many animals, especially of birds, has its source in their nature as releasers and in the general tendency of all releasers to develop in the direction of the more improbable. This would also explain the astonishing rhythm that we meet in very nearly every releasing action. The more or less pure spectral colors which so often appear in color patterns functioning as releasers, very probably also find their explanation in this way, since the reflexion of one wavelength among the wave-mixture of white light is in itself rather improbable, so improbable indeed that color alone may, in some cases, function as a releaser. It is for very much the same reasons that pure colors are applied in all optical signals used by man. It may very well be that the same explanation holds true for the pure and 'beautiful' sounds occurring in bird song, as it quite certainly does for the great number of rhythmical movements of limb and body which play so important a part in most releasing actions found in birds. The begging movements of many altricial young birds represent a good example of this so that very nearly all the waving movements theoretically possible are realized in different species. In this they actually resemble all the different waving movements used in marine signalling by man. To cite but a few instances: up-and-down movements as begging-releasers have been independently evolved by parrots, gulls, spoonbills and many others; swinging the head sideways is found in many finches; young European Orioles (*Oriolus*, not the icteride bird) perform a rotating movement of the head which has for its axis a line drawn through the upper mandible; young warblers of the genus *Sylvia* perform an incredibly rapid trembling movement of the head and neck.

All these movements and structures which function as releasers, by their essential quality of rhythmic regularity, have appealed strongly from time immemorial to the sense of beauty in man. It is no wonder that a vast amount of theorizing has been spent on their behalf. Darwin, in his work on 'The Expression of the Emotions in Man and Animals', has indeed come very close to our conception of releasers, yet it is strange that he attributed so little survival value to their functioning that he could not believe any bodily organ was ever evolved for their special use. He states expressly that not a single facial muscle was ever differentiated in monkeys for the sole end of expressing some emotion. Contrary to this, we must state that we have good reason to believe that not only muscles, but very complicated structures in some species, have been evolved for the purpose of expressing one single emotion or, to be more precise, of transmitting this emotion to a fellow-member of the species. A good example of this is the erectile crest in all night herons, evolved for the purpose of indicating peacefulness, and comparable in its function to the tail-wagging of a dog. Darwin's well-known view about the function of bright colors and striking structures of male birds is so far correct, as that there are certainly a considerable number of species in which these releasers, in the male, function in eliciting sexual reactions in the female. Yet it would be an error to generalize this so far as to conclude that all male coloring and all male structures have been evolved for this function only. Noble and Bradley have shown that in a great number of reptiles the bright coloring of the male does not evoke any sexual responses in the female but has its chief function in intimidating other males. What is true of some reptiles has also been regarded as a general rule throughout the animal kingdom. It was Hingston who propounded the theory that all bright coloring encountered in animals, as well as all peculiar structural designs have been evolved solely for frightening other animals, particularly, but not exclusively, those of the same species. In his opinion even the axillary hair of man is there to frighten the enemy into non-resistance when the aggressor displays it in raising his fists. There is one indubitable fact underlying both this extreme theory, and the sexual theory, namely, that structures and colors are evolved to influence fellow-members of the species. Yet this absolutely correct thought common to both theories was discarded by Wallace, in whose opinion "the more developed plumage and more vivid colors of the males . . . . may be wholly due to their greater vital energy and those general laws which lead to such superior development even in domestic breeds; but in some cases the need of protection by the female, while incubating, may have suppressed a portion of the ornament which she would otherwise have attained." To this we must retort that there are a considerable number of birds in which it is the female and not the male that carries 'ornamentation.' Also the very animals in which the ornamentation of the males reaches about the highest development it ever attains,—the spiders of the families Attidae and Lycosidae,—cannot well be said to have "more vital energy" in the male sex, since the male is much smaller than the female. In these spiders the Peckhams as early as 1889, correctly recognized the releasing function of the male colors and structures which, by eliciting specific sexual responses in the female, prevent her from reacting to the male in an unadaptive way by simply devouring him.

Every theory which, like that of Wallace, leaves to chance the particular regularity of detail in all display coloring and structure, commits a serious error against the laws of probability. If we refuse to resort to an altogether metaphysical, vitalistic explanation, which involves entelechial factors, it is only by regarding these colored and structural patterns as releasers that we can hope to find some reason for the regularity and 'beauty' of their design. The very word 'ornamentation' smacks of a metaphysical assumption. That this so-called ornamentation does not necessarily have some sexual significance, is exemplified by the many instances where its releasing function is of a purely social nature. Nothing can be more ornamental than the crest of night herons or the striking patterns of the wings of many ducks. Yet the former functions as the organ of a peace-making ceremony without any sexual meaning, while the latter serves as a releaser of the reactions of flying in a flock or of holding socially together.

Our assumption that most of the bright colors and peculiar structures, or what are commonly called secondary sexual characters, which we meet with in the bird world, actually function as releasers of social reactions, receives a convincing confirmation by the fact that there are hardly any of them that do not take part in an instinctive ceremony, and are quite evidently differentiated in such a manner as to be strikingly unfolded by the coordination of movements characteristic of the latter. It is hardly an exaggeration if we state that all striking color designs and bizarre structural devices, such as elongated plumes, inflatable pouches, turgescent naked spots and the like, find their exclusive use in some instinctive act representing a releasing ceremony. Supposing I should shoot, in some far country, a bird unknown to science and that this bird had somewhere on its body a circumscript patch of feathers longer than those of the adjoining regions, I would confidently assert that this particular species was in possession of some releasing ceremony in which just that patch of elongated plumes found its use. There are indeed very few structural and color designs that function as releasers automatically, without the aid of special instinctive acts displaying them. The only example of such 'automatic releasers' at present known to me, is represented by the devices eliciting the flying-in-pursuit reactions in a great many social birds. All of them are color patterns invisible in the sitting bird, but are suddenly and strikingly unfolded at the moment of taking flight. Such patterns are often found in the tail, as in case of the blue-and-yellow design of the Shell Parakeet, the white lateral feathers in the tails of tits, shrikes, doves and hosts of other birds. Often the lower back, covered in the sitting bird by the wings, is white or of some striking color, as in the Bullfinch, the Bean Goose and others. A very high differentiation of this type of automatic releaser has been attained by numerous species of the anatide order, of which many bear special releasing patterns on their wings. Heinroth has made an extensive study of these releasers and their function.

Lastly, we have to speak of releasing actions, the function of which is not dependent on any structures or colors evolved for their special use. A great many such actions are familiar to any student of bird behavior, so that I may confine myself to just one example. The male Raven has a most striking threatening attitude, in which all the plumage of the bird's head is tightly depressed, excepting a sharply defined area just above the eye where the feathers are stiffly erected at right angles to the surface of the skin, so that two ears or horns suddenly seem to sprout on the angry Raven's front. In a certain ceremony of courtship, the male Raven stretches forward his head and neck horizontally while fluffing the plumage of the whole head to the utmost and drawing nictitating membranes over his eyeballs. The picture thus presented by the Raven is so totally different in each of these two attitudes that it can be readily understood that two answering reactions or, more exactly, two different innate perceptory patterns, are released by them in the fellow-member of the species.

Releasing actions lacking structural or color designs are of special interest to us in cases where closely related species do possess such bodily differentiations, because they often tend to throw some light upon the phylogenetic development of the structure used in the releasing action. We know of a considerable number of instances where a certain releasing ceremony is common to some closely related species and is executed in all of them in so precisely similar a way that even by studying the single frames of a motion-picture film, not the slightest difference of movement can be found. Yet it may be that one of these different species does not possess the least bit of structural differentiation to emphasize the optical stimulation issuing from the movements executed in the ceremony, while a closely related species has the most striking colors and structures that come into play in the very same coordination of movement. The Mallard (*Anas platyrhynchos*), as well as the closely related Black Duck (*Anas rubripes*), and the two species *Anas superciliosa* and *Anas* (*Polionetta*) *poecilorhyncha*, have, in the male sex, a communal display ceremony quite alike in all four species. I need not go into the details of movement executed in this reaction, as it suffices to state that, while *A. rubripes* and *A. superciliosa* do not possess structures or colors taking part in this action, *A. poecilorhyncha* has a bright color pattern on the bill and pure white elbow-feathers, while the brilliant color design of the Mallard drake is well known. In the ceremony in question, a certain movement of tilting up the posterior part of the body, together with a raising of the elbows as strikingly displays the ringlet in the Mallard drake's tail-coverts, as it does the white elbows of the *poecilorhyncha* male. Similarly, in another motion of the same ceremony, consisting of a quick dipping of the bill followed immediately by a stretching-up of head and neck, two characters different in both species are strikingly displayed. In *A. poecilorhyncha* this down-and-up movement is made eminently conspicuous by the colors on the bird's bill while in the Mallard the same movement is optically emphasized by the disappearance and subsequent surprising broadening of the white stripe encircling the drake's neck. All the conspicuous characters of the male of both species have one thing in common: they are all so placed on the bird's body as to be *displayed by the very same movements*, which are exactly alike in both species. The night herons of the three genera *Nycticorax, Nyctanassa* and *Cochlearius* have exactly the same greeting or peace-ceremony, the function of which I have likened above to that of a friendly dog's tail-wagging. In this ceremony the upper side of the head is presented to the fellow-member of the species who is to be appeased. All of the three genera possess elongated plumes on the top of their heads that serve to emphasize the movements executed in the ceremony and evidently they were especially evolved for this particular end. Yet the ceremony is executed with success also by young birds, though still lacking the elongated and conspicuously colored plumes. As a third example of the same principle, I would cite the differentiation of the head-plumage in grebes. In the smallest of European species, the Dabchick, a certain ceremony can be observed in which a most singular shape of the head and neck is brought about by depressing the feathers of the neck up to a sharply defined line just below the lower mandible, upward from which the plumage of the head is erected. The sharp boundary between the fluffed and the depressed parts of plumage in the Dabchick is purely functional, no difference in feather length or color being visible in the quiescent or the dead bird. Yet this line, in most other grebes, forms the boundary between the short, plush-like plumage of the neck and the area covered with elongated and brightly colored feathers on the bird's head.

In the grebes as well as in the ducks and night herons we find that an instinctive action, common to a number of closely related species, has caused some of them to evolve colors and structures serving to make their movements more conspicuous. The evolution of structure and color has gone on independently in the different species, but a certain similarity in its results is caused by the common origin of all bodily differentiations from the source of one instinctive releasing ceremony. I do not think it either a far-fetched or an incautious hypothesis to assume that in all such cases the releasing ceremony is phylogenetically older than the colors and structures used by it. Systematic comparative study of instinctive actions in birds has shown very clearly that the phyletic age of instinctive reactions is commonly as great as that of organs. In very many cases indeed, its special form proved to be a much more conservative character than that of any organ. Whitman and Heinroth were the first to use instinctive actions as taxonomic characters and the latter's famous paper on the ethology of Anatidae has found a very impressive and convincing confirmation in the work of Poll. This author made an extensive study of the fertility of hybrid birds drawing conclusions therefrom on the blood-relationship of the parent species. His results confirmed those attained by Heinroth in literally every point in which the latter were at variance with those generally held by systematic zoologists of the time. The taxonomic value of releasing actions, for very simple reasons, is even greater than that of other instinctive reactions. Since releasing actions are what we might call a private signalling code of the species, and as such pure conventions, they are largely independent of environmental influences. Their special differentiation is explainable from a predominantly historical point of view and not at all on the ground of their function. It is but a 'convention' that the tail-wagging of a dog expresses and transmits a peaceable mood to the fellow-member of the species while a similar movement in Felidae is the expression of quite a different and nearly contrary emotion. As regards the function of tail-wagging, its meaning in the different animals could just as well be distributed in the opposite way. If ever we find an explanation of why the movements are executed just so and mean just that, this explanation will be chiefly historical. This is most relevant for the estimation of the taxonomical import of releasing actions, because it greatly reduces the likelihood of equality of releasing actions ever being attained in two species by convergent evolution. Equality in instinctive releasing actions always means homology and it is just this that often makes it possible for the student of instinctive actions to analyze phylogenetic relations with an exactitude hardly ever attained by the morphologist. It was necessary to explain at some length the phylogenetic age as well as the taxonomic importance of releasing actions, so as to give some background to my assertion that the inherited coordination of movement functioning in releasing ceremonies is, for the most part, phylogenetically older than the structures and colors used in them.

It has been said already that we know very little about the phyletic origin of releasing actions themselves, so little indeed that it seems worth while to set it forth here in detail. In regard to most releasing actions, as in the case of the tail-wagging of the dog, we are completely at a loss concerning their evolutionary origin. The only exceptions to this are a few instances where we can trace the origin of releasing ceremonies to instinctive actions of an altogether different function. It may be regarded as true for all or most instinctive reactions that the very contrary of an 'All-or-nothing-law' governs their performance. Even at the lowest degrees in intensity of instinctive reaction, the animal will show its internal processes by certain movements which, to anyone familiar with the reaction in question, are recognizable as its initiating movements. If the reaction is very low in intensity, no further movements but these slight beginnings of the action will be observed. As long as the reaction is too low in intensity to carry the animal through the whole sequence of expected movements, it may break off at any point. There are all theoretically possible gradations between the slightest movements, hardly noticeable even to one thoroughly familiar with the reaction initiated by them, up to the complete performance of the reaction, and attaining the full survival value representing its biological end or goal. The frequent occurrence of a reaction remaining incomplete and inconsequential because of its being too low in intensity, is of the greatest theoretical importance. It shows with particular clearness that the biological end, or survival value of instinctive action, must not be confounded with the purpose pursued by the animal as a subject. This is most evident in case the action, through sheer lack in intensity, is broken off at the very last moment, falling only just short of attaining the end for which it has been evolved by the species. Nobody, who has ever had occasion to observe this phenomenon, can doubt that the animal performs the movements pertaining to the reaction for their own sake and not for the sake of any biological advantages. As C. O. Whitman puts it, the animal goes through the movements of instinctive reaction because "it finds it agreeable to do so and disagreeable not to do so." If, in early spring, we observe a night heron sitting in a tree and rather suddenly breaking into the action of tugging at and shaking a near-by twig, only to relapse incontinently into its former state of quiescence, it becomes directly and quite indubitably evident that these initiating movements of nest-building are executed for their own sake and not with a view to their possible ultimate result and also that at the present low intensity of the reactions the bird's craving to perform them is quite satisfied by once or twice shaking a twig.

As a matter of course, these incomplete reactions are of no survival value for the animal or its species, unless we attribute to them the function of improving the action by exercise. Even when we admit the questionable value that exercise may or may not have for the performance of purely instinctive reactions, we must state that incomplete reaction is of no survival value in regard to the primary biological end for which the complete reaction was evolved by the species. Yet there is a way by which even the slightest initiating movement of an instinctive reaction may attain an altogether new and biologically important function. Some initiating movement, just hinted at in the behavior of a bird, may tell to the human observer in what direction actions of the birds are to be expected. Because such initiating movements are able to convey the intentions of the animal, they have been termed 'intention movements' (Intentionsbewegungen). It is a well-known fact that this kind of initiating movement in social animals is perfectly 'understood' by the fellow-members of the species. A few words must be said about this so-called understanding. On seeing one animal beginning to perform some action and thereby inciting a fellow-member of the flock or herd to do likewise, the human observer is prone to assume an 'instinct of imitation' on the part of the second individual to explain its behavior. The process, however, on which this seeming imitation is really based, very closely resembles that very direct transmitting of moods from one individual to another which we can so often observe in ourselves. The 'contagious' reactions of laughing, yawning and the like, at first sight seem very different from the complicated serial actions transmitted in a similar way in animals, yet, being also inherited possessions of the species, they are directly comparable to them. In social animals the transmitting of specific excitation may clearly become of very considerable survival value. All those functions of coordinating the behavior of the individual members of society which, in the human species, represent one of the chief tasks of speech, are performed either by releasing ceremonies or by the transmitting of specific excitation which we have just described.

There is no sharp boundary line between the simple transmitting of excitation, as we may say, "by contagion" and releasing actions in the strict sense of the word. Responding to a certain reaction of a fellow-member of the species by reacting in the very same way is evidently wholly innate. We have, therefore, to assume the existence of innate perceptory patterns corresponding to certain sets of stimuli emanating from the individual first showing the reaction, an assumption which we have to make in all cases where an unconditioned reaction is released in so specific a manner. By the evolution of this kind of innate perceptory pattern, almost any instinctive reaction in a social species may be appointed to the secondary and purely social task of releasing like reactions in the fellow-member of the flock or herd. Now as a matter of course, this secondary releasing function is not dependent on the reaction being executed completely and with full intensity. Even slight initiating movements, wholly inconsequential as to the primary meaning of the reaction, may transmit its specific excitation to the next bird, and thereby gain an undeniable survival value in social species. The correlation of releaser and corresponding innate perceptory pattern once being established, a new development of the intention-conveying initiating movements may set in. By special adaptation to their releasing function, they may be gradually alienated from the reaction, the beginning of which they originally represented. This, to the best of our knowlege, has been the origin of all those instinctive actions which, with some inexactitude, we are accustomed to describe as 'symbolic.' It is only in very few cases that we are able to illustrate this theory by a series of 'phylogenic stages' represented in living species, none of which is more convincing than the following: a reaction which, in large birds especially, always seems to require a considerable amount of 'nervous energy' or, more precisely, of reactional intensity, is that of taking to wing. Everyone familiar with bird behavior knows that none of the larger birds ever takes wing without noticeable preparations, gathering themselves a number of times in quick succession for the effort of leaping into the air and, seemingly at the very last moment, refraining from doing so. It is only after a considerable repetition of these initiating movements that the bird finally takes the plunge. The importance of taking to wing synchronously is evident in all species flying in flocks, so that it is no wonder that these initiating movements of taking the air have attained a special function as releasers in social birds. They transmit the specific excitation from one bird to the other until, after an interval of mutual stimulation, the threshold of the whole reaction is so far lowered that the final stimulation issuing from the first bird actually taking wing, is sure to cause all members of the flock to follow. In the Greylag Goose this kind of mutual stimulation is so important that flocks containing many members actually take the air much more often than others which consist of only a few birds. The individual bird sending out specific stimulation receives it back 'with interest' from the fellow-members of the flock and it is this 'interest' that increases with their number. An isolated Greylag spends so little of its time on the wing that it will become noticeably fatter and weaker of muscle than geese living under the same conditions but in the society of their kind. The same phenomenon causes large herds of horses or cattle to be much more prone to stampede than are small numbers of the same animals.

The mutual stimulation to take wing seems to be especially important in the anatide order, probably because these birds are particularly slow in their resolve to fly up. It is in this order of birds that we find not only the highest differentiation of movements releasing this reaction, but also an exceptionally complete series of what we may regard as phylogenetic stages in the evolutionary progress of this differentiation. In the Mallard, the movements transmitting the specific excitation of flying up are easily and convincingly recognizable as beginnings of the actual reaction itself. Any ornithologist not acquainted with their special importance as releasers would, on observing them, at once grasp the bird's intention to fly up. Crouching low and ready for the effort of leaping off, the duck in a brief interval throws up its head, neck and the anterior part of its body in a way extremely similar to, but yet a little different from the actual motion of jumping upward. One might say, the action is a little *over-emphasized,* as symbolic actions characteristically are. In the Greylag Goose, a species in which all social reactions have attained a higher degree of specialization than in the Mallard Duck, the movement which indicates the bird's intention to take flight and transmits the same to the other members of the flock is quite different, consisting in a sidewise shaking movement of the head and beak alone, the neck being all the while held stiffly upright. No one knowing only the movement of the Mallard just described, would ever suspect that this shaking movement which looks exactly as if the bird were shaking something off its bill, has the same meaning. Yet we can, with great probability of being correct, assert that both these actions of the two different anatides are phylogenetically homologous, because we find all manner of intermediate forms of the same ceremony in other species of this order. The Egyptian Goose, for instance, in its flying-up ceremony, stands just midway between the Mallard and the Greylag, for its expressional movement, as in the latter species, is strictly confined to head and beak, but, like that of the Mallard, goes 'still' perpendicularly upward. Anybody familiar with the movement expressing the flying-emotion in the Egyptian Goose would, without any doubt, recognize at first sight that of the Mallard as well as that of the Greylag. Considering the great many intermediate stages in the development of movements expressing and transmitting flying-emotion in other anatides, I think we are fully justified in assuming (a) that the movements found in the Mallard and in some other ducks represent a more primitive evolutionary stage when compared with those of other birds of the same order, among which those of geese are to be considered the most differential; and (b) that all these ceremonies have been derived phylogenetically from initiating movements and represent abortive performances of the reaction of taking wing, which must be regarded as one special case of the many instances of an instinctive action remaining incomplete through lack in intensity.

There are a great many 'symbolic' releasing ceremonies for which a very similar origin seems extremely probable, though we are not in possession of such a complete series of intermediate links as in case of the flying-up ceremonies of anatides. I am referring, among some others, to the great many actions of symbolic nest-building, which play so important a part in the mating of a great number of birds. Especially interesting is a certain symbolic movement of the Gannet, in which the bird sitting on the nest site 'pretends' to take building material from the bill of an imaginary mate and to build it into a nest which at the time being does not yet exist or need not necessarily exist. I have seen fit to deal with these symbolic ceremonies with some detail, because they actually represent the only case in which we have some inkling as to the evolutionary origin of a releasing action.

JAKOB VON UEXKÜLL'S CONCEPTION OF THE 'KUMPAN'

Apparently it is in birds that the parallel differentiation of releasers and innate perceptory patterns has reached the highest development it ever attains in animals. This differentiation is one of the two alternatives which confront a species whenever there arises the biological need of one individual consistently treating another throughout a series of separate actions. The first of the two possible ways to secure such consistency of object-treatment is represented by the animal's possessing insight into the goal or end of its actions and also into the permanent identity of the object toward which its actions are directed. The second possibility lies in the differentiation of a specific innate perceptory pattern for every single one of the actions on the part of the agent, and also on the part of the patient in receipt of the actions, in the differentiation of a releaser separately eliciting each of them. The uniting factor which ensures the consistent cooperation of the several instinctive actions thus does not lie in the agent at all, but in the object of the reactions which, by representing the issuing station common to all the different sets of releasing stimuli, guides every single reaction to its evolutionally predetermined end. The agent as a subject need not, even in the vaguest way, be conscious either of the survival value of his actions, or of the identity of their neutral object. The object in the agent's world need not be represented as that kind of unit in space and time which we are accustomed to call a "thing," if only it is sending out the specific set of stimuli and releasing every one of the actions which must be executed toward it. Complicated and far-fetched though this devious method of object-treatment may seem to the human mind, it is certain that for animals on the mental level of birds this has been easier to attain through evolution than have the mental powers necessary to effect an object-treatment of equal complication and consistence by insight and purpose.

By supplying abnormal objects which do not send out the several sets of releasing stimuli in a way to secure the normal cooperation of reactions, it can be proved experimentally that in many cases it is the object of the reactions, the patient and not the agent, who unites them with a functional unit of definite survival value. For example, in a female Mallard whose ducklings are just hatched, the reaction of defending them is released exclusively by the call emitted by a duckling in distress. Other reactions of taking care of the young, especially that of specifically allowing the duckling to remain near her instead of unspecifically chasing it away, as she would all other small living creatures, are dependent upon certain color patterns on the down of the young. These specific down-patterns vary somewhat in closely related species of ducks, while any difference in the distress signal of the young is hardly discernible in the numerous species belonging to the anatide order. The result of these circumstances is that a mother duck's defending reaction can be released by the young of very different species while other reactions normally directed toward the same object cannot. A mother Mallard, on hearing the distress peeping of a Muscovy duckling, will respond by defending it exactly as she would her own young, but, having just 'heroically saved' it from the hands of the experimenting human, she will incontinently proceed to attack and even kill it when she sees it trying to mix with her own flock of ducklings.

The possibility of experimentally separating functions which ought to be united in the treatment of one particular fellow-member of the species, certainly precludes the assumption that this fellow-member of the species appears as an unit in the bird's world. In all cases where such a separability of the single instinctive acts can be proved, we have reason to think that the fellow-member of the species is perceived as a different thing in every experimentally separable part-function. The most peculiar rôle which the fellow-member of the species thus plays in the agent's world, being perceived as one thing when representing the object of one reaction and as a different one when being that of another, has been termed that of a "Kumpan" by Professor J. von Uexküll. The German word, *Kumpan,* means a fellow who is our companion so far as concerns but one particular kind of occupation, such as hunting or drinking (*Jagdkumpan, Saufkumpan*). It implies that no deeper and nobler bonds link us to our fellow in this kind of companionship. The word certainly meets the case exceptionally well, although it is hardly translatable into English. The word 'companion' certainly lacks the detracting implication which is so essential for the wonderful way in which Uexküll's term describes this lowest type of animal companionship.

INBORN RECEPTORY PATTERNS AND 'CONDITIONING'

It would be a fundamental error if, on the ground of such observational examples as that of the mother Mallard which I cited above, we should assume that all birds in every case are unable to perceive a fellow-member of the species, such as their mates, their young or their social companions as personalities remaining identical in space and time. In fact, as soon as any bird attains the faculty of individually recognizing one fellow-member of the species who represents the mutual object of several of its instinctive actions, this personal acquaintance may serve as an uniting factor. It may fail, however, to do so, and it is interesting to observe how, in one of two closely related species, personal acquaintance may dominate instinctive actions as released by innate perceptory patterns, while in the other blind instinctive reaction reigns supreme. I am referring to the social defending reaction in the Jackdaw and in the Raven. Of both these species I possessed a very tame individual who was extremely attached to my person, responding to me with all its social reactions. When I tried to elicit the response of defending a companion by gripping a fellow-member of the species and showing it thus to each bird, I got exactly contrary reactions in the two species. The Jackdaw instantly attacked me with the utmost intensity and pecked viciously at my hand that was holding the other Jackdaw, although the latter was an individual for whom it had a strong personal hate and whom, not very long before, it had so maltreated that I had to separate the birds. The Raven, on the other hand, displayed a much less reflex-like response. When I grasped a young Raven, whom my tame old male thoroughly disliked, he instantly flew on my shoulder and from this position took advantage of the young bird's helplessness to peck at it, without giving the call and the movements characteristic of social defense. But when, sometime later, his mate, by playing with my mother's knitting, got so entangled with it that she could not get away, the male furiously attacked the servant girl who was trying to extricate her. On this occasion he displayed the full reaction of social defense which, in the Raven, is similar to that of the Jackdaw. A female Mallard, in defending her young, actually shows both types of behavior displayed by the Daw and the Raven in their defending reactions. Soon after the hatching of the young she just responds blindly to stimuli emanating from them, but six or seven weeks later, her behavior appears on a much higher mental level. We find now that personal recognition of her own young has developed to a degree that releases her defending reaction. Again, in the Muscovy Duck, which is considerably more stupid and also less social than the Mallard, the mother bird keeps on defending blindly all other ducklings besides her own throughout the entire summer.

From the point of view of Professor von Uexküll's "Umweltforschung" this conditioning of innate reactions to a personally recognized object means a radical change in the bird's world. At first, in the world of the mother Mallard, there do not exist young ducklings individually recognized as things and units, but just stimuli, blindly releasing her brooding reaction in one case, or her defending reaction in another. Later on, the acquired ability to recognize individually every one of her ducklings unites the formerly independent sets of stimuli which correspond to her several innate perceptory patterns. Thus by true learning on the part of the mother duck, what first may have appeared in her world as quite different things fuse into the unit of one thing. The 'thing to be brooded' and the 'thing to be defended' finally are united in the identity of what, following von Uexküll, we may term a 'child companion'.

Although I have followed von Uexküll's terminology in calling such a compound object of several reactions a 'Kumpan', coining the expressions of 'child-Kumpan', 'parent-Kumpan', and the like, it must not be forgotten that these terms imply a slight broadening of the original conception of the 'Kumpan', as the object releasing but one single, independant function. I feel inclined to use the English word 'companion' as a term for this somewhat different conception of a fellow-member of the species who acts as a releasing object in regard to several instinctive actions of the agent.

Such a thing as a 'parent-companion', a 'child-companion,' owes its appearance in the bird's world to an *acquiring process*, that is to conditioning in a broad sense of the word. We have already said that it is true associative learning which unites the different sets of releasing stimuli emanating from an individual companion. There is, however, a very peculiar acquiring process, differing in some respects from associative learning, which unites and guides to their proper object innate reactions directed to fellow-members of the species in general, but not to the object as an individual, as is the case with the process of personal recognition just described. This process of acquiring the biologically 'right' object of social reactions by conditioning them, not to one individual fellow-member of the species, but to the species as such, is so very peculiar that I have thought it necessary to use a particular word to describe it. I have called it '*Pragung*' in German, which I purpose to translate into English by the term 'imprinting'.

IMPRINTING

It is a fact most surprising to the layman as well as to the zoologist that most birds do not recognize their own species 'instinctively', but that by far the greater part of their reactions, whose normal object is represented by a fellow-member of the species, must be conditioned to this object during the individual life of every bird. If we raise a young bird in strict isolation from its kind, we find very often that some or all of its social reactions can be released by other than their normal object. Young birds of most species, when reared in isolation, react to their human keeper in exactly the same way, in which under natural conditions they would respond to fellow-members of their species. In itself this phenomenon is in no way surprising. We know of a great many reflex actions that can be conditioned to very different releasing factors without being changed as to their coordination of movement. Also we know that a great many animals, when deprived of the normal object of some instinctive reaction, will respond to a substitute object, or, to be more precise, will react to other than the usual set of stimuli. In all these cases the animal will prefer the normal object as soon as it is proffered, but the bird raised in isolation refuses to react to its kind. In most cases experimentally investigated, the biologically right object, that is, the fellow-member of the species, was not even accepted as a substitute for the abnormal object, acquired under the conditions of experiment, when the latter was withdrawn and the bird left severely alone with other individuals of its species. Heinroth failed to breed hand-reared Great Horned Owls, Ravens and other birds, for no other reason than that these tame individuals responded sexually to their keepers instead of to each other. In a very few cases known, the bird whose sexual reactions were thus directed toward man, finally accepted a fellow-member of the species which, however, was always regarded as a rather poor substitute for the beloved human and was instantly abandoned whenever the latter appeared. Portielje, of the Amsterdam Zoological Gardens, raised a male of the South American Bittern (*Tigrisoma*) who, when mature, courted human beings. When a female was procured, he first refused to have anything to do with her but accepted her later when left alone with her for a considerable time. The birds then successfully reared a number of broods, but even then Portielje had to refrain from visiting the birds too often, because the male would, on the appearance of the former foster-father, instantly rush at the female, drive her roughly away from the nest and, turning to his keeper, perform the ceremony of nest-relief, inviting Portielje to step into the nest and incubate! What is very remarkable in all this is that while all the bird's instinctive reactions pertaining to reproduction had been repeatedly and successfully performed with the female and not once had been consummated with a human being for their object, they yet stayed irreversibly conditioned to the latter in preference to the biologically proper object. The performance or better the successful consummation of an instinctive reaction is evidently quite irrelevant for this peculiar way of acquiring its object. The object-acquiring process can be completed months before the action is executed for the first time. I once had a pair of Greylag Geese hatch a Muscovy Duck's eggs. The parent-child relations in this artificial family dissolved sooner than is normal for any of the two species, owing to some hitches in mutual understanding which occurred because the key and lock of the releasers and innate perceptory patterns of both species did not fit. From the seventh week of their life, however, the young Muscovies had nothing more to do with their former foster-parents nor with any other Greylag Geese, but behaved socially toward one another, as well as toward other members of their species as a perfectly normal Muscovy Duck should do. Ten months later the one male bird among these young Muscovies began to display sexual reactions and, to our surprise, pursued Greylag Geese instead of Muscovy Ducks, striving to copulate with them, but he made no distinction between male and female geese.

These few observational examples are sufficient to illustrate in a general way the peculiarities of the acquiring process in question, but I wish to call the reader's attention more especially to the points in which this process differs from what we call associative learning. (1) The process is confined to a very definite period of individual life, a period which in many cases is of extremely short duration; the period during which the young partridge gets its reactions of following the parent birds conditioned to their object, lasts literally but a few hours, beginning when the chick is drying off and ending before it is able to stand. (2) The process, once accomplished, is totally irreversible, so that from then on, the reaction behaves exactly like an 'unconditioned' or purely instinctive response. This absolute rigidity is something we never find in behavior acquired by associative learning, which can be unlearned or changed, at least to a certain extent. In 1936, I kept a young Greylag isolated from its kind for over a week, so that I could be sure that its following-reaction was securely attached to human beings. I then transferred this young goose to the care of a Turkey hen, whom it soon learned to use as a brooding-Kumpan for warmth instead of the electric apparatus it had hitherto favored. The gosling then followed the Turkey hen, provided that I was not in sight, and kept this up for a fortnight; but even during that time I had only to walk near the two birds, to cause the gosling to abandon the hen and follow me. I did this but three times, to avoid conditioning the gosling to my person as a leader. When, after two weeks, the gosling began to become more independent of the warming function provided by the Turkey hen, it left her and hung around our front door, waiting for a human being to emerge and trying to follow it when it did so. Now this gosling, excepting the few necessary trial runs, each of which did not last more than about a minute, had never actually consummated its following-reaction with a human for its object. On the other hand, for more than two weeks, it had been in constant contact with the Turkey hen; yet its following-reaction did not become conditioned to the Turkey in preference to the human. I would even suspect that its instinctive following-reaction was never really released by the Turkey at all, and that its following the hen was predominantly a purposive act, directed to the necessity of getting a warm-up from time to time. It never ran directly after the Turkey hen in the intensive way in which it would follow me and in which Greylag goslings follow their normal parents, but just kept near her in a most casual and deliberate sort of way, quite different from the normal reaction. Most impressive is the fact of the irreversibility of imprinting in such cases, in which birds become conditioned to an inaccessible object or to one with which it is physically impossible to perform the reaction. (3) The process of acquiring the object of a reaction is in very many cases completed long before the reaction itself has become established, as seen in the observations on the Muscovy drake cited above. This offers some difficulties to the assumption that the acquiring process in imprinting is essentially the same as in other cases of 'conditioning', especially in associative learning. To explain the process in question as one of associative learning, one would have to assume that the reaction is, in some rudimentary stage, already present at the time when its object is irreversibly determined, an assumption which psychoanalysts would doubtless welcome, but about which I have doubts. (4) In the process of imprinting, the individual from whom the stimuli which influence the conditioning of the reaction are issuing, does not necessarily function as an object of this reaction. In many cases it is the object of the young bird's begging-reactions, or the following-reactions, in short the object of the reactions directed to the parent-companion, that irreversibly determines the conditions which, more than a year later, will release the copulating reactions in the mature bird. This is what we might call a super-individual conditioning to the species and certainly it is the chief biological task of imprinting to establish a sort of consciousness of species in the young bird, if we may use the term 'consciousness' in so broad a sense.

I would not leave the subject of imprinting without drawing the reader's attention to some very striking parallels existing between imprinting and a certain important process in the individual development of organs known in developmental mechanics (Entwicklungsmechanik) as indicative determination. If, at a certain stage of development, cellular material of a frog embryo be transplanted from one part of its body to another, the transplanted cells owing to influences emanating from their new environment, are induced to develop in a way fitting to it, and not in the way they would have developed in their original position. This process of being influenced by environment, termed 'induction' by Spemann and his school, is confined to very limited periods in the ontogenetic development of the embryo. After the lapse of this period, transplantation of tissue results in the development of abnormal monsters, because any transplanted material will develop in a way exactly fitting the place of its provenience. Also, cells transplanted before the critical time and afterward replaced in their original situation, will develop in harmony with the part of the embryo in which they are implanted during the critical period of inductive determination. It is certainly a very suggestive fact that the two chief characteristics of imprinting, in which it differs from associative learning, namely, in being irreversible and in being strictly confined to definite phases of ontogenesis, coincide with those which imprinting has in common with inductive determination in Spemann's sense of the word.

Of course, it is a matter of personal opinion how much or how little importance one should attribute to these differences from associative learning, and to analogies to inductive determination. My object in drawing the parallels to the latter, is to show that not only the phylogeny of instinctive reaction, but also its ontogeny more closely resemble those of an organ than those of any of the higher psychological processes. Also, it is a purely conceptional dispute whether imprinting is to be regarded as a special sort of learning, or as something different. The decision of this question depends entirely upon the content we see fit to assign to the conception of 'learning.' Imprinting is a process with a very limited scope, representing an acquiring process occurring only in birds and determining but one object of certain social reactions. Yet rarity does not preclude systematic importance, but I should think it rather unwise to widen the conception of learning by making it include imprinting. Such an increase of its content would bring the conception of associative learning dangerously near to including inductive determination as well, and experience has shown that this kind of stretching the boundaries of a conception is apt to destroy its value. This is exactly what has already happened to the conception of the reflex and to that of instinctive action. Since it determines the conditions for the releasing of a certain reaction, imprinting certainly must be regarded as 'conditioning' in a very broad sense of the word, but I think that English-speaking scientists should be glad to possess this term because it describes a conception less specific than that of learning.

INTERACTION BETWEEN INNATE PERCEPTORY PATTERNS AND IMPRINTING

There is a dual connection between innate perceptory patterns and the process of imprinting. On one side it is the normal function of innate perceptory patterns to guide a reaction to their biologically proper object, and we have already mentioned that sets of stimuli releasing one reaction are, strange as it may seem, factors inducing the choice-of-object of an entirely different action. For instance the sets of stimuli which, through innate perceptory patterns, release the following-mother reaction in many species of precocial birds, in doing so determine the object of sexual reactions not displayed until a year later. On the other hand, such characters of the object which are not present in the innate perceptory patterns, but to which the reactions must become conditioned in individual life, serve as a uniting factor to the different reactions once their acquisition is accomplished. This uniting of hitherto independent functions has already been illustrated by the example of the mother Mallard learning to know her ducklings individually. A very similar uniting function must be attributed to the process of imprinting as well, though it never concentrates reactions on one individual object, but only in the species as such. If normal imprinting is prevented experimentally, the social functions of a bird may be distributed between a considerable number of species. Thus, I had a tame Jackdaw, all of whose social reactions were, once for all, directed toward Hooded Crows as a species, while it would court human beings and respond with all its caring-for-progeny reactions to a young Jackdaw. One might say metaphorically, that imprinting fills out the spaces left vacant in the picture of the proper species, outlined in the bird's perceptory world by the data given by innate receptory patterns, very much as medieval artists in drawing astronomic maps, accommodated the pictures of the heraldic creatures of the zodiac between the predetermined points given by the position of the stars. Just as the imagination of such an artist is given the more freedom the smaller the number of stars which must be accommodated in the picture, so also is the scope of imprinting the greater, the fewer and the less specific are the characters of the species represented in innate perceptory patterns. With very many species it is practically impossible to direct experimentally the social reactions of the young to any but the normal object, because their innate perceptory patterns are so highly differentiated as to prevent the successful 'faking' of the corresponding sets of stimuli. This is the case with most birds of the Limicolae. Especially Curlews (*Numenius arcuatus*), even when hatched artificially and never having seen any living creature but their keeper, cannot be brought to respond to him with any reactions but those of escape. Most instructive are those cases where it is just possible to imitate releasing stimuli normally emanating from the parent bird, and thus to direct the imprinting of some reaction to a substitute object. This is the case with the following-mother reaction of young Mallards. It was long regarded by me as an established fact that Mallard ducklings would not accept their human keeper as a foster-parent, as would young Greylags, cranes and a number of other birds. I began experimenting by having Mallards hatched by a Muscovy Duck, with the result that they ran away from her as soon as they could, while she continued incubating on the empty shells. Foster-mother and young failed completely to respond to each other. Heinroth had exactly the same experience when he tried to let young Wood Ducks hatch under a Mallard. On the other hand I knew, from former experience, that young Mallards without any difficulty accept a spotted or even a white domestic duck as a foster-mother. The optical stimulation emanating from such a domestic duck was indeed more different from that provided by the small, brown mother Mallard, than was that of the small and rather shabby Muscovy with whom I had been experimenting. The characters relevant for the responding of innate perceptory patterns of the young must then, I concluded, be those common to the Mallard and the domestic ducks. These characters evidently were represented chiefly by the call note and by the general demeanor, both of which have not been changed much in the process of domesticating the Mallard. I decided to try experimenting on the call note which it is happily well within the powers of the human voice to imitate. I took seven young Mallards and while they were drying under the electric heater I quacked to them my imitation of the mother Mallard's call. As soon as they were able to walk, the ducklings followed me quite as closely and with quite the same reactional intensity that they would have displayed toward their real mother. I regard it as a confirmation of my preconceived opinion about the relevance of the call note, that I could not cease from quacking for any considerable period without promptly eliciting the 'lost peeping' note in the ducklings, the response given by all young anatides on having lost their mother. It was only very much later, probably after much conditioning to other characters inherent to my person, that they regarded me as their mother-companion even when I was silent.

The distribution of function between the innate perceptory patterns and the acquisition by imprinting is very different in different species. We find all possible gradations between birds like the Curlew whose innate perceptory patterns, corresponding to stimuli emanating from their own species, are so specialized as to leave hardly any room for the acquiring of characters by imprinting, up to birds like the Mallard, in which just one character, but a very 'characteristic' one, represents the evolutionally predetermined condition which must be fulfilled to make the object 'fit' into the general pattern of the companion. Finally we know of species whose innate perceptory patterns are so reduced as to form but a very rough and sketchy outline of the companion which, under the conditions of an experiment, may become filled out by a very different object. A good example of this is represented by the reactions of the newly hatched Greylag Goose who, on coming to the light of day for the first time, looks upward in a marked manner and will respond to actually any sound or movement by giving its specific greeting reaction. If the moving and sound-emitting object begins to move away from it, the gosling will instantly start in pursuit and will most stubbornly try to follow. It has been credibly reported that boats were followed by Greylag goslings when the parent birds had been driven away, very probably at exactly the right moment to elicit the looking-up reaction above described. I intend to experiment on the general form and on the limits of size which the object, thus releasing the young gosling's following-reaction, must possess. The lack of specificity which is so remarkable in the gosling's first responses to form and sound is, to an extent, compensated by its specificity in time. The looking-up reaction once performed, it is extremely difficult and possible only by very forceful means to induce the gosling to follow any other object than the one releasing its very first greeting reaction. In a natural environment it is extremely unlikely that a moving and sound-emitting object other than the parent bird ever encounters the gosling just at the critical moment and, even if some enemy of the species should do so, it does not matter whether the still very helpless gosling runs away from it or toward it.

Another example of a species with wide and little specific innate perceptory patterns is the Shell Parakeet (*Melopsittacus undulatus*). I raised in isolation a young bird of this species, which was taken out of the nest of its parents at the age of about one week. It was reared in such a way as to expose it to as little stimulation from the keeper's side as possible. When fledged it was confined to a cage in which a celluloid ball was so attached that it would swing to and fro for a considerable time if accidently touched by the bird. My intention to transfer the sexual and general social reactions of this bird to the very simple contrivance mentioned, succeeded beyond all expectations. Very soon the bird kept continuously near the celluloid ball, edged close up to it before settling down to rest and began performing the actions of social preening with the ball for an object. Notwithstanding the fact that the celluloid ball had no feathers, the bird minutely went through all the movements of preening the short plumage of another bird's head. One most interesting item in the behavior of this bird was that evidently he was treating the celluloid ball as the head of a fellow-member of the species. All actions which he performed in connection with it were such as are normally directed toward the head of another parakeet. If the ball was attached to the bars of the cage in such a manner that the bird was at liberty to take any position relative to it by holding on to the bars, he would always do so at such a level that his own head would be at exactly the same height as the celluloid ball. When I attached it closely to a horizontal perch, so that it was much lower than the head of the sitting bird, he would be at a loss what to do with his companion and looked 'embarrassed.' Throwing the ball loosely on the floor of the cage elicited the same response as the death of the only cage-mate does in Shell Parakeets, namely, the bird fell absolutely silent and sat still in the 'fright-attitude' with feathers depressed close to the elongated body. The only instinctive reaction not normally addressed to the head of a fellow-member of the species that I could observe in this isolated bird, was the following: males in courting a female excitedly run up and down a perch in a quick sidewise movement and finally sidling up to her, they grip in a playful way at her lower back or at the base of her tail, using one foot and standing on the other. When my parakeet grew to mature age and began more seriously to court the celluloid ball, he would execute exactly the same movements, but, as he was aiming them in such a way that the ball represented the female's head, his thrust-out claw would grip only vacancy below the celluloid sphere dangling from the ceiling of his cage. All this seems to indicate that some of the innate perceptory patterns of the Shell Parakeet must, in some way, be adapted to the *receiving of formed stimuli* representing, at least in rough outline, the head and body of a companion. Portielje got analogous results in his most interesting investigation of the European Bittern (*Botaurus stellaris*). This bird possesses an innate perceptory pattern corresponding to formed stimuli emanating from the enemy who releases its defence-reaction. This pattern also represents the head and body and also consists of a very rough outline only. The Bittern in defending itself, strikes at the head of the enemy, not at its eyes as was formerly believed. Portielje could show that the bird in this reaction was guided by the fact that a smaller shape representing the head of the enemy, was situated just above a larger one, representing the body. Two disks of cardboard were sufficient to meet the requirements of this simple innate perceptory pattern.

The observations of the Budgerigar[1] may serve us as an example, of how, under the abnormal conditions of captivity, the rough sketch representing the companion, outlined in the bird's perceptory world by innate patterns, may be 'filled out' in an incomplete way by accepting an object only partially corresponding to the innate sketch, so that some parts of the latter are left vacant, as the space reserved for the companion's body was left vacant by the celluloid ball. Instinctive reactions directed to such vacant spaces, as the one of gripping the female's tail in the Shell Parakeet, very often prove their fundamental independence by attaching themselves to an independent object, to a separate 'Kumpan.' The Jackdaw mentioned above supplies a good example of this. More transparent perhaps and susceptible of a simpler explanation is the behavior of man-reared young Greylag Geese. This species, as mentioned before, has particularly wide and sketchy innate perceptory inlets which, by reason of their very wideness enable the experimenting human to step in and supply all the needs a Greylag has for companionship, much more completely than is possible

---

[1] The Shell Parakeet, a corruption of Betcherrygah, native Australian for 'good parrot,' probably introduced into Great Britain at the time of the Crystal Palace Exhibition in Hyde Park, London, in 1851, when it soon became a favorite cage bird.

with any other species of bird hitherto investigated. There is, however, one reaction of the Greylag which constitutes an interesting exception to this rule by having a very definite and highly differentiated 'lock,' an innate perceptory pattern corresponding to the one and only structural releaser ever evolved by the species. I am referring to the reaction of flying after another member of the flock which is dependent upon a striking and beautiful grey-and-black color pattern on the wings of the preceding bird. This color pattern which represents one of the prettiest examples of an 'automatic releaser', is quite invisible in the sitting bird, as all the parts of the wings then open to view are colored in the same 'protective' gray-brown as the rest of the bird. It is only the plumage of the propatagial membrane, which disappears beneath the shoulder plumage when the wing is folded, and furthermore the base of the remiges of the hand and their primary coverts, then covered by the dull plumage of the arm, which display a light silvery gray appearing almost white when seen at a distance. The sudden transformation of a grayish-brown bird into one predominantly black and white at the moment of taking to wing, is very impressive, even for the human observer, and most probably is essential for the following- or flocking-together reaction of the fellow-member of the species. This highly differentiated way of releasing the reaction makes it impossible for the human companion to elicit it in the isolated goose, which results in an apparently inconsistent behavior on the part of such a bird. The young goose seems to undergo a complete mental transformation at the moment of taking to wing. While being completely indifferent to any fellow-member of the species and most intensely and affectionately attached to its keeper as long as it stays on the ground or on the water, it will suddenly and surprisingly cease to respond to the human in any way whatever at the moment it takes to wing in pursuit of another Greylag. My Greylags used to follow me on my swimming tours in the Danube as a dog would, and in walking and swimming, the leader-companion of a Greylag Goose releases its following-reaction without the use of specially differentiated bodily characters; therefore, when walking or swimming in front of the bird, it is able to supply the necessary stimulation, but leaves unfulfilled the conditions releasing the following-reaction of the bird on the wing, and leaves vacant a place which may be taken by any object which supplies specific stimulation.

The releasing of one separate social reaction independently of all others which normally cooperate with it in the social life of the species, as exemplified in these observations, is indeed a very common occurrence in birds reared by man. Abnormal though these phenomena undoubtedly are, they yet tend to throw some light on the normal processes upon which social life is built up in birds. As in the case of the reflex processes, our knowledge of what is the normal sequence of reactions is almost entirely founded on a careful analysis of abnormal reactions produced experimentally.

SPECIAL CONSIDERATION OF THE PARENT-COMPANION, CHILD-COMPANION AND THE LIKE

Five chapters of my work deal with five different cases in which one definite fellow-member of the species plays an important part in the bird's world, as the parent-companion, the child-companion, the sex-companion, the social-companion and finally the brother-and-sister-companion. These chapters are made up almost exclusively of examples of all these phenomena which I have already mentioned in the preceding sections of this abstract. Observational evidence is difficult to condense, so perhaps I should conclude this paper with a list of the contents of the 'companion' chapters. Each of them begins with a short account of the innate perceptory patterns which represent the innate sketch or outline of the companion in the bird's world. Next comes 'personal recognition of the companion', and after this I consider all the separate reactions released by the particular companion in question. Finally, I deal with the independence and experimental separability of the different releasing functions performed by the companion.

To enumerate a little more in detail the releasing functions of each type of companion: the releasing functions of the parent-companion: (a) the releasing of begging reactions, (b) of food-taking reactions, (c) of following reactions, (d) of responses to warning, and (e) of the responses to being defended by the parent.

The releasing functions of the child-companion: (a) the releases of feeding reactions, (b) of nest-cleaning reactions, (c) of leading reactions, (d) of defence reactions, (e) of other life-saving reactions, (f) of brooding reactions, and (g) the responses to the disappearance of the child-companion.

The releasing functions of the sex-companion: (a) the interlocking of instinctive actions pertaining to mating, (b) the synchronization of mating cycles, (c) the interlocking of instinctive actions in nest-building, (d) the releasing reactions leading to copulation, (e) the interlocking of instinctive actions pertaining to nest-relief, and (f) the responses to the disappearance of the sex-companion.

The releasing functions of the social companion: (a) inducing of reaction by 'contagion' and so-called imitation, (b) the releasing of following reactions, (c) of responses to warning, (d) of social attack reactions, (e) the interlocking of instinctive actions pertaining to the pecking-order and to nest-protection, and (f) responses to the disappearance of the social companion.

The releasing functions of the brother-and-sister-companion: (a) the releasing of following reactions, (b) inducing of reactions by 'contagion', (c) the releasing of responses to warning, (d) of communal defence reactions, (e) the responses to the diasppearance of the brother-and-sister-companion; and (f) the interlocking of instinctive actions pertaining to the pecking-order.

The paper, which I have attempted to summarize, concludes with a brief discussion of all the instances in which my results appear to be at issue with opinions generally held in comparative psychology.

Altenberg, Post Greifenstein,
Nieder-Oesterreich, Austria