

SEX RHYTHM IN THE RUFFED GROUSE (*BONASA  
UMBELLUS* LINN.) AND OTHER BIRDS.<sup>1</sup>

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*Plates VIII-XI.*

THE sex instinct is generally conceded to be the most powerful of all agencies controlling the actions of birds. It may seem heretical, therefore, to begin this paper with the statement that, after fifteen years of rather intensive study of the Ruffed Grouse,<sup>2</sup> I am convinced that this species, and perhaps all species of birds, are not cognizant of sex as such, even during the breeding season, and that sex reactions are based primarily upon differences in size or vigor of individuals irrespective of sex.

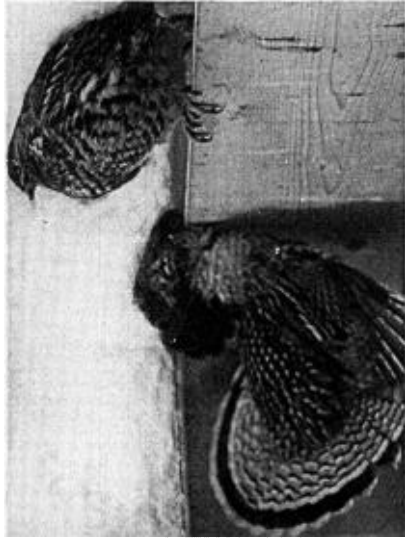
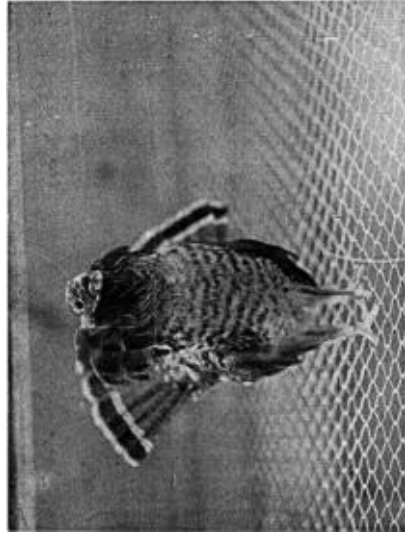
My observations on Grouse are based primarily upon birds reared in captivity, because these birds, being devoid of fear of man, react toward one another before one's eyes in a perfectly normal manner, and one is able to repeat and check his observations dozens of times for every single observation made on wild birds. Some of the observations have been made in large woodland enclosures, others in small pens, and, during the past three years, largely in pens with wire floors where, incidentally, the birds seem to behave exactly like others in the woods. In 1931 I reared 57 birds, in 1932, 77, and in 1933, 50, so that I have had plenty of captive birds to watch, and they have behaved quite uniformly according to the pattern which I shall attempt to describe.

In the first place it may be well to call attention to the external differences between male and female Grouse, so that it will be understood that there is no excuse for a male not recognizing a female if it were necessary to do so. Adult Eastern Ruffed Grouse vary in weight from one to nearly two pounds, averaging perhaps

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<sup>1</sup> Read at the Fifty-first Stated Meeting of the A. O. U. New York, November 14, 1933.

<sup>2</sup> During these fifteen years of study of the Grouse, I have received much encouragement and direct financial assistance, firstly from the Haeckscher Fund for the encouragement of research at Cornell University; secondly from the American Game Association and, during the past three years, from the New York State Conservation Department, through its Bureau of Game.



UPPER: (A) INTIMIDATION DISPLAY OF MALE. (B) NORMAL DISPLAY OF MALE BEFORE FEMALE.  
LOWER: (A) DISPLAY BEING COLLAPSED BY STRONG RIVAL MALE. (B) GROUSE THAT DISPLAYED BEFORE  
WOMEN AND CHILDREN BUT NOT BEFORE MEN.

twenty-four ounces, two year old birds being heavier than first year birds, and females averaging about three ounces lighter than the males. All female measurements average less, particularly the tail, which is nearly an inch shorter. If this were all, a small male might pass for a large female, because both birds wear ruffs, though these are much smaller in the females; and females show the same range of color variations as the males. A fairly conspicuous color difference, however, is that of the breast which, in the females, is pinkish brown and not crossed by the short black (or brown) feathers of the fore part of the ruff. In the males, on the other hand, the ruff is indicated across the breast, even when the long lateral feathers are retracted, as a line of much darker feathers.

The black band on the tail is never solid and continuous across the tail of the female, being interrupted or broken up on the two central feathers. The majority of males, on the other hand, have the band continuous on the middle feathers, though in at least ten per cent it resembles that of the female.

In the juvenile plumage I have discovered no certain way of determining the sex of Ruffed Grouse by the plumage, as all of the adult characters are so imperfectly and irregularly developed. The young males, however, grow faster and seem larger from at least six weeks of age. Previous to that age I have not banded my young stock and have no way of knowing definitely which develop into male and which into female birds, and many individuals seem intermediate until their adult tails and ruffs are matured at about fifteen weeks of age.

"Male" behavior commences, however, long before this age is reached. Indeed, quite frequently I have observed a vigorous young Grouse scarcely more than a week old strutting for the benefit of its companions, fighting and subjugating a weaker bird and actually going through the actions of coition. One would naturally suppose this bird to be a male, and doubtless the majority of times it is, though, as I am about to show, if a female Grouse feels itself stronger or more vigorous than a companion, it will go through what is ordinarily the behavior of a male.

Let us first consider the normal behavior of the male Grouse, in which it is ordinarily thought to be displaying its maleness:

### 1. *The Intimidation Display.*

The normal display of plumage, usually spoken of as the Courtship Display, is too well known to need detailed description. With ruffs elevated, tail erected and wings drooped, he walks very deliberately, occasionally pecking the ground or giving his head a rotating shake. As he approaches the object of his attention the head shaking becomes more rhythmical and more rapid and is accompanied by a hissing sound, until finally he takes a short run in front of his victim and strikes a pose to the accompaniment of a prolonged hiss. This pose he may hold for minutes at a time or he may conclude it with a rush at the other bird and an attempt to deliver blows upon its head, particularly if the bird runs from him, or in any way registers inferiority. If it fights back, the displaying bird may partially or completely collapse its feathers and withdraw, but this seldom occurs for the reason about to be stated. I have called this the "*Intimidation Display*" rather than the Courtship for, so far as I can see, it is given indiscriminately before males or females, but almost always before a smaller or weaker bird. It seems to have little to do with actual mating, except as the bird is able to prove itself stronger than its opponent, and in confinement, it occasionally results in the death of a weaker bird, either male or female.

This display may start when a bird is only seven or eight days old, and is quite frequently observed among immature birds when they have completed their juvenile plumage at about six or seven weeks of age. During the following month it is seldom seen, but from about the last of September, when the larger birds have come into their adult plumage, it can be expected at almost any time, but particularly on cloudy days. It reaches its highest development in the most vigorous males and weak or undersized birds seldom undertake it. In its completeness it is apparently confined to male birds, but females, when fighting, have a somewhat similar display, and I have on several occasions seen a *female* display in a very similar and almost as vigorous a manner as a male before a small *male* that had been completely subjugated by a larger companion and lay flat in a corner of the pen. In one case the female actually attacked the subjugated male, pecked it on the head and went through the actions of coition as a male would have done

under similar circumstances.<sup>1</sup> A bird that has been completely subjugated, as in this case, is subjected to attack from every other bird in the enclosure. He has developed an *inferiorism* and usually, unless removed, he remains in the corner until he dies. His resistance completely shattered, he dies, not from mechanical injury nor from starvation, but from some sort of nervous shock, and death is likely to occur within twenty-four hours. If he is removed and placed in solitary confinement, he usually recovers, but it may take weeks before he will offer resistance to other Grouse.

This *Intimidation Display* occurs not only for the benefit of less vigorous Grouse, but seems to be a reaction to a dominating complex energized by the sight of a weaker individual of any species. It is apparently what Schelderup-Ebbe<sup>2</sup> (1924) calls "despotism" carried to the extreme. One male bird that was kept by himself during the spring of 1932 was always inspired to the display by the sight of a woman or a child of either sex. It was impossible to get him to "show off" for the benefit of masculine visitors unless a woman or child were present, and he always selected the weakest individual for his attentions. Women in knickers or riding breeches were immediately recognized as women, especially when accompanied by a man.

With these various reactions of male and female in mind, I have come to the conclusion that the Grouse are not cognizant of sex as such, that they certainly do not distinguish between male and female, and that they have a very strong instinct for judging the relative strength of other Grouse and other creatures. With this instinct exist strong superiority and inferiority complexes, or what we may call "*superiorisms*" and "*inferiorisms*" which, when there is any competition, quickly result in what Darwin called "the Struggle for Existence and the Survival of the Fittest."

## 2. *The Drumming.*

The drumming of the Grouse, which I have described elsewhere,<sup>3</sup>

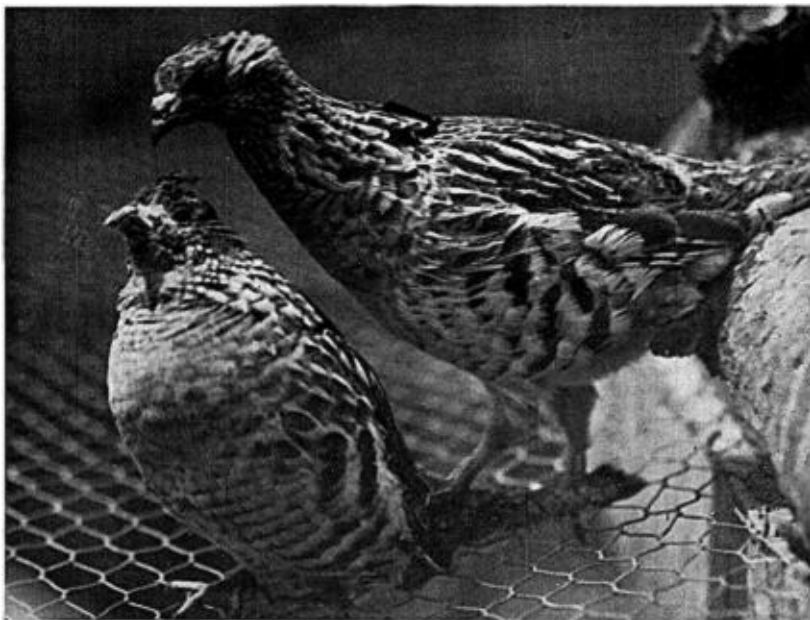
<sup>1</sup> Carpenter in his observations on gonadectomized Pigeons (1933), reports similar behavior with certain of his female Pigeons. C. R. Carpenter: Psychobiological studies of Social Behavior in Aves. *Journal of Comparative Psychology*, Vol. XVI, No. 1, Aug. 1933, p. 41.

<sup>2</sup> Despotism Amongst Birds by Thorlief Schelderup-Ebbe, Ph.D. *Scandinavian Scientific Review*, Vol. III, Nos. 3 and 4, pp. 10-82.

<sup>3</sup> See A. C. Bent: *Life Histories of N. A. Gallinaceous Birds*, pp. 142-147.

apparently takes the place of the territorial song in other birds. It is an expression by the male of his feeling of superiority. In the spring it becomes an announcement to females, and a challenge to other males. It is indulged in by adult wild birds at all seasons of the year except the molting period of July and August, but naturally reaches its height during late March and early April, at which time it is more frequent during the night than during the day. Some wild Grouse apparently lead their lives without drumming, and in captivity, as long as the females are kept with the males, they can feel their superiority without expressing it with their wings, and seldom if ever drum.

In the spring of 1932, however, I separated a two year old male from the rest of the flock and put him in a small enclosure on the ground by himself some thirty feet from the rest of the birds. The pen measured about 6 x 10 feet, and I placed a short log at one end where he could drum if he so desired. This bird had never been placed in solitary confinement before, nor had he, to the best of my knowledge, ever heard another Grouse drum, nor had he attempted to drum himself. Ten minutes after he had been placed in this new pen, however, and after a few minutes of reconnoitering, he mounted the log and almost immediately assumed the drumming pose, first patting the log with his feet as though to test the stability of the spot which he had chosen. Then followed the quick stroke of the wings, another and another, and finally the roll and a blur of wings that made the dead leaves fly from in front of the log. There was no question that he knew instinctively what a drumming log was for, and knew how the drum should be produced; but he made scarcely a sound. I stood ten feet from him, and while I could hear the rush of air and the rustle of the leaves, there was none of the characteristic thumping. Indeed it required nearly two weeks of constant practicing before the bird's drum sounded like that of a wild bird. It reminded me of a youngster trying to snap a whip—knowing just how it ought to be done and apparently doing it right and yet producing no snap. Since this bird had never seen nor heard another Grouse drum (having been hatched by a bantam and reared in a brooder), I think we are justified in concluding parenthetically that Grouse inherit an instinct to drum, just as I believe other birds inherit the instinct to sing the char-



UPPER: GROUSE THAT DRUMMED BY INSTINCT.

LOWER: TWO MALE GROUSE IN MATING CYCLE; DO NOT DISCRIMINATE BETWEEN SEXES.

acteristic song of their species, but that both need a little practice to become perfect.

I have never known of a female Grouse trying to drum, though at times I have kept solitary females through the breeding season and had them come into oestrus and lay eggs without the presence of a male.

### 3. *The Mating Display.*

A third reaction of the male Grouse is what I have called the *Mating Display*. This is very different from the *Intimidation Display*, both in form and purpose. The bird is no longer trying to impress others with his superiority; he is completely overpowered by his mating instinct. Instead of being vicious, he is gentle; instead of erecting his feathers, they are depressed; his tail drags on the ground and his head is held slightly upward in a beseeching attitude. He walks around slowly, occasionally shaking his head, and when he gets close to another bird he pecks lightly at the base of its bill or places his foot on its back. He seems not to recognize differences in sex and approaches other males as well as females. If the other male is in the same stage, he permits the advances and there even may be attempted coition, though the receptive male never actually assumes the posture of the female in oestrus. If the approached male is not in his "head shaking stage" he pecks the advancing bird and drives him away.

The duration of this *Mating Display* varies with different individuals and is apparently sometimes omitted entirely. It appears not to be essential to the accomplishment of coition, since one male in 1933 was known to have had successful matings following immediately upon the "*Intimidation Display*." The *Mating Display*, however, suggests a protection for weaker or timid females, since the male in this stage is gentle and never rough with other birds.

This *Mating Display* is occasionally indulged in by a female when she comes into oestrus and has not found a mate, but ordinarily where males are available in the same enclosure, it seldom lasts long.

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Let us now consider the behavior of the female.



In addition to what has been said about the plumage differences of the female, her intimidation displays, mating display and lack of drumming, there remains to mention the approach of the oestrus period and its effect on her appearance and behavior.

The enlargement of the ova and the thickening of the oviduct register externally by a filling out of the area back of the legs and the depressing of a line of feathers between the legs and the tail. This becomes quite conspicuous during the period that eggs are being laid so that egg laying females are easily recognized among their less advanced sisters.

I do not have many data on the exact time at which oestrus begins, but one female that was kept without a male became receptive, as indicated by her posturing before me when I brought her food, six days before the laying of the first egg, and this stage lasted for two weeks or until three days before the laying of the eleventh and last egg, when she began to get broody. The posture assumed by the receptive female is that of a stiffened depressed body with its wings slightly spread and the tail slightly raised.

Another indication of the approach of oestrus is the head shaking as already described, and the beginnings of nest building. This is first indicated by feeble attempts at tossing leaves over her shoulder on to her back as she sits or even as she walks. A little later she starts her nest at the base of a tree or under some brush, by excavating a little hollow and lining it with the materials within reach as she sits in the depression. The leaf throwing continues during the egg-laying period and for several days after incubation starts, so that at first she sits with her back more or less completely covered. This doubtless accounts for the differences noted in the covering of the eggs with leaves amongst wild birds. The more advanced the incubation the less likely the eggs are to be found covered, for she ceases covering her back with leaves after a few days, and there is none to fall on the eggs when she departs.

I have been unable to determine any relationship between the nest site and the drumming logs, and I have known nests with fertile eggs located in wood lots, even on the Cornell Campus, where no male could be found within half or three quarters of a mile; on the other hand, nests are sometimes found within fifty feet of a drumming log.

The male bird, in the wild, apparently never incubates, but in 1932, one of my largest red-ruffed males got broody and insisted on sitting on a nest egg for over two weeks, until I took it away from him, his behavior being exactly like that of adjacent females.

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Thus far I have been speaking only of Ruffed Grouse (*Bonasa umbellus* Linn.). Before expressing again my conviction that birds are not sex conscious, or that they do not discriminate between the sexes, I should like to describe briefly a few experiences with other birds.

A few years ago when Dr. Herbert Friedmann was making his Cowbird (*Molothrus ater ater* Boddaert) studies<sup>1</sup> at Cornell, we kept a male bird in a flying cage on my grounds, and in an effort to make him go through his plumage display on a branch where the camera was focussed, we fastened a stuffed female just below the desired spot. The bird was rather poorly mounted but was apparently easily recognized as a Cowbird, for not only did the captive male display for its benefit, but time and again attempted coition. We thought at the time that the position in which the female was fastened might have suggested a mating posture to the male, so in 1931 I repeated the experiment with a House Wren (*Troglodytes aëdon aëdon* Vieillot), placing a mounted bird, from the museum, standard and all, on the sloping roof of a bird house occupied by a pair of House Wrens. The slope to the roof gave the mounted bird an almost vertical position. Nevertheless the male responded immediately, flew at the brazen visitor, pecked it on the head, and again and again attempted to mate with it.

Still another experience with Canada Geese (*Branta canadensis canadensis* Linn.) in captivity. For years I kept two females which behaved exactly like a mated pair, except for one year when a gander mated with one and drove away the other. They travelled together continuously and seemed very much attached to one another. During March or early April, one of them would build a nest and lay four or five eggs, while the other stood guard like a gander. After about a week this bird would build a nest alongside of her mate and lay four or five eggs. Then they would sit side by side and spend their time stealing each other's eggs until they all

<sup>1</sup>The Cowbirds. A study in the Biology of Social Parasitism. 1929.

got broken. It was obvious that the slightly larger female was behaving like a male until her actual nest building and egg-laying began.

Another experience was during the spring of 1932, with a Yellow Warbler (*Dendroica aestiva aestiva* Gmelin) that came to a Spiræa bush near my study window. He was happy until he espied his reflection in the window, and assuming it to be another Warbler intruding in his territory, he flew at the window to drive it away. To determine conclusively that it was his reflection that caused him to fly against the window, I hung a mirror alongside the window to make it more worth his while. He immediately transferred his attention to it, behaving like the monkey in the zoo, looking at his reflection from all angles, singing, flying at the glass in a rage, and peering around behind it as though expecting to find his rival in the bush behind the mirror. He continued this for about three days, until his newly arrived mate had about completed a nest in an adjacent pear tree, when his ardor cooled.

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What is the relevance of these disjointed observations and their connection with the behavior of the Grouse? They all are, in my belief, expressions of the same blind instinct which recognizes so quickly and yet without reason, differences in strength or vigor; and the natural law among lowly-organized creatures, that the strong shall destroy the weak, a law which seems to me more powerful than the actual mating instinct itself, and which is not cognizant of any sex difference as such.

The male Yellow Warbler that selects a territory instinctively drives out all other Yellow Warblers, males and females (and reflections) from his territory, so that when a female arrives that is in the same stage of the reproductive cycle as himself, he will be the only male around when she comes into the oestrus period.

In a flock of Ruffed Grouse, birds that are equally vigorous are apparently oblivious to one another, but let one make a single misstep, fly into the wire, or misjudge his landing place so that he alights somewhat confused, immediately any other Grouse near by takes a peck at him, and unless he fights back and is able to disprove his weakness, he or she is immediately relegated to the inferiority class. A flock of apparently timid, gentle Grouse becomes a

“pack of wolves,” and the reaction is entirely devoid of sex relationship. A male Grouse drums and displays to show his superiority, and until he actually comes into the final mating stage of his display, he is as much interested in killing a female as in mating with her or disabling a rival. If he is able to prove his superiority—and a female is strong enough to resist or elude his attacks until they are both in the same mating cycle—fertilization takes place and the world is assured of the reproduction of the strongest individuals. The Survival of the Fittest still seems to be the strongest law of Nature.

Howard in his illuminating book on Bird Behavior<sup>1</sup> (p. 74) states “A bird is like a mammal. Throughout the cycle the male is physiologically prepared to conjugate, but the female is under stricter physiological control; her prior sex condition corresponds to prooestrus, and her condition when the secondary physiological control is removed to oestrus.” He describes the actions of a pair of Hedge Sparrows and their inability to produce fertile eggs in spite of being together from February 21 to April 10, and explains it on a basis of lack of intensity of reaction in spite of all the posturing and sexual flights that took place. Lack of sufficient stimulation in this and other birds he ascribes to variations in the weather, food, metabolism and unknown factors.

My explanation would be somewhat simpler. It is my belief that birds are *not* like mammals and that the males are *similar* to the females in having a short definite mating period.<sup>2</sup> The period may be longer than that of the female or it may be shorter; it varies with species and with individuals, especially with age. In domestic poultry the period is either very long or it recurs at such frequent intervals that it confuses our conception of its status in wild birds. The male comes into and passes out of a definite mating cycle irrespective of the presence of a female and any posturing or sexual flights. The whole framework of bird behavior during the breeding season is built around securing *synchronization* of the cycles in male and female. The selection of territory, display

<sup>1</sup> Howard, H. Elliot; An Introduction to the Study of Bird Behavior, 1929.

<sup>2</sup> Note in this connection the work of Prof. Thomas Hume Bissonnette with Starlings, 1930. Studies on the Sexual Cycle in Birds. I. Sexual maturity, its modification and possible control in the European Starling. *Am. Jour. Anat.*, Vol. 45, pp. 289-305.

—intimidation— driving away of other males (and females early in the season) is an effort not only to provide an area in which the young can be reared without competition for food, but primarily to insure the acquisition of a female in approximately the same reproductive cycle as himself, so that their mating periods will synchronize. If he is not successful in keeping other males away, the female which has settled in his territory—when she comes into oestrus is just as likely to mate with some other male as with him. On the other hand, if he permitted the first female that arrived to settle in his territory, he might well get one with which his mating period would not synchronize. Hence the intimidation displays—sexual flights, etc., to determine whether the two birds are approximately balanced before either one comes into the mating cycle. Hence the strong instinct to “dominate” as previously described. Birds in the same reproductive stage are rather evenly balanced and neither one can dominate the other, irrespective of sex. The condition of the reproductive glands is very easily influenced by the metabolism of the bird and by any sense of inferiority. A bird that has developed an *inferiorism* from having been dominated by another may never come into the mating cycle.

Hence, when the male selects his territory, he drives away all others of his kind, male or female, that are not as far advanced in the reproductive cycle as he himself. Finally a female arrives which is in the same rhythm as himself. He drives her out but she immediately returns.—When she stands her ground, he leaves her alone and feeds beside her; when she runs or flies from him, he pursues her, and the “Sexual Flights” described by Howard develop.

If the species is rare, territories large, competition not severe—a lack of synchronized rhythm and resulting infertile eggs is likely to occur. The more common the species, and therefore the greater the competition and the smaller the territories, the greater is the likelihood of absolute synchronism.

Final extirpation of species on the verge of extinction, such as the Heath Hen and the Passenger Pigeon, I believe might well have been accomplished because of a lack of synchronization in the mating cycles of the few males and females left toward the end of their existence, and we can look for the same thing in the Trumpeter Swan, Whooping Crane and Ivory-billed Woodpecker. Failure to

synchronize the mating rhythm may likewise be an important factor in delimiting breeding ranges of species, those few birds at the edge of the breeding range being less likely to produce fertile eggs. The high percentage of infertile eggs among captive birds of all species, where forced matings are necessary on account of the few individuals available, is explainable on this same basis rather than on any inherent weakness of the males. The failure to establish foreign species when few individuals are liberated or the stock widely scattered is likewise explainable on these grounds.

Furthermore, the changing of mates between broods reported by Baldwin<sup>1</sup> and Nice<sup>2</sup> may well be accounted for by the short mating period in the male and the necessity for synchronization with that of the female.

The Hedge Sparrows of Howard that produced infertile eggs after associating for nearly two months were doubtless out of tune. The male may well have passed through his mating cycle before the female came into oestrus.

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The test of a theory is its practical application, and fortunately I was able to test mine on my Ruffed Grouse during the spring of 1933, with rather satisfying results. In the past the fertility of Grouse eggs has averaged about 70% in captivity—in the wild state over 90%. If my theory were correct, I had merely to synchronize the periods of males and females perfectly in order to insure higher fertility. Furthermore, if males are not sex conscious and depend upon their dominating instinct to insure proper mates for themselves, one should be able to bring them into their mating cycle while isolated and determine when they are ready to mate by offering them a stuffed bird as I had done previously with the Cowbird and the House Wren.

Accordingly on March 27 when my male Grouse, which had been kept together all winter, began to fight more actively in an effort to dominate one another, I placed the six worst offenders in separate pens. Some were displaying at this time and some not, but practically all started to display as soon as the restraining influence of

<sup>1</sup> Baldwin, S. P. The Marriage Relations of the House Wrens. *Auk* 33, pp. 232-244.

<sup>2</sup> Nice, M. M. Do Birds Usually Change Mates for the Second Brood? *Bird-Banding* 1, pp. 70-72.

stronger birds was removed. Now if this characteristic display of plumage was an evidence of reproductive maturity and if, as Howard states, the males are ready to conjugate throughout the cycle, each displaying male should have been ready to mate with any female that came into oestrus. This, however, was not the case. On April 12, the first one year old female came into oestrus, as evidenced by her following me about the enclosure and crouching in characteristic pose whenever I reached toward her. This bird was submitted to successive males. Three were disinterested, two wanted to fight and subdue her, but showed no desire to conjugate, and only one attempted coition. This reaction was exactly as I had anticipated, because I had previously offered to each male a stuffed Grouse mounted in the oestrus pose.

I soon learned that it was as simple to determine when a male Grouse had come into his mating cycle as to observe when a female came into oestrus. One had merely to place in his cage each morning a stuffed Grouse or a Grouse skin or a dead Grouse—the exact pose was unimportant so long as it was more or less flattened, or at least not mounted in an attitude of display, and the sex of the stuffed bird was equally unimportant. Depending upon the cycle in which the male happened to be, he would pay no attention to the proffered bird; he would fight it—pecking it on the head and pulling out feathers; or he would attempt to mate with it.

It would be expected from Howard's statement that once a male Grouse had become sexually mature, he would remain so throughout the breeding season. On the contrary, with the males experimented with in 1933, the number of days that each bird was ready to mate varied considerably, but in no case was greater than two weeks. Some males were ready for only two days, and then reacted negatively for from a week to ten days before being ready once more for a few days. Some never came back into the mating cycle and some birds, including the largest, heaviest, and best looking bird I had, never arrived at the mating stage during the entire season.

Now for the practical application of the theory—an attempt to increase the percentage of fertile eggs laid by the captive Grouse. The females were divided into five groups, as follows:

- (1) Six second generation females one year old.



UPPER: (A) NORMAL FEMALES IN PRE-LAYING CONDITION. (B) A LAYING FEMALE WITH ABDOMINAL FEATHERS DEPRESSED.

LOWER: (A) FEMALE IN OESTRUS POSTURE. (B) REACTION OF MALE DURING MATING CYCLE TO STUFFED MALE.



(2) One second generation and five first generation females—one year old—these birds inferior in appearance to group (1).

(3) Two first generation females one year old in a pen by themselves.

(4) Ten first generation females one year old.

(5) Eighteen first generation females two years old.

In pens 1 and 2—no male was given until he had been tested and found ready to mate. He was then placed with the females and watched to see if he were acceptable. The females would immediately try to dominate him as they would any strange bird placed in the flock. If the male was not strong enough to subdue the fighting females (those which had not yet come into oestrus) he had to be replaced by another immediately, lest he be killed by them. If he were strong enough to subdue the females that wanted to fight, he was left for as many days as he gave the proper mating reaction to the stuffed bird when it was placed in the cage each morning. When he was apparently no longer interested he was replaced by another good male, and returned to solitary confinement until he should again come into the mating cycle and be ready to mate with the stuffed bird. This was sometimes a week later, at other times never.

I had learned from experiment that a male would mate with a stuffed bird at least four different times during the day; and whether this was always necessary or not, at least there was a male in readiness for conjugation whenever a female should come into oestrus. How successful the experiment was can be judged by the fact that in pen No. 1, 96% of the eggs were fertile, in pen No. 2, 92%.

In the third pen with two females, one of the females never came into oestrus nor laid an egg, and the one male introduced on April 7 was left throughout the season and apparently synchronized satisfactorily for 12 out of 13 of the eggs were fertile, or 92%.

In pen No. 4 with ten yearling females, males were introduced, one after another, as they came into the mating cycle, until there were five in the large 8 x 36 foot enclosure with the females. This method was unsuccessful because not only did the females raise initial objection to each new male, but the males, previously introduced, raised even more strenuous objection and so much fighting

ensued that it apparently upset all of the birds, both male and female, and very few eggs resulted, and the fertility was but 82%.

In the fifth pen which might be considered the "check," 18 females and nine males (two years old) were kept together all winter and not disturbed during the mating season. A certain amount of fighting naturally ensued, but the birds were rather evenly balanced and serious fights were usually interrupted by other birds. One would naturally expect that with so many males present that at least one would always be in the mating cycle and ready to conjugate whenever a female came into oestrus, but the fact remains that while egg production was better than in pen No. 4, only 70% of the eggs were fertile.

The conclusions from these experiments are the following:

1. The female has an oestrus period when she is ready to mate which lasts from less than a week before the laying of the first egg to about three days before the laying of the last one.

2. When not actually in oestrus, a female is oblivious to sex and attempts to dominate weaker birds just as does a male.

3. Male birds have quite as definite mating cycles as females which last varying periods of from two days to two weeks—possibly longer.

Previous to this period and throughout the period, the males are oblivious to sex differences and do not differentiate between males and females even in mating. At all times they are very sensitive to differences in physical strength and apparently also to *superiorisms* and *inferiorisms* in other birds. Variations in metabolism and in the degree of domination by other birds apparently radically effect the rate of development of the gonads and the time at which the male comes into his mating cycle; possibly also the duration of the cycle.

4. In order to produce fertile eggs there must be absolute synchronization of the two mating cycles, one fertilization perhaps lasting for as many as three eggs.

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Now to apply our observations on Grouse to other birds:

If it is true that birds in general are oblivious to sex differences and that when the male is in his mating cycle he will mate with any bird of his species (and sometimes with other species) that dares to

remain in his territory, then perhaps a mounted bird placed in his territory will be just as acceptable as a receptive female because, of necessity, it must remain immovable and not try to escape. Since the mating cycle is short, however, one can expect quite different reactions on succeeding days accordingly as the placing of the mounted bird synchronizes or not with the mating cycle of the bird experimented with. I have already related my experience with the Cowbird, the Yellow Warbler and the House Wren. In 1933 I experimented with a Song Sparrow (*Melospiza melodia melodia*, Wilson) and a Yellow-breasted Chat (*Icteria virens virens*, Linn.). The experience with the Chat was short and while suggestive, was not altogether conclusive, as I could not follow it through to its natural conclusion. On June 6 I placed a blind at the edge of some shrubbery in a Chat's territory, and erected a dead branch in front of it to which I could fasten a mounted Chat. The only specimen I had for use was the flat skin of a male bird, but I blackened the white cotton eye with my fountain pen and ran a wire into the body of the skin so that I could fasten it to the branch in a semi-natural condition. I entered the blind—gave a few whistles in imitation of a Chat and proceeded to await the arrival of the owner of the territory which had been heard calling when I first came with my blind, but which had been quiet during the operation of setting it up. I had not long to wait. Like a flash of gold he shot from the shrubbery to the prepared branch with his throat puffed out as large as a pigeon's egg and full of clucks and whistles. Wings down, and tail up, he landed on the branch below the skin, and twisting and turning and peering he climbed the branch in characteristic clownish manner. Nor did he waste much time in preliminaries. When the stuffed bird did not fly away or fight back, his one reaction, in the particular cycle in which he apparently was on this day, was to mate with it. There was left little to the imagination, and three different times he advanced to the skin in characteristic manner, mounted it and attempted coition. The third time, owing to the insecurity of the wire holding it, the skin pitched head foremost to the sedges below, where he followed it and attempted once more to mate with it. Having used up my motion picture film and wishing to return the next day for some close-ups of the singing bird, I frightened him away—took the skin and camera with me but left

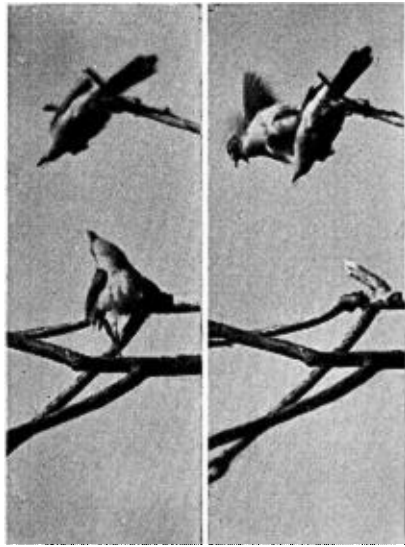
the blind and branch. The next morning when I returned a change had apparently come over the male Chat. He was not calling when I arrived and answered me rather feebly when I whistled. However, I made the same set-up as the day before and attempted to call him to his stuffed mistress. This time, however, he was disinterested. Eventually he came to the branch and looked over the intruding bird but with none of the concentration of the day before, so that the rattle of the camera frightened him away and he did not come back. My assumption is that his behavior paralleled that of my male Grouse which pass abruptly out of the mating cycle, so that while they may be ready to mate with a stuffed bird one day, the next day they register no interest. Owing to other duties I was unable to proceed further with this experiment.

Later in the summer I became interested in two male Song Sparrows (*Melospiza melodia melodia*, Wilson), which had settled in my garden earlier in the season. Each had a female with eggs in bushes about fifty feet apart and on opposite sides of the driveway, which was apparently a boundary to their territories, and where considerable fighting had taken place earlier. On July 8 one of the most severe hail storms I have ever experienced destroyed both nests and the female birds disappeared. What became of them I do not know—nor apparently did the male Song Sparrows, for almost immediately their song, which had almost ceased, was resumed with springtime fervor, and once again they began fighting in the road and flying at one another whenever the boundary was crossed. The birds seemed evenly balanced and each was supreme in his own territory.

It occurred to me that this might be a good opportunity to repeat the Chat experiment. Accordingly I arranged a perch over the deserted nest of one of the birds, on which I fastened a mounted Song Sparrow as in the case of the Chat. I was not able to imitate the Song Sparrow's song, so I merely got into the blind and awaited developments. Soon the male bird in going the rounds of his territory espied the Song Sparrow's skin and swooped down at it in characteristic fashion.<sup>1</sup> It did not fly from him and it did not fight back. According to my theory, if he were in the mating cycle,

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<sup>1</sup> See Relations Between the Sexes in Song Sparrows by Margaret Morse Nice, Wilson Bulletin XLV, June 1933, pp. 51-59.



UPPER: (A) REACTION OF MALE CHAT TO A STUFFED BIRD IN HIS TERRITORY. (B) MALE YELLOW WARBLER THAT FOUGHT AND SANG TO HIS REFLECTION.

LOWER: (A) FEMALE CANADA GOOSE THAT BEHAVED LIKE A GANDER BUT LATER BUILT A NEST. (B) MALE COWBIRD'S REACTION TO A STUFFED FEMALE DURING MATING CYCLE.

he should attempt to mate with it, but this he did not do. He sang rather feebly a couple of times, picked at the label on its leg and departed in the direction of the other Song Sparrow that was now singing. Apparently he was not in the mating cycle or else he was more intelligent than the Chat and recognized a dead bird when he saw it.

To determine which, I captured the other Sparrow at a feeding station and placed it in a small cage (4 x 4 x 12 inches) above the deserted nest. Unfortunately it was necessary to introduce a second factor at the same time, for not only was this captive bird alive but it was able to attempt either to fight back or try to escape, and either reaction would produce a different result in the attacking bird. The reaction of the caged bird, however, was quite unexpected, for though it had accepted its confinement and was not apparently very much afraid of me, when its rival appeared on the scene and tried to reach it through the wire, it was thrown into a paroxysm of fear. I have never seen more conclusive evidence of the power of "domination" of one bird over another. The bird in the cage was perfectly safe from the attack of the other as long as it remained in the middle or on the opposite side of the cage. But the bird on the outside strove frantically to get at it and the bird on the inside fluttered just as strenuously to keep out of reach. After a few minutes both birds were panting as they often had before when they rolled over and over in the drive. This time, however, the caged bird was obviously terrified and made no effort to fight back, and when by chance the aggressor got hold of one of its primaries and held on—the poor thing quivered and expired from the shock. The fight had been of no more duration than many I had watched in the drive, and there had been no mechanical injury to either bird, so that fear and shock alone must have caused the death of the bird in the cage.

This might never happen in a state of nature, but it gives evidence of the sensitiveness of the bird's organization to the dominating influence of others of its kind, and the value, therefore, of intimidation displays, on the part of the male birds in driving away rivals. Carrying the thought still further, the action of natural selection in developing the ornamental or conspicuous plumes, or bright colors or loud songs of male birds may have as its activating

principle—this fear of the rival which was apparently so real to the little caged Song Sparrow as to cause its death; that fear which, in the case of my Grouse, gives them an inferiorism from which they often never recover sufficiently to come into the mating cycle during the entire season. It is difficult sometimes to understand how little differences in color or song can have much survival value, but if their presence indicates greater strength to rival males and therefore helps to produce fear or an inferiorism, then their value cannot be measured by their slightness. They have real value in the eyes or ears of rival males and therefore real significance in the action of natural selection.

Well, what of the victorious little Song Sparrow? Was he exhausted by the experience? Apparently not at all. He mounted to the telephone wire and sang and sang, and eventually a female arrived and built a nest in a neighboring bush and laid four eggs. It was now, however, the first of August, and whether or not he had been in the mating cycle—weeks earlier when he refused to mate with the stuffed bird but killed his rival—he was so no longer, for the eggs never hatched and upon examination proved to be infertile.

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In conclusion let me lay before you for your consideration, further observation, and experiment the following outline of bird behavior during the breeding season which has been forced upon me during the past few years as the culmination of my study of the Ruffed Grouse and the application of my observations on Grouse to other birds:

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1. Birds are not sex conscious, that is, they do not discriminate between the sexes as such.
2. Courtship displays, including song, are one form of intimidation and the stronger bird, irrespective of sex, is the more active performer.
3. Domination and fear are the important principles in the development of secondary sexual characters and even in controlling the mating cycle.
4. Female birds have a short oestrus period during which fertilization must take place. It begins a few days before the laying of the first egg.

5. Male birds have a similar short mating period during which they are able to fertilize eggs.

6. Bird behavior, including the earlier arrival of males than of females on the nesting ground, and of adults than first year birds; selection of territory, song, fighting, and display of plumage are explainable on the basis of the necessity for synchronizing the mating cycles of male and female.

7. In order to insure the propagation of the strongest birds, the virile male must keep all the other males out of his territory and must drive out all females that are not in the same reproductive cycle as himself lest another male mate with his female, or lest he waste his energy on a female that does not synchronize with him.

8. The stage of the reproductive cycle each spring is determined primarily by the vigor of the bird which depends first on *metabolism* of the individual influenced by a great many factors such as age, food, temperature, sunlight, parasites, etc., and secondly by the *mental state* of the individual, and this is determined largely by the results of his conflicts with others of his kind. An inferiorism resulting from a disastrous conflict may keep a bird from arriving at a mating period, while successful conflicts stimulate the development of the gonads which, with most birds, are not fully functional at the time of arrival on the nesting ground.

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