

A STIMULUS CONTROL ANALYSIS OF IMPRINTING IN

A HUMAN-REARED PIGEON

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Events that occur early in the life of birds greatly influence social and sexual preferences throughout the course of life. Traditionally, this is explained by a learning process known as imprinting. Young birds are thought to imprint to early stimuli, causing the development of permanent preferences for those stimuli. In the present study, imprinting is examined with respect to behaviors of an adult human-reared pigeon in several conditions. The subject was either presented with no stimulus, a conspecific stimulus, a novel stimulus, a human stimulus, or the human and novel stimuli simultaneously. Several phases within these conditions were employed to pinpoint the variables that produced the most social and sexual behavior. The results showed that while some conditions produced unclear behavior, other conditions produced very clear indications of sexual preference for humans and fear of conspecifics. The results suggest that the concept of imprinting may not be needed to explain the sexual preference of the subject, and that operant contingencies may play a large role in sexual behavior.

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## INTRODUCTION

Imprinting is a form of learning popularized by Konrad Lorenz originating from descriptions of the behaviors of goslings (1935). In nature, hatchling geese follow their parents. However, Lorenz found that the young birds would follow the first object to which they were exposed, without regard to species. The birds were said to “imprint” to this object. In the context of his research, the birds imprinted to Lorenz, and as a result followed him much like wild goslings would follow their parents.

The process of imprinting has primarily been used to explain the rapid acquisition of the following behavior of hatchling precocial birds. This process is known as filial imprinting. The young birds follow the imprinted object, and avoid other conspicuous objects. The long-term consequence of filial imprinting is the development of sexual preferences later in life (Guiton, 1961; Sluckin, 1973, p. 120). This process is known as sexual imprinting. Both filial and sexual imprinting are thought to cause birds to develop species recognition (Immelmann, 1972b; Lorenz, 1935).

### Behavior

Lorenz (1937) suggested that the process of imprinting differs from other forms of learning such as operant and respondent conditioning. However, some researchers feel that it is not possible to draw a sharp distinction between imprinting and other types of conditioning (Fabricius, 1951). Others suggest that imprinting is not fundamentally different from other forms of learning (Hinde, 1955). For example, Hoffman and Ratner (1973) suggest that imprinting is not a specialized phenomenon, but instead can be interpreted in terms of behavioral processes that are relevant to a wide range of species.



Although researchers do not agree that imprinting can be explained completely by operant and respondent processes, the function of reinforcement in imprinting has been clearly demonstrated with the following-response of precocial birds. The following-response was initially thought to be a key feature of filial imprinting (Sluckin, 1973, p. 23). Later research discovered that the topography of the response was irrelevant. Instead, the contingency of reinforcement was found to be more important. Proximity to the imprinted stimulus acts to reinforce any behavior. Peterson (1960) was first to demonstrate that an arbitrary behavior, in this case key pecking, could be reinforced with presentation of the imprinted stimulus. Even behaviors that are incompatible with following can be reinforced with the presentation of the imprinted stimulus. Hoffman, Stratton, and Newby (1969) later expanded on this work and demonstrated that the removal of the imprinted stimulus could be used to punish behavior. The behavior that was punished in this experiment was the natural behavior of following. The birds undergoing this procedure remained still in order to maintain the presentation of the imprinted stimulus. In regards to this research, Skinner (1969) suggests that what is innate is not the behavior, but the sensitivity to reinforcement in the form of proximity to the imprinted stimulus (p. 187).

Other researchers agree that the following response is not an instinctively elicited reflex and suggest that the behaviors evoked by the imprinted stimulus are innately reinforced (Hoffman & Ratner, 1973) or strengthened by “self-reinforced learning” (Hinde, Thorpe & Vince, 1956). However, the work of Peterson (1960) and Hoffman et al. (1969) appears to indicate that the seemingly innate following-response is likely captured and maintained through operant contingencies, with proximity to the imprinted

stimulus acting as a reinforcer. Skinner (1969) suggests that this type of behavior, though learned and maintained through operant contingencies, still presents an example of “species-specific” behavior, in the sense that it is “the product of ontogenic contingencies which prevail for most members of the species” (p.187). Considering the evidence that indicates the following response of filial imprinting is maintained through proximity to the imprinted stimulus, and the similarities between filial and sexual imprinting, it is also possible that species-specific responses related to sexual imprinting are also maintained by natural contingencies of reinforcement.

In addition to the behavior caused by imprinting, Lorenz (1937) stated two other defining features: First, the process is confined to a brief and fixed period of the individual’s life called the critical period. Second, once this process occurs, it is completely irreversible. The resulting behavior will appear as if an unconditioned or purely instinctive behavior. Lorenz suggests that this kind of inflexibility is something that is never found in associative learning.

#### Critical Period

One historically defining feature of imprinting is that it can only occur during a small window of time, early in life, called the critical period. After the critical period ends, the animal cannot imprint to a new stimulus. In precocial birds, the critical period for filial imprinting typically occurs within the first few days of life (Hess, 1964). The critical period of filial imprinting in altricial birds has not been studied greatly, likely because the birds are physically unable to emit obvious responses at a young age. The critical period of sexual imprinting shows more variation among species in onset and duration, occurring in mallards from 5 to 19 days (Schutz, 1965), ringdoves from 7 to 9 days

(Klinghammer & Hess, 1964), and zebra finch from 13 to 30 days (Immelmann, 1972a). Although the critical period and learning of stimuli takes place at a young age, some behaviors resulting from imprinting, particularly sexual behaviors, are not expressed until a much later age.

Although the critical period was initially thought to be very rigid, some exceptions were later noted. Hoffman and Ratner (1973) suggest that prolonged exposure will produce imprinting after the critical period ends. In one extreme exception, Eiserer (1980) found imprinting like behavior to develop in ducks 5 months after the end of the critical period. Due to the exceptions observed in the length of the critical period, several researchers suggested that the use of the term requires additional considerations. Bateson (1966) suggested the term “sensitive period” because the term “critical period” implies an all-or-nothing effect, while “sensitive period” implies that the behavior is more flexible. Immelmann (1972b) notes that despite the common use of the terms “critical period” and “sensitive period,” there is not an exact definition that is consistently used throughout the literature. He also suggests that the definition should remain an operational one, as the onset and duration of the period is a function of the procedures used.

The end of the critical period is thought to mark the development of fear of novel stimuli (Hess, 1959). After the critical period ends, a young bird will avoid novel stimuli. A gradual increase in fear and avoidance behavior occurring at 4 to 6 days of age has been documented in several species of precocial birds (Schaller & Elmen, 1962). Once this fear develops, it can prevent imprinting to new stimuli. Hess (1959) states that fear prevents an animal from engaging in the social behaviors that are necessary for

imprinting to occur. However, Bateson (2000) claims that while it may be possible for a bird to overcome fear of a novel stimulus, it will only become tame with respect to this stimulus; it will not become imprinted to it.

### Permanence

Another key feature of imprinting is the permanent effect on behavior. Immelmann (1972b) states, "The great persistence of preferences has always been regarded as one of the most important characteristics of imprinting." Several researchers have found that sexual preferences remain for many years. Long-term preference has been documented in 5-year-old turkeys (Schein, 1963), in 7-year-old Bengalese finches (Immelmann, 1972a), and in 9-year-old mallards (Schutz, 1965). These preferences appear to be very long lasting, even when the birds were imprinted to humans, as in the case of Schein (1963). Other researchers have found some evidence that imprinting may not be completely permanent. In ringdoves, Klinghammer and Hess (1964) found that sexual imprinting to humans was reversed with prolonged exposure to conspecifics. Although Klinghammer and Hess suggested this is a sign of reversibility and a lack of permanence, Immelmann (1972b) suggests that researchers claiming to disprove the permanence of imprinting often overlook critical features in their methods. He suggests that researchers frequently attempt to produce reversibility before the critical period ends and are not demonstrating true irreversibility.

An analysis of the literature reveals that two separate processes may work together to maintain the permanence of imprinting and make behavior difficult to modify. After the end of the critical period, the development of fear of novel stimuli prevents responding to new stimuli, as suggested by Hess (1959) and Bateson (2000).

Responding to the imprinted stimulus may simultaneously be strengthened and maintained by “automatic” reinforcement as suggested by Hinde et al. (1956) and Hoffman and Ratner (1973), or by a naturally occurring reinforcer such as proximity, as suggested by Peterson (1960). When working in conjunction, these processes may account for what is considered to be the permanence of imprinting. Unless procedures to modify imprinting address both fear of novel stimuli, and reinforcement that strengthens responding to the imprinted stimulus, reversals of preference will be difficult to engineer.

#### Methods to Test Imprinting

Sluckin (1973) describes two common procedures typically used to test imprinting. The recognition test of imprinting entails exposing subjects in an experimental group to an object, while subjects in a control group do not receive any exposure with this object. Then, to test if the exposure the experimental group received caused imprinting, the object is presented to all subjects in both groups. If subjects in the experimental group approach and follow the object significantly more than subjects in the control group, the exposure can be said to cause imprinting (p. 19). This method is typically used to study filial imprinting, but not frequently used to study sexual imprinting.

Sluckin (1973) also describes a second method, the discrimination test of imprinting. In this method, two experimental groups are exposed to different objects. Then, all subjects are tested individually in a situation where both objects are presented simultaneously. Subjects may choose to respond to either object. If subjects in each group primarily respond to the object to which they were previously exposed, the

exposure can be said to cause imprinting to that object (p. 20). This method has been used to study both filial and sexual imprinting.

Sluckin's descriptions were primarily in reference to the following response occurring as a result of filial imprinting. A large majority of the work on filial imprinting follows these general methods. The typical measures of imprinting are latency to approach and the following response (Bolhious & Johnson, 1988; Brown & Hamilton, 1977; Campbell & Pickleman, 1961; Cheng, Shoffner, Phillips, & Sharpiro, 1979; Collins, 1965). Several studies used additional measures such as enhancement of responding to the imprinted stimulus in the presence of fear-inducing stimuli (Eiserer, 1980; Hoffman, Searle, Toffey, & Kozma, 1966; Stetner & Tilds, 1966), the amount of self-maintenance behavior that occurred in the presence of the imprinted stimulus (Eiserer, 1980), and the occurrence of distress calls when the imprinted stimulus is removed (Hoffman, Eiserer, Ratner & Pickering, 1974).

The research on sexual imprinting primarily uses the discrimination test. The primary subject of study in sexual imprinting is the zebra finch, *Taeniopygia guttata*. Studies with these birds often recorded song fragments directed towards stimulus birds, as well as duration spent near stimulus birds (Oetting, Proeve, & Bischof, 1995; ten Cate, 1986; Vos, 1995; Witte & Sawka, 2003). Studies with different species used other courtship or copulation measures (Gallagher, 1977; Klinghammer & Hess, 1964; Warriner, Lemmon, & Ray, 1963).

### Single-subject Designs

Single-subject designs have been crucial to providing an understanding of the mechanisms controlling filial imprinting. Such experiments have allowed an

understanding of the operant contingencies that play a role in the development and maintenance of the following response (Peterson, 1960), the distress call (Hoffman et al. 1969), and the ability of these contingencies to develop arbitrary behavior (Peterson, 1960). Single-subject designs may provide a similar benefit to the study of sexual imprinting.

Sexual imprinting typically follows the discrimination method described by Sluckin (1963). Although these designs provide an abundance of data, many features of the behavior are still unclear, and warrant further analysis at the level of the individual. One area of study in which single-subject designs would be beneficial is the occurrence of area biases. In some experiments, when two stimuli are presented simultaneously, certain individuals display a bias to a particular area. This occurs without regard to the stimuli currently occupying that area. The bias is unexplained, and data from these individuals is often removed from analysis (Witte & Sawka, 2003). Another area of interest is the occurrence of “dithering.” Several researchers described some individuals as ditherers. These birds display an equal preference to multiple stimuli, despite procedures intended to produce imprinting to only one (Hollis, ten Cate & Bateson, 1991; ten Cate, 1986, 1987). These outliers seen in group-designs must exist because of other variables that are not controlled.

In addition to the outliers seen in group-designs, the method of testing imprinting may create additional uncontrolled variables. Some research indicates that responding to the imprinted stimulus in filial imprinting is enhanced by the presence of a novel stimulus (Hoffman et al. 1966; Pitz & Ross 1961; Sluckin & Salzen, 1961; Stettner & Tilds, 1966). This may also occur in sexual imprinting. As the majority of the research

on sexual imprinting presents the imprinted stimulus and a novel stimulus simultaneously, procedures intended to test imprinting may unintentionally enhance responding to the imprinted stimulus. Measuring behavior directed to both stimuli individually, as well as simultaneously, could alleviate this potential methodological issue.

The outliers in group-designs and the potential methodological issues created by presenting a novel and the imprinted stimulus simultaneously could be avoided by controlling variables more closely. Single-subject designs allow variables to be controlled and changed as orderly behavior emerges. This level of control, coupled with additional conditions to test imprinting, would allow a functional analysis of imprinting to be conducted.

#### Applied Relevance

In addition to gaining a better understanding of sexual imprinting, single-subject designs would allow an understanding of individual behavior needed to solve behavioral problems. Imprinting to improper stimuli presents a problem in captive breeding programs. Such programs are intended to allow the maintenance of populations of animals to ensure that various ecological threats will not eradicate the species until reintroduction into the wild is possible (Conde, Flesness, Colchero, Jones, & Scheuerlein, 2011). In recent years, captive breeding programs have played a major role in 25% of vertebrate species whose threat level was reduced (Hoffmann et. al., 2010). Even with these successes, there are many difficulties faced in captive breeding programs. Inappropriate behavior, such as a lack of fear of humans, and a lack of critical species-typical skills are a common problem (Conde et al., 2011). Imprinting to



an improper stimulus, in particular humans, may be at the root of these behavior problems.

In captive breeding programs, animal keepers are frequently required to raise young birds independent of their parents. The effects of hand-rearing a bird and imprinting it to humans are unclear. Captive breeding programs are particularly concerned about the reproductive capability of human-imprinted birds. As a result of imprinting to humans, some species have been described as displaying reproductive deficits (S. Ellis, 2005), and dangerous levels of aggression to humans (D. Ellis, Gee, & Mirande, 1996). Others human-imprinted individuals may also be socially dysfunctional, disrupting the breeding efforts of other birds (S. Ellis, 2005). These problems may also extend to non-avian species. Although imprinting is typically described in birds, it may occur in other groups of animals (Immelmann, 1972b). Some researchers are confident that the occurrence of imprinting in mammals is only a matter of terminology (Sluckin, 1973, p. 135).

The potential problems caused when animals imprint to their human caretakers have resulted in a variety of methods to prevent imprinting to humans (Brown; D. Ellis et al., 1996; S. Ellis, 2005). However, no procedures currently exist to modify social and sexual behaviors after the end of the critical period. If procedures to modify imprinting in sexually mature individuals are developed, increased conservation options will be made available to captive breeding programs. An understanding of sexual imprinting at the level of the individual is a prerequisite to the development of these techniques.

The present experiment is intended provide an understanding of individual behavior, and the outliers seen in group-designs by exploring variables that may

contribute to such outliers. In this experiment, sexual imprinting is studied in a human-reared pigeon using a single-subject multi-element design. Several conditions were used to measure different aspects of behavior. In these conditions the subject was either presented with no stimuli, a conspecific stimulus, a novel stimulus, a human stimulus, or the conspecific and human stimulus simultaneously. In each of these conditions, several phases were used to isolate the variables that most affected behavior.

## METHODS

### Subject

The subject of the experiment was an adult female feral pigeon, (*Columbia livia*), approximately 13 months old. The subject was removed from the nest at approximately 15 days of age. Age was estimated by the date eggs were laid, and by developmental features of the subject at acquisition. After acquisition, the subject was raised exclusively by the experimenter. The experimenter cared for and fed the subject up until about one month of age. The subject was then mature enough to be able to feed herself. Food and water were made constantly available after the pigeon became independent.

After the subject was removed from the nest, she was not in visual contact with other birds. The few days the subject was cared for by other birds were not a concern for this experiment. The results of Klinghammer and Hess (1964) suggest that although there may be an optimal age for imprinting, caring for the birds from hatching is not required. Warriner et al. (1963) suggest that the close and constant attention needed to care for the young birds is a strong influence on imprinting and sexual preference.

The subject emitted many behaviors that indicated she was sexually imprinted to the experimenter. The subject frequently allo-preened the experimenter's hands. If any tactile contact was provided while the bird was allo-preening, the bird would crouch with the neck retracted and the wings slightly opened. This behavior is described as a species-typical behavior indicating a female's willingness to copulate (Goodwin, 1983, p. 303).

The subject was sexed by physical and behavioral characteristics, primarily the presence of the mating solicitation behavior. Sexing pigeons in this manner appears to be a fairly reliable measure after sexual maturity. Warriner, et al. (1963) accurately sexed sixty out of sixty-four birds in this manner. After the end of the experiment, the subject began producing eggs, confirming the sex of the subject.

The subject's home cage was a 35 x 35 x 25 cm hardware cloth enclosure. The subject was housed adjacent to six other pigeons in similar enclosures. The birds were visually isolated, but not acoustically isolated.

The subject lived in the home cage prior to the start of the experiment and lived in the experimental apparatus during the experiment. Illumination was presented on a twelve-hour light/dark cycle. Interaction with human stimuli during the experiment was limited to brief apparatus maintenance.

### Apparatus

Figure 1 provides a diagram of the experimental apparatus. Figure 2 is an image of the apparatus taken from the attached camera. The apparatus consisted of several components. The living chamber measured 68 x 68 x 25 cm. The front of the chamber was made from clear acrylic, allowing observation. The remaining walls were made from plywood. The floor and ceiling of the living chamber were made from hardware cloth. A wooden lid with a light covered the top of the apparatus and provided illumination. A peephole was built into the lid to allow unobtrusive observation. Food and water bowls were mounted on the right side of the apparatus. An adjacent door permitted the apparatus to be serviced. The left side of the apparatus contained two sliding doors.

Each door spanned 20 cm, with another 20 dividing them. Opening the doors revealed two stimulus chambers.

The stimulus chambers were separate, identical units, each measuring 26 x 26 x 25 cm. The walls adjacent to the experimental chamber were made from hardware cloth. The other walls and tops were made from wood. The back walls were mounted on a hinge allowing stimuli to be placed in the chamber. The floors were made from hardware cloth. The tops contained a window of acrylic diffuser, allowing light to enter the chamber, but not allowing a clear view in or out of the chamber. This was intended to provide illumination without allowing the subject to view outside of the apparatus through the top of a stimulus chamber.

A bright red wooden grid under the floor of the living chamber was used to visually divide the chamber in nine areas to assist visual measurement. Each square of the grid was 20 x 20 cm. These dimensions permitted each square to contain a pigeon in the center, with little overlap into other squares.

A separate unit containing a video camera was attached to the front of the apparatus to permit unobtrusive data collection. The camera unit covered the entire viewing panel on the living chamber, preventing the subject from seeing outside of the apparatus.

## Measurement

### *Locations*

Four areas were used for measurement. Two large areas adjacent to the stimulus chambers and outlined by the red grid were known as Area 1 and Area 2. Each area was 20 by 20 cm. They were separated by an additional 20 cm so that the subject

could not be in both areas simultaneously. Inside these areas were two smaller areas, marked by a red bar next to the stimulus door. These areas were denoted Area 1-close and Area 2-close. These areas corresponded to the 5 cm of the larger area closest to the stimulus chambers.

The location of the subject was recorded at all times. The subject was noted as entering an area as soon as any part of the foot overlapped the red wood designating that area. The subject was noted as leaving that area as soon as no parts of the feet were in the area outlined by the red wood. As Area 1 included Area 1-close, and Area 2 included Area 2-close, the subject was not considered to be leaving the larger area when entering the smaller area.

### *Behaviors*

Pecks, attacks, allo-preening, and mating solicitation were scored with respect to the area they occurred, and only when they occurred within 5 cm of the stimulus chambers, anywhere in height within that area. These behaviors were distinguished by a visual assessment of topography from videos of each session. The following descriptions describe the general topographical characteristics that were used to distinguish the behaviors.

*Peck.* A peck was defined as a quick head movement directly toward an object. The subject's beak was not required make contact with the object. When beak contact was made, the beak lightly touched the object, and was retracted immediately. After the beak was retracted, the subject's head would often remain in close proximity to the object. Frequently, several pecks were emitted in rapid succession before the subject's head and neck returned to a resting position. A peck was considered to begin with the

motion of the head toward an object and end when the head was moving away from the object.

*Attack.* An attack was defined as a fast head movement directly toward an object, with a different thrust topography than a peck. The head movement of an attack was faster than a peck, and the thrust was less direct than a peck. In an attack, the head often moved in an arc down to the object, similar to the swing of a hammer. After the attack ended, it often recoiled quickly away from the object. The subject's beak was not required to touch the object. The subject's eyes were often closed during prolonged beak contact. An attack was considered to begin with the motion of the head toward an object. If beak contact was made, the beak often clamped down on the object. The beak was then frequently used to twist, push or pull the object. The attack was considered to end when the head was moving away from the object.

*Allo-preening.* Allo-preening was defined as an open beak movement toward an object with prolonged beak contact. Allo-preening was not considered to occur if no contact was made with the object. When in contact with the object, the beak opened and closed rapidly. Allo-preening differed from pecking in that the thrust of the head was not as fast as in a peck. Additionally, allo-preening frequently entailed prolonged beak contact while prolonged contact never occurred with a peck. Allo-preening differed from attacks in the speed of the thrust and topography of the topography of the contact. The thrust of the head was slower in allo-preening than in an attack. When open beak contact was made in allo-preening, the subject did not grasp, twist, push or pull the object as in an attack. Allo-preening was considered to begin when the open beak made contact with an object, and end when the head moved away from the object. Although

the subject may momentarily break beak contact, allo-preening was still considered to be occurring until the head moved away from the object.

*Mating solicitation.* Mating solicitation was defined by the body position of the bird. The defining characteristics were a retracted neck, and a crouched body position, such that the back was parallel to the ground. The subject often crouched so that she was completely resting on the floor. The wings were also often slightly extended. Neck retractions did occur on occasions when a mating solicitation was anticipated. Although this may indicate that mating solicitation was likely to occur, it was not scored unless the subject crouched to some degree. Mating solicitations were considered to begin when both the neck was retracted and the back was parallel to the ground, and ended when either the neck was no longer retracted, or the back was no longer parallel to the ground.

#### *Dependent Variables*

The dependent variables in this study were the duration the subject spent in each area, frequency of pecks, frequency and duration of attacks, duration of allo-preening, and duration of mating solicitations.

#### *Measurement System*

A custom computer program was used to capture data from videos of the sessions. The program played the video file of the session, while the observer pressed and held keys to record behavior. For each behavior the individual onset, individual duration, total number of occurrences, and total duration were recorded.

#### *Inter-observer Agreement*



Inter-observer agreement was conducted using 16% of all sessions. Two other observers each scored a selection of these sessions. The second observers were trained using the preceding definitions and video examples of behaviors. The second observers then used the computer program to play video of the sessions and record data independently of the primary observer. Data files were then compared to determine inter-observer agreement. Agreement was calculated by dividing the smaller of the two measurements by the larger, then multiplying the result by 100.

Average agreement for the duration the subject spent in each area was good, at 93% across all areas. Average agreement on time the subject spent in Area 1 was 93%; Area 1-close, 90%; Area 2, 95%; and Area 2-close, 93%.

Average agreement of frequency of pecks was 76%. Four reports of 0% agreement between pecks occurred when one observer scored 1 peck while the other observer scored 0 pecks. Removal of these 4 sets of observations brings the average agreement to 82%. For attacks, average agreement was 82% for frequency, and 88% for duration. Average agreement on duration of allo-preening was 91%. Average agreement on duration of mating solicitations was 80%.

### Procedures

Several conditions were used in this experiment to provide a greater understanding of behavior. The multiple conditions were intended to demonstrate the effects of individual stimuli on behavior in addition the preference measure used in most sexual imprinting experiments. Several additional conditions were used as controls. In each session, stimuli were presented to the subject by placing them in the stimulus chamber and opening the door to that stimulus chamber. Location of the stimuli was

counterbalanced. Each session lasted five minutes. Video of each session was recorded and scored at a later time.

### *Alone Condition*

In the alone condition, the subject was not presented with any stimuli. Each session in the alone condition alternated between having both stimulus chambers closed, stimulus chamber 1 open, stimulus chamber 2 open, and both stimulus chambers open. The alone condition was intended to act as a control, providing a comparison to sessions where stimuli were presented. Additionally, it assessed the effects of the apparatus on behavior.

Sixteen sessions of the alone condition were conducted. In the first eight sessions, a wire barrier prevented the subject from entering the stimulus chambers. In the second eight sessions, an opening in the barrier allowed the subject to extend her head and neck into the chamber.

### *Conspecific Condition*

In the conspecific condition, another pigeon was presented to the subject. The stimulus pigeon was a wild caught adult male. The same stimulus bird was used throughout the experiment. Two phases were used in the conspecific condition. In the closed-wire phase, a wire barrier prevented any interaction between the two birds. In the open-wire phase, a small opening allowed either bird to extend their head and neck through the wire opening.

### *Novel Condition*

As the subject had not been exposed to a conspecific prior to the start of the experiment, other birds were novel to the subject. The behavior of the subject in the

presence of the conspecific could be attested to either the novel effect of the stimulus, or innate species recognition. In order to clarify this possibility, an artificial novel stimulus that the subject was unlikely to innately recognize was presented in the novel condition. As both the novel stimulus, and the conspecific stimulus were novel to the subject, an artificial novel stimulus was needed to act as a control. This stimulus consisted of a stuffed hedgehog toy. The novel stimulus was always presented with an opening in the wire barrier, permitting some degree of contact.

#### *Human Condition*

In the human condition, a human stimulus was presented. Four phases were used. In the closed-wire phase, a human hand was presented behind a solid wire barrier. In the open-wire phase, an opening in the barrier allowed the subject's head to enter the stimulus chamber and interact with the hand. In the preening phase, a human hand was presented behind a wire barrier with an opening. In this phase, if the subject allo-preened the experimenter's hand, the experimenter would extend a finger through the opening in the wire barrier, and gently touch the head and neck of the subject. This tactile contact occurred as soon as the subject began preening the experimenter's hand, and ended as soon as the subject ceased allo-preening. In the face phase, a human hand and face were presented behind a wire barrier with an opening. As in the preening phase, the experimenter would gently touch the head and neck of the subject if the subject preened the experimenter's hand.

#### *Preference Condition*

In the preference condition, both the conspecific stimulus and human stimulus were presented simultaneously in opposite stimulus chambers. The same phases used

in the human condition were used in the preference condition. When the phase required an open-wire barrier for chamber containing the human stimulus, an open-wire barrier was also used for the chamber containing the conspecific stimulus.

### Experimental Design

The experiment used a multi-element design with 5 conditions, and 4 phases in those conditions. One session was conducted a day at noon. Only one condition of each type occurred during a daily session. The order of conditions rotated each day through a repeating pattern listed in Table 1. Each day, the alone condition always occurred before other conditions. The novel condition alternated between occurring immediately after the alone condition, and occurring after all other conditions. Each day, the human and conspecific conditions were always presented before the preference condition so that the preference condition did not affect behavior in the presence of the individual stimuli. A phase change in the conspecific, human, or preference condition, also entailed a phase change in the other two conditions. Thus, all three conditions changed from the closed-wire to open-wire phases simultaneously. As the behavior of the stimulus bird was not under the experimenter's control, the analog of the preening and face phases in the human condition was the open-wire phase in the conspecific condition.

## RESULTS

### Alone Condition

Figures 3, 4 and 5 show the range of duration the subject spent in each area in all sessions of the alone condition. The box plots illustrate the median, upper quartile, lower quartile, maximum, minimum and outliers in the range of data collected.

Figure 3 shows the duration the subject spent in each area across all sessions of the alone condition. Each box plot was derived from 16 data points. The results show that the subject spent more time in Area 1 and Area 1-close than in Area 2 and Area 2-close.

Figure 4 shows the duration the subject spent in Area 1 and Area 2 when the stimulus chamber doors were both closed, opened individually, or both opened. Each box plot was derived from 4 data points. The data shows that when both chambers were closed, the subject spent more time in Area 1 than Area 2. When only one stimulus chamber was opened, the subject spent much more time near the opened chamber. When both chambers were open, the subject spent a similar amount of time in both Area 1 and Area 2.

Figure 5 shows the duration the subject spent in Area 1-close and Area 2-close when the stimulus chamber doors were both closed, opened individually, or both opened. The data shows that when both chambers were closed, the median, upper quartile and lower quartile of Area 1-close was higher than those for Area 2-close. However, Area-2 close had a higher maximum. When only one stimulus chamber was opened, the subject spent much more time near the opened chamber. When both

chambers were open, the subject spent slightly more time in Area 1-close than Area 2-close.

The data collected when both chambers were closed likely accounts for most of bias towards Area 1 and Area 1-close seen in Figure 3. Interestingly, Pecks were the only behavior to occur in the alone condition. They occurred very infrequently with an average of only 3 pecks in each session. Because of the low occurrence of pecks in the alone condition, they are not reported in additional detail.

### Conspecific Condition

Figure 6 shows the duration the subject spent near the stimulus bird in the open-wire and closed-wire phases of the conspecific condition. In general, the time spent near the conspecific was variable across all sessions. In the Session 1, the subject did not spend much time near the conspecific. In the Sessions 2 to 8, of the first closed-wire phase, the subject generally spent more than 200 seconds within 20 cm of the conspecific, and more than 100 seconds within 5 cm of the conspecific. In Sessions 9 to 37, the first open-wire phase, the subject generally spent more than 200 seconds within 20 cm of the conspecific. In Sessions 9 to 25, the subject generally spent a similar amount of time within 5 cm of the conspecific as she did within 20 cm of the conspecific. In Sessions 26 to 37, the subject spent much less time within 5 cm of the conspecific, around 75 seconds each session. In Sessions 38 to 68 a distinction emerged between the closed-wire and open-wire phases. In closed-wire phases, the subject generally spent more than 200 seconds within 20 cm of the conspecific, and more than 150 seconds within 5 cm of the conspecific. In the last 12 sessions of the open-wire phases, the subject spent much less time near the conspecific, an average of 136 seconds

within 20 cm of the conspecific, and 32 seconds within 5 cm of the conspecific. This is less than average time spent near an empty stimulus chamber in the alone condition reported in Table 4.

The topography of the subject also changed across sessions. In Session 1, as the subject approached the conspecific, the feathers on the subject's back were raised, the tail feathers slightly spread, and the wing facing away from the conspecific slightly opened. Goodwin describes this posturing as a defensive-threat display, and suggests it occurs when a pigeon is simultaneously compelled to escape and to attack, and is an indicator of fear (1983, p. 294). Although this topography disappeared after Session 1, it returned in Sessions 8 and 9, the first two sessions the conspecific was presented with an opening in the wire barrier.

Figure 7 shows the number of pecks and attacks occurring near the stimulus bird in the closed-wire and open-wire phases of the conspecific condition. In Sessions 1 to 8, the first closed-wire phase, the subject pecked around 10 times each session. In Sessions 9 to 27, the first open-wire phase, the primary behavior to occur was attacks, at around 10 each session. After the first open-wire phase, attacks become less frequent, and a difference between closed-wire and open-wire phases emerged. In the closed-wire phase, the subject pecked much more than in the open-wire phase, with peaks in pecks at over 50 pecks in a session. Very little pecks or attacks occurred in the last two open-wire phases.

Although the stimulus bird could not always be observed in the video of each session to allow a record of its behavior, several bouts of fighting between the stimulus bird and the subject were noted. Figures 8 and 9 show two such bouts of fighting.

Figure 8 shows a bout of fighting between the subject and the stimulus bird, and the time the subject spent near the stimulus bird in Session 26. The subject and the stimulus bird attacked each other throughout the entire duration of the session. The subject began the session near the stimulus bird. The birds attacked each other during the first 100 seconds, and then the subject left the area. At around 175 seconds the subject returned to the area near the stimulus bird. The stimulus bird attacked the subject twice, and then the subject left the area. At around 200 seconds the subject again entered the area near the stimulus bird, attacked the stimulus bird 4 times, the leaves momentarily and is attacked by the stimulus bird twice.

Figure 9 shows a bout of fighting between the subject and the stimulus bird, and the time the subject spent near the stimulus bird in Session 32. The subject and the stimulus bird rapidly trade attacks during the first minute of the session. After 12 attacks, the subject's rate of attack decreases while the stimulus bird's rate of attack maintains. The subject did not spent much time within 5 cm of the conspecific until the bout of fighting was over.

#### Novel Condition

Figure 10 shows the duration the subject spent near the novel stimulus in the novel condition. The subject spent very little time near the novel stimulus in Sessions 1 and 2. In Sessions 3 to 10, the subject spent some around 175 seconds within 20 cm of the novel stimulus, but little time within 5 cm of the novel stimulus. Starting in Session 11, the subject spent around 225 seconds near the novel stimulus, most which was within 5 cm.



In Sessions 1 to 5, as the subject approached the novel stimulus, the feathers on the subject's back were raised, and the tail feathers were slightly spread, similar to defensive-threat display observed in conspecific Sessions 1, 8, and 9.

Figure 11 shows the number of pecks and attacks occurring near the novel stimulus. Pecks began occurring frequently in Session 11 and continued to occur frequently for the remainder of the sessions. Session 11 also marked the first time the subject spent a notable amount of time within 5 cm of the novel stimulus, suggesting a relation between pecks and proximity.

Attacks occurred in Session 4 and 5 then subsided, to later return in Session 13. The attacks in Session 4 and 5 were accompanied with the defensive-threat display similar that seen in early conspecific sessions. Attacks in Sessions 13 to 20 were not accompanied with the defensive-threat display, and often possessed longer durations. When attacking in Session 13 to 20, the subject frequently gripped the stimulus and pushed, pulled or twisted with the beak. When this topography of attack occurs between conspecifics, is interpreted as territorial aggression (Goodwin, 1983, p. 291).

The topographical distinction of attacks and different ethological interpretation warranted a closer analysis. Figure 12 and 13 show several properties of attacks in sessions when attacks occurred.

Figure 12 shows the average and maximum duration of attacks occurring in the novel condition. Attacks in Sessions 13 to 20 generally possessed a longer maximum and average duration.

Figure 13 shows that the average inter-response-time (IRT) of attacks decreased across sessions. For the purpose of calculation, attacks occurring over 5 seconds apart

were considered to be in different bouts of attacking, and an IRT value was not derived in these occurrences. In Session 16, no attacks occurred within 5 seconds of each other and an IRT value could not be determined.

In Sessions 11 and 12 there were 1 and 14 occurrences of allo-preening, respectively. These behaviors were very brief in duration, accounting for only 6 seconds total.

### Human Condition

Figure 14 shows the duration the subject spent in the areas adjacent to the human stimulus in the closed-wire and face phases of the human condition. For the purpose of clarity, Sessions 9-23 and 29-37, the open-wire and preening phases, were excluded from this graph. Generally, the subject spent over 200 seconds of the session near the human stimulus in both phases. The duration the subject spent within 20 cm of the human stimulus and within 5 cm of the human stimulus generally corresponded closely. A slight difference between the closed-wire and face phases was noticed. In the closed-wire phases the time spent within 20 cm and within 5 cm of the human stimulus was more variable. In Sessions 62 to 68, the last closed-wire phase, a downward trend in time spent near the human stimulus was noticed. In the face phases, time spent near the human stimulus was more stable, and the subject more frequently spent over 250 seconds within 20 cm of the human stimulus.

Figure 15 shows the number of pecks occurring near the human stimulus in the closed-wire and face phases of the human condition. Pecks consistently occurred more in the closed-wire phases than the open-wire phases, frequently at around 50 pecks per sessions. Attacks occurred more in the face phases than in closed-wire phases. Attacks

generally occurred at a much lower frequency than pecks, at around 10 each session. The distinction in pecks and attacks between the closed-wire and face phases became less pronounced after several reversals.

Figure 16 shows the duration of allo-preening and mating solicitations in the closed-wire and face phases of the human condition. With the exception of 1 second in Session 65 the subject never allo-preened the human hand in the closed-wire phase. The occurrence of this behavior does indicate that allo-preening through the wire barrier is possible. In the face phase, the subject generally allo-preened the human stimulus around 100 seconds each session. Mating solicitations never occurred in the closed-wire phase, but did occur in small durations in the face phase.

Figure 17 shows the duration the subject spent attacking and allo-preening the human stimulus in Sessions 9 to 37 of the human condition. This figure includes the open-wire and preening phases that were excluded from previous graphs. There was an inverse relationship between the durations attacking and allo-preening. Peaks in attacking, at around 100 seconds each session, occurred at Sessions 11 to 14. This corresponded to low points in allo-preening. Conversely, the highest points in allo-preening, at around 150 seconds, in Sessions 20 and 25 to 33, correspond to very low durations of attacking. Additionally, the occurrence of the first face phase may have produced an effect on the second preening phase. The subject attacked very little in the second preening phase. The behavior more closely resembled the face phase.

Table 3 lists the number of sessions in each phase of the human condition that began with a peck and an attack. Because only two sessions began with other behaviors, only pecks and attacks are discussed in detail. In the closed-wire phases,

most sessions began with a peck. In the open-wire phases, a similar number of sessions began with pecks as did attacks. In the preening, and face phases, more sessions began with an attack.

Table 4 lists the average latency in seconds to the first peck for sessions that began with a peck, and the average latency to the first attack for sessions that began with an attack. In the closed-wire phase, the average latency to the first peck was 43 seconds, while the average latency to the first attack was 16 seconds. In the open-wire, preening and face phases, average latencies to both pecks and attacks were similar, at around 10 seconds.

#### Preference Condition

Figure 18 shows the duration the subject spent within 20 cm of the human and conspecific stimuli in the closed-wire and face phases of the preference condition. For the purpose of clarity, Sessions 9-23 and 29-37, the open-wire and preening phases, were excluded from this graph. A consistent pattern emerged in the amount of time the subject spent within 20 cm of the stimuli. In the closed-wire phase, the subject generally spent time around 150 seconds near each stimulus, with slightly more time overall spent near the conspecific. In the face phase, the subject spent almost the entire 300-second session near the human stimulus, with little time being spent near the conspecific.

Figure 19 shows the duration the subject spent within 5 cm of the human and conspecific stimuli in the closed-wire and face phase of the preference condition. The duration the subject spent within 5 cm of each stimulus followed a pattern similar to that seen with the duration spent within 20 cm of each stimulus. In the closed-wire phase, the subject generally spent time around 100 seconds near each stimulus, with slightly

more time overall spent near the conspecific. In the face phase, the subject spent around 250 seconds near the human stimulus each session, with very almost no time spent near the conspecific.

Figure 20 shows the duration the subject spent within 20 cm of the human and conspecific stimuli in Sessions 9-37 of the preference condition. This graph includes the open-wire and preening phases that were excluded from previous graphs. The initial open-wire and preening phases showed that most of the sessions were spent almost exclusively near human stimulus, with several sessions being nearly equally divided between the two stimuli. In Sessions 23 to 37, the face phase and the second open-wire and preening phases, the subject spent with almost the 300-second session near the human stimulus, with very little time spent near the conspecific.

Figure 21 shows the number of pecks and attacks occurring near the conspecific in the closed-wire and face phases of the preference condition. Similar to the conspecific condition, pecks primarily occurred in the closed-wire phase. An increase in pecks occurred throughout the closed-wire phase. In the first closed-wire phase, around 10 pecks occurred each session. The number of pecks increased each closed-wire phase, to around 25 each session in the last closed-wire phase.

Figure 22 shows the number of pecks and attacks occurring near the human stimulus in the closed-wire and face phase of the preference condition. Pecks occurred frequently in the first two closed-wire phases. After Session 44, pecks and attacks did not occur frequently in either phase.

Figure 23 shows the duration of allo-preening and mating solicitations directed to the human in the closed-wire and face phases of the preference condition. Similar to the

human condition, allo-preening only occurred in the face phase. The duration of allo-preening in the face phases was generally around 100 seconds. Mating solicitations did not occur as frequently as in the human condition. Session 60 was the only session that a notable duration, 15 seconds, of mating solicitation occurred.

### Summary Table

Table 4 summarizes the time the subject spent near each stimulus, and allows for a comparison between effects of an empty stimulus chamber and the effects of stimuli in the chamber on time spent near stimulus chambers. The average and standard deviation of duration spent within 20 cm and within 5 cm of the stimulus chambers in each condition is reported. Two sets of averages were provided for the alone condition. The first set, one chamber open, averages the time the subject spent near open stimulus chambers when only one chamber was open. This can be compared to the data reported for the novel, conspecific, and human condition.

When one stimulus chamber was opened in the alone condition, the subject spent an average of 161 seconds within 20 cm and 115 seconds within 5 cm of the empty stimulus chamber. This was more than the average time spent near the novel stimulus in Sessions 1 to 10 of the novel condition; 136 seconds within 20 cm and 0 cm within 5 cm, but less than the average time spent near the novel stimulus in Session 11 to 20 of the novel condition; 247 seconds within 20 cm and 211 cm within 5 cm. In the conspecific condition, the subject spent an average 211 seconds within 20 cm and 123 seconds within 5 cm of the conspecific stimulus, notably more than the time spent near empty stimulus chambers in the alone condition. In the human condition, the subject spent an average 255 seconds within 20 cm and 221 seconds cm within 5 cm of the

human stimulus. This greater than both the time spent near empty stimulus chambers in the alone condition and time spent near the conspecific in the conspecific condition.

The second set of averages reported for the alone condition, both chambers open, was derived from sessions when both stimulus chambers were open. This can be compared to data in the preference condition. When both stimulus chambers were opened in the alone condition, the subject spent an average of 76 seconds within 20 cm and within 5 cm of the empty stimulus chambers. In the preference condition, the subject spent an average of 66 seconds within 20 cm and 44 seconds within 5 cm of the conspecific stimulus. This is slightly lower than the time the subject spent near empty stimulus chambers in the alone condition. The subject spent an average of 188 seconds within 20 cm and 159 seconds within 5 cm of the human stimulus in the preference condition. This duration is much greater time than time spent near empty stimulus chambers or near the conspecific stimulus.

## DISCUSSION

### General Results

The general results show that empty stimulus chambers produced an effect on proximity. Generally, the subject spent more time near occupied stimulus chambers than empty stimulus chambers, with two exceptions. The first exception was observed in the conspecific condition, and the second during the novel condition. With regards to occupied stimulus chambers, the subject spent the most time near the human and novel stimulus, after Session 10. The subject spent the least time near the conspecific, in later open-wire phases. If proximity to stimuli was the only measure of imprinting, this would suggest that the subject was imprinted to the human stimulus, and became imprinted to the novel stimulus as sessions progressed. Other measures, however, suggest otherwise.

Pecks occurred in the highest frequency in the human condition. Pecks also occurred at a high frequency in the second half of the novel condition, but did not occur in the first half. In the conspecific condition, pecks occurred at lower rates than in the human condition or the second half of the novel condition. The lowest general frequency of pecks occurred in the preference condition with respect to both the conspecific and the human stimulus. Interestingly, across the conspecific, human and the preference condition, the closed-wire phase produced more pecks than other conditions. Although many of the pecks made contact with the wire, very few pecks occurred in the alone condition, indicating that the wire did not produce pecks in the absence of other stimuli. If the number of pecks occurring near a stimulus was taken as a measure of imprinting,



the subject would seem most imprinted to the human stimulus and similarly imprinted to the novel stimulus after Session 10, and least imprinted to the conspecific stimulus.

Attacks occurred in the highest frequency in the second half of the novel condition, but very little in the first 10 sessions. Attacks also frequently occurred in the open-wire and preening phases of the human condition. Attacks occurred at a lower frequency in the first open-wire phase of the conspecific condition. Across all sessions, attacks occurred the least in the closed-wire phase. While attacks may indicate imprinting if they are interpreted as intra-species aggression, they may also indicate a lack of imprinting if they are interpreted as avoidance behaviors. The effect of the experimental condition on attacks as well as the multiple interpretations suggest that attacks do not provide a clear interpretation of imprinting and need to be analyzed in greater detail before making any suggestions about imprinting.

Allo-preening and mating solicitations occurred almost exclusively in response to the human stimulus. The only exceptions noted were a few seconds of allo-preening in two the novel condition. The almost exclusive occurrence of these behaviors in response to the human stimulus, as well as their ethological interpretation, suggests that the subject was only sexually imprinted to the human stimulus. Interestingly, these behaviors were not observed in the closed-wire phase, indicating that stimulus conditions play a strong role in the expression of sexual imprinting.

#### The Alone Condition as a Control

The results show that empty stimulus chambers do produce an effect on behavior. When either stimulus chamber is opened, the subject spent much more time near the opened chamber than the closed chamber. This data, compared to the amount

of time the subject spent near occupied stimulus chambers in other conditions, allows for an assessment of the magnitude of the effect of stimuli on behavior. The amount of time the subject spent near stimuli must be notably different than the amount of time spent near empty stimulus chambers to demonstrate an effect of the stimulus on behavior. The alone condition is necessary for this type of assessment to be made. Data from the alone condition is needed to demonstrate that the effect of stimulus presentations in other conditions is caused by the stimuli inside the chambers, instead of the chambers themselves. Experiments without this control may be able to state a difference in the effect of one stimulus versus another, but they cannot confidently state the magnitude of the effect of either stimulus on behavior.

In addition to serving as a control condition, the alone condition may also serve a practical purpose. Some researchers have removed subjects from experiments because of area biases similar to that seen in the present experiment (Witte & Sawka, 2003). In the present experiment, the occurrence of an area bias only when both stimulus chamber doors were closed suggests that a modification of procedures could be useful for researchers that consider removing subjects from experiments. Subjects in sexual imprinting experiments require a significant amount of time from hatching to reach sexual maturity. During this time the subjects must be kept in controlled conditions, often isolated from other individuals. The age of the subject varies by species and procedure and ranges from 60 days (Gallagher, 1977; ten Cate, 1986), 100 days, (Oetting et al., 1995; Witte & Sawka, 2003), 120 days (Vos, 1995), 300 days (Warriner et al., 1963), to 540 days (Klinghammer & Hess, 1964). As each subject represents a considerable time investment, further analysis of individuals that show area biases

could be of great benefit, and potentially lead to better methods to test sexual preference. The inclusion of an alone condition in experiments presents one such analysis to locate the cause of area biases.

#### Aversive Characteristics of the Conspecific

In the conspecific condition, the duration the subject spent near the conspecific was variable, and often very low. Additionally, some approaches to the conspecific in initial sessions were accompanied by a defensive-threat display. The defensive-threat display occurring in earlier sessions, the reduced amount of time spent within 5 cm of the conspecific in the open-wire phases after Session 25, and the suppression of pecks in the last two open-wire phases suggest that the conspecific may have been aversive.

If the conspecific was aversive, as suggested, an avoidance contingency may prevent appropriate social interaction from developing (Hess, 1959). To cultivate social interaction and the development of an appropriate repertoire, avoidance contingencies first need to be removed. With respect to filial imprinting, Hoffman and Ratner (1973) suggest that filial behavior will emerge if fear of a stimulus is removed. Several researchers have produced this effect through prolonged exposure to a fear-inducing stimulus (Bateson, 1964; Hoffman, Ratner, & Eiserer, 1972; Sluckin & Salzen, 1961). A similar emergence of behavior may also occur in sexual imprinting if fear of a stimulus is removed. A lengthy exposure to the conspecific in this experiment did not produce such a change, possibly because the behaviors of the stimulus bird maintained fear and an avoidance contingency. Thus, it is important to note in experiments of sexual imprinting, the behavior of living stimuli is important. The interaction between subject and stimulus should be studied to better understand the behavior of the subject.

## The Development and Maintenance of Avoidance Behavior

Avoidance contingencies that prevent social interaction may develop quickly through initial interactions. Consider a human-reared bird that has never been exposed to a member of its own species. As it has not interacted with other birds, it has no reinforcement history for approach or interaction with conspecifics. If the human-reared bird is attacked by another bird on its first encounter with another member of its species, it may learn to avoid other birds. As long as avoidance behaviors and a lack of interaction result in a lack of aggression, these behaviors may be reinforced. These behaviors may become considerably strong even if reinforced and maintained superstitiously.

Parent-reared birds may also encounter aversive interactions with other birds. However, a lengthy history of reinforcement of interaction, derived from the rearing process, may prevent parent-reared birds from coming to avoid other birds. The reinforcement history originating from their parents may also allow them to easily come in contact with additional communities of reinforcement with other birds.

The suggestion that initial interactions may produce avoidance contingencies requires that some aggression occur frequently in interaction. Consider Tables 3 and 4. In the human condition, the phase that produced the most sexual behavior, the face phase, also frequently began with an attack occurring within the first 18 seconds of the session. If a human-reared bird was subjected to this initial attack, would it be likely to remain near the other bird until social and sexual behaviors were emitted, or would it retreat some distance? A parent-reared bird at least possesses some reinforcement history with other birds, due to the rearing process, so that interaction behaviors may

not be easily extinguished. Parent-reared birds could then come in contact with social and sexual behaviors that occur later.

This interpretation suggests that contingencies of reinforcement are important factors affecting the social and sexual behavior of an individual. Early contingencies may be especially important, as they not only affect behavior, but the likelihood of encountering other contingencies of reinforcement (see Rosales-Ruiz & Baer, 1997). If initial contingencies strengthen approach behaviors, it may be more likely that approach behaviors can be reinforced in the future and be further strengthened. Conversely, if initial contingencies strengthen avoidance behaviors, it would be less likely that approach behaviors could be reinforced in the future, and more likely that avoidance behaviors would be maintained and strengthened. This interpretation also suggests that the behavior occurring in the presence of a non-imprinted stimulus may be primarily related to fear and operant contingencies. The concepts of imprinting and species recognition may not be needed to explain behavior.

#### Comparison of Behavior in Conspecific and Novel Conditions

The novel condition was intended to act as a control to the conspecific condition. Although the conspecific was novel to the subject, there was likely some phylogenetic history. The novel stimulus was used as a control because it possessed no ontogenic or phylogenetic history. The initial responses to the conspecific and novel stimuli showed some similarities. In both the conspecific and novel conditions, the subject initially spent little time within 5 cm of each stimulus, and approaches and attacks were frequently accompanied with the defensive-threat display. Several differences between the conspecific and novel conditions were also noted. The subject began spending a

notable amount of time within 5 cm of the conspecific stimulus much sooner than she began spending time within 5 cm of the novel stimulus. However, in later sessions of the conspecific condition, the subject began spending much less time within 5 cm of the conspecific. This may be due to some innately reinforcing properties of conspecifics. Conversely, in the novel condition once the subject began spending time within 5 cm of the novel stimulus, this duration remained consistently high.

The reduced amount of time spent near the conspecific in later sessions suggests that although fear of the conspecific was overcome quickly, some degree of avoidance was maintained or cultivated through the course of the experiment. This may be due to the behavior of the stimulus bird. As the stimulus bird was able to move about in the small stimulus chamber and reach through the chamber in the open-wire phases, the stimulus bird possessed a much greater ability to reinforce and punish behavior than the inanimate novel stimulus. From this perspective, a further analysis would be needed to determine the differences in response to the conspecific and novel stimuli. The differences may have been caused by the ability of the conspecific to change the subject's behavior, rather than an issue of novelty versus innate recognition.

In addition to the differences in the amount of time the subject spent near the conspecific and novel stimuli, there were also differences in behavior. The most notable of these differences was the occurrence of allo-preening in the novel condition, and a complete lack of allo-preening in the conspecific condition. In the novel condition, allo-preening occurred a few times in later sessions, after attacks accompanied by the defensive-threat display ended, and after the subject began spending most of the session within 5 cm of the novel stimulus. It is possible that this behavior represented

an unreinforced emergence of allo-preening occurring as a function of loss of fear. A similar emergence of allo-preening was not seen in the conspecific condition, likely because the conspecific always produced some degree of fear. It is also possible that the allo-preening observed in the novel condition was not the same allo-preening behavior that was observed in the human condition. Although the behavior in the novel condition did fall under the same operation definition, and no topographical distinctions were noted, the distinctions between the topographies of attacks in the novel condition indicate that operational definitions may take serious consideration to accurately capture all aspects of the species' natural repertoire.

#### Functions of Attacking and Allo-preening

In the human condition, attacking and allo-preening showed a close relationship. Figure 17 shows that allo-preening and attacking occurred inversely in duration. A strictly topographical analysis of the behavior would propose that the behaviors have different functions. The ethological interpretations would suggest that the topography of the attacks observed in the human condition occurred because of aggression, territoriality, and function to remove a stimulus from the environment (Goodwin, 1983, p. 291), while allo-preening is a social behavior, functioning to maintain social bonds and divert aggressive tendencies of the individual being preened (Goodwin, 1983, p. 301). Despite this ethological distinction, in the present experiment allo-preening and attacking appear to have similar functions.

In the open-wire phase of the human condition, attacking and allo-preening both produced the same consequence. Regardless of the subject's behavior, the human stimulus remained unmoved and consequently, no obvious pattern was discernable. In

the preening and face phase, however, allo-preening received a programmed consequence, while attacking did not. If the subject allo-preened the human hand, the experimenter attempted to gently touch the face and neck of the subject for the duration of the allo-preening. However, even with this additional consequence, allo-preening did not always occur in greater duration than attacks. On some occasions, reciprocated preening was met with a cessation of allo-preening or an occurrence of an attack. On other occasions, the subject switched rapidly between attacking and allo-preening, with no clear predictor of a change in behavior. This suggests that attacking and allo-preening may be functionally similar, or that the behavior definitions used were not accurate enough to completely distinguish between the behaviors.

Although attacking and allo-preening may have functioned similarly in the human condition, two topographies of attacks were observed in the novel condition, suggesting that some attacks may function differently. Several distinctions were seen between attacks in the novel condition. Attacks in earlier sessions occurred with a defensive-threat display while attacks in later sessions did not. With respect to topography, attacks in later sessions more closely resembled attacks to the human stimulus. In addition to the topographical distinction, the earlier attacks generally had shorter durations and longer IRTs than later attacks. The difference in topography and temporal characteristics suggest that the attacks may be functionally distinct. Early attacks may have served the function of avoidance behaviors. The topography of the attack was consistent with that described by Goodwin (1983) as a fearful attack (p. 294). These attacks likely dissipated either because they were not reinforced by removal of the novel stimulus, or because the novel stimulus became less aversive over time. Attacks later



sessions possessed a topography similar to that intra-species territorial aggression (Goodwin, 1983, p. 291). Goodwin suggests that the long holds of the attacks, coupled with pushing and twisting are used to throw a rival from a ledge. The duration and the IRTs of the attacks support the distinctions observed in topography.

#### Conditions Required to Demonstrate Imprinting

In the human condition, reversals between the closed-wire and face phases did not greatly effect the time spent near the human stimulus. However, in both the human and preference conditions, the closed-wire and face phases did greatly affect the behaviors that were emitted. Pecks occurred much more in the closed-wire phase than the face phase. Conversely, consistently high durations of allo-preening and exclusive occurrences of mating solicitations were observed in the face phase.

The lack of social behaviors in the closed-wire phases of the human and preference conditions suggests that the full wire barrier did not allow the full range of social and sexual behaviors to emerge. When appropriate stimulus conditions were presented in the face phase, the subject was then able to display a full range of behavior. Although, the behavior of the subject prior to the experiment was a clear indicator of imprinting to humans, this behavior was not immediately clear within the experimental context. In the experiment, mating solicitations only occurred when the face was presented, and did not occur when only a hand was presented. Although the subject was raised by human hands, and directed social and sexual behavior to human hands, this stimulus alone was not enough to evoke sexual behavior in the apparatus. This suggests that research on sexual imprinting to humans should use methods to determine and present the relevant stimuli, similar to the ones used in the present

experiment. Other solutions include presenting the entire human as in Klinghammer and Hess (1964), or maintaining more controlled imprinting procedures that only allow the subject to come in contact with the intended human stimulus.

The occurrence of sexual behaviors in only specific phases should cause us to reconsider interpretation of data from subjects that display a "failure to imprint." Are these occurrences actually a failure to imprint, or a failure of the methods to detect imprinting? Although we cannot assume imprinting will occur from any given history, the enormous amount of research on the topic should increase our confidence that imprinting will occur, given some early experience. If a procedure does not detect any degree of imprinting, we should first assume that the methods, before assuming that no imprinting occurred in spite of the history.

Another interesting feature of the face phase was the effect it had on the phases that occurred afterwards. In sessions of the human condition preceding the first face phase, the duration of attacking and allo-preening was erratic. The onset of the face phase brought stability to the data, attacks subsided while allo-preening stabilized at higher duration. This stability remained for several sessions after the face phase ended.

A similar effect was observed in the time spent near the conspecific and human stimuli in the preference condition. In sessions preceding the first face phase, the subject divided some time between the conspecific and human stimuli. After the onset of the first face phase, the subject began spending almost the entire session length near the human stimulus. This exclusive preference remained for several sessions after the face phase ended.

The persistence of these trends after the end of the face phase suggests that the effect of the face phase gave new functions to some aspects of the experimental context. This conditioning effect suggests that it may be possible to condition the evocative effect of the face phase not only to another aspect of the imprinted stimulus, but also to a more appropriate stimulus such as the conspecific.

### Mechanisms of Preference

Two reasons for the lack of preference in the open-wire phase and the clear preference in the face phase of the preference condition are suggested. First, the conspecific may be more aversive in the face phase as it is presented with an opening in the wire. In the face phase, the stimulus bird may attempt climb through the wire opening, and may peck or attack the subject. Data from later reversals between the closed-wire and open-wire phases in the conspecific condition support this suggestion.

Second, in the face phase, the human stimulus may be more reinforcing than in the open-wire phase. In the face phase, appropriate stimulation was provided to evoke allo-preening and mating solicitations. Data from reversals between the closed-wire and face phases in the human condition support this suggestion. The reinforcing effect of the face phase may be derived through some form of automatic reinforcement, or a natural reinforcer such as proximity. These types of reinforcers have been suggested by other researchers (Hoffman & Ratner, 1973; Peterson, 1960).

In every session of the preference condition, the subject is in a choice situation. The subject may approach the stimulus that produces the greater overall reinforcement, avoid the stimulus that produces the greatest aversive stimulation, or some degree of both. Carrigan and Sidman (1992) use the terms “select” and “reject” to describe these

types of behaviors. Subjects are said to select a stimulus if they respond to it due to a history of positive reinforcement, while they are said to reject a stimulus if they respond to a different stimulus in order to avoid the rejected stimulus. In the present experiment, the subject responds nearly equally in the closed-wire phase, suggesting approach to either stimulus is reinforced nearly equally. However, in the face phase, the subject appears to be selecting the human stimulus, or rejecting the conspecific stimulus. Although the data clearly suggests these contingencies occurred, it is difficult to distinguish the effect of one contingency from another. Carrigan and Sidman (1992) suggest that it can be difficult to distinguish between selecting and rejecting behaviors, because both lead to the same response and both are reinforced. Further research would be needed to gain a detailed understanding of these kinds of contingencies and how they operate in experiments and the natural environment.

The lack of preference in the closed-wire phase of the preference condition has been described as dithering in sexual imprinting experiments with finches (Hollis et al. 1991; ten Cate, 1986, 1987). Dithering, if stable, is said to indicate imprinting to multiple stimuli (ten Cate, 1986). The subject in the present experiment appears to be a “ditherer” in the closed-wire phase. The behavior is certainly stable through the experiment even after several phase changes. However, in the face phase, the subject demonstrated a clear preference, and would not be considered a ditherer. This clear and immediate control over behavior suggests that changes in methods may produce orderly behavior in subjects that do not initially show clear preferences.

Research in other areas suggests some methods that may produce distinct preferences. With human subjects, several researchers have noticed emergence or

reversals in preferences for reinforcers occurring as the response requirement to obtain the reinforcers increases (Deleon, Iwata, Han-Leong, & Worsdell, 1997; Tustin, 1994). Tustin (1994) suggests that preferences are not static properties, and instead are affected by the response requirement, and availability and quality of alternative reinforcers. The suggestions on preference assessments in humans could easily be translated into useful methods to study sexual imprinting in birds. For example, if presentation of stimuli were contingent on some behavior, then increases in requirements of these behaviors may show an emergence of preference. Increases the requirement of behaviors such as key pecks would present a more traditional approach, while increases in requirements of in other behaviors such as travel time, or number of song phrases may present a more ecologically valid approach.

#### Imprinting: Mechanism or Description

The present experiment shows that testing stimulus conditions is very relevant to the study of imprinting. The face phase consistently produced sexual behaviors and a strong preference for human over conspecific stimuli. However, the closed-wire phase consistently produced no sexual behavior, and an unclear preference. The control these phases have on behavior suggests that different operant contingences may be in effect during each phase. In the closed-wire phase, very few behaviors can be reinforced or punished by either stimulus, resulting in a lack of behavior or preference. In the face phase, the human stimulus is able to reinforce more behavior through proximity to an aspect of the imprinted stimulus that is more predictive of reinforcement. At the same time, the conspecific is able to punish more behaviors through pecks and attacks to the subject. These operant contingencies are likely the cause of the differential responding

to stimuli and the distinction between phases. Considering this, imprinting may not be a special kind of learning.

With respect to sexual behaviors, sexual imprinting is thought to be the mechanism for both the development and maintenance of sexual preference. However, if we consider the concepts of other researchers, operant contingencies may explain the acquisition and maintenance of sexual preference. First, consider that social and sexual behaviors will emerge to stimuli that do not evoke fear (Hoffman & Ratner, 1973). These behaviors may be reinforced by naturally occurring reinforcers such as proximity. Second, consider that newly hatched birds are fearless (Sluckin, 1973, p. 85), that fear of novel stimuli arises at a young age (Hess, 1959), and that fear prevents social and sexual responding to novel stimuli (Hess, 1959). If these behaviors never occur, they cannot be captured and maintained by a naturally occurring reinforcer. Other researcher's work suggests that, early in life, social and sexual responses to some stimulus will emerge and be reinforced, while later in life, these responses will not develop to new stimuli and thus cannot be reinforced. In this way operant contingencies can explain the development of sexual preferences.

Additionally, much of the maintenance of sexual preferences can be explained by operant mechanisms. Once an animal sexually responds to a stimulus and receives some reinforcing consequence, it will likely continue to respond to this stimulus. An animal may simultaneously learn to avoid any stimuli that are associated with aversive stimulation, and thus will never have the opportunity to respond sexually to this stimulus. Working together, these two operant processes have the effect of maintaining sexual responding to one stimulus while preventing sexual responding to another.

With these concepts in mind, the word imprinting is not needed to explain sexual preference. This suggests that imprinting is better suited as a description for these events while further research is conducted to discover the specific operant contingencies involved in the development and maintenance of social and sexual behavior.

Table 1

*Repeating Pattern of Order of Sessions*

Order	Day 1	Day 2	Day 3	Day 4
First	Alone	Alone	Alone	Alone
Second	Novel	Novel	Human	Conspecific
Third	Human	Conspecific	Conspecific	Human
Fourth	Conspecific	Human	Preference	Preference
Fifth	Preference	Preference	Novel	Novel



Table 2

*Number of Human Sessions Beginning with Pecks and Attacks*

Phase	Sessions beginning with a peck	Sessions beginning with an attack
Closed-wire	20	7
Open-wire	3	5
Preening	2	12
Face	4	13

Table 3

*Average Latency to First Behavior in Human Sessions*

Phase	Average latency to the first peck	Average latency to the first attack
Closed-wire	43	16
Open-wire	10	8
Preening	10	8
Face	18	12

Table 4

*Average Time Spent Near Stimulus Chambers Across Sessions*

Condition	Within 20 cm		Within 5 cm	
	Average	SD	Average	SD
Alone: One Chamber Open	161	62	115	67
Alone: Both Chambers Open	76	52	76	52
Conspecific	211	83	121	93
Novel: Sessions 1-10	136	86	0	0
Novel: Sessions 11-20	247	46	211	50
Human	255	30	221	44
Preference: Conspecific Stimulus	66	79	44	62
Preference: Human Stimulus	188	92	159	93

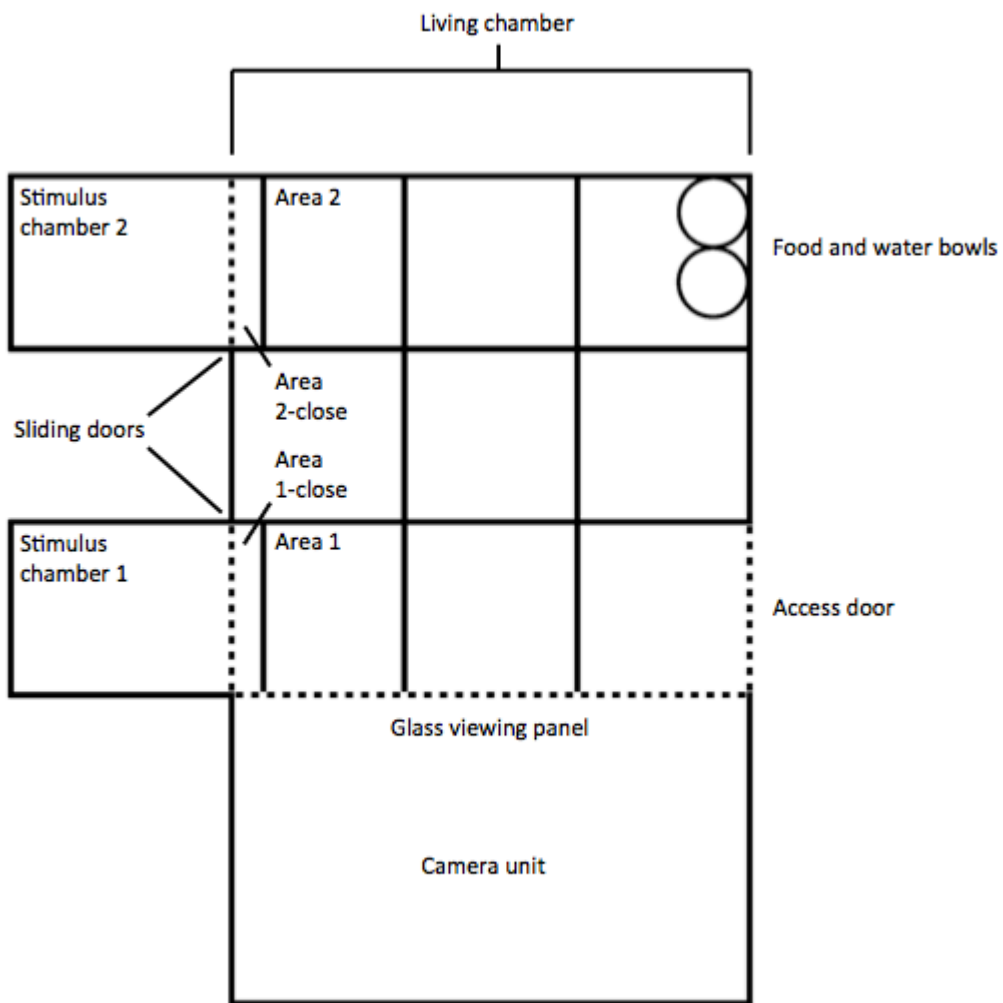
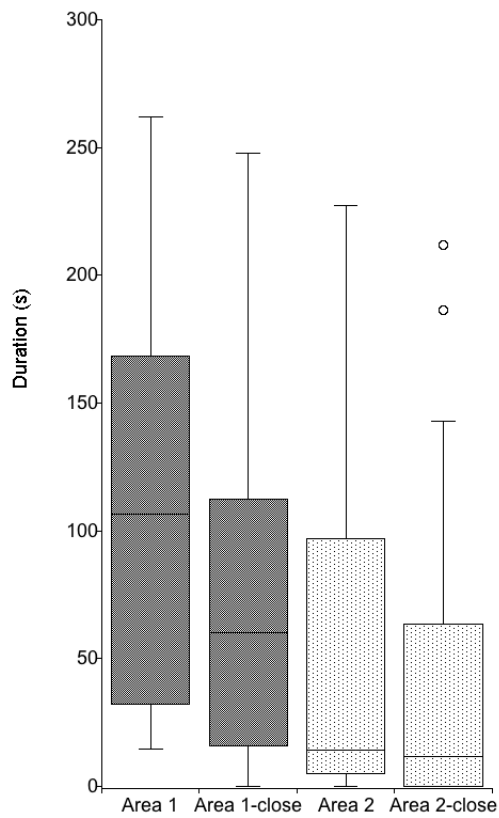


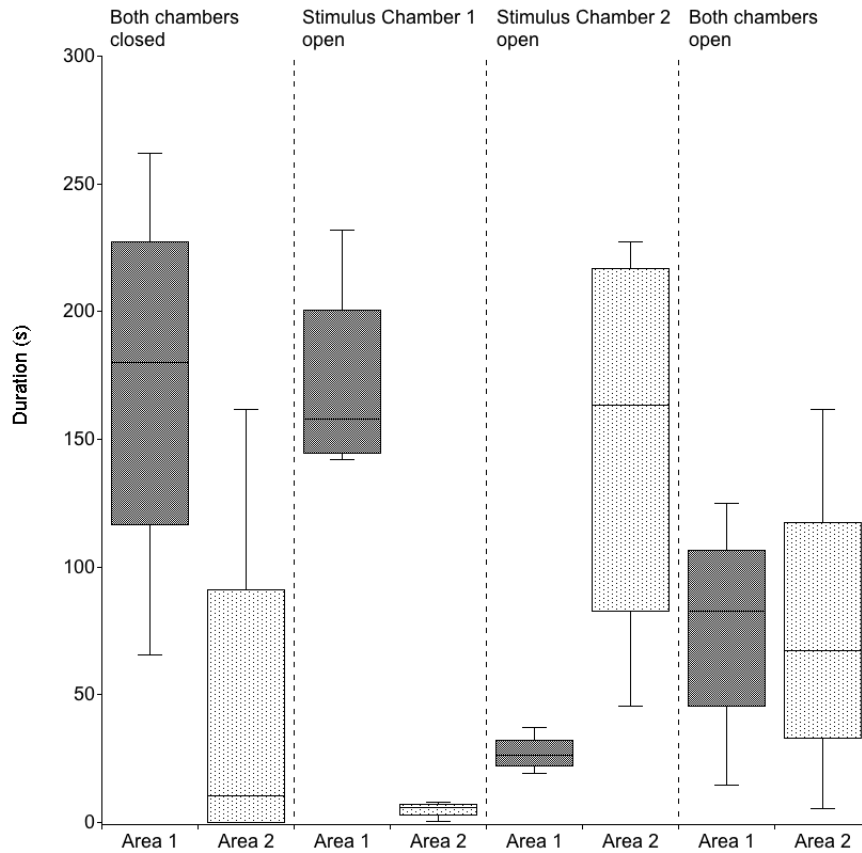
Figure 1. Diagram of the apparatus.



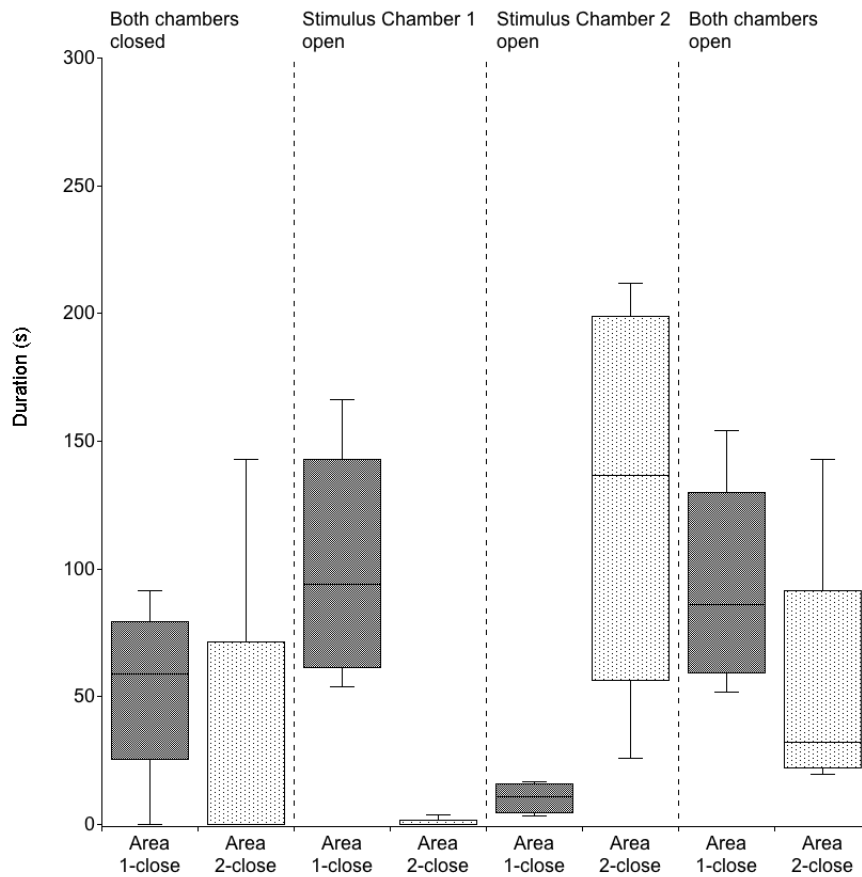
*Figure 2.* Image of the apparatus taken from the attached camera.



*Figure 3.* Range of duration the subject spent in each area in the alone condition. The box plots illustrate the median, upper quartile, lower quartile, maximum, minimum and outliers in the range of data collected.



*Figure 4.* Range of duration the subject spent in Area 1 and Area 2 in the alone condition when both stimulus chambers were opened, each chamber was opened individually, and when both stimulus chambers were closed. The box plots illustrate the median, upper quartile, lower quartile, maximum, minimum and outliers in the range of data collected.



*Figure 5.* Range of duration the subject spent Area 1-close and Area 2-close in the alone condition when both stimulus chambers were opened, each chamber was opened individually, and when both stimulus chambers were closed. The box plots illustrate the median, upper quartile, lower quartile, maximum, minimum and outliers in the range of data collected.



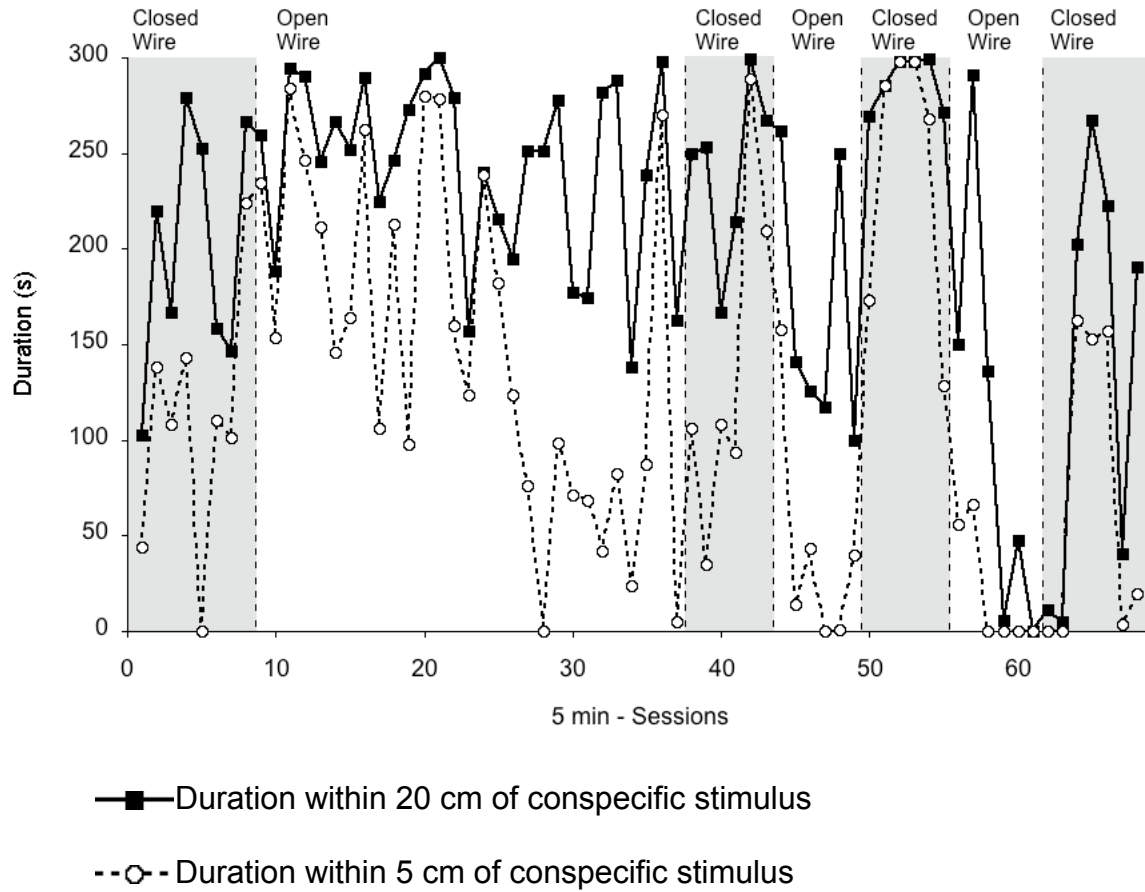


Figure 6. Duration the subject spent near the conspecific stimulus in the conspecific condition.

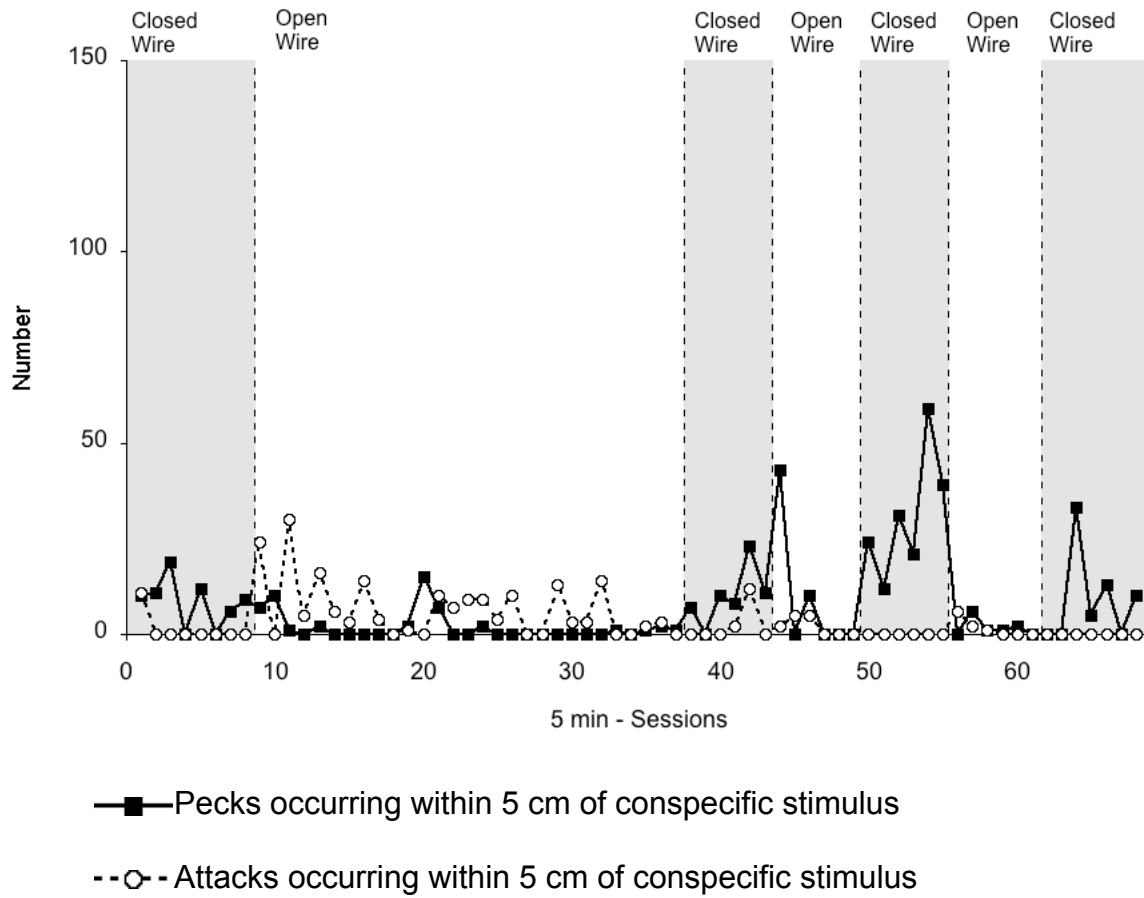


Figure 7. Pecks and attacks occurring near the conspecific stimulus in the conspecific condition.

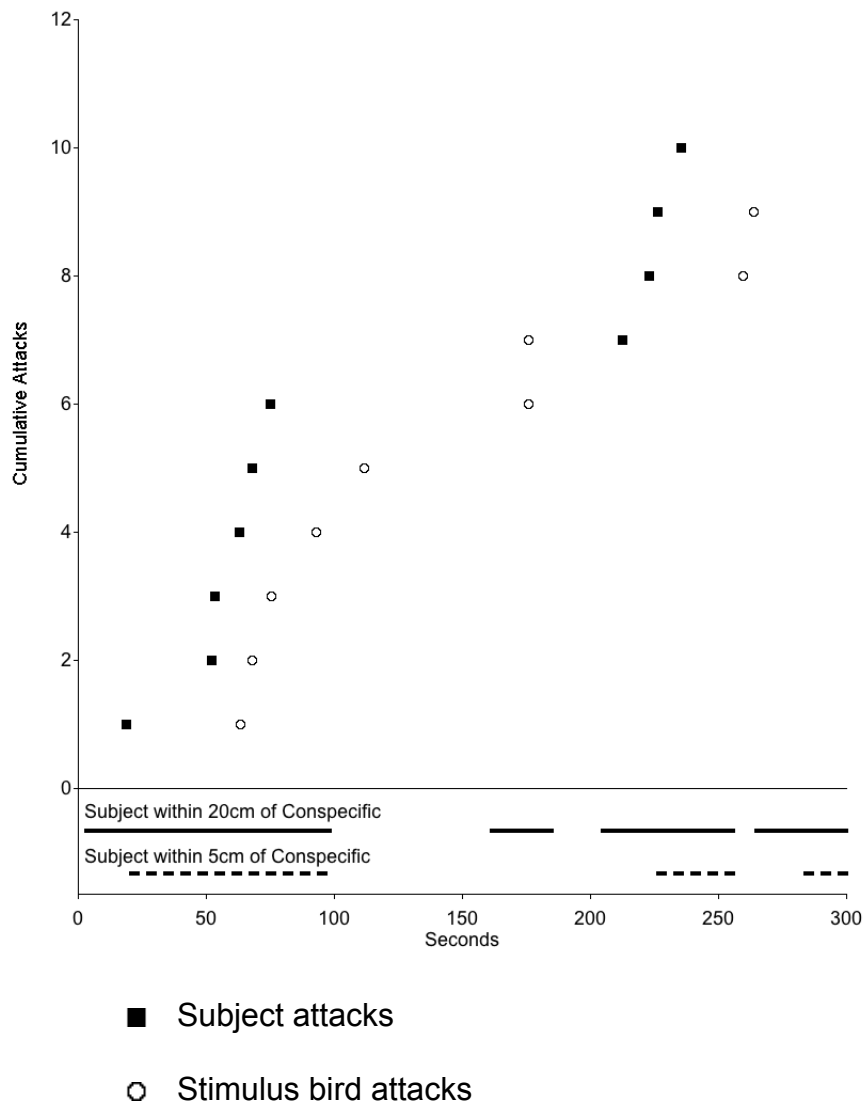


Figure 8. Cumulative attacks of the subject and the stimulus bird, and time the subject spent near the stimulus bird in Session 26 of the conspecific condition.

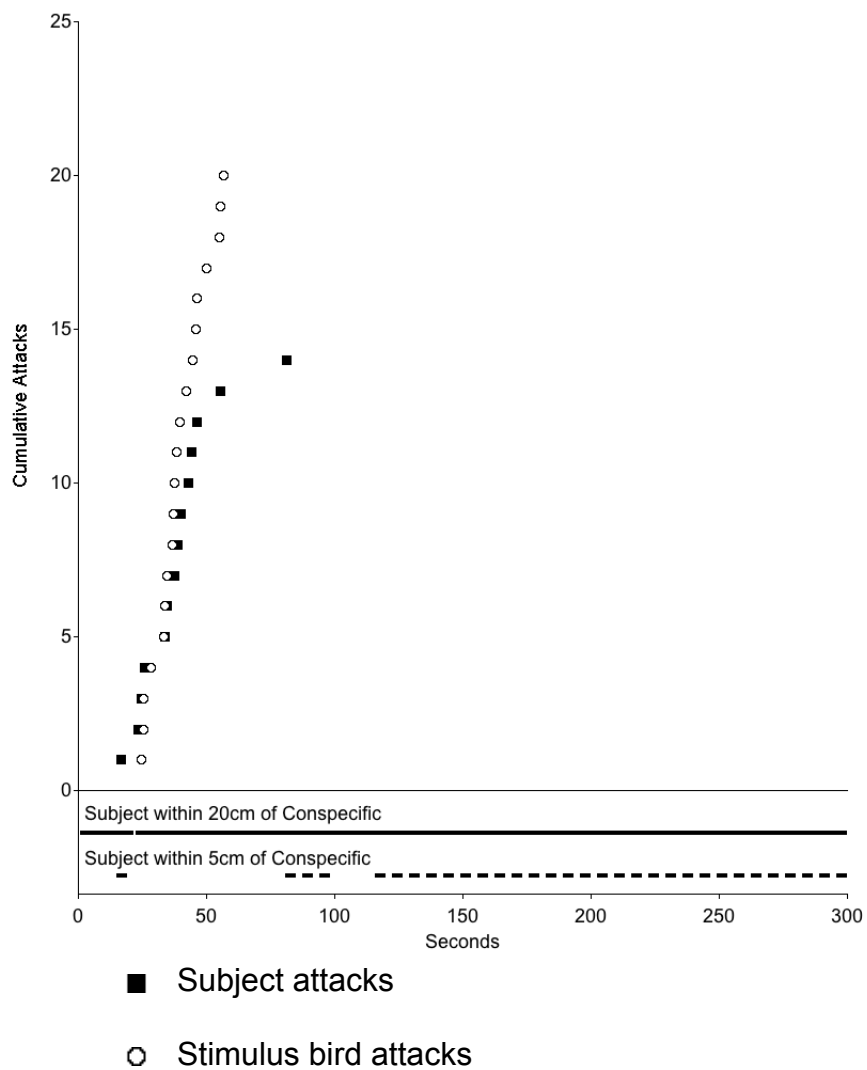


Figure 9. Cumulative attacks of the subject and the stimulus bird, and time the subject spent near the stimulus bird in Session 32 of the conspecific condition.

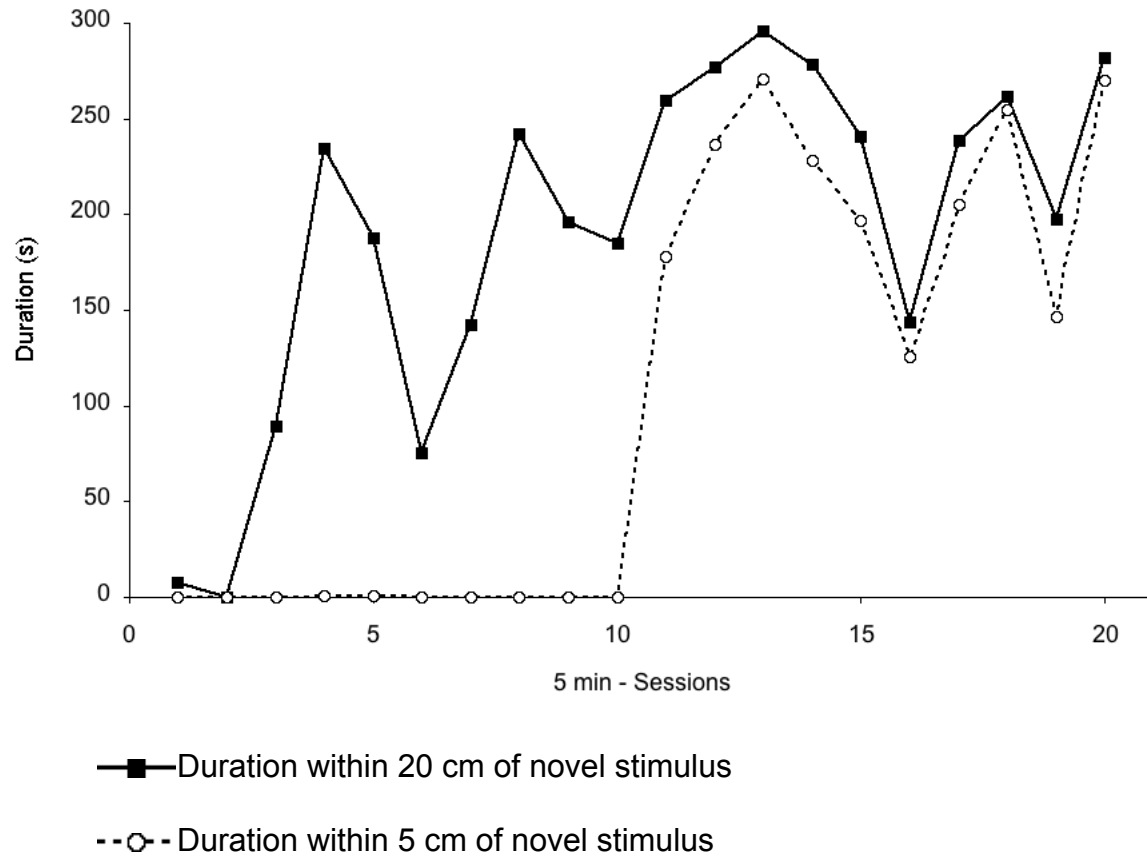


Figure 10. Duration the subject spent near the novel stimulus in the novel condition.

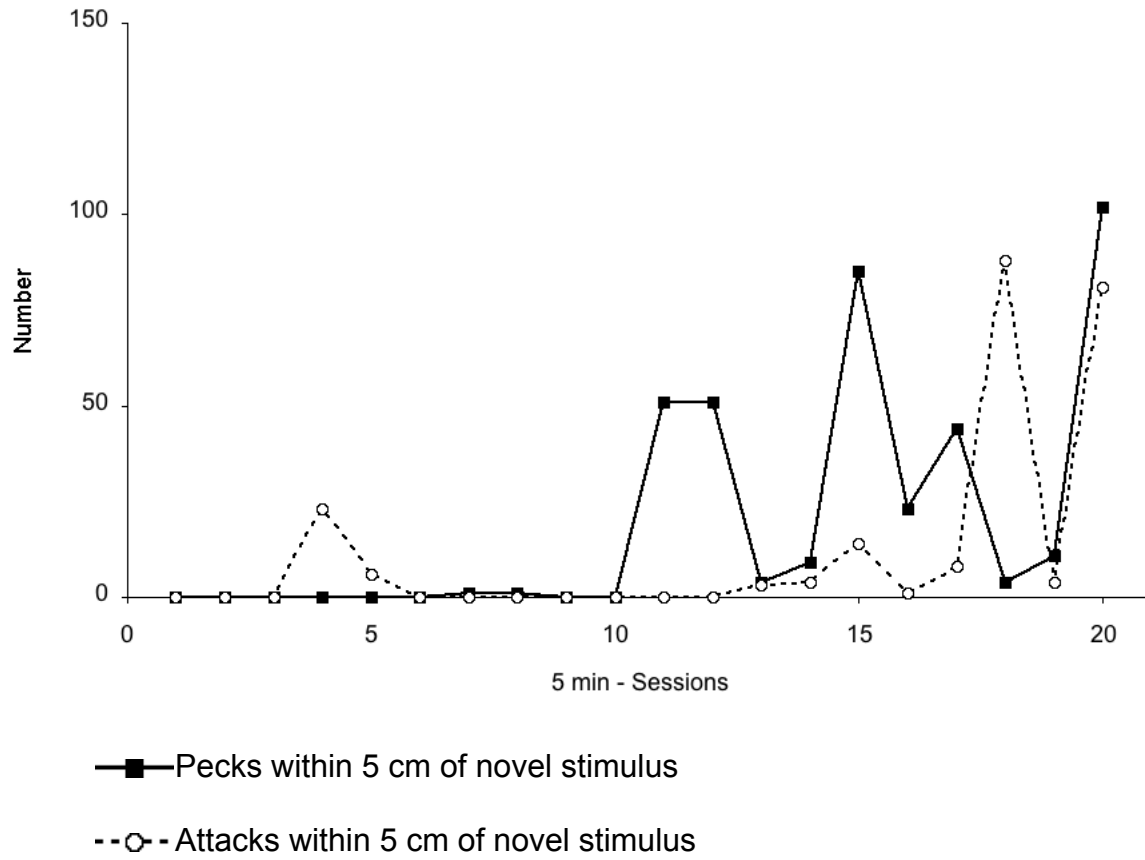


Figure 11. Pecks and attacks occurring near the novel stimulus in the novel condition.

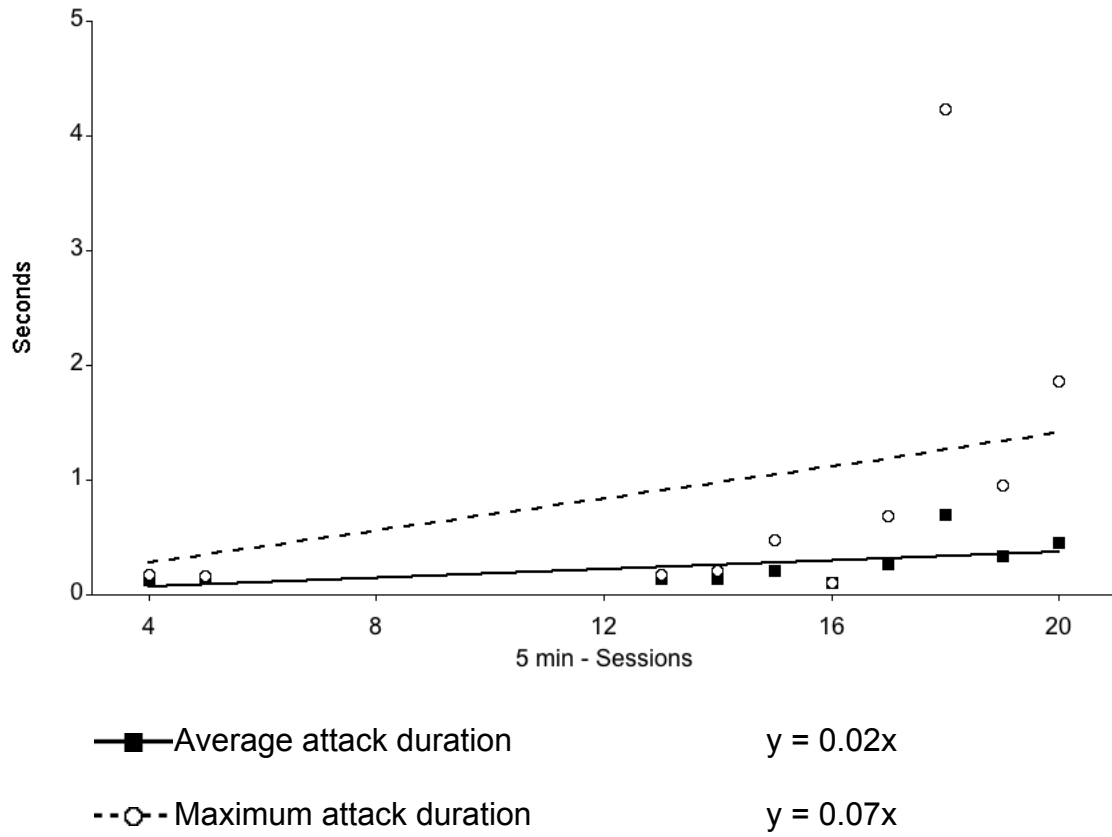


Figure 12. Average and maximum duration of attacks in the novel condition.

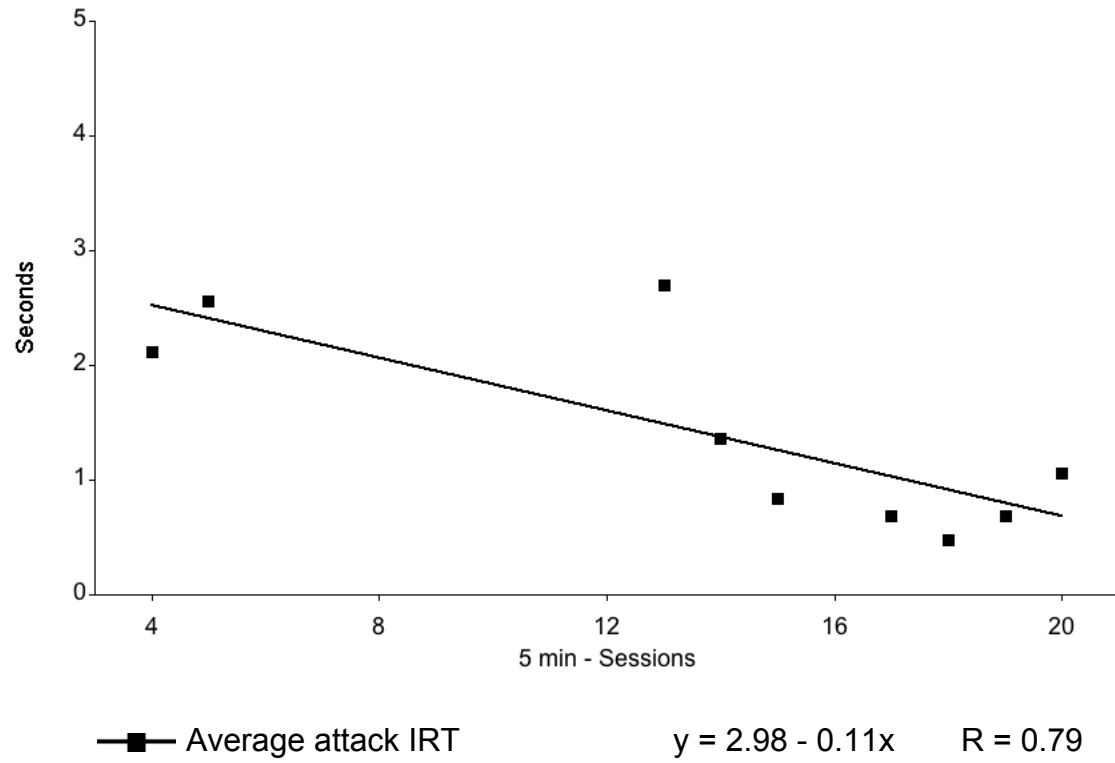


Figure 13. Average attack IRT in the novel condition.



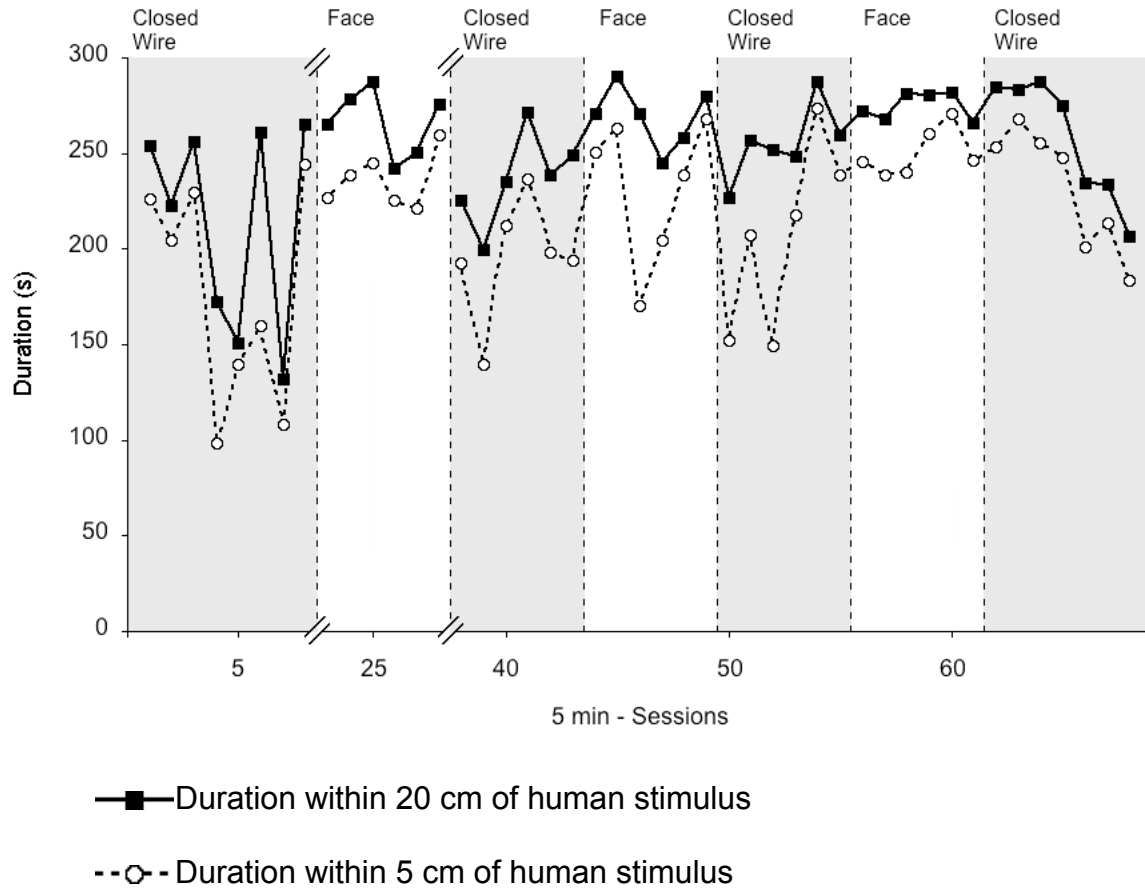


Figure 14. Duration the subject spent near the human stimulus in the closed-wire and face phases of the human condition.

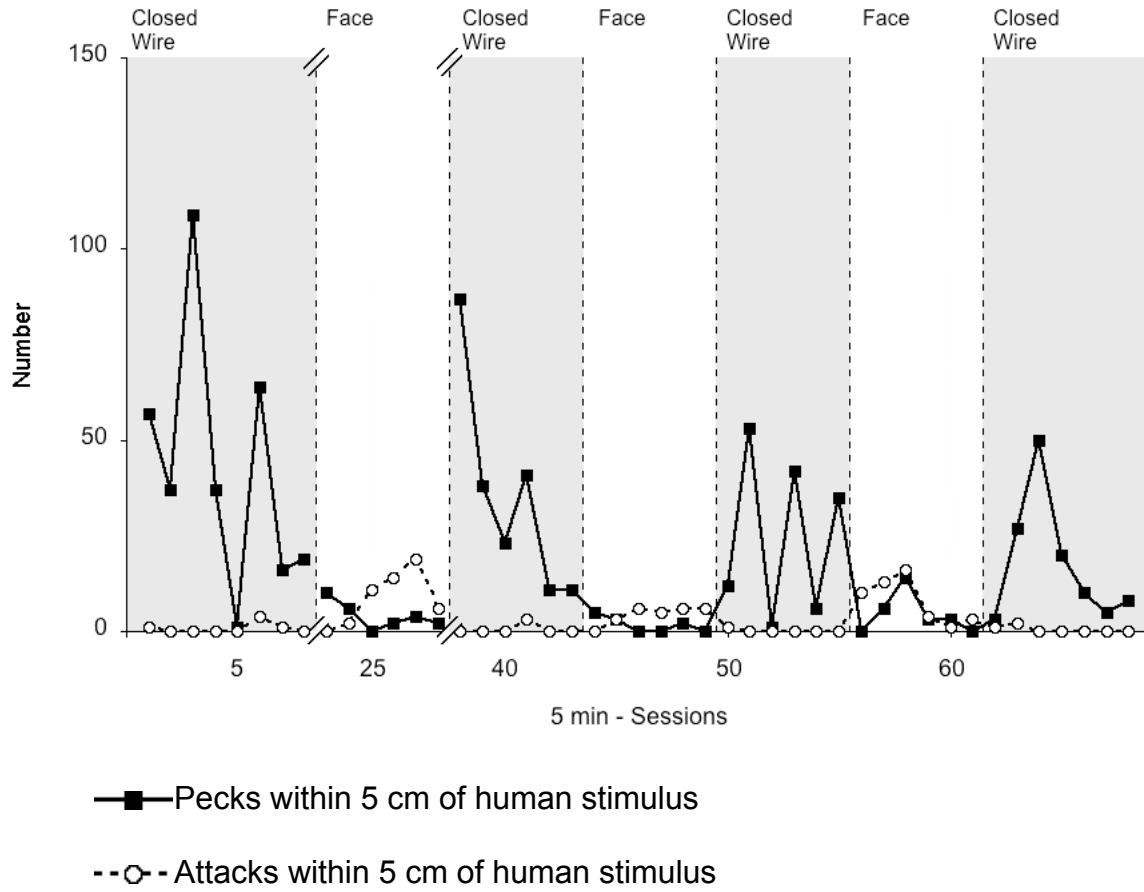


Figure 15. Pecks and attacks occurring near the human stimulus in the closed-wire and face phases of the human condition.

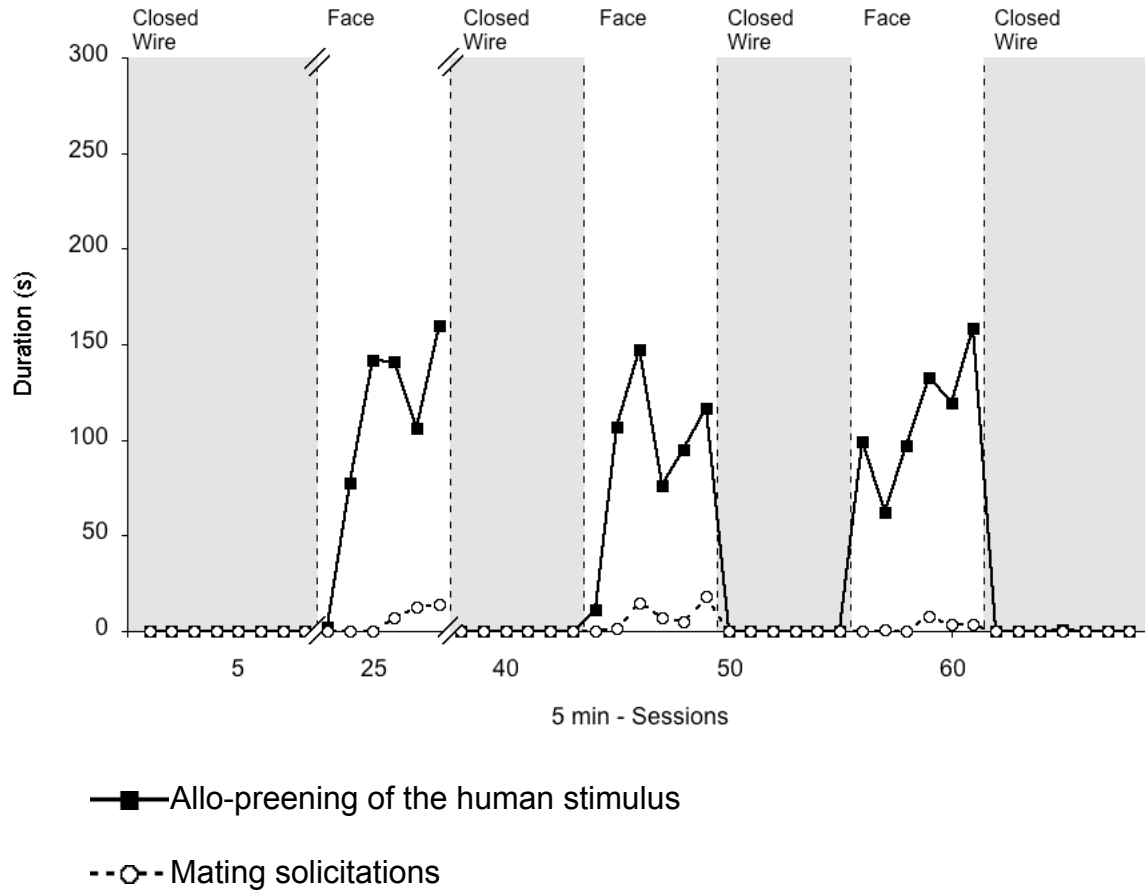


Figure 16. Duration of allo-preening and mating solicitations in the closed-wire and face phases of the human condition.

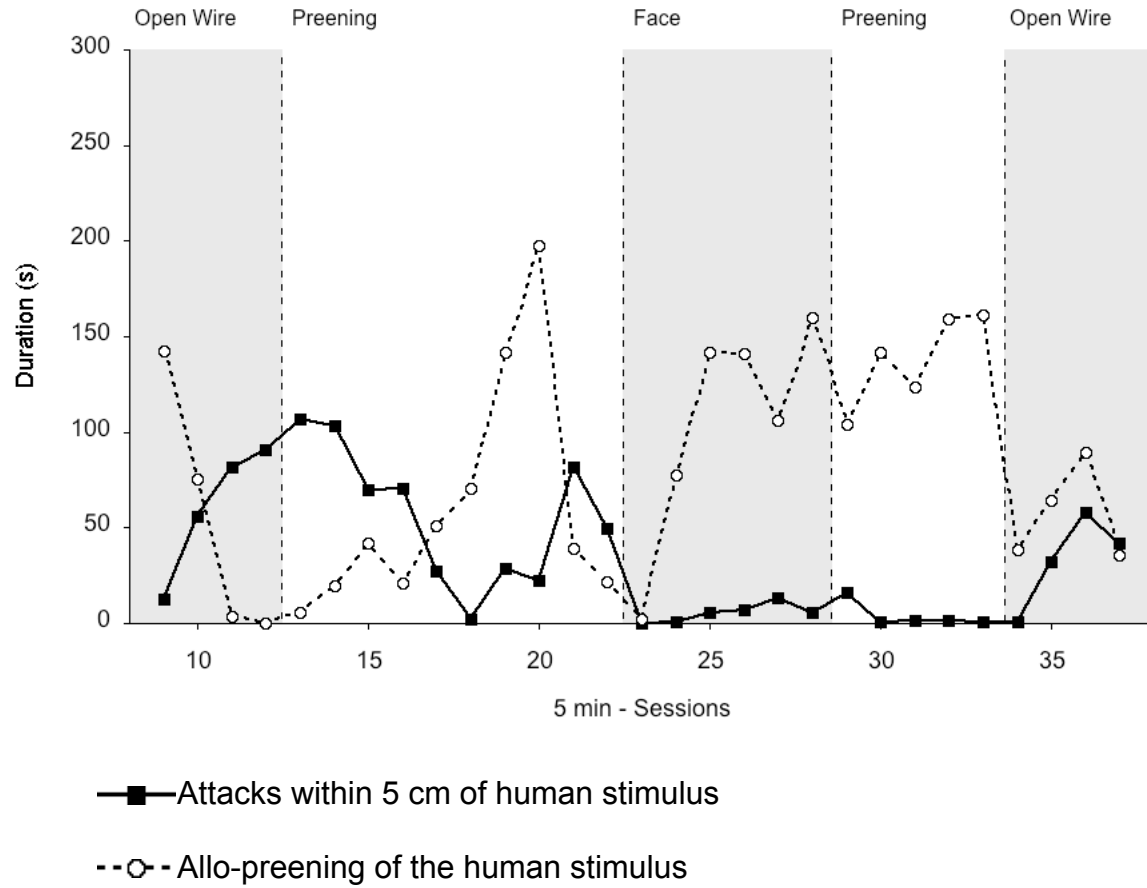


Figure 17. Duration of attacks and allo-preening in the closed-wire and preening phases of the human condition.



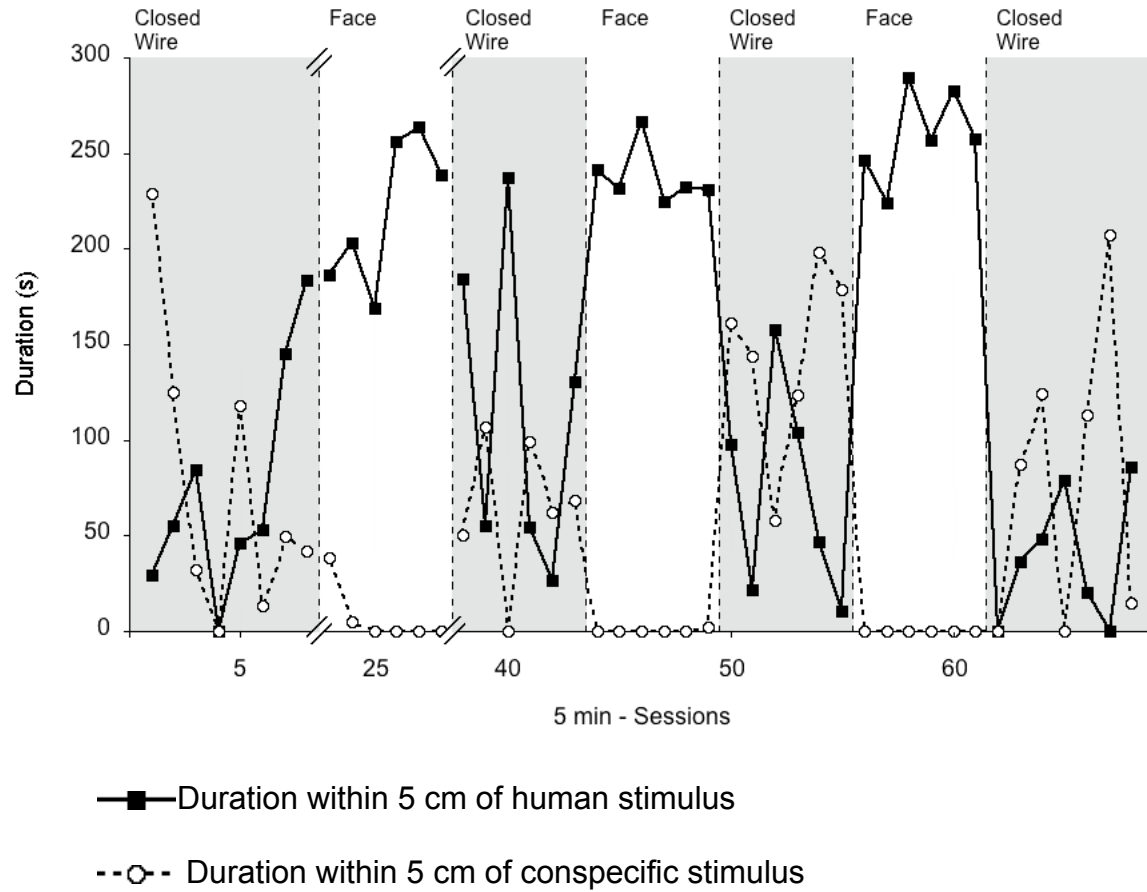


Figure 19. Duration the subject spent within 5 cm of the human stimulus and conspecific stimulus in the closed-wire and face phases of the preference condition.

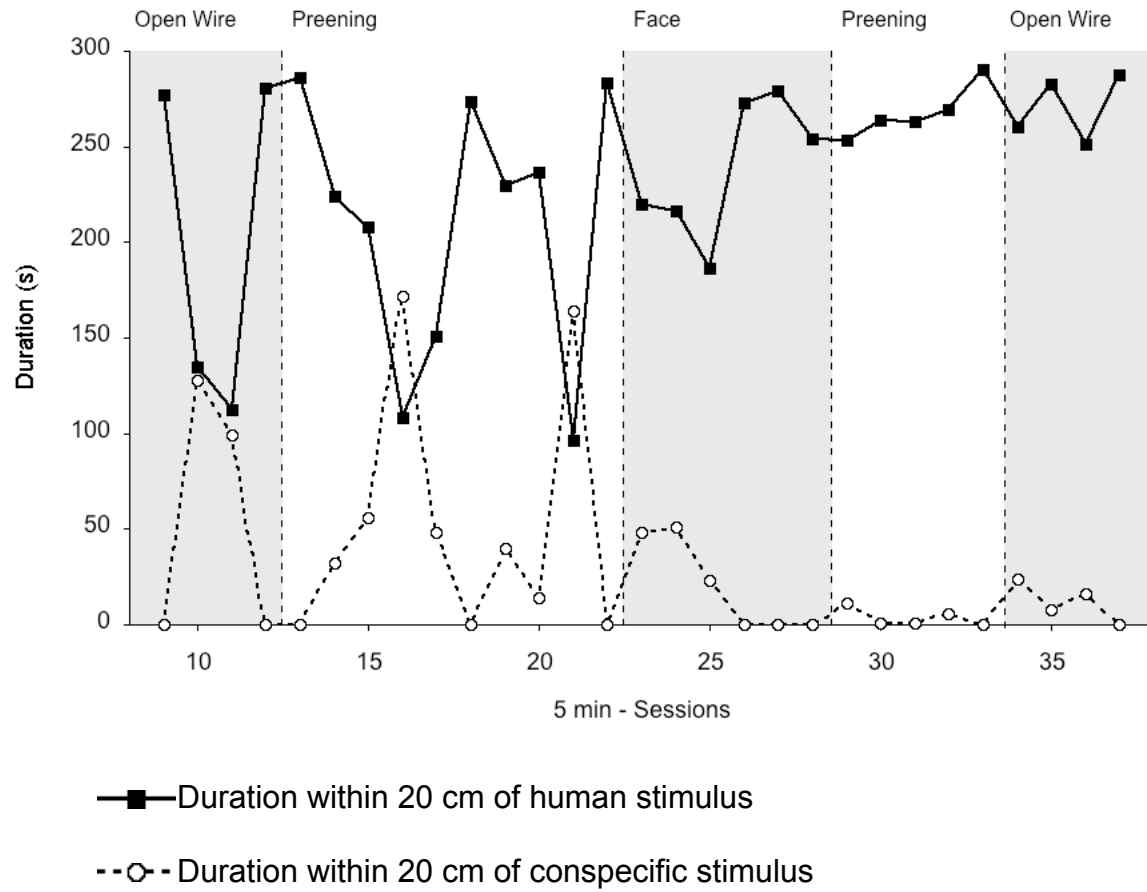


Figure 20. Duration the subject spent within 20 cm of the human stimulus and conspecific stimulus in the open-wire and preening phases of the preference condition.

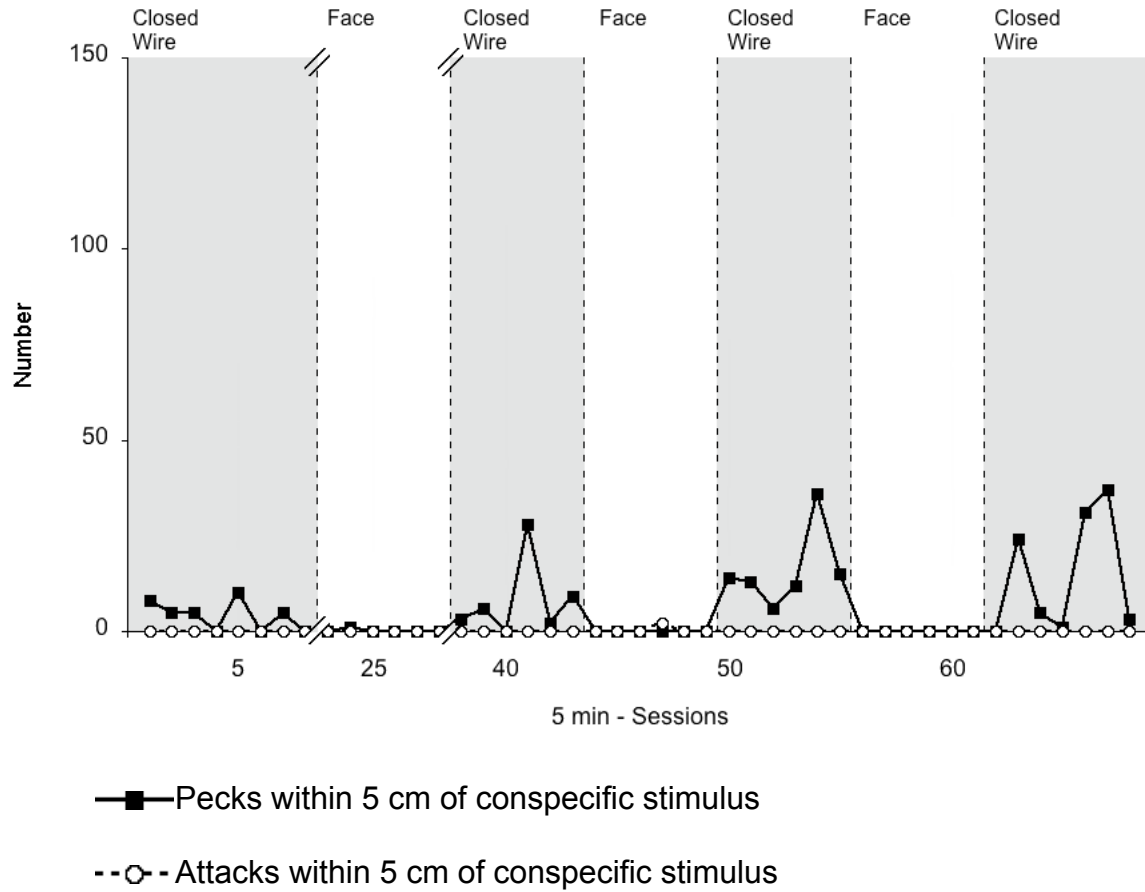


Figure 21. Pecks and attacks occurring near the conspecific stimulus in the closed-wire and face phases of the preference condition.



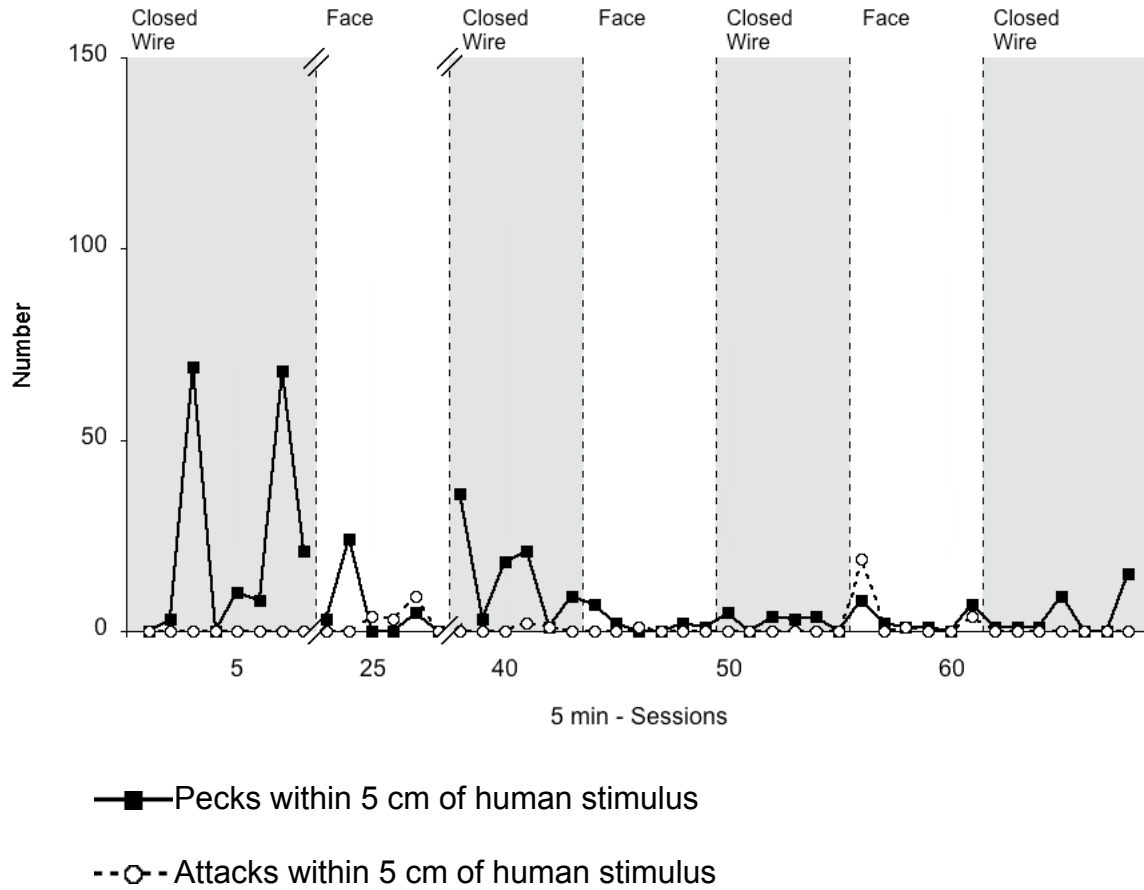


Figure 22. Pecks and attacks occurring near the human stimulus in the closed-wire and face phases of the preference condition.

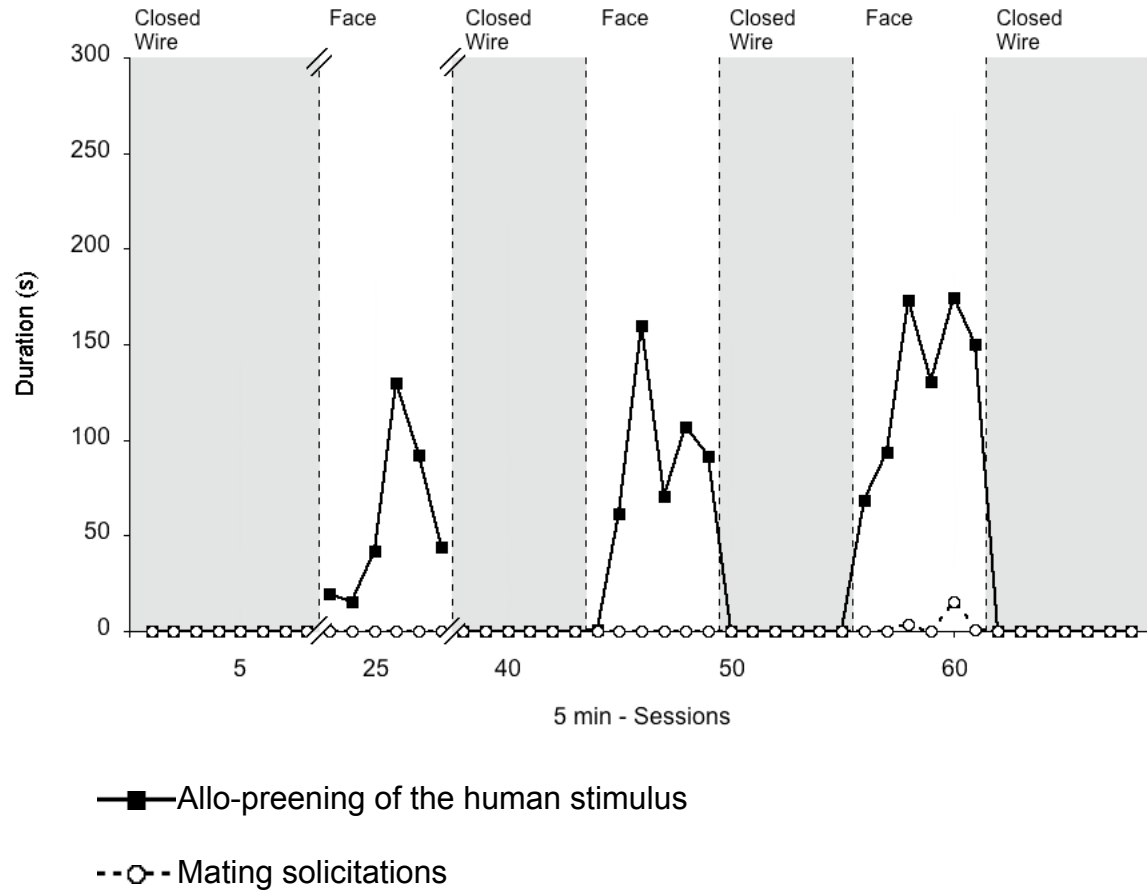


Figure 23. Duration of allo-preening and mating solicitations directed to the human stimulus in the closed-wire and face phases of the preference condition<sup>d</sup>.

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