

AN EXPERIMENTAL STUDY OF SEX RECOGNITION IN BIRDS.

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Plates XIV-XV.

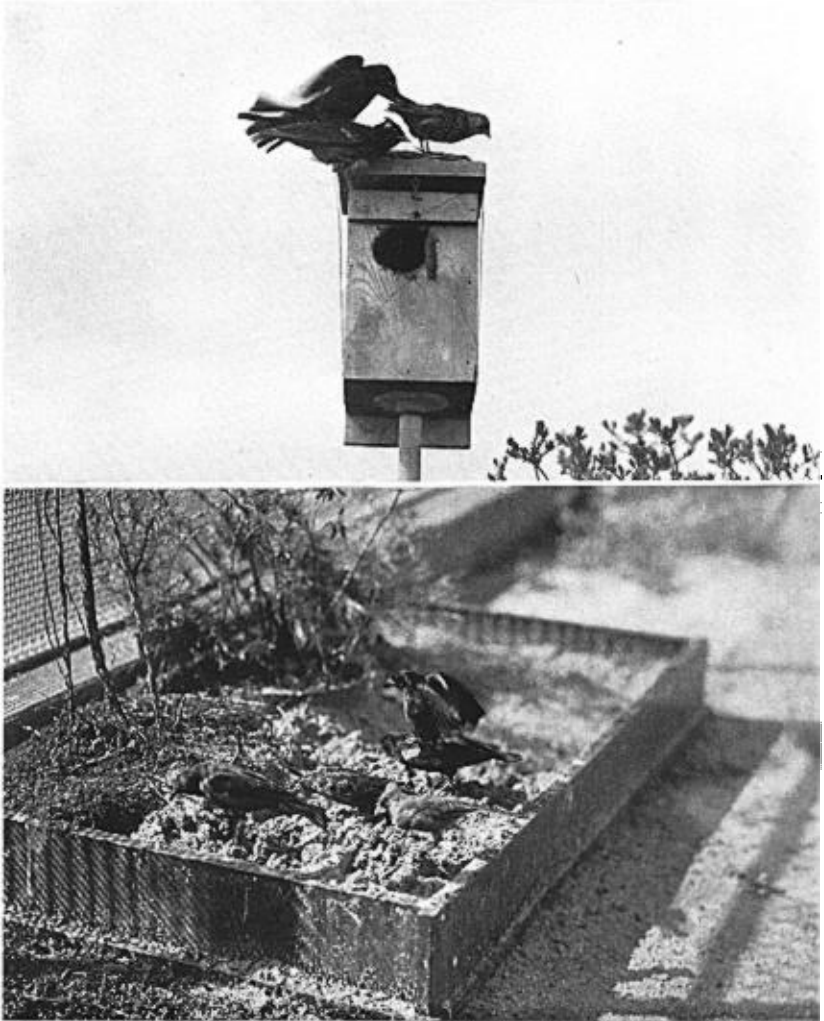
THE methods of sex recognition in domesticated, or at least captive, birds, have been extensively studied by Craig, Whitman, Heinroth, Schjelderup-Ebbe and others, but the conclusions reached by these investigators have not been widely applied to problems of field ornithology. Whitman, in his exhaustive monograph on the behavior of Pigeons, states that captive Mourning Doves, for example, "like ring-doves, do not know the differences between the sexes until they meet and exchange salutations. The male's place is to coo and strut, while the female retreats, bowing and showing herself off if she happens to be disposed. If she does not retreat, the male tests her by pecking and claiming his mastership. The behavior is the only guide they have in selecting a mate of the right sex. This may seem incredible, but it is certain." (Publ. 257, Carnegie Inst., Washington, Vol. 3).

In some domesticated birds, as well as in some wild species, the behavior by which the male identifies the receptive sex may be extremely simple. Long ago Audubon described the fierce conflicts between male Wild Turkeys. When one bird has been killed "the conqueror treads him under foot, but, what is strange, not with hatred, but with all the motions which he employs in caressing the female." In the Ruffed Grouse, where the courtship ceremonies closely approach in their simplicity those of the Turkeys, Allen (Auk, 1934, pp. 180-199) has secured abundant evidence that the male will frequently mate with a prostrate bird of either sex. Allen's experiments led him to conclude that the Ruffed Grouse "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."

This conclusion is at variance with the views of the above mentioned investigators who have studied domesticated birds. Craig, for example, concluded: "The male pigeon usually knows the sex of each bird in the flock, and is always ready to play up to the females. When a new bird comes to the flock he does not seem to be so sure of its sex at first; but he tests it by display behavior. If the newcomer proves to be a male, he then pays less attention to it." (In Whitman l. c.)

In other species of domesticated birds the identity of each individual in a flock is well known to the members of the flock, for each has a particular place in the pecking-order (Schjelderup-Ebbe¹). This is the more remarkable in that individual differences in the members of the flock often cannot be seen by the human observer. If birds are endowed with such a

¹ Forsch. Völkerpsych, Soz. 10: pp. 77-137.



SEX DISCRIMINATION IN RED-WINGED BLACKBIRD.

UPPER: MALE ATTACKS MOUNTED MALE BIRD; MATES ONLY WITH FEMALE.

LOWER: YOUNG RED-WING MALE FAILS TO DISTINGUISH SEX OR SPECIES IN SEVERAL MOUNTED BIRDS.

keen sense of vision and have such a memory for personalities among their bird associates, as Craig, Schjelderup-Ebbe and others have proved, it would seem remarkable that sexually dimorphic birds should not make use of the sexual differences in form or color as visual cues. Nevertheless, in spite of the considerable amount of work in recent years on the courtship of birds, no one has shown by experiment to what extent this holds true.

In view of this situation, we have considered it desirable to test the ability of several species of wild birds to discriminate sex solely on the basis of visual cues. Allen, Chapman and others have shown that males of several species will attempt to mate with mounted females of their own species. Where there is little sex dimorphism, as in the Ruffed Grouse, males will also mate with the skins of males. This was one of the reasons why Allen assumed that birds were not cognizant of sex. No one has previously offered to males of strongly dimorphic species mounted birds of both sexes for discrimination tests. Here, of course, the males would have a greater opportunity of making use of visual cues if these were actually of importance in sex recognition.

We turned our attention first to the Red-wing Blackbird (*Agelaius phoeniceus phoeniceus*) for the species is abundant in the brackish marshes of the Jones Beach State Bird Sanctuary which were available to both of us. We tested males in this area before any females had arrived on their territories. These birds apparently had had no sexual experience for the greater part of a year. Nevertheless, their responses to the female mount were markedly different from those to the male.¹

The following observation, made April 18, 1934, when the temperature stood at 55° F., illustrates the response of a male that has not yet received a female into his territory:

At 8.34 A. M. the male Red-wing fluttered toward the male mount, which had been placed on the edge of bird house well within the territory of this bird. He flattened himself close to the boards and with tail spread, wings drooped and epaulets erected he lifted up his head and sang. After some time he climbed to the ridge on the back of the bird house and began to peck at the male mount. He did this rather casually until 8.44, when he knocked the mount from the house and followed it down into the grass.

Three minutes later, at 8.47, the mount was fastened back to the top of the bird house. The observer had scarcely returned to the observation post when the male flew to the mount and attacked it vigorously. After hammering with his bill for some time he sang for about 10 seconds from the top of the bird house and then once more attacked. This time, standing on the back of the mount, he used his feet as well as his bill.

At 9.00, after this complex response lasting 13 minutes, he pursued another male flying across his territory. (It should be emphasized that up to this time the owner-

¹ The mounted birds employed in this study were loaned by the Department of Education of the American Museum of Natural History.

male did not pay a great deal of attention to nearby males; they were permitted to cross the territory without molestation.) This interloper was driven off, however, and the owner-male now apparently spied the female mount for the first time. This had been placed on another bird house a hundred feet from the male mount but still within the territory of the same owner-male. He rushed to the female mount, copulated with it, flew away, and dashed back to repeat the performance. He then flew in a wide circle, repeatedly giving the *keening* note so familiar to intruders near a Red-wing's nest, but which had not been heard previously this spring.

At 9.03:30 he flew back to the female mount and attempted copulation. He then pecked this mount at the base of the tail, both above and below, before again attempting copulation. It should be noted that the female mount was gently pecked in the cloacal region, whereas the male mount was so furiously attacked in the head as to tear a large hole in the skin. When the male did not evoke a response on the part of the female mount, he again resumed the cloacal pecking until he knocked the mount to the ground.

The male and female skins used in the above experiment were mounted in nearly the same pose. The long axis of the body was nearly parallel with the ground and the head was turned slightly. Later in the season we used a female Red-wing that had been mounted with the tail lifted at an angle of 45 degrees to the ground, and the bill directed downward. The male copulated no more frequently with this bird than with the other. Both female mounts would eventually evoke a gentle pecking in the cloacal region. This was apparently a sign of annoyance on the part of the male.

We were able to secure a differential response to the mounted male and female birds as late as May 26. On this date a male, presumably the same individual tested in the above experiment, copulated with a female mount and fought a male mount when these were placed either together or alternately on top of the same bird house utilized in the above experiment (Pl. XIV, a). The male returned again and again to peck viciously at the male mount, while he usually ignored the female mount. Only twice on this day did the male copulate with the female mount. A mounted female Chewink (*Pipilo erythrophthalmus erythrophthalmus*) and a mounted Starling (*Sturnus vulgaris vulgaris*) in winter plumage placed in the same spot as the female mount had occupied, were entirely ignored. Hence there was not only a sex but a species recognition on this late date. The fact that the male directed his attack only toward the male mount showed that late in the season the male defends his territory more against males of his own kind than against birds of other species. Further, the fact that this bird fought far more frequently than he copulated was evidence that sexual interest fades earlier than an interest in territory defense.

It was a significant fact that while the male, in attacking a male mount during either April or May, usually erected his epaulets, these were less frequently displayed before copulating with the female mount. Hence these ornaments, which are usually assumed to be employed by the males

to stimulate the females to mate, have an even more important function as intimidating devices to be directed against rival males.

We repeated our experiments with the Northern Yellow-throat (*Geothlypis trichas brachidactyla*). Again we selected a male that seemed to have assumed guard over a territory and after making sure that no females had yet arrived in this territory we placed mounted individuals of the two sexes in conspicuous places within this area. These mounts were similarly posed and they were placed in a variety of positions within the territory. Again the male, that had presumably no sexual experience that year, differentiated readily between the mounts. He attacked only the male and copulated only with the female. We recorded 11 attacks on the male mount and 15 copulations with the female. These observations were made on May 11 and 16, 1934.

Since the mounts were similarly posed, it seemed that the male Northern Yellow-throat was discriminating between the sexes primarily on a basis of color pattern. In order to secure further evidence to support this assumption, we drove the bird from the female mount immediately after copulation and quickly placed a mask of black paper across the mount's eyes. This mask was glued to the mount's face and gave a rough approximation to the distinctive facial pattern of the male. Two minutes later the male returned to the mount and began to copulate. Suddenly he jumped into the air and dashed away. Apparently he had seen the mask. This was removed at once but the male did not return until 24 minutes later when he flew at the mount and began to peck viciously the top of the mount's head from above. After a few seconds he slipped posteriorly and again copulated with the mount. Since this was the only attack on the female mount at any time it seems highly probable that the mask, or rather the memory of it, was the disturbing factor.

The above experiments with Red-wings and Northern Yellow-throats show that the males of some dimorphic species clearly distinguish between sex on the basis of visual cues alone. The question arises: Were these sexually experienced birds that had become conditioned to the sexual differences in pattern the previous year? The birds we tested were not banded and we had no way of determining their age. Nevertheless the observations of Whitman and others have shown that birds reared with other species will attempt to mate with these instead of with their own kind when they mature. Aside, then, from any basic pattern of courtship which may be an inherited characteristic of the species, birds become conditioned to their associates. The male Red-wings and Northern Yellow-throats had presumably learned from experience to fight with individuals having the color pattern that identifies the male sex. Although this conclusion would seem certain from the observations of Craig¹ on Pigeons reared in isolation,

¹ Jour. Animal Behavior, IV, pp. 121-133.

we decided to test the question by working out the responses of young birds to mounts. Unfortunately this could not be done in the field because we could not locate the territories of any male Red-wings in their dapple plumage of the first year. Many of these males with yellow epaulets and brown superciliary stripes were congregated on the edge of one of the swamps and we captured a series for testing under controlled conditions. At the same time a series of fully adult males was captured and the two lots were released in a large flying cage, 18' x 6'10" x 7'10". When these birds were offered a series of mounted birds of many species we found that the old birds, those in second nuptial plumage and having bright red epaulets, usually copulated only with the female Red-wing mount, while the birds in first nuptial plumage would copulate with nearly every species presented. Brightly colored species, including a male Cardinal (*Richmondia cardinalis cardinalis*), a Blue Jay (*Cyanocitta cristata cristata*), a Meadowlark (*Sturnella magna magna*), a male Chewink, and a Love Bird (*Melospittacus undulatus* Shaw), were mated with as frequently as were dull colored forms, including a Wood Thrush (*Hylocichla mustelina*), a Fox Sparrow (*Passerella iliaca iliaca*), a Northern Shrike (*Lanius borealis borealis*), a female Chewink, a Rusty Blackbird (*Euphagus carolinus*), a Cowbird (*Molothrus ater ater*), and a female Red-wing. The male Red-wing mount was never attacked by any male, although there was considerable bickering among the live males. This was probably correlated with the fact that all the birds were in a strange territory. Still it is of interest that the copulatory responses continued with as great or even a greater frequency than in the field.

A few of the experiments may be described in detail: May 20, 12.20 P. M. Mounts of a male Red-wing, a Hermit Thrush (*Hylocichla guttata faxoni*), a female Chewink and a male Cardinal were arranged facing the same way and six inches apart in a single row. At 12.22 a fully adult male copulated with the female Red-wing mount. A moment later a first nuptial male mated with the male Cardinal mount. At 12.30 another young bird copulated with the male Red-wing mount. At 12.40 a fully adult male again selected the female Red-wing mount.

Although the males with a maximum amount of red on the shoulders tended to mate only with the mounted female Red-wings, they were not infallible, especially when the test was difficult. One case will illustrate the point:

May 20, 10.02 A. M. The following mounted birds were placed in a row with their long axis making an angle of 45° to the margin of the sand box (Pl. XIV, b) in which they were placed: Cedar Waxwing (*Bombycilla cedrorum*), female Cowbird, female Red-wing, Pine Grosbeak (*Pinicola enucleator leucura*) in winter plumage, male Red-wing and Blue Jay. The Cowbird, Grosbeak and Blue Jay were placed approximately 2 inches higher than the others, making it easier for the birds to mate with them.

At 10.03 a fully adult male copulated with the female Cowbird mount and then turned immediately to the female Red-wing mount and repeated the movements.

At 10.09 another adult male walked past 3 of the mounts and selected the female Red-wing mount to give a series of typical copulatory thrusts.

At 10.10 a fully adult male flew to opposite edge of the sand box and walked deliberately around the Waxwing and female Cowbird to give full copulatory movements while clinging to the back of the female Red-wing mount.

At 10.14 a first nuptial male copulated with the Blue Jay.

At 10.45 the series of mounts was arranged: female Robin (*Turdus migratorius migratorius*) female Red-wing, male Red-wing, female Cowbird and male Cardinal, in single file and only 2 inches apart. The female Cowbird was placed half an inch higher than the others but since it was not next to the female Red-wing there was presumably less chance for confusion.

At 10.52 a fully adult male walked deliberately around the Robin and copulated with the female Red-wing.

Between May 17 and June 5, 11 male Red-wings were tested with the mounted birds arranged in a great variety of ways. During this time the males with the maximum amount of red on the shoulders selected the female Red-wing mount and copulated with it on 37 different occasions. Only 7 times did these same males copulate with mounted birds of other species or with mounted males of their own kind. On the other hand, male Red-wings that were undoubtedly birds of the first season, selected and copulated with the female mount of their own species only 3 times while they exhibited copulatory behavior 24 times with mounts of other species or with mounted males of their own kind. On 28 different occasions, the male Red-wings that copulated with mounts of other species or with males of their own kind were birds of intermediate age. Some red was present in the epaulets but there was less of this color than on the fully adult birds. These birds lacked the buff of the males in the first nuptial plumage. Since the male Red-wing in approaching the mounted bird to copulate rarely displays, it was difficult to be sure that some of these intermediates were not fully adult. This grouping of the birds into fully adult, definitely young and an intermediate group, while inexact, was sufficiently definite for the purposes of this experiment. The young birds tested in exactly the same way as the birds with maximum amount of red had far more difficulty in selecting females of their own species. But even the males with the maximum amount of red did not make perfect scores and no doubt the crowded conditions in the flying cage made selecting of the proper mount far more difficult in the laboratory than in the field.

As stated above, Allen and others have shown that some birds with little sexual dimorphism are apparently incapable of recognizing the sex of birds of their own kind. The question remains, Are these birds capable of distinguishing their own kind from other species approaching them in form and color? We have tested this question with the House Wren (*Troglodytes aedon aedon*). A male House Wren that was cleaning out a bird house shortly before a female joined him in his labors was tested on May 9 with

a mounted House Wren of unknown sex. He copulated with the mount at once. On May 12, after the female had arrived, he was tested again and with the same result. The female attacked the mount twice, but soon both birds grew indifferent to the mount. On May 19, a mounted Winter Wren (*Nannus hiemalis hiemalis*) and a mounted Long-billed Marsh Wren (*Telmatodytes palustris palustris*) were placed alternately where the mounted House Wren had been. The male copulated with the Winter Wren and ignored the Long-billed Marsh Wren. Very soon, however, he grew indifferent to the mounts.

On June 17, this same male, apparently, had moved to the vicinity of another bird house and was calling for another mate. The House Wren, Winter Wren and Long-billed Marsh Wren were placed in a row 3 inches apart on one of the stout branches of a rose bush near the house. In the course of 2 hours the male had copulated 7 times with the Winter Wren, twice with the House Wren, and had approached the Long-billed Marsh Wren only once in a mating attitude. The Winter Wren resembles a House Wren far more closely than does the Long-billed Marsh Wren and hence it was not surprising to find the male more interested in the mounted Winter Wren. It was, however, interesting to note that the House Wren would mate as readily with the mounted Winter Wren as with a mount of his own species (Pl. XV, b).

Although the unrestrained Red-wing males had shown no interest in mounted birds of other species and had neither attacked them nor displayed any sexual behavior toward them, the question remained: To what extent are other sexually dimorphic birds so discriminating? We have tested 3 male Golden Pheasants (*Chrysolophus pictus* (Linn.)) at the Jones Beach State Bird Sanctuary. One of these had killed his own mate a week previously and the others had mates in the cages with them during the experiments. A mounted female Ring-necked Pheasant (*Phasianus colchicus torquatus*) when placed in the cage of the lone male, in either a standing pose or a prone one, called forth first a display, and later copulatory movements. Sperm preparations were secured during these movements. A Golden Pheasant male mounted in the same pose, in the cage of this bird, brought forth no display and no mating, even when his legs were buried until his body made contact with the ground (Pl. XV, a). A Ring-necked male also stimulated no courtship behavior, no matter what the pose. On the other hand, a female Silver Pheasant (*Gennaemus nycthemerus* (Linn.)) mounted in exactly the same pose as the other mounts, called forth a display but not a persistent one. The Ring-necked female resembles a Golden female more closely than does the Silver. Hence, the greater the divergence from the female Golden type, the less the persistence of courtship.

A live Golden Pheasant introduced into the cage called forth a vigorous

attack. Here were factors of cage ownership and threat of attack entering in. A mounted male Golden Pheasant, in the cage with a mated male, had its head ripped to pieces by the enraged owner. These observations, although few, clearly show that a male Golden Pheasant a week after the loss of his mate can distinguish between the sexes, and not on the basis of posture but presumably on the basis of color pattern differences.

The male Golden Pheasant, unlike the male House Wren, Northern Yellow-throat or Red-wing Blackbird, displays to the female mount before copulating. The Wren would frequently raise his wings to a horizontal position and flutter them nervously while hopping rapidly toward the mount. Male Red-wings would also elevate their wings during their approach, but this was not a definite display such as the Golden Pheasant exhibited. Friedmann (The Cowbirds) has shown that a male Cowbird will display to a mounted female. This difference in mode of response to a mounted female is correlated with the greater amount of display in the courtship of the Cowbird and Golden Pheasant than in that of the Wren. It is interesting that the Red-wing, which is frequently supposed to display with his epaulets, should react toward a mounted female more as the Wren does, than as the Pheasant. It raises the question of the real function of the epaulets in the social life of the Red-wing.

Many birds exhibit a series of mate feeding or sham nesting ceremonies instead of display during courtship. No one has previously tested the responses of this group of birds to a mount. We have made a single experiment with the Common Tern (*Sterna hirundo hirundo*). A mounted bird placed near a nest of 3 eggs in a Tern colony on South Oyster Bay induced well marked courting responses in a bird that may or may not have been the owner of the eggs. The bird approached the mount in silence, settled down on the sand, and revolved on its breast to make a "cock nest." While revolving, it kicked sand out behind with vigorous thrusts of its small feet. Then it rose in the air and settled behind the mount to make another cock nest on the other side. As shown by Tinbergen (Ardea, XX, pp. 1-18) this is part of the typical courtship of the Common Tern. Whether the courtship would have reached the fish passing stage earlier in the season is impossible to say. Chapman¹ found that the courtship of Gould's Manakin was shortened in the presence of a mounted bird. It is possible that the silent, quiet form of a mounted female is sufficiently stimulating to make other birds abbreviate or entirely give up their courtship. The behavior induced by a mounted bird may give a very incomplete picture of the full courtship of a species. Nevertheless, the mounted bird technique as employed in the experiments reported above has shown that some wild and domesticated birds recognize sex difference and carry these differences in their minds for long periods.

¹ Natural History, Vol. 32, pp. 470-480.

CONCLUSIONS.

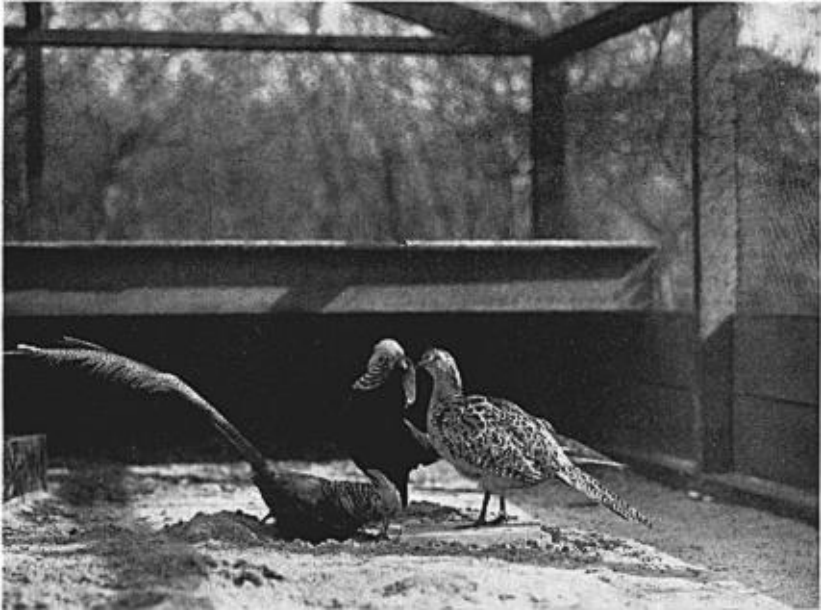
The male Red-wing Blackbird (*Agelaius phoeniceus phoeniceus*) and the male Northern Yellow-throat (*Geothlypis trichas brachidactyla*) can distinguish the sex of mounted birds of their own species, even early in the year before females have arrived on the breeding territories. These highly dimorphic birds are therefore sex conscious at this season in that they respond differentially to sex when only visual cues are available to them.

Under laboratory conditions, Red-wing Blackbirds in the first nuptial plumage are less successful in selecting mounted birds of their own species and opposite sex than are the fully adult males. Even under natural conditions, a bird may not be able to select his own species with accuracy. A House Wren (*Troglodytes aedon aedon*) will mate as frequently with a mounted Winter Wren (*Nannus hiemalis hiemalis*) as with a mounted bird of his own species. On the other hand, a mounted Long-billed Marsh Wren (*Telmatodytes palustris palustris*) is usually avoided.

A male Golden Pheasant (*Chrysolophus pictus*) will court and mate with a mounted female Ring-necked Pheasant (*Phasianus colchicus torquatus*) or court a mounted female Silver Pheasant (*Gennaecus nyctemerus* (Linn.)). The latter, which diverges more from the pattern of the Golden female, aroused less interest in the Golden Pheasant. The posture of the mounted bird has no influence on the type of response. Mounted male Pheasants are either ignored or attacked but not courted.

A mounted Common Tern (*Sterna hirundo hirundo*) will call forth a courtship performance in a breeding bird. The Tern and the Pheasant differ in their response from the House Wren, Northern Yellow-throat and Red-wing Blackbird, which usually attempt to mate without courtship. This difference in behavior is correlated with the more elaborate courtship performance of the first two species.

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RESPONSE OF MALES TO MOUNTED BIRDS OF OTHER SPECIES.

UPPER: MALE GOLDEN PHEASANT DISPLAYS TO MOUNTED FEMALE RING-NECKED;
IGNORES MOUNTED MALE GOLDEN.

LOWER: MALE HOUSE WREN MATES WITH MOUNTED WINTER WREN IN PREFERENCE
TO MOUNTED HOUSE WREN.