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Gregariousness in the animal world.

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BOSTON UNIVERSITY

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Thesis

GREGARIOUSNESS IN THE ANIMAL WORLD

by

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INTRODUCTION

Gregariousness occurs so frequently in the animal world that it is an adaptation which must be of great biological significance. Several well-known scientists, including Allen (1920), Miller (1922), Allee (1931), and Balfour-Browne (1936), have paid considerable attention to this subject, but our knowledge concerning gregariousness among animals is still far from complete.

Balfour-Browne (1936) believes that the highest types of animal societies have, perhaps, evolved from gregariousness. Wheeler (1923), on the other hand, is of the opinion that true societies have evolved from a closer association between mother and offspring, also a very common phenomenon in the animal world.

The line between strictly solitary and strictly social animals is very difficult to draw, because by imperceptible gradations, the one shades off into the other. At one extreme is the most specialized and most successful of all units: that found among the Isoptera (termites) and Social Hymenoptera (ants, bees, and wasps), where complete organization and unification of the com-

munity is the rule. At the other extreme are the solitary animals which never seek out other individuals of their own species.

Transitions occurring between these two groups include the Quasi-Social animals, among which there are two general types; one, where the young remain with the mother and form incipient families, and the other, where strict gregariousness occurs. Some authors use the term "society" rather loosely, for example, Zuckerman (1932), who considers a school of fish as forming a society, while Allee, and others, differentiate between mere gregariousness and true societies. In general most authorities concede the fact that true gregariousness is the habit of individuals of collecting in groups. However, not all aggregations are the result of gregariousness, e.g., tropistic and catastrophic aggregations. Only when the individual voluntarily seeks or remains in the company of other individuals when conditions are equally favorable elsewhere, can the term "gregariousness" be applied. Gregarious aggregations may be formed by like individuals, or by individuals of different species.

The most obvious advantage of the gregarious habit, according to Miller (1922), is that it offers a multiplicity of eyes, the chances of sighting an enemy

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from afar being thus greatly increased. Another advantage is the fact that numbers distract attention from any one individual, and in consequence all are likely to escape. As an illustration, Miller calls the attention to the fact that a hunter who, shooting into a flock of ducks, has less chance of bringing one down, than he does when he waits for a duck to rise from the reeds and then shoots at it. In the same way, a hawk, pursuing a flock of birds, may become distracted to the point of not concentrating on any one individual, thereby increasing the chance of escape on the part of the pursued.

GREGARIOUSNESS AMONG THE INVERTEBRATES

The first evidences of gregariousness among the Invertebrates is found in the "Sea Butterflies", Pteropoda. Weyssse (1922) describes them as minute pelagic animals, very transparent, and rarely attaining a length of two or three centimeters. Hegner (1935) has found that these creatures live in vast schools, sometimes covering the sea for many miles. Their movements along the surface of the water give them the appearance of tiny butterflies.

Isopods offer a more striking example of gregariousness among the lower forms. According to Allee (1932), Land Isopods tend to collect in moist regions. These aggregations are frequently such as might result when shelter is limited, provided there is a tolerance for the presence of other animals, but at times they collect in much closer units than can be entirely explained on that basis. They do not occupy all the available space, but group together in one place. They do not move in a straight line, but by a sort of random movement. When there is no difference in the dampness of their environment, they tend to wander until one of

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them stops, and then, in time, all the rest collect on or near this quiet animal. On the approach of certain adverse conditions, they collect in groups. Because of this, Allee (1926) believes that the element of mutual attraction is present.

According to the same author, immense numbers of Water Isopods occur in swamps in early spring and in the winter. As in the case of Land Isopods, they tend to use other Isopods in place of inanimate elements of their physical environment when the former are present in considerable numbers and the latter are lacking in their usual ratio of abundance in proportion to the numbers of animals.

Another subdivision of the Crustacea which has been shown to have gregarious habits is the Order Decapoda. Along the mudbanks of the creeks in Stratford, Connecticut, the writer has repeatedly seen the small holes of hundreds of Fiddler Crabs (Uca, sp.). By paddling a canoe through the creeks with as little noise as possible, one has a fine opportunity to observe these interesting creatures.

Hyman (1920) has also found the common species of Fiddler Crabs occurring in thousands on favorable beaches. Burrows dug along the beach just below the high tide

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line extend downward a foot or more at a very steep angle. Although there is a continual daily loss of their members, the thousands of Fiddlers on the beach do not get smaller year by year, since these crabs are very prolific. The group on the beach is always being recruited by late arrivals of larvae from the sea, because the breeding season of Fiddlers is a long one. When the weather begins to get cold in the late autumn, all the crabs on the beach crawl into their burrows for hibernation.

Gregariousness is far more common among the Insecta than any other group of Invertebrates, as will be shown by examples discussed in the following insect orders.

Order Pseudoneuroptera

The lowest order of insects which show gregarious habits are the Mayflies (Ephemera). Dr. Plath reports that on several occasions he has seen small numbers of Mayflies moving up and down about ten feet above the ground, not far from Boston.

Order Orthoptera

It is a well-known fact that Locusts (Acrididae) are gregarious.

Uvarov (1928) asserts that all typical Locusts are characterized by the inclination of their nymphs to live in close groups from the time of their hatching to the adult stage. He believes that the formation of the groups depends upon the presence, in the gregarious species, of a special biological faculty, which compels the nymphs to keep close to each other, and to repeat each other's movements. During the moulting period the nymphs are even more intensely gregarious, but later may temporarily lose all connections with a group.

The migration of Locusts is an occurrence that has been recorded as far back as Bible times. At that time in their life history they become very serious pests. Hegner (1935) has reported that in the Middlewest the Rocky Mountain Locust is hated by all. At one time in Kansas, Iowa, Nebraska, and neighboring states, hordes of these insects were brought by the northerly winds from their breeding grounds in the Northwest, and proceeded to eat all the crops. Nothing green was left, and on one occasion, what almost amounted to a famine resulted. "Falling upon a cornfield," writes Hegner, "the insects converted in a few hours the green and promising acres into a desolate stretch of bare, spindling stalks and shrubs..... Their flight may be

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likened to an immense snowstorm, extending from the ground to a height at which our visual organs perceive them only as minute, darting scintillations, leaving the imagination to picture them indefinite distances beyond..... In a-lighting they circle in myriads about you, beating against everything animate or inanimate, driving into open doors and windows, heaping about your feet and your buildings, their jaws constantly at work, biting and testing all things in seeking what they can devour.... The young that hatch from eggs laid by the insects after their migration do not thrive in their new home and die before reaching the adult stage, hence the spread of this destructive species is prevented."

Uvarov (1928) describes the mass wanderings as follows: "Some of the hoppers become restless, make irregular small jumps, which cause reflex jumps on the part of others, and in this way some centers of movement arise in different sections of the band; movement is at first irregular, but soon a common direction is found, owing to the inclination of hoppers to move parallel to each other. This common direction of each band is, therefore, determined by accidental conditions, and separate bands may begin

to move about in different directions. In some cases, however, the direction of movement of individual hoppers and, consequently, of their bands is determined by external factors; thus, for example, bands of the Moroccan Locust very often march downhill..... All attempts to connect the direction of the wind, have given so far most contradictory results, and none of these factors are likely to play any serious part in determining the direction of movement, though they may perhaps influence it to some extent.

"A band once started on its march positively cannot stop, since the hoppers, owing to their gregariousness, strive to keep as close as possible to each other and produce continuous mutual stimuli resulting in jumps and crawling. The band therefore must move, regardless of where this movement may lead it, and the result is the blind march of masses of hoppers.

"The bands usually move, not in dense masses, but in a formation with a broad but not very deep front. In front the band is defined very sharply, the first rows of the hoppers being particularly dense, while behind they become less so.

"When two bands moving in different directions meet,

they usually form one large band that continues to move in the direction of the larger of the two; there is, of course, no general rule for these cases, except that it is seldom possible for each band to continue on its own way. As a result of such chance encounters and of the fusion of bands, enormously large bands, stretching for miles and blindly marching along, are formed; picturesque descriptions of such great bands of hoppers abound in various books of travel. The relentless march of such masses of hoppers, regardless of obstacles, creates an impression of some dark purpose, of a movement towards an objective, and has led to numerous more or less fantastic explanations of the causes of movement based on the imagination of the observer and not on facts.

"Obstacles to the moving bands, in fact, do not seem to exist; they pass over hillocks and boulders; holes and ditches in the ground are filled with the bodies of the first coming hoppers, and their comrades pass over them as if over level ground; absolutely insurmountable obstacles, such as smooth vertical walls, cause only an alteration in the direction of movement; across canals and streams the bands swim to the other side and continue their march. This crossing of streams and even of broad rivers had nothing extraordinary in it, as the

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hoppers enter the water, of course, without any understanding what is before them, while swimming itself consists, as we know, of the same movements as marching."

According to Parker (1925), it is only rarely that the migrations of bands of young locusts can be attributed to a search for food, the usual stimuli being temperature and light. He suggests that the tendency for all to move in the same direction is a response to visual perception, perhaps a reflex due to the formation of moving retinal images which leads each locust to move simultaneously and in the same direction as its neighbor.

Parker discredits the idea that adult locusts migrate to escape their natural enemies, and believes that migrations are the result of certain physiological changes that take place just after the insect becomes adult. Temperature and vibration of air are given by Parker, as the immediate stimuli to the daily flights, and the tendency for all to move in the same direction is explained in the same manner as for the crawling young. Dissections made at this time show the fat body to be large and the air sacs enormously developed, and the author believes these conditions stimulate and make

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possible long flights. As the fat body is used up and the air sacs grow smaller due to the development of reproductive products, migration ceases and eggs are deposited.

While Uvarov agrees that the search for food plays no part, and that temperature and other external conditions play a great part in migration, he, too, is convinced that the flight is both induced and regulated solely by physiological factors.

Parker, by field observation, rearing experiments, and morphological studies, has gathered evidence which proves that if the migrating swarms of Locusta migratoria settle in an environment similar to that in which they originated, their offspring will be typical migratoria; whereas if they settle where temperature and humidity conditions are quite different, the progeny of the migrating swarm may be indistinguishable from L. danica, which is non-gregarious in habit, has shorter wings, differently proportioned pronotum and different color markings, danica being merely a solitary "phase" of migratoria.

Order Hemiptera

Most of the aggregations formed by Hemiptera are the result of environmental conditions. The Water

Boatman is an exception. Hegner (1935) has the following to say concerning this insect. "Sometimes Water Boatmen occur in enormous numbers..... Soon after reaching Mexica City, we visited Lake Texcoco, where we found the water near the shoresso crowded with Boatmen that we collected hundreds of them in our insect neb in a few minutes and could have fulfilled our obligation, with respects to the number of insects to be secured -20,000- in half an hour had we so desired."

Order Lepidoptera

Kenyon (1898), Howard (1922), Holland (1922), and Williams (1930) all report that certain species of butterflies are extremely gregarious. Williams (1930) informs us that it is interesting to note the partial interrelation of gregariousness and the migratory instinct. "It has been found in some locusts," he writes, "that overcrowding sets up a series of physiological and psychological processes which result in the migratory phase and instinct . Nothing of this nature has been proved in butterflies, but a remarkable comparison can be drawn between the incidence of the two instincts in D. plexippus and V. cardui, the two butterflies whose migrations are best known.

"In D. plexippus the process is as follows:-

(1) Development of the gregarious instinct resulting in great massing of adults in the autumn in the N.

(2) Gregarious instinct continues, migratory instinct develops, resulting in mass flights to the S.

(3) Gregarious instinct continues, migratory instinct ceases and is replaced by hibernation, resulting in mass hibernation of adults in the Gulf States.

(4) Gregarious instinct ceases, migratory instinct reappears (with opposite direction-determination), resulting in break up of flocks and individual flights to the N. in the spring.

"In cardui, on the other hand, it is in the spring that we find the gregarious instinct together with the migratory instinct, resulting in mass flights more or less to the N., both instincts ceasing more or less simultaneously when the insects disperse over their new territory. It also appears almost certain that if there is a return southerly flight of cardui in the autumn, it is without the gregarious instinct, with the result that the insects fly one by one to the S., thereby accounting for the almost complete lack of evidence of any such movement."

Many species of butterflies have been seen in dense masses far out at sea. Williams relates that migratory flights of butterflies may stretch across a front of several hundred miles, may continue over land and sea for two thousand or more, and the number of insects concerned may run well into thousands of millions.

According to Kenyon (1898), in Topeka, Kansas, the butterfly Anesia plexippus was present in such extraordinary abundance as to prevent people from working out of doors, These insects gathered on the rails of the Union Pacific Railroad in such numbers as to stop a train by their bodies greasing the rails. "The air was full of insects, which were flying lazily southward, paying no attention to the flowers in their way. They were not quite as numerous, however, as the Topeka report makes them out to have been. Large swarms of this species are not infrequent, being noticed from time to time."

Animals that are fierce and strong can afford to be solitary, but the individuals of many species band together and lead a gregarious life, not so much, apparently, because they enjoy each other's company, as for mutual protection. The Tent Caterpillars that hatch from a single batch of three or four hundred eggs, according to Essig (1929) unite in the spinning of a

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web that often takes the form of a tent. Into this they retire every morning, and from it they emerge every evening when they start out on their foraging expeditions.

Order Diptera

The Cluster Fly (Pollenia rudis) according to Essig (1929) is gregarious. The adult flies often collect in great numbers in houses during the winter, hibernating on the reverse sides of pictures hanging on the walls or in other dark places.

Dr. Harris reports that in mid-June ^{Several years ago,} he found a compact mass of what he believed to be Cluster Flies between the window and the shutter of the Madison Spring Hut on Mt. Madison, at an altitude of 4800 feet. The mass was large, nearly filling the window sash.

Order Coleoptera

Among the Coleoptera we find several members which are gregarious. The writer has noticed giant aggregations of Whirligig Beetles occurring on the surface of still water in ponds and streams. Although at times they rest quietly, they generally exhibit what appears

to be a perfect frenzy of erratic activity. It appears that the behavior of these beetles is largely due to visual stimuli, since the aggregations break up in the dark.

Allee (1931) has made some unusual experiments with Fireflies (Lampyridae) and has discovered that sometimes the Fireflies in one locality seem to flash all at the same time. This has been noticed especially in the Philippines, where thousands have been seen to flash in unison. Similar observations have been made in this country, but the explanation as to how the flashing is regulated is unknown. Partial control of the flashing can be obtained by the use of a pocket flash.

Certain species of Ladybird Beetles of the genus *Hippodamia* collect in great numbers in favorable places year after year, even though, to man, nearby unoccupied niches seem equally desirable. Some hibernating aggregations of Ladybird Beetles in northern California form large masses among the pine needles.

Hawkes (1926) found eighteen clusters of Ladybird Beetles among the dead leaves under the Azaleas in the

Sierra Mountains. Each cluster of insects was congregated into a ball-like mass the size of one-half to one fist in bulk. There was a complete separation of the various clusters. The impulse which caused the Beetles to congregate was so strong that there were no stragglers between the masses, but it was not strong enough to consolidate all the clusters into one group.

Hawkes disturbed several clusters of Ladybird Beetles to see how they would reassemble. A number began at once to climb up the main stem and collected at the very top, where some remained. Others also went up gradually, and pressed as near as possible to the first settlers. Still more followed, and the late-comers crawled on top of those already assembled. Finally the mass was so top-heavy that gravity became a greater force than the ability to hold together, and the top part of the mass toppled and fell.

Order Hymenoptera

So-called Solitary Wasps may collect to the number of some hundreds in one locality. Thus, for example, Wasps belonging to the family Sphecidae form spaced aggregations. Those of another genus (*Prionyx*) sleep crowded together on the top of a weed. Marked individuals

have been known to return to the same sleeping place several times in succession.

Just before dusk in California one night, Bradley (1908) observed a group of Black Wasps (Prionyx atrata) asleep on a dried stem of wild oats. Upon investigation, he found scores of these resting Wasps grouped on wild oats or other plants. Each group contained from one or two to a couple of dozen individuals. In about an hour's time Bradley was able to collect about five hundred individuals. Seven species of Aculeate Hymenoptera were represented in large numbers, belonging to three different families, four sub-families, and five genera, and each species, so far as observed, was always grouped separately. Though a group of one species was in close juxtaposition to that of another on a neighboring stem, there was no intermingling of individuals. Returning on an evening a week later, (but perhaps not finding the precise place at a favorable time) Bradley found the aggregations of Wasps less abundant, but still present.

GREGARIOUSNESS AMONG THE VERTEBRATES

Gregariousness is even more highly developed and more common among the Vertebrates, and occurs in all the sub-divisions, such as fishes, amphibia, birds, and mammals.

PISCES

Among the fishes, schooling or shoaling is a "sense" that is highly developed. Norman (1931) has observed that two individuals of aggregarious species, when brought close enough together to perceive each other clearly, approach to within a certain distance, and then change their course so as to swim forward side by side. If some influence tends to stop the forward progress of a school, the advance members of the shoal stop abruptly, turning backwards, and a "milling" movement is set up.

Parr (1927) in his observations on the schooling behavior of fishes has divided the schools into two groups; first, the occasional travelling in bands kept together as a reaction to impulses created by a temporary situation; and second, the apparently permanent schools. Schools of the first sort are of slight stabil-

ity and disperse as soon as the conditions for their gathering disappear. The schools of the second group are characterized by great stability through the most varied of environmental conditions. Such schools disperse only under the influence of rather violent stimuli, and immediately reassemble. Schools of this type are chiefly formed by pelagic fishes such as mackerel, sprat, and herring. The existence of these schools must be dominated by internal factors of the school as a whole, or of the single individuals, and not by direct influence from the changing environment.

Parr believes that the apparently social behavior of schooling fishes may be only an incidental result of mechanically integrated, comparatively simple and automatic responses of the single individuals.

Order Selachii

The smaller species of shark often form immense schools which follow mackerel or other migratory fishes. Kingsley (1888) reports that a certain species, (Cetorhinus maximus), has received the common name, Basking Shark, from the fact that it collects in large schools, which lie motionless, the dorsal fins and backs rising above the surface of the water.

Order Teleostei

By far the largest number of gregarious species belong to this order.

Certain species of minnows, travelling in schools, are an easy prey to their enemies. At night the writer has seen large schools of them congregate in that part of the water that was lighted by a search light in the Housatonic River. Repeated observations showed no apparent activity among them, except minor movements as they remained in the circle of light. Attempts to disperse them proved unsuccessful, as they merely scattered for a time, returning almost immediately beneath the light.

Shad, at first dispersed about the sea, become gregarious and gather to form groups when ready to swim up the river to spawn. That they come together in shoals was observed by Roule (1933). The males arrive first, the females coming along shortly afterwards. Each shoal is made up of individuals which have reached the same degree of sexual development, and breaks up and comes together again according to the variations of the qualities of the water which it seeks, and which are suitable to it. In the spring,

when the water is warm, spawning is accomplished in a final gathering of reproductives collected in great numbers.

Gregarious to a large degree, herring shed their sex products as they move about in immense schools. Roule (1933) explains the gathering in shoals in the open sea as spontaneous, since he believes the sexes attract one another. These vast herring shoals, according to Roule, are genetic assemblies, concentrations for the purpose of spawning, and they break up afterwards when the motive for their existence is no longer present.

Schools of Mackerel appear along the coast of New England in the spring and remain until fall. When Mackerel are "running" in Maine, they bite so readily that there is little time in which to bait one's hook. The gregarious tendency of these fishes causes them to congregat^e in schools, rather than swim singly over a greater area. The writer has watched them "milling" not far from the surface of the water. Even when their enemy the dogfish appears, they do not separate, but swim off in school-formation.

Bluefish are extremely gregarious, and hunt their prey in large schools. The writer has spent many hours

fishing for them, and has observed that because of the tendency to form schools, they do not occupy all the available space. While one fisherman is making a fine catch, another, a few rods away, may sit in idleness until the school swims in that direction.

"Skippers" (Scomberesocines), according to Kingsley (1888), are gregarious. They live in large schools which, when pursued, come to the surface of the water. The individuals of which these schools are made up crowd each other when pursued by an enemy, and in this way become easy prey, since progress cannot be as speedy under such conditions.

Large Mulletts begin to assemble along the coast of Florida in schools in the height of the summer, probably preparatory to spawning. They school best with a north-east wind, according to the same author.

Atlantic Flying Fishes are gregarious, travelling in large schools. Hegner (1935) has the following to say concerning them: "When the iron monster of a steamer approaches, they rise terror-stricken, in large groups, spreading out over the tops of the waves like a flock of silvery insects".

AMPHIBIA

A striking example of gregariousness which occurs during the breeding season is found among the Anura . Frogs are practically solitary during the year, except for possible hibernation groups, but they form aggregations during the breeding season. In certain parts of New England, Leopard Frogs are to be found in almost every pond, stream, marsh, and meadow, often far from water, and are so abundant and easy to capture that they are used more than any other vertebrate for the study of anatomy and physiology. The actual egg-laying and fertilization of eggs is accompanied by the formation of a compact aggregation in a pond or stream. The writer has watched them force themselves together as closely as possible, and when the eggs are deposited, the latter form a continuous mass. Repeated efforts to separate pairs resulted in their pushing and shoving to another position among the frogs as soon as they are released.

When thousands of tadpoles change to minute toads, they leave the ponds to find a suitable living place, especially during a rainstorm. Unfortunately most of them meet an early death. Miller(1909) has observed toads congregating in such fashion that 90% of the eggs were laid within a radius of fifteen feet. Males form

groups a day or two before the females arrive.

Newly transformed toads must remain in a damp place for a few days, consequently many congregate, seeking shelter. Toads do not hibernate singly as a rule, and a dozen or more may be found closely packed together under a rock, board, or in some sheltered spot.

REPTILIA

In this group, two orders have been found to contain gregarious species, the Alligators and Crocodiles, and certain species of Snakes belonging to the Order Squamata.

Alligators may, at almost any times, be found piled one upon another in the zoo. Their gregariousness causes them to collect at one end of the available space, leaving unused an amount of space which would easily accomodate them, making compact grouping unnecessary. Motion pictures of tropical scenes show that Alligators and Crocodiles have the same gregarious tendencies in nature. Johnson (1931) found thousands of Crocodiles grouped on various rocks at the water's edge below Murchison Falls, in Africa.

Order Squamata

Tightly entwined groups of Snakes have been found

by Ellicott (1880) heaped together on a rock and between big stones, in warm sunny locations. Hundreds of them were together in one group, and all were very active. Stones thrown at them did not cause them to alter their position. In the winter Banded Rattle-snakes congregate in a "den" which is often a fissure in the rocks, where they can hibernate without being disturbed by other animals, or injured by the cold.

AVES

Almost all birds are gregarious to some degree. Miller (1922) considers the Bush-tit of the Pacific Coast, a bird in which the gregarious instinct is highly developed, as one of the most successful species in its group.

Order Sphenisciformes

The form in which gregariousness is manifested by the Penguins is worthy of study. Observations by Gain (1912) show that the Macaroni Penguin (Catarrhactes chrysolophus) is found in rookeries of a few hundred individuals on the South Shetland Islands. The rookeries are often intermingled with those of the Antarctic Penguin with which it lives peaceably.

The Antarctic Penguin (Pygoscelis antarctica) lives in huge rookeries that include sometimes as many as several hundred thousands of individuals. Their rookeries not infrequently extend as high as a hundred meters on the rocks, and in order to reach the sea, the Penguins set out in little bands, in Indian file, following the paths they have worn in the snow. Their nests are protected by guardians who await the return of those who have been fishing before they set out in their turn for the sea.

The Adelie Penguin (Pygoscelis adeliae) according to Gain (1912), is the most abundant in the Antarctic, and settles in numerous rookeries during the period of breeding and the raising of their young. The Adelies abandon their rookeries for the winter, but gradually return in the early spring. Each day they are more numerous, until it is finally difficult for new comers to procure suitable stones, whereupon, they resort to attempts to steal them from neighboring nests.

Order Ciconiiformes

Habits of gregariousness have been observed in many groups under this order, of which the Gannets, Pelicans, and Cormorants and Flamingoes will be discussed.

Suborder Steganopodes.

Gannets nest in large quantities on the rocks at the seashore, for which reason these rocks are ordinarily known as Bird Rocks. A famous breeding place is Bass Rock at the Firth of Forth in Scotland.

Hegner (1935) has the following to say concerning them. "Upon reaching the Bass, a few Gannets may be seen sailing dreamily about, but you have no idea of the immense numbers until you have climbed the rugged hill. But when the summit of the cliff is reached, the scene that burst's upon one's gaze is one that well-nigh baffles all description. Thousands upon thousands of Gannets fill the air, just like heavy snowflakes, and on every side their loud harsh cries of "carra-carra-carra" echo and reecho among the rocks. The Gannets take very little notice of our approach, many birds allowing themselves to be actually pushed from their nests. Others utter harsh notes, and with flapping wings offer some show of resistance, only taking wing when absolutely compelled to do so, and disgorging one or two half-digested fishes as they fall lightly over the cliff into the air. On all sides facing the sea Gannets may be seen. Some are standing on the short grass on the edge of the cliffs, fast asleep,

with their heads buried under their dorsal plumage; others are preening their feathers; whilst many are quarreling and fighting over standing-room on the rocks."

The Pelicans are gregarious in their nesting, and show a remarkable trait in their method of fishing. A flock of birds, according to Friedmann (1935), fly out to a likely place and then form a large circle, thus surrounding a school of fish. They then begin to close in and as the fish swim together in denser and denser masses, the birds begin scooping them up from all sides. At other times these birds make a semicircle and gradually drive the fish shorewards into shallower water where they become an easy prey to the birds. The nesting colonies are remarkably free from quarrels and confusion.

According to the same author the size of some of the Cormorant colonies is enormous. On the Chincha Islands of Peru, ^{Friedmann found that} about fifteen acres of ground were covered with Cormorant nests. The nests were very uniformly spaced, and not an available meter of ground within the outside limits of the rookery was unoccupied.

Suborder Phoenicopteriformes

Johnson (1931) found Flamingoes nesting in large groups in which there were estimated to be as many as two thousand birds. One of the most beautiful spectacles to be seen, so far as companies of animals go is a flock of Flamingoes when they make a rose-pink cloud above the shallow water where they stand.

Order Anseriformes

Wild Ducks and Geese are easily domesticated, but when time for migration arrives, they will join the flocks that fly overhead unless their wings are clipped, a precaution in which the writer has taken part. These birds love to congregate in grain fields, and are known to have sentinels ^{which} warn the flock of approaching danger.

Order Galliformes

← According to Allen (1925)
Our Quail, or Bobwhite, as this bird is more popularly called, is extremely gregarious, living throughout the winter with others of his kind in coveys. At night the covey roosts together in shrubbery or under an evergreen tree in a close circle with their heads facing outward.

Order Charadriiformes

Among the suborders in this group we find much evidence of gregariousness. It is best illustrated by the Sandpipers, Gulls, and Auks, and Murres.

Suborder Limicolae

According to Allen (1925) flocks of Sandpipers in migration are quite often dense and swift. In their maneuvers, they twist and turn all in unison so that one moment the entire company flashes white in the sun and then darkens again when they all turn their backs toward the observer. In alighting, those that follow are apt to pass over those already down and alight farther on, so that their whole action is like the waving of a great scarf.

Suborder Laridae

The gregarious habits of the Gulls are interesting because they are so easily observed. The writer is extremely fond of Sea Gulls and scarcely ever loses an opportunity in which to observe them. Rarely is one of these birds seen soaring gracefully above the water in solitude. As a rule, several, flying close together, wheel about the sky in company, even when no immediate

supply of food is apparent. The Mormons have a special affection for Sea Gulls, because in the early days, when their precious crops were threatened by hordes of locusts, thousands of Gulls appeared as though heaven-sent, and devoured them.

The gregariousness of Gulls can be seen in their preference for certain roof-tops, and their aversion to others. In North Haven, Maine, the writer has watched them perched in a string along the peak of some roof on a dock shed at the water's edge, solemnly facing the wind. Although other roofs were apparently as favorable, the birds always crowded together on one or two roof-tops and ignored the others. They always face the wind. Their gregariousness leads them to collect at one end of a sand-bar or break-water when apparently there is no "choice" spot on either place.

Suborder Alcae

The Great Auk became extinct about 1850. According to Hegner (1935), large numbers used to nest on the coast and islands of the North Atlantic, where sailors collected them by the thousands when they needed fresh meat.

According to Pearson (1936), the California Murre

congregates in large numbers on rocky shores. There seems to be no reason why they should crowd so closely together. The spirit of neighborliness that is evident in the case of the Penguins seems to be lacking among the Murre, for they continually quarrel and spar with their sharp bills.

Order Coraciiformes

Another Order of Aves which has been described as gregarious is the Order Coraciiformes. To this group belong the Chimney Swifts, great gatherings of which occur as they congregate in late summer preparatory to migration. Blanchan (1923) and Allen (1925) have observed hundreds of them flying around a tall chimney in a funnel-shaped flock, and one by one, as they reached the point of the funnel, raising their wings and dropping into the chimney for the night. They sleep clinging to the rough surface, supported by their spiny tails. Other species of Swifts actually cling to one another as bees do when swarming.

Order Passeriformes

It is a generally known fact that the gregarious habit is highly developed among the Passeriformes.

Rooks, Crows, Ravens, and Purple Grackles, according to Blanchan (1923) and Allen (1925), are extremely gregarious. The Purple Grackle is described by Blanchan as a "gregarious bird of the first order", travelling in immense flocks of its own kind.

Starlings, Allen (1925) reports, are very gregarious and frequent fallow fields, pastures, and meadows, often in company with the Rook. After the young are able to care for themselves, they congregate with the parents in vast numbers which resort each evening to some chosen resting place, where they congregate in tens and even hundreds of thousands, resembling a gigantic black cloud.

The gregariousness of the Cowbird cannot be disputed, since a peculiar situation arises. In a certain species of Cowbird, the females deposit their eggs in the nests of some other birds and leave them to be cared for by that bird. When able to fly, these young Cowbirds, according to Blanchan (1923) and Friedman (1929), reared by foster-mothers of different species, join the well-known Cowbird flocks. Such flocks have no family ties and can form only by the coming together of individuals which are total strangers to one another.

Allen (1925) has observed that a group of Martins will join together for their mutual protection and drive away hawks and crows that might molest them and their young, and, incidently, protect the property of the farmer wise enough to provide a nesting^{place} for them.

Blanchan (1923) found that after rearing^{several} broods, Bluebirds congregate in small groups in pastures, stumpy fields, and cleared woods, and seem loath to leave, but finally depart for their winter home.

Observations by Howard (1929) show that from September to early February the behavior of the Reed-Bunting is determined partly by the attraction of the flock. In search of companions small parties wander forth, and associating with other species, form composite flocks which drift from place to place as the food supply changes. At night^{these} composite flocks split up and the different units retire to roost.

House Sparrows often sleep in small trees on Boston Common. On a winter's night a dozen or more may be seen perched along the branches. In Bridgeport, Connecticut, the writer has observed sparrows that gather nightly on the eaves of a certain building in the shopping district. Their incessant chatter

keeps on until late at night. During the day they may be seen perched along the wires overhead, but as darkness comes on, they retire to the eaves where they continue their noise.

Thomson (1926) explains that gregariousness is the characteristic feature of the migration of a majority of species of birds, including many of those which show in special degree the tendency to be solitary in the breeding season and hostile to all intruders on the chosen territory of the pair. Many species customarily migrate in flocks. Birds of prey and raptors are among the best examples of habitually non-gregarious migrants, although even in these cases small parties may at times be formed.

The flocks formed by gregarious migrants, Thomson has found, vary in size. Geese often migrate in what appear to be small family groups. Many small Passerines and Timicoline species commonly travel in small bands of from twenty to fifty birds, but larger flocks may be formed. Flocks of hundreds or more are common in the case of the Hooded Crow, the Starling, and other birds. Storks and Cranes are sometimes seen in thousands. No rule can be stated, but some species seem to

show a greater tendency than others to form very large flocks. On migrating, different species often fly in company in mixed flocks, as in the case of Rooks and Jackdaws, or of Swallows and House Martins.

MAMMALIA

Gregariousness is an almost universal phenomenon among the Mammals, the question being whether there is any Mammal that is not gregarious.

Order Cetacea

Many Whales are gregarious and follow a leader just as sheep do, so that if one gets stranded by venturing too close to a shelving shore, the chances are that the whole "school" will share its fate. Daghish(1931)reports that in one case a large school of more than one hundred whales became stranded in a shallow bay not far from Cape Town. They lay about helplessly for some days, and some of them took nearly a week to die. A similar incident occurred when a school of Pilot Whales ran ashore in Mount's Bay, Cornwall.

Sperm Whales roam about in tropical and sub-tropical seas. When caught, they are found to be males, according to the same author, and it is supposed that they are young or very old members of a herd

that have been driven away by the stronger bulls.

The black-fish - a kind of whale - which roams the ocean in large companies comprising as many as a thousand individuals, rush blindly after their leader no matter what mischance may overtake him, Daglish (1931) reports. Should he swim into a patch of water so shallow that he is stranded and unable to escape, the whole band will accompany their leader to share his misfortune.

The Killer Whale usually travels in schools or packs from three to a dozen or more individuals. Unlike most whales, the members of these schools do not travel in a straggling party, but swim side by side, according to Stone and Cram (1922).

The writer has seen many schools of Porpoises and believes them to be responsible for the stories of sea-serpent, since the motion of the Porpoises as they rise one after another above the water and sink out of sight again is not unlike the gliding movement of the coils of a great serpent. Porpoises always travel in schools, keeping close together and sporting and frolicking as they swim.

Order Ungulata

Johnson (1931) has made some interesting observations regarding the Ungulates. He has found that Elephant bulls live a solitary existence a large part of the year, but when migrating in search of food, they all join together in herds of a few to a hundred or more. Females may travel in groups, and are always in the company of their offspring.

Musk Oxen and Chamois, Johnson relates, are gregarious and travel about in herds of a dozen or more. When attacked by wolves, they form a circle with their heads pointed outward, that no wolf can hope to penetrate.

According to Heape (1931), after the mating season the males of the American Elk collect in large bands and as winter advances, they descend to the feeding grounds in the lowlands. In the spring they scatter. In May the hinds leave the herd to give birth to the young.

Heape describes the behavior of Caribou and Black-tailed Deer as gregarious. During the summer the bulls of the Caribou gang away by themselves, not associating with the cows and calves, but as winter approaches, they congregate in herds again. Formerly the herds frequently contained hundreds of thousands of Caribou, but are now

much smaller, due to widespread destruction by white men with guns.

The same author explains that during the winter the Black -tailed Deer congregate in good-sized bands, but when the snow melts in the spring and the animals are free to move about, they scatter and are usually seen as individuals or in small groups of two or three. In the summer the bucks and does do not mingle, but the sexes keep by themselves. The bucks may be found in small bands of ten or more.

Johnson (1931) describes Water Bucks as living in small herds which are to be found in hilly country near water. The females keep constantly on the alert for possible danger, which they recognize by means of their keen sense of smell and hearing.

Order Rodentia

The best example of gregariousness among the Rodents is the Prairie Dog. According to Hegner (1935) this animal is extremely gregarious. Companionship is necessary for their happiness, and groups form colonies which extend from a few acres to many miles, and are scattered through the plains country. One group has been reported from

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Texas that covered an area one hundred miles wide and two hundred fifty miles long, and has been estimated to contain four hundred million Prairie Dogs.

Order Chiroptera

Bats are exceedingly gregarious and are fairly well-known for their gigantic numbers in caves or barns where they sleep.

According to Hegner (1935) Fruit-eating Bats are gregarious in habit. They have no tail and may reach a wing-spread of five feet. They congregate at night in large numbers in orchards, searching for fruit. At night or on a dull day, the individuals making up these flocks wake up and perform extraordinary antics, engaging in fierce arguments with each other. Their fights to secure the most comfortable places from which to hang are responsible for a great uproar.

Allen (1921) reported a few interesting experiments in banding bats. The only ones he found nesting in colonies were the Little Brown Bats and the Pipistrelle, the former occurring during the breeding season in groups often of several hundreds, in dark attics and cupolas, while the latter usually roost in small clusters.

The largest he has ever seen contained eighteen individuals.

At one time Allen was called to observe a cluster of four Bats in the dark corner of a porch. To determine whether it was always the same Bats that came back each summer, or whether it was a roosting place known to many Bats, Allen captured and banded the Bats. Three years later he was informed that Bats were again in the corner of the porch. Allen secured the Bats, of which there were again four, and three of them bore the bands he had put on three years before.

Discovering a cluster of eighteen Pipistrelles clinging to the gable of his barn, Allen captured and banded each Bat. Most of them returned to the barn sooner or later. The young were born, and a month later Allen captured ten adults and sixteen young, nine of the adults bearing the bands that had been placed upon them the previous month.

The Small Brown Bat has been found in congregations composed chiefly of adult females and nearly grown young. Allen believes that while the sexes are normally about an equal number, they segregate during the season of

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gestation and care of the young. The presence of males may indicate that the males rejoin their mates for a short time between litters.

Order Carnivora

Wolves and Seals are the best examples of gregariousness among the Carnivores.

Suborder Fissipedia

Johnson (1931) observed a group of wild dogs sunning themselves peacefully in front of a wooded donga on one of his trips into the interior of Africa. These brown and white animals are notoriously wild and they hunt in packs. The dogs were apparently little concerned as Johnson ground out foot after foot of film. Suddenly a line of giraffes appeared out of the donga behind the pack. The dogs leaped to their feet, wheeled about and raced away in mad pursuit of the herd.

Suborder Pinnepedia

Seals, according to Daghish (1931), range the North Pacific in herds for seven or eight months of the year, hunting mainly for squids and different kinds of octopi that are in great abundance in the ocean. In

the spring they turn towards the California coast. The adult males land first, and then follow the younger males and females. The beaches soon swarm with them. Each of the older and stronger males gathers about himself a varying number of females and keeps guard over them. The younger males form separate rookeries of their own.

The writer has observed that Seals in Penobscot Bay, Maine, tend to occupy the rocks on which other Seals are sunning themselves, and thus many apparently equally favorable rocks are left unoccupied.

Order Primates

Monkeys and Apes, coming close to Man in the system of classification used here, are all gregarious.

According to Carpenter (1934), White-faced Capuchin travel about in groups. The troops consist of thirty or more individuals which travel in single file. When the foremost of the group reaches the outer branches of an unusually lofty tree, it springs forward into the air without a moment's hesitation and alights in the yielding foliage belonging to the neighboring tree, maybe fifty feet beneath, all the rest of the group following its example.

Baboons, Zuckerman (1932) relates, are gregarious, going about in small groups. This habit helps to make it possible for them to live on the ground in the same surroundings with such Carnivores as lions, leopards and hyenas. The old male baboon in his prime is ready to fight anything that threatens his troop.

Carpenter (1934) found Howling Monkeys to be extremely gregarious. They form clans which may be composed of several sub-groups. That the tendency in Howlers to group is strong is shown by the fact that when forced to choose between continued feeding and following the group, a Howler will join the group. There seems to be no one leader of a clan. In conditions where there is a network of arboreal pathways or a lack of clearly defined routes, much exploratory "random" searching is shown. Each male of the clan participates as a rule. When a male finds a suitable route, he gives deep clucking vocalizations; the females and young begin to follow him closely, and associated males cease their exploratory behavior and fall in line with the moving column of animals. If the controlling animal stops, progression ceases until he resumes his locomotion. New clans are formed by sub-groups which have

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split off from parental groups.

Hartmann (1880), Yerkes (1929), and Johnson (1931) agree that the Gorilla is gregarious. They live in bands of twenty to thirty individuals. Apparently these are not family groups, since there may be more than one adult male present. Yerkes writes of them: "The gregariousness of the Gorilla implies a measure of sociability, but the habits and habitat of the animal render naturalistic observation of social relations extremely difficult, and little indeed is known about this aspect of life in freedom".

Bingham (1932) on the other hand, reports from actual observation: "Responses of individual gorillas within the group were by no means stereotyped. They were not uniform throughout the band or troop and they were not constant from group to group, but there was in each instance a social homogeneity that suggested leadership and discipline. Individuals, and possibly subordinate units in the whole troop, seemed to adapt one to another under different circumstances and with varying degrees of confusion and appropriateness. Whether or not there was round-about translocation in the temporary division of the gorilla group at the termination of the

100 hour trail, there was convincing evidence of re-adjustment that kept the society together. If it represented an initial maladjustment there were connections which followed."

Bingham goes on to say, "There were other indications of adjustment among the subordinate members of the group that seemed to involve in the same situations both imagination and affective processes. Varied and modified chest beating with vocalizations and exploratory translocations by some, seemingly playful demonstrations by others and lethargy in another group, all took place simultaneously or in appropriate succession. Decisive changes also occurred within the group as a whole. There were abrupt reversals by individuals between exhibitions of aggression and silent retreat. The observed groups regularly withdrew in a padded silence and there were observations of individuals in the file who looked back over their shoulders as though slinking away."

Bingham points out that the gray-haired leaders of two different groups appeared to concentrate on opposite aspects of the social environment. The one seemed to concentrate entirely on the task of retiring with eight gorillas. The leadership in the other

seemed to rely on established discipline among twenty-two gorillas and to use a variety of devices for sizing up the human observers.

A Digest of the Thesis --- Gregariousness
in the Animal World

This thesis represents an attempt to trace gregariousness throughout the animal world. The lowest form of life in which gregariousness is found is in the "Sea Butterflies". These tiny creatures form immense aggregations in the sea. Isopods show a definite-tendency to attract each other, since when one Isopod comes to rest, the others eventually come to rest near it, forming a close aggregation by which not all the available space is occupied.

Among the Insecta, the most spectacular, and probably the best-known form of gregariousness is to be found in gigantic swarms of Locusts. Uvarov (1928) has explained these migrations entirely on the basis of gregariousness, believing that attempts on the part of the Locusts to keep as close as possible to each other produces continuous stimuli, thereby resulting in continuous progression.

Among the fishes, schooling is a "sense" that is

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highly developed. The apparently permanent schools are characterized by great stability through the most varied of conditions, dispersing only under the influence of rather violent stimuli. Parr (1927) believes that the schooling of fishes is based on purely visual stimuli.

Almost all birds are gregarious to some degree. Miller (1922) believes that the bird in which the gregarious "instinct" is most highly developed is the most successful species in its group. The flocking of Cowbirds can be explained on no basis other than gregariousness, for these birds are reared by foster-parents, and therefore have no recognition of their true parents, and no family ties. Yet, as soon as they have become old enough, young cowbirds join a flock of their own species, where they remain throughout their lives.

The characteristic grouping of Ungulates is a sight which is familiar to almost everyone. Herds and packs are formed by various species, in which there are leaders, sentinels, signals, and some degree of group cooperation.

Among the Primates gregariousness is extremely

well-developed, there being, again, group leaders, sentinels, signals, and varying degrees of cooperation. There are indications of adjustment among the subordinate members of the group, and an attempt toward an established discipline, especially among the gorillas.

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