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RUSH, Jane Evelione, 1947-
BROOD DEFENSE BEHAVIOR IN GALLUS HENS.

City University of New York, Ph.D., 1978
Zoology

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BROOD DEFENSE BEHAVIOR IN GALLUS HENS

by

JANE E. RUSH

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment of the
requirements for the degree of Doctor of
Philosophy, The City University of New York.

1978

Jane Rush

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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ACKNOWLEDGMENTS

I would like to acknowledge the efforts and influence of certain individuals in the development and production of this dissertation. Without their various and generous contributions, I would have been unable to attain my objective.

For his enduring support and direction, I am especially grateful to my major advisor, Joseph G. Griswold.

For his instruction and criticism in the application of statistical techniques and for his commitment to the completion of this work, I thank Robert Rockwell.

For extensive editorial help and good counsel during many crucial moments, I thank Joseph Turkel.

In addition, I sincerely appreciate the thoughtful advise and specific suggestions offered by other members of my committee: R.-G. Busnel, Maria Miller, W. N. Tavolga and H. P. Zeigler.

The actual experiments were carried out with the unstinting assistance of Julianna Caguiat. She also persevered through the tedious reviewing of videotaped tests. I am thoroughly grateful to her for her extraordinary reliability and continued encouragement.

Further, I would like to thank Robert Cope for his help in building housing for the birds and John Hagen and Joseph Turkel for their photographic services and coaching.

Computer analyses were executed on the PDP 10 in the C. C. N. Y. physics department and the IBM 360 which is available through the biostatistics laboratory of the C. C. N. Y. biology department. I thank Robert Rockwell, Joshua Wallman and George Kleiner for demystifying the machines.

Finally, I want to give special thanks to my husband, Clair Martin, for the graphic design and to my friend, Martin Branner, for the drawings of the intruders and the hens.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Statement of the Problem

There are many factors that can reduce the probability of survival of young animals. Certain of these factors can be affected by the behavior of the parents, and this broadly defines the range of parental behavior: those activities of the parents that increase the probability of survival of the offspring. Parental behavior, as a category within the more general one of reproductive behavior, can also be divided into categories. These divisions are often made on the basis of the function of a particular activity or behavior. In parental behavior of birds, there are three major functions: assistance in thermoregulation, nourishment of the young, and protection of the young against intruding animals. The allocation of parental activities to thermoregulation and nourishment categories is usually clear. By contrast, the definition of so-called "defense behavior" is more difficult. Edmunds (1974) defines defense as "any adaptation which reduces the chances of success of an attack by another animal." Thus, selection of a nest-site which diminishes accessibility to predation (e.g., cliff-nesting in kittiwakes, Rissa tridactyla, Cullen, 1957) and cryptic coloration of eggs or young (e.g., camouflaged eggs and chicks of the black-headed gull, Larus ridibundus, Tinbergen, et al., 1962) are examples of adaptations within the defense repertoire of an animal. Further, behavioral responses by parent birds to predators which approach the nest or young purportedly serve to distract the predator from the offspring: these reactions of breeding birds to intruders have been described in myriad field observations (Nice, 1943; Armstrong, 1947; Simmons, 1952, 1955). Despite this apparent significance of brood defense behavior, there are few experimental investigations of this phenomenon. Generally, the descriptions are derived from uncontrolled field observation. These qualitative accounts provide much valuable information but their accuracy and the extent to which they characterize the species is unknown.

Variability has been noted (Nice, 1943; Armstrong, 1947; Kruuk, 1964; Curio, 1975) and, on the basis of field observation, many researchers have suggested that the stage of the breeding cycle and the type of intruder influence the behavior of birds toward intruders. Strong evidence demonstrating the effects of these factors is limited, however. For example, when birds are observed in their natural habitat, it is often difficult to ascertain the reproductive state of the individual. Sometimes, a nest and eggs or chicks are discovered and they permit one to deduce the breeding condition of the bird; more often, inferences are made on the basis of the season or on the basis of the birds' behavior. Claims for the influence of the type of intruder on responses are weakened by the lack of control over such basic factors as the behavior of the intruder vis à vis the subject; in addition, information concerning the parent bird's prior experience with similar circumstances is unknown.

It is the aim of this research to provide an accurate description of the behavior of parent birds when they are confronted by an intruder and to determine the variables that influence these responses.

Background

The information presented here on the responses of parent birds to intruders was selected from an extensive literature; these representative examples have been chosen to indicate the many forms of brood defense and to introduce some of the variables thought to affect its expression. A separate section summarizes what is known about brood defense in Gallus since domestic chickens have been chosen as the subject species. The specific experimental rational follows the literature review.

Modes of Expression

Adaptive responses to predators include special calls which announce the predator's presence, explicit attack, fleeing of various forms and defense displays (Nice, 1943; Kear, 1970).

Special calls. Vocalizations are uttered by many avian species at the approach of a predator (Frings and Frings, 1964). During the period of parental care, the number and types of calls elicited by an intruder my change from those elicited during the non-breeding season. Furthermore, some calls occur uniquely when embryos or chicks are present. The song sparrow (Melospiza melodia) demonstrates this modification of its vocal repertoire in response to intruders during the breeding season. Nice (1943) reports that if song sparrow parents are tending eggs or young nestlings, they give a 'tchunk' call at the approach of a human being, a cat or a dog. Later in the rearing period, nearer fledging, the female in particular produces a wider variety of notes including 'tik', 'ick', 'yip' and 'jib' upon encountering an intruder. Another example of a species changing its vocal responses during the breeding season is provided by the European avocet (Recurvirostra avosetta) which adds a second alarm call which is elicited specifically by gulls, a major predator of the species (Makkink, 1936).

Attacks. Explicit attack by prey species on potential predators are most commonly reported during the breeding season. Many field observations attest to attacks by mocking birds (Mimus polyglottos) on potential predators such as cats. Song sparrows will attack cowbirds (Molothrus ater) and small snakes (Nice, 1939). Brown thrashers (Toxostoma rufum), swallows (family Hirundinidae) and numerous colonial nesting sea birds such as gulls and terns (family Laridae) intersperse actual attacks on intruders with series of aerial swoops (Nice, 1943). Among waterfowl, overt attacks are known to occur in screamers (Chauna spp.), the males of which are notable for their spread wing posture and the blows they deliver with carpal spurs. The Magpie goose (Anseranas semipalmata) employs its beak as its chief defensive weapon while swans (Cygnus spp.), steamer ducks (Tachyeres spp.) and the larger anserine and sheld-geese (Anser and Tadomini spp., respectively) use both wings and bill (Kear, 1970).

Flight. An option widely used to evade a predator is flight. In this instance, flight is used generically to mean "rapid locomotion away from the stimulus source" (Edmunds, 1974). In non-breeding as well as breeding birds, fleeding often occurs when the prospective prey notes the presence of an intruder at some distance; this response reduces the probability of direct confrontation. For example, numerous species of grebes (family Podicipedidae), swans, ducks and geese swim away with the young carried on the parent's back (Kear, 1970). Flight also may follow other defensive responses which have not succeeded in dispatching the imminent danger. For example, many small gallinaceous game birds are known to remain motionless when hunters and hounds are nearby. If the covy is discovered in spite of its crypsis (immobility and camouflaging plumage), the adult birds will flush from cover in a whirr of wings (Blanchan, 1902). At the same time, the young typically dash to fresh cover and freeze once again (Bent, 1932). In cases of surprise assault, the predator's target(s) may attempt to fly, swim or run from the immediate vicinity. For example, Johnsgaard and Kear (1968) report that at least 16 species of waterfowl purportedly carry their young to a new location. While in flight, the parent usually holds the young by the beak. Even more remarkable is the adaptation of the American finfoot (Heliornis fulica): the adult male has pockets of body skin under each wing in which he carries the blind and naked young. They remain secure while he is either flying or swimming (del Toro, 1971).

When eggs or nidicolous young are involved, fleeing by the parent birds means leaving the offspring behind, a situation which may increase the risk to reproductive success. Commonly, in lieu of direct flight the parent bird(s) give a display or take leave by moving in an erratic fashion. This latter adaptive pattern of fleeing may contain elements of many behaviors including walking, hopping, and rapid changes in form and orientation. Chance and Russell (1959) and Humphries and Driver (1970) called this highly unpredictable behavior "Protean defense." It is thought to have its effect by confusing the predator, thereby giving the prey animal or the brood more time to escape.

Defense displays. In some cases, the prospective prey neither attacks nor flees definitively. Instead, the bird engages in a species-typical pattern of various postures and locomotor activities that purportedly have the effect of deflecting the attention or attack of a potential predator from the young to the adult. Armstrong (1949a) suggests calling such behavior diversionary display. This type of defense adaptation is especially prevalent among non-colonial ground nesters. The following examples detail its extent and variety. Wading birds, for example, are especially well-known for "injury-feigning," one type of diversionary display. Killdeer plover (Charadrius vociferus vociferus) and black-necked stilts (Himantopus himantopus mexicanus) exhibit a "broken-wing display" in which they flutter conspicuously in a manner suggesting disablement. This display is sometimes alternated with another behavior: squatting on the bare ground as if on eggs (Lack, 1941; Deane, 1944). False brooding, as this manoeuver is called, may lure chicks away from a dangerous location (as in the case of the avocet, Makkink, 1936) or deceive the predator as to the actual whereabouts of the brood (Armstrong, 1947). While various tactics, of which the foregoing examples are a few, seem to form certain categories of distraction displays, Armstrong (1949a) rightly cautions that the boundaries are blurred and, at best, categorical distinctions can provide guidelines for description.

Factors Influencing Responses to Intruders

The numerous qualitative accounts of reactions to predators depict great variety in the behavior. Even intraspecifically, responses to intruders are reported to be variable. Differences in the immediate stimulus situation and in certain intrinsic factors have been suggested as causes of intraspecific variability.

Reproductive condition. Situations demanding defensive countermeasures confront adult birds in both breeding and non-breeding conditions. Conceivably, one system of behavioral defense could serve these two phases of the birds' life. As mentioned earlier however, evidence indicating that defense behavior is elaborated in incubating and brooding birds is extensive. Notably, displays and attacks are observed much more commonly among breeding birds. Armstrong (1949b) states that "distraction displays in general and injury simulation in particular are confined almost entirely to situations in which reproductive impulses are active." In contrast, it is flight which figures predominantly in the anti-predator behavior of non-breeding birds (e.g., Simmons, 1955). Song sparrows, for instance, give alarm calls to groung enemies during the breeding season but ignore them outside of it (Nice, 1943). More recently, Vowles and Harwood (1966) demonstrated that aggressive and defensive behavior in ring doves (Streptopelia risoria) depends firmly on the hormonal state characteristic of birds incubating and rearing young. Experiments testing the effect of estrogen, progesterone, progesterone plus estrogen and prolactin revealed that prolactin and progesterone (with and without estrogen) increased defensive behavior in both sexes towards a predator (a model spider). In females only, these hormones increased defensive behavior toward conspecifics as well. The authors suggest that the hormones have a direct effect on the central nervous system mechanisms mediating the behavior.

Generally, marked differences in defense behavior between breeding and non-breeding birds do not appear abruptly. Rather behavior toward intruders changes gradually from personal defense to defense of territory, eggs and young. The main change in defense behavior as the breeding season approaches is a decrease in immediate fleeing as a means of escape (Simmons, 1955). Once the bird(s) begin to incubate the eggs, their responses to intruders have been reported to include a variety of displays performed in the intruder's vicinity; for some species, direct attacks on the predator have been observed (Nice, 1943; Simmons, 1955). The intensity of displays peaks commonly at hatching and continues until fledging (little ringed plover, Charadrius dubius, Simmons, 1952, 1955; song sparrow, Melospiza melodia, Nice, 1943; black-headed gull, Larus ridibundus, Kruuk, 1964). Kruuk's study (1964) of anti-predator behavior in the black-headed gull clearly demonstrated that responses to predators change with the stage of the breeding cycle and are adapted to the needs of the chicks and to patterns of predation. Further evidence of this general pattern is supplied by pied-flycatchers (Ficedula hypoleuca) which mob pygmy owls more intensely as the breeding season progresses, as well as by willow warblers (Phylloscopus trochilus) and Darwin's finches (family Fringillidae, subfamily Geospizinae) (Smith. and Hosking, 1955; Curio, 1969).

It has been suggested that the patterns of change in brood defense during incubation of the clutch and rearing of the offspring correlate with the developmental pattern of the young (Nice, 1943; Armstrong, 1949b; Barash, 1975). Many altricial species have been observed to show strong brood defense behavior until fledging (Armstrong, 1949b). In fact, the Alpine accentor (Prunella collaris), a ground-nesting altricial species, increases the conspicuousness of its display as the egg-nestling unit grows older (Barash, 1975). Yet other species defend their offspring most vigorously around the time of hatching and, subsequently, they show a progressive decrement in response.

Experience. Few investigations have touched upon the question of whether repeated experiences in defending a brood change parental responses to intruders. One study (Hinde, 1954a) considered this problem with regard to mobbing in non-breeding chaffinches, which also mob during the breeding season. The primary response component that was recorded, the 'chink' call, waned (declined in frequency) with repeated presentations of a live owl. This decrement in responsiveness seemed maladaptive if one assumed that vocalizations associated with mobbing enhance the probability of avoiding predation. Of course, the decrease in the 'chink' calls might not be indicative of the complete mobbing pattern which includes various postures and movements. Further, it is not known whether a similar result would be observed in breeding chaffinches. The exploration of the consequences of multiple encounters with predators on subsequent responsiveness during care of young seems particularly relevant to concepts of adaptive significance since it examines a situation which is probable for many individuals of various species.

Another category of experience that seems potentially important is parental experience. Although no empirical comparison of the intruder responses of maternally naive birds and maternally experienced birds has been made, anecdotal reports (Smith and Daniel, 1975) indicate that domestic hens are less successful in rearing their chicks if they are inexperienced. Insofar as parental anti-predator behavior can increase the probability of offspring's survival, it is reasonable to consider that prior maternal experience might affect multiple aspects of parental care. Clearly, the implication is that the effects of such experience are beneficial to species' survival.

Type of intruder. Many avian species have the ability to reorganize their defense behavior according to certain contingencies. Which tactics are used seem to be determined in great measure by the nature of the intruder. The killdeer plover that feigns injury when approached by a human attacks a grazing cow about to trample her nest (Deane, 1944). The reed bunting (Emberiza schoeniclus) will attack a rat (Rattus norvegicus) (Smith, 1945) but flutters about in an advertising display when encountering a ferret (Mustela furo) (Howard, 1929). Pied-flycatchers (Ficedula hypoleuca) mob owls (Glaucidium passerinum) but deliver "snarling attacks" on woodpeckers (Dendrocopus major) and red squirrels (Sciurus vulgaris) (Curio, 1975). Pickwell and Smith (1933) noted that a man approaching on all fours elicited a threat display from a Texas nighthawk (Chordeiles acutipennis); when the man walked upright toward the bird, it simulated distress and left the nest.

Different responses may be given to the same intruder during one encounter. Nice (1943) provides an example of a lapwing which initially froze as a sheep approached, then switched to a distraction display, and finally attacked the intruder directly.

Besides heterospecific predation which may have the parents and brood as its target, certain species risk loss of their chicks to conspecifics (e.g., Parsons, 1971; Kruuk, 1964). The opportunity for such predation is especially prevalent in ground nesting birds which form colonies during the breeding season. Black-headed gulls (Larus ridibundus) are an excellent example (Tinbergen, et al., 1962). Intraspecific encounters rarely result in damage to the adults as highly ritualized displays usually settle boundary disputes that would precede the pirating of eggs or chicks from a neighboring bird's nest (Tinbergen, 1959; Stout, et al., 1969). In cases of general alarm, however, when most of the colony takes wing, untended chicks are completely defenseless against marauding neighbors that return before the chicks' parents.

Brood Defense in Gallus Hens

Intruders. In precocial species such as chickens, the social unit is mobile shortly after hatching and yet requires maintenance of spatial contiguity for most aspects of parental care. Adequate proximity is maintained by visual and auditory communication between the hen and her chicks (Collias and Joos, 1953; Busnel, 1963). In the absence of the hen, chicks show a type of searching behavior which tends to restore the contact on which their survival depends (Hinde, 1974). To such a group, an intruder poses a secondary threat: chicks separated from the parent and lost have only a slim chance for survival, especially during the first 2 weeks when dependency on the hen for thermoregulation, food location and protection from predators is still high (McBride, Parer and Foenander, 1969). Thus, destruction of the spatial organization characteristic of the hen-chick unit by an intruder has consequences potentially as inimical to survival as direct predation.

While heterospecific predation on Gallus is universally recognized as a threat to survival of adults and offspring, the threat posed by conspecifics to the young is not intuitively obvious. For example, broody hens incubate their clutches at some distance from the flock and from one another. Further, they generally maintain their chicks in a discrete group which is separate from all other flock members. Occasionally, however, chicks do become vulnerable to conspecifics. McBride, et al. (1969) documented that broody hens and non-broody hens may congregate at a group feeding site. This proximity usually resulted in broody hen displays toward other adult birds. On several occasions chicks that wandered close to other hens were pecked severely.

Responses to intruders. The information about the responses of Gallus hens to intruders has resulted primarily from McBride, et al.'s study (1969) of the social behavior of feral domestic fowl. In the course of their observations, the investigators witnessed broody hens defending their young in various situations. For example, when a broody hen with very young chicks was disturbed by a man, she ruffled her body feathers, retracted her head, and arrayed her tail in a fan while holding it vertically over her back. This posture is called the "full broody hen display." When pressed closely, the hen hides her chicks, regularly turns and makes a charge at her pursuer. Both cats and low-flying birds elicited charges. In several incidents described, broody hens protected young chicks from other hens by displaying with ruffled feathers and charging the conspecific. No differences between the displays to con- and heterospecific intruders were mentioned.

Hypotheses concerning hens' responses. Review of the literature leads me to certain expectations about the responses of Gallus hens to intruders. A separate hypothesis is presented in each of the following paragraphs.

Based on several observations by McBride, et al. (1969), the responses of broody hens to intruders have been described as containing visual display and approach components. In many other avian species as well, elaborate postural and motor behavior has been observed when parent birds are confronted by an intruder; in contrast, their response during the non-breeding season is predominantly flight. Although no description of the intruder responses of non-broody Gallus is available, it seems reasonable to predict that, in parallel with other avian species, the responses will differ from those of hens in the broody condition and that the tendency to flee will be a prominent feature of the behavioral responses of non-broody hens.

In numerous avian species, changes in defense behavior during the period of chick care have been reported. As the chicks develop, various aspects of the responses to intruders may intensify or diminish and such alterations in the behavior are thought to have adaptive significance. No information on this aspect of Gallus behavior exists, so any expectation is based on data from species classified in different orders. While changes in hens' intruder responses during the post-natal care phase will probably occur, too little is known even generally to predict the type of changes which may occur.

During the care of a brood, it is possible that an intruder may be encountered more than once. While repeated presentations of a stimulus have been reported to cause habituation of responses that are not reinforced, decrements in responses to intruders would seem maladaptive and, therefore, unlikely. It is known, however, that laboratory settings which commonly present rather stereotyped stimulus situations, even those introducing a predator, augment the tendency of some responses to decline in intensity and/or frequency. Since the stimulus situation I have designed (described in the following section) involves pursuit of the subjects by the intruder, an amelioration of the effect of laboratory monotony might be expected: habituation would not occur. On the other hand, since the removal of the intruder is contingent on elapsed time and not on the hen's behavior, the resolution of the "intruder-present" situation is independent of the bird's responses; if certain aspects of the behavior depend on consequent changes in the stimulus situation such as absence of the intruder, the tendency to perform certain responses may be altered, but in unpredictable ways.

Previous research on the effect of maternal and intruder experience on behavior toward intruders is completely lacking. As an integral part of parental care which reputedly improves with experience, however, there is a modest expectation that having reared a brood and having encountered an intruder during care of that brood will affect the hen's behavior toward intruders encountered subsequently. The nature of the differences awaits empirical investigation.

Reports on Gallus indicate that responses to a wide variety of intruders are similar. These descriptions, however, are qualitative and leave open the possibility that wuantitative differences may distinguish behavior toward intruders of different types. Particularly since many avian species exhibit diversity in intruder-responses it seems reasonable to expect that broody hens' responses to different intruders may be characterized by at least differences of a quantitative nature.

Experimental Rationale

The general goals of this research are to provide a detailed quantitative description of brood defense behavior and to investigate possible factors that influence its expression. In particular, the effects of the reproductive condition, prior maternal and intruder experience and certain stimulus properties are explored. In order to obtain the information necessary to determine the relationship between the behavior observed and the factors under study as efficiently as possible, the responses of parent birds to intruders were studied in the laboratory. The experience of the subjects could be controlled to a greater degree than free-living birds and individual's histories could be recorded. In addition, details of the external stimulus situation could be determined by the experimenter. Control over the type of intruder, the frequency, duration and physical setting of encounters permit stronger inferences to be made from data since the characterisitic limitations of field observation, non-uniformity of stimulus conditions and lack of information about the subjects, were minimized.

Broody bantam hens were chosen as subjects because they exhibit all phases of the reproductive cycle including the laying and incubation of eggs and the rearing of chicks under laboratory conditions. In addition, preliminary observations revealed that the responses of bantam hens to intruders were similar in most aspects to those of feral domestic fowl. Thus, even under captive conditions, the bantams perform apparently species-typical brood defense behavior.

In order to describe a more complete range of responses to intruders and to obtain a representative estimate of quantitative features of the response pattern, I observed broody hens with and without prior maternal experience and with varying amounts of contact with intruders. Furthermore, changes in the responses of these hens were recorded as experience with both of these independent variables accrued.

A predator was chosen as an intruder for the description since disruption by this type of animal is highly probable in the natural habitat. Specifically, a ferret (also called a polecat, _Mustela putorius_) was selected as the stimulus animal.

Ferrets are well-known predators of Gallus and hunt both during the day and at night. The family Mustelidae, of which ferrets are a member, are common throughout a large geographic range. If the putative functional category of brood defense exists, it seems reasonable to assume that a ferret would elicit a strong response. Their reputation as a formidable predator is undisputed and they are known to kill surplus prey when the occasion arises. The ferret had to be restrained and controlled in these experiments in order not to kill or damage the hen. The restraint also provided a control over the ferret's behavior so that the presentations to the hens were more uniform. Some pursuit behavior by the ferret was permitted. If the ferret were too restrained, then the hen's behavior might be atypical. If one considers that a natural predator-prey encounter may include a complete sequence of approach, pursuit, attack and capture, this experimental protocol emphasized approach, diminished pursuit and eliminated attack and capture. Thus, a compromise between the experimental objective of a realistic description of the hens' behavioral responses to a predator and the implicit limitations on the verisimilitude of the stimulus situation has been reached. In fact, the approach-pursue sequences are representative of many predator-prey encounters (Errington, 1967) since predators are often unsuccessful in their attempts to secure prey.

In addition to predators, other hens occasionally intrude upon and disrupt the activities of broody hens and their chicks. This situation is more likely to occur when birds are housed in close quarters or when resources such as food are spatially and temporally restricted. Although few reports of such encounters appear in the literature, McBride, et al. (1969) do describe a broody hen that fluffed her feathers and charged another hen in the vicinity. The "charged" hen responded by moving away. Preliminary research by this author confirmed that broody hens do confront conspecifics which approach. The broody hens express a variety of responses, some of which successfully arrest the approaching animal. The preliminary tests were conducted with live non-broody hens which were introduced into the living space of broody hens and their chicks. Although it was not unusual for the stimulus hens to approach the broody hens, the infrequency of these approaches and the general variability in gross and fine movements of the non-broody hens made them unsatisfactory stimuli for collecting sufficient data for a substantial description of the responses. In order to gain control over the spatial relationship between the stimulus hen and the subject and over the subtle postural changes of the stimulus hen which seemed to influence the broody hen's response, the use of a hen puppet was adopted. The hen puppet (HP) used was an abstraction of certain morphological features of a live hen. In addition, the movement of the hen model was patterned after aspects of live hen behavior observed in pilot studies associated with approach responses. Nevertheless, I do not assume that the salient features for conspecific recognition were necessarily the ones chosen for the puppet. For example, initial observations indicated that the hen puppet elicited responses that were qualitatively similar to the behavior observed in response to the live ferret and to non-broody hens. In this sense, the hen puppet was a satisfactory intruding stimulus.

Reproductive condition. Many students of avian behavior suggest that the responses to intruders of birds that are caring for young differ from the responses of birds that are not in the breeding phase of the reproductive cycle. In general, immediate fleeing is common in non-breeding birds whereas parent birds display a complex pattern of conspicuous behavioral elements within sight of the intruder. Peculiar locomotion, special postures and attack of the intruder have been observed. However, no attempt has been made to describe the precise changes in response to intruders that occur as a function of reproductive condition.

In addition to distinctions between the behavior of breeding and non-breeding birds, many parental responses change as the chicks grow. Among the parental behavior reputed to change is the response to intruders. The interpretation of a majority of observations, however, confounds prior intruder experience and factors associated with the brood and the internal state of the hen. Hence, it seemed reasonable to ask under controlled conditions: Do parent birds respond to an intruder encountered early in the period of chick care in the same manner as one encountered when the chicks are older? Under laboratory conditions, one can naturally control for prior intruder experience of the subjects.

Specifically, then, one aim of this research is to determine the effect of reproductive condition on responses to intruders.

<u>Experience</u>. In a great deal of previous research, implications that responses to intruders were a function of reproductive condition and intruder type have been strong. A general criticism, however, is that the subjects' prior maternal and intruder experience have been unknown factors. Since experience with particular stimulus situations often has consequences for subsequent responses to them (e.g., nut-opening in squirrels, Eibl-Eibesfeldt, 1967; drinking behavior in chicks, Shet-

tleworth, 1970), conclusions that do not take experience into account must be interpreted with caution.

In order to determine whether prior maternal and intruder experience influences the behavior of broody hens toward intruders, several steps must be taken. First, a behavioral baseline describing changes in the responses which are correlated with an accrual of experience must be established. If birds which are exposed repeatedly to an intruder throughout the period of chick care show no changes in their behavior, further analyses are unwarranted. On the other hand, if changes do occur, the second step is to determine whether they may be due to repeated encounters with the intruder or to the stage of broodiness which includes a cumulative experience with the chicks as well as the physiological state of the hen. An interaction of these factors is also possible. The influence of these factors can be determined by changing the point at which hens are tested in the period of brood care while holding intruder experience constant. If the responses are different, it would suggest that breeding cycle stage and/or the experience with the brood do not exert major control over the behavior. Moreover, intruder experience gained during care of one brood may have consequences for the behavior a hen shows toward intruders encountered during the care of subsequent broods.

Responses of hens which are broody for the first time can be compared with hens that have reared a previous brood and have had prior intruder experience. If there be a difference between the two groups, the relative influence of maternal and intruder experience can be dissociated by further studies.

In an experimental framework, the questions about the effects of experience with intruders can be answered by asking whether responses to intruders change as a function of repeated encounters with that intruder and whether hens that have reared a previous brood and have encountered intruders during the care of the former brood respond differently to intruders they encounter during care of a subsequent brood.

Intruder type. Reports in the literature indicate that many species respond differently to intruders of different types. However, since the bulk of these observations were made under field conditions and many potentially influential factors were not controlled, the inference that birds consistently discriminate among intruders is necessarily tentative. Furthermore, there are reports, such as one on Gallus, which gives no indication that responses to different types of intruders are different. McBride, et al. (1969) described a similar pattern of response by feral broody hens to a cat, some low-flying birds and to other hens. No other information on responses to intruders of more than one pattern is available for this species. One inference which may be drawn from these similarities is that an important aspect of the stimulus situation for the broody hen is the physical disruption of ongoing activities. The differences in responses to the ferret, the live hens and the hen puppet observed in pilot research could be related either to differences in movement or form of the stimuli.

To determine whether broody hens respond in the same manner to any object which disrupts the activities of the hen-chick unit, behavior recorded in encounters with a hen model was compared with the responses to an abstract object. An abstract intruder was chosen as a control stimulus to determine whether some aspects of the response are due to intrusion per se and if others are influenced by differences in the visual form of the stimulus objects. Models were used so that differences in movement pattern could be minimized. Further, an attempt is made to use virtually identically matched samples for testing the two objects since the variables of individual experience and stage of broodiness may influence the response.

METHODS

Materials and Methods

Subjects

Twelve bantam hens (Gallus gallus domesticus) formed the pool of animals out of which various experimental groups were organized. The bantams were purchased as nulliparous adults from a local supplier (Pitman Farms, Wyckoff, New Jersey) and had been maintained in outdoor flocks prior to acquisition. None of the birds used in these experiments was injected with hormones to encourage incubation, since Saeki and Tanabi (1955) suggested that hens with chemically induced broodiness. Thus, the supply of subjects was limited to hens which became broody in our simulated summer environment.

Housing

Housing conditions were of three types corresponding to particular stages of the hens' reproductive cycle. During the breeding period, the bantam flock of 12 females and 1 male was housed in a 6.1 m^2 wire and wood frame enclosure (Figure 1) having a chipped wood substrate. This structure was located in a quiet room of the animal facilities. Grower and layer pellets and fresh water were available ad libitum from standard poultry feeders and water dispensers. Ten metal nest boxes for laying and incubation were also present in the enclosure. To enhance the probability that the hens would become broody, summer conditions were simulated. A 14/10 hour light-dark cycle was maintained throughout the year and temperatures ranged between 30°C during the day and 14°C at night.

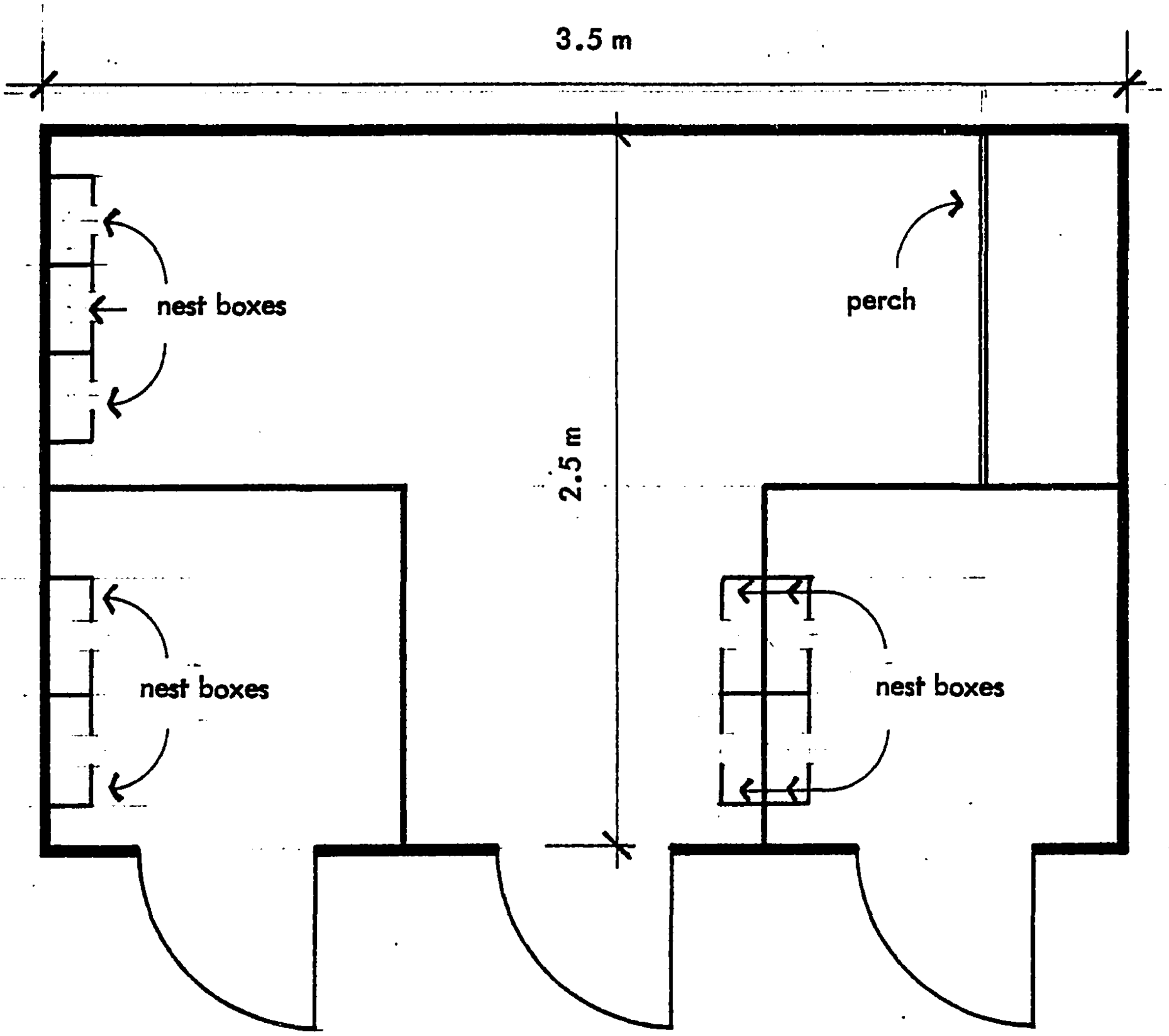


FIGURE 1. Housing for the flock. (Scale 1:20)

When hens shifted from egg laying to incubation, each took up solitary residence in a metal nest box within the colony enclosure. Nest boxes measured 33 cm X 33 cm X 30 cm and were enclosed on three sides. Since hens more readily incubate clutches located in dimly lit areas, entrances to nest boxes were curtained by opaque fringed cloth which reduced light in the interior. Excelsior, used as a nesting material, was fashioned into a cushioned depression within the nest box. During the incubation period, hens spent most of the time sitting on their eggs, so contact with the flock was limited to their occasional excursions from the nest for food and water.

Chicks hatched after 20-21 days of incubation and remained in the nest until dry. When the chicks' feathers were dry, the hens with their hatchlings were removed to individual enclosures (Figure 2) in different rooms within the laboratory complex. Generally, each housing unit was placed in a separate room. Occasionally, however, space limitations made it necessary for two housing enclosures to be maintained in a single room.

The enclosures were wood-frame structures having dimensions of either 3 m X .9 m or 1.8 m X .9 m. The floors were strewn with wood chips to a depth of 4 cm. Plywood walls .3 m in height bordered the enclosures at ground level. Above these solid walls, opaque material mounted at a height of 1.35 m was draped from verticle corner posts and cross beams. Food and water were available _ad libitum_ in dispensers identical to those used for the flocks; however, they stood directly on the substrate instead of supporting stands so that chicks could reach the troughs. The food provided was a composite of chick starter mash and grower crumbles. Am-

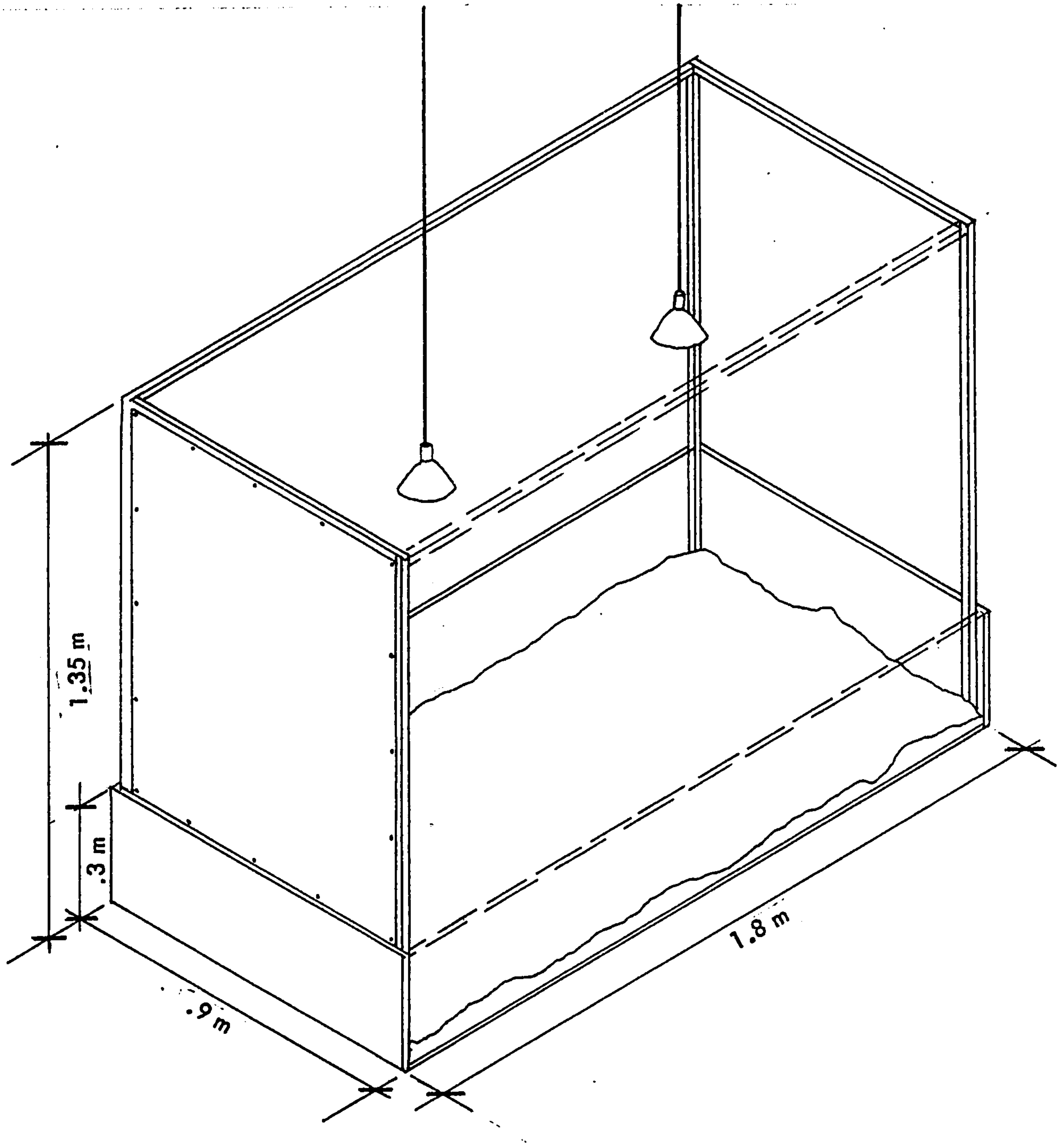


FIGURE 2. Individual housing unit for a broody hen and her chicks. This enclosure served also as the test arena.

bient temperatures varied between 30° C during the 14 hour light period and 19° C during the 10 hour dark period. The post-hatch housing units described above were also used for testing in order to minimize disturbance of the birds by handling.

Since the effect of substituting the eggs of other chickens on maternal care is not known, it was preferable that a brood consist of chicks hatched from a hen's own eggs. However, on the occasions when clutches proved infertile or fewer than three chicks hatched, pipping leghorn chicks which had been artificially incubated were gently placed under the hen. This procedure of introducing supplementary chicks generally achieved a brood size of 4-5 which approximates the average reported for feral domestic fowl (McBride, et al., 1969).

Experimental Design

For the purpose of describing the responses of parent birds to intruders and investigating the effects of reproductive condition and maternal experience on those responses, bantam hens were tested with intruders at different times in their reproductive cycles. Changes in the reproductive condition of a hen are mediated by physiological factors that are correlated with a complex of attendant intrinsic and extrinsic stimuli (Burrows and Byerly, 1938; Ramsay, 1953). Since the experimental subjects were allowed to cycle normally, the presence or absence of incubation behavior or a brood and the age of the brood were used as estimates of a hen's reproductive condition. The bulk of data has come from broody hens tested repeatedly throughout the first 4 weeks after the chicks hatched. To test the influence of reproductive status on the response patterns, three subject categories were established:

broody hens with young chicks (≤1 week), broody hens whose chicks hatched 3-4 weeks earlier, and non-broody hens. To assess the effect of maternal experience, hens' responses to intruders during the care of their first brood were compared with their responses to intruders during the care of a second brood.

Stimuli

Three different stimulus objects were selected as intruders. The selection of each intruder and its relevance to the experimental questions are discussed separately.

Predator intruder. Since mammalian ground predators are a widespread, naturally occurring threat to the survival of a hen and her chicks, an adult, female ferret (*Mustela putorius*) was used as one of the intruders (Figure 3). Typically, the ferret showed a consistent, strong tendency to pursue the hen and her chicks. To prevent possible attacks on the hen and to control the hen-intruder distance, the ferret was restrained by a harness and leash. In spite of these precautions, there were three cases in which the ferret killed one or two chicks.

Whereas a composite description of the responses of broody hens to an intruder could be successfully generated by using the live ferret, the limited control over its behavior and possible behavioral changes resulting from multiple encounters with broody hens made the live predator unsuitable for assessing the influence of repeated testing, maternal experience or reproductive condition. A standard stimulus presentation was necessary for this purpose. The substitution of a ferret model was considered but the behavior constituting the approaches of the live ferret was

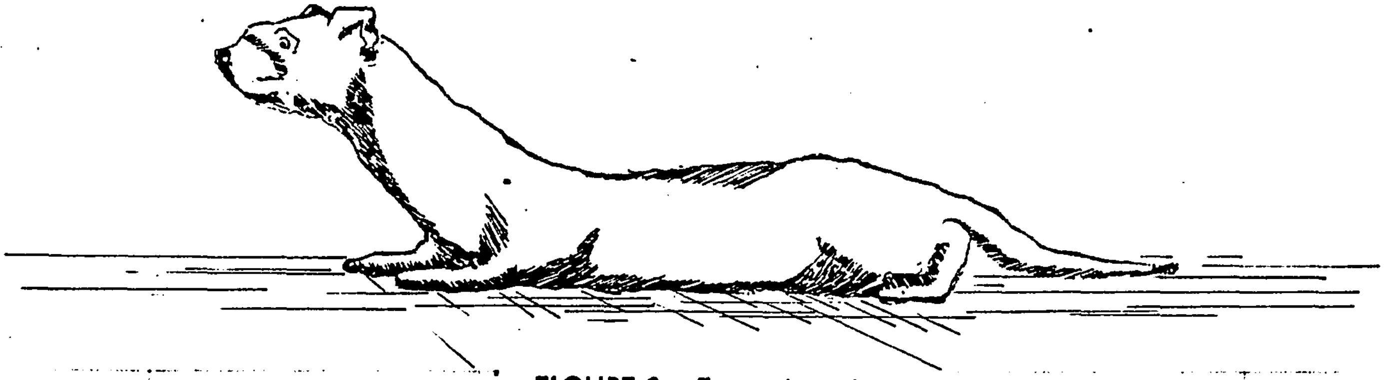


FIGURE 3. Ferret intruder.

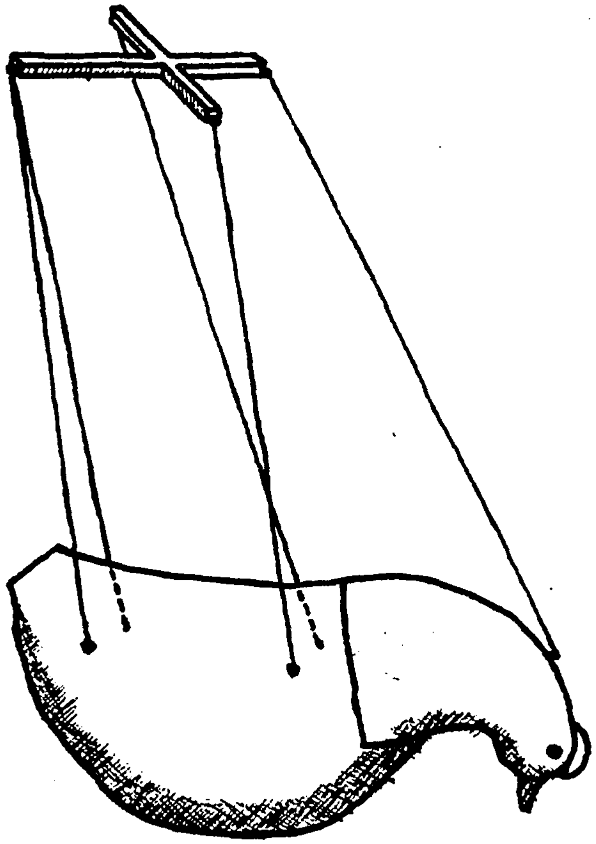


FIGURE 4a. Hen Puppet intruder.

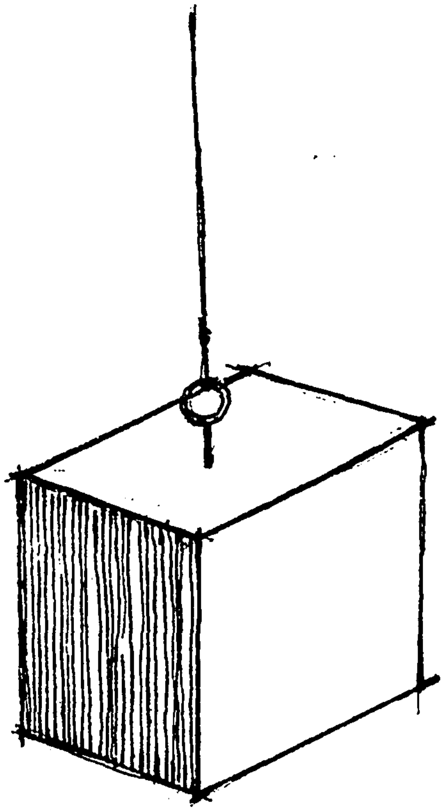


FIGURE 4b. Green Cube intruder.

complex and erratic. In general, the ferret moved rapidly around the enclosure, often alternating a gamboling gait with a slithering movement on her ventrum that partially buried her in wood chips. Accurate duplication of this pattern using a ferret model and interpretation of data procured with such a model would have been difficult.

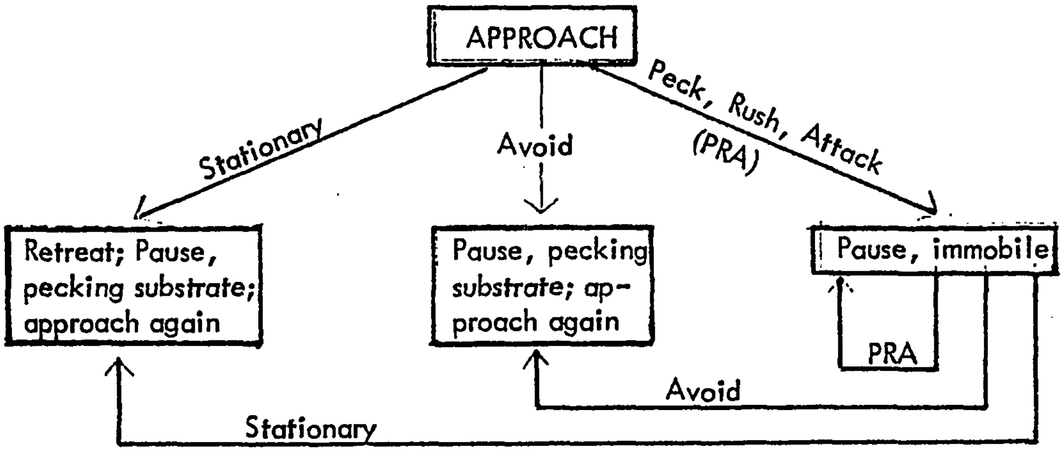
Conspecific intruder. Although broody hens generally remain some distance from other flock members, adult conspecifics intrude periodically into the activity area of a brood and disrupt interactions between the hen and her chicks. In preliminary attempts to determine how a broody hen responds to this situation, non-broody hens were introduced singly into enclosures housing test subjects. The non-broody hens tended to wander slowly around the arena and remain some distance from hens and their chicks. Occasionally, the stimulus animal approached a broody hen; this event seemed more likely to occur if the broody hen was near a food dispenser or was foraging vigorously with her chicks. Almost invariably, the broody hen responded with particular vocalizations, fluffing of the plumage, and movements toward the stimulus hen which sometimes included pecks or attacks. The non-broody hen responded by moving away, and thereafter, tended to stay at a distance and/or approach in a more hesitant manner. Thus, although the live non-broody hen's behavior was relatively simple, the infrequency of approaches and irregularity in orientation vis à vis the broody hen rendered live birds unreliable as stimulus animals for studying the effects of the experimental variables. The idea of curbing a live hen and thereby controlling the hen-intruder distance was neither feasible nor sufficient. First, hens are generally intractable when harnessed and resist being guided and stimulated to locomote. Second, intermittent eye contact and subtle postural adjustments such as head position often evoked strong responses from broody hens. Harnessing could not regulate this inconsistency. These difficulties in presenting a standard stimulus situation were overcome by substituting a hen puppet for the live bird. The hen puppet, which is described below, could be manipulated in a manner that accurately mimicked particular features of live conspecific behavior but eliminated variability in posture and orientation.

The life-sized hen puppet (Figure 4a) was fashioned out of styrofoam, covered by white plush cloth and suspended by 50 cm lengths of monofilament line from wooden cross-bars designed to be hand-held by the experimenter. Red felt wattles and comb, an ochre beak and black eyes detailed the head region of the puppet. The marionette was mute since acoustical signals were rarely emitted by live non-broody hen intruders.

Because the puppet's choreography was derived from observations of live hen interactions, it consisted in various standard movement patterns whose particular activation depended on the behavior of the broody hen (Table I). The subjects' responses to the marionette closely resembled those shown toward live hen intruders in that most components observed in the trials with the hen and the hen puppet had also occurred in tests with live hens. In addition, the behavior toward the hen and hen puppet appeared qualitatively similar to the behavior toward the ferret. Evidence supporting this statement is presented in Appendix A.

In summary, the choice of the hen puppet as the stimulus object to investigate the effect of reproductive condition, maternal experience and repeated testing was

TABLE I . Choreography for the Hen Puppet and the Green Cube. The movement patterns of the intruder are contingent on the responses of the subject. The boxes enclose the movement of the stimulus object and the lines represent the response options of the subject.



based on two considerations. First, preliminary tests had demonstrated that the hen puppet produced responses in broody hens that were qualitatively similar to those observed when live hens or a ferret intruded into the living space of the hen and her chicks. Second, due to the nature of the behavior of live hens in contrast with that of the ferret, the degree of accuracy in duplicating the behavior of hen intruders with an inanimate facsimile was greater. Therefore, it seemed reasonable to combine the advantages of consistency in stimulus form and movement with accuracy in reproducing the movement patterns of a live intruder by using the hen puppet to explore the effects of the independent variables.

Abstract object intruder. The question of whether broody hens would respond differently to intruders that behaved similarly but were unlike in appearance was investigated by testing hens with an abstract object and comparing those responses with the hen puppet data. This abstract form lacked most features of naturally occurring intruders and followed the same choreography of the hen puppet. Any difference in response, therefore, could be attributed primarily to differences in visual configuration.

A green styrofoam parallelepiped having the proportions 18 cm X 18 cm X 13 cm served as the abstract object (Figure 4b). It was suspended from a cross bar by 50 cm of thin monofilament and manipulated by the experimenter. In the interest of simplicity, if not precision, this intruder is referred to throughout as the "green cube."

Test Groups

Subjects differing in reproductive condition (hens without chicks, hens with broods of different ages) and amount of previous maternal and intruder experience were tested under different stimulus conditions. The eight experimental groups formed are summarized in Table II. Data generated by the groups were used in various combinations to answer the specific experimental questions. The relationship between the experimental groups and the questions they were designed to answer is presented in Table III.

Both groups I and II were designed to test broody hens' responses to the hen puppet and the green cube during the first four weeks after hatching. The groups are composed of the same subjects: in Group I, birds were both experimentally and maternally naive while in Group II, the hens were rearing their second brood and had had previous experience with the test objects. Data from these groups are pertinent to the effects of repeated testing, reproductive condition, maternal experience and intruder type.

Groups III, IV and V were concerned with responses to the ferret during the early post-hatch period. In Group III, the responses of naive broody hens were tested, while hens which had had no previous exposures to the ferret but did have maternal experience were tested in Group IV. Group V subjects had experienced both prior broods and the test predator. The responses recorded from these three groups primarily provided the data from which the composite description was made.

Certain aspects of maternal behavior, such as the time spent brooding chicks, change as the age of the chicks advances. To determine whether the stage of broodiness influenced the response pattern, Group VI was established in which hens whose broods had attained three weeks of age were tested for the first time with the hen puppet and the green cube.

TABLE II. Summary of all experimental groups.

Test Group	Reproductive Condition	Stimulus Object	Previous Experience		Span of Testing	No. of Subjects	I.D. #'s of Subjects
			Maternal	Test Object*			
I	Broody	H, C	no	no	1-4 wks	6	1,2,3,4,5,6
II	Broody	H, C	yes	yes	1-4 wks	6	1,2,3,4,5,6
III	Broody	F	no	no	1-3 wks	6	9,10,11,13,14,15
IV	Broody	F	yes	no	1-3 wks	2	2,4 **
V	Broody	F	yes	yes	1-3 wks	2	4,5 **
VI	Broody	H, C	yes	yes	3-4 wks	6	1,2,4,5,6,9
VII	Broody	none	yes	yes	1-3 wks	5	2,4,5,6,9
VIII	Non-broody	H,C,F	yes	yes	n. a.	6	2,3,4,5,6,9

Key: H = hen puppet
C = green cube
F = ferret

* = has had experience with the test object during care of a previous brood

** = hens 2,4 and 5 had experience with the ferret during care of an earlier brood (not shown on this chart)

TABLE III. Relevance of tests groups to experimental questions. Certain experimental groups were used to answer several questions. The relationship between the experimental groups and the questions are given in this table.

Test Group		I		II		III	IV	V	VI		VII	VIII		
Stim. Obj.		H	C	H	C	F	F	F	H	C	-	F	H	C
Results														
Composite	Ferret tests					■	■	■						
	Intruder present/absent						■				■			
Responses to Hen Puppet and Ferret		■				■								
Reproductive Condition	Broody/Non-broody			■									■	
	1 vs. 3 week broods			■					■					
Repeated Testing		■												
Maternal Experience		■		■										
Different Intruders		■	■											
Individual Variability		■	■	■	■	■		■						

Key: means that the data from this group was used to answer the question

H = hen puppet

C = green cube

F = ferret

To control for the experimenters' presence and data collection procedures, behavior of broody hens was recorded during normal test periods with no stimulus object present (Group VII).

In the final test group, Group VIII, non-broody hens were exposed to the hen puppet, the green cube and the ferret, so that their responses could be compared with those of broody hens. Since the subjects available for this group had had prior maternal and intruder experience, they were compared with experienced broody hens.

Since any one bird from the pool of experimental animals may have been used in several of the test groups, the subjects used in each group are identified in Table II. For example, Test Group VI is composed of hens that had been tested during the care of previous broody (Groups I, II, III).

Test Schedules

Exposure-brood age correspondence. At the outset of the experiments, it was not known whether or how responses to intruders changed as a function of differences in broody hen behavior related to the chicks' development and/or recent experience with intruders. By selecting several post-hatch dates on which to begin multiple exposure sequences and by varying inter-trial intervals for all subjects, a broader range of relationships among intruder experience and on-going hen-chick interactions was sampled. The number of days since the chicks hatched is used as an estimate of the stage of broodiness which is a complex of internal (e.g., hormonal, experiential) and external (e.g., social) factors. The relationship between the stage of broodiness and repeated exposures is that the stage of the hens' broodiness progresses as the exposure numbers increase. Correspondence between the exposure number and the inter-trial interval was unsystematic and assumed to be random.

Range of exposures. The number of exposures for the test groups was determined by the function(s) each group served in the overall design. As can be seen in Table II, all birds in Groups I and II received a minimum of 7 exposures. In the ferret tests (Groups III, IV, V), the number of exposures was regulated primarily by consideration for the stimulus animal. On occasion, the hens physically attacked the ferret which was prevented from retaliating. Although she received no actual wounds, such repeated experiences might modify the quality of subsequent hen-ferret interactions and it seemed reasonable to limit the potential for these effects. Thus, although some hens were tested 7 times to allow statistical comparisons among the hen puppet and green cube test sequences, most were terminated earlier.

Since the effects of repeated testing on the responses of birds in Groups VI, VII and VIII were not of interest, subjects were tested no more than 3 times.

Test Protocol

To begin a test, the room lights were switched off and the stimulus object was lowered into the test arena as noiselessly as possible and positioned 1.2 m from the hen. The lights were then phased on using Variac, an autotransformer, and data recording was begun.

Hen puppet and green cube tests. For both the hen puppet and the green cube, an exposure consisted of a progressive reduction in the intruder-hen distance.

Initially, the object was maintained for 30 s at the original distance of 1.2 m after which it was moved slowly to a position .6 m from the hen where it remained for 30 s. A third 30 s interval at .3 m also was included in most tests (75%). In the final 120 s, the object made a series of approaches to within 1 cm of the hen.

During the 30 s intervals at 1.2 m, .6 m and .3 m, the models made periodic bobbing and pecking movements and, if the hen increased or decreased the space between herself and the intruder, frontal orientation and the specified distance were reestablished by a slow, compensatory movement of the model.

The number of approaches during the 120 s period was regulated by the behavior of the hen. If spatial contiguity within the brood disintegrated during an approach, its restoration was required prior to the next advance. On the other hand, if the hen and her chicks were merely displaced as a group by the intruder, the model retreated and approached again when the hen resumed non-intruder oriented behavior such as foraging or brooding (see choreography in Table I).

At the end of the 2 minute period, the lights were extinguished, the object removed, and the pre-test conditions reinstated.

Ferret tests. The protocol of the ferret tests differed from that of the hen puppet and green cube only in that the 120 s of approaches to 1 cm began immediately. As soon as the lights were restored, the hens' sighting the ferret typically resulted in constant locomotion and the maintenance of stable hen-intruder distances was impossible. The number of approaches was regulated by the same criteria as those set up in the green cube and hen puppet tests.

In general, the ferret's behavior included consistent orientation toward and active attempts to approach the hens. On occasion, however, the ferret had to be coaxed by tugging on the leash.

Baseline tests. Tests in which no stimulus object was presented consisted of a 3-minute sample of a subject's behavior under technical conditions identical to those described for the experiments with intruders.

All multiple object test groups. In all test groups where more than one model was involved, the objects were presented to the hen in separate trials on the same test day. The order of presentation was non-systematic in an attempt to randomize the effects of order (Appendix B) and the time elapsing between tests, usually 5 to 15 minutes, was determined by the hen's behavior. A return to either foraging or brooding was the criterion set for beginning the next test.

Although the data generated from the green cube tests in Groups II, VI and VIII were not used to evaluate the effect of the experimental variables (as shown previously in Table III), it was necessary to test subjects with the green cube as well as the hen puppet for a balanced design. This procedure ensured that the hen puppet data from different experimental groups was comparable.

Behavior Recorded

The behavioral components comprising a hen's response to the presence of an intruder fall into three categories: acoustic behavior, phasic motor behavior and feather postures. Each discrete behavioral component is described below; the letters in brackets after each behavior are the abbreviation used for it in figures, tables and text. During a test, the frequency of initiation was tabulated for each component; the duration of scratching bouts and each feather posture's maintenance were recorded. These measures form the data base of the experimental results.

Acoustic Behavior

During the tests, hens emitted eight distinct calls. Of these, six were routinely recorded. The roosting and food calls (Collias and Joos, 1953) were excluded due to unreliable audibility and infrequent occurrence, respectively.

The descriptions of the signals included in this study emphasize the spectral characteristics detailed by earlier investigators of the vocal repertoire of the domestic fowl (Collias and Joos, 1953; Baeumer, 1962; Konishi, 1963). Semantic content of the calls has been presented only where a clear demonstration of the relationship between the signal emitted and the complex eliciting situation has been made. Any tendency to use the presumed stimulus situation as a basis for interpretation of a vocalization was avoided by monitoring only the auditory portion of the taped record when quantifying the various calls. Furthermore, should a call seem ambiguous, two listeners independently evaluated the sound segment and a decision was reached.

The calls recorded were these:

Clucks (Cluc). Only broody hens are known to cluck. There is little doubt that the primary social function of this call lies in maintaining or reestablishing contact with the chicks as demonstrated by Bruckner (1933) and reemphasized by Baeumer (1962), and Collias and Joos (1953). A cluck consists of two short pulses, separated by approximately 50 msec. There is a predominance of lower frequencies (below 400 Hz) and the pulses vary greatly in amplitude. Clucks are identical with the "glucke" (#18) described by Baeumer (1962), and, of course, the "cluck" discussed by Collias and Joos (1953).

Chirrs (Chir). These usually short, harsh, low frequency notes are composed of very rapidly delivered pulses (50-60 pps), which sound slurred. This call has many variable aspects including duration and amplitude modulation. Collias and Joos (1953) called it the "broody hen alerting call" while Baeumer (1962) labelled it #25/26 in his study.

Alarm Call, Type I (AC I). This call is given in short (ca 40 msec) pulses over a wide range of frequencies and amplitudes. The fundamental frequency has been identified as 1 kHz. Both the length of calling bouts and the inter-pulse interval are highly variable. Most recently, Konishi (1963) named this vocalization the "Type I Alarm Call" and it is call #6 , the "kleines gackern" in Baeumer's study (1962).

Alarm Call, Type I hybrid (AC Ih). While similar to the AC I in the timing of pulses and the stimulus-response situation in which they are emitted, the tonal quality of AC Ih approximates the more grating and harsh sound of chirrs. Since a classification as a chirr or AC I would indicate clarification of the nature of this ambiguous call, which has not been achieved, this vocalization has been recorded separately from the few subjects (2) which produced it.

Alarm Call, Type II (AC II). This call has two segments, the last generally louder and longer-lasting than the first. Characteristically, one AC II follows a train of AC I's. Konishi (1963) considered the entire sequence of multiple AC I's followed by an AC II as the "Type II Alarm Call." I restrict my designation to the specific element ending the train which differentiates it from the Type I calls. The occasional emission alone of an AC II, without preceding AC I's, is therefore not overlooked and the analysis of frequency of occurrence is accurate. Baeumer (1962) called this vocalization "grosses gackern" (#7).

Shriek (Shri). A shrill, raucous, multisyllabic (ca 3-7) call wherein the first syllable is usually stressed by having high amplitude, which decreases on successive syllables. On rare occasions, a shriek is repeated without other intervening calls, but, more often, it is preceded by increasingly rapid and intense AC I's or AC Ih's. A shriek may be followed by alarm calls as well, although they are usually given at a lower rate and amplitude. Shrieks typically accompanied vigorous forms of avoidance such as flying out of the test arena or fast dodging manoeuvers involving wing flapping.

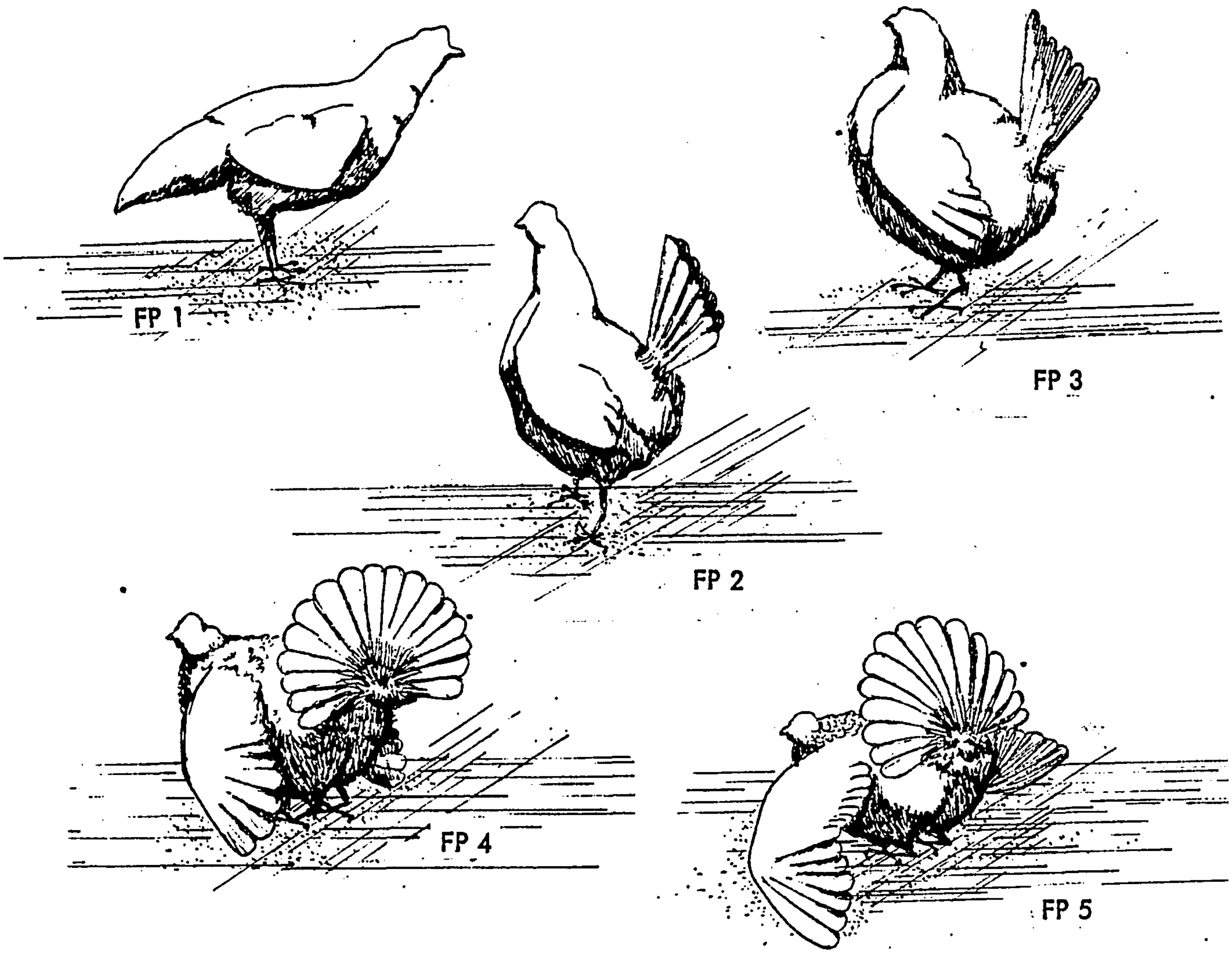
Screech (Scre). This harsh, usually loud, grating monosyllable is always prolonged, although its actual duration varies. Not all hens were observed to give this call and, when it occurred, a screech was not necessarily repeated during a test. A screech was usually but not invariably accompanied by elaborate threat components and was delivered when the hen squarely faced the intruder. The quality of the sound resembles that of a chirr and, in fact, that pattern of rapidly repeated pulses obtains. In the screech, however, the pulses sound slurred in the characteristically extended expiration.

Feather Postures

During interactions with both juvenile and adult conspecifics and in response to various other stimulus situations, the visual appearance of a hen may change quite remarkably. In addition to modification of head and body orientation, alterations in body image are accomplished by various degrees of vaned body feather ruffling or fluffing and by arraying the feathers of the alar and caudal tracts in several ways (Morris, 1956). Although the contour feathers of the body, wings (remiges) and tail (rectrices), in fact move through individual positional continua, certain arrangements are adopted much more regularly than others, thus making distinct configurations recognizable. Since the hackles of the neck region were not raised except in concert with the body feathers of broody hens, the erection of hackles is considered with that of the body feathers. Five categories, designated as feather postures 1 through 5, were established in order to record this constituent of responses. The distinguishing features of each feather posture are presented in Table IV. Despite collective references to these feather postures, no a priori assumptions about their causal and functional relationships have been made.

On the few occasions when the feather configuration straddled 2 categories or appeared ambiguous due to an impaired view of the hen, the tail position was given precedence as a determinant since there was minimal overlap from one category to the next and no case arose where the other features of the feather posture were contradictory to the posture signalled by the highly visible tail.

Feather posture 1 (FP 1). Observations during pilot studies suggested general temporal characteristics of feather postures and the social contexts in which they often occur. Feather posture 1 (FP 1) has been observed in broody hens during the brooding of young chicks but has also been noted in non-broody hens while sleeping or during an agonistic encounter as a sign of submission. The feathers are relaxed with a sleek overall contour. The tail position, the tip angled toward the



	Wings	Tail	Body Feathers
FP 1	folded flat against body	angled down, folded fan	flat
FP 2	folded flat against body	erect, closed "V"	flat
FP 3	slightly lifted out from body	erect, open "V"	slightly fluffed
FP 4	lifted out from body, elbow bent, carpals near ground	erect, open, completely spread	very fluffed
FP 5	lifted out from body, elbow and carpal joints straight	angled forward, completely spread	very fluffed

TABLE IV. Descriptions of the feather postures: wing, tail and body feather characteristics.

ground, is unique.

Feather posture 2 (FP 2). Both broody and non-broody hens commonly exhibited feather posture 2. Observations indicate that it could be considered the basic relaxed posture of an undisturbed hen, the least transient of the five postures and the one around which the others revolved. However, FP 2 was also associated with active avoidance of an intruder as well as a general state of alertness. These three situations have in common an evident absence of aggression, threat or ambivalence in both social and asocial contexts. The feathers of the tail are held vertically, almost perpendicular to the bird's back, and the body's contour is sleek, these features thereby producing a usually crisp, unambiguous silhouette.

Feather posture 3 (FP 3). Intermediate posture, FP 3, appears to soften the angles and enlarge the visual image of a broody hen. While FP 3 had been observed in undisturbed hens as well as in ones confronted with an intruder, it was seen more frequently when a hen was locomoting toward specific stimuli such as food or away from a specific stimulus such as an intruder. Since the transition from a feather posture 3 to feather posture 2 was often very gradual, a firm point of discrimination between the two was often difficult to fix. In this case and all others when a posture seemed to have certain elements of two adjacent postures, judgments were consistently conservative. That is, should a doubt prevail as to whether a hen had slid from FP 2 to FP 3, the lower numerical value was recorded.

Feather posture 4 (FP 4). The fourth feather posture was observed almost exclusively during hen-intruder confrontations. The body feathers are fluffed; the tail is spread and held vertically over the back; the wings are extended toward the ground and are lifted slightly from the body. This configuration gives the bird a formidable aspect and, not uncommonly, outright aggression was performed in this posture. Furthermore, escaping or avoiding birds were never seen exhibiting FP 4.

Feather posture 5 (FP 5). The most fleeting posture, FP 5, was noted only in conjunction with aggressive approach which usually included a rush or an attack. While the body feathers are similar to FP 4, the fully spread wings are extended horizontally from the body and the open-fan tail is thrust forward in an acute angle over the back.

Phasic Motor Behavior

The frequencies of the following phasic behavior patterns were also determined.

Peck (Peck). A sharp, rapid thrust of the bill striking the intruder. Pecks were delivered from a variety of feather postures and object-hen orientations. Although substrate pecks were recorded, they were infrequent and did not warrant analysis.

Rush (Rush). A rapid forward lunge toward the object, usually involving locomotion. Contact with the object may or may not result from a rush.

Attack (Attk). Hen-initiated aggressive contact with the intruder which often took the form of wing beating and thrashing the object with her feet. If pecking occurred while an attack progressed, the pecks were counted separately.

Scratch Bouts (Scrt). Grating or scraping the substrate with the feet occurred in two contexts. In the absence of an intruder, scratching regularly contributed to general foraging activities wherein the hen orients her head toward the substrate and, often pecks at unidentified debris.

As a component of defense behavior, however, scratching typically occurred in an erect posture while the hen scanned the enclosure rapidly, her visual attention not focussed on the ground. Only scratching dissociated from concurrent foraging was considered in this analysis. If a pause greater than one second occurred during scratching, or a discrete behavior such as preening or locomotion intervened briefly, the episode was counted as two bouts. Both frequency and duration (DScrt) measures were taken.

Avoids (Avds). Sudden increases in the hen's rate of locomotion away from the stimulus object enlarging the hen-intruder distance constituted avoids. Avoids form a heterogeneous category in that they include both ground and aerial manoeuvers ranging from short dashes out of the path of an approaching model to flying out of the test arena entirely.

Data Collection and Reduction Procedures

All tests were conducted by the author and an assistant and were recorded on videotape. While one experimenter manipulated the model, the other videotaped the responses of the hen. The same two experimenters simultaneously reviewed the preserved tapes. The components of the behavior exhibited in each test were identified and recorded quantitatively with an Esterline-Angus event recorder. Since the components fall into three categories which can occur simultaneously (e.g., a hen clucking while scratching in a #3 feather posture), accurate recording of these events was accomplished by replaying tests so that one experimenter recorded one category (which consisted of mutually exclusive behavior) on each viewing. Very complex responses were reviewed until we were satisfied that the translation was precise. Also, any ambiguity was clarified by replaying the test with both observers recording the same category. Resolution depended on agreement of the independent evaluations of the two observers. If the interpretations of a component were different on reviewing, the data were so labelled. Since the occurrence of persistent ambiguity or contradictory reports was rare, such data were eliminated from the final analysis. The ongoing practice of checking and rechecking the tapes and one another assured a high degree of accuracy and consistency in the translation. Preliminary analyses of the data from the main experimental groups were carried out subsequently on the PDP-10 computer using programs written by the author.

Statistical Methods

The results were described quantitatively by calculating mean values and percentages. To describe the quantitative characteristics of behavioral components, an arithmetic mean was determined. This mean value which is called the typical frequency or duration is based only on those encounters in which the component occurred at least once; it indicates the mean number of times or mean length of time a component was expressed during 2-minute tests. The standard error is provided for each component as well. These values are employed exclusively in the composite description of responses to convey a sense of the extent to which a component is expressed when it occurs as part of the response.

To ascertain whether a given variable affected the expression of components comprising responses, a mean based on all tests under the experimental conditions was used. This value defines the average frequency or duration and indicates the mean number of times or mean length of time a component was expressed during the 2-minute tests. The advantage of its use over that of typical frequency or duration in determining whether a variable affected the response is that the average over all tests takes into account not only the possibility that frequency or duration within tests might change, but also that the component might be completely eliminated from the repertoire in some cases. In other words, both of these possible outcomes are reflected in a mean that includes all tests.

During a 2-minute test, a hen's response might or might not be composed of the same components. To discover how often a given component appeared at least once in hens' responses, the percentage of tests in which it occurred was calculated. This value does not take into account the frequency or duration during a test.

Comparisons of data generated by different experimental conditions were made using standard statistical methods. Analyses of variance (ANOVA) and Student's t-tests were applied by IBM Stat Pack^{TM}. The data subjected to ANOVA were based on single observations in each cell. As such, the ANOVA was of a Space/Time design (Winer, 1971) in which hens were treated as a bona fide factor. To determine whether 2 sets of percentages could be considered different from one another, a modification of the Student's t-test was used (Sokal and Rohlf, 1969: p. 607).

RESULTS

Composite Description of Responses

Qualitative

So that the reader may have a sense of the behavior observed during a test, I would like first to present a general account of the responses of broody hens to a ferret before presenting the quantitative analyses of the effects of the independent variables. The composite description is based on data from broody hens that had had different prior experience with intruders and with chicks.

When a broody hen and her young were undisturbed by the introduction of an intruder into the arena, they typically foraged during the observation period. Foraging included ground pecks and substrate scratching which was sometimes accompanied by slow locomotion around the enclosure and was typically accompanied by head orientation toward the substrate. Occasionally, clucks, chirrs and a few alarm calls punctuated this activity. In all tests without intruders, the body feathers of the broody hen were laid flat.

In contrast, when the ferret was introduced into the arena, a broody hen immediately changed her behavior. She increased her locomotor activity and the frequency of her vocalizations. Furthermore, she fluffed her feathers to various degrees which changed during the encounter. The hen's movements included ones which brought her closer to the ferret (pecks, rushes and attacks) and others which increased the distance (avoids) between them. In addition, the broody hen scratched the ground in a manner quite different from that observed during foraging in that the hen never oriented her head toward the substrate; instead, the animal held her head up and apparently scanned the environment. Many alarm calls were given as well as shrieks, clucks, chirrs and screeches. When the ferret was removed, the broody hen continued to give alarm calls, but began to intersperse increasing numbers of clucks among them. This vocal activity was accompanied by locomotion toward the usually dispersed, peeping chicks.

Quantitative

This overview of the responses of broody hens to a ferret is derived from observations of 6 subjects tested with the ferret a total of 43 times during the first 4 weeks after their chicks hatched. Of the 16 components defined in the Behavior Recorded section, some were present in virtually every test, others in only a few. To ascertain how often a behavioral component contributed to intruder defense, the percentage of tests in which the component occurred was calculated (Figure 5). Certain components such as clucks were observed in most encounters (77%) while others, such as feather posture 1, appeared rarely (5%). Figure 5, then, describes the probability of seeing each component in a randomly selected encounter between a broody hen and the ferret.

In addition to the percentages of tests in which each component occurred, the typical frequency and duration (where appropriate) of expression in those encounters is described (Figure 6). To determine the typical frequency or duration, a mean based only on those tests in which the component occurred was calculated. From this estimate, it is evident that alarm calls and clucks, for example, were emitted in relatively large numbers whereas attacks occurred infrequently during an encounter with the ferret.

FIGURE 5. Ferret Composite. The percentage of tests in which each component occurs. Based on 43 tests.

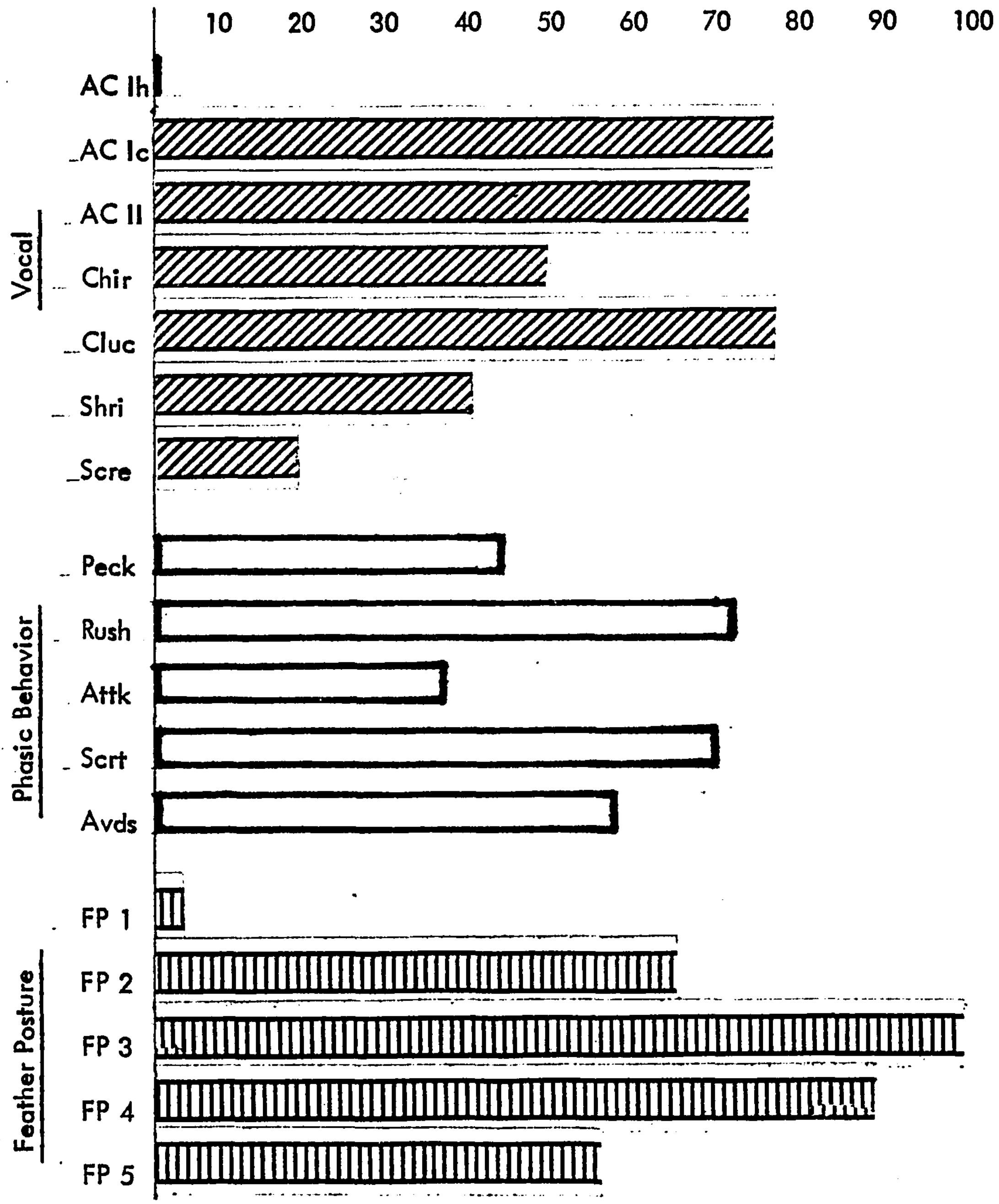
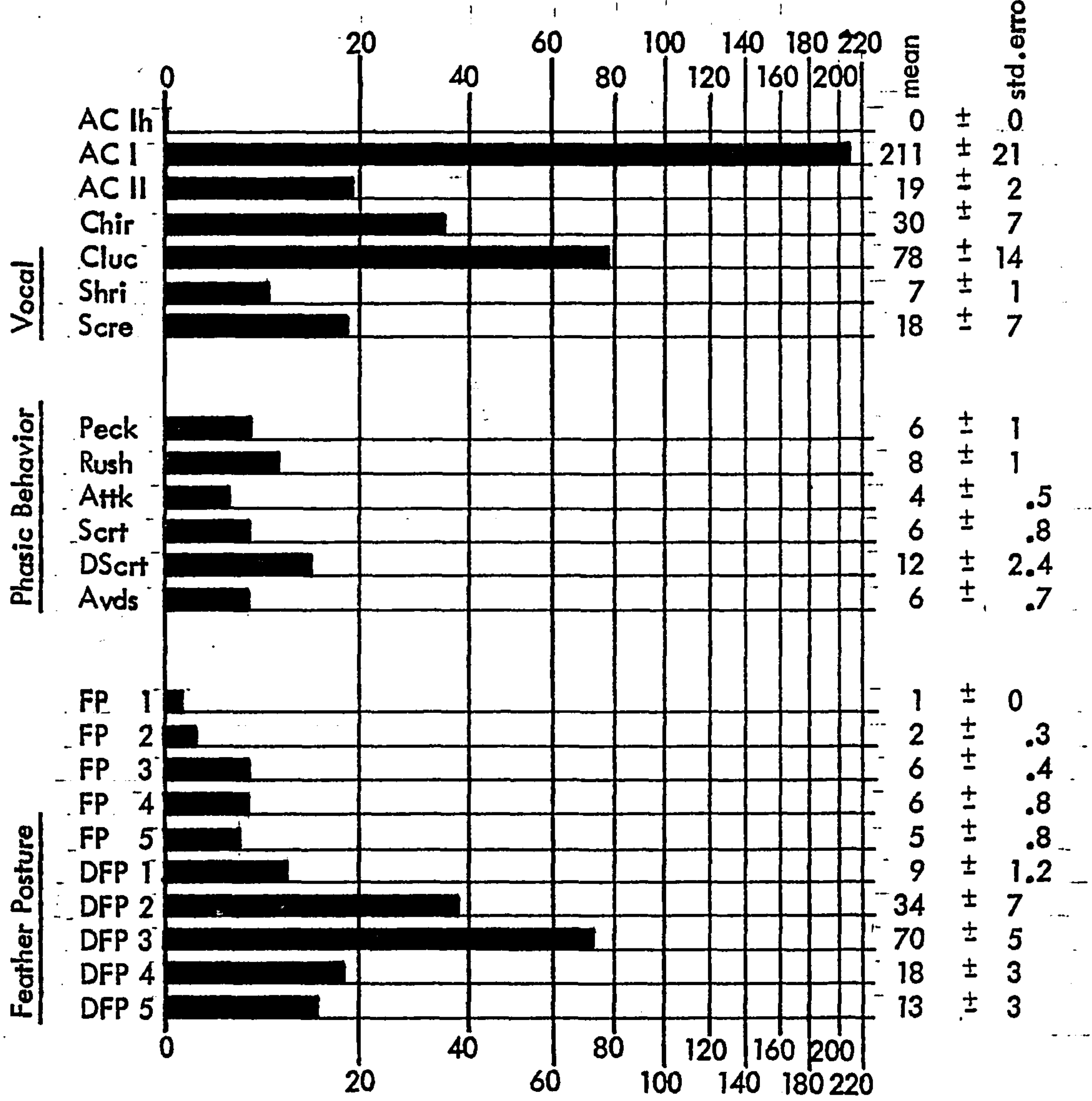


FIGURE 6. Typical frequency per 2 minute test of each component. The values are based on the mean frequency or duration of those tests in which the component occurred. Only tests administered to broody hens during the first four weeks after hatching and using the ferret as a stimulus object were considered.



Ferret present/ferret absent. In order to quantify how the behavior recorded during an encounter with a ferret is different from behavior in its absence, a control group was established in which experienced broody hens were observed while no intruder was present in the enclosure. A comparison of the percentages of tests in which each component occurred for the ferret present and the ferret absent groups was made. Of the 16 components recorded, 12 occurred in a greater percentage of tests when the ferret was present (Figure 7). Only chirrs, clucks, screeches and feather posture 1 occurred in approximately the same percentages of tests when the ferret was present as when it was absent.

In addition to the occurrence of 12 components in more tests when the ferret is present, the average frequency and/or duration during an observation of five components differed. Unlike typical frequency and duration which is based exclusively on those tests in which the component occurred, the average frequency and duration include all tests and are therefore less easily biassed by the possibly multiple factors responsible for the large variance characteristic of many components. Eight measures differed significantly under the ferret present and ferret absent conditions (Table V). Experienced broody hens shrieked and gave alarm calls more often and fluffed their feathers more frequently (FP 3, FP 4) and for longer durations (FP 3, FP 4) when the ferret was present than when no intruder was present. In contrast, when the ferret was absent from the arena, broody hens maintained either FP 1 or FP 2 and made no transitions to other feather postures throughout the entire tests.

Responses to the hen puppet. Before using the hen model as the stimulus object to test the effect of certain variables on the responses of broody hens to an intruder,

FIGURE 7. Percentages of tests in which each component occurs in the "ferret present" and "ferret absent" test groups. (An asterisk indicates a significant difference when p ≤ .05.)

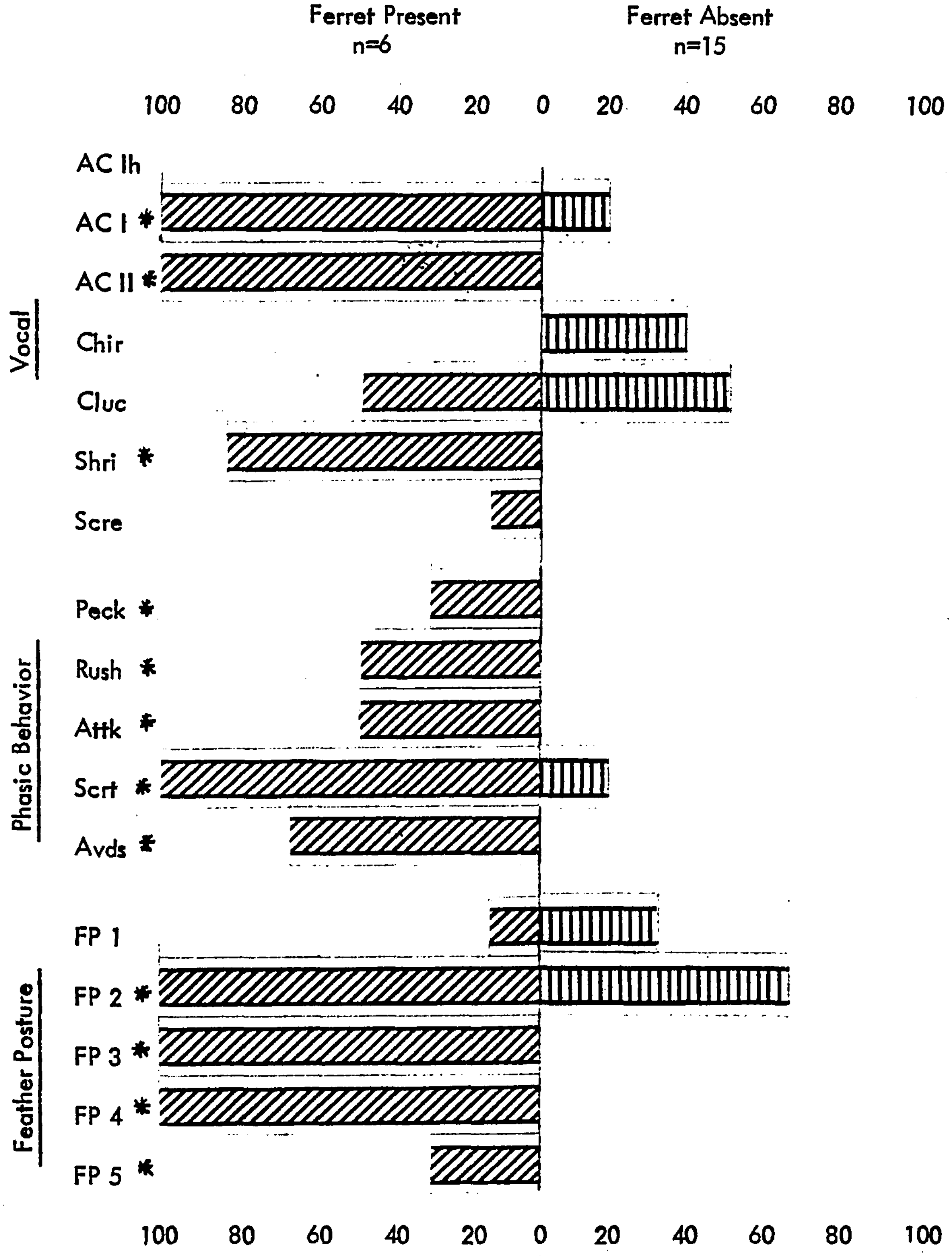


TABLE V. Significant differences between the Ferret Present and the Ferret Absent groups. The symbol's placement indicates the condition in which the mean for that component was significantly greater. (Based on exposures 1, 2 and 3; Student's t-tests, $p \leq .05$)

	Ferret Present n=2	Ferret Absent n=2
AC I	■	
AC II	■	
Shri	■	
FP 3	■	
FP 4	■	
DFP 2		■
DFP 3	■	
DFP 4	■	

the responses of 6 naive broody hens tested with the hen model (42 tests) were compared with the responses of 6 other naive broody hens tested with the ferret (30 tests). All 16 components recorded in the ferret tests occurred also in the hen model tests. Furthermore, only one component that had not occurred in the ferret tests appeared in the hen puppet tests: Type I alarm call hybrids.

Although virtually all the components comprising the responses were the same, the percentages of tests in which each component occurred at least once differed in encounters with the hen model and with the ferret. Three components (AC Ih, peck and FP 2) were present in a greater percentage of tests with the hen puppet whereas 6 components (AC I, AC II, rush, attk, FP 4 and FP 5) occurred in more tests with the ferret (Figure 8).

Another estimate of the effect of the ;hen puppet compared with the ferret was the average frequency and/or duration of expression of components during tests. Student's t-tests were performed on data from exposure 1 of the test sequences (Table VI). In exposure 1, pecks were delivered more often to the hen puppet while rushes and the average frequency and average duration of feather posture 5 were greater in ferret tests.

In general, responses of broody hens to the ferret and the hen puppet include the same components, though not necessarily in the same proportions in response to the 2 intruders. In encounters with the ferret, hens were more apt to rush and attack, fluff their feathers and give alarm calls than when confronted by the hen puppet. On the other hand, pecks and the hybrid alarm calls appeared more often in responses to the hen puppet intruder. Additionally, when comparing selected exposures

FIGURE 8. Percentages of tests in which each component occurs when naive broody hens were tested with the hen puppet and with the ferret. (Separate test sequences; an asterisk indicates a significant difference when p ≤ .05).

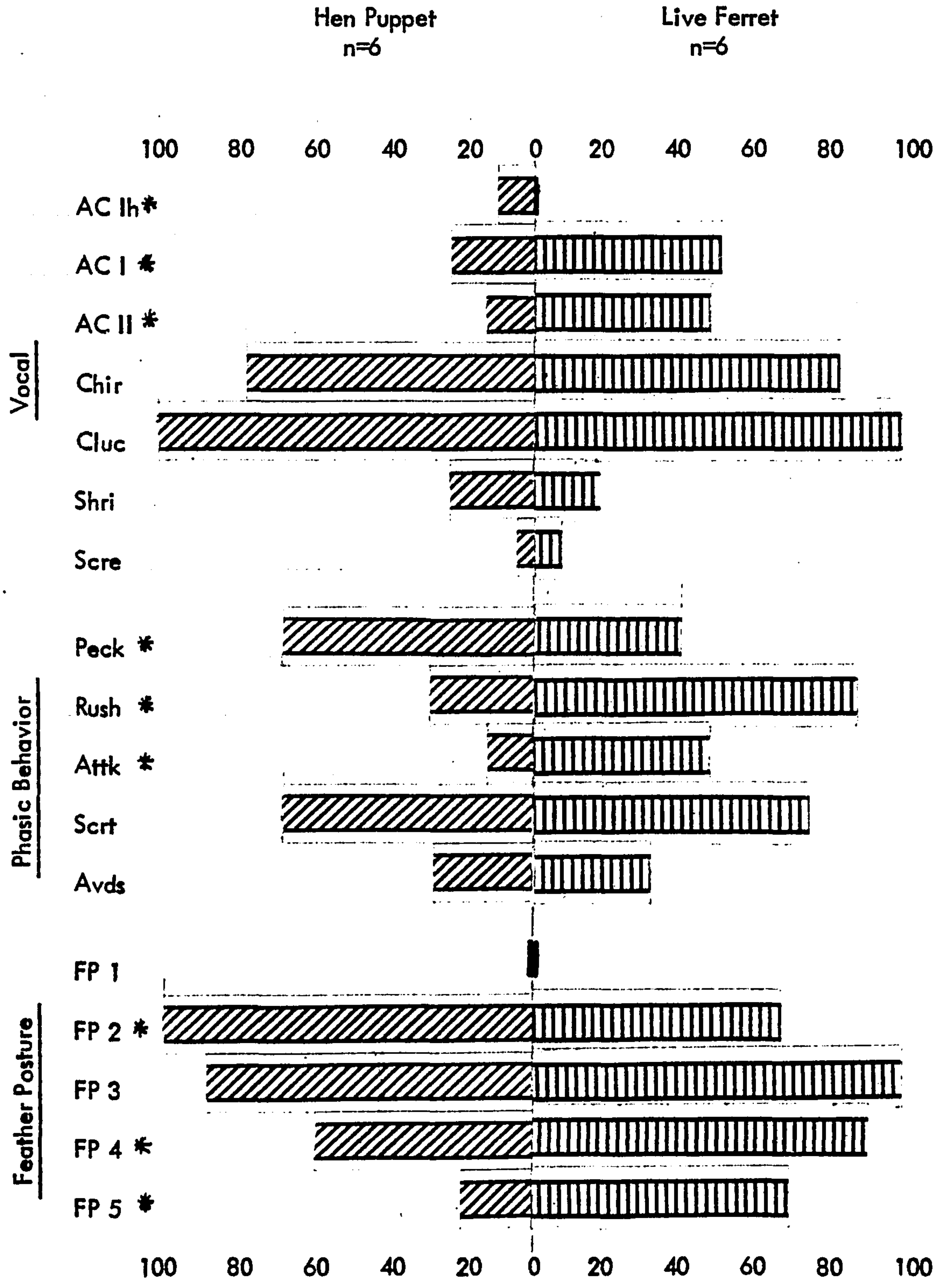


TABLE VI. Significant differences in the expression of components to the hen puppet (HP) and to the ferret (F) by maternally naive broody hens. Student's t-tests were performed on exposure 1. (Based on 6 hens in tests with the hen puppet and on 3 hens in tests with the ferret; $p \leq .05$)

	Exposure 1
Peck	HP > F
Rush	F > HP
FP 5	F > HP
DFP 5	F > HP

from the test sequences, it is evident that differences are more prevalent in the initial encounter than in subsequent ones.

Effect of Reproductive Condition

Broody Hens and Non-broody Hens

To determine whether reproductive condition influenced hens' responses to intruders, the behavior of 5 experienced broody hens toward the hen puppet was compared with the behavior of 5 experienced non-broody hens toward the hen puppet. Although 12 of the 15 components observed in tests with the broody hens were also present in tests with non-broody hens, numerous quantitative differences in the responses were found. For example, 5 components (chir, cluc, scrt, FP 3, FP 4) occurred in a higher percentage of tests when the subjects were broody hens (Figure 9), whereas three components (AC Ih, avds, FP 2) occurred in more of the non-broody hen tests.

The average frequency and duration of each component expressed by broody and non-broody hens during tests were also compared. Table VII illustrates that the responses of broody and non-broody hens differed in the average frequency in 8 components and in the average duration of 4 components. Broody hens gave more chirrs, clucks and pecks and initiated scratching, feather posture 3 and feather posture 4 more frequently than non-broody hens. Broody hens also maintained the fluffed feather postures and bouts of scratching for longer durations than non-broody hens. In contrast, non-broody hens gave more Type I alarm calls, avoided and maintained feather posture 2 more than broody hens.

In summary, distinct differences in the responses of broody and non-broody hens

FIGURE 9. Percentages of tests in which each component occurs in the broody and non-broody hen test groups (Based on exposures #1 & #2 to the hen puppet; an asterisk indicates a significant difference when p ≤ .05).

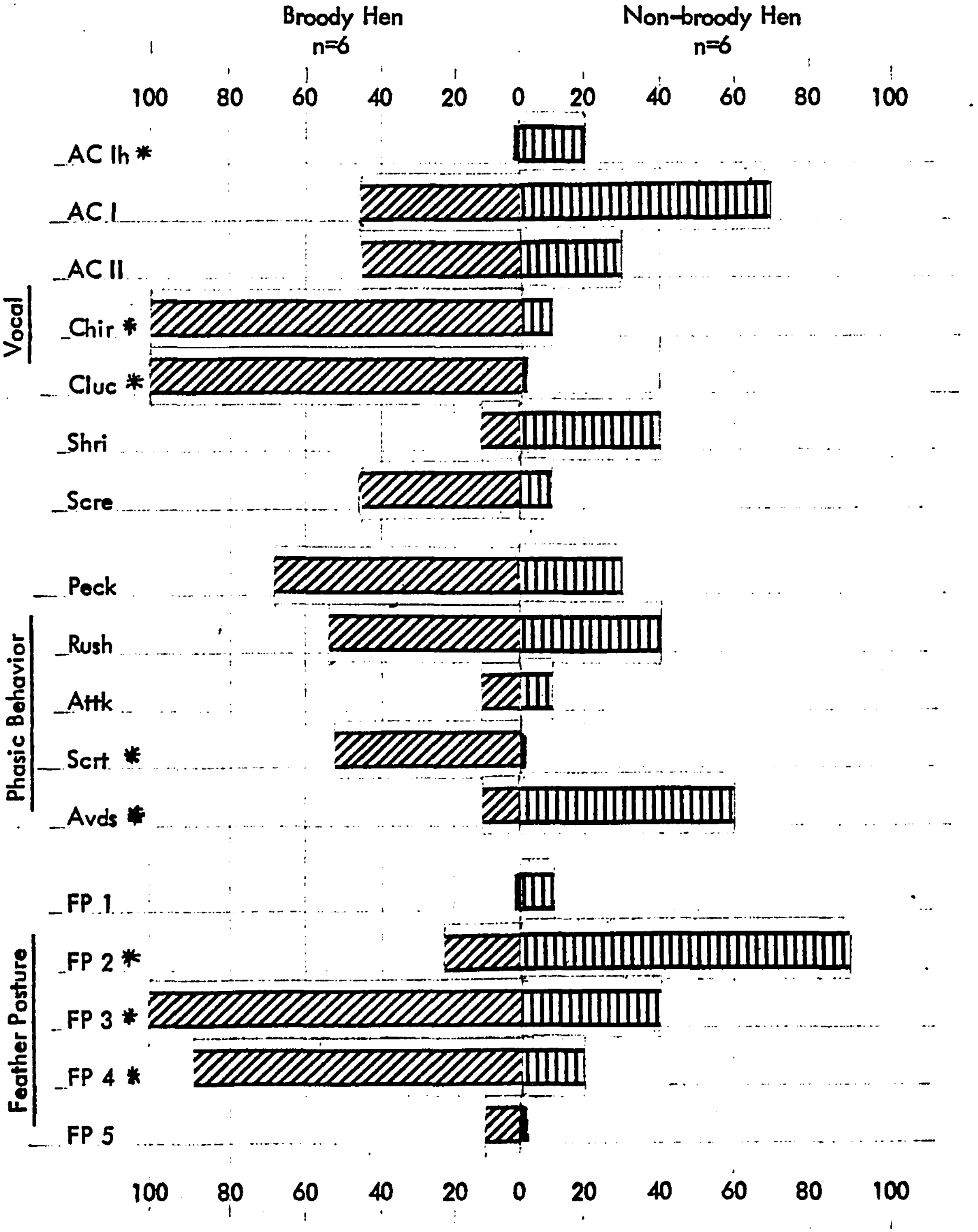


TABLE VII. Significant differences between the responses of broody and non-broody experienced hens tested with the hen puppet. Student's t-tests, $p \leq .05$; based on 2 exposures, $n = 5$ in each group. Placement of the symbol under Broody or Non-Broody for any given component signifies that the mean is greater in that experimental group.

	Broody	Non-Broody
AC Ih		
AC I		■
AC II		
Chir	■	
Cluc	■	
Shri		
Scre		
Peck	■	
Rush		
Attk		
Scrt	■	
Avds		■
FP 1		
FP 2		
FP 3	■	
FP 4	■	
FP 5		
DFP 1		
DFP 2		■
DFP 3	■	
DFP 4	■	
DFP 5		
DScrt	■	

to the hen model were observed. When broody hens were subjects, they clucked, chirred, scratched and fluffed their feathers more than non-broody hens. The distinguishing characteristics of the responses of non-broody hens were that they rarely fluffed their feathers and avoided often.

Different Points in the Period of Chick Care

The question of whether broody hens' responses to an intruder change as a function of the stage in the broody phase required that the behavioral responses of hens be observed at different points during the period of brood care. Using the hen puppet as an intruder, the behavior of 4 hens having ≤ 1 week old chicks was compared with that of 5 hens having chicks of 3 to 4 weeks in age. One difference between these groups was the probability of observing certain components in encounters with the hen model (Figure 10). For example, hens with younger chicks chirred and screeched in a greater percentage of encounters than hens with older chicks. On the other hand, hens that encountered the hen puppet for the first time when their chicks were 3 to 4 weeks old gave more Type I alarm call hybrids, rushed, avoided and initiated feather postures 2 and 5 in more of the tests.

The average frequency and duration calculated for components revealed that the frequency of avoidance and duration of feather posture 2 were greater among hens with older chicks while the duration of feather posture 4 was lower (Table VIII).

In summary, the behavior of broody hens encountering an intruder for the first time at different points in the period of chick care is not the same. The strongest difference was that hens with young chicks avoided less and maintained fluffed feather postures more than hens with older chicks. Hens with older chicks however

FIGURE 10. Percentages of tests in which each component occurs in tests of maternally experienced broody hens with the hen puppet. One test group was tested when their chicks were younger (≤ 1 week) and the other group was tested when their chicks were relatively older (3-4 weeks). (Based on exposures #1 & #2; an asterisk indicates a significant difference when $p \leq .05$).

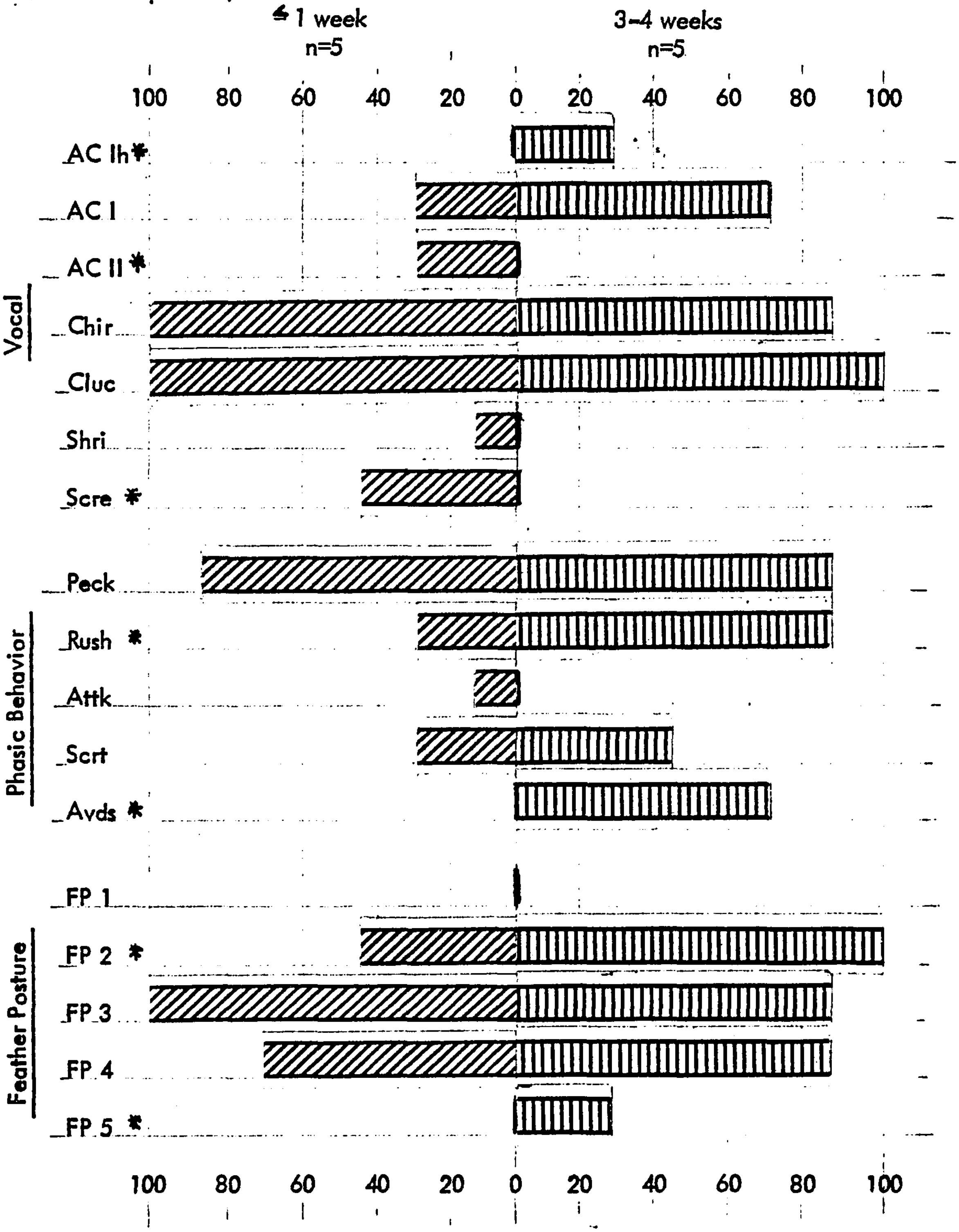


TABLE VIII. Significant differences between hens with younger chicks (≦ 1 week) and hens with older chicks (3-4 weeks) tested with the hen puppet. (Based on exposures 1 and 2; Student's t-tests, $p \leqq .05$) *The symbol's placement under the* ≦ 1 week or 3-4 weeks column indicates that the mean for that hen group was greater for that component.

	≦ 1 week	3-4 weeks
Avds		■
DFP 2		■
DFP 4	■	

did rush the hen puppet and exhibit feather posture 5 in more encounters than hens with younger chicks, although the frequency during a response was not greater. Differences between the test groups were marked also by the percentage of tests in which 3 vocalizations occurred: screeches and Type II alarm calls were associated more often with the responses of hens with younger chicks while hybrid alarm calls appeared exclusively in the responses of hens with older chicks.

Effect of Repeated Testing

The behavior of hens confronted repeatedly by an intruder during the care of their brood changed over successive encounters. In tests with the hen model, naive broody hens showed an effect of repeated testing in eight component measures. Shrieks, chirrs, scratching and feather posture 4 and feather posture 5 changed significantly in frequency while scratching, feather posture 2 and feather posture 4 changed significantly in duration (Figure 11). The patterns of change in the test sequences for these components were not the same. For example, the average duration of feather posture 2 appeared to increase while the frequency of chirrs fluctuated irregularly from one exposure to the next. The remaining 6 measures seemed to decrease as testing progressed so that the incidence of feather fluffing, shrieks and scratching had notably declined by the 7th encounter with the hen puppet.

Effect of Maternal Experience

In contrast with the findings on naive hens presented above, maternally experienced subjects showed no behavioral changes that could be attributed to repeated exposures (Table IX). In addition to this difference in the apparent influence of repeated testing on the responses of birds which differed in terms of maternal experi-

FIGURE 11. The components illustrated in the figure below showed significant variation across exposures (2-way anova; p ≤ .05; 6 maternally naive hens tested with the hen puppet over 7 exposures). The values given under each exposure are the mean hen scores for that exposure. By following the mean hen score across exposures for a given component, an indication of the pattern of change with repeated testing can be gained.

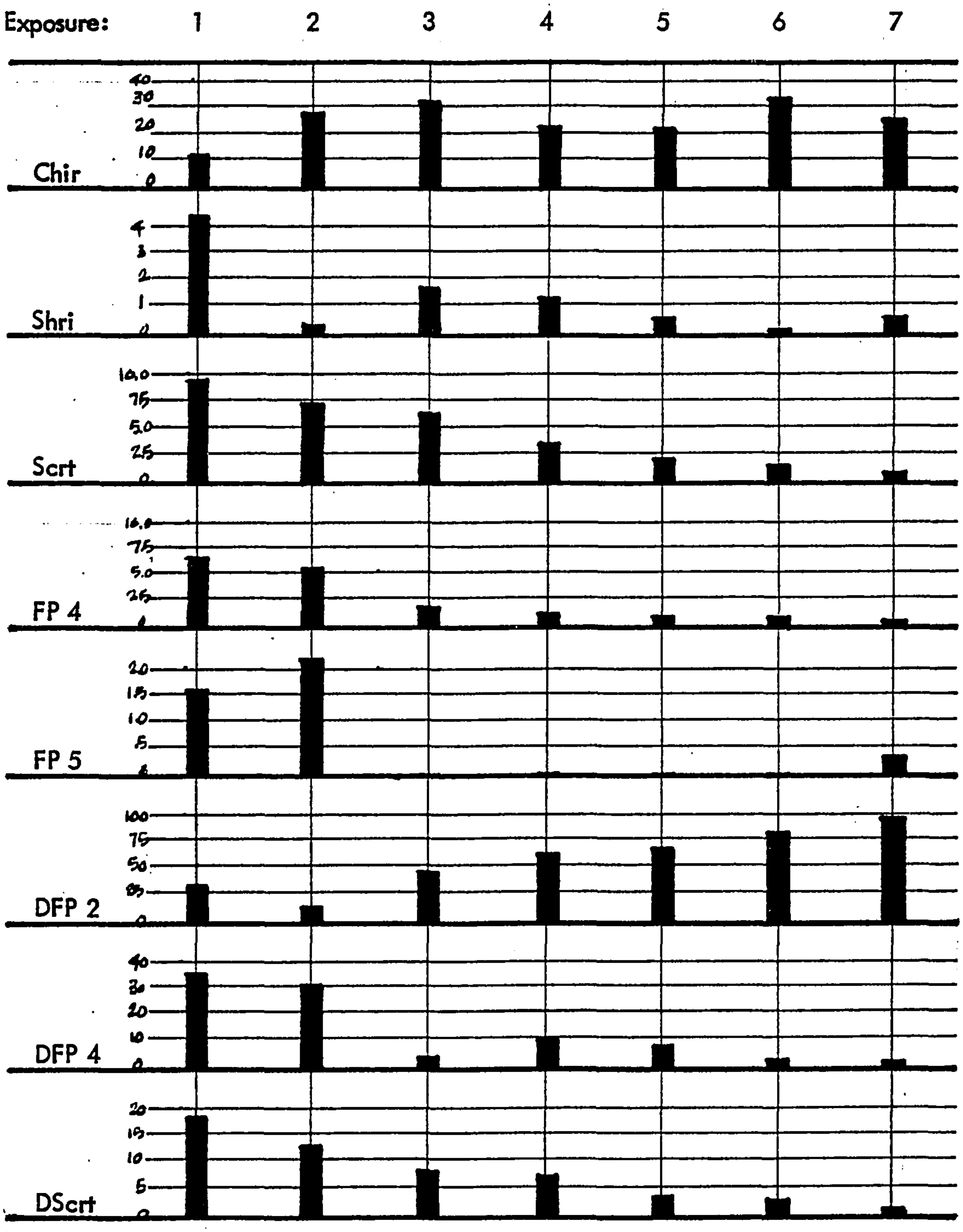


TABLE IX. Significant variation across exposures in naive and experienced broody hens tested with the hen model. (Based on 6 hens tested over 7 exposures; 2-way ANOVA, $p \leq .05$)

	Naive	Experienced
AC Ih		
AC I		
AC II		
Chir	■	
Cluc		
Shri	■	
Scre		
Peck		
Rush		
Attk		
Scrt	■	
Avds		
FP 1		
FP 2		
FP 3		
FP 4	■	
FP 5	■	
DFP 1		
DFP 2	■	
DFP 3		
DFP 4	■	
DFP 5		
DScrt	■	

ence, 4 components occurred in different percentages of tests when maternally naive and maternally experienced hens were compared (Figure 12). Naive hens exhibited head-up scratching, avoids and feather posture 2 in more tests than maternally experienced hens but gave the chirr vocalization in fewer of the encounters.

In order to determine whether the average frequencies and durations of components during tests differed for maternally naive and experienced hens, exposures 1, 3 and 7 were compared (Table X). Analysis of individual exposures was necessary to permit the separation of the influence of naivete regarding intruder encounters and naivete regarding the rearing of chicks since maternally naive hens are inexperienced in relation to both factors on exposure 1, but only in relation to the rearing of a brood on exposures 3 and 7. In exposure 1, the frequency of scratching and the duration of feather posture 3 was significantly less for naive hens. No significant differences between naive and experienced hens were found for any components in exposures 3 and 7.

Effect of Different Intruders

A comparison of the test results of 6 naive broody hens tested separately with the hen puppet and the green cube (42 tests each) showed that, with one exception (FP 1) the responses to these intruders included the same components. Differences in the responses, however, were evident in the percentage of tests in which components appeared, in the average frequency and duration of some components during a test, and in the effect of repeated testing. For example, 7 components were observed in significantly different percentages of tests with the hen model and the green cube

FIGURE 12. Percentages of tests in which each component occurs when maternally naive broody hens and maternally experienced broody hens were tested with the hen puppet. In both test groups, the same 6 hens were tested 7 times during the care of their 1st and 2nd broods, respectively. (An asterisk indicates a significant difference when p ≤ .05).

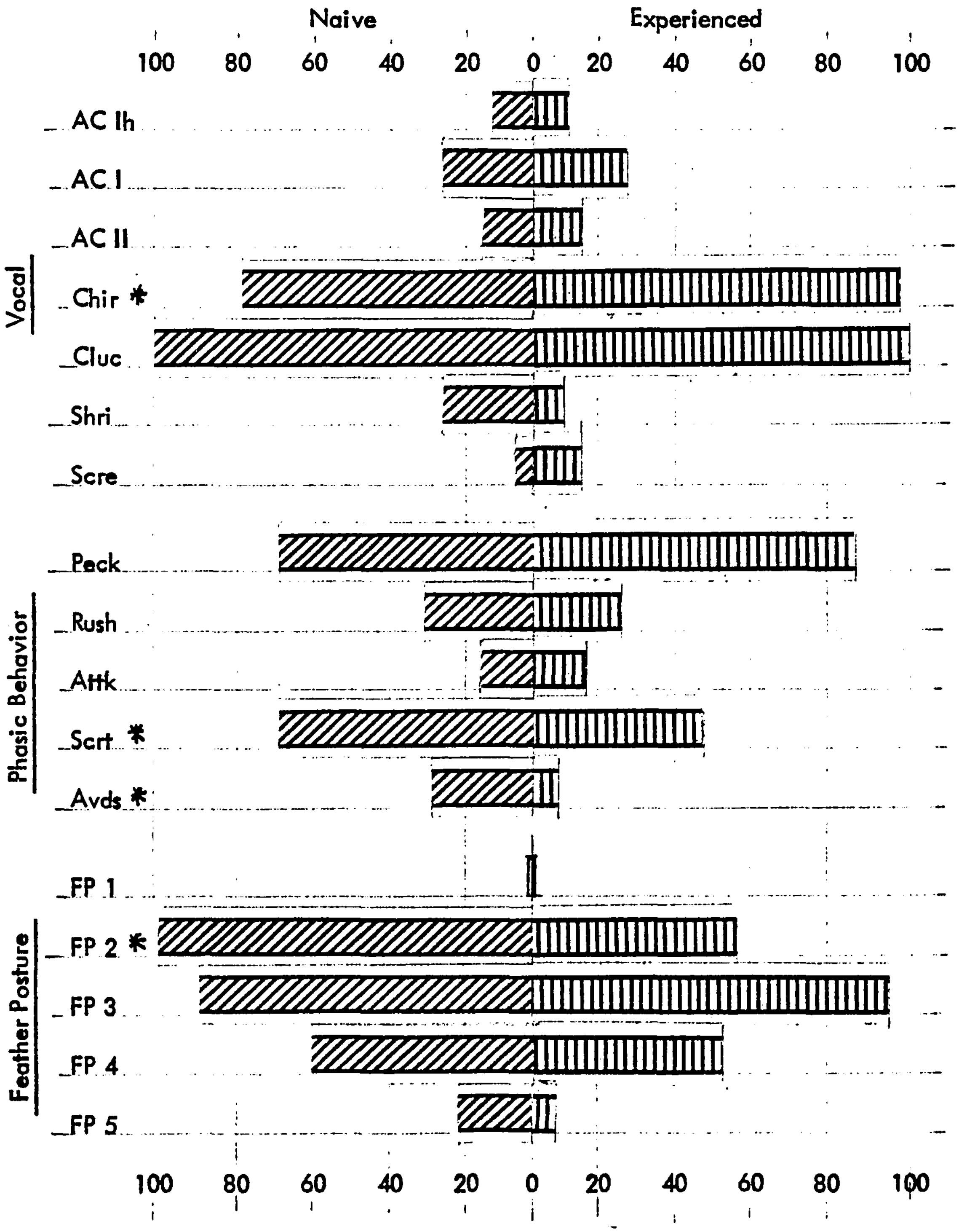


TABLE X. The results of paired comparison tests (2-way ANOVA; $p \leq .05$) on exposures 1, 3 and 7 for naive and experienced hens tested with the hen puppet. The placement of the symbol under naive or experienced was determined by a comparison of the means. It signifies that the component was given in greater measures under that condition. No measures differed significantly in exposures 3 and 7.

Exposure # 1

	Naive	Experienced
Scrt	■	
DFP 3		■
DFP 4	■	

(Figure 13). Six of these were represented in more tests with the hen puppet. Specifically, clucks, pecks, rushes, attacks, feather posture 4 and feather posture 5 occurred in a greater percentage of tests when the subjects were confronted with the hen puppet. The one component which was observed in more tests with the green cube was feather posture 1. In summary, broody hens were more likely to include feather fluffing, approach components and clucking in their responses if the intruder was the hen puppet than if the intruder was the green cube.

The hen puppet and the green cube also differentially influenced the average frequencies and durations of some components in responses of broody hens. In the first exposures, the average number of chirrs and rushes and initiations of feather posture 3 occurred in greater frequencies in tests with the hen puppet (Table XI). The data from exposures 3 as well as 7 were also compared and, in exposure 3, chirrs, pecks and feather posture 4 were given in greater measure to the hen puppet. In exposure 7, the only significant differences were found in clucks and avoids which occurred more frequently on the average in response to the green cube.

Another aspect of the responses to different intruders that was compared is the effect of repeated testing. In tests with the hen model, the green cube and the ferret, both the number of measures which showed significant changes and the identity of many components which changed were different (Table XII). The greatest number of measures (11) changed with repeated exposures when naive broody hens were tested with the ferret. In the green cube tests, repeated testing resulted in significant changes in only 2 feather posture measures while 8 measures changed in tests with the hen model. The identity of components in the phasic behavior and vocalization categories which showed significant variation among exposures was never

FIGURE 13. Percentages of tests in which each component occurs when maternally naive hens were tested separately with the hen puppet and the green cube. (Based on 7 exposures with each intruder; an asterisk indicates a significant difference when $p \leq .05$).

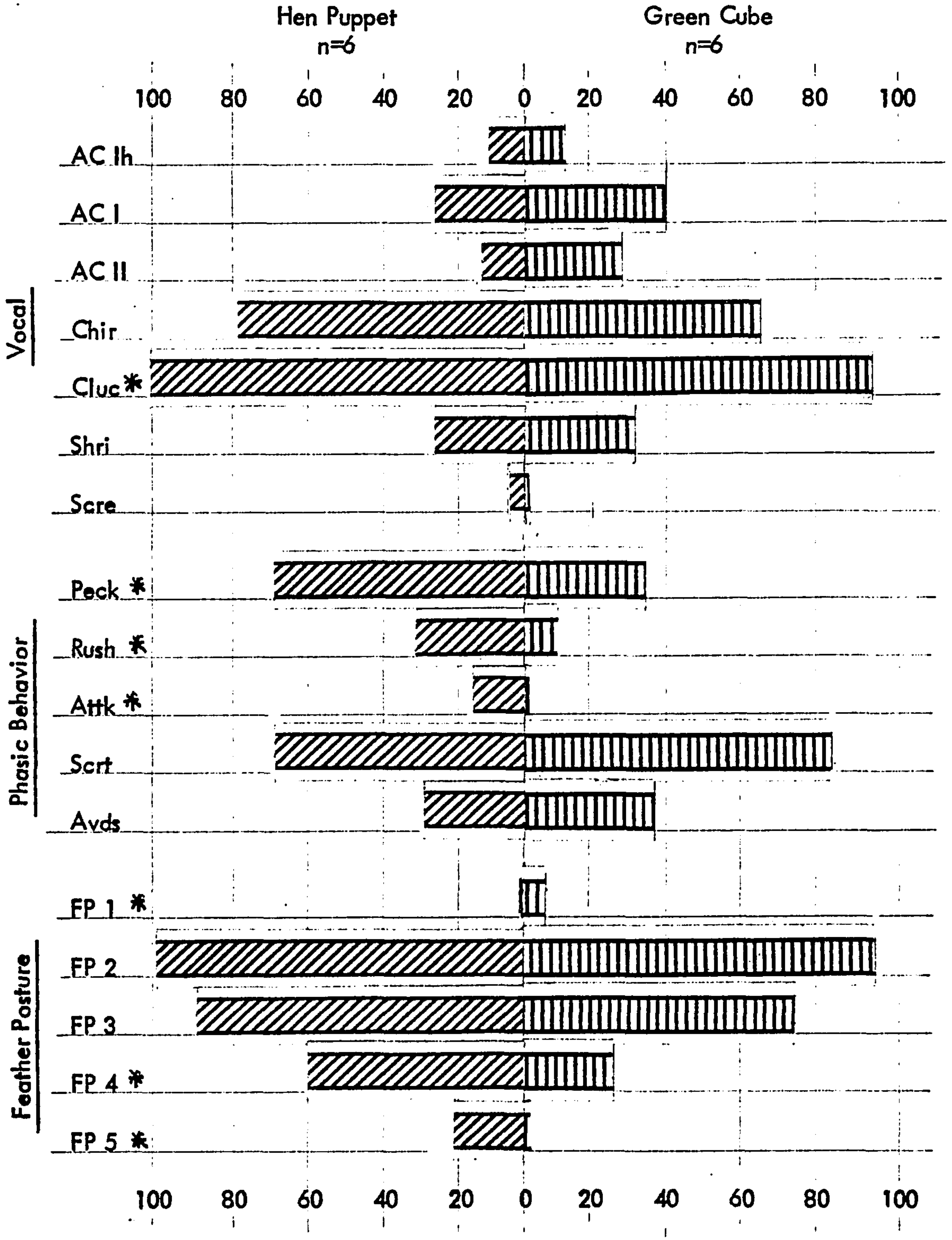


TABLE XI. Significant differences in the expression of components to the hen puppet (HP) and to the green cube (GC) by maternally naive broody hens. Paired comparison tests (2-way ANOVA; $p \leq .05$) were performed on exposures 1, 3 and 7. Based on 6 hens.

	Exposure 1	Exposure 3	Exposure 7
Chir	HP > GC	HP > GC	
Cluc			GC > HP
Peck		HP > GC	
Rush	HP > GC		
Avds			GC > HP
FP 3	HP > GC		
FP 4		HP > GC	

TABLE XII. Differences in the effect of repeated testing for different types of intruders. The components which varied significantly across exposures are indicated by the symbol. The subjects were maternally naive in all groups presented here. (2-way ANOVA, $p \leq .05$)

	Ferret	Hen Puppet	Green Cube
AC Ih	■		
AC I	■		
AC II			
Chir		■	
Cluc			
Shri		■	
Scre	■		
Peck			
Rush			
Attk			
Scrt		■	
Avds	■		
FP 1			
FP 2	■		
FP 3			
FP 4	■		
FP 5	■	■	
DFP 1			
DFP 2	■	■	■
DFP 3	■		■
DFP 4	■	■	
DFP 5	■		
DScrt		■	

the same for any 2 intruders. In the feather posture category, however, the duration of feather posture 2 showed a significant exposure effect for tests with each intruder; the duration of feather posture 3 changed with repeated exposures in tests with both the hen puppet and the ferret.

So, the effect of repeated testing was influenced by the type of intruder. Except for certain feather postures, the number and identity of components that changed as testing progressed were different in groups tested with the hen puppet, the ferret and the green cube. A common effect of all intruders was that feather fluffing generally declined which resulted in hens' spending more time in feather posture 2.

Individual Variability

The composite of broody hens' responses to the ferret described the components observed and several of their quantitative aspects. One striking feature of many components is the variability in their expression. Analyses to determine potential effects of repeated testing, maternal experience and intruder type revealed that individual differences among hens were often a significant source of variability. Since the number and identity of those components were often different under different experimental conditions, it seemed important to describe hen variation in relation to the major experimental variables.

Maternal Experience

In tests with the ferret, naive broody hens showed individual variation in 7 measures (Table XIII). The main category of behavior that reflected hen differences was

TABLE XIII. Significant variation among hens in the maternally naive and maternally experienced hens tested with the ferret. (Based on 3 naive hens and 2 experienced hens; all were tested over 7 exposures; 2-way ANOVA, $p \leq .05$)

	Naive	Experienced
AC Ih		
AC I	■	■
AC II	■	
Chir	■	
Cluc	■	
Shri	■	■
Scre		
Peck		■
Rush		■
Attk	■	
Scrt		■
Avds		■
FP 1		
FP 2		
FP 3		■
FP 4		
FP 5		■
DFP 1		
DFP 2		
DFP 3		■
DFP 4		
DFP 5		■
DScrt	■	■

vocalizations (AC I, AC II, cluc, chir). When maternally experienced hens were tested with the ferret, 11 measures varied significantly among hens but the dominant category of behavior that reflected hen variation was that of phasic behavior (peck, rush, avds, scrt), not vocalizations. More components varied among hens when hens tested with the ferret were maternally experienced; also, the identity of the components reflecting hen variation changed. To determine whether this trend occurred in tests with other types of intruders, the data from tests with the hen puppet and the green cube were also analysed. As shown in Table XIV, neither the increase in number nor change in identity of components holds for naive and maternally experienced hens tested with the hen model. The same number of components varied significantly and most measures that varied among naive hens also varied among experienced hens. In tests with the green cube, the number of components that varied significantly among hens was greater in the maternally experienced group (15 versus 11) but many measures that varied under one maternal condition also varied under the other. Thus, considering the 3 intruder types, maternally experienced hens showed individual variation in the same or in a greater number of components than naive hens. Furthermore, components from all 3 categories were represented in the hen model and the green cube tests while vocalizations or phasic behavior more strongly reflected individual differences in tests with the ferret.

Intruder Type

Individual variability in the expression of components is also influenced by the intruder type. An average of the number of component measures which varied significantly among maternally naive and maternally experienced hens for each intruder

TABLE XIV. Significant variation among hens in the maternally naive and maternally experienced hens tested with the hen puppet and the green cube. (Based on 6 hens tested over 7 exposures in all groups; 2-way ANOVA, $p \leq .05$)

	Hen Puppet		Green Cube	
	Naive	Experienced	Naive	Experienced
AC Ih	■	■	■	■
AC I	■		■	■
AC II	■		■	■
Chir	■	■	■	■
Cluc	■	■	■	■
Shri	■	■	■	■
Scre	■			
Peck	■	■	■	■
Rush	■	■		
Attk		■		
Scrt	■	■		■
Avds	■		■	■
FP 1				
FP 2	■	■		
FP 3	■	■		■
FP 4	■	■		■
FP 5		■		
DFP 1				
DFP 2	■	■	■	■
DFP 3		■	■	■
DFP 4	■			■
DFP 5		■		
DScrt	■	■	■	■

showed that the largest number of measures (16) varied significantly in tests with the hen model, while an average of only 13 varied in tests with the green cube. The smallest number of measures (9) varied significantly in tests with the ferret.

Individual Variation of Certain Components

From the data presented above, it is evident that some components of the response to intruders tended to vary in individual expression under more test conditions than others. Shrieks, for example, varied significantly in every exposure sequence: maternally naive and maternally experienced subjects tested with the hen model, the green cube and the ferret. The frequency of attacks, in contrast, varied significantly among hens in only one test condition: maternally experienced hens tested with the hen puppet (Tables XIII and XIV). Thus, the components are differentially consistent in expression from one hen to another. This information lends an important detail to the description of responses of broody hens confronted by an intruder since components best-suited to the experimental goals and constraints of any subsequent studies of brood defense behavior can be selected as measures.

DISCUSSION

This study identified seventeen components that comprise the behavioral repertoire of hens confronted by intruders. Vocalizations, phasic motor activities and feather postures were the three general descriptive categories appropriate to the behavior observed. In individual encounters with intruders, hens' responses consisted of one or more components from each category.

The particular expression of behavioral components was influenced by the hen's reproductive condition, her prior maternal and intruder experience and the type of intruder. Controlled manipulation of these variables revealed which components changed in their probability of occurrence, their frequency and, where appropriate, their duration.

It is the aim of the discussion that follows to consider separately the influence of each variable on the responses of broody hens to intruders.

Reproductive Condition

Broody and non-broody hens. The reproductive condition of Gallus hens clearly influences their responses to intruders. The predominant response of non-broody hens consists in avoiding and giving alarm calls while broody hens fluffed their feathers, gave clucks and chirrs and engaged in head-up scratching bouts. The tendency during the non-reproductive phase to flee and during the reproductive phase to remain and perform various displays in the vicinity of the intruder is a general motif that has been observed in many avian species (Armstrong, 1947; Simmons, 1955).

Despite the significant differences in the probability of observing particular components in the responses of broody and non-broody hens, it is worth noting that broody hens exhibit all components observed in non-broody hens' responses and most components (14 out of 17) observed in broody hens occurred at least occasionally in the responses of non-broody hens. It is possible that testing in an enclosed space might be responsible for the appearance of particular components which might not occur in a field situation. For example, the opportunities for escape from the intruder are particularly limited in the experimental situation. When a hen in her natural habitat flees, she has a chance of evading the intruder, whereas in the laboratory, avoidance only temporarily increases the hens distance from the intruder. Although spatial restrictions operate in tests of both broody and non-broody hens, the behavior of non-broody hens might be expected to show the effect of testing in an enclosed area more strongly because they avoid the intruder more often. Perhaps forced proximity presents the non-broody hens with aspects of the stimulus situation with which they are not usually confronted; responses more specific to the particular intruder then are elicited.

Hens with chicks of different ages. The responses of hens to intruders changed during the period of chick care. Hens with younger chicks (≤1 week of age) incorporated screeches and Type II alarm calls in more encounters and fluffed their feathers (FP 4) for longer durations than hens with older chicks (3-4 weeks of age). Clearly, these birds were disturbed by the intruders since screeches, Type II alarm calls and fluffed feathers are given primarily in stimulus situations that interrupt on-going activities of the birds. None of the aforementioned components occurred in tests of broody hens without an intruder present. Baeumer (1962) reported that screeches were given in situations of "imminent danger" such as direct confrontation with a predator from which the hen did not flee. Type II alarm calls begin to be interspersed with Type I alarm calls as an initial disturbance intensifies (Baeumer, 1962; Konishi, 1963), but the caller does not necessarily move from the immediate area (Baeumer, 1962; personal observation).

In contrast to hens with young chicks, hens with older chicks gave hybrid alarm calls, rushes, avoids and feather posture 2 and 5 in more encounters. Further, hens with older broods avoid more often and stay in feather posture 2 for longer durations. While the responses of hens with broods of different ages depart from the undisturbed behavior of foraging and brooding, the character of their behavior is different; hens with older chicks exhibited more locomotor responses with regard to the intruder as both avoids and rushes figure prominently in the pattern.

One explanation for these differences might be that the gradual change in the hen-chick spatial relationship which occurs as the chicks mature affects the probability that particular components will be expressed. As chicks develop, they spend less time near the hen and increase the distance they range from her (Bateson, 1963). This progressive increase in chick mobility is a function of the chicks' improving ability to regulate their own internal temperature (Bateson, 1963; McBride, et al., 1969). Since it is locomotor aspects in particular which differentiate the intruder-responses of hens with older chicks from hens with younger chicks, it seemed plausible that the proximity of young chicks to the hen in some way functions to restrict her movements. For example, McBride, et al. (1969) observed that hens with young chicks (<2 weeks of age) responded to intruders by hiding the chicks and hens with older chicks (>2 weeks of age) ran away from intruders. Further research, however, is needed to determine whether the correlation between the spatial relationship of the brood and the hen and differences in intruder responses indicates causation.

The finding that the responses of hens to intruders changes as the period of chick care progresses provides an opportunity to examine the hypothesis of Barash (1975) that birds with precocial young show a progressive decline in the conspicuous aspects of the responses, whereas altricial species show an increase until the young are fledged. In his study of the Alpine accentor (Prunella collaris), Barash (1975) reported that this ground-nesting altricial species increased the intensity and conspicuousness of its display progressively after hatching. In altricial species, the young are dependent on their parents until fledging. Since the reproductive success of any parent is measured by the survival of the offspring, a significant role in protection of dependent young by the parents might be expected. The increase in conspicuousness and intensity which Barash equates with a mounting risk of parental mortality, is explained by assuming further that an inverse relationship exists between the age of the brood and the probability that the parents could re-nest to compensate for its loss. Thus, the temporal pattern of increase in efforts by the parent(s) to ensure their offsprings' survival is an adaptation specifically suited to the reproductive success of altricial species which hinges increasingly on survival of the particular brood on hand. From this interpretation of the data on the Alpine accentor, Barash predicted that the change in occurrence of conspicuous elements in displays toward intruders would be different in precocial species. He assumed that these offspring have some chance of survival without parental assistance and, therefore, that parental investment can be diminished since the chicks' independence from parental care increases rapidly shortly after hatching. The reproductive success of the parents consequently is not jeopardized by a reduction in their role as protectors of the young. According to Barash, then, conspicuousness and intensity will decline after hatching in precocial species.

Three issues raised by Barash's report can be considered in light of the results of my experiments with Gallus hens, a precocial species: first, the interpretation of "conspicuousness" and "intensity" with regard to the responses of birds to intruders; second, the assumption that conspicuousness and intensity are directly related to risk; and third, the assumption that chicks are increasingly independent of the parental response to intruders for their own survival.

The application of the same behavioral criteria for conspicuousness and intensity used for the Alpine accentor to the responses of other species seems arbitrary. For example, Barash used three measures on which to base his assessment of the accentor's response: (1) the distance between the intruder (Barash) and the parent bird before it flushed, (2) the distances from the nest at which the bird settled prior to performing its distraction display and (3) the extent of wing spreading and occurrence of bill clapping in the display itself. Progressively after hatching, the flushing and settling distances became shorter and the degree of wing extension and the incidence of rapid opening and closing of the mandibles increased. If feather fluffing, low levels of avoidance and screeches are equated with conspicuousness and intensity, the data from broody hens are consistent with Barash's distinction between the temporal patterning of intruder responses in altricial and precocial species because these components are more prevalent in hens with younger chicks. If complexity in form and movement, however, are the criteria for conspicuousness and intensity, the results from hens with older chicks contradict the hypothesis because they exhibit greater variety in feather postures and locomotor patterns. Thus, it seems difficult to ascertain what pattern actually obtains, since human observers can readily select different features of the response to identify as "conspicuous" and "intense" with the result that the temporal patterns described oppose one another. Also, two further aspects of this problem warrant investigation as well: what constitutes conspicuousness to an intruder biologically relevant to the survival of a species, and whether that conspicuousness finds consistent application across all species in a category (i.e., precocial).

Even if an unequivocal pattern of decline in conspicuousness and intensity could be demonstrated for all precocial species, equating risk with conspicuousness and intensity is tenuous. An independent assessment of the mortality of parent birds in the two groups would offer a strong supporting argument for Barash's hypothesis if it revealed, for example, that relatively more parents with young precocial chicks but relatively fewer parents of young altricial chicks fall prey to predators. In lieu of such direct evidence, an appropriate procedure is to consider the consequences of response patterns in which avoidance progressively supplants approach or distance-maintaining behavior. The results of my experiments revealed that broody hens increased avoidance as their chicks matured; the increase in avoidance, however, was accompanied by a concommitant increase in the incidence of rushes. Since fleeing has been cited as an important stimulus for the eliciting and directing of pursuit and attack (Errington, 1967), and further, since some hens with older chicks also approach the intruder on more occasions, it is uncertain that this response pattern improves the hen's probability of survival (escape). The complexity of the interaction characteristic of many intruder-encounters makes any prediction of outcome difficult, and the relationship between actual risk to the parent and the behavior exhibited can be clarified only through direct observation. The differences in the behavior pattern observed may reflect a qualitative rather than a quantitative change in parental investment.

The precocial chick's progressive independence from the parent for thermoregulation and food location has been measured directly (Bateson, 1963; Tuculescu, personal communication) whereas the assumption that chicks become increasingly independent of the parents for defense is based on indirect evidence, that is, changes in parental responses to intruders. The decrease over time from hatching in the conspicuousness and intensity of parental responses to intruders which has been reported by Barash (1975) provides inconclusive evidence of a reduction in the chicks' dependency on parental behavior. For example, in the foregoing discussion, the increased avoidance by broody hens with older chicks in intruder encounters was tentatively considered to be associated with the chicks' enhanced mobility. Even if the suggested relationship is not causal, interpreting the change in the hen's response as indicative of a decline in the importance of parental behavior to chick survival seemed unwarranted since avoidance might function either as a crucial stimulus to the chicks to scatter themselves or as a cue to direct their flight. Experiments comparing responses of chicks to intruders with and without the parent bird would help to establish an interpretation.

Maternal and Intruder Experience

The present results indicate that the behavior of maternally naive broody hens toward intruders is less consistent than that of maternally experienced broody hens. In the maternally naive group, 8 components of the response to the hen puppet changed with repeated exposures whereas in the maternally experienced group, no components of the response changed. Of the components that changed, the frequencies of shrieks and feather posture 5, and the frequencies and durations of head-up scratching bouts and feather posture 4 decreased over successive encounters. Since the presence of these components is correlated with disturbance by the intruder, their waning indicates decreasing interference with ongoing activities caused by the hen puppet. This interpretation is supported by the concommitant increase in the duration of feather posture 2 since observations of undisturbed hens revealed that they remained in feather posture 1 or 2 throughout test periods.

A decline in responsiveness to repeated presentations of a stimulus is a widespread phenomenon in the animal kingdom (Hinde, 1970); the results of these experiments are consistent with that generalization. Two basic processes have been suggested to account for the observed changes and both fall under the rubric of learning (Hinde, 1970). The first, habituation, is defined as a "relatively persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Thorpe, 1963). In addition, the reduction in response level cannot be due to sensory adaptation or motor fatigue (Hinde, 1970). The second possibility is broadly defined as relatively persistent changes in behavior which are systematically related to the contingencies of responding. The main distinction between these types of learning is that habituation describes response decrements in which no conventional reinforcement has been identified while response-contingent learning assumes that the particular feedback from the external stimulus situation changed the probability of subsequent responding. Whichever process is responsible for the observed decline in fluffed feather postures, scratching and shrieks, the strong waning effects seem particularly paradoxical in behavior toward intruders since repeated encounters with potential predators are probable under natural conditions and survival appears directly dependent on the responses of the prey (Hinde, 1954a, 1954b; Kruuk, 1964).

One explanation for response decrements has been the artificially monotonous laboratory conditions under which such results were obtained. For example, Lorenz (1965) explicitly stated that a habituation of responsiveness to predators is an artifact of the testing conditions that does not occur in the wild. The results of an experiment by Curio (1975) support this contention. He showed that pied-flycatchers (Ficedula hypoleuca) which saw a predator near their nest boxes daily did not change the strength of their response. The explanation for the maintenance of response strength in the field is that the conditions in which the predator is encountered change. This hypothesis is borne out by Curio (1969) who found that ducks and geese habituated to dogs at one shore of a lake but renewed their responsiveness when encountering the same dogs on the opposite shore. Since my test conditions did not provide variety in the circumstances of the encounter comparable to those in the natural habitat of Gallus, the stable aspects of laboratory testing might be responsible for the decrements in fluffed feather postures, head-up scratching and shrieks.

In addition to the influence of an identical physical setting on responses to intruders, the mode of stimulus presentation probably affects the behavior. For example, bobwhites (Colinus virginianus) stopped responding to repeated overhead flights of a red-shouldered hawk (Buteo jamaicensis) (Martin and Melvin, 1964). Paulson (1973) suggested that the responses of prey waned because "capture attempts" so characteristic of predator-prey interactions in the field were not made. If the hawk had swooped close to the quail rather than simply passing at some distance above them, Paulson predicted that the prey would have continued to respond. In my experiments, the presentation of the intruders was an actual physical disruption of the activities of the hen by persistent approaches. Presumably, such a protocol which more closely approximates the stimulus situation of pursuit in the field reduced the probability that a lack of this potentially important stimulus feature was responsible for the observed decreases.

A more probable explanation for changes in behavior of broody hens as a function of repeated exposures is that the maintenance or elimination of particular components is contingent on specific feedback from the intruder. For example, Gramza (1967) proposed that repeated withdrawal of a human intruder might actually reinforce distraction behavior just as the normally occurring withdrawal of an owl is believed to reinforce mobbing in chaffinches (Hinde, 1954b). In my experiments, removal of the intruder was not contingent on the behavior of the hen although cessation of approach was determined by particular responses. Therefore, the reinforcement necessary for the subsequent expression of certain components might have been lacking. On the other hand, it is possible that the removal of the intruder coincided with behavioral components that occurred with greater than random frequency at the end of tests so that the probability of observing those components in subsequent encounters was enhanced. It is also known that repeated approaches among conspecifics constitutes "dominant" behavior and, as a result, aggression (pecks, rushes, attacks, feather erection) declines particularly in subordinate birds (Collias, 1944; Potter and Allee, 1953; Kuo, 1967; Candland, Matthews, Taylor, 1968). Since the protocol of the hen puppet may be considered similar to a dominant hen, the conditions may be analogous to those which occur in agonistic encounters.

Several explanations have been offered to account for the changes in certain components with repeated testing. In maternally and intruder experienced hens, however, no effect of repeated testing was observed. One interpretation of this finding is that prior maternal experience affects subsequent maternal behavior. In fact, naive birds scratched the substrate and avoided the intruder in more encounters than experienced hens and experienced hens chirred in more encounters than naive birds. Other studies have shown that the parental care of maternally naive and experienced mammals and birds differed in various ways. Primiparous cats (Felis catus), for example, lick their neonates less during parturition than multiparous cats (Schneirla, Rosenblatt, Tobach, 1960). In ring doves (Streptopelia risoria), inexperienced parents demonstrated a longer latency to first feeding (Lehrman, 1955) and Hansen (1973) showed that naive doves spend more time lifting up and looking at the brooded young while the experienced birds sit quietly on the young for longer periods.

The significance of greater consistency of experienced broody hens from one encounter to another cannot be readily interpreted since there are no independent measures of the consequences of one pattern or another. By analogy with other aspects of maternal behavior and behavioral development, however, it does appear that increased stability has been acquired through individual experience.

Types of Intruders

These experiments clearly establish that the form of the stimulus object influences the responses of broody hens to intruders. Although the same behavioral components occurred in tests with both the hen puppet and the green cube, there were significant quantitative differences in the expression of components to the two intruders. In tests with the hen puppet, there was a greater probability of observing clucks, pecks, rushes, attacks and fluffed feather postures 4 and 5 in the responses. Behavioral differences were also demonstrated in individual exposures. Generally, then, approach components and fluffed feather postures were the predominant features distinguishing the responses to the two intruders. From what is known about many other avian species (e.g., song sparrows, Nice, 1943; review by Armstrong, 1947; pied-flycatcher, Curio, 1975), the results demonstrating differences in the responses of broody hens to different types of intruders are not surprising; earlier descriptions of broody hens' responses, however, departed from the generally recognized trend in that similar reactions to a wide variety of intruders were observed. The main features of the reported behavior were fluffed feathers accompanying a charge toward other broody hens (McBride, et al., 1969), non-broody hens (Collias, 1944; McBride, et al., 1969), cats (McBride, et al., 1969), dogs (Darwin, 1872), low-flying birds (McBride, et al., 1969) and human beings (Aldrovani, 1599). The common denominator shared by all these stimulus animals is approach in a manner that interrupted the ongoing behavior of the hen and her chicks. Hence, an undifferentiated response to any object which disrupted the prevailing behavior of the parent and young seemed to be indicated.

This alternative to multiple response patterns reported for other bird species was not demonstrated for broody hens. The present results show instead a behavioral organization that changes in response to different intruder types; this pattern is analogous to other species such as the black-headed gull (*Larus ridibundus*) which both attacks and flees from crows (*Corvus corone* and *C. cornix*) and peregrine falcons (*Falco peregrinus*) but the probabilities of attack and flight differ for the two predators (Kruuk, 1964).

The differences between my results and existing descriptions apparently reflects the rudimentary nature of the qualitative accounts. In contrast, my description included more details of the responses and is based on a quantitative analysis of the behavioral components. In fact, the present results are consistent with the picture of a hen with her feathers fluffed, charging an intruder drawn in earlier reports. The quantification of the response which had not been done before expands the description to include accompanying details and refined expectations about the observation of particular components.

Before the proximate factors accounting for the differences in response pattern are considered, one interpretation of the quantitative differences in hens' behavior toward the intruders is that the hen puppet is actually a more potent stimulus than the green cube since it evoked more feather fluffing and approach than the green cube. These two categories of components were demonstrated to indicate disturbance by an intruder in the ferret present/ferret absent tests. Other components indicating disturbance such as avoidance occur in response to both intruders so they do not contradict this judgment. By the same criteria, a comparison of the responses to the ferret and hen puppet indicate that the live predator was a stronger stimulus than the hen puppet. In fact, a difference in protocol was necessitated by the marked disturbance of the hen at first sighting of the ferret (see Methods).

Although these experiments with the hen puppet and green cube were designed primarily to determine whether the intruder's form influenced the hen's response, several factors which potentially distinguish the hen puppet and green cube can be suggested. One possibility is that the discrimination between the hen puppet and green cube is based on conspecific recognition or, more parsimoniously, by considering the hen puppet as an unfamiliar stimulus having a more complex visual configuration than the green cube. A difference in visual complexity is defined by the greater number of distinguishable elements (Berlyne, 1960) characterizing the hen puppet configuration. A third factor which affects behavior is novelty of the stimulus object (Berlyne, 1960; Menzel, Davenport, Rogers, 1963; Curio, 1975). Even though it is conceivable that the hen puppet and green cube are not equivalent in this property, novelty can largely be dismissed on the ground that the data base consisted of a 7-exposure sequence. After the first exposure, the differences in relative novelty between stimulus objects are assumed to decrease (Berlyne, 1960).

Finally, these experiments demonstrate that one stimulus feature, gross movement pattern, is not essential for intruder discrimination since the hen puppet and the green cube followed the same choreography.

Variability

The present results showed significant variability in the behavior of individual hens. Individual variability changed under different experimental conditions. Even though these experiments were not designed to identify causes of individual variability, several possible sources will be discussed.

One possibility is that the individual differences might represent genetically-based physiological differences among subjects. Such differences have been identified as influences on parental behavior in Gallus by several investigators although responses to intruders were not specifically examined (Burrows and Byerly, 1938; Nalbandov and Card, 1945; Wood-Gush, 1955; Saeki, 1957). Since the bantams used as subjects in these experiments were not drawn from a highly inbred stock, they are assumed to be more genetically heterogeneous than most other domestic strains which have been bred for commercial purposes (Guhl and Fischer, 1969).

A second possible contributor to variability among hens is different experiences with conspecifics. The subjects were drawn from a single flock and presumably they occupied different positions in the dominance hierarchy (Schjelderrup-Ebbe, 1922, 1935; Collias, 1943; Guhl, 1955). In consequence, I infer that the individual hen's experiences involved in determining and maintaining dominance relationships in the flock (e.g., approaching, pecking, attacking other birds) were heterogeneous. Collias (1943) and Potter and Allee (1953) demonstrated that a hen's social rank had consequences for her behavior toward strange hens. For example, hens dominant in the home flock tend to initiate dominant behavior toward unfamiliar hens sooner than submissive hens lower in the hierarchy. In another study, the development of maternal behavior as measured by a hen's tendency to approach or flee from chicks was related to the social rank of the hen (Ramsay, 1953). Although these examples concern responses to conspecifics exclusively, it is conceivable that interactions with flock members also affect individual responses to other types of intruders. This consequence seems more likely for species such as Gallus in which the same components comprised responses to live conspecifics, heterospecific intruders and inanimate models. An experiment correlating the behavior of the individual broody hen toward intruders with her position in the social hierarchy would provide pertinent evidence for determining whether the experience of hens in agonistic encounters influences subsequent behavior in confrontations with intruders in general.

A third possible source of hen variability is non-uniformity of experience both outside of and in the intruder context. For example, the hen-chick relationship may have an individual character and such idiosyncracies might affect the hen's behavior in confrontations with intruders. One such documented difference is that the maximum distance chicks range from their mothers is directly correlated with the peck order rank of the broody hen (McBride, et al., 1969). Further, the cumulative experience of hens was probably unequal even at the time of their acquisition since their histories were known only in the most general terms. Additionally, the test groups of experienced hens were composed of subjects whose prior intruder experiences were not identical (see Table II).

Clearly, these potential sources of variability are not mutually exclusive or exhaustive. Only specifically designed experiments can provide conclusive evidence regarding causal factors responsible for individual variability among hens. But in addition to individual differences among broody hens in their expression of various components, responses to intruders have been shown to change as a function of the stage of chick care, maternal experience, repeated testing and intruder types. This flexible organization characteristic of Gallus hens' responses to intruders has been described in other species although the descriptions have been qualitative (Armstrong, 1947; Simmons, 1955). The prominence of variability in the responses to intruders compels further consideration.

The changes in probabilities of observing particular components which have been shown to depend on numerous factors which operate naturally in the life of the individual produces great variety of response patterns and raises the question: Why is the organization of intruder responses so variable? Recently, the hypothesis that variability in response to potential predators is selected for directly as an effective anti-predator strategy has been suggested (Chance and Russell, 1959; Humphries and Driver, 1967, 1970). Humphries and Driver (1967) stated that "In general, other things being equal, those prey individuals which employ escape patterns unfamiliar to predators will tend to be at a selective advantage." Theoretically, the effectiveness of variability operates by arousing conflict and interfering with the information processing capabilities of the predator, lengthening reaction time and reducing the effectiveness of predatory mechanisms. Humphries and Driver (1967) called this type of adaptation "protean defense" after the sea-god Proteus whose changes in form made him disconcertingly difficult to capture (Hamilton, 1940). Such highly unpredictable behavior tends to prevent possible counter-measures by the predator since the predator presumably cannot learn any simple strategy for dealing with the prey (Humphries and Driver, 1970). Similarly, the variability in behavior of broody hens to intruders may be an important response characteristic functioning to reduce predation.

Conflicting Tendencies and Responses to Intruders

During encounters with intruders, broody hens were observed to alternate approaches with avoidance, to fluff their feathers to varying degrees and to scratch in head-up postures. This general pattern of behavior is reminiscent of the approach/withdrawal oscillations and context-specific feather postures observed in territorial disputes (e.g., Tinbergen, 1952, 1959), in threat displays (e.g., Blurton-Jones, 1968) and in diversionary displays toward potential predators (Armstrong, 1947, 1949a, 1949b; Simmons, 1952, 1955). One interpretation of the form of the behavior postulates a conflict between tendencies to perform incompatible responses such as attack and escape (Hinde, 1955; Tinbergen, 1959; Blurton-Jones, 1968). Certain aspects of the intruder-responses of broody hens seem consistent with this interpretation. In particular, Tinbergen (1959) described three criteria to assess motivation: 1) 'form analysis' which compared the morphology of context-specific display movements with movements of known function and causation; 2) 'situation analysis' which considered the situations in which the various movements occur; and 3) 'time scores' which look for temporal correlations between display movements and movements of known function and causation.

An examination of the morphology of feather postures 4 and 5 shows that they contain postural elements which are recognizable as parts of motor patterns used in escape and in attack. In particular, the wings are extended to some degree from the body in both feather postures and the tail is spread and held vertically over the back. Raised wings are movements preparatory to escape involving flight as well as to wing-beating, a common feature of attack; the wing position thus implies dual options of approach and avoid. The open-fan tail position is characteristic of flight (McBride, et al., 1969). The third defining characteristic of feather postures 4 and 5, fluffed body feathers, has been reported by Morris (1956) to be dependent on arousal of the autonomic nervous system. Morris (1956) argues that various degrees of feather fluffing are indicative of situationally-produced conflict.

The situations in which responses to intruders that include feather fluffing occur seem to be composed of extrinsic stimuli which have the potential of causing simultaneous contradictory locomotor tendencies. Specifically, the intruder is known to elicit both avoidance and attack, depending on a nexus of concommitant factors. Further, there is a tendency to stay near the chicks so that if they are immobile or their movements are restricted, a broody hen's tendency to flee would be counterposed with the tendency to remain in proximity to her brood. Where this complex of stimuli are not simultaneously present, such as in tests of non-broody hens without chicks and in observations of broody hens without an intruder present, behavioral components such as fluffed feather postures occur much less often.

The third method for discovering the motivational variables in operation, 'time scores', was not applied to the present results. It does seem pertinent, however, to report that the overwhelming impression from observing the behavior is that feather postures 4 and 5 frequently but not invariably accompany or precede rushes and attacks on the intruder. The present observations are consistent with those of McBride, et al. (1969) who described charges and/or attacks on a variety of intruders by hens in fluffed feather postures ("the typical broody hen display"). This preliminary evaluation thus does not contradict the indications from the 'form analysis' and 'situation analysis' that conflicting tendencies to perform incompatible behavior may be responsible for the pattern of responses observed when broody hens are confronted by an intruder.

On other indication of conflicting tendencies is the presence of head-up scratching in responses of broody hens to intruders. This component meets the criterion for a displacement activity (Tinbergen, 1952; Zeigler, 1964; Hinde, 1970) in that it seems anomalous in the intruder context. Specifically, scratching the substrate is typically associated with foraging in both broody and non-broody hens; effective foraging usually requires visual orientation to the substrate so that edible material can be recognized and seized. In the scratching observed during tests of broody hens with intruders, however, the typical head orientation to the substrate does not appear; instead, the hen holds her head in an upright position and appears to be scanning the enclosure. Thus, head-up scratching differs substantially in form from the normal pattern and seems divorced from its usual function. Kruijt (1964) labels ground scratching dissociated from food consumption as an "irrelevant movement" in agonistic encounters of non-broody hens and pointed out that its form suggests similarity to the motor patterns that could be in conflict. That is, leg movements which characterize locomotion occur and yet, the bird remains in approximately the same location.

In summary, even though these experiments were not expressly designed to elucidate motivational variables that might account for the form of the responses, an argument marshalling several types of evidence appears to support the notion that broody hens confronted by intruders tend to perform incompatible behavior. Further research is needed to provide a more critical appraisal of the conflict model _vis à vis_ the responses of broody hens to intruders.

CONCLUSIONS

1. This study has described the responses of broody hens to intruders both quantitatively and qualitatively. The components comprising the responses are vocalizations, phasic motor activities and various feather postures.

2. Many of the components recorded have been observed primarily in an intruder context; in particular, the phasic motor activities and the feather postures involving fluffing of the body feathers and changes in wing and tail position characterized the hens' behavior in the presence of an intruder. Other components, particularly the vocalizations, have been observed in stimulus contexts that do not include the presence of an intruder.

3. Based on the number of components which differed in the average frequency or duration in contrasting conditions, the effects of the independent variables were of different magnitudes. Reproductive condition, whether the hen was broody or non-broody, had the strongest effect on the birds' responses toward intruders. The second most influential factor was the type of intruder confronting the hen. The factor placing third in influence was experience with intruders during care of a previous brood. Moreover, components which did change under one or more experimental conditions were not necessarily influenced by the same factors.

4. Under most test conditions, a majority of components showed significant variation in expression by individual hens. Several explanations for the origins of this variability are considered. Further, the hypothesis that individual variation may serve to

enhance the adaptive value of responses to predators is presented. The determination of causation and function of this highly characteristic variation in intruder responses requires further research.

SUMMARY

The responses of broody bantam hens to intruders are highly variable. Seventeen discrete components were recorded and these behavioral units fell into three general categories: vocalizations, phasic motor behavior and feather postures. The probability of observing a particular component was influenced by the reproductive condition of the hen, her previous maternal and intruder experience and the visual form of the intruder. In addition, individual variation among hens characterizes the expression of many components under most stimulus conditions. These results are broadly consistent with the existing information on other avian species. Interpretations of the specific differences observed in the experimental groups led to several testable hypotheses which have been proposed to explain the findings. Further, having recorded most discrete components comprising responses to intruders rather than a selected few provides useful information on which components are particularly suitable for further evaluation of independent variables in a way which is affected as little as possible by various factors other than the one under investigation.

Appendix A. Comparison of components present in the responses of maternally naive broody hens to three types of intruders: a live ferret, a live non-broody hen and an inanimate hen puppet. Key: + = component present; o = component absent.

	FERRET	LIVE HEN	HEN PUPPET
AC Ih	o	o	+
AC I	+	o	+
AC II	+	o	+
Chir	+	+	+
Cluc	+	+	+
Shri	+	o	+
Scre	+	+	+
Peck	+	+	+
Rush	+	+	+
Attk	+	+	+
Avds	+	o	+
Scrt	+	o	+
FP 1	o	+	o
FP 2	+	+	+
FP 3	+	+	+
FP 4	+	+	+
FP 5	+	+	+

Appendix B. In tests in which one stimulus object was presented and subsequently (5 to 15 minutes later) a second tests with another stimulus object was conducted, the order of presentation was non-systematic and assumed to be random. The order of presentation for test groups involving multiple stimulus objects is given below. H = hen puppet, C = green cube, F = ferret. The letter given indicates the object used in the first test for that day.

Test Group I

subject no.	1	2	3	4	5	6	7	8
6	C	H	C	H	C	H	C	
5	H	C	C	C	H	C	H	C
4	H	C	C	H	C	H	C	H
3	C	H	C	H	C	H	C	C
2	C	H	C	C	H	C	H	C
1	C	C	H	C	C	C	H	H

exposure no.

Test Group II

subject no.	1	2	3	4	5	6	7	8
6		C	H	C	H	C	H	C
5	C	H	C	H	C	H	C	H
4	C	H	C	H	C	H	C	H
3	H	C	H	C	H	C	H	H
2	C	H	H	C	H	C	H	C
1	H	C	C	H	C	H	C	H

exposure no.

Test Group VI

subject no.	1	2
9	H	
6	C	H
5	H	C
4	C	H
2	C	
1	C	H

exposure no.

Test Group VIII

subject no.	1	2
9	C H	C H
6	H F C	H F C
5	C H F	C H F
4	C F H	C F H
3	H C F	H C F
2	H C	H C

exposure no.

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