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A Contribution to the Comparative Sociology of Colonial-Nesting Birds

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For some considerable time I have been endeavouring to collect observations which might possibly throw some little light upon the problem of instinct, that most debatable question of comparative psychology. I have found that for several reasons, which I need not detail here, birds were by far the most suitable animals for my observations and experiments, so much so, that for a couple of years I have worked almost exclusively on them.

Originally it was not by any means my intention to specialize on bird sociology, but my choice of a species on which to experiment was very much influenced by the relative ease with which different kinds of birds were tamed. As birds with highly developed social instincts are apt to become much more attached to their keeper than those of non-social species, when choosing the best kind of bird to tame and to keep tame I deliberately selected the one with the most specialized social reactions. This bird was the Jackdaw, *Coloeus monedula spermologus.*

The first single Jackdaw that I kept at once showed a number of reactions, the import of which I could not understand. They apparently were instinctive ceremonies, meant to induce some answering reaction in another bird of the same species. But what those answering reactions were like, I naturally could not guess. To learn the biological value of these curious ceremonials it was evidently necessary to observe the intercourse between a number of Jackdaws, and so I decided to rear a flock of young Daws in captivity. I am of the opinion that intricate details of behaviour are best studied in tame animals, because being devoid of fear of man, they react towards one another in a perfectly normal manner before one's eyes. Also, and this is most important, it is possible to repeat and check observations dozens of times for every single observation made on wild birds. (This sentence is quoted from A. A. Allen, but I might just as well have written it myself.)

But, after all, there might be a way to combine the advantages of field observation with those on tame animals. It was quite easy to accustom my first Jackdaw to fly about in full freedom and yet to return regularly to its home. Why not try the same with a whole

flock of Jackdaws? I will not go into details about all the difficulties I encountered in executing this plan, psychologically interesting though they often were, nor how I finally succeeded in establishing a Jackdaw colony in the roof of our house. But when I had done so, I had a really unique opportunity to acquire first-hand knowledge about Jackdaw sociology. I could study the social reactions of my birds not from afar, but sitting right amidst them, although they enjoyed full freedom, and consequently the full health and vigour of wild birds.

After I had studied Jackdaws for more than three years, I began to wonder how many of the reactions I had observed were common to colony-breeding birds in general and how many were peculiar to the Jackdaws, and perhaps their closest relations. To answer this question it was clearly necessary to study another colony-breeding species, and one which was as different from the Jackdaw as possible.

I chose the Night-Heron, *Nycticorax nycticorax,* chiefly because this bird is so very easy to breed in captivity. The attempt to plant a colony of Night-Herons in our grounds was even more successful than it had been with the Jackdaws. While the latter needs constant attention and some artificial aid to prevent the colony from dying out, the small heronry is really flourishing and constantly increasing in numbers, and that not only by breeding. In 1934 two wild Night Herons joined the colony, one of which bred with a tame female and successfully reared two young. This is all the more interesting, as I have never seen a Night-Heron in the forests of the Danube near our home, nor heard of one reported, which seems to indicate that the nightly excursions of my birds extend much farther than I had previously thought.

I will now proceed to give a short summary of the social behaviour of Jackdaws and Night-Herons, though I would prefer to give you my observational diaries *in extenso.*

I may begin by saying that the vital point in which the reactions of the Jackdaw differ from those of related non-social species of Corvidae lies in the difference in their reactions on establishing a territory. While other birds will tolerate only their mates in their own territories, a Jackdaw does not object to sharing the territory with the well-known co-citizens of the colony. Territorial instincts are nevertheless existent in the Jackdaws, but they are only elicited by *strange* Daws coming near the nesting colony during the breeding season. In that case the trespassers are unanimously attacked and ruthlessly driven away *by the whole of the community.* Thus the Daws

of my colony, when they numbered about twenty birds, refused to admit strangers. As the reaction is evidently conditioned by the birds personally recognizing every member of their flock, it would be important to know how the birds of a really large colony, numbering several hundred Daws, would react to the intrusion of unknown individuals. One would expect that in this case it would be impossible for the birds to know whether strangers were trespassing on their grounds. In my colony, however, new members were only received during autumn and winter, generally by flying in with birds that had been away for some days on a short excursion. It seems that away from home, where the reactions of territory do not prevent the forming of new acquaintances, the conditions are more favourable to the assimilation of new members of the flock.

It is not by any means a matter of course that, even when the territorial factor is excluded, a large number of mated pairs of birds can successfully breed so close together as do the Jackdaws. If a correspondingly great number of non-social birds are forced to live in so small an area, hardly ever more than one pair will go through all the actions of their cycle of reproduction. If more than one pair of Swans are kept on a pond, or more than one pair of Magpies in a flight cage, the birds will establish what we call a 'pecking order'. In such an artificial assembly the birds may even gradually become accustomed to share their 'territory' with other individuals of the same species. The reactions of territorial fighting get 'run down' by being released constantly, so that after a time even the bird, or pair of birds, which is topmost in the established pecking order ceases to try to chase away all other cage-mates. But even so the simple fact that these despots are able to move freely all over the enclosure, while all others have to give way to them, has as a consequence that only the topmost pair can breed successfully. All the others are too often disturbed and too intimidated to be in the mood even to begin the instinctive actions of reproduction. Every one who has observed the behaviour of Swans that were kept in a number greater than two on one pond during their breeding season has seen a typical example of this phenomenon.

Now the Jackdaw society is by no means without a pecking order, but its pecking order differs materially from that which we have just encountered in an artificial assembly of birds. In the latter the despot is apt to persecute the individuals low down in the order with even greater intensity than the ones ranging higher up, so that on the lowest rung of the ladder there usually is to be found the typical ugly duckling, pecked by all and sundry, and very often dying

from sheer continuity of persecution. In a Jackdaw society, on the other hand, the despot is only jealous of the individuals who are nearest to himself in the social order. Active persecution will occur if another bird actually endangers his leading position and becomes a potential usurper of the crown. But birds belonging to much lower social layers simply do not exist for him. They will give way before him even without his adopting a threatening attitude, and he would never deign to pursue them actively. All this is to be observed best in the top animal himself, but of course it holds true for all other members of the colony also. Every bird is jealous of his own position, constantly bickering with those that are his direct subordinates, but distinctly tolerant of those that range far below himself.

Through this characteristic indulgence of the strong for the weak, even the weakest individuals are at no disadvantage from the existence of a 'pecking order' as regards their own persons. But to protect the nest of the birds low in the social order the species has had to evolve an instinctive reaction, which must be counted among the most interesting phenomena that we encounter in animal sociology. If a Jackdaw is beaten by a rival during the breeding season, it invariably flies to its nest and, if further pursued, utters a certain characteristic cry, which is difficult to render in letters, and which I do not propose to reproduce. On hearing this cry, all birds of the colony, first of all the mate of the one calling, come rushing up to the scene of the fight, and if the aggressor does not give way immediately, he is unanimously attacked by all birds present. Usually matters do not reach this last stage. Generally the pursuing bird is sufficiently intimidated by the crowd of opponents. Often he very characteristically reacts himself in the same way as do all the others and joins in the chorus, uttering the same cry, and going through the same ceremonial movements, which consist in ducking low down while throwing up and spreading the tail-feathers. An anthropomorphistic observer would think that the bird was trying to conceal the fact that he himself was the root of all the trouble, but we shall not go wrong if we refuse to attribute such motives to a bird and prefer to assume that the cause of all the commotion really does not know that he has been its originator, and that he simply reacts, just as any other bird would do, to the acoustic stimulus of the specific cry. Typically instinctive and even reflex-like as this behaviour is, it nevertheless produces exactly the same results as the conscious co-operation of human beings does by suppressing unsocial behaviour on the part of any member of society. It prevents all aggressions by birds high up in the pecking order and thus

abolishes all detrimental consequences of the latter, without taking away its advantages.

While this is indisputably the most interesting consequence of the social reactions of the Jackdaw, another one may be said to be even more impressive to a casual observer. I mean the reaction of defending a fellow Jackdaw which has been caught by some animal of prey. If any normal and healthy Jackdaw sees a bird of its own species carried away by a predacious animal, it will utter a curious grating sound and flutter its wings in a peculiar way. In an instant all Jackdaws within sight and hearing are affected in the same way, and if the enemy is not too powerful the whole flock will attack him regardless of their own danger. Tame Jackdaws, with whom familiarity with man has bred contempt for his fighting powers, will invariably attack him whenever he takes a Daw into his hand. The co-operation of the community is even more unanimous, and if possible more instantaneous, in this reaction than in the reaction tending to suppress tyrants which we have described before. It was an unforgettable experience when I inadvertently caused this kind of social attack on the part of my Jackdaws, by picking up and carrying away a bird which had unexpectedly died during the night.

It can be experimentally shown that this reaction of defending fellow Jackdaws that have been caught by some animal is purely instinctive. It is even very reflex-like in the way in which it is released by a curiously simple combination of stimuli: anything black being carried by any living thing will release the reaction with an almost absolute certitude. This extreme simplicity of the key unlocking the gates of this defending reaction often causes it to miscarry in a very characteristic way. I once saw an instance of its error when a wet black bathing-suit was carried across the lawn by a human being. Another time it was released by a female Jackdaw carrying a primary that had just dropped out of the wing of a moulting Raven, *Corvus corax*. On the other hand, my Daws did not defend their own young when I took these out of the nest and presented them to their parents on the flat of my hand, as long as no black feathers had sprouted on the chicks. But on the day on which the tips of the growing quills burst open, showing the ends of the black feathers, the same experiment caused the parent Jackdaws to attack me furiously in the way described above.

Lack of time prevents me from describing some other interesting social reactions of the Jackdaw in detail, so I will merely mention their existence.

A very curious reaction is elicited when one member of the flock

is observed to be missing. The reactions of fear and flight seem to be then far more readily evoked by initial stimuli, so that all birds appear nervous and alarmed. If not on the actual site of the colony, the flock is evidently ready to leave the place where it has lost one of its members.

Another characteristic reaction takes place when one inexperienced member of the flock loses its orientation. It is at once sought out and led home by some bird which knows the way, very often by the despot of the colony himself, who seems to have some special 'responsibility' in such cases. It is interesting to note how the bird which is about to guide the lost sheep instinctively recognizes the latter's aimless and undecided flying movements as a sign of distress and how promptly he reacts to them, in a way which reminds one of the actions of a well-trained collie-dog.

All these instinctive reactions tend to make the Jackdaw community one of the most highly organized societies which we know among vertebrates. Now let us proceed to the social structure in the case of the Night-Heron and compare it with what we have learned about the Daws.

I shall again begin with the reactions which concern territory. There are two ways in which evolution can change the indubitably primitive territorial instincts so as to make colony-nesting possible. Either one common territory must be shared by all the birds of the colony, or else the territories of individual pairs must shrink to such an extent that the nests can be built so closely together as to produce the outward appearance and the advantages of a rookery. This latter possibility has been realized in the colony-breeding Herons and in a number of other birds. The nesting territory of a pair of Night-Herons has an area of but a few cubic feet, yet it retains all the characteristic features of the typical territory of other birds. Of course its extreme smallness makes it necessary for the birds to seek their food on some neutral ground, but many other birds do the same, as, for instance, according to Howard, the Yellow Bunting does. But the chief characteristic of territory is the fact that any individual will fight with very much more vigour if the combat is decided in his own territory. To my mind it has not been sufficiently emphasized that this increase of fighting power is not equal all over the ground defended by one individual bird, but that it always increases in proportion to how near a certain centre of the territory the fight takes place. This causes territories to 'behave' like pieces of elastic substance, the counter-pressure of which is proportional to the deformation caused by some outward influence. Any one who

wants to study these phenomena at first hand can easily do so by keeping a number of males of the common Stickleback, *Gasterosteus aculeatus,* in an aquarium large enough to hold the corresponding number of Stickleback territories. If one fish crosses the boundary of his neighbour's territory, he will be attacked and invariably beaten by its owner. He will retreat in the direction of the centre of his own ground, and the victorious enemy will pursue him even across the former boundary. On nearing his own head-quarters, the vanquished fish's spirits gradually rise to a point where he will suddenly turn and vigorously attack his pursuer, vanquish him and instantly pursue him in the direction of his centre of action. This will be repeated a number of times, till at last both adversaries come to rest approximately on the same spot where the first transgression had been committed, the boundary between the territories behaving all the time exactly like a pendulum that has been moved out of its normal position. This essential phenomenon of territory is very much the same in a great number of territorial animals. It is extremely prominent in the colony-nesting Herons because of the small size of their territories and the correspondingly rapid increase of fighting power which takes place when the bird moves a few yards from the outer boundary of his territory to its centre. This increase more than compensates for any difference in vigour that may exist between two birds within the normal range of variation peculiar to the species. Naturally this protects the nests of even the weakest birds so effectively against any invasion of other Night-Herons that such wonderful instinctive reactions as those which guard the nests of Jackdaws are quite unnecessary and therefore absent.

The predominance of territorial reactions in the Night-Heron precludes the pecking order from being of real consequence. It was difficult to prove even the existence of such an order, because it was not easy to observe the birds on really neutral ground. Near the heronry in our garden every patch of ground soon became allotted to an individual Night-Heron, who would treat it as his own, no matter how far it was from his actual nesting-territory or whether it was an *enclave* between similar outside possessions of other Night-Herons, exactly as a Power treats one of its colonies. It was only when I succeeded in observing the birds in localities where they had never been before (which I was only able to do by baiting for them), that I could convince myself that to some extent a pecking order actually existed among them. It was interesting to note that the birds had quite a different way of walking when on neutral ground. When they were in their own territory, every step they took was freighted

with some meaning that conveyed a message to their neighbours, always signifying either aggression or retreat, making their movements look ridiculously dignified and consequential. It was only on neutral land that I ever saw a Night-Heron actually moving at a trot. So quick a movement would certainly cause trouble of some sort if executed near the frontier of a distrustful neighbour. Whenever I had enticed the birds on to some place that was new to them and therefore neutral, this neutrality lasted only for a very short time. After feeding them for a couple of days in the new locality I noticed that individual birds were continually standing on the same spots, and soon afterwards they would begin to defend successfully these places against stronger birds, thus confirming their newly acquired proprietary rights.

Night-Herons show these territorial reactions not only during their breeding season, but even the young birds develop them as soon as they become independent of their parents. This early establishment of territory, together with the overpowering urge to drive out of it any other Night-Heron, regardless of sex, naturally is apt to prove an obstacle to mating. The Night-Herons, like very many other birds, do not recognize the sex of another individual of their own species on seeing it, so that the possibility of a male admitting just one female to his own territory, as do a great number of other territorial birds, simply does not exist for the Herons. The evolution of the species has overcome this difficulty by developing a very complicated instinctive ceremonial, which is indispensable for the understanding of Night-Heron behaviour, so that I must describe it here at length.

An unmated male Night-Heron begins his cycle of reproduction by choosing a potential site for the building of a nest, which may or may not be on the exact spot of the formerly described headquarters, but in the latter case it instantly assumes this function. Here the lone male begins to build and at the same time to call for a female. With head and wings lowered, he executes a queer sort of courting dance on the spot of the future nest, treading from one foot to the other with a peculiar weaving action. From time to time he suddenly lowers his head and neck vertically, while his shoulders lift as if in a hiccough, and he utters his courting cry. This cry is very deep and quite low, sounding like steam escaping through the safety-valve of a boiler. All this ceremonial is executed whether or not another bird is within sight or hearing, and its intensity rises with a bound if another Night-Heron approaches while he is calling. The other bird's sex has absolutely no influence upon this stimulating

effect, any male which fortuitously comes near the calling bird will excite him exactly in the same way as a female approaching with the purpose of mating. When at last such a female is attracted by the persistent calling of the male, she is by no means allowed to join him immediately on his nest or nesting-site, nor does she try to do so. Verwey has observed in the Grey Heron, *Ardea cinerea* (in which species the mating ceremonial is somewhat similar), that the males could not repress their territory-defending reaction when the females joined them too suddenly on the nesting-site where they had been uttering their courting call, so that they actually drove away their prospective brides for whom they had been calling longingly for weeks on end. This never actually happened to my Night-Herons, but when at last the females began to take an interest in the calling males and slowly drew near the boundary of their territories, one could clearly see how the latter were torn between two conflicting impulses. In spite of the fact that the behaviour of every male was clearly meant to attract a female, it was apt any moment to change quite suddenly into one of territorial defence, if the female approached beyond a certain limit. It is typical of instinctive action that in the case of two conflicting reactions being released by the same object, the resultant behaviour never shows a purposeful compromise between the two impulses, but a perfectly aimless intercalation of two actions that serve absolutely contradictory biological ends. The absence of conscious purpose in instinctive behaviour hardly ever becomes so strikingly apparent as in this phenomenon. The distance at which the approaching female releases this abrupt change from courting into territory-defending behaviour now gradually decreases, possibly because the male becomes accustomed to his prospective mate's proximity, possibly because of some internal change taking place in the male with the progression of the cycle of reproduction. It is my opinion that during this time of getting slowly acquainted there takes place what A. A. Allen calls the synchronization of mating cycles. Some females seem very anxious to join the male in his nest and are at work day and night trying to get him accustomed to themselves, while others, characteristically often young or weak birds, spend only a few hours daily near the calling male and often take weeks in approaching the nesting site. The male seems to be able to stay almost indefinitely in the physiological state of the courting call, waiting for the female to arrive and to attain her oestrous phase. Things do not begin to move again till the stage which I call the 'appeasing ceremony' is reached.

Strong instinctive urges have been overcome in the male to induce him to allow another bird to trespass on his territory, but now matters become even worse: the female must come within actual touching distance of him on the small area of the nest. Ordinarily any other Night-Heron which comes within reach of a bird's bill will release its 'repelling reaction', the swift, snake-like stab with opened beak, which, surprising by its suddenness and by its unexpectedly long reach, has most undeservedly earned the Herons a refutation for conscious and malicious dissimulation. If we are not well versed in Heron psychology, we are prone to overstep the limits beyond which a tame Heron's repelling reaction is released, only to be reminded of its existence by a double puncture in our skin!

To overcome the apparently very strong impulse to take a stab at the other bird when the latter comes within striking distance, the Night-Heron has developed the appeasing reaction to which I referred before. It is a ceremonial that must be gone through each time the members of one family come within striking distance of one another. The movements of the ceremony are as follows: all feathers of head and neck are erected to the utmost extent, the three white crest plumes standing out nearly at right angles to each other. Then the beak is lowered and head and neck are stretched far forward in the direction of the bird to be mollified. At the same time a low disyllabic call, with the accent on the second syllable, is uttered. The lowering of the beak brings the top of the head into a nearly vertical position, so that the black crest with the three white plumes rising out of it are presented most impressively to the view of the other bird, which reacts by performing in exactly the same way in token that his repelling reaction has been suppressed and that a mutual approach may be made without danger.

The appeasing ceremony is first observed when the females actually join the males on their nest or on the chosen site, which at this point already has acquired the 'meaning' of a nest. As it is generally the approaching bird who thus 'greets' first, it is the female who at first seems more intent on this ceremonial, the male answering rather perfunctorily, but soon afterwards it is the other way round; now the female stays in the nest nearly all the time, while the male is busy carrying nesting material to her. It is always the bird approaching the nest which is most anxious to appease the one that is standing in it, even when the former is represented by the parent arriving with food and the latter by a small chick.

I want to emphasize that the striking pattern of a Night-Heron's

crest is not used in any other kind of display. It is there strictly as an organ developed in the evolution of the species to control the normal repelling reaction by releasing a greeting reaction which supersedes it. The appeasing or greeting reaction of the Night-Heron becomes even more interesting through the fact that its geological age is at least approximately known. The rather aberrant South American Night-Heron, *Canchroma cocblearia,* has exactly the same appeasing ceremony, although its crest feathers are quite different from those of *Nycticorax.* Since a purely ceremonial reaction that has nothing whatever to do with environment can hardly be expected to become absolutely equal in two species through converging development, we must assume that the ceremony is older than the separation of the genus *Canchroma* from the other Night-Herons, and, incidently, older than the signalling organ used in it.

Little more remains to be said about the social reactions of *Nycticorax.* The strong territorial reactions guaranteeing the immunity of the individual nests, the appeasing ceremony taking place on the nest to prevent the birds belonging to the same from fighting each other, are the two main factors underlying the social behaviour of the Night-Heron. Perhaps I ought to add that the young birds, newly fledged and inexperienced, can stray all about the heronry regardless of territory without ever being chased away by an old bird. The young birds do not seem to recognize their parents, or else their begging reactions are released on seeing any adult, so that they will most obtrusively molest every old bird they meet, crowding against him and trying to seize his bill. Such impudent youngsters are not only absolutely immune from attack, but the old birds actually seem afraid of them and will retreat whenever they see one coming. Adult dogs normally show very much the same reactions, when worried by puppies. This rather astonishing tolerance gradually disappears as the begging reactions of the young birds subside, but when that time arrives they have grown strong and experienced enough not to be stampeded off the colony altogether, a danger which would be very serious indeed if they had to fight for territory immediately after leaving the nest.

If we compare the social reactions of Jackdaws and Night-Herons, of which I have briefly tried to convey to you some notion, we must admit that the phylogenetic development of social instincts in these two species has reached somewhat similar results by astoundingly different means. Think how outwardly similar their rookeries are, and how fundamentally different is the structure of society on which

the existence of each is based! This should be a warning not to generalize too rashly from any rules or laws that we find underlying the behaviour of any animal we observe. What may be true in one species may be absolutely untrue of a closely related one, and if any one makes an assertion of which 'animals' are the subject, you may rest assured that the statement is erroneous!