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Social parasitism among insects and birds.

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BOSTON UNIVERSITY

GRADUATE SCHOOL

Thesis

SOCIAL PARASITISM AMONG INSECTS AND BIRDS

by

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A. Introduction

Parasitism is a common condition throughout the entire animal and plant kingdoms. For instance, the Conopidae, a family belonging to the Diptera, are known to be parasitic in the bodies of adult bees, wasps and ants. In ordinary parasitism the parasite belongs to a species which is not closely related to the host species.

Social parasitism, on the other hand, occurs only in connection with species which are closely related. It represents the parasitism of members of one species by members of the same or a closely related species, and may be either temporary or permanent.

In this thesis, the writer wishes to give a rather detailed résumé of what is known concerning social parasitism in insects and birds. We shall see how the social parasites of these very different orders possess the common habit of avoiding the task of raising their young by depositing their eggs in the nests of related species, which rear the parasitic brood.

B. Social Parasitism Among Insects

As regards the insects, social parasitism apparently occurs only in the Social Hymenoptera, i.e. the ants, wasps, and bees, and even here only in connection with certain species.

Among the ants, social parasitism may be divided into three forms: temporary social parasitism, permanent social parasitism and dulosis.

In the case of temporary social parasitism the queen seeks and obtains adoption in a small colony of another species and permits the alien workers to bring up her brood. In many instances she seeks a queenless colony but some times the host queen is present, in which case she must be destroyed. Her presence would afford a continual production of her own young such that her workers would neglect the progeny of the alien queen. Since the queen ant is really the reproductive organ of the colony, the elimination of the host queen may be said to castrate the colony, for its sterile workers are compelled to nurture the broods produced by the fertile parasitic member of the nest. The workers gradually die off and the parasitic queen and her offspring are left in possession of the nest, which is then a pure colony capable of independent growth and development. Furthermore, the nest exhibits not the slightest trace of anything that would indicate its parasitic origin.

Some of the most remarkable temporary social parasites are members of the genus Formica. Wheeler (1913) divides

the genus into two groups according to the size of the females in relation to the size of the workers: the microgynous Formicae, and the macrogynous Formicae. Although both of these groups are widely distributed and extremely common in certain localities, no one has ever seen one of the females establishing a colony independently. Some of the species, however, enlarge their colonies by the adoption of queens of the same species or even of different subspecies.

The microgynous Formicae embrace Formica rufa and its allies and are most abundantly represented in North America. In this group the females are a little larger, or sometimes even smaller, than the workers. F. difficilis and its variety consocians possess females that are as small as the large workers and, like other members of the rufa group, consocians is very pugnacious.

Consocians queens have been found associated with workers of Formica incerta, a rather cowardly ant whose workers are about the same size as the consocians queen. Wheeler (1913) inferred that these colonies must owe their origin to the adoption of consocians queens by incerta workers. He performed numerous experiments which left no doubt concerning the correctness of this inference. The following is an account of one of these experiments: "July 21, 4.30 P.M., an artificially dealated consocians female was placed in a nest

with twenty incerta workers and several worker cocoons taken from one of the most vigorous colonies found during the entire summer. The workers were unusually large and more like the workers of pure schaufussi, but with the coloration and pilosity of incerta. The female seemed discinclined to approach the workers, which were brooding over their cocoons, but she moved towards them when the illumination of the chamber was reversed. She was at once seized by a worker and showered with formic acid. She escaped to a corner of the nest. By 5.15 P.M. she had returned, mounted the pile of cocoons and was licking the workers, who were submitting to this treatment as if it were a matter of course. A few moments later she fed one of the workers and then kept alternating between feeding and caressing them with comical rapidity and perseverance. The colony was watched till 7.45 P.M., but no hostilities were seen. July 22, 7 A.M.: The previous night had been cold and the female seemed to have passed it hanging from the roof pane in a corner of the nest. Later, as it grew warmer, she returned to the incerta and their brood, caressed and fed the workers and took food from their lips. Only once during the day was a worker seen to tug for a few moments at one of her antennae. On the four following days (July 23 to 26) no hostilities were observed. The consocians female had been definitively adopted."

The size and structure of the parasitic females are particularly significant. They are yellow and about the same size as the incerta workers which are reddish-yellow. The tiny queen gains the favor of the incerta workers by her mimetic resemblance to them and by such conciliatory actions as licking and feeding. Once adopted, she lays her eggs and the larvae that hatch from them are reared by the incerta workers. Since the parasitic queen instinctively seeks out colonies which have no queen, or if she does enter a colony with a queen she becomes responsible for her host's elimination, she becomes the sole reproductive organ of the nest. In this way her workers are continually produced and the incerta gradually die of old age until the colony becomes pure and independent.

Other North American Formicae of the rufa group are: rasilis, impexa, nepticula, nevadensis, microgyna and dakotensis. All of these are known to have tiny females as small or even smaller than those of consocians, and to display habits similar to those of consocians. The diminutive size of the females is probably the result of the elimination of the necessity of nourishing their young with substances prepared from their own tissues. This, in turn, becomes a saving to their parental colony, for it is able to rear a much greater number of queens on a given amount of food than

can a colony rearing macrogynous females.

The macrogynous Formicae also include F. rufa and its allies. The typical European rufa with its subspecies, pratensis and truncicola, and the American subspecies obscuriventris, obscuripes, and integra, with several varieties, and the species ciliata, crinita, comata, dreas and specularis are members of this socially parasitic group. The fertilized females of these groups force different races and varieties of Serviformica fusca to adopt them.

The Formicae of the exsecta group are characterized by having the head of the worker and female deeply excised behind. In Europe this group is represented by the typical Formica exsecta, its subspecies pressilabris and suecica, and in North America by F. exsectoides, its subspecies opaciventris and F. ulkei. Formica exsectoides is our common mound-building ant, and is a successful temporary social parasite on F. fusca variety subsericea.

The Myrmicine ants, Aphaenogaster tennesseensis and probably A. Mariae, found their colonies with the aid of Aphaenogaster picea and rudis, varieties of fulva, one of most common ants in the Northern States. There is little doubt that the queens seek out the nests of fulva and start their colonies in them as does consocians in the nests of incerta. The fact that tennesseensis occurs only in localities where some form of fulva is abundant tends to bear

this out. Moreover, like consocians, the parasitic Aphaenogaster produce great numbers of small females whereas the non-parasitic Aphaenogaster are kept busy bringing up a few of their large queens. These ants have an interesting habit of migrating into old logs and stumps after the host workers have become extinct, and there, let the colony attain its full development.

Other colonies of temporary social parasites are composed of two species of Dolichoderine ants. Bothriomyrmex meridionalis and Tapinoma erraticum colonies have been found on the Borromean Islands and colonies of B. atlantis and T. nigerrimum have been observed in the Tunisian desert. In all cases the method of adoption and elimination of the female was the same. The Bothriomyrmex queen, after descending from her nuptial flight, wanders about on the ground until she is seized by the Tapinoma workers and dragged by her antennae and legs into the nest. Once in the nest she may be attacked from time to time by the workers, but she hides behind the brood or takes refuge on the back of the Tapinoma queen. Moreover, she purposely seeks out the queen, climbs on to her back, fixes her mandibles firmly into her neck, between the head and the pronotum, and thus decapitates her. By the time the Bothriomyrmex queen has accomplished the decapitation of her host she has acquired the nest odor and is adopted by the Tapinoma workers. She is now sole queen of the nest and lays

eggs which are reared by the Tapinoma workers. This continues until these workers die of old age and then the nest becomes a pure colony of Bothriomyrmex.

There is convincing evidence that all of the sub-ganus Oxygyne, including emmae, ebenina, soror, travancorensis, dalyi, aberrans, ranavolonae, agnetic, daisyi, marthae, and depressa from Madagascar, India and the Malayan region, are temporary parasites. Actual proof is lacking but various structural peculiarities of the Oxygyne queens point to this habit of parasitism. For instance, the curved and pointed mandibles, which are present in the queens but lacking in the workers, are comparable to those of the amazon ants and point to a method of assassinating the host queen similar to that employed by the Bothriomyrmex queen. Moreover, the queens are unusually small, but the gaster of the aged female becomes enormously enlarged and subspherical like that of the mother queens of the permanently parasitic Anergates.

There are more than a dozen genera of ants from various parts of the world which are known to be permanent social parasites. These ants live in the nests of other species after the host queens have been assassinated by their own workers. Moreover, they differ from other groups of social ant parasites in lacking a worker caste. In this respect they resemble the social parasites of the wasps and bees. The more common

permanent ant parasites are: Wheeleriella santchii, Symphei-dole pelecebra, Epipheidole inquilina, Epoicus pergandei, and Anergates atratulus.

The fertilized queens of Wheeleriella santchii, which lives in the nests of the common North African Monomorium salomonis, runs around on the ground until she finds a colony of the host species. She runs as quickly as possible to be able to make the nearest approach to the nest before the inhabitants come out and "arrest" her. She is generally "arrested" near the entrance of the nest and then taken by the legs and dragged into the nest. While this harsh treatment is going on, the W. santchii queen caresses the Monomorium workers. Once inside she wanders around the galleries unmolested and finally the workers begin to feed her and finally adopt her. She pays no attention to the Monomorium queen which is later killed by her own workers.

Anergates atratulus is the most specialized of these social ant parasites. It is found in every part of central and southern Europe, but its colonies are rare and very far apart. Its host is Tetramorium cespitum. Whenever these colonies are found, only the fertile Anergates queen, adult females and males, and some adult Tetramorium workers are in evidence. This queen mother of the colony is only a living ovary or egg-laying machine. Her gaster has become so

swollen, because of the enlargement of the ovaries, as to cause the abdominal segments to show as small black islands on a dull white background. This condition is brought about after the entrance into the Tetramorium nest.

The Anergates males are large grayish-yellow ants without wings. The virgin females are very small and black, and much more lively than the males. In fact, due to the apterous and sluggish condition of the male, mating takes place in the nest among the offspring of the same mother; a condition which Forel(1930) calls "adelphogamy." Both the male and female parasites are fed by the hosts, for they are quite unable to feed themselves. The males, however, are given much more attention than the females, and are often carried about and licked constantly.

Several experiments have been performed to ascertain the method whereby the Anergates female becomes associated with Tetramorium. It was found that in experimental nests, under unnatural conditions, the Anergates female was almost always amicably received. By introducing the queens into nests of Tetramorium in the field, varied results were obtained. In all cases, however, the behavior of the queens was very uniform. They sought out the nests of the host species as if they belonged to them, and if they were roughly handled they rolled up and feigned death. The response of the

colonies

Tetramorium to the intrusion of the Anergates queens, as has been pointed out, varied. As a rule, they treated the females with great leniency and, in some cases, carried them into the nests. The males, on the other hand, were rejected. It would seem that the acceptance of the parasites by Tetramorium, under natural conditions, is not as immediate as under conditions in the artificial nests. The fact that Anergates is so rare shows that permanent adoption is not easily brought about. If the enormous number of females produced in these scattered colonies in regions inhabited by innumerable Tetramorium colonies were easily adopted, T. cespitum would become rare if not extinct.

Anergates, the most specialized of all the permanent social parasites is thought to be a very degenerate dulotic ant as is suggested by the dwindling of the worker caste in Strongylognathus testaceus. Another theory is that they have arisen from the temporary social ant parasites. However, owing to their excessive specialization and loss of their worker caste, there is nothing in their structure to definitely determine whether they have arisen from temporarily parasitic or dulotic species.

In this connection Wheeler (1928) has the following to say: "The permanent parasites which have lost their worker caste are therefore really solitary insects and may be

regarded as symphiles. The enormous disparity between the abundance of parasites and that of their host, shows clearly that the former cannot owe their peculiarities to amical selection on the part of the latter, and the fact that the parasites actually castrate or lead to the castration of the colonies which they infest and never undertake the rearing of the male offspring of host workers, proves there can be no hereditory basis for the development of symphilic instincts on the part of the host species. As in the case of the myrmecophiles, the peculiar adaptions, both structural and behavioristic, to particular hosts, are therefore initiated and deviloped entirely by the social parasites themselves and there is nothing to indicate that these adaptions requiring fundamentally different biological explanations from those which have been advanced for countless cases of parasitism among solitary insects, other animals, or plants."

Another form of social ant parasitism is known as dulosis or slavery. The alliances between parasite and host are more permanently symbiotic than are those of the temporary parasites which are more or less transitory since they are formed as a means of establishing colonies which later become independent. Colonies formed by dulosis, with one or two exceptions, are the result of the adoption of the larvae and pupae of particular alien species after raids on their form-

icaries. Like the temporary social parasites, with the exception of Oxgyne, the slave-making ants are confined to the north temperate regions and extend far up into the boreal and alpine regions. Wheeler (1913) suggests that "it is not improbable that the development of the slave-making habit is connected in some way with the long, winters, short summers, and small amount of food in the subarctic belt."

All of the slave-makers occur in four genera: two genera of the Formicinae, Formica and Polyergus, and two genera of the Myrmicinae, Strongylognathus and Harpagoxenus. These groups represent three phylogenetic stages in the phenomenon of dulosis: first, the primitive stage in Formica; secondly, the culminating stage in Polyergus, and the degenerate stage in Strongylognathus. The habits of Harpagoxenus are little known but they are included in the last stage.

The typical species of the genus Formica, F. sanguinea, the sanguinary or blood-red slave-maker, which is common th throughout temperate Europe and northern Asia. This species, as well as the American sanguinea, can readily be distinguished from the other species of the genus by the pronounced notch im the clypeus so that the worker and queen look as if they were hare-lipped. Moreover, F. sanguinea is not an obligatory slave-maker for it is able to excavate a nest, secure its own food, and bring up its young without the aid of slaves.

Even

Even when the slaves are present the sanguinea workers do most of the work of the colonies. In fact, there is nothing to show that the slaves contribute anything more to the activities of the colony than would be carried out by the small sanguinea workers. The normal slaves of F. sanguinea are members of the fusca group, namely: glebaria, rubescens, gagates, rufibarbis and cinerea, and occasionally members of the rufa group are enslaved. It has been observed that the youngest colonies have the greatest number of slaves, while the old colonies may contain very few slaves, or, perhaps, none at all. In this respect the colonies bear some resemblance to those of the temporary parasites.

The slave-making expeditions take place in July and August after the marriage flight of the slave species. These expeditions, it must be remembered, are not of regular occurrence, but are limited to two or three a year. They generally begin in the morning from nine to eleven o'clock and last until mid-day, or even later. Ants leave the nest in troops and each troop when at a certain distance from the nest sends back emissaries to the nest to call out more workers. They take the most direct route possible but sometimes they are forced to turn aside because of some obstacle in their path. They proceed slowly and hesitate continually. At the very head of the column there is no one leader but

merely an ever-changing group of workers. In order to explain their direct advance to the nest of the slave species we must presuppose a high development of memory in those scouts which singly must have acquired the knowledge of the nest in sufficiently large numbers over a period of weeks to control the movements of the marching column. Furthermore, we must presuppose some form of communication to explain the common attack of only one nest out of many lying in different directions from the sanguinea nest.

No one has observed the sanguinea queen establishing her colony, but it is thought that these colonies of the facultative slave-makers arise either from adoption by some colony of the slave species, or that the sanguinea queen brings up, unaided, her own brood which can, by dulosis, continue to maintain the mixed character of the colony. Wheeler (1906), after experimenting in this connection, arrived at the conclusion that queens of the slave species are not allowed to live in the dulotic colonies of the sanguinea type. These colonies, in this way, resemble those of the temporary and permanent social ant parasites.

We come now to the consideration of the amazons or obligatory slave-makers. These ants belong to the genus Polyergus, whose distribution parallels that of Formica sanguinea. It has only one representative in Europe (P. rufescens)

there

whereas in North America there are at least four subspecies and a few undescribed varieties. These subspecies are: P. breviceps, ranging from the Rocky Mountains eastward to Illinois and Kansas; mexicanus in Mexico; bicolor, known only from Wisconsin and Illinois; and lucidus, ranging from the seaboard north of the Carolinas, to the eastern slopes of the Rocky Mountains.

The amazons, in spite of the long hours they pass in stolid idleness within the nest, display remarkable speed and untiring energy. Polyergus has been known to attack its enemies despite the fact that it was outnumbered, and to allow itself to be beheaded without retreating. It is said that no Polyergus ever runs away. The sickle-shaped mandibles, which are admirably adapted for piercing the enemy's armor, prevent the amazons from clinging to the legs of their adversaries so that they always fight face to face.

Polyergus usually sets out on its slave raids in the afternoon, somewhere between two and five o'clock. By seven the troop has always returned. As a rule, it consists of the majority of the amazons of the formicary. Just before the departure of the army an increasing number of ants may be seen walking about on their nest which they do not do in the morning. Shortly afterwards, the workers rush back into the nest, give the signal of departure by striking their companions' heads, and

they start out. Usually the guidance is left to the scouts which have been out since spring exploring potential slave species' nests. Once on their way they usually make straight for the colony to be plundered, but occasionally they lose their way and have to retrace their steps and start off in a different direction. They move forward in a compact mass at a high rate of speed. In fact, according to Forel (1930) if man were to move at such a pace, increased proportionally to his size, he would be walking as fast as a railway train of average speed travels.

The armies of Polyergus show a more perfected tactical organization, and the subjugation and plundering of slave colonies are effected with much greater dispatch and precisionthan those of the facultative slave-makers. In fact, they cause themilitaristic efforts of the sanguinary ants to appear clumsy and amatsurish. The amazons, therefore, represent a more specialized and perfected stage of the dulotic habit.

At the approach of this formidable army the workers of the slave species usually flee in dismay. Some, however, offer resistance and are promptly pierced in the head by the sickle-shaped mandibles of the amazon worker. The Polyergus army then enters the nest without delay, picks up the brood and starts a somewhat slower journey homeward. Sometimes

it does not enter the nest but merely drops its plunder at the nest opening where it is cared for by the slaves. The young emerging from this kidnapped brood excavate the nest, feed the Polyergus and bring up their brood, but never accompany the armies on their raids.

Because of the absence of domestic instincts, the amazons have been thought to be unable to establish colonies without the aid of slave workers. Numerous experiments have supported the theory that Polyergus can be easily adopted in Formica nests. In fact, a F. fusca queen received a Pol. rufescens queen amicably and failed to attack her as did the workers. They lived together for several weeks until one morning the fusca female was found dead. Apparently, the rufescens female, which had been adopted by the colony had pierced her head with her mandibles.

Wheeler (1913), however, got rather conflicting results in experiments with our American amazons. When her introduced artificially dealated queens into nests containing incerta workers with their brood, the queens behaved like sanguinea under similar conditions. They killed the alien workers, but paid absolutely no attention to the brood. In other cases they were more passive and conciliatory, but equally indifferent to the incerta cocoons. As a result, Wheeler explains that "it will be necessary, therefore to study this question further before making definite statements in regard to the method employed

by our American amazons in establishing colonies. But even if the method of rufescens should be found to obtain also in our subspecies, we should not be justified in deriving it from that of the temporary social parasites, for we might conceive it to have arisen secondarily by involution or degeneration from that employed by sanguinea."

The dulotic instincts have reached their culmination in development in Polyergus. At the same time, however, this ant is a social parasite on its host, the slaves. Moreover, it abounds in degenerate tendencies which in the further course of evolution are expected to become supreme so as to overwhelm and replace the predatory instincts. This

This brings us to the degenerate slave-makers which are all Myrmicinae, and, therefore, cannot be said to have arisen from sanguinea and Polyergus which are members of the Camponotine subfamily. However, these ants resemble the host species so closely that it is supposed that they have been derived from them. This supposition is open to doubt since the resemblance may be due to mimicry rather than to a true morphological relationship. The degenerate slave-makers include two genera, Strongylognathus and Harpagoxenus, which resemble Polyergus in some respects, but unlike Polyergus allow the queens of the host species to survive and reproduce in the colonies.

Strongylognathus alpinus, an Alpine species of these degenerate slave-makers, is particularly interesting. These ants are likely to make spontaneous slave raids which take place only at night. The slaves accompany their masters on these forays and together they form narrow, unbroken files which tend to connect the home-nest with the formicary to be raided. Once the pillaging begins, the alpinus prove to be less formidable than their slaves, Tetramorium cespitum, which do all the fighting. Apparently the slaves are really the masters in this case, and the Strongylognathus are taken along merely to disconcert or terrify the cespitum colonies whose brood they are bent on kidnapping.

While the slaves are fighting, the S. alpinus concern themselves mainly with the intimidation of the callows, but at the end they leave this to the slaves. Forel (1930) gives the following interesting description of one of these battles: "The fighting tactics of the alpinus were extremely comical. They prudently grasped hold of their enemies from behind, preferably by the thorax. Without doing them any serious harm, they obtained mastery over them by a notable tactic. The T. cespitum seized in this way would fold up its legs and the abdomens of the two ants would begin to tremble violently, especially that of the Tetramorium. The alpinus soon relaxed her hold and went away, as though overcome with disgust for ther-

cespitum, and also as though she had no other means of overawing this creature, which was at least as strong as herself." This curious fighting method of S. alpinus, which consists solely of intimidation, may facilitate their final alliance with the T. cespitum which they defeat. After the battle is over the slaves carry home the brood of their own species.

The genus Harpagoxenus embraces two known species, which are rare local ants closely allied to Leptothorax, the genus to which their hosts belong. One species, Harpagoxenus sublevis, is more or less confined to boreal Europe but has been found near Dresden where it lives in the nests of Leptothorax acervorum and muscorum, and occasionably L. tuberum. The slave-raiding expeditions and the return homeward have never been observed but it is thought that they raid colonies, as Polyergus does, and not to content itself with the brood of the ergatoid females. These ergatoid females form the principal sex in these colonies and it is they who found new nests by attacking L. acervorum or muscorum colonies alone or with the aid of companions. They drive out all the inhabitants and annex their nymphs of all sexes, which they rear as slaves. Often they cut off the wings of the males and possibly mate with them. Moreover, they often cut off the wings of virgin Leptothorax females as soon as they are hatched in order to make them slaves also.

The phenomenon of slavery may be said to resolve itself into a form of social parasitism in which the slaves are really the hosts. "These dulotic ants," says Wheeler (1905), "differ from the temporary and permanent parasites not only in the peculiarity of the worker instincts but also as representing parasites with a synthetic host. In other words, when they hatch the larvae and pupae from different nests of one or more varieties of Formica fusca or schaufussi, they are actually constructing a unitary colony out of the fragments of several colonies of the host species. This peculiarity, as I have shown, arises from the inheritance of female instincts which the worker slave-makers share with this caste in many other Formicidae."

If this interpretation of the dulotic instincts is correct we must admit that dulosis has grown out of temporary social parasitism and tends to form a permanent social parasitism through such a series as represented successively by Polyergus, Strongylognathus and Anergates. This interpretation is, in part, at variance with that of earlier authors who supposed that dulosis had grown out of abnormal mixed colonies.

Unlike the ants, comparatively little is known concerning the social parasites among the wasps. We know of only two parasitic species: Vespula adulterina (= Vespa arctica) and Vespula austriaca.

The rare wasp, Vespula adulterina, has been found as a social parasite in nests of Vespula arenaria (= diabolica), the common yellow-jacket. Like V. austriaca, it lacks a worker caste which suggests that it is parasitic. Moreover, no other species of Vespula shows this lack of the worker caste except these two: Vespula austriaca and V. adulterina

V. adulterina belongs to the Canadian and Upper Transition zones and instances of its appearance have been recorded in Connecticut and, more rarely, in eastern Massachusetts in the Forest Hills region. It is here that Wheeler and Taylor (1921) made their observations that confirm the contention of Fletcher that adulterina is a social parasite.

A nest of arenaria (= diabolica) was taken which contained about 62 workers of arenaria, a queen of the same species and a queen of adulterina. The upper and older comb contained the eggs of young larvae in diverse stages of development. Apparently the brood in this comb represented workers of arenaria.

The lower comb had a circle of 20 pupae of arenaria on one half its area, while the center of the other half was occupied by a clearly defined cluster of 11 extremely elongate cells, each of which contained remarkably large larvae. The remaining cells were small and short, containing eggs and very young larvae. Nearly all of the brood except the large

larvae, belonged to adulterina. It was evident from their size that they were carefully nurtured and their development favored by the arenaria workers.

The two queens, which were of the same size, showed that their wings had been mutilated. The apical halves of both wings of adulterina on the right side had been destroyed or bitten off. Wheeler and Taylor (1921) suggest that: "As both queens were still fresh when found in the nest on the morning of July 8 (the diabolica [= arenaria], when stimulated still moved her tarsi) we may infer that both were living together in the nest though probably not on the best terms, that the arctica [= adulterina] queen probably entered the nest just as the workers were beginning to build the second comb and oviposited in 11 of its cells, and that the resulting lafvae were being actively fed by the diabolica workers, because the parasites' wings were too much mutilated to permit her to leave the nest and forage."

Vespula adulterina is definitely a permanent social parasite in the nest of V. arenaria. Furthermore, it is probable that the over-wintering queen of adulterina appears late in spring when the nests of the host species are well enough established to contain workers to nurse her brood which consist mostly of males and fertile females. In some cases the adulterina queen is found living side by side with the arenaria

queen. At other times the host queen is not found. What becomes of her in cases of this sort is still a matter of conjecture. It is possible, however, that she voluntarily deserts the nest when the parasitic queen enters. She may even be killed by the parasitic queen or her own workers.

The only other known parasitic wasp is Vespula austriaca, which ranges over the entire Holarctic region where it shows a marked preference for higher altitudes up to 5,500 feet. It has been found as an inquiline in the nests of Vespula germanica, but shows a decided preference for V. rufa, to which it bears a remarkably close resemblance, In America it is found in nests of V. consobrina which is probably the American race of V. rufa.

A close kinship between austriaca and rufa is certain, for even the characters which distinguish one from the other tend to show a variation toward the other. It is probable that they have diverged from common stock in comparatively recent times, and that V. austriaca represents the ancestral stock of V. rufa, which shows a greater tendency to vary.

A small, paper-covered nest, suspended from grass roots and almost on the surface of the ground was taken and carefully described by Carpenter and Pack-Beresford (1903). The comb had two layers. The upper layer consisted of 16 to 18 central cells, all of which were empty. Around these were 60 to 70 capped cells and outside of these there was another belt

of cells. The cells in this belt were for the most part empty but a few were capped and later produced austriaca drones.

The lower layer of the comb was composed entirely of large cells, with the exception of an outside belt of about four cells deep, which contained larvae. Some of the cells in this area, moreover, were not finished. Next to these there was a ring of cells which contained 25 capped cells. Most of these capped cells contained queens. In the center of the comb were 18 empty cells.

The comb and its contents, together with several escaped austriaca males, one rufa male, five rufa workers, and an old austriaca queen with frayed wings and nearly hairless body, were put into an insect cage. The wasps were then supplied with honey and carefully watched. Of the results Carpenter and Pack-Beresford (1903) write: "During the next week or so queens and drones of the austriaca occasionally emerged from the capped cells, but on August 16th a drone emerged from one of the large cells in the lower comb, undoubtedly referable to rufa, but with the face yellow, except for a small central black dash, and with yellow spots on the scape of the antennae. In the course of the next day or two another rufa male, very similar, but with three small black dashes on the face exactly like those that characterize the austriaca queen, appeared and also a male, which was a typical rufa. On August 18th, to our great surprise, an apparently typical rufa emerged from the

layer of comb....."

From this study one can see that the structure and markings of V. rufa and V. austriaca demonstrate a very close relationship between the two. Moreover, Carpenter and Pack-Beres-ford infer that the old, hairless austriaca queen was the founder of the nest and that both the austriaca and rufa forms were her offspring. Wheeler and Taylor (1921),in this connection, state that "the evidence with which they (Carpenter and Pack-Beresford) support this inference seems to us to be very inconclusive. It is indeed surprising that such accomplished entomologists should have failed to take account of the habits of other parasitic Aculeata such as Psithyrus and the workerless ants which are all so much better known than the wasps they were studying.

Robson (1898),many years earlier, suggests that the parasitic habit in V. austriaca will probably be found to be correlated with some modification of structure. For example, Psithyrus, which he calls "a modified and degenerate Bombus,"" possesses no corbicula, the apparatus conveying the bee bread, nor the wax plate extractors or nippers. This loss prevents the Psithyrus from conveying food as well as disqualifying her for building cells. Consequently, Psithyrus is unable to rear her own young so she forces that occupation on the true Bombus.

In such a manner the Vespula austriaca queen may lack

some structure which would not enable her to build her nest a and live a normal life. At the same time Robson suggests that there may be some deterioration of the salivary glands which secrete saliva. This saliva is of primary importance in nest-building for without it paper-making is not possible. Therefore, without a nest the rearing of the brood is impossible, so the task is thrust upon other members of the group, namely, Vespula rufa. In this connection Robson has the following to say;"Hence, the parasitism of this wasp austriaca upon Vespa [= Vespula] rufa from whom one need scarcely question she has descended, and from whom she will probably be gradually differentiated more and more as a result of this different mode of life, is unavoidable. In her we have an example of a comparatively recent and modern differentiation or evolution of a species and genus, a genus, so far as I am aware, yet to be named and rightly founded on this difference in habit and constitution."

It is interesting to note that Carpenter and Pack-Beresford (1903) believe, to the contrary, that V. austriaca is the ancestral stock of rufa or that the inquiline is the ancestor the industrious ones. Saunders (1903) expresses the hope "that the inquiline bees might some day prove to be the ancestors of the industrious ones," but he adds: "There are so many points apparently distinctly in opposition to such a

theory, that I have never been able to see how it would work out." The great majority of writers, however, believe that austriaca bears the same relation to rufa as Psithyrus to Bombus: one of direct evolution from the host species.

In any case, both austriaca and adulterina were at one time non-parasitic like their hosts, but now their broods are reared by the workers of the species which nurture them as their own. As a result of such care, the parasitic stock has lost its worker caste and is represented only by males and fertile females. They have reverted, therefore, from a state of social independence with distinct female castes to the status of the solitary insects which also have a single type of female.

Among the bees, social parasitism is known to occur in at least two subfamilies, the Halictinae and the Bombinae. Various species of the Halictinae are victimized by certain species of the closely related genus Sphecodes.

The old Halictus female, as well as her daughters, violently resists the intrusion of the Sphecodes queen. Ferton (cf. Wheeler 1928) gives the following description of the encounter between a Sphecodes subquadratus and the"guard" at the nest entrance of Halictus malachurus: "Unable to seize the sentinel that obstructed the entrance with her head, she burrowed towards the bees' gallery and thus succeeded in seizing and killing the guardian and cast her backwardsout of

the tunnel. A second and then a third Halictus endeavoured to replace the first but met with the same fate." In some cases, however, the Sphecodes female is stung to death.

Once the Sphecodes has entered the nest of the host species she apparently destroys the eggs in the Halictus cells and lays her own in their place. In this way her larvae do not have to compete with the larvae of the lawful owners for the use of the stored pollen and nectar.

The most interesting social parasites among bees are the dozen or more species of bumblebees belonging to the genus Psithyrus (=Apathus). Psithyrus has long been known to breed in colonies of Bombus (=Bremus), the latter representing the nest-building bumblebees. Like the permanent social parasites of the ants these parasitic species lack a worker caste. It is easy to distinguish a Psithyrus female from a Bombus female by the former's lack of corbiculae or pollen baskets. Both sexes, however, so closely resemble the genus Bombus that anyone other than a specialist would see no difference between them.

The Psithyrus female, like the Bombus queen, hibernates alone but reappears later in the spring than the latter does. However, because of the lack of a pollen collecting apparatus, she is, unlike the Bombus queen, unable to found a colony of her own. Therefore, she must enter and secure adoption by a Bombus colony, usually after the first batch of workers have

emerged. The Bombus workers, then rear her larvae rather than their own. Let us now turn to a more detailed account of the behaviour of these "cuckoo" bees.

Once the Psithyrus queen has left her winter resting place, she starts a search for a Bombus colony. It has been suggested by Sladen (1912) that she is guided in her search by a remarkably keen olfactory sense. In support of this view Sladen (1912) suggested that Bombus lapidarius and B. terrestris have longer tunnels than other species in order to escape being parasitized. Plath (1934), however, has shown that, at least in our American species, these precautions are of no avail. He found a considerable number of nests of B. affinis and B. impatiens which were parasitized by Ps. laboriosus and Ps. ashtoni even though they had tunnels ranging from five to ten feet in length and also by the not infrequent appearance of Psithyrus females in Bombus colonies kept thirty feet above the ground. These experiences led him to believe, at first, that Psithyrus possessed a truely remarkable olfactory sense, until further observations and experiments suggested that it was not any keener than that of Bombus. "As early as the summer of 1921," he says, "I had noticed that females of Ps. laboriosus often appeared in the nests of my bimaculatus colonies and sometimes remained for several days without any serious objections on the part of the owners. In taking colonies of

this species, I have also repeatedly found a laboriosus female lodging in the nest, but since Ps. laboriosus apparently never breeds in the nests of B. bimaculatus, I have come to the conclusion that not infrequently one or more laboriosus females may know the location of a nest of this species, and use it merely as a kind of hotel. That this -- and not a keen olfactory sense -- is probably the correct explanation for the frequent appearance of laboriosus females while colonies of B. bimaculatus are being taken, is indirectly confirmed by the fact that not a single Psithyrus has ever appeared during the process of transferring nearly 175 nests belonging to other species."

Many times, admittance to a colony is not possible without a struggle, in which case, the Psithyrus female has the advantage over the individual members of the colony for she possesses a tougher integument and a stouter and more curved sting than her opponents, In fact, her integument is so thich that her adversaries are unable to penetrate it with their sting. But she is vulnerable in the neck, and because of this fact she is not always successful in entering the nest.

However, the Psithyrus queen sometimes gains admittance to a Bombus colony without being killed and may remain there the rest of her life. The attitude of the members of the host colony toward the alien queen differs with the various

species of Bombus. Plath (1934) observed a Psithyrus ashtoni and a Bombus affinis queen living together with no indication of antagonism. Moreover, during the two months they lived in this state, none of the other members of this Bombus-Psithyrus colony exhibited the slightest sign of hostility.

The behaviour of B. vagans and Ps. laboriosus toward each other, with the exception of the first three or four days, was the same as that of Ps. ashtoni and B. affinis. Of the peculiar behaviour of the laboriosus queen during these first few days in the nest, Plath (1934) has the following to say: "On the first day after the laboriosus female entered the nest, she seized nearly every worker with which she came in contact and rolled it toward the ventral side of her abdomen, making movements as if to sting her victim. This mauling lasted only a few seconds, when the worker, which in every case remained passive, was again released. In seizing the workers, both the mandibles and the first pair of legs were usually employed simultaneously, but on one occasion the Psithyrus first lifted a worker by the pile of its thorax with her mandibles and then rolled it below her body. None of the workers seemed to be any worse for this mauling. On the second day, the Psithyrus female only occasionally seized a worker and treated it in the manner described. These attacks upon the Bombus workers occured still less frequently on the following day, and thereafter no animosity was noticed between the Psithyrus female and the

vagans workers.

The attitude of B. impatiens toward a Psithyrus female is quite different from that of either B. bimaculatus or B. vagans. When the females are introduced into a colony of B. impatiens a great turmoil arises in the nest. Workers rush frantically about seeking the cause of the uproar, and once the Psithyrus queen is found, each worker attempts to sting her. The result is an agglomeration of workers about the poor creature which practically renders her helpless. Those unable to get at her seize their own nest mates with their mandibles and attempt to sting toward the Psithyrus queen in the center of the struggling mass. Some of these workers are killed.. Moreover,during the struggle the Psithyrus female vigorously opposes her adversaries with attempts to sting them, which,uâsiarule, results in several deaths.

Plath (1934) gives the following interesting description of a case where such a struggle ended quite differently under different conditions: "On July 24, 1921, nineteen workers of a colony of this species, which had been transferred to one of the Bussey buildings on the preceding day, were caught at the old nest-site and placed in a glass jar. A few minutes later, a female of Ps. laboriosus was discovered on some comb which had been left in the empty nest-cavity of a colony of B. fervidus. Just to see what would happen, the laboriosus female

was also placed in the jar. All the inmates, including the Psithyrus, were ill at ease, and tried to escape, but one or two of the workers nevertheless attacked the laboriosus female as soon as they came in contact with her. The latter now went on the warpath herself. She quickly seized one worker after another, whether attacked by them or not, rolled them below her abdomen and stung them to death. This done, she seemed to feel quite at home in the jar, and began to lap up the honey which was oozing from the bodies of her victims."

Now that we have seen that the attitude of the workers of the host colony toward the intruding queen varies with the species and the environment, we might ask how the host queen and the parasitic queen react toward one another. Sladen(1912) states that in the case of Psithyrus rupestris and Ps. vestalis the Psithyrus queen murders the host queen, after which the Bombus workers assume a hostile attitude toward their queen's murderer and await the opportunity to depose her. Sladen, in describing the preparations of the Psithyrus queen for her atrocious deed, says: "Her first care is to ingratiate herself with the inhabitants, and in this she succeeds so well that the workers soon cease to show any hostility towards her. Even the queen grows accustomed to the presence of the stranger, and her alarm disappears, but it is succeeded by a kind of despondency. Her interest and pleasure in her brood seem less,

and so depressed is she that one can fancy she has a presentiment of the fate that awaits her. It is by no means a cheerful family, and the gloom of impending disaster seems to hang over it."

But while the queen grows more dejected, the Psithyrus grows more lively, and takes an increasing interest in the comb, crawling about over it with unwonted alacrity, and examining it minutely." The queen, according to Sladen is eventually killed by the parasite which starts to lay her eggs.. The Bombus workers are soon reconciled to the strange larvae and rear them as their own brood.

It is difficult to determine which is the aggressor in this "duel of the queens", but Sladen (1912) suggests that it is probable that the Bombus queen starts the procedure as soon as she discovers that the Psithyrus female is about to lay,"an unpardonable fault in a member of her household at this early stage."

The assertion of Sladen that the Bombus queen is invariably killed by the Psithyrus female not only conflicts with the observations of Hoffer (cf. Sladen, 1912), another European authority on this subject, but also with those of Plath, an authority on our American Psithyri. Plath (1922), in this connection, tells of taking, June 26, 1922, a nest of Bombus vagans which contained,"(1) the old queen and about 40 workers of Bremus [= Bombus] vagans; and (2) a Psithyrus queen belong-

into the Laboriosus group." Another nest taken July 20, 1922 consisted of the old queen and 61 workers of Bombus, and a Psithyrus queen belonging to the Laboriosus group. A considerable number of Psithyrus males and several Psithyrus females were reared from one of these colonies.

When the Ps. laboriosus queen enters the nest of B. vagans she pays little or no attention to the Bombus queen. The latter, however, avoids the Psithyrus female whenever they meet for a period of a few days. Moreover, she turns the tip of her abdomen toward the intruder as if to ward off the attack. Such signs of animosity, however, gradually decrease until after the fourth or fifth day the two are reconciled to one another.

Sladen (1915), moreover, was later forced to admit the possibility of two queen living in an amicable relationship, for he asserts: "Ps. insularis does not apparently kill the Bombus queen, as I have found Ps. vestalis and rupestris do in England, but both females seem to live together in the nest, laying eggs..... This seems to be in accord with Hoffer's observations on Ps. campestris, the Old World representative of insularis. He found Ps. campestris living on good terms with its hosts B. agorum and helferanus, both queens producing young."

In regard to the actions of two Psithyrus queens which might meet in the same host colony Sladen (1912) has the following

to say: " I believe the Psithyrus queens do not kill one another, for I have never found a dead Psithyrus in a nest ruled by a Psithyrus. If several Psithyri find the same nest only one remains, although the others may make it their headquarters for a few days,....." Plath (1934), however, has prooved experimentally that this is not true of Psithyrus laboriosus. He placed two Ps. laboriosus females looking for bumblebee nests in a colony of B. bimaculatus. The results are vividly described as follows: "The two Psithyrus females usually attacked each other at once, and within a minute or two, sometimes even within a few seconds, one toppled over, mortally stung. Occasionally the second Psithyrus female tried to avoid a conflict by making a dash for the flight-hole as soon as she noticed the other Psithyrus. But if both females were in a pugnacious mood, they generally seized each other by one of the legs and endeavoured to use their stings. As soon as one had succeeded in accomplishing this, she attempted to extricate herself from the embrace of her vanquished foe. During these encounters it sometimes happened that legs were torn off, or that the dead Psithyrus had fastened her mandibles so firmly to one of the legs of the victor that the latter had to be released. Such a Psithyrus in turn was not infrequently killed a few minutes later by a third Psithyrus that was introduced into the nest."

Another interesting problem concerning the members of the genus Psithyrus is that of oviposition. Hoffer (cf. Plath, 1934), although never having observed Psithyrus ovipositing, expresses the opinion that the Psithyrus female lays her eggs in pollen masses in which Bombus eggs or larvae are already present. The Ps. laboriosus female, at least, does not exhibit the above habit, but has been observed by Plath (1934) building small cells from wax which she had gathered from Bombus cocoons. Later, as she laid each egg, she penetrated the wall of the cell with her sting. Before building the cell she had been seen tearing open a cell containing Bombus larvae so that they rolled out on the floor and were thrown out by the Bombus workers. These facts are important in connection with parasitism for they serve to refute Hoffer's suggestion that the Psithyrus larvae devour the larvae of their host.

Still another important consideration has to do with the similarity of size and coloration of Psithyri and their hosts. Hoffer (cf. Plath, 1934) believes that the European Psithyri which most closely resemble their Bombus hosts are those which parasitize Bombus species of the same size or perhaps larger than themselves; whereas, those which show the least resemblance victimize smaller Bombus species. This, according to Plath, does not apply to the American Psithyri. For instance, the queens of B. affinis are larger than those of Ps. ashtoni, and

yet there is little or no similarity in coloration between the parasite and host. The same is true of Ps. variabilis and B. americanorum. The queen of B. vagans, however, is smaller than her parasite Ps. laboriosus, and in this case, particular- between the Psithyrus male and host, there is a considerable degree of similarity.

The manner in which this permanent parasitic habit came about has been suggested as being the result of temporary social parasitism by Sladen (1912). He says, in this connection; "The origin of Psithyrus, more especially of its peculiar parasitic instincts, is an interesting question. If a specimen of Psithyrus be compared with a specimen of Bombus it is seen that the resemblance is not merely superficial but extends to nearly all the important details of structure, so that it is impossible to avoid the conclusion that Psithyrus has sprung from Bombus, and this at quite a recent period in the history of life. Moreover, the Bombi — and this is particularly interesting — show parasitical tendencies leading to the parasitism of Psithyrus. We have seen .... how the Bombus queens may enter the nests of their own species and kill one another, and how, in the case of the twin species, B. terrestris and lucorum, terrestris has extended this habit so as to prey on lucorum, killing the lucorum queen and getting the lucorum workers to rear her young in practically the same manner as the Psithyri

prey on the Bombi. It is a remarkable fact that the sting of the terrestris queen differs from that of the lucorum queen and approaches that of Psithyrus in being somewhat stouter and more curved, and having its thickened basal portion more parallel-sided when viewed sideways than in lucorum. There is, however, no evidence to show that any species of Psithyrus has sprung from the particular species of Bombus on which it preys, such resemblances as it may show to it in coat-colour, etc., being pretty clearly attributable to mimicry or exposure to the same conditions of life, and not to ancestry."

As Sladen points out, temporary social parasitism, as exemplified in the relations between B. terrestris and B. lucorum, may have been the original state leading to permanent social parasitism in the members of the genus Psithyrus. Psithyri, according to Lutz (1916), are "closely related to, and have been derived from the Bombidae by degeneration," and their parasitic habit originated in the temporary parasitic habits of their ancestors.

Similarly, permanent social parasitism among the ants, and probably among the wasps, may have originated from temporary social parasitism. For instance, as in the case of Bombus terrestris, queen ants of Formica consocians may not start colonies of their own, but may enter colonies of Formica incerta where they secure adoption and bring forth their brood which

is reared by the workers of the host species. In this way a mixed colony arises. The incerta workers gradually die off, while the parasitic queen keeps on laying eggs and producing more workers. The result is a pure colony of Formica consocians. Many other species of ants likewise form their own colonies by temporarily parasitizing other species, and it is but a step from this temporary social parasitism to permanent social parasitism.

C. Social Parasitism Among Birds

Social parasitism is also found among the birds and the condition is entirely comparable to that existing among the insects. Here again, the eggs are laid in a nest belonging to a member of some closely related species who then assumes the responsibility of hatching and bringing up the parasitic brood. The habit, however, is not nearly so common, being found in relatively few species of birds.

Formerly it was believed that the European cuckoo, Cuculus canorus, was the only bird having this peculiar habit. Less than two centuries ago, however, it was found that many cuckoos in Asia were also parasitic; but it was still supposed that the habit was limited to this one family of birds. Early in the last century it was discovered that the cowbird of North America, Molothrus ater, a bird belonging to an entirely different order, also possessed this peculiar habit. Later some of the neotropical cowbirds of southern South America were added to the list. Recently a South American Duck, Heteronetta atricapilla, or Black-headed Duck, was shown to have attained a state of social parasitism. South American Orioles known as Hang-nests, African Honey-guides, and the Weaver-birds, have but recently been added to this group of parasitic birds which constitutes but a very small portion of the thousands of kinds of birds known to science.

Therefore, at present, the parasitic breeding habit is

known to occur in five widely separated and distantly related families of birds--the Cowbirds (Icteridae), the Cuckoos (Cuculidae), the Weaver-birds (Ploceidae), the Honey-guides (Indicatoridae), and the Ducks (Anatidae). Of the family Icteridae, the Cowbirds and the closely related Rice Grackles, constituting about a half dozen species in all, are known to be parasitic; of the Cuculidae, about seventy species; of the Ploceidae, only three; of the Indicatoridae, or Honey-guides, less than half a dozen; and of the Anatidae, we have knowledge of but a single species.

Let us first consider the role of the Cowbird in the study of social parasitism in the bird world. The Cowbirds belong to three genera--Agelaioides, Molothrus, and Tangavius, of which the first is the most primitive.

The members of the genus Agelaioides, restricted to Argentina, Paraguay, Uruguay, and Brazil, are characterized as being "non-parasitic Cowbirds with short, rounded wings, no sexual plumage dimorphism, and no court-ship display." (Friedmann, 1929) This genus consists of two species--A. badius and A. fringillarus. A. badius, whose primaries according to Friedmann (1929) are of a "bright chestnut-brown, broadly tipped with fuscous", giving it its name, "Bay-winged Cowbird," is found in Argentina, Uruguay, Paraguay, Brazil, and Bolivia, and is generally restricted to the lowlands. Little is known concerning A. fringillarius, and since no field observations have ever been recorded and

few actual specimens collected, it is probable that it is a rare local bird. From the few specimens in the museums of the world, its geographical distribution has been determined to be restricted to eastern Brazil with a rather extensive coastal range. It is known as the Pale Cowbird since its primaries are dull olive brown, narrowly edged with pale chestnut. Its habits are very similar to those of its near relative, A. badius.

A. badius, or Bay winged Cowbird, has an important place in this treatise because it represents the most primitive species of the group, as well as the original condition of the ancestral cowbird family. These birds do not migrate in the winter, but wander about in small flocks until spring arrives. At that time they leave the flocks in pairs. Unlike the rest of the Cowbirds, there is no courtship display of any sort; simply a monogamous pairing off, giving no indication of polyandry.

These paired birds then look about for a nest, already built, as a suitable breeding place and, on finding one, they take possession of the nest. If the nest happens to be occupied at the time, the Cowbirds fight for possession of it. In this way, unlike other birds where the male establishes a "territory" in which he allows no other male to settle and from a "singing tree" announces to all the females that he wants a mate, both the female and male Cowbirds mutually establish a "territory". Then, after the

capture, some part of the tree in which the nest happens to be becomes the favorite singing perch of the male. Even then, the female shares in the choice of this particular spot, which is selected after the capture of the nest.

This mutual establishment of the "territory" and of the "singing tree" has other manifestations as well. The "territory" is not established with a view to its promise of food supply as it is among other birds, but as a nest-site. Furthermore, instead of the "territory" being of basic interest, as it is among other birds, it is secondary to the nest among Bay-wings, and the female and male of this species vigorously defend the nest. This more theoretical "territory" leads toward a possible polyandry in the more highly evolved Molothrus and Tangavius.

These cowbirds show a decided preference in the choice of breeding nests, generally building in the nests of Lenateros (Anumbius) and Spinetails (Synallaxis) and to a lesser extent in those of Ovenbirds (Furnarius). The fact that the Bay-wings are the last of the Argentine land birds to breed assures an abundance of available nests. In fact, this late breeding season is probably due to the greater supply of nests, since earlier in the season available nests are fewer and the competition is greater.

Having decided on a nest, the Bay-wings defend their empty nests for some time before laying in them. During this time the female seems to be more belligerent and audacious in

the defense of the nest than after the eggs are laid. This also becomes a period of repair carried out by both the male and the female. The male, however, seems to do most of the work. The preparations for egg laying consist of throwing out any eggs or young of the previous occupant that happen to be present, and making a little addition to the lining of the nest, or perhaps only a rearrangement of the lining, or even enlarging the entrance. The repairs, however, are not extensive for the birds are idle during most of the two weeks in which they stand guard over the nest before laying in it.

If, however, they are unable to gain possession of a nest built by another bird, they build a rather creditable affair of their own. In this case it is always open and off the ground. Their favorite materials seem to be dead grass, straw, and occasionally feathers, horsehair, and mosses are used for linings. Furthermore, they are built fairly early in the season when the supply of ready built nests is less extensive. As I have stated above, both males and females possess the nest-building instinct, which is only brought to the fore when other means fail them or is manifested to a slight degree when repairing usurped nests.

After the nests have been renovated or completed, the females lay their dirty white, heavily mottled eggs which are usually five in number. After all the eggs have been

laid the females begin incubation and rear their young much as do normal nesting birds. In this connection Friedmann (1929) has the following to say: "In his earlier papers Hudson wrote that this species sometimes lays an egg now and then in nests of other birds and leaves them to be cared for by the foster parents. This is not the case. The Bay-wing is not parasitical at all and the eggs which misled Hudson were probably those of the Screaming Cowbird."

He goes on to say: "Hudson found that occasionally two or more females laid together in one nest. Allowing for the possibility that many of these extra eggs were not Bay-wing but Screaming Cowbird eggs, it is still possible that in some cases more than one female Bay-wing used the same nest. I have never found instances of this kind myself, and Senor Pablo Girard, a resident naturalist in Tucuman, tells me, that of sixty-six nests of the Bay-winged Cowbird found by him in the past twenty years he has never found eggs of two different Bay-wings together, but that every single nest contained eggs of the Screaming Cowbird as well as of the Bay-wing.....I feel that it is quite likely that once in a while two Bay-wings may lay together but that such instances are rather rare. The protecting instincts of the female are very weak and two may lay together because of this weakness." If this is true we have here the actual beginnings of the social parasitical brood habit.

Belonging to the genus Molothrus are the typical

parasitic Cowbirds with long, pointed wings, and dark plumaged males. To this genus belong three species with many races--M. rufo-axillaris, or the Screaming Cowbird, is found in the northern half of Argentina, Uruguay, Paraguay, southern Bolivia, and southeastern Brazil; M. bonariensis, known as the Shiny or Argentine Cowbird, has a far more extensive range than any of the other South American Cowbirds, since it occurs as far south as northern Patagonia and as far north as Panama; M. ater, known as the North American Cowbird, is limited, in general, to temperate North America from the highlands of central Mexico to the region of Lake Athabaska, and from the Atlantic to the Pacific.

The Screaming Cowbird, Molothrus rufo-axillaris, is in a direct evolutionary line from the Agelaioides badius. The juvenal plumage is exactly alike, both having the coloration of the Bay-winged Cowbird, but the adult plumage of the two species is quite different. The bird gets its name, Screaming Cowbird, from the fact that it gives a harsh scream just when it is about to alight or take off in flight; otherwise it is not excessively noisy as the name might suggest.

Like the Bay-wing it is not migratory and is strictly monogamous. Friedmann (1929) who has made extensive and intensive observations on the habits of Cowbirds, states that he knows of no case of polygamous relationships, and, in fact, this species often remains in pairs the year round.

After their ostentatious courtship has been going on from the second week in September to the middle of November, some female pairs with the male and this monogamous state exists throughout the breeding season and even, in some cases, the year round. This pairing off takes place rather early when one considers that the Screaming Cowbird is a very late breeder, the season for the eggs being from December to the end of February as is the case with the Bay-winged Cowbird. Throughout the months of October and November the birds establish their "territories" and often two months may pass, during which they perch day in and day out on their "singing trees", before the actual laying of eggs occurs. This early establishment of "territories," which remain unused for a considerable length of time, not infrequently results in a weakening of the territorial instinct such that the birds desert their first choice and establish another.

The Screaming Cowbird never builds a nest. As I have said above, the Bay-wing is a late breeder because there are more nests available and unoccupied later in the season. The Screaming Cowbird shows in several ways that it is an offshoot of the Bay-winged Cowbird and hence its delayed reproductive season has a phylogenetic origin in its ancestral stock. Strangely enough, since M. rufo-axillaris is parasitic and since no other birds are breeding so late in the season, the Bay-wing (Agelaioides badius) becomes its chief, or

perhaps its only, victim. In this way the Bay-wing, which breeds late in the season to avoid work in the form of nest building, passed on the habit to the Screaming Cowbird, which became almost wholly dependent on the Bay-wing because so few birds breed so late in the season. As a result, the Bay-wing, which postpones its breeding period to avoid work, has the additional work of raising the young of the Screaming Cowbird.

The eggs of M. rufo-axillaris are so similar to those of Agelaioides badius that it is not always easy to distinguish between them. The number of eggs laid in one season is generally stated as being five. These are laid at intervals of one day. Friedmann (1929) states that he has never found more than two eggs belonging to any one female Screaming Cowbird in any one nest of the Bay-winged Cowbird. In one case he found the eggs of the same female Screaming Cowbird in another Bay-wing's nest about 200 yards from the first one. It is also interesting to note that the Screaming Cowbird does not remove one of the Bay-wing's eggs when laying into the nest of the latter.

Following the egg laying there is an incubation period of twelve to thirteen days. At birth the young Screaming Cowbird is able to right itself if placed on its back, and it possesses a food reaction exactly like that of the Bay-wing. Its initial call note is a faint peep which also resembles that of the young Bay-wing. After the young bird

opens its eyes its food reaction becomes more vigorous. Unlike the young Bay-wing, however, it does not associate this food reaction with the nest or the presence of its foster parents. Moreover, the instinct of fear is not as fully developed as in the Bay-wing.

When the bird is about twelve days old it leaves the nest with its foster brothers and from that time on until the post-juvenal molt it is difficult to demonstrate any difference between the young Bay-winged Cowbirds and the young Screaming Cowbirds. Not only is their plumage identical but also their habits. Both Hudson (1920) and Friedmann (1929) agree that this close resemblance is due to a common descent rather than to any adaptive mimicry. This is further substantiated by the fact that other parasitic Cowbirds get along well with a great variety of species whose young often do not even closely resemble them.

Molothrus bonariensis, known as the Shiny Cowbird because of the bright metallic sheen of the male, has a range over about four-fifths of South America, extending from Northern Patagonia to Panama. It occurs at sea level and even at altitudes over 12,000 feet above sea level. This varying geographical distribution has given rise to local subspecies in many cases.

Again, as was the case with the Bay-wing and Screaming Cowbird, the size of the "territory" varies with the number of available nests to be found within it and not with the

food supply. Hence, the denser the Cowbird population, the smaller the "territory" of each Cowbird. Furthermore, the sexual relations of the bird are influenced by the comparative density of the population of its own kind, as well as the actual demarkation of the "territory" in a thickly settled district.

The Shiny Cowbird is chiefly monogamous and each mated female sticks to her own "territory" if the pressure of population is not too great. However, if the section is densely settled by her own kind, territorial demarkations become indefinite and may even be destroyed so that any particular area becomes the domain of any female that desires to use it, and a semblance of sexual promiscuity results.

Furthermore, the Shiny Cowbird presents a differential sex ratio, there being about three males to every two females. In the first two species discussed the sexes were about equal in number. The Shiny Cowbird's system of mating takes care of this superfluity of males that would otherwise be sexually unsatisfied. Every male has his "territory" and there he stays until a mate comes along. The female having utilized all the nests in the "territory" of any one male, passes on to another male's domain. If, however, she finds that field already occupied by another female and the supply of nests inadequate, she passes on to still another, or she may lay an egg or two in passing. This

arrangement gives the female a chance of laying her maximum number of eggs, and also provides for the appeasement of each male's sexual desire. Nor can this be called polyandry on the part of the females, or polygyny on the part of the males which do not leave their "territories" to collect a harem but take whatever comes their way. Furthermore, the male possesses no parental instinct, and the female has only one mate at a time in any one "territory."

It would seem that this excess of males is due directly to the parasitic habit for it allows an increase in the species without too great an increase in egg-producing individuals. Since the numerical status of the parasite depends on that of the host species, the natural equilibrium would be upset if too many eggs were produced so that too few of the foster parents would be able to bring up their own young to be the victims for the next season.

Remnants of the ancestral nest-building instinct are seen in the Shiny Cowbird, which has become entirely parasitic. These birds show an intense interest in the nests they are to parasitize. Both female and male walk over to the nests and inspect them carefully, peering into the entrances, and may even persist in these investigations for several hours without even entering the nest. Instances have been recorded in which the Shiny Cowbird has been seen attempting to build nests of its own. In most cases they are never completed, but they serve to demonstrate the recurrence of an ancestral

habit.

The eggs of the Shiny Chowbird exhibit a greater variety of color, size, and marking than any other member of its genus, resulting in the lack of markings which are characteristic of the species. The number of eggs laid during one breeding season is open to question, but in view of the number of eggs wasted, it is believed to be somewhere between sixty and a hundred eggs. These are laid at intervals of a day. The eggs are wasted by being laid in old forsaken nests, by not infrequently being dropped to the ground, by being laid in nests where incubation has already begun, so that if incubation is too far advanced the parasitic young will not be reared, and by being punctured by the Cowbirds themselves.

This wasteful habit of pecking holes in the eggs probably has arisen from the Bay-wings which destroy the eggs of the species which they oust from the nest. The builders' eggs are probably pushed over the side with the bill which, in time might lead to the destruction of the eggs by pecking them. Hence, we are here dealing with a habit derived from a more primitive non-parasitic stock. However, the habit is not universal among the Shiny Cowbirds, and is probably the result of desertion by the victim so that its eggs, as well as those of the parasite, were doomed.

One female often lays several eggs in the same nest and several females often lay in one nest. Thirty-seven

Cowbird's eggs were found in a nest of the Rufus Ovenbird which seems to be a favorite victim. Any nest containing such a large number of eggs is generally deserted, for such a number makes incubation impossible. As many as thirteen Cowbirds have been found laying into the same nest, and individual females have been known to lay as many as four eggs in the same nest. These, however, are extreme cases found late in the breeding season. A more conservative estimate would be of two females laying in the same nest, and where conditions are less crowded parasitized nests contain the eggs of only one Cowbird. The ratio becomes about three nests with single eggs to two with more than one.

Long lists of the victims of the Shiny Cowbird have been published, and more are being added as new data are supplied. The total is now definitely around 98 species and subspecies of birds, but when the bird life of its region is as well known as that of the Molothrus ater the total will probably be many hundreds. Most of the victims seem not to mind the eggs of the intruder; others, like the Yellow Browed Tyrant (Sisopygis icterophrys) sometimes bury the parasitic eggs by building a new floor to the nest. Still others desert if a Cowbird lays an egg in their nests, but the general rule is desertion if large numbers of parasitic eggs are found in any one nest.

The incubation period varies from eleven to twelve days,

at the end of which time the blind and helpless Cowbird is hatched. After the first feeding its growth is nothing short of phenomenal. On the fourth day its eyes open, and with that comes an interest in its surroundings. It differs from other altricial birds in that it never develops any alarm calls, nor does it respond to the alarm calls and danger signals of its foster parents.

The young Cowbirds are usually larger, can hold their heads higher, and open their mouths wider than the young of the foster parents. Since most birds feed the young birds that seem to be the hungriest instead of feeding them in sequence, the Cowbird's young are fed first. Moreover, this young parasite has been known to trample on the other young in the nest and competition for food is overcome in this way. They are fed for about two weeks after hatching and in some cases probably longer.

The North American Cowbird, Molothrus ater, is very similar in habits to the Shiny Cowbird, but it exhibits a more efficient phase of parasitism. It doesn't waste such large quantities of eggs.

Molothrus ater ater, the main subspecies, ranges over temperate North America in general, breeding as far north as 49 degrees in the more eastern provinces, south to Georgia and Texas, and from the Atlantic coast to the state of Washington with the exclusion of parts of the Pacific coast. In the winter the birds migrate as far south as

central and southeastern Mexico.

If the range of the Molothrus ater obscurus, a dwarf subspecies, is added to that of the Molothrus ater ater, we have the representative range of the entire species of Molothrus ater. This includes, in addition to the range given above, the greater part of Mexico including Lower California, and nearby portions of the United States. It is generally believed that the ancestral home of Molothrus ater was in South America and that, by migrating through Central America, the species came to Texas which became the dispersal area.

Among the Molothrus ater as among the M. bonariensis, there are more males than females, the ratio being about three to two, and it is still questionable as to whether they are strictly monogamous. It is generally thought, however, to vary with local conditions but to lean strongly toward monogamy. Because of this superfluity of male birds it seems remarkable that there are not more cases of polyandry than there are. In one case of polyandry a male established himself in the "territory" of another male and both answered the flight rattle of the female. In no case of this sort was the original settler of the "territory" seen to offer any defense of his area against intrusion by outsiders except, perhaps, what is thought of as being an intimidation display. Apparently the fighting instinct has degenerated as have the nest-building, and incubation

instincts in the female.

Molothrus ater possess, however, a fairly strong "territory" complex during the breeding season. Birds which have lost the nest-building and other instincts to such an extent as to have become parasitic, can hardly be though to be attached to a nest at this time. Therefore, it has been decided that the "territory" is the prevailing influence which limits the movements of the birds to a certain area.

Not only has the female a breeding area marked off but also the male has his "singing tree" where he sings and displays. This bears no direct connection with any of the nests parasitized within his "territory", but seems to be at a definitely high point so that he can see most of his domain in which the victimized nests are. As I have previously stated, the males exhibit no desire to defend their "territories" through physical combat but merely through intimidation display, which consists of pointing the bill toward the zenith whenever another male is near.

North American Cowbirds have been seen watching, while perching motionless, for a long time the nest-building operations of the prospective victims. When ready to lay an egg, the female went directly to the nest as if that nest had been selected far in advance. The eggs, moreover, are laid during the absence of the owners of the nests and generally in those already containing eggs. One case is

recorded where a Cowbird laid an egg in the nest of an Indigo Bunting containing young, although normally they do not lay in nests where incubation has been started.

In some cases the Cowbird may remove an egg belonging to the victim and the fact that the egg was often found on the ground was offered as a proof that it was removed by the female Cowbird. However, in many cases, there were fewer rightful eggs deposited in the nest in proportion to the number of Cowbird eggs. In other words, the foster parent probably never laid the eggs but retained them in her body because her brood number had been reached. The latter seems a more probable explanation.

Sufficient evidence of the actual puncturing of eggs is lacking. It is true that eggs have been found from time to time that have holes in them. Nevertheless, it cannot be definitely stated that the Cowbird deliberately punctured the eggs. Other birds might be responsible or the claws of the Cowbird might be accountable since the bird is generally too large for the nest it parasitizes.

Rowley (1930), however, tells of having actually observed the dwarf Cowbird, Molothrus ater obscurus, destroying an egg of its victim. In describing this action he says: "The total time the Cowbird remained on the nest could not have exceeded two or three minutes. During this time she laid her egg, either kicked out, or, with the use of her bill, removed one of the Oriole's eggs, and was gone. The

thing happened in such quick time that I hardly had time to see whether she took the oriole egg out of the nest before she laid the egg or afterwards. However, I know there was an egg removed to make room for this 'parasite' because I found the oriole egg where it was dropped."

In the majority of cases one egg is laid in a nest although more than one egg may be laid, and more than one bird may lay in one nest. The eggs are of a generalized type and coloring, having a ground color varying from pure white to bluish white and with speckles from yellowish tan to dark brown. It is interesting to note, however, that the eggs are small in comparison with the size of the Cowbird, even though they are usually larger than the eggs with which they are found.

The incubation period is about the shortest of any of the passerine birds. Here again, is the perfection of the parasitic habit demonstrated. This enables the birds to hatch a day or two before the other birds in the nest, and the larger size of the egg brings it nearer to the body of the nesting bird in such a way that more heat is obtained. Moreover, if the egg is laid after incubation has started, the short incubation period of the parasitic eggs enables the young parasite to survive.

By 1929, eight orders, twenty-five families, 103 genera, 158 species, and 195 species and subspecies of birds had been recorded as being victims of the Molothrus ater, and some have

been added since. There are only nine non-passerine birds on the list, but these are rare victims. These birds are not well suited for bringing up young Cowbirds. To make a suitable foster parent, a bird must be altricial; it must lay eggs that are not much larger than those of the parasite, for, if larger, the parasitic egg would not get enough heat from the incubating body; the manner of feeding of the host must resemble that of the Cowbird rather closely; and the nature of its food must not vary too much from that of the parasite, although a robin has been seen feeding a young Cowbird a small garter snake.

Some birds are spared the task of bringing up these young parasites because of their peculiar temperament. The pugnacious character of the Kingbird is an example. Birds nesting in holes are generally not molested, for the Cowbird prefers an open nest with the exception of that of the Ovenbird. In some localities, those birds which live in swamps are not parasitized, while in other areas they are commonly affected.

During the period of infancy lasting from birth to the age of four days, the young Cowbird exhibits powers of orientation (righting itself if it falls on its back), food reactions (elevation of the head with the widely opended mouth accompanied by rapidly beating wings and loud calls for food), and lastly, the initial call note which is a faint "peep" not often heard. The Cowbirds, unlike their foster

brothers do not crouch down and remain quiet at the approach of any creature other than the parent bird, but clamor for food and apparently have made no mental association with the nest or foster parents.

Tangavius armenti, Arment's Cowbird, is known from four museum specimens, of which only one is an adult. Because of this scarcity, our knowledge of its life history is far from complete, but its geographical distribution seems to be limited to the Cartagena district of Columbia. Tangavius aeneus, the Red-eyed Cowbird, is an important species with three subspecies: Tangavius aeneus aeneus, found in the lowlands of Mexico; Tangavius aeneus involucratus, found in eastern Mexico and Central America; and Tangavius aeneus assimilis, which frequents southwestern Mexico. This species is only partly migratory.

In the case of the Red-eye the males outnumber the females. They have been seen to pair off but not to the extent of indicating that they have no promiscuous relations. The males establish their "territories" and "singing trees" about the first of May and perhaps desert them about the beginning of July.

Aeneus parasitizes relatively few species, and the orioles seem to be its chief victims. This may be explained by the fact that, unlike the Screaming Cowbird, the Red-eye's nearest relative, it has no non-parasitic Cowbirds to parasitize so it turns to a closely allied genus, Icterus.

The largest number of eggs found in one nest was four and usually none of the host's eggs are destroyed. Although one female commonly lays only one egg in a nest, occasionally two females may lay in the same nest.

Upon hatching, the young Red-eye exhibits the same powers of orientation and the same food reactions as other Cowbirds. Like a true member of the Cowbird group its lusty clamoring for food results in being well fed. However, the young parasite gets along with its foster-parents better than the young Molothrus ater. In most cases the competition with the Red-eye becomes too great and the rightful young may last but a few days. Here again the close relationship of this species to M. rufo-axillaris, which does not starve out the rightful young of the nest but grows up along with them, may explain this more congenial behavior toward its foster brothers.

From the description of the geographical distribution and the habits of the Cowbirds one thing should be evident--the evolution of the Cowbird as well as of the parasitic habit. It is believed that Agelaioides badius represents the least development of social parasitism of all the Cowbirds. Molothrus rufo-axillaris is very closely related to A. badius and has given rise directly to Tangavius on one hand and Molothrus bonariensis on the other. Molothrus ater is in a direct evolutionary line with Molothrus bonariensis.

According to Friedmann (1929) the Rice Gracke (Cassidix

oryzivora) is the only other parasitic member of the Icteridae. This bird seems to be an enlarged edition of Tangavius aeneus to which it is related. It is found generally distributed from Mexico to Paraguay. Goeldi (1897) came to the conclusion that Cassidix oryzivora is parasitic everywhere, and parasitizes the Cassidix species whose nests correspond to its own in size.

The Rice Grackle is so persistent in its attempts to parasitize its victims that frequent repulsions on the part of the owners of the nests fail to discourage it. It succeeds in laying one or two eggs in a nest but as many as six have been found.

In the preceding paragraphs I have given an account of the parasitic habits of the Icteridae. Now let us turn to the more universally discussed group, the Cuculidae. The European Cuckoo, Cuculus canorus, was the only species of Cuckoo known to Aristotle and it was of the strange habits of this bird that he wrote cautiously as follows: "People say that they have been eyewitnesses of these and similar things." Since that time strange things have been reported about these birds. Recently, however, more accurate and precise observations have been made as is exemplified in the scientific work of Chance (1922).

Of the Cuckoos about seventy species are known to be parasitic. The true Cuckoos of the genus Cuculus are widely distributed in the Old World and seem to be generally parasit-

ic. The American species apparently have not developed the trait, though occasionally Cuckoo's eggs are found in nests of other species. The South African species, Cuculus gularis, is parasitic as well as the Red-chested Cuckoo (Cuculus solitarius) and the Black Cuckoo (Cuculus clamosus), which are also of that region. Members of the genus Chrysococcyx, or African Golden Cuckoos, are also parasitic as well as those of a third genus, Coccystes. The individual Indo-Malayan Cuckoos, called Koels (Eudynamis) parasitize the same species of allied birds and represent remarkable cases of host specificity. Members of the genus Centropus, or the Spurred Cuckoos, however, are not parasitic for they build their own nests and care for their young as do normal birds.

Unlike most birds, the selection of the breeding territory is left almost wholly up to the female since there is no nest, incubating mate, nor young which require the protection of the male. Furthermore, there is no necessity for birds to pair, in the usual sense of the word, when they do not rear their own young. The Cuckoos are both polyandrous and polygynous. The hen Cuckoo, it has been found, not only becomes attracted to the territory of her upbringing but also prefers to victimize the nests of the species which happened to be her foster parents. Those that have occupied any particular territory the previous year naturally return to it and defend it against all outside opposition.

The dominating female makes use of whatever nest of the

foster species are in the neighborhood and all other females are kept out until she has finished laying. Other females may then enter and deposit their eggs in the very nests utilized by the dominant. It is probable that these other females are wanderers in the vicinity and must be content with dropping occasional eggs into the nests of the dominant Cuckoos until such a time when they will become dominant birds themselves.

These female wanderers, which find the nests of their natural hosts in territories ruled by a dominant female and have an egg at a stage of development compelling deposition, must lay in strange nests. In other cases the Cuckoo may be particularly prolific and start laying before the nests of the host species have been built. Such was the case of a Cuckoo (Cuculus canorus) which used the Sedge Warbler's (Acrocephalus phragmitis) nests early in the season before the Reed Warblers (Acrocephalus streperus) had begun to build.

As I have said, each individual of the European Cuckoo shows a particular attraction for some one species. In this way one female Cuckoo may deposit all of her eggs in the nests of the Meadow pipit (Anthus pratensis), while another may victimize only the nests of the Hedge-sparrow (Accentor modularis). The numerical list of hosts is very large and includes almost every species of small bird breeding where Cuculus canorus ranges, but each individual tends to use the

nest of but one kind. Therefore, the parasitic habit in Cuculus canorus canorus (the European Cuckoo) is characterized by individual host specificity.

On the other hand, the parasitic Cuckoos of the Indo-Malayan region exhibit specific host specificity. For instance, the Indian Koel, Eudynamis honorata, lays its eggs wholly in the nests of crows and jays. In Burma it victimizes the Burmese crow (Corvus insolens) and the Burmese jay (Pica sericea); in British India it parasitizes the Indian crow (Corvus splendens), and the jungle crow (Corvus macrorhynchus); and its victim in southern China is the starling (Graculipica nigricollis). In the above cases, the individual Koel victimizes the same species of bird in any given district so that over a large range the host species are few in number and so closely related that the individual host specificities are so similar as to be characterized as specific.

This may be explained by the fact that the Koel and its egg are too large to be successfully incubated by small species of birds. The most abundant, accessible bird, which comes fairly close to being the size of the Eudynamis, is the crow. Hence, those Cuckoos not making use of these more common nests would be gradually eliminated because of the uncertainty of their young being successfully reared.

Still another situation is found among the African Cuckoos. Here the host specificity is limited because of the

ecological factors affecting the ranges and habitats of the various Cuckoos. Some of them live in the open country, others live in dense forests; and even in the same type of locality, some may restrict their parasitic habits to arboreal nests while others lay only in low domed nests in low branches or on the ground. Thus we find the Golden Cuckoos (Lampromorpha) victimizing birds whose nests are domed or covered, such as the Weaver-birds and Grass Warbler; while the Crested Cuckoos (Clamator) parasitize open, arboreal nests which are never molested by the Golden Cuckoos.

This specificity of habit allows the survival of the parasitic habit in a land where the number of species and of individual birds is very large for any given area: then there is no conflict as there would be if all were parasitic on the same host species. However, there is no real environmental reason for an individual parasite to further restrict its activities toward extreme host specificty.

Furthermore, the African species of Cuckoos establish breeding territories to which they adhere throughout the egg-laying season. This territory is selected not because of the adequacy of food for the young but because of the availability of suitable nests within that area. In the case of the Golden Cuckoo which parasitizes Weaver-birds (Ploceus, Hyphantornis, Otyphantes), the territories are often restricted to a single tree. Since a single tree seldom contains more than one species of Weaver, the Cuckoo is automatically

limiting its parasitism to one host species. It may be that such individual host specificities, correlated with the breeding territory, are responsible for similar cases among other individual Cuckoos. The development of these host specificities seems to depend on the strict adherence to individual breeding areas and indicates that the parasitic habit in the Cuckoos has not resulted in the diminution of the territory such as we find in the Cowbirds.

The dominant hen Cuckoo watches and searches until she discovers in advance the nests of those birds in which she intends to deposit an egg. Thereafter, she visits the nests of the host species in turn, and surveys her dupes hard at work constructing their nests. Concerning this fact Chance (1922) says: "I think that it is only reasonable to assume that a Cuckoo does not lay until the incentive to do so has first of all been provided by the sight of a pair, or probably more than one pair, of her particular dupes actively engaged in the preparation of their nests. The eggs thus 'conceived' are subsequently fertilized, and ready to be laid at a time when her intended dupes have arrived at a period in their domestic affairs suitable to their reception. In the meanwhile the Cuckoo usually pays one or more visits to the destined fosterer's nests, probably in order to locate them precisely, and to assure herself of their satisfactory progress. From this can be deduced the reason for eggs of even dominating Cuckoos appearing in the nests of

rare and uncommon fosterers and for Cuckoos normally parasitic upon one species to make occasional use of a nest of another species. The reason is that some abnormal delay has occurred in the completion of the nest by the pair of dupes on which the Cuckoo had 'conceived' her egg, and when the time comes that she is forced to lay it, she resorts to a nest of some other species that has come within her ken."

Chance (1922) was the first one to suggest the theory that watching her dupes stimulates the reproductive organs of the Cuckoo to such a degree that an egg is ready to be laid five or six days later, and such a theory is well founded from records of his observations. Moreover, it follows that the number of eggs she might lay in a season depends on the number of nests of the host species available. Any shortage of nests would check the stimulus of reproduction so that, until the female became reconciled to the adoption of another species, laying would be checked.

Only one egg is deposited by the same Cuckoo in the same nest. It is possible to explain this fact by imagining the result if two eggs were laid in, say, 5 nests. Since the first instinctive action of the young Cuckoo when hatched is to throw out all the other contents of the nest, his own brothers and sisters would go overboard along with the rest. The result at the end of the season would be five Cuckoos.

The manner in which the Cuckoo deposits her egg in the nest of her host has frequently been discussed, but the

manner in which she lays her eggs in inaccessible nests still remains a matter of speculation. However, in the more accessible nests, such as the cup-shaped structures of some birds, the Cuckoo lays her eggs directly in the nest. This requires only about eight seconds. The astonishing rapidity with which she lays her eggs causes less likelihood of being discovered in the act by the host. In this way there is less chance of the foster bird forsaking her nest after the Cuckoo's visit.

There seems to be ample evidence that in many instances the egg is laid on the ground, transferred to the bill, and in this way is taken to the nest. This would seem to be the method generally used where it is difficult or impossible for the Cuckoo to enter or sit on the nest. There is indisputable evidence that Cuckoos may carry away the dupe's egg in their bills, so that there may be a question as to the identity of the egg being transferred. On the other hand, one might use the argument that if the Cuckoo is able to carry someone else's egg it is quite capable of carrying its own.

Others suggest that the Cuckoo, while clinging to the side of a domed nest, or the opening of a hollow limb, might bring its oviduct to the nest-entrance and in this way deposit her egg. It has even been suggested that the Cuckoo may carry her egg from the ground to the nest of her dupe in her claws. This is very questionable since the flight of

the Cuckoo is rather awkward and there would be difficulty in controlling it in such a way as to make a successful landing without breaking the egg. Furthermore, it is questionable that the Cuckoo possesses a sufficiently precise sense of touch in its claws to enable it to perform this exacting achievement.

The Cuckoo has the habit of removing one of the dupe's eggs from the nest in exchange for its own and in some cases the instinct is so strong as to bring about the removal of two eggs from the nest. This habit prooves very beneficial in that it enhances the acceptance of the parasitic eggs and in this way they stand the best chance of survival.

The methods of removal vary; but a more common method is to carry the egg away in her bill. Other Cuckoo females merely push the eggs over the sides of the nest, where they drop to the ground. On rarer occasions they have been known to swallow the dupe's egg, leaving no trace of it in the nest. More frequently, eggs are merely pierced, but this may be unintentional and caused by attempts to lay eggs in the nest.

Elliot (1930) found a broken shell of a Cuckoo's egg beneath a Pied Wagtail's nest in which was a still warm egg of a Cuckoo but no eggs of the Wagtail. He has the following to say in this connection: "Although the Cuckoo's eggs were of similar type (possibly related birds) one was of a more greenish tinge and distinctive, and I do not think the

same female Cuckoo has ever been recorded laying twice in the same nest. No trace of the contents of the first egg could be detected in or about the nest and no doubt, as is usual it had been cleanly swallowed; at times, by personal observation, I know this removal takes place subsequent to laying.....On may twenty-third two eggs of the would-be fosterers had been laid in the company of the egg of the Cuckoo, and on May twenty-seventh I found a usual full clutch of five eggs had been laid by the Wagtail, which is in favor of her not having commenced laying until after the laying of the second Cuckoo. The egg of the Cuckoo had disappeared but the dried yolk of a broken egg adhering to several others was in evidence. This fact raises in one's mind the query: Did the Wagtail remember the premature laying in her nest and subsequently distinguish the intruder's egg for removal as is undoubtedly done by some unusual foster parents?".

Another very remarkable thing in the parasitic life of the Cuckoo concerns the coloration of the eggs, since the latter show a remarkable range of coloration corresponding to the number of birds used as dupes. Moreover, the eggs of each female are all of the same type and bear a more or less close resemblance to the eggs of the host species. When this doesn't hold true it is probable that the Cuckoo was unable to find a nest of her normal host and was forced to lay in the available nest.

The eggs laid by the Cuckoo are remarkably small in proportion to the size of the bird. Here, again the law of survival may be the explanation. Since the female has to wait for a fovorable opportunity to deposit her egg, it is conceivable that the smaller the egg in relation to her size the more easily it can be retained until a suitable nest can be found.

Moreover, the eggs are extremely thick shelled. Swynnerton (1918) writes as follows concerning this fact: "It is just as conceivable, again--the point could be tested experimentally--that the thick shell of a Cuckoo's egg, explicable I believe as a result of the reduction in size without a corresponding reduction in the amount of lime used, and useful as enabling it to be carried about, may also protect it from being pierced by such weak birds as Warblers.. .....and that this, with the difficulty of handling it otherwise, which must be experienced by such small birds, may account for the Cuckoo's egg being so often left deserted in the nests of Wrens, Willow Warblers, etc."

The incubation period lasts from twelve to thirteen days and under normal circumstances (where the egg of the parasite starts on equal terms with the eggs of the host) the young Cuckoo is the first to hatch. When the young Cuckoo first breaks out of the shell it is naked, blind, an ugly squat-shaped creature of fleshy hue whose body is remarkably large for the size of the egg.

When but a few hours old, the young Cuckoo seems to anticipate the need of the undivided attention of its foster parents, for it musters up enough strength to eject its foster brothers, and even young members of its own species from the nest. Hindwood (1930) watched a Cuckoo, thirty hours old, blind, and utterly devoid of feathers, eject the young of a Rufus Fantail from the nest. The Cuckoo "struggled until the smaller and helpless Fantail was lodged partly on its back and partially against the nest. Then vigorously backing, the Cuckoo gradually worked its way upwards with its back to the steep, sloping side. During the early stages of ejectment the neck of the Cuckoo was stiffened so that its head rested against the bottom of the nest, thus giving the support necessary for attaining the initial position. Later when nearing the rim of the nest, the neck and head hung limply downwards and in no way helped the Cuckoo, whose body was semi-upright, with the rump still pressed against the wall.....Throughout the extraordinary act the wings of the Cuckoo were constantly in motion and bent backwards to keep the hapless Fantail in place, but it was not till the concluding movements that they became the paramount factor. Finally with considerable exertion, and when the Fantail rested on the rim of the nest it was pushed over after which the murderer moved its wings about for a few seconds before reclining."

Chance (1922), in his book entitled, "The Cuckoo's

Secret", has an actual photograph of a most amazing feat: a young Cuckoo ejecting a Meadow Pipit's egg while the female Meadow Pipit is on the nest. Strangely enough, the Meadow Pipit takes no apparent notice and even lifts herself up to allow the young Cuckoo a greater range of activity. Is it possible that such actions have evolved from Cuckoos, that once knowingly threw out the other young or eggs in the nest, to present stage where all movements are controlled by inherent impulse?

The young Cuckoo's growth is rapid and within three days its skin has blackened. Shortly after this the feathers begin to grow. After remaining in the nest for three weeks it leaves, but is still fed by the foster parents. The foster parents may even cater to the insatiable appetite of its changeling for a period of three weeks after it has left the nest. It will remain for hours on its perch and keep up an incessant wheezing note until its foster parents return with some morsel which it snaps up with a gaping mouth.

The attitude of the foster parents regarding their foreign offspring is far from being one of distaste for the young Cuckoo. In fact there seems to be more demonstration and activity about a young Cuckoo than about the legitimate young. This is probably due to the incessant demand for food which exceeds that of the host's young in lustiness.

Heteronetta atricapilla, a rare duck, found in the basin of the La Plata and in Central Chile has recently been

described as being the only social parasite among the Anatidae.

In discussing the breeding habits of this Duck, Phillips (1920) says: "It is very extraordinary that no nest of this species has ever been found, or at any rate described. This gap in our knowledge of the bird's life-history may be due to the fact that the species is extraordinarily parasitic, depositing its eggs in the nests of such birds as the Coscoroba Swan (Coscoroba), the Crested Screamer (Chuana), the South American Limpkin (Aramus), Gulls (Larus), Coots (Fulica), White-faced Ibises (Plegadis), Black Rails (Pardirallus), and even the Chimongo or South Carocaro Hawk (Milvago chimongo). Eggs found in such situations were at first attributed to the Rosy-billed Duck (D. Rodriguez, 1918) but a later writer (Daguerre, 1920) has discovered that these parasitic eggs are slightly different from those of the Rosy-bill, being more whitish with a very finely granulated surface; they are also thicker and more blunt. Most convincing is his statement that these supposed Rosy-bill eggs are identical with a mature egg which was taken from the oviduct of a female of the Black-headed Ducks."

Friedmann (1932), in explaining the development of the parasitic habit of Heteronetta, considers the cases of the Ruddy-duck, Redhead, Shoveller, and others, which sometimes drop eggs in the nests of other ducks or coots, while at other times they build very poor nests of their own. With such indiscriminate deposition of eggs in the nests of other

ducks, it was not surprising when one of the Anatidae, Heteronetta atricapilla, was found to be entirely parasitic.

It was found that the Ruddy-duck (Erismatura oxgura), which lays most often in the nests of other birds, has the largest egg of any of the Ducks except Heteronetta which also lays a relatively large egg for its size. The eggs of both are usually larger than those of the owners of the nests in which they lay. Furthermore, it has been shown that they incubate but little after the first few days, which suggests that the eggs may allow development of the embryo even under adverse conditions.

If this is the case, the eggs possess heat-retaining, or perhaps heat-generating, properties which are correllated with the size of the egg, and both are possibly correllated with the parasitic habit. However, these heat-retaining properties have not been experimentally demonstrated in the case of Heteronetta, but Friedmann (1932) believes there are two alternatives to be considered. "If they are not heat adaptive, then the parasitic habit is the sole cause for the survival of the species, for eggs, unable to cope with thermal difficulties, are laid in nests where they are uncared for, as in the 'dumping nests' (nests in which large numbers of eggs are deposited but apparently not incubated). If, however, they are laid in nests where they are given incubation of some other bird, they will have a good chance to hatch out. If they are able to cope successfully with the

thermal difficulties attendant in the lack of regular incubation, then the parasitic habit is due merely to the loss of the nest-building instinct, as the eggs would get along in uncared for nests just as well as in others where they receive incubation. If the eggs were laid in uncared for nests, that is old or abandoned nests, the birds could hardly be called parasitic. Whichever of the two possibilities is correct however, the fact remains that the Heteronetta appear to have lost the nest-building habit."

The fact that the females carelessly lay eggs in other nests demonstrates that the territorial boundaries are indefinite. Moreover, when ducks are hatched, the parents take them into the water and territorial limitations are completely forgotten. Therefore whatever territorial limitation there is lasts only as long as incubation.

As in the case of Heteronetta, a few of the African Weaver-birds have quite recently been shown to be parasitic, but as yet comparatively little has been written about them. Vidua macroura and Vidua serena are definitely known to be parasitic but there is still some question about Anomalospiga imberis.

It seems that there exists a general tendency among the Weaver-birds (Ploceidae) for two females to lay in the same nest. Granvik (1933), in describing the nests of Plocepasser mahali, explains: "Most of the nests contained only two eggs. In two cases I found four eggs but the

different shape and color show distinctly that two females had used the same nest." He also found four or five eggs in a nest belonging to Plesiositagra vitellina uluensis where, as a rule there are only three eggs. Here again, it is evident that two females used the same nest. It is possible that this occasional deposition of eggs in the nests of other females has led to true parasitism among other members of the Ploceidae.

Of Vidus serena, the Pin-tailed Widow-bird, Roberts (1917) writes: "I am positive from my numerous observations that this bird never builds its own nest but deposits its eggs in the nest of some other bird, by whom they are incubated and the young birds reared. I have known it to leave its eggs in the nests of four species of Finches, those being the Common Waxbill (Estrilda astrilda), Dufress's Waxbill (Coccopygia dufresni), Ruddy Waxbill (Lagonostica rubricata), and the Red-collared Widow-bird (Coliuspasser ardens), the first three of which are smaller and the last rather larger than the Pin-tailed Widow-bird."

The parasite may lay more than one egg in a nest or may replace the whole clutch of the owner. When depositing her eggs it is evident that the Widow-bird destroys one of the owner's eggs for every egg of her own. Like Honey-guides however, the young parasites do not eject their young foster brothers from the nest but grow up along with them.

The Honey-guide family (Indicatoridae) is not a large

one, comprising only five genera, and about twelve species, two of which are found in the Oriental region, and the remainder in Africa south of the Sahara. Of these a few species are parasitic: Indicator indicator, ranging from the Cape Colony to Northeast Africa and across the Sudan to Senegal; Indicator variegatus, the Scaly-throated Honey-guide of east and south Africa; and Indicator minor (the lesser Honey-guide), Indicator major (the Yellow-throated Honey-guide), and Indicator sparrmani (Sparrman's Honey-guide), generally distributed through South Africa.

The Black-throated Honey-guide (Indicator indicator), the common African Honey-guide, resembles the Cowbirds and Cuckoos in its parasitic habits yet it is not related to these birds but to the Woodpeckers. Moreover, it deposits each of its white eggs in the nests of Barbets which, like Woodpeckers, nest in cavities of trees. According to Chapin (1924): "Whenever possible the adult Honey-guide breaks the legitimate eggs, it is said, and when the young is found, it is always the sole occupant of the nest." However, this fact might be explained by the ejection of the young foster brothers from the nest by the Honey-guides.

Haagner (1907) has taken photographs of young nestling Honey-guides which show the extremities and lower mandibles furnished with a pair of hooks, which are hard, strong, and very sharp. He suggests that these are used in ejecting the young of the rightful owner from the nests. One can easily

see the damage that might be done by the firm grip of these hooks which overlap in a way to assure a strong hold. These hooks apparently fall off when the bird becomes an adult. Haagner describes them as being recurved appendages which are "semi-transparent and appear to be an exaggeration of the shell-breaking scale which occurs on the beaks of chickens--this being epiblastic in origin, whereas the teeth of Odontornithes and Archaeopteryx were true teeth and consequently partly epiblastic and partly mesoblastic in origin."

"It will thus be seen that the teeth of the ancient reptile-like ancestors of modern bird life, and the projections on the beak of the nestling Indicator, are in no way related; consequently it does not appear to be a case of reversion, and would seem more after the nature of a subsequent development engendered by the bird's habits of life." Supporting this theory is the evidence that among those Honey-guides that are not parasitic, such as Melignothis conirostris and Melichneutes robustus, these hooks do not appear.

There still seems to be some question as to whether Indicator variegatus is parasitic but Haagner (1907) tells of seeing a young bird in the nest-hole of the Diamond Sparrow (Petronia petronella). Sclater and Moreau (1932) record a case where one was fed by Dendropicus lafresnayi hartlaubii, while a native collector reports having watched a Mescopicos grisecaphlus feeding a young Indicator variegatus

side by side with its own fledgling on a branch in the Amani forest. He also noted that the two young birds were uttering similar hunger calls.

The Honey-guides are very persistent in their attempts to usurp the nests of other birds and they are generally fiercely attacked by the owners. In one case the Honey-guide, which had flown to the nest-hole of a Barbet, was opposed by the male which was later joined by the female; and the intruder was successfully ousted from the hole. The Honey-guide came back, however, in five minutes and the same procedure was repeated over and over again for an hour, when the birds were shot. It was found that an egg was actually protruding from the oviduct of the Honey-guide. But once the parasite has entered the nest-hole, she breaks the eggs of the foster parents to make room for her own.

It is also interesting to note that, in general, the creamy white eggs resemble those of the birds usually parasitized, as in the case of the Cuckoos where the eggs are speckled and colored like those of the host species.

Many theories have been advanced concerning the origin of the parasitic habit among the birds. Since, in most cases, our knowledge of the characteristics and life history of the various parasitic species is incomplete, it is probable that no one of these theories will be able to survive in the light of continual accumulation of additional data. It might be well, however, to present some of the leading current

hypotheses.

Pycraft (1910) is the chief exponent of the theory that the source of the parasitic habit lies in the polyandrous condition which all parasitic birds are supposed to exhibit. Concerning this theory he asserts: "That parasitism is due to polyandry--and to a less extent to polygyny--we believe is almost certain. And this because such sexual relationship tends inevitably to lower the parental instincts, just as monogamy tends to strengthen them. Among the polygamous game birds there are not wanting sings of degeneracy in the parental instinct. Thus the males commonly leave the care of their offspring entirely to the females, which indeed, often have to guard them from the violence of parental jealousy, while two females will frequently share a common nest, a custom which offers an easy means of shelving responsibility altogether, as in the case of parasitic species."

While this reasoning may hold true when applied to some species, it is evident that the theory breaks down when applied to Vidua macroura, parasitic African Weaver-bird, which is strictly monogamous, and to the Cowbirds, which tend to be monogamous. In fact, in the latter case, what promiscuity does occur, appears to be a result of the parasitic habit.

Chance (1922), a student of the Cuckoo problem, wisely avoids the issue. In the statement, "How and why her para-

sitic habit originated is, of course, probably insoluble, and I have no intention of theorising about it," he suggests the futility of attempting to find a solution. However, Allen (1925) was among the first to realize that social parasitism has been acquired in different ways and that no one theory is enough to explain the penomenon. He comes to the conclusion that "one must be prepared to find that this habit has been acquired in more than one way, and independently in the groups mentioned."

There are two general theories that the parasitic habit was originally caused by an external stimulus. The first points out that there are birds that can be induced to ovulate and lay eggs by artificial means. Examples of this phenomenon can be seen in the fact that a nest egg may encourage a hen to lay, and that certain doves can be induced to ovulate by a constant caressing of their heads and necks. It is probable then, that among the Ducks, the habit of parasitism had its inception when the stimulus--the sight of a nest with eggs resembling their own--brought about the response--the addition of eggs to the number already in the nest.

The second theory in this group is that the habit merely arose from the very close relationship between the parasitic bird and its victims, as well as a resemblance both in appearance of their eggs and in the style of the nest each originally constructed. This hypothesis can be applied

successfully to the Honey-guides, which parasitize hole-nesting species--Woodpeckers and Barbets.

Herrick (1907) suggests that the habit may have originated with the maladjustment of egg-laying to nest-building so that the eggs were ready to be laid before the nests had been built. In accepting this conclusion he points out that, "The door is thus opened wide to parasitism in its initial stage, whenever the acceleration of egg-laying or the retardation of the nest-building instinct becomes common, with or without irregularity in the egg-laying intervals." He applied this idea both to the Cowbirds and to the Cuckoos.

If this is the case social parasitism of birds is of a very ancient origin, having become characteristic of many of the Cuckoos before there was evidence of any demarkation from the parent stock. Among the Cowbirds and some Cuckoos, however, the trait is more plastic, for some species still retain the nest-building instincts. The fact that female Cuckoos pick up and hold pieces of straw for over a minute during the courtship may be reminiscent of the time when they built their own nests.

The Cowbirds exhibit an evolution from normal nesting through partial nesting to the complete parasitic habit. This is not the case among the Cuckoos, of which there are but two normal nesting species in America, and the subfamily Centropodinae (Coucals) which have not reached complete parasitism. Therefore the habit must have descended from some

ancient stock, for all other members of the family have reached complete parasitism.

Friedmann (1929) discusses at length the origin and the evolution of the parasitic habits, particularly those of the Cowbirds. He gives several reasons for believing that the original condition was not one of parasitism: most birds of the world possess nest-building and brooding instincts so that it is likely that this was the primative condition of the Cowbirds; all the other members of the family Icteridae are splendid nest builders; the life histories of the various species of Cowbirds give evidence of the evolution of parasitism; the fact that they are now fairly monogamous indicates that they were monogamous and nested in the fashion of all monogamous birds; the most primative of the present species is the Bay-winged Cowbird which is not parasitic.

Accepting this conclusive evidence that normal nesting was prevalent among primative Cowbirds, we must seek the method whereby the original habits were lost. Friedmann (1929) believes that the immediate cause of the origin of the parasitic habit in the Cowbirds was the loss of the protecting instinct of the male. In explaining the loss of this instinct he says: "Inasmuch as the Bay-wing is non-parasitic and inasmuch as the Screaming Cowbird is a direct off-shoot of this stock it seems probable that originally the latter species was also non-parasitic. In other words the change from the normal to the parasitic mode of reproduction occurred within the racial history of Molothrus rufo-axillaris.

Assuming that in most ways the original habits of the Screaming Cowbird were similar to those of the Bay-wing, we should suspect that the birds tried to breed in the nests of Ovenbirds, Woodhewers, etc., but tried to do so early in the season. As elsewhere indicated the struggle for the nests is much greater early in the season than later on, and the Screaming Cowbird, handicapped hereditarily by a weakened territorial instinct, probably could not succeed in this struggle. We have seen that sometimes Screaming Cowbirds establish territories in the spring, occupy them for considerable periods, and then desert them without ever having utilized them. This indicates very strongly that the weakened territorial instincts of the male are often insufficient to maintain their influence long enough to 'make connections' with the somewhat more vernal development of the egg-laying instincts of the female. In this lack of attunement between the territorial instincts of the male and the egg-laying instincts of the female the parasitic habit probably had its origin. This lack of attunement seems to have been caused by the diminution of the protecting territorial instincts of the male and this diminution seems in turn to have been started by the reversal of the territorial and the nest-building instincts in the stock from which the Screaming Cowbird evolved."

The Cuckoos have never had a very highly developed nest-building habit and it was, therefore, comparatively easy to

lose. The Indicatoridae (Honey-guides) represent the same condition as the Cuckoos. Among the Hang-nests (Icteridae) and the Weaver-birds (Ploceidae) the nest-building instincts are developed to the highest degree, and of these two groups but a few species are parasitic. The change here, then, has been an internal, physiological change and not an external or environment change.

D. Literature Cited

Allen, G.M.

____ 1930. Birds and Their Attributes. Marshall Jones Co., Boston.

Carpenter, G.H. and Pack-Beresford, D.R.

____ 1903. The Relationship of Vespa austriaca to Vespa rufa. Ent. Month. Mag., Vol. 14, pp. 230-242.

Chance, E.E.

____ 1922. The Cuckoo's Secret. Sidgwick and Jackson, Ltd., London.

Chapin, J.P.

____ 1924. Profiteers of the Busy Bee. Natural History, Vol. 24, pp. 329-336.

Elliot, J.S.

____ 1930. Removing Another Cuckoo's Egg from a Nest and its Sequel. British Birds, Vol. 24, pp. 53-54.

Forel, A.H.

____ 1930. The Social World of the Ants. Translated by C.K. Ogden. Charles Boni, New York.

Friedmann, H.

____ 1929. The Cowbirds. A Study in the Biology of Social Parasitism. Charles C. Thomas, Springfield, Ill.

____ 1932. The Parasitic Habit in the Ducks. Proceedings of the U.S. National Museum, Vol. 80, pp.1-7.

Goeldi, E.A.

____ 1897. On the Nesting of Cassicus persicus, Cassidix oryzivora, Gymnomystax melanicterus, and Todirostrum maculatum. Ibis, pp. 361-370.

Granvik, H.

____ 1933. The Ornithology of North Western Kenya Colony. Rev. Zool. Bot. Afr. Tervueren, pp. 133-190.

Haagner, A.

____ 1907. Contribution to our Knowledge of Indicatoridae. Pretoria, Journ. So. African Ornithological Union, pp.76-116.

Herrick, F.H.

____ 1907. Analysis of Cyclical Instincts of Birds. Science, Vol. 25, pp. 725-732.

Hindwood, K.A.

____ 1930. Observations on the Habits of Cuckoos. Emu, Vol. 30, pp. 17-21.

Hudson, W.H.

____ 1920. Birds of La Plata. 2 Vols., Dent, London and Toronto.

Lutz, F.E.

____ 1916. The Geographic Distribution of Bombidae (Hymenoptera) with Notes on Certain Species of Boreal America. Bull. Amer. Mus. Nat. Hist., Vol. 35, pp. 501-521.

Phillips, J.C.

____ 1925. A Natural History of the Ducks. Vol. 3, The

Riverside Press, Cambridge, Mass.

Plath, O.E.

____ 1922. Notes on the Nesting Habits of Several North American Bumblebees. Psyche, Vol. 29, pp. 189-202.

____ 1934. Bumblebess and Their Ways. The Macmillan Company, New York.

Pycraft, W.P.

____ 1910. A History of Birds. Methuen and Co., London.

Roberts, A.

____ 1917. Parasitism amongst Finches. Annals of the Transvaal Museum, Vol. 5, pp.259-262.

Robson, J.E.

____ 1898. Vespa austriaca, a Cuckoo Wasp. Science Gossip, Vol. 5, pp. 69-73.

Rowley, J.S.

____ 1930. Observations on the Dwarf Cowbird Molothrus ater obscurus. The Condor, Vol.32, pp. 130-131.

Saunders, E.

____ 1903. The relationship of Aculeate Inquilines and their Hosts. Ent. Month. Mag., Vol. 14, pp. 272-279.

Sclater, W.L. and Moreau, R.E.

____ 1932. Birds of the Northeastern Tanganjika Territory. Ibis, Vol. 2, pp. 664-683.

Sladen, F.W.L.

____ 1912. The Humble-Bee, Its Life-History and How to Domesticate It. Macmillan & Co., London.

____ 1915. Inquiline Bumble-Bees in British Columbia. Canad. Ent., Vol. 47, pp. 84.

Swynnerton, C.F.M.

____ 1918. Rejections of Birds of Eggs Unlike Their Own. Ibis, Vol. 6, pp. 127-154.

Wheeler, W.M.

____ 1905. An Interpretation of the Slave-making Instincts in Ants. Bull. Amer. Mus. Nat. Hist., Vol. 21, pp. 1-16.

____ 1906. On the Founding of Colonies by Queen Ants with Special Reference to the Parasitic and Slave-making Species. Ibid., Vol. 22, pp. 33-105.

____ 1913. Ants, Their Structure, Development and Behavior. Columbia University Press, New York.

____ 1928. The Social Insects, Their Origin and Evolution. Harcourt Brace and Co., New York.

Wheeler, W.M. and Taylor, L.H.

____ 1921. Vespa arctica Rowher a Parasite of Vespa diabolica De Saussure. Psyche, Vol. 28, pp. 135-144.