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OBSERVATIONS ON THE BREEDING BEHAVIOR OF THE RING-NECKED PHEASANT

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The object of this study was to follow the behavior of individual, wild Ring-necked Pheasants (*Phasianus torquatus*), particularly cocks, through the breeding season in order to ascertain and interpret the various behavior patterns and apply this knowledge toward a better understanding of the total reproductive effort of this species.

The breeding behavior of the Ring-necked Pheasant in the wild has been studied and observed in part by many authors. Bent (1932) has assembled much of the work done in this country prior to 1931, including that of Leffingwell (1928); in addition, he quotes Millais (1909), the student of English game birds. Beebe (1931) and, more recently, Kozłowa (1947) have given partial descriptions of the breeding behavior of several members of the genus in their native habitats. Wight (in McAtee, 1945) was the first to describe the entire breeding season of this pheasant from the game manager's viewpoint; Hiatt and Fisher (1947) have critically examined some of Wight's findings and added new data. Baskett (1947) has made incidental observations on breeding behavior and examined the problem of territoriality. Einarsen (1945) has described some aspects of social friction in a high-density population. Several of these papers appeared subsequent to the inception of the present study in 1947.

The study area consisted of a 349-acre marsh lying along Nine-Springs Creek in the Town of Fitchburg, Dane County, Wisconsin, and the surrounding uplands. This marsh, which includes the Nevin State Fish Hatchery Refuge, is typical of winter pheasant habitat in southern Wisconsin. It has been described by Buss (1946:29), who did much of his work on pheasants in the area: "At one time the marsh . . . was a shallow lake, but drainage in 1922 converted it into a marsh which now consists of optimum cover for pheasants. A spring-fed stream flows from the Madison Fish Hatchery adjoining the marsh to the center of the marsh where it joins the drainage system. Numerous springs that arise within the marsh meander to the ditches. Both the spring(s) and the ditches are densely grown to water cress (*Radicula officianale*) The stream bank is grown to willows (*Salix* sp.), while the ditch banks are covered with a succession of giant ragweed (*Ambrosia trifida*), nettle (*Urtica gracilis*), and some elder (*Sambucus canadensis*). Dredging, plowing, grazing and burning at various times and places within the marsh have caused a variety of plant successions. Part of the succession is original and ungrazed." The principal winter roosting cover is formed by stands of *Phragmites communis* on slightly elevated areas and *Carex stricta* in the lower spots. The uplands are under cultivation, in part; the principal crops are corn, hay and small grains.

The various genetic strains of pheasant which have been interbred at the Wisconsin State Garm Farm have been discussed by Leopold and Grimmer (in Buss, 1946:15-17). While it is impossible to describe with accuracy the exact mixture represented by the wild pheasants on the study area, their appearance is that of *Phasianus torquatus* as described by Delacour (in McAtee, 1945:8).

Drive censuses of the study marsh were made by the staff and students of the De-

partment of Wildlife Management, University of Wisconsin, in the winters preceding the periods of observation, those of 1946-47 and 1947-48:

Date	Cocks	Hens	Total	Ratio
January 25, 1947	43	119	162	28:100
January 24, 1948	81	231	312	35:100

A crew of about 20 men in line systematically beat through the marsh, counting those birds which flew out of the marsh or into an area already covered. This census method is more fully described by Leopold (1943:383).

Trapping and banding of this population have been carried out during the winters from 1940-41 to 1946-47, inclusive. The complete file of trapping records at the Department of Wildlife Management for these years facilitated the checking of previous age and weight records for retrapped birds. In the seasons of 1946-47 and 1947-48, the author did all the trapping in this marsh; this afforded him opportunity to mark numbers of birds.

Season	Cocks trapped	Hens trapped	Total	Sex ratio	Previously marked	
					Cocks	Hens
1946-47	12	85	97	14:100	10	62
1947-48	38	170	208	22:100	32	131

In 1946-47, the markers consisted of dyed chicken contour feathers glued to the pheasants' contour feathers, plastic tail plaques of the type described by Trippensee (1941), and plastic tags glued to the pheasants' contour feathers. In addition, each trapped birds was banded with an aluminum band on one leg and an overlapping plastic band (numbered) on the other.

Although a number of birds were identified individually during the following breeding season, the markers were not considered satisfactory. The following winter the marking problem was solved satisfactorily by use of a new type of marker (Taber, 1949). This marker consisted of a pair of numbered rubber film tags, one projecting in front of each wing, which were attached to a silver-plated safety pin fastened through a pinch of skin at the back of the bird's neck. In addition, each bird trapped the second season was banded with colored aluminum bands in an individual combination; these bands were colored by the Alumilite process of the Chicago Thrift Company.

The yearly period of observation started each season in February as soon as the first breeding behavior was noted. It extended until September 6 in 1947 and June 24 in 1948. Hours of observation totaled 204 on 116 days in 1947 and 82 on 52 days in 1948. In the first season, a limited area was studied intensively; in the second season, this intensive study was continued but an effort was also made to follow the seasonal changes of the whole population. Two 20-foot portable tower blinds, five tree blinds and eight ground blinds were used as the occasion warranted. Every effort was made to keep from disturbing the birds during periods of observation. Most of the observations were made with the aid of a 20× telescope loaned by the Wisconsin Conservation Department.

Since no phenological differences were observed in the two consecutive breeding seasons, the discussion is presented as though it pertained to a single season. The actual year in which an observation was made, however, is indicated in every case. The various stages of the breeding season have been related to the stages in the development of the gonads of cocks, as shown by a concurrent study of pen-reared birds (Greeley, MS).

THE EARLY BREEDING SEASON

Prebreeding season.—The prebreeding season lasted until late January. In December and January, the pheasant population was distributed generally through the marsh. While a few birds left the marsh in the daytime to feed in shocked corn in the nearby

uplands, the bulk of the population fed in the marsh. All birds roosted there. There seemed to be a rough segregation of sexes. Although the birds were generally in groups, the composition of each group was continually shifting (Collias and Taber, MS).

During this period, the only call heard was the cackle of the cock. This was given either as one flew off when suddenly startled or spontaneously from the ground, espe-

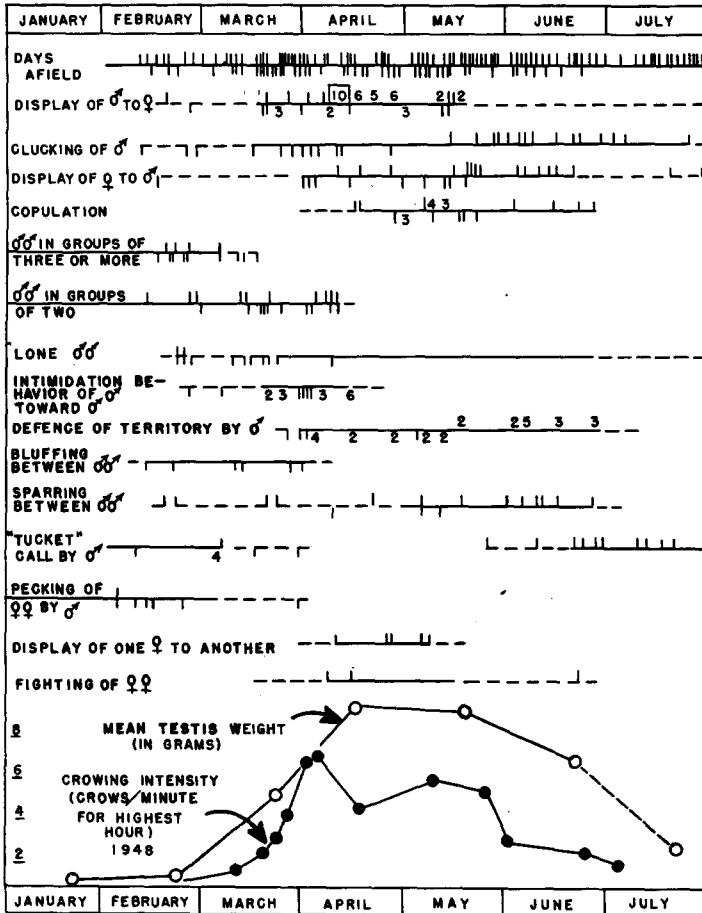


Fig. 21. Comparison of behavior with testis weight and crowing intensity. Figures above the lines indicate number of times behavior was observed on given date in 1947; those below lines, number for 1948; numbers of 10 or more are boxed. A solid line indicates behavior was common or continuous; broken line, rare or discontinuous. Data on testis weight obtained from Greeley, who examined 12 individuals per month from July, 1947, to June, 1948. Crowing records only for clear, calm mornings in 1948.

cially in the late evening. An evening cackle was sometimes answered by a second cackle from a different cock. This call has been described by Leffingwell (1928:24) as a trisyllabic call, *tucketuck*; it is given in a series which trails away at the end.

The transition period.—The period of transition from the prebreeding to the breeding season lasted from late January to the middle of February. About January 20, a

new call was heard which seemed identical with the alarm call or two-syllabic *tucket* described by Leffingwell (1928:24). Since this call is reported to be an alarm note, and since it has been observed to be given by startled cocks at all times of the year (Aldo Leopold, verbal communication), it might be supposed that its occasional rendering about the end of January had no significance. However, since it diminished as crowing built up at the beginning of the breeding season, and became more common as crowing diminished at the end of it (fig. 21), I believe it to be a transitional call, indicative of a close approach to the crowing threshold. When heard in late January and early February, it was given in series, each *tucket* covering an interval of about half a second. It was unlike the cackle in that it did not terminate in a trailing diminuendo and was never given in flight.

In early February, there was a concentration of pheasants in that portion of the marsh which lay adjacent to the newly-manured fields. Whether the concentration was based wholly upon this new food supply or was connected with the urges of the incipient breeding season, I do not know; however, it was my impression that the concentration of birds began before the manure was spread.

Pecking of hens by cocks during feeding, indicative of sexual quiescence (Collias and Taber, MS) continued until mid-February (fig. 21). In late January and early February of both years, groups of from two to ten cocks began to work out from the marsh-edge in the daytime, returning to the marsh to roost at night. No sexual antagonism was detected among these birds at this time.

A study of the testis weights of southern Wisconsin pen-reared birds (Greeley, MS) showed that the testes were increasing in weight very slightly during this period from late January to mid-February (fig. 21).

Period of first breeding behavior.—The first breeding behavior took place between mid-February and mid-March. Wight (in McAtee, 1945:143) states that the behavior typical of the breeding season is first observed in the first warm days of February. Such was the case in both seasons in the present study. Male behavior patterns of the breeding season may be divided into those directed toward hens, or courtship behavior, and those directed toward cocks, or antagonistic behavior. A similar division may be made in the behavior of hens.

Courtship behavior.—In 1948, the most dominant cocks began to cluck and display to hens sporadically in mid-February (fig. 21). The clucking was of two sorts, a conversational cluck and a food call. The conversational cluck has been described by Kozłowa (1947:424) for *Phasianus colchicus bianchii* as "a number of confused, low cooing notes . . . *coo - coo - coo - co - co - crow*, with a slight howl at the end of the cooing, heard now and then." Also described by Kozłowa (1947:425) is the food call, which she calls "a softly muttered *kutj - kutj - kutj*." My observations agreed with these descriptions except that the food call as heard by me seemed to be rather clear and definite rather than softly muttered.

The display of the cock to the hen has been described many times. That observed in this study agreed with published descriptions in being a lateral display, the tail and back feathers of the cock being shifted toward the hen, the tail spread, the pinnae raised, the wing dropped, the contour feathers raised and the wattles swollen. With head held low and close to the breast, the cock strutted in an arc around the hen (fig. 22c). If she ran a few steps, as she usually did, he either stopped displaying or ran after her with head held low and against his breast and rump elevated (fig. 22a), and displayed again; if she stood still when he had completed his strut, however, he remained stationary in full display until she moved. As many as 12 displays in series have been observed in late February, but early season displays were generally in shorter series.

During the early breeding season, the wattles of the cock diminished rapidly to their resting condition after each series of displays was completed. The nature of the wattles has been studied intensively by Regnier (1927) who found them to be secondary sexual

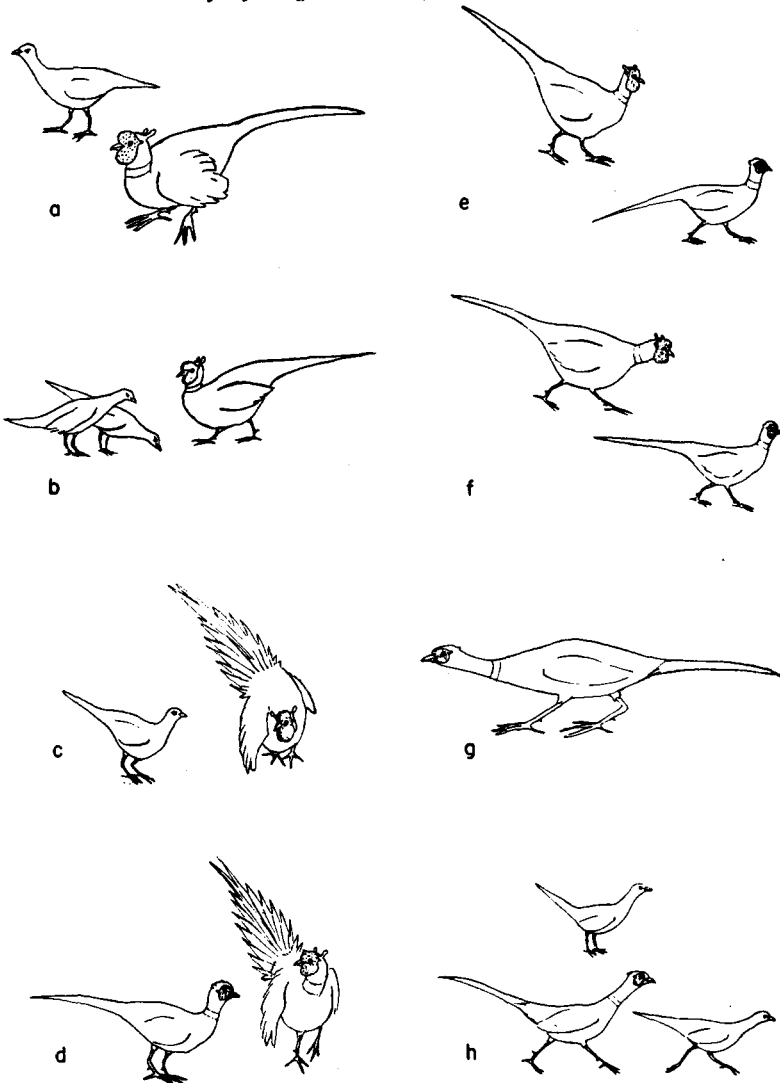


Fig. 22. a. Predisplay run of cock in courtship; b. predisplay run of cock upon re-entering his territory; c. courtship display of cock to the hen; d. intimidation display of dominant cock to submissive cock; e. walking pursuit of dominant cock toward submissive cock; f. running pursuit of territorial cock toward intruding cock; g. pose of non-territorial cock while trespassing upon a territory; h. non-territorial cock chasing hen, illustrating lack of pre-display run.

characters developing suddenly with the onset of spermatogenesis. Wodzicki (1931) describes the arrangements of blood vessels which provide the mechanism of their erection.

Leffingwell (1928:11), in a description of the display which otherwise agrees substantially with that given above, says, "Apparently the air sacs are partly inflated, for

after the pose is held for several seconds the plumage is allowed to fall back in its natural position as the bird gives out a hissing sound." The hissing sound has also been described by Kozłowa (1947:424) who further states that it is accompanied "by a low clapping, brought forth by the vibration of the tail feathers, which sounds like the flutter of a large sail in the winds." Neither of these sounds was heard by me, possibly because of imperfect hearing in the higher ranges.

Not all cocks displayed during the early breeding season; those that did display seemed to limit their attentions to certain hens. These particular hens exhibited some postures of which I can find no published description. These consisted of the following: a half-squat, of extremely short duration, as if the hens' "knees" had buckled momentarily; a flirting hop, like that of a tethered hawk, consisting of a short horizontal jump, made with the wings slightly opened and both feet off the ground; and a stretch, in which the wings were opened and raised while the hen rose up on her toes and stretched her neck. None of these poses was oriented strictly toward the male although all took place near a male (fig. 25). The presence of one or all these patterns in the action of a hen, along with a nervous, jerky manner of walking and occasionally a definite depression of the tail seemed to stimulate courtship display by the cock. Since these actions in the hen were relatively inconspicuous, the frequency and duration of their occurrence through the two seasons as shown in figure 21 may be inaccurate.

Antagonistic behavior.—Antagonistic actions between cocks consisted of bluffing, sparring and intimidation display. In a bluffing contest, two cocks of approximate equality in dominance stood facing one another or stalking along parallel to one another with heads held high. A few seconds after the start of the contest their neck hackles rose, their wattles swelled and they emitted a hoarse *krrrrah*, a pose and call of which I can find no published description. One of the contestants then generally gave way, but if this did not happen a sparring contest sometimes ensued. Fragmentary observations in dense cover indicated that the same growling call might be used as a warning by a dominant cock against an inferior.

In a sparring contest, the two antagonists crouched beak to beak, or walked on parallel courses, heads low, one occasionally pecking at the other. At intervals one or both would spring into the air like gamecocks. This behavior is very conspicuous and so the ratio of observation to occurrence should be high. It is significant, then, that sparring during the early breeding season was very rare. This is contrary to the findings of Wight who said (1930:223) that "Actual fighting apparently occurs only early in the season before or at the time of mating."

The intimidation display, which was made by one cock to another, was similar to the courtship display of the cock to a hen. There were, however, differences between the two displays. The intimidation display was not as complete, the wing being but partly spread and the lateral display of the plumage not as extreme. In addition, the cock giving the intimidation display almost never strutted, but displayed from one position, following the other cock, if he should run a few steps, with the same head-down, rump-up run that precedes display to the hen. Lastly, the head of the displaying cock was held high during the intimidation display (fig. 22d) whereas it was held low during the courtship display (fig. 22c).

While I have found no previous description of this behavior in the pheasant, intimidation displays which resemble courtship displays have been observed in many birds, including the Ruffed Grouse (*Bonasa umbellus*) (Allen, 1934; Bump, *et al.*, 1947).

The intimidation display was commonly given only once, although occasionally several were given in succession. In complete form it was preceded by the predisplay run described above and followed by the walking pursuit (fig. 22e), in which the pursuing

cock, feathers fluffed and wattles full, stalked along slowly after the other, who avoided him. As seen in figure 21, where these three postures are grouped as "intimidation behavior," they were more common after mid-March than during the period of first breeding behavior (mid-February to mid-March). Antagonism between hens was manifested in much the same way that it was among cocks (see p. 171).

As a result of the growing antagonism between cocks during this period, the cock flocks were almost all reduced to groups of two by mid-March (fig. 21). As early as late February (fig. 21), a few lone cocks had established a daily route covering essentially the same ground that would form the territory in April. They did not, however, defend it as this time.

Crowing.—Crowing, being the song of the pheasant, partakes both of courtship and antagonistic behavior. In this area, crowing has first occurred in past years anywhere from early January to early March (Leopold, 1947:86). In 1948, the first crow was heard on February 18; thereafter, crowing was generally infrequent until mid-March, but it was heard every morning when more than an hour's observation was made.

Summary of events of the early breeding season.—1. During a transition period which extended from late January through early February, testis growth was just beginning, the *tucket* call was characteristically heard, there was a concentration of birds in one part of the marsh and cock flocks appeared on the marsh edge.

2. During the early breeding season, which extended from mid-February to mid-March, there was courtship display by cocks to hens and antagonistic behavior between cocks. Crowing began and the first lone cocks were seen during this period, near the end of which the cock flocks had been reduced to groups of two.

SPRING DISPERSAL PERIOD

During this period, from mid-March through April, the average testis size increased rapidly and reached its peak. Courtship behavior, both of cocks and hens, now became more general (fig. 21).

Antagonism between cocks.—Baskett describes the breakup of cock flocks as follows (1947:6): "In early spring, the males become progressively less companionable and by March immediate proximity of two usually results in strife." Such was not found to be true in the present study. Dominant cocks were generally separated from each other by the end of February, but submissive cocks continued to associate with dominant cocks in some degree until mid-April. These associations were in pairs after mid-March. Beginning about mid-March, the tension between the members of a pair of cocks rose, especially in the dominant member, and was expressed by increasingly frequent intimidation displays and walking pursuits directed at the submissive member (figs. 22e and 22f). The wattles of the dominant cocks were swollen most of the time and their body feathers were held out, giving the impression of bulk. The wattles of the submissive cocks swelled only when they displayed to hens or to other cocks of low dominance, both of which they occasionally did during this period; their body feathers were generally held flat.

The last cock pairs broke up in mid-April. Thereafter the dominant cocks endeavored to keep all other cocks away from their territories; the submissive cocks generally remained in the same general area but did not defend territories.

Crowing.—Crowing intensity (measured in crows per minute for the highest hour) rose rapidly through March, reaching a first peak in early April. This rise could have been due to one of two causes: (1) increase in the number of crowing cocks; (2) a rise in the crowing intensity of individual cocks. While both of these occurred, the effect of the first is believed to have been greater.

Individual cocks continued to push out of the marsh into the uplands through March, but by late March only a few were established in the uplands. About the first of April, however, as the new growth of vegetation increased, the spring dispersal became general. This is shown graphically in figure 21, through the rapid drop in crowing intensity to mid-April. Since the crowing counts were taken in the marsh, cocks moving

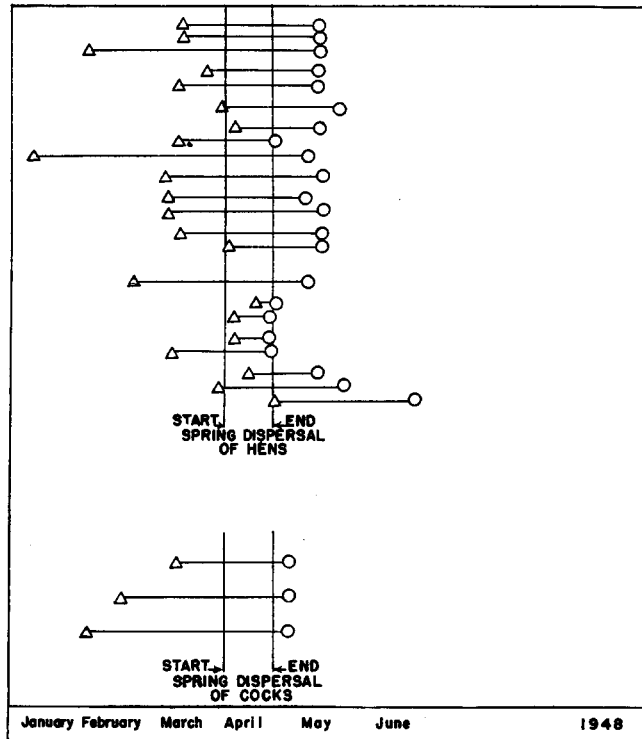


Fig. 23. Records of individual birds before and after spring dispersal. Triangles mark last observation in marsh; circles, first in upland. Vertical lines mark principal period of dispersal.

to the uplands beyond earshot were not counted. There are, of course, other possible explanations of this sudden drop. Some cocks may have stopped crowing; this is possible, but is considered unlikely. Cocks in general might crow at a lower intensity, but where individual birds were followed this did not occur.

In addition to this negative evidence, there is positive evidence of an exodus of crowing cocks from the marsh. Figure 23 shows the last dates on which three marked cocks were seen in and around the marsh and the first date of subsequent observation in the uplands. The data for hens are more complete. Twenty-two hens were seen both in the marsh and, later, in the uplands in this period. Additional evidence of the departure of hens from the marsh during early April, 1948, is presented in figure 24. Here the frequency of hen observations around a mid-marsh observation post is shown to have dropped off sharply from the end of March to mid-April. The coincidence in time of this drop with that of crowing intensity (fig. 21) is striking.

To sum up this evidence, there appeared to be a dispersal of both cocks and hens

from the marsh during March and April of 1948, with most of the movement starting in the first two weeks of April.

Similar spring dispersal periods have been reported in other studies. Randall (1940: 304), writing of Pennsylvania, states that a spring movement from winter cover occurred during late March and early April. Baskett (1947:7) mentions a movement away from winter cover concurrent with the breaking up of winter bands of pheasants in Iowa, and states that ". . . as dispersal progresses, males begin crowing." This is contrary to the evidence of the present study, which indicates that crowing began before much dispersal had taken place. A more detailed study of spring dispersal has been made in South Dakota (Janson, 1947). There a ten-mile movement from winter to summer range

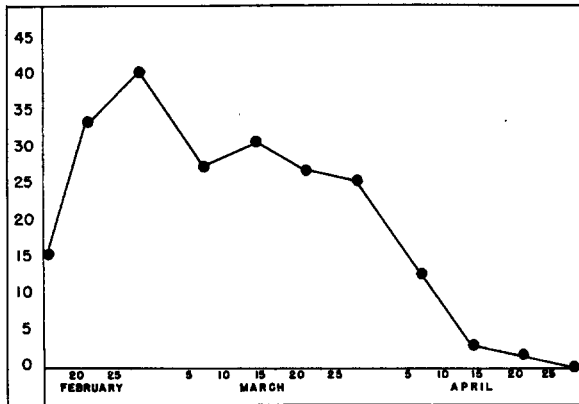


Fig. 24. Number of marked hens seen about a mid-marsh feeding station in 1948. February peak reflects period of large-scale marking.

was traced by means of crowing intensity samples. This dispersal began in late March.

Because the density of the vegetation hinders observation, it is not practicable to measure directly the proportion of the cock population leaving the immediate vicinity of the marsh during this dispersal period. Such a measurement might, however, be achieved indirectly. The rise in crowing intensity of the "normal" cock as the season progresses could be determined from an average of individual counts and this curve magnified until its peak coincided with the second peak in the seasonal crowing curve (fig. 21). The difference, then, between the hypothetical curve and the first peak in the seasonal crowing curve should give an approximation of the proportion of cocks moving beyond earshot.

Distribution of birds in the uplands.—During May and June, 1948, 26 hens, which had been marked the previous winter in the "hatchery" marsh, were found in the surrounding uplands; most of them were within one-quarter of a mile of the marsh. Another was found, dead, six miles away in the center of the city of Madison; it had been run over but how it reached that spot was not ascertained. Since there is no question as to the origin of these hens, a spring dispersal, up to one and a half miles is demonstrated. Most of these hens were observed in harems in early May but three were killed during mowing in late June or shortly before.

Summary of events of spring dispersal period.—1. Antagonism between cocks resulted in the dissolution of cock pairs in early April.

2. A spring dispersal period in March and April was indicated by sight records; the principal period of dispersal was shown to be late March and early April by mid-marsh crowing intensity counts and by sight frequency records.
3. The greatest observed radius of spring dispersal of hens was one and a half miles.
4. Cocks showed a rapid gonad weight increase through the whole period.

PERIOD OF COURTSHIP AND MATING

In the spring dispersal some birds went no farther than the marsh edge. These marsh edge birds were studied intensively and the subsequent accounts are based on them. The period of courtship and mating started in April and continued through June.

Period of territory establishment.—Territories were established during the first half of April. The increasing tension between pairs of cocks that culminated in the complete breakup of cock flocks has already been described. This disappearance of cock pairs, although complete by mid-April, was accomplished largely in early April; the final rupture between pairs was characterized by the change in the dominant member from a display pose (figs. 22d and 22e) to a chasing pose (fig. 22f). The appearance and duration of the chasing pose are shown in figure 21, as "defense of territory by male."

As soon as a given cock had begun consistently to chase off any other cock, he was considered to have a territory. Although territories were first defended during the first two weeks of April, the actual daily ranges of individual dominant cocks along the marsh edge did not change essentially from February through June. Not all cocks established territories; those not doing so were usually of low rank in the dominance order.

Crowing.—Despite the drop of total crowing intensity due to spring dispersal, the crowing frequency of individual cocks continued to rise during the first half of April.

Courtship.—The first half of April was the period of greatest courtship display activity. Not only the territorial cocks but also some nonterritorial cocks displayed. This was possible in the case of the latter because the hens were not so closely oriented toward territorial cocks as they were in the succeeding period, tending to wander somewhat more within their habitual range. Thus they often foraged beyond the orbits of the territorial cocks and the nonterritorial cocks could then court them with impunity.

In the typical courtship of the early breeding season (mid-February to mid-March) the hen being courted ran, after each display, in such a way that in the course of a series of displays the cock and the hen often covered a considerable distance (30 to 150 yards) in a straight line. In early April, however, this type of movement on the part of the hen was gradually replaced by one in which, while still eluding the cock, she remained in a circumscribed area.

Formation of the harem nucleus.—Like the cocks, hens in general used one area habitually every day through the early breeding season (mid-March). Subsequently, a number of hens dispersed from the marsh. Certain hens, however, did not change their daily range appreciably and these formed the nucleus of the marsh-edge harems. In one particular cornfield, which was a well used feeding area during the early breeding season, the membership of these early-April harem-nuclei was studied in both years. After the period of spring dispersal, it was found that the majority of hens remaining were two years old or more. In two harems studied intensively, one in each year, the total number of hens remaining after spring dispersal, or joining the harems later, was 18. Of these, 12, or 66 per cent, were old birds. In the area as a whole the percentage of old hens was considered to be about 20 per cent as determined by winter trapping records, corroborated by sight records. Thus the concentration of old hens in this particular cornfield was probably higher than that at any other spot; the old hens remained near their winter range while younger birds dispersed to the uplands.

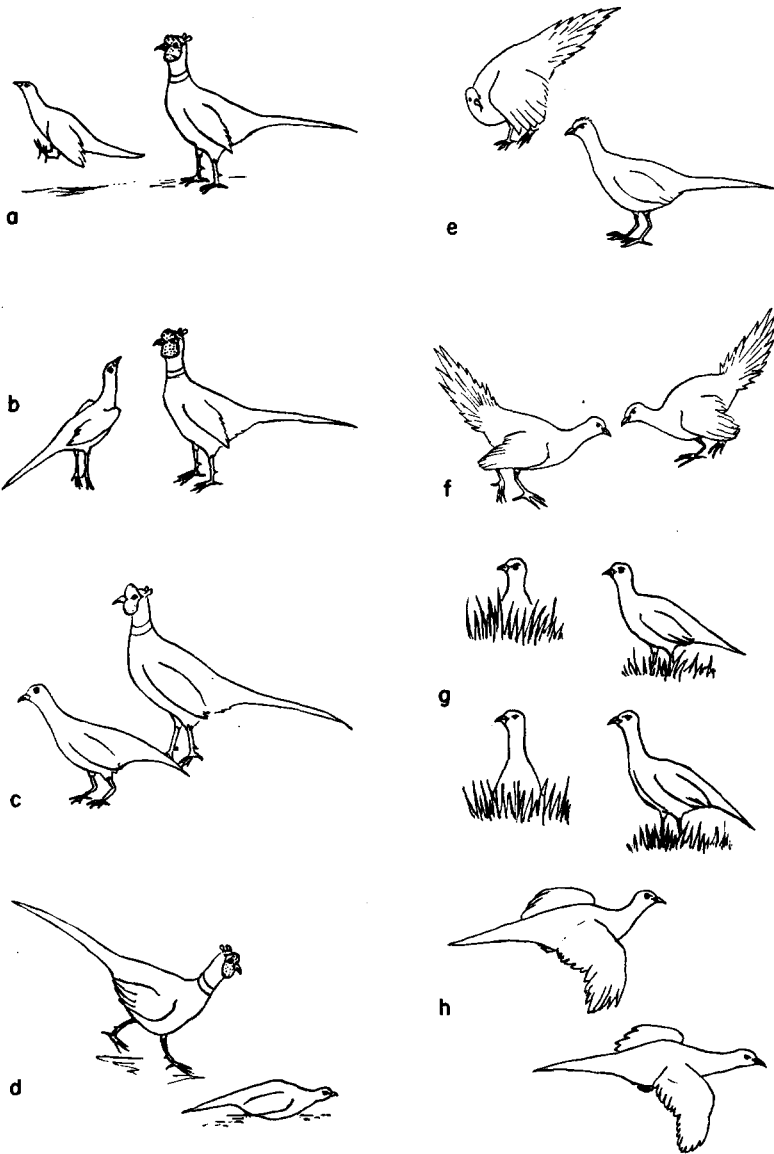


Fig. 25. a. Courtship display of hen, the flirting hop; b. courtship display of hen, the stretch; c. courtship display of hen, the half-squat; d. precopulatory behavior, type 3, the hen squats; e. the intimidation display directed by one hen toward another hen; f. two hens fighting; g. upper, posture of a hen without chicks, neck not stretched; g. lower, posture of hen with chicks, neck stretched; h. upper, posture in flight of hen with chicks, head held high; h. lower, posture of a hen without chicks, head held in line with body.

Mating period.—Late April and early May was found to be the period of peak testis weight (fig. 21). The hens which remained at the marsh edge during the spring dispersal period became more closely associated with territorial cocks in late April; that is, harems were formed. These harems were joined by new hens during late April and May. A harem count on any particular day in this period was often lower than the known harem membership; presumably this was due to the fact that the missing hen or hens, while nearby, were masked by vegetation. Because of this and because, as shown later, harems gain some hens while others are leaving to incubate, a harem count on any particular day gives a value which is probably lower than the number of hens which are actually members of the harem. Early May, however, was considered as the time in which the greatest percentage of hens were in harems in both years of study.

After early May, courtship was found to be of a different sort than previously. Display of the cock to members of his harem grouped around him in the feeding period was

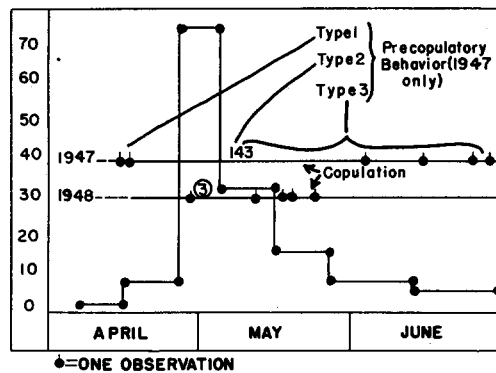


Fig. 26. Date of first egg in successful nests of 1947 (derived from Kozlik) plotted with observations of copulation (figures on horizontal lines indicate numbers of observations when more than one).

rare, but very often if one hen emerged from cover on to the feeding grounds later than the others, the cock ran to her and gave a series of displays in rapid succession. This, taken in conjunction with the fact that during the period of territory establishment (early April) a hen which was being displayed to could always terminate the cock's attentions by joining a group of other hens, suggests that a single hen was a greater stimulus to courtship than a group of hens.

From mid-April on, nonterritorial cocks did not court hens; although attracted by hens, they were driven off by the territorial cocks. Even on those rare occasions when they came near hens, they did not display, but simply chased them (fig. 22h).

Copulation was seen for the first time each year in the latter half of April, 14 being recorded in 1947 and eight in 1948 (see fig. 21). The curve for the date of laying of the first successful egg in 1947 (derived from Kozlik, 1947: 51-76) is presented in figure 26; a repetition of the copulation records has been included in this figure to facilitate comparison. In 1947 the first copulations were noted shortly after the first successful eggs were laid, but the bulk of copulations were seen when the "average" hen had just finished her clutch (Kozlik, 1947: 51-76). Whether this discrepancy represents a true phenological difference between the marsh edge, where most of the mountings were observed, and the uplands, where most of the brood-counts were made, or whether it was due to a sampling error, is not known.

Three distinct types of precopulatory behavior were observed. The earliest of these consisted of a series of rapidly repeated displays by the cock, followed by the squatting of the hen, whereupon the cock mounted. In the second type, the cock pursued the hen, seized her by the feathers at the back of the neck and mounted. In such an instance the hen sometimes struggled and on one occasion was apparently lifted clear off the ground for an instant. The only time a nonterritorial cock was seen to copulate with a hen was preceded by precopulatory behavior of this type. The third type consisted simply of the hen squatting and the cock mounting (fig. 25d). In 1947, two cases of the first type only were observed in late April; six of the second type only were seen in the third week of May; and seven of the third type only were seen from late May to late June, mostly in late May (fig. 26).

The existence of territories.—There seems to be a general agreement (Leffingwell, 1928; Wight, MS; Randall, 1940; Baskett, 1947) that the pheasant is territorial. Baskett, however, expressed an opinion common among students of pheasants when he stated (1947:8) that “. . . there probably was a tendency toward the establishment of crowing areas or territories by the male pheasants, but that these territories were very plastic and subject to frequent readjustments probably even through the nesting phase.” The findings of the present study support this opinion insofar as the plasticity of territorial boundaries is concerned.

The size and shape of a territory were sometimes modified by environmental changes, the extension of the daily cruising radius of the hen, and pressure from adjacent territorial cocks. In order to define the limits of each territory, I plotted each observation of a given cock on a large-scale map; the resulting outline, in conjunction with data on cover, adjacent territories and the movement of hens, aided in analyzing territorial requirements.

Figure 27 shows the changes in boundaries of several adjacent territories from mid-April to the end of May in 1947. The ground cover was classified as (1) that affording concealment to a crouching pheasant (over six inches) and (2) that of lesser height. Examples from figures 27 and 28 illustrate cases where the three modifying factors mentioned above were operative.

The importance of open ground for courtship.—Relatively open ground, where the cock and hens may see one another and where trespassing cocks may be more readily seen, played an important part in the function of the harem. The bulk of sexual activity took place during the morning and evening feeding periods, and these periods were spent on, or at the edge of, relatively open ground. Over 25 cocks' territories which were partly or completely known included some open ground by late April. In figure 27 the extension of the territory of cock III toward the north, with the result that his territory continued to include some open ground, may be observed. Such cases were common.

Kozłowa (1947:423), discussing the habitat of the related form, *Phasianus colchicus bianchii*, in its native Tadjikistan, describes several types of interspersed open and brushy cover, as well as a park-like area, as being typically inhabited by the birds. From this it would appear that in the area of her study, as well as that of mine, the daily range of a breeding cock contained open ground. Wight (1933) maintained that on southern Michigan farmland, territories could be made most desirable for pheasants by protecting the area from cutting, burning and grazing and by replanting where necessary. His intention was to furnish (*op. cit.*:7) “. . . good winter roosting cover, which will continue to stand into the spring and prevent the hens from scattering before the breeding season.” There is no indication that he considered openings of any importance.

Contrary to Wight (in McAtee, 1945:146) I found no evidence that a patch of brush

or woods is an essential part of the territory. Some heavy herbaceous vegetation was always present where brush or woods were absent.

The effect of the cruising range of the hen on territorial boundaries of males.— Generally, the cock followed the hens out from cover and then, when the feeding period

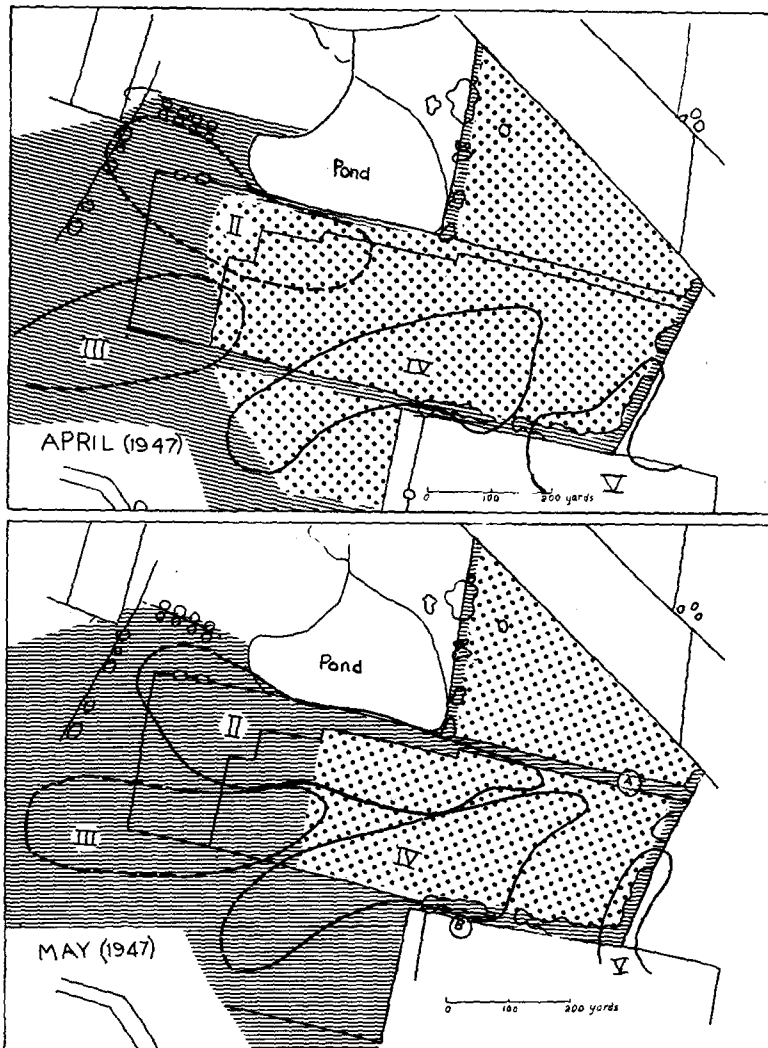


Fig. 27. Territorial boundaries of males in April and May, 1947. Solid lines, exact boundaries; broken lines, approximate boundaries. Stippled areas, vegetation under six inches in height; lined areas, vegetation over six inches. Encircled letters mark nest sites.

was over, led the way back. He seemed to be more strongly oriented roostward than they. However, since he was also strongly attracted to the hens, he followed them until stopped by some obstacle, like another cock's territorial boundary. An example of the way in which this tendency on the part of the cock to follow the hens could modify territorial boundaries is given below; in this case the movement of the hen was toward her nest.

The difference in shape of territory IV between April and May consisted largely of an addition of a fingerlike projection (fig. 27) toward the northwest in May. In May an incomplete nest, believed to belong to one of the hens of harem IV, was found just beyond the point of this finger (symbol A). Although the individual hens were at that

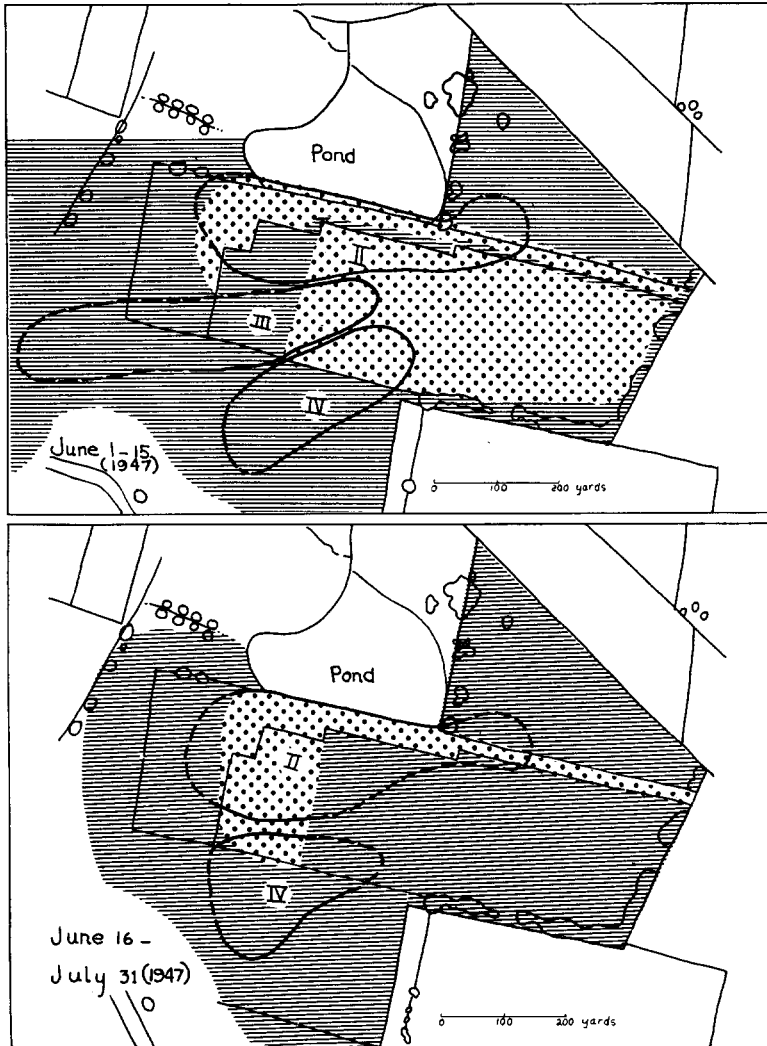


Fig. 28. Territorial boundaries of males in June and July, 1947. Symbols as in figure 27.

time too imperfectly marked for certain identification, it seemed that one hen led the harem in this direction during the feeding period while the cock followed the harem. This particular nest was watched and was soon deserted, whereupon the movements of the harem toward this location were greatly reduced.

A second similar instance was observed in May. The nest (B, fig. 27) was completed and incubation began about the middle of May; the part of territory IV which had extended to the immediate proximity of the nest was no longer used by the cock after

incubation began (fig. 28), presumably because that particular hen did not associate to any extent with the rest of the harem while incubating.

Baskett, however, believes (1947:10) that "... nest sites were probably defended by males." The findings of the present study, while based on limited evidence, are more in agreement with Wight, who states (1933:7) "The nests are usually situated within or near the crowing area."

The effect of adjacent territorial cocks on territory boundaries.—Wherever territorial boundaries are shown running close together in open ground in figures 27 and 28, fights between adjacent cocks were fairly frequent. The principal cause seemed to be the tendency of hens to wander over boundaries and of cocks to follow them. These fights sometimes took on a pendulum pattern in that the intruding cock slowly retreated, when attacked, into his own territory; there he rallied and, in turn, gradually drove back his attacker. After a few jumps in which the antagonists met breast to breast in the air, the conflict took the form of a beak-to-beak crouch, with a sparring of heads, varied with parallel stalking of the cocks. Eventually they drifted apart; no definite "winner" could be determined. Even more commonly, however, the intruding cock, whether territorial or nonterritorial, simply retreated when attacked by the territorial cock, who abandoned the chase near his boundary.

It has been pointed out in this study that the male, in running toward another bird to display, uses the predisplay pose, with head low and in, and rump up. After mid-April, when dominant cocks replaced the intimidation display to other cocks with the chasing pose, this predisplay run was directed only at hens. Generally, but not always, such a run ended in a courtship display. It was interesting to note that when a territorial cock left his territory, whether because of chasing off a trespasser or because he had been flushed by some animal, he returned to the territory in a predisplay pose (fig. 22b). It seemed as if, in the words of Tinbergen (1936:7), "a territory is, to the male, a 'potential female'."

Territory size.—Foote (1942:51) described five territories which he considered to vary in size from 30 to 112 acres, whereas Gould (1939:7) found the range in size of five other territories to be from 30 to 50 acres. The density of pheasant population in neither case is clear. Twining (1946:146), in an area thought by me to be of high pheasant density (estimated at one bird per two acres), found 11 territories to range in size from 3 to 13 acres. In the present study, a single territory (IV, figs. 27 and 28) was found to vary from 12 or 13 acres in April and May to six acres by mid-June. Twelve other territories in this area were 6-12 acres in size. Territory size is probably modified principally by population pressure and factors limiting vision, that is, cover and topography.

Nonterritorial cocks.—Wight (in McAtee, 1945:146) states that, "if a male is entirely vanquished in his quest for an area, he usually moves out completely, and becomes a wanderer . . ." This is not supported by the findings of the present study. Individual nonterritorial cocks were occasionally found to wander as far as half a mile, but generally were almost as localized as territorial cocks during the breeding season. Their range was somewhat larger than the average territory, however; several nonterritorial cocks were observed to have daily ranges of about 80 acres. The range of a nonterritorial cock frequently included areas within the territories of territorial cocks. These were entered both in the course of foraging and when attracted by the hens of the harem. Generally a trespassing nonterritorial cock was driven from the territory, but often the territorial cock did not see him or, if he saw him, was engaged otherwise at the moment. A striking example of this latter situation was observed on May 18, 1947. Two territorial cocks were fighting at their mutual boundary line in an open field while two hens stood nearby.

A nonterritorial cock entered the field and began to chase one of the hens; she ran in a circle around the fighting cocks, while he pursued. Within 30 yards of the two territorial cocks he seized her by the neck feathers and mounted. Neither of the fighting cocks gave any indication of having noticed this performance.

The pose of nonterritorial cocks was generally furtive while trespassing (fig. 22g). However, they persisted in returning time after time only to be chased directly off again by the territorial cock. When the territorial cock was elsewhere, they often fed at his accustomed spot unmolested. Incidents of this sort are probably the basis of Baskett's (1947:8) statement: "Throughout spring, there were numerous cases in which a field which the observer had come to regard as the domain of a particular male was traversed by another male without apparent strife resulting."

I found nonterritorial cocks to have several characteristics: (1) they were never seen to crow; (2) their wattles were always small unless they were actually in close contact with hens (a rare event); (3) they did not cluck; (4) they did not fight; (5) they did not court (display to) hens after mid-April.

The fact that these nonterritorial cocks were continually attracted to the harems raises the question of the extent to which a hen away from the harem is subject to harassment by them. On several occasions they were observed to pursue hens which were apparently on their way to the nest. When a hen was with a harem, she was protected from this form of attention, but when she left it she was liable to pursuit. The actual effect of such a surplus of males upon the reproductive success of the hen population was not determined in this study. Two authors, however, have given descriptions of the effects of a heavy excess of cocks. Beebe (1931:47) says that under certain conditions "cocks may become so numerous in a locality as to interfere seriously with the breeding. They disturb the hens while sitting on the eggs and often acquire the egg-eating habit, if they do not, indeed, actually kill the young birds." Einarsen also writes (1945:5): "It is very probable that territorial competition among the birds adversely affected reproduction. Cock birds have been seen persistently molesting hens and chicks."

During the season of 1948, a tally was kept of all territorial and nonterritorial cocks on the study area. The results were: territorial, 18; nonterritorial, 8; doubtful, 3. The proportion of nonterritorial cocks in the thinner populations of the uplands seemed to be lower than that at the marsh edge.

Since a direct count of nonterritorial males is seldom feasible, an indirect method was devised wherein the proportion of nonterritorial cocks was estimated from the sex ratio and the average harem size. A series of observations of harem size made by R. A. Ellis was used. Fifty-four harems were counted on and near the University of Wisconsin Arboretum in April, 1946; the average number of hens per harem was 1.8, both in the marsh edge and in the uplands. The sex ratio of the population, determined through the drive-census of the previous winter, was 70 cocks per 100 hens. Before proceeding with the simple calculations necessary to determine the proportion of unsuccessful breeders, we must list the four assumptions upon which the validity of the result will rest: (1) both sexes were flushed proportionately during the drive census; (2) no important differential mortality occurred during late winter and early spring; (3) no important differential ingress or egress occurred through April; (4) the harem spotter was successful in seeing all hens of every harem. No information invalidating the method on any of the first three assumptions has been found, but it may safely be assumed that the observer will discover something less than 100 per cent of the hens in the harems he spots.

The winter census of 1946 showed a total of 152 hens in the Arboretum marsh. Dividing this number by 1.8, the average harem size in April, we get 85, the number of harems which might be formed from such a population. Dividing this by the number

of cocks tallied in the winter census, 106, we get 0.80. According to this computation, then, 80 per cent of the Arboretum cocks were successful breeders. However, since we know the average harem size to be something higher than 1.8, the percentage of successful cocks must be something lower than 80.

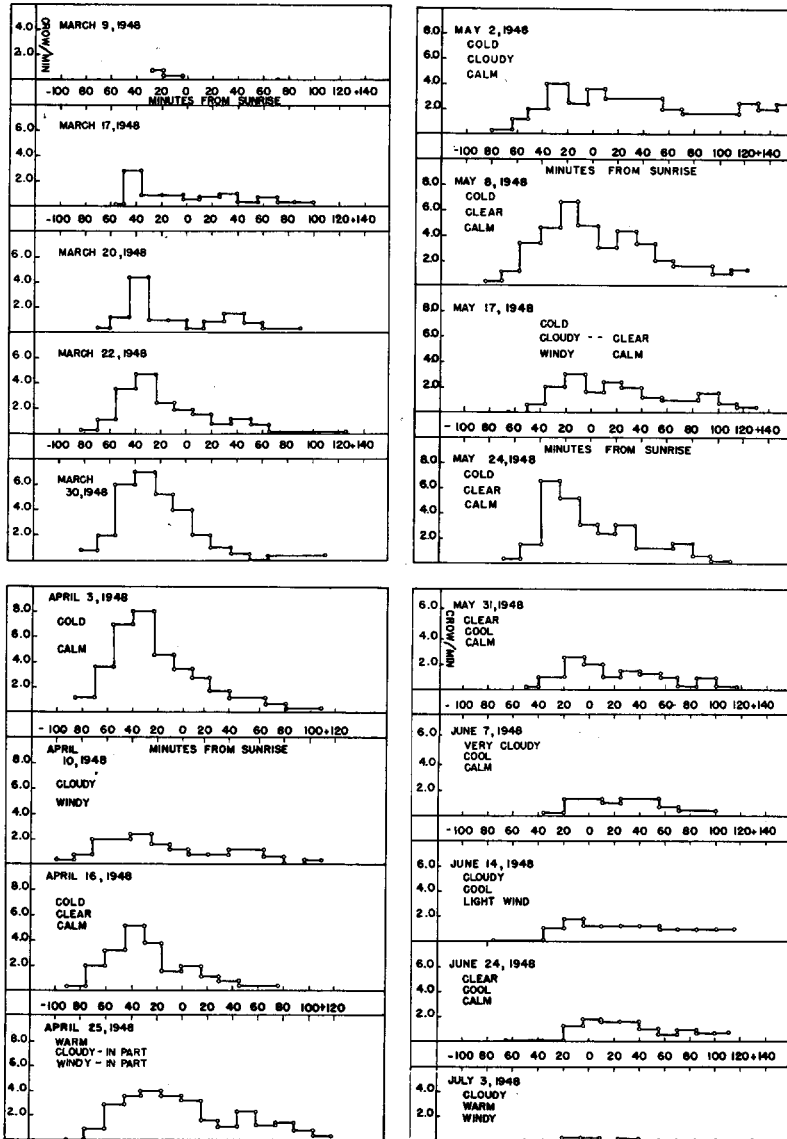


Fig. 29. Records of crowing intensity for individual mornings expressed in crows per minute. All crows within earshot were recorded. The weather on each of the March mornings represented here was clear, cool and calm.

Excess cocks in a hunted pheasant population represent an unharvested surplus. The above method of measuring this particular excess, while crude, indicates that in this case it is substantial and therefore of potential importance in management.

Antagonism between hens.—Concurrent with harem formation (late April and early May) were fighting between hens and display of one hen to another. Both of these were presumably expressions of antagonism. In a hen fight, both hens spread the tail, lowered the wings and forepart of the body and rushed at one another (fig. 25f). When close together, they sometimes jumped against each other, with the head up, but generally one gave ground and retreated after a single dash together.

The intimidation display of the hen was very much like that of the cock; the head was held low, the rump raised, the tail spread and canted toward the object of the display, the wing on that side somewhat spread and the contour feathers ruffled (fig. 25e). The display was often repeated several times, like the display of the cock. The hen which was displayed to acted much the same in either case, dashing alertly away for a few steps and then stopping while the displaying bird came up and displayed once more. The occurrence of these two types of behavior is given in figure 21. Whether antagonism between hens in these or other forms might be a factor limiting harem size is not known. However, it is a possible instrument for such limitation.

Crowing.—In late April and early May, crowing rose to a second peak which coincided with that of testis weight (fig. 21). Individual crowing counts indicated that this rise was due to a general increase in the crowing intensity of individual cocks, a continuation of the rise which had begun in March.

Crows audible from a mid-marsh observation post during the morning period were recorded on many days; these records are expressed in terms of crowing intensity (crows per minute) in figure 29. As may be seen, cloudy or windy weather resulted in a flattening of the morning curve as well as an extension to the right. On cold, clear, calm mornings, on the other hand, the peak or peaks of the curve were much more pronounced. The seasonal development of curves of such mornings is traced below.

The typical crowing curve of late March and early April was found to be single peaked, the peak occurring about 40 minutes before sunrise (fig. 29). After mid-April, a second peak in the morning curve began to develop due to the crowing of territorial cocks upon entering the feeding grounds; this second, and smaller, peak was found about half an hour after sunrise. Following the feeding period there was a third and still smaller peak of crowing which occurred as the birds were leaving the feeding grounds, about 125 minutes after sunrise. These prefeeding and postfeeding peaks became more pronounced in May (fig. 29). As the season advanced, the first morning peak became gradually later until by the end of May it occurred at about ten minutes before sunrise. It is interesting to note that in the Wild Turkey (*Meleagris gallopavo silvestris*), which also "sings" on the roost during the breeding season, there is a similar increasing lateness of this singing as the season progresses (A. S. Leopold, verbal communication).

The morning crowing intensity curve has been used as an aid in establishing the time that crowing counts should be taken as an index to pheasant populations (Kimball, 1949). Kimball (p. 107) says: "Fortunately crowing intensity between -40 to +50 [minutes from sunrise] is relatively constant, the maximum variation being ± 7.5 per cent of average," and considers this period suitable for counts.

My findings were in agreement with this statement only with respect to cloudy, windy days. On clear, calm days the drop in crowing intensity after the presunrise peak was very sharp. This indicates that under the conditions of this study a crowing "census" taken before sunrise on a clear, calm day could not be compared directly with one taken after sunrise on the same day without a considerable error.

Weather and daily routine.—It is difficult to assess the influence of weather on daily routine since weather includes so many variables; however, my findings are in only partial agreement with those of Baskett, who says (1947:7): "During intemperate

weather, all diurnal activities are often altered . . .” The morning routine in late March, April and May was found to conform to a rather definite pattern; this pattern was most closely adhered to on clear, calm days but was by no means abandoned when it was cloudy, windy or even raining. This pattern was found to be about as follows: the birds left the roost about sunrise and moved to the feeding grounds, sometimes flying. My impression was that they flew only on mornings of heavy dew, but data on that specific point were not gathered. The feeding period began about 35 minutes after sunrise; the early part of the feeding period was spent in walking slowly out from cover and the end of the period in returning to cover, while the middle part was devoted to feeding and loafing. It has been seen in a previous section that crowing intensity was higher at the beginning and the end than during the middle of the period.

Summary of period of courtship and mating.—During this period (late April and May), (1) territories are established; (2) harems are formed; (3) copulation takes place; (4) the first eggs are laid; (5) crowing reaches a second peak and starts diminishing.

THE LATE BREEDING SEASON

Crowing.—Crowing intensity dropped in late May, June and July, the curve following closely that for gonad weight for the same period (fig. 21).

Incubation.—During this period, the harems continued to decline in size as more and more hens left them to incubate. Baskett (1947:7) states that hens “probably are solitary only while incubating; even then they may consort with other females and a male during rest periods.” I found no evidence that incubating hens joined the harems to feed. Solitary hens exhibiting a skulking posture were occasionally seen apart from the harems at this time; these may have been birds which had left the incubated nest to feed alone.

The increase in trespassing.—As the harems diminished in size in late May and June, some cocks found themselves with only one hen or none at all. If there was only one hen, she often led the cock into a neighboring territory. Without demonstrable proof, I suspected that the gregariousness of the hen might have attracted her to some adjacent harem. Whatever the reason, if a single hen strayed from a harem of five, for example, the cock remained with the four which did not stray, but if a cock had but one hen, his tendency was to follow her; and single hens appeared to wander farther afield than hens in groups. Each trespass of a cock on his neighbor’s territory resulted in a defense by the resident cock, providing the intruder was detected.

The end of territorial behavior.—When his last hen is gone, the cock seems to lose his territorial proclivities very rapidly. In figure 28 it may be seen that the territory of cock III, who lost his last hen about the middle of June, was soon deserted by him; the ground was then added to the territories of his neighbors who still had hens. Note also how cock IV modified his territorial boundary to include open ground (in this case a closely grazed pasture). Pressure from cock IV possibly speeded the relinquishment of territory by cock III.

A few observations suggested that between the time of losing his last hen and the relinquishment of territory a cock might for a time be attracted to the hens of an adjacent cock, trespassing on neighbors’ territories in consequence. Also there was evidence of a transitional period near the end of territoriality, comparable to that near its beginning, when trespassers were subjected to a walking pursuit (fig. 22e) rather than a chase (fig. 22f).

Cocks which had abandoned territories seemed to stay in much the same area they had occupied when behaving territorially; frequently they were seen near hens and chicks, but there was no definite association comparable to that of the harem.

On the other hand, if a cock had abandoned a territory, he might be stimulated to resume part, at least, of his sexual activities. In 1947, I observed one cock which, by the end of June, had apparently become nonterritorial (he had maintained a territory earlier that season). A hen appeared near him one day and went through her sexual antics. He responded with a partial swelling of the wattles and an imperfect display. During July and August I observed these same two birds frequently and was able to observe signs of increasing sexual excitement in the cock. His wattles, which at the end of June had swollen only partially when the hen performed, swelled to their fullest extent when she danced by him in late July. Similarly his display became more complete over the same period. In August this cock was still displaying occasionally to the same hen and showed signs of antagonism toward other cocks even though his molt had progressed in the meantime so far that all his old tail feathers had been lost and the new ones were about four inches long. It seemed to me that this was a case of sexual recrudescence based on stimulation by the hen. All that is known of the hen is that she was at least two years of age.

Brood observations.—In 1947, whereas a few broods were brought off in May, the bulk of the successful hatch occurred in June. In July and August I made many brood observations; while the bulk of the findings will be reported elsewhere (Collias and Taber, MS), certain aspects of behavior are reported here.

A limited number of observations indicated that hens with chicks up to at least five weeks of age could be distinguished from hens without chicks by their frequent assumption of a craning posture (fig. 25g). In addition, hens with small chicks, when flushed, were observed to hold their heads higher in flight than hens without chicks (fig. 25h). The potential value of these revealing postures in surveys of percentage of reproductive success among hens seems to warrant verification of these findings.

Although complete records were not kept, it was my impression that chicks of six weeks and above generally followed the daily routine of the adult birds, feeding half an hour to an hour after sunrise and retiring to cover. Younger chicks, however, seemed to appear later, perhaps an hour after sunrise and remained active for a longer period. Possibly this difference in time of appearance was correlated with food habits, the insects upon which the young chicks fed not being active at the earlier hour. Another possibility is the avoidance of early morning dew by a hen with a young brood. If this difference in routine were true, the accuracy of brood counts would be affected.

Summary of late breeding season.—During this period (June, July and August), (1) crowing ends; (2) territories are relinquished; (3) the peak of the hatch occurs.

GENERAL SUMMARY

The first courtship behavior was detected in February, when cocks began to cluck and to display to hens, which also displayed. Clucking by dominant cocks continued throughout the season. Courtship displays by cocks became increasingly numerous through the first half of April; thereafter they declined in number. At the same time, the area covered by a series of courtship displays changed from a linear to a circular form. After mid-April, courtship display by the cock was largely directed toward single hens appearing late on the feeding grounds.

Copulation was first seen in mid-April and continued through May and June, being seen most often in May. It was preceded by three types of precopulatory behavior, each type occupying a definite part of the total seasonal period of copulation. Nonterritorial cocks displayed to hens until mid-April, when harems were formed, but simply chased them thereafter.

Antagonistic behavior between cocks began in February, when cocks of approxi-

mately equal dominance began to have bluffing contests and to spar occasionally. Cock flocks were reduced to groups of two by mid-March. Of these groups of two, the dominant member then intimidated the submissive member by means of the predisplay run, the intimidation display and the walking pursuit. By the first of April, some cocks were defending territories by actively chasing trespassers and by mid-April all cocks which were going to defend territories had begun to do so. A residue of nonterritorial cocks remained. Toward the end of June, when territoriality was waning, there was a change in attitude on the part of a territorial cock toward trespassers from an active chase to a walking pursuit.

Antagonistic behavior between hens, as manifested by fighting and the rendering of the intimidation display, occurred largely in late April and May.

Crowing began in February and continued at a low level until early March, when crowing intensity in a marsh area began to build up rapidly. The first peak of total crowing intensity came in early April; there was a subsequent decline to mid-April, indicative of the spring dispersal of some crowing cocks to the uplands. A second peak came in late April and early May; this was thought to represent the true peak of crowing of individual cocks. Crowing declined rapidly thereafter and was at a very low level by mid-July.

The daily curve of all crowing in the marsh came to a peak about 40 minutes before sunrise and declined rapidly thereafter in late March and early April, but after mid-April a second, smaller peak appeared about 35 minutes after sunrise; a third, still smaller peak about 90 minutes after sunrise was also sometimes noted. These two secondary peaks represented the increase in crowing intensity of each territorial cock when entering and leaving the feeding area.

Nonterritorial cocks were not observed to crow.

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