foreground. The flock resting upon the water is composed mainly of Canvas-backs (*Marila valisineria*), a deep water species that feeds but little upon land.

These birds arrive about October of each year. After the close of the shooting season they begin to scatter, for, with general protection elsewhere there is no longer need of congregation within this sanctuary; so that the ducks cease to be a conspicuous feature of Lake Merritt some time before their departure for distant breeding grounds.

Oakland, California, February 14, 1917.

Fig. 35. Same flock as in figs. 33 and 34. There is a limit to the trustfulness of even very tame wild ducks and phlegmatic mudhens.

SOME FACTORS INVOLVED IN THE NESTING HABIT OF BIRDS

By CLARENCE HAMILTON KENNEDY

WITH TWELVE DRAWINGS BY THE AUTHOR

ONE OF the most interesting series of problems in ornithology is that connected with the high development of the nesting habit in birds. But little has been done to correlate bird anatomy and nesting habits, or even to figure out the causes leading to the great diversity of nests which birds build, for when the present writer wished to look up some obscure points on the nesting habits in this group, great was his surprise that in a group so thoroughly worked, so little had been done in the study of nidification other than the mere collection of data on the nesting habits of individual species. No group in the animal kingdom has been so thoroughly worked as that of the birds, yet the attempts to figure out the biological reasons for the various developments in nidification are comprised in a few pages of printed matter. A. R. Wallace has given an interesting theory of the relation of the nest to the coloration of the species building it, in his "Theory of Birds' Nests" (Journal of Travel and Natural History, 1868). This has been discussed and criticised by Dr. J. A. Allen, in the Bulletin of The Nuttall Ornithological Club. A few limited and cursory discussions of various phases of the subject are given in various general works such as Knowlton's "Birds of the World", but no extended study of the subject has been made.

Just why the individuals of one generation of a given species in the animal kingdom should occupy themselves in any manner with the rearing of the succeeding generations is a philosophical enigma, for after the production and fertilization of the egg no physical necessity of their own is satisfied by it. Nevertheless we find the beginnings of such care even among the lowest animals.

Nidification first appears in the vertebrates among the aquatic forms, for among fishes the little stickleback and the pugnacious sunfish guard their nests with great fearlessness, while the humble bullhead, after the eggs are hatched, may be seen leading his dusky young about as they learn the business of fish life. Fish nests are usually very simple affairs, being seldom more than shallow basins in the stream bottom, but when we get among the higher vertebrates we find more ambitious structures. For among all vertebrates the nest has reached its most elaborate development with man, though in the other great group of warm-blooded vertebrates, the birds, it has reached a development in which many nests show a wonderful ingenuity and exquisite care in construction.

The nesting habit among birds is probably anticipated by the nesting habits which are found among reptiles, as from the ancient reptilian group of Dinosaurs have probably arisen our modern birds. The nesting habits of the higher modern reptiles and some of the more primitive birds are so similar that they can be said to bridge over the gap from the slovenly nidification of the average indifferent reptile to that solicitous care of the young characteristic of the highest birds. Many of the modern snakes deposit their eggs in holes in the ground or in the soft wood of rotten stumps, and turtles dig jug-like holes in the sand. Some tropical alligators deposit their eggs in warm sandbanks, while those found in the cooler latitude of the southern states bring together a mass of rotting vegetation, by the warmth of which the eggs are hatched, after which the young are guarded for a time by the mother. Now this method of nesting occurs among some of the lower birds, though here it is a reversion from, or more probably a special development of, the general bird type. The interesting fowls which have this primitive nesting habit are the Megapodes of the Australian region. Of these, the Australian Brush Turkey (*Catheturus lathami*) rakes together a pile of decaying leaves and rotten wood, and in this mound at intervals deposits its eggs, which are incubated by the heat from the decomposition of the nest materials. Other members of this same curious group deposit their eggs in the warm sands of the sea shore, where they are left without further care.

Similar to this were probably the beginnings of the nesting habit among birds. Careful guarding of the eggs early developed into a definite period of incubation, which was made possible by the high temperature of the body. The development of the four-chambered heart meant the possibility of the great development of the brain, as this delicate organ was no longer poisoned by quantities of venous blood; then, with this increase in brain power, could come the dexterity and ingenuity displayed by the average bird in constructing his home.

We may add to the above factors some others, and discuss the series as follows:

1. Perhaps the first factor leading toward the care of eggs by the oviparous vertebrates is the reduction of the number of eggs in a clutch and the increase in the amount of yolk and food materials. This reduction in number, from the hundreds or thousands of eggs laid by the lower vertebrates to the few laid by the average reptile or bird, makes possible better care for the few. This decrease in number and increase in care already appears in the fishes. Here, however, the problem is complicated by the factors of environment, for the highly specialized pelagic mackerels strew their thousands of eggs uncared for on the surface of the sea, while the more primitive catfishes, using the opportunities afforded them by the stream beds, guard jealously in a nest the few hundred eggs they produce each season.

The vertebrate egg, denuded of food and protective envelopes, is a single cell, which in the chicken is but one twentieth of a millimeter in diameter. As such these cells occur in the ovary of the fowl. In the later development food in the form of yolk is added inside this cell until it may become more than an inch in diameter, then, during its passage down the oviduct, there are wrapped about it the nutritive envelopes of albumen and the fibrous and calcareous envelopes, which we know as the egg-shell. Fig. 36*a* shows the later development of the egg in the ovary, where yolk is being added to it, and the arrangement of the oviduct in which those parts other than the yolk are added. Fig. 36*b* shows a hen's egg in section in which the eye of the yolk is the only living part.

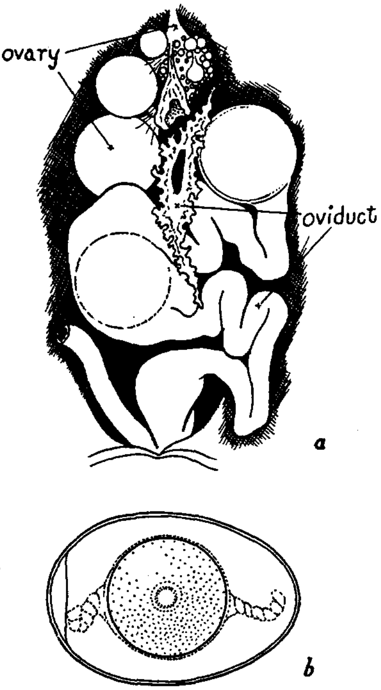

Fig. 36. *a.* OVARY AND OVIDUCT IN THE CHICKEN, SHOWING THE EGGS OF THE OVARY EACH IN ITS FOLLICULAR SAC WHERE IT IS ACQUIRING YOLK. BELOW THE OVARY THE GLANDULAR OVIDUCT, WHICH, WHILE THE EGG PASSES THROUGH IT, SECRETES AROUND THE EGG THE WHITE AND THE SHELL. *b.* DIAGRAM OF A HEN'S EGG IN WHICH THE "EYE" OF THE YOLK IS THE INCIPIENT EMBRYO, THE ONLY LIVING PART OF THE EGG.

2. Immediately associated with this increase in the amount of yolk material and the addition of the nutritive albumen is the development, first, of the fibrous, and then of the calcareous, shell. This hard shell was probably necessitated by the change of the reptilian ancestors from a semi-aquatic to a purely terrestrial environment, for the eggs then required such an impervious shell to protect them from dessication. As the results of a change are seldom simple, we find that the hard shell made possible more elaborate nests, and these placed in a greater variety of situations, as the developing embryo was then protected from mechanical injuries as well as from drying.

3. One of the greatest steps in advance towards avian nidification was the increase and stabilization of the body temperature. This probably occurred slowly as the birds became more and more differentiated from the reptiles. Indications of this slow increase still remain, as in Apteryx and others of the lowest

living birds the body temperature is at an average of from 5 to 10 degrees lower than in the more highly specialized forms such as our songbirds, where it may reach 111 degrees F. With this increase in temperature the guarding of the nest by the parents became more and more a definite act of incubation in which the heat was furnished by the body of the parent. Thus the hatching was speeded up and removed from the uncertainties of weather or the irregularities of decomposing vegetable matter. It is interesting to note at this point that the Megapodes, which leave their eggs to be incubated by the warm sand or by decaying vegetable matter, of which group I have already mentioned the Australian Brush Turkey, nearly all occupy islands in the Australian region where there are few or no small predaceous mammals. This style of nesting would be of little protection against such enemies, for the mounds are conspicuous, the eggs are relatively large, and incubation is slow. The heat is low and the young have to be advanced enough at hatching to burrow out of the sand or mass of debris and hustle a living for themselves at once. We might speculate that this simple form of nesting and those birds that practiced it have been eliminated in other parts of the world by some such enemy.

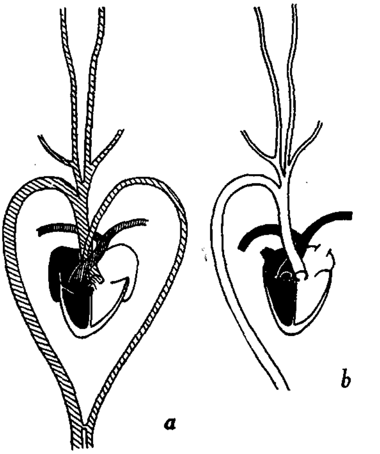

Fig. 37. *a*. CIRCULATORY SYSTEM IN THE ANTERIOR END OF A REPTILE, WITH THE MIXED VENOUS AND ARTERIAL BLOOD BATHING THE BRAIN. *b*. CIRCULATORY SYSTEM IN THE ANTERIOR END OF A BIRD, IN WHICH ONLY FRESH ARTERIAL BLOOD REACHES THE BRAIN.

4. A corollary to this increase in body temperature is the development of the reptilian scales as a whole or in part into the delicate fimbriated scales of birds which we know as feathers. These made a high body heat possible, and made the heat for incubation more reliable, as they helped cover the eggs. Incidentally they made flight possible in this group, and with flight the high development of arboreal nests so characteristic of the more specialized forms. Birds were probably evolved from the bipedal Dinosaurs and came into existence without that ability to climb which is the birthright of the small quadrupeds, where the possession of both fore and hind feet in a generalized form mechanically fits the owner for an arboreal life. Instead birds probably hopped awkwardly from limb to limb, flight at first being merely a lengthening of such leaps. The scansorial birds, such as woodpeckers, creepers, nuthatches, certain parrots and others, are highly specialized groups in which the climbing habit has been only recently redeveloped.

The preceding factors are especially associated with the actual incubation of the eggs. The succeeding are more immediately associated with the art of nest building itself.

5. Coming at this same time of transition, when the birds were differentiated from their reptilian ancestors, was the change in the heart from a three-chambered to a perfect four-chambered organ. Thus in the anterior end of the body were the venous and arterial bloods entirely separated. This great advance in the circulatory system meant that only the freshest and purest blood went to the brain, the delicate cells of this organ being stimulated and nourished by the

pure arterial blood, by which change was brought about the wonderful development of the brain in the warm-blooded vertebrates. With development of the brain could come the cleverness necessary to the building of the average bird nest. Fig. 37*a* shows the circulatory system in the anterior end of a reptile (crocodile), with the mixed venous and arterial blood bathing the brain, while in fig. 37*b* is shown the circulatory system in the anterior end of the bird, where only fresh arterial blood reaches the brain. Fig. 38 shows the difference in the development of the brain in the alligator (*a*) and in the bird (*b*). The main differences are the greater development of the cerebral hemispheres and the cerebellum in the bird. In the cerebral hemispheres are located all those centers which give to birds that greater intelligence which separates them at once from existing reptiles, while in the cerebellum are probably located those stores of great energy and centers of coördination that give the birds their intense activity and great cleverness.

6. As the anterior limbs of birds are highly specialized for flight, they must use for their actual nest building tools the mouth or the hind limbs. Many birds use both, though the bill is used most often, for the hind limbs are usually too highly specialized in their own way to admit of much use in nest building. In the use of the bill as a building tool lies the birds' one great handicap in ever developing nest building beyond what we see today. The great awkwardness that comes from having the eyes, which must gauge and judge the work, on the very base of the tool itself, will make impossible a much higher development of this art among birds. The most efficient tools are those such as the human hand, where the judging eye is undisturbed by the motions of the tool itself, and where the eye can, as it were, remain aloof and attend exclusively to the business of overseeing. In many groups of the animal kingdom correlations between the tools used and the work performed are very close, but in birds, adaptation of the bill to the work of nest building is only a secondary use for this organ, the main duty of which is that of food getting. Fig. 39 shows two bills, of the Bank Swallow (*a*) and of the Belted Kingfisher (*b*), which, while almost as dissimilar as any two bird bills can be, yet are used in constructing similar burrows in earth banks. The key to this difference lies in the adaptation of the two bills to the kinds of food used. The short and frail swallow bill is used to scoop up delicate insects on the wing, while that of the kingfisher is for seizing fish in the water.

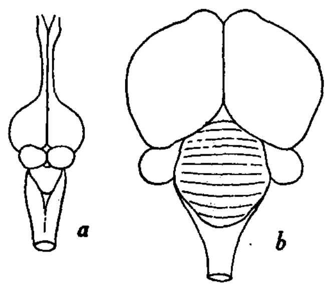

Fig. 38. *a*. Brain of the alligator showing the small cerebral hemispheres and small cerebellum. *b*. Brain of the golden eagle, showing the large cerebral hemispheres and cerebellum.

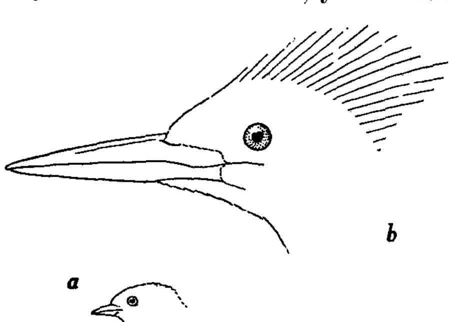

Fig. 39. *a*. Head of a Bank Swallow. *b*. Head of a Kingfisher.

7. The remaining factors in the development of the bird into a nest building animal, are those connected with the perfection of the bill as a nest building tool. Several minor developments may be grouped under this head,

of which the most important are those anatomical peculiarities, which give the bird a long and flexible neck. In birds there are generally more neck vertebrae than among many other vertebrates, and these are longer than usual and have remarkably flexible joints. Fig. 40 shows the articulatory surfaces of a crow's vertebra. These do not form a ball and socket joint, which theoretically would be the most flexible possible articulation, but each is convex in one direction and concave, or saddle-shaped, in the other. Several such joints in series make a neck as flexible as a similar number of ball and socket joints.

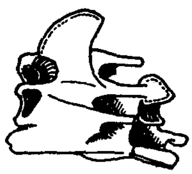

Fig. 40. NECK VERTEBRA OF CROW SHOWING THE SADDLE-SHAPED ARTICULATION.

Next to the flexibility of the neck as a factor in increasing the usefulness of the bill, is the rather flexible articulation of the mandible itself. In reptiles and birds an extra bone, the quadrate, is inserted between the articulatory tip of the mandibular ramus and the base of the cranium. This bone in the mammalia forms the incus of the middle ear according to a generally ac-

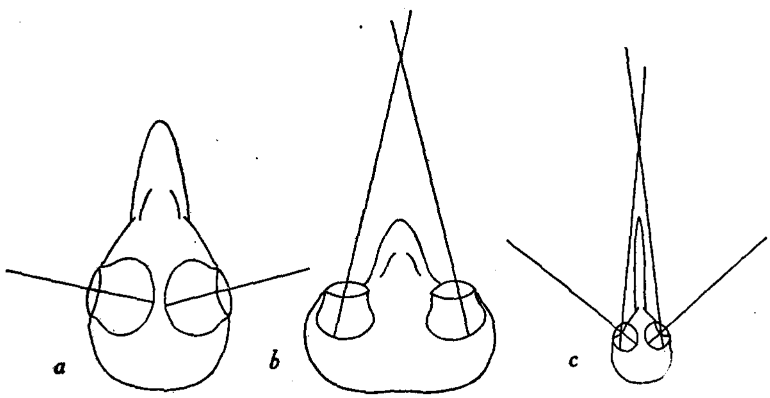

Fig. 41. *a*. DIAGRAM OF THE MONOCULAR VISION OF A CHICKEN. *b*. DIAGRAM OF THE BINOCULAR VISION OF AN OWL. *c*. DIAGRAM OF A HUMMINGBIRD'S HEAD. EACH EYE WITH TWO CENTERS OF ACUTE SIGHT GIVING BOTH MONOCULAR AND BINOCULAR VISION.

cepted view. In most reptiles the insertion of this quadrate in the articulation of the mandible makes a true double joint, but in the birds it is so firmly fused to the cranium that the hinge of the jaw lies between the quadrate and mandible. Nevertheless, the joint is perhaps freer, at least than in mammals, as it is farther removed from the base of the cranium.

With this, but of considerably more importance, is the length of the bill, which removes the grasping tip far enough from the eyes at its base to bring the work of the tip within the range of vision. As one result of this we find that the very finest nests are built by such birds as hummingbirds and the longer-billed insectivorous species, rather than by the conical-billed sparrows, whose nests are usually loosely constructed as compared with the nests of the preceding.

The smooth horniness of the bill, and the lack of teeth, are characters that permit the use of the bill as a shuttle or needle, making it an organ that can produce the beautiful woven nests of such forms as the orioles, or the interesting nests of the tailor bird, with leaves sewed about them. But even with these characters, the primary food getting use of the bill overshadows all else, so that we do not find that all birds with needle-like bills make compactly woven nests. This form of bill merely permits such use rather than absolutely conditioning it.

An anatomical device that perfects nest building in certain species is binocular vision. Not all birds are possessed of this, as the primitive condition among reptiles was probably monocular vision. The common hen of the poultry yard looks her friends or enemies over, first with one eye, then turning her head, checks her observations with the other eye. She is handicapped by monocular vision. Not so those birds that pursue active prey, for in the hawks, in the owls, in many predaceous sea fowl and in most insectivorous groups the two eyes work together, both focussing simultaneously on the same object, giving these fortunate ones that greatest privilege of the senses, binocular vision. As a general rule vegetable feeders among birds do not possess this. Now of the birds pursuing active prey, which possess binocular vision, those that produce the most cunningly constructed nests are found among the insectivorous forms, common examples of which are the bush-tits, hummingbirds and orioles. However, binocular vision does not necessarily carry with it exquisite nesting habits, because, as stated before, the bill is primarily adapted to food getting, so, when such vision is associated with a raptorial bill as in the hawks and owls, the form of the bill itself precludes delicate work in nest building. Other factors than the form of the bill also enter into the type of nest built by birds with binocular vision. For example, the Limicolae, with this type of sight, together with bills that could be used for any ordinary nest building, usually construct the merest excuses of nests, frequently not much more than a depression in the ground. In this case probably the terrestrial habits of the group control the form of nest, for on the solid ground there is not needed that unity of structure and thoroughness of execution essential to nests attached to swaying limbs many feet above the earth. Nests are meager constructions or entirely lacking in the case of many predaceous sea fowl, in some instances perhaps because of the hooked bill, in others because the nest is secondary to the nesting site. Food being the primary consideration in a bird's life, sea fowl frequently occupy cliffs and rocky islets, which, though swept by every storm, are close to their fishing grounds and free from predaceous mammals. Because of their exposure such places are usually barren of nesting material; in the birds inhabiting such homes we often find instead of a nest to retain the eggs, that the latter are obovoid to the extent of being almost conical to prevent them from rolling off the rocky ledges.

Such is a brief sketch of some of the factors involved in the nesting habit of birds. It is an interesting subject, and would prove a rich mine of biological material to one well enough acquainted with birds to make use of the great mass of available data.

Cornell University, Ithaca, New York, February 24, 1917.