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Individual Recognition in Japanese Quail Requires Physical and Behavioral Cues

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Individual recognition is a complex social learning process in which idiosyncratic characteristics of a conspecific are learned and later used to discriminate this conspecific from others. Many social species of birds appear to be capable of individual recognition. However, it is possible that at least under some circumstances these and other species discriminate conspecifics not based on individual recognition but instead, by recognizing them as members of one or more social categories. Many references to individual recognition in the literature have neglected to address this distinction. For example, Riters and Balthazart (1998) reported that male quail were capable of recognizing individual females with which they had and had not copulated, but their experimental design may have unintentionally created two social categories of females (sexually receptive and non-receptive). The present set of experiments replicated Riters' and Balthazart's findings (Experiment 1) and then tested male quail for their ability to recognize females based on physical cues only (Experiment 2), physical and behavioral cues (Experiment 3), and the social categorization cues associated with female receptivity (Experiment 4). The results suggested that male quail are capable of recognizing individual females with which they have and have not copulated, but this recognition is not based on physical, non-sexual, or sexual receptivity behaviors in isolation. Instead, individual recognition occurred only when the males were able to utilize all of these potentially distinctive female attributes in combination. The results also suggested that female receptivity responses may be unique and idiosyncratic, varying along one or more dimensions.

Recognition of conspecifics is important to the survival and reproductive success of many species of social animals. The maintenance of dominance hierarchies, territories, pair-bonds, and parent-offspring relationships all depend upon remembering information associated with specific individuals. The recognition of one particular individual of an animal's own species is referred to as individual recognition. This specific form of conspecific recognition requires that the observer process and remember the idiosyncratic cues of a conspecific (Gheusi, Goodall, & Dantzer, 1997; Sherman, Reeve, & Pfennig, 1997). The evolution of individual recognition has been documented in wide variety of animals including insects (Tibbetts, 2002), fish (Johnsson, 1997) rodents (Johnston & Bullock, 2001), aquatic invertebrates (Karavanich & Atema, 1998), horses (Proops, McComb, & Reby, 2008), dolphins (Janik, Sayigh, & Wells, 2006) and both non-human and human primates (Seyfarth & Cheney, 2009).

The ability to recognize individuals also has evolved in a variety of avian species including spectacled parrotlets (Wanker, Apein, Jennerjahn, & Waibel, 1998), penguins (Clark, Boersma, & Olmsted, 2006), pigeons (Watanabe & Ito, 1991) chickens (Ryan, 1982; Ryan & Lea, 1994), and flycatchers (Lovell & Lein, 2005). However, the specific signature traits that form the basis of individual

recognition vary among these birds. Penguins and spectacled parrotlets, for example, recognize individuals based on vocalizations, (Jouventin, 1982; Wanker et al., 1998; Wanker & Fischer, 2001) while turnstones and pigeons rely more on idiosyncratic visual and behavioral cues (Jitsumori, Natori, & Okuyama, 1999; Whitfield, 1987).

Many adaptive social behaviors rely on an animal's ability to recognize individual conspecifics (see Tibbetts & Dale, 2007 for a review). In territorial species, for example, it allows animals to discriminate neighbors from non-territorial floaters (Temeles, 1994). It also can play an important role in the maintenance of dominance hierarchies, reducing the need for aggressive interactions once the hierarchies have been established (Benard & Burk, 1979). In mating interactions, the ability to recognize individuals of the opposite sex can help maximize outbreeding.

Although it is pervasive and highly adaptive (Seyfarth & Cheney, 2009), individual recognition in social situations is a challenging cognitive task. It requires that animals attend to, remember, and then accurately recall the idiosyncratic characteristics of the individuals with which they interact. The challenge becomes more difficult as the size of the social group increases so some species have evolved alternative identification strategies to compensate. For example, under conditions when individual recognition is not possible, large flocks of domestic hens shift from a dominance hierarchy system based on actual aggressive encounters to a more passive social organization, likely making use of reliable markers highly correlated with dominance such as large body and comb size (Pagel & Dawkins, 1997). Situations like this when animals rely on species typical physical or behavioral characteristics to successfully interact with conspecifics require a simpler form of learning, social categorization.

Unlike individual recognition, social categorization requires that animals need only recognize the species-typical characteristics of particular categories and then identify these characteristics in the individuals they encounter (Gheusi et al., 1997; Payne, Payne, Rowley, & Russell, 1991; Tibbetts & Dale, 2007). The unique attributes of individual conspecifics within each category may in fact never be learned or even attended to. There is substantial evidence that birds recognize many social categories including familiarity (Bradshaw, 1992; Dawkins, 1982), dominance (King, 1965; Syme, Syme, & Barnes, 1983), sex (Domjan & Nash, 1988), and kin (Bateson, 1982). For social categorization to occur, species typical characteristics must be highly stereotyped within the individuals of each social class and vary noticeably between social classes (Wanker & Fischer, 2001). Under some circumstances, a categorical distinction such as male–female, or dominant–submissive, is sufficient to successfully interact with a particular individual even during a first encounter. Social categorization is likely to occur in species that maintain relatively simple social structures where individual recognition is not necessary (Jitsumori et al., 1999) or in very large groups of animals where individual recognition is not possible.

Individual recognition and social categorization can be easily confused, especially in the study of non-human behavior. For example, Ryan and Lea (1994)

used a dishabituation procedure in an attempt to demonstrate individual recognition in pigeons. Subjects were repeatedly exposed to a stimulus bird for short periods of time. Once the subject bird's agonistic behaviors decreased the presentation a novel stimulus bird caused the agonistic behaviors to return. The authors concluded that the return of agonistic responding was evidence of individual recognition (Ryan & Lea, 1994) even though sorting the stimulus pigeons into familiar and unfamiliar categories would have resulted in the same behavior. Other researchers have tested for individual recognition by presenting visual or auditory stimuli associated with a mate or a stranger, creating a similar familiarity confound (e.g., Clark, Boersma, & Olmsted, 2006).

Riters and Balthazart (1998) conducted a similarly ambiguous experiment using male Japanese quail as subjects and live female quail as discrimination cues. Males were permitted visual access to a female before being allowed to copulate with her. The same males also were exposed to a different female with which they were not permitted to copulate. The males spent significantly more time viewing the copulation female, a result suggestive of individual recognition. However, the copulation females may have displayed sexual anticipatory squatting responses that distinguished them from the non-copulation females. If this occurred, a categorization strategy using female sexual receptivity responses also would have allowed the males to successfully discriminate between the two females. Therefore, as in the Ryan and Lea (1994) experiment, the results of the Riters and Balthazart (1998) experiment may not have represented individual recognition.

The present experiments were conducted to identify the mechanisms by which male Japanese quail discriminate between the females with which they have and have not copulated. Evidence of true individual recognition would suggest a level of cognitive complexity not yet documented in this species. The experiments also were designed to provide information about the mating strategies used by male quail in their natural environment, and which particular female cues are most salient to males as they make their mating decisions.

Experiment 1 replicated the procedures used by Riters and Balthazart (1998) with slight modifications to regulate the male subjects' familiarity with each stimulus female. Experiment 2 used taxidermic models of female quail to examine whether males were capable of recognizing females based only on their physical characteristics. Experiment 3 examined the ability of males to recognize live females based on their idiosyncratic, non-sexual characteristics. The design of Experiment 4 tested the extent to which males utilize social categorization to regulate their social interactions. In this experiment the male subjects had to discriminate between live females based on the presence or absence of sexual anticipation behaviors.

General Method

Subjects and Stimulus Birds

Forty-eight male Japanese quail served as subjects and 58 female Japanese quail served as stimulus birds. The birds were raised from eggs randomly selected from a colony of quail maintained at The University of Texas and housed in mixed sex brooders until 30 days of age. The birds were

then sexed and transferred to smaller wire cages (GQF Manufacturing, 55 cm long x 25.4 cm wide, with a sloping floor creating a height of 20 cm at the back and 25.5 cm at the front of the cage). Males were housed individually and females were housed in pairs.

Potential male subjects were screened for abnormally low sexual motivation with a 5 min copulatory pretest at 6 month of age. Only males that achieved cloacal contact during the pre-test were selected as subjects. The copulatory pretest was the only sexual experience the male subjects had prior to beginning the experiments and none of the males were previously involved in any other experiments. Sexually and experimentally naïve female quail that were at least 4 months of age served as the conditioned and unconditioned stimuli.

The lights in the colony and experimental rooms were set on a 16 hr light: 8 hr dark cycle. This simulation of long days allowed the birds to remain in reproductive condition throughout the experiment. Food (Purina Poultry Chow) and water were available at all times.

Apparatus

Twelve identical experimental chambers were used (Figure 1). Each subject was housed in a large test chamber (90 cm wide x 90 cm deep x 50 cm high). The top, bottom, back, and side walls of each large test chamber were constructed of sealed plywood. The front of the chamber was made of wire mesh to allow for behavioral observations and hinged to act as a service door. Two side-by-side stimulus chambers, also constructed of sealed plywood, rested on a sliding track that was mounted just outside the large test chamber. They were used for presentation of the conditioned and unconditioned stimuli. Each stimulus chamber measured 20 cm wide x 15 cm deep x 15 cm high. The stimulus chamber wall that faced the large test chamber was made of opaque Plexiglas. It could be removed to reveal the contents of the stimulus chamber. A doorway (14 cm wide x 16.5 cm high) with a guillotine-style door (stimulus door) separated the large test chamber and the small stimulus chambers. The door contained a narrow Plexiglas viewing window (1.3 wide x 15.2 cm high) that allowed visual access into only the stimulus chamber that was aligned with the doorway. During most experiments the CS presentations began by removing the stimulus chamber's opaque Plexiglas wall so that the subject male could view the CS through the viewing window. Sliding the stimulus chambers and/or raising the stimulus door allowed for the presentation of the unconditioned stimulus. The configuration of the test enclosures did not permit the experimenters to regulate the degree to which the subject and stimulus birds could hear one another. Although the vocalizations in this species are sex-specific there is no evidence that either sex uses vocal cues to discriminate individuals.
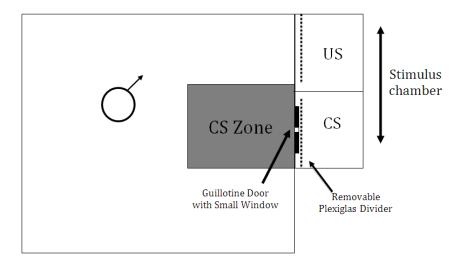

Figure 1. Experimental Apparatus – Stimulus chambers slid along a track so that the contents of only one of the stimulus chambers (CS or US) was visible through the window in the guillotine door.

Procedure

One week prior to starting an experiment, subjects were housed in the large test chambers to facilitate habituation to the testing environment. Food and water were available in the test chambers at all times. The experiments utilized a Pavlovian discrimination procedure in which one conditioned stimulus (CS+) was paired with sexual opportunity and another conditioned stimulus (CS-) was not. The nature of the conditioned stimulus differed between experiments (see Table 1) but all of the conditioned stimuli were presented in a similar fashion.

Table 1
Conditioned Stimuli (CS+ & CS-) and Unconditioned Stimuli (US+ & US-) for each experiment
Letters indicate whether the same or different females served as CS and US for each subject within an experiment. The plus and minus signs used in the boxes for Experiment 4 indicate female categories (CS+, CS-)

	CS+	US+	CS-	US-
Exp 1	Window Viewing of Live Female (A)	Full Access to Live Female (A)	Window Viewing of Live Female (B)	Visual Access to Live Female (B)
Exp 2	Window Access to Taxidermic Model (A)	Full Access to Live Female	Window Access to Taxidermic Model (B)	No Access to Female
Exp 3	Window Access to Live Female (A)	Full Access to Live Female (B)	Window Access to Live Female (C)	Visual Access to Live Female (D)
Exp 4 (Disc)	Window Access to Live Female (A+)	Full Access to Live Female (A+)	Window Access to Live Female (B-)	No Access to Female
Exp 4 (Transfer)	Window Access to Live Female (C+)	---	Window Access to Live Female (D-)	---

During reinforced trials the CS+ was placed in one stimulus chamber and then revealed to the subject by removing the opaque Plexiglas wall. The subject could then view the CS+ through the window in the stimulus door for 5-min. At the end of the CS+ period the stimulus door was raised in order to release a sexually receptive female quail (the unconditioned stimulus or US+). The subject was permitted to interact with the female in the large test chamber for 5 minutes, during which copulation invariably occurred. In some experiments the CS+ and US+ were the same female, but in others, the CS+ and US+ females were different. To achieve the latter, immediately after the CS+ period the other stimulus chamber containing a female was shifted to align with the doorway and the stimulus door was raised, simultaneously hiding the CS+ and allowing the male and the US+ female to interact.

During CS- trials, the opaque Plexiglas wall was again removed to reveal the CS- in one of the stimulus chambers. After 5 min, the stimulus chambers were shifted to reveal the US- condition. There was some variation in the US- across experiments (see Table 1), but the US- never involved the opportunity to copulate with a female.

Every subject received one CS+ and one CS- trial each day for 10-14 consecutive days in Experiments 1, 2, and 3. The CS+ and CS- trials were conducted at least 2 hours apart and the order of CS+ and CS- presentations was randomized with the single constraint that no subject experienced the same type of trial first on more than three consecutive days. In Experiment 4, trial type was randomized such that two trials of the same type could occur on the same day. Each trial was video recorded for subsequent scoring and two behaviors were measured to assess the effects of discrimination training: time in the CS zone and orientation towards the viewing window. The CS zone (30 cm^2) was marked on the floor of the cage directly in front of the viewing window. A subject

was considered to be in the CS zone when both feet were within the marks. Orientation was measured using a point sample technique. Orientation of the subjects beak (towards or away from viewing window) was recorded every 5 sec for the 5 min CS period.

Experiment 1: Social Categorization or Individual Recognition

Experiment 1 was conducted to replicate the previous finding that male quail can discriminate between females with whom they have and have not copulated (Riters & Balthazart, 1998). Twelve live females served as conditioned and unconditioned stimuli. Each male subject (n = 12) was assigned a pair of stimulus females. One female served as the CS+ and one as the CS- throughout the experiment. During CS+ trials, subjects could see a live female (the CS+) through the viewing window for a 5 min period then were allowed to copulate with the same female during the 5 min US+ period. During CS- trials, a different female (the CS-) was visible in the stimulus chamber. The CS- period lasted for 5 min and was immediately followed by the US- period when the door was raised to reveal the CS- female behind a transparent Plexiglas wall. During the 5 min US- period, the subject had visual access to the female but no physical access. Each stimulus female served as a CS+ for one subject and a CS- for a different subject. Subjects received one CS+ and one CS- trial per day for 10 consecutive days. Like the experiment conducted by Riters and Balthazart (1998) this procedure did not distinguish between social categorization and individual recognition. Either identification strategy would permit the subject males to successfully discriminate between the CS+ and CS- female.

Results and Discussion

The average amount of time that subjects spent in the CS zone during the 5 min CS period increased across trials (Figure 2, top panel). Furthermore, there was a consistent trend for subjects to spend more time in the CS zone during CS+ trials than CS- trials. These impressions were supported by a repeated measures analysis of variance (ANOVA) with Days (1-10) and CS type (CS+ and CS-) as within subject variables. The analysis revealed significant effects of Days ($F(9,99) = 4.13$, $p = 0.0002$) and CS Type ($F(1,11) = 11.70$, $p = 0.0057$) but the Days X CS Type interaction was not statistically reliable, $F < 1.0$.

Orientation towards the CS window (Figure 2, bottom panel) tended to occur more frequently on CS+ trials than CS- trials. However, when the data were analyzed with a repeated measures ANOVA with Days and CS Type as independent variables, the main effect of CS Type was marginally significant, $F(1,11) = 4.50$, $p = 0.058$. The main effect of Days was significant, $F(9,99) = 2.088$, $p = 0.038$; but the Days X CS Type interaction was not, $F(9,99) = 1.28$, $p = 0.256$.

Orientation

Frequency

45
40
35
30
25
20
15
10
5
0

Trial 1 Trial 2 Trial 3 Trial 4 Trial 5 Trial 6 Trial 7 Trial 8 Trial 9 Trial 10

● CS+
○ CS-

CS Zone

Seconds

300
250
200
150
100
50
0

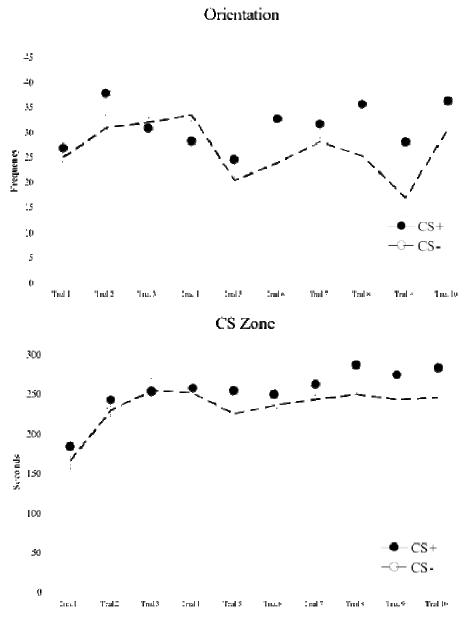Trial 1 Trial 2 Trial 3 Trial 4 Trial 5 Trial 6 Trial 7 Trial 8 Trial 9 Trial 10

● CS+
○ CS-

Figure 2. Mean time (±SE) spent in the CS zone (top panel) and number of orientations towards the CS window (bottom panel). Subjects were allowed to copulate with CS+ females after the 5 min exposure but were not allowed to copulate with CS- females.

In discrimination tasks that require one or more trials for subjects to become familiar with the stimuli and the nature of the task, evidence of successful discrimination by the end of the experiment can often be diluted by poor performance early in training when learning was still occurring. Therefore, it was necessary to isolate behavior during the last few trials to assess whether subjects

were able to truly discriminate between the identities of the female stimuli. Subsequent analyses examined data from the final 3 days of training to assess the extent to which learning had occurred independent of the early phase of learning (Figure 2). A repeated measures analysis of time spent in the CS zone during CS+ and CS- trials on days 8, 9, and 10 revealed a significant main effect of CS Type $(F(1,11) = 7.77, p = 0.018)$ indicating more time spent near the CS+ than the CS-. Neither the main effect of Trials nor the Trials x CS Type interaction were significant (Fs<1.0), suggesting that learning may have been complete at that point. Evaluation of orientation data during the last 3 days of training also revealed a significant main effect of CS type, $F(1,11) = 8.32, p = 0.015$. Subjects spent significantly more time in the CS zone when the CS+ was visible through the viewing window than when the CS- was visible. The main effect of Trials was also significant, $F(2,22) = 7.56, p = 0.003$, but the Trials X CS Type interaction was not, $F < 1.0$.

These results were very similar to those obtained by Riters and Balthazart (1998). The male subjects learned to discriminate between the females with which they had and had not copulated. However, it remained unclear from these results what type of cues the males were using to make this discrimination. One possibility is that they relied on the physical characteristics of the females like overall size or plumage variations to identify individuals. This possibility was tested in Experiment 2.

Experiment 2: Individual Recognition Using Only Physical Cues

Experiment 2 was designed to determine if male quail could recognize individual females based solely on their physical attributes. In a small pilot study, it was determined that human observers were able to easily distinguish same-sex quail based only on their physical characteristics (shape, size, plumage variation, etc.) so it was theorized that male quail would be capable of doing the same. The contribution of idiosyncratic behaviors to individual recognition was eliminated by using taxiderimic models of female quail as the CS+ and CS- and all of the models were placed in a squatting position to eliminate the use of sexual receptivity as a categorical cue. In the absence of behavioral and categorical cues, the male subjects had to rely on their ability to recognize individual females based solely on their physical characteristics. Twelve naïve males participated as subjects and 12 naive female quail served as unconditioned stimuli.

Six female quail were prepared as taxidermic models to serve as conditioned stimuli. Each model was a CS+ for four subjects and a CS- for four different subjects. During CS+ trials, the CS+ model was visible through the viewing window for 5 min before a live female (US+) was released into the test chamber by shifting the stimulus chambers. During CS- trials, the subject could see a different model (CS-) through the viewing window for a 5 min period, but no US- was presented. In order to avoid subjects discriminating CS+ from CS- conditions based on the presence of cues produced by the US+ female (e.g., vocalizations, movement), a live female was placed in the concealed stimulus

compartment during CS- trials as well. Subjects did not see or interact with the concealed female at any time. However, as was the case during the CS+ model presentations, males were able to hear the live females when the CS- model was visible. Sliding the opaque Plexiglas wall between the viewing window and the stimulus chamber ended the CS- period. Because subjects failed to show evidence of discriminating between the CS+ and CS- conditions after day 10, discrimination training was extended for an additional 4 days to determine if the difficult nature of the task required additional training sessions before individual recognition was evident.

Results and Discussion

Time in the CS zone and orienting towards the CS window during the 5 min CS periods are represented in the top and bottom panels of Figure 3. Subjects showed an increase in both behavioral measures across trials, indicating that learning occurred with training. However, the subjects showed similar amounts of approach to the CS window and orientation towards the CS window regardless of whether the CS+ or CS- taxidermic model was visible.

The CS zone data was evaluated using a repeated measures ANOVA with Trials (1-14) and CS Type (CS+ and CS-) as within group variables. The analysis revealed a significant effect of trials, $F(13, 91) = 6.498$, $p < 0.0001$, reflecting increased time spent in the CS zone with training. However, the main effect of CS Type was not significant, $F(1,7) = 2.13$, $p = 0.188$. Subjects did not discriminate between the taxidermic models that predicted copulatory opportunity and the models that did not. The Trials X CS Type interaction also did not reach significance ($F < 1.0$).

The orientation data was analyzed with the same statistical tests and similar results were found. Orientation towards the CS window during the 5 min exposure period increased significantly across trials, $F(13,91) = 4.746$, $p < 0.0001$. However, neither the main effect of CS Type nor the Trials X CS Type interaction were significant (Fs < 1.0) indicating that the subjects did not react differently to the CS+ and CS-.

These results suggest that male quail are not capable of recognizing female quail based solely on their physical characteristics. The lack of discrimination in Experiment 2 was not likely due to insufficient training. Unlike the 10 days of discrimination training used in Experiment 1, this experiment used 14 days of discrimination training. His was done to increase the opportunity for subjects to learn the association between the CS+ and copulation, and this length of training has been more than sufficient to sexually condition male quail in previous experiments (Crawford, Holloway, & Domjan, 1993).

The results of Experiment 2 also suggest that the males in Experiment 1 were relying on behavioral cues to successfully discriminate between individual females. Experiments 3 and 4 were designed to determine whether sexual or non-sexual female behaviors were more important to the males during their discrimination training.
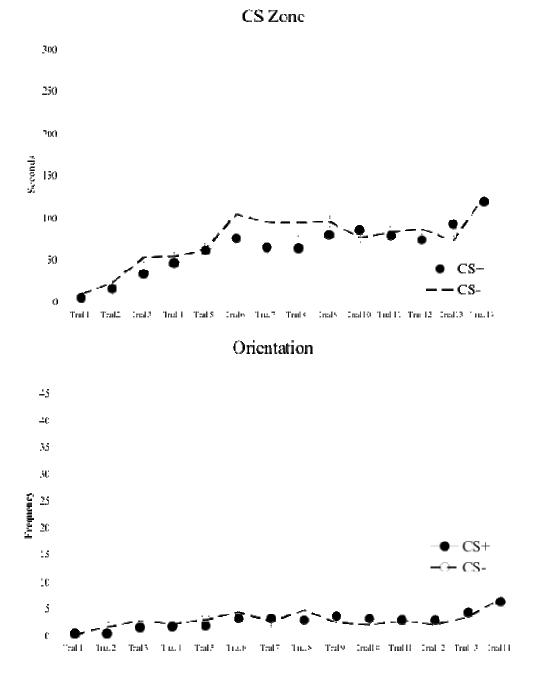
CS Zone

Orientation

Figure 3. Mean time (±SE) spent in the CS zone (top panel) and number of orientations towards the CS window (bottom panel). The presentation of the CS+ taxidermic model preceded opportunity to copulate whereas the CS- taxidermic model was never paired with copulation.

Experiment 3: Individual Recognition Using Physical and Behavioral Cues

Female quail that are sexually receptive show species-typical squatting behavior (Gutiérrez & Domjan, 1997; Domjan, Mahometa, & Mills, 2003). This species-typical, sex-specific response consists of the female remaining immobile while at the same time bringing her body in contact the ground. Thus it is possible that the males in Experiment 1 were using this squatting behavior to separate females into social categories – those that are sexually receptive and those that are not. In contrast, female quail also exhibit individual variation with respect to their non-sexual behaviors. Males could presumably use these unique non-sexual behaviors to distinguish one female from the next. It is unclear what female behaviors to which the males were attending in Experiment 1 but the distinction is important because only the use of the idiosyncratic behaviors, physical cues, or some combination of the two would represent true individual recognition.

Experiment 3 was designed to determine if male quail could recognize individual females in the absence of the categorical cues associated with sexual anticipation. This was accomplished by using the presentation of a live female bird (the CS+) to predict copulation with a different female (US+). A similar procedure in which a live rat acted as a CS to signal impending food was used by Timberlake and Grant (1975). In our CS+ trials, the CS+ female was visible through the viewing window for 5 min before a different female (US+) was released into the test cage for copulation. The presentation of yet another live female (the CS-) predicted non-copulation with a different female (US-). During CS- trials, the CS-female was presented in the stimulus chamber for 5 min then the stimulus chamber was shifted to expose a different female (US-) behind transparent Plexiglas. The Plexiglas partition prevented physical contact but allowed visual access to the female US-. As in Experiment 2, each male subject experienced two trials daily for 14 consecutive days. Twelve male quail served as subjects and 24 females served as stimuli (12 as CSs and 12 as USs). Unlike Experiment 1, the CS+ and CS-females in the present study remained sexually naïve for the duration of the experiment, and therefore, were prohibited from anticipating sexual opportunity during discrimination training. Periodic observations of the female stimulus birds during discrimination training confirmed that the females did not engage in squatting behavior while in the stimulus chambers. In the absence of such categorical information, the males needed to rely on the unique physical and non-sexual behaviors of the females to successfully discriminate.

Results and Discussion

The average amount of time that the subjects spent in the CS zone on CS+ trials and on CS-trials across the 14 days of discrimination training is represented in the top panel of Figure 4. In general, time spent near the CS female increased across trials regardless of whether or not the stimulus predicted impending sexual opportunity. Analysis of the data using a repeated measures ANOVA with Trials and CS Type as independent variables revealed a significant main effect of Trials,

$F(13, 143) = 4.70$, $p < 0.0001$, but neither the main effect of CS Type, $F(1,11) = 2.88$, $p = 0.118$, nor the Trials X CS Type interaction $F(13, 143) = 1.54$, $p = 0.111$, were significant. The subjects did not discriminate between the CS+, which predicted sexual opportunity, and the CS-, which predicted no sexual opportunity.

The orientation data (bottom panel of Figure 4) also was analyzed with a repeated measures ANOVA. Orientation towards the CS window during the 5 min exposure period increased significantly across trials, $F(13, 143) = 4.00$, $p < 0.0001$). However, neither the main effect of CS Type ($F(1,11) = 1.94$, $p = 0.188$) nor the Trials X CS Type Interaction ($F(13, 143) < 1.0$, $p = 0.774$) were significant indicating that the subjects did not learn to discriminate between the CS+ and CS- females.

By using virgin females as conditioned stimuli, the males in this experiment were forced to rely on general behavioral cues such as overall activity level or idiosyncratic behavior patterns to discriminate between individual females. Without the benefit of sexual anticipation cues, the males failed to recognize the differences between the CS+ and CS- females, even after 14 days of discrimination training. These results suggest that female sexual anticipatory responses were important in the recognition exhibited by the male subjects in Experiment 1 and that these males may have simply separated females into receptive and nonreceptive categories. This possibility motivated the design of Experiment 4.

This change in procedure created a difference in the amount of time that a subject was exposed to the CS/US+ female (5 min CS period + 5 min US period per trial) compared to the CS- female (5 min CS period only per trial) allowing for the possibility that the subjects would be more familiar with the CS+ female than the CS- female. To eliminate this inequality, the number of CS- trials was doubled so that by the end of training, subjects had visual exposure to each stimulus female for 140 min (CSs+: 10 min on 14 trials; CS-: 5 min on 28 trials). Eight stimulus females served as either a CS+ or as a CS-, but not both. Additionally, each female was used to train three different subjects to ensure that the female's sexual anticipation would develop in response to cues associated with the stimulus chamber rather than in response to the individual identity of the subject.

A transfer test was conducted immediately following discrimination training to determine if males were utilizing social categorization to discriminate between the CS+ and CS- females. On this day, each subject received a 5 min CS+ trial and a 5 min CS- trial with, respectively, a CS+ female and a CS- female that were used in the discrimination training of another male. Therefore, the physical characteristics and individual behaviors of each female were unfamiliar to the subject male, but the sexual anticipation behaviors of the CS+ females (i.e. immobility and squatting) were similar to those the male observed during the discrimination training. If males categorize females using the presence or absence of anticipatory squatting behavior, the subjects during the transfer test should successfully discriminate between unfamiliar receptive and nonreceptive females even when seeing them for the first time.
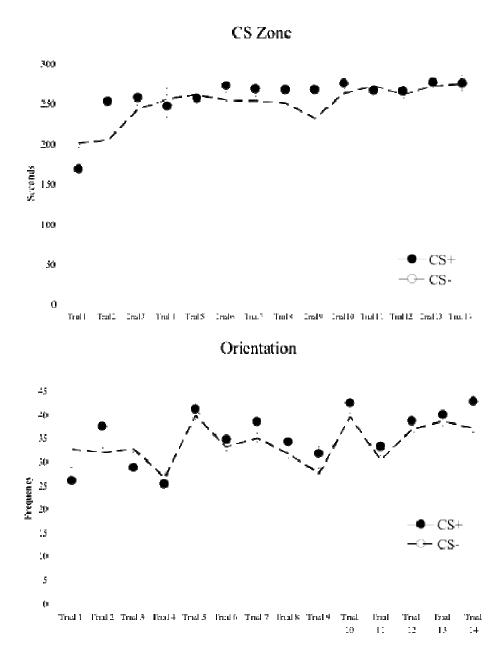
CS Zone

Orientation

Figure 4. Mean time (±SE) spent in the CS zone (top panel) and number of orientations towards the CS window (bottom panel). The CS+ (a live female) predicted an opportunity to copulate with a different live female whereas the appearance of the CS- (yet another live female) was not followed by sexual opportunity.

Results and Discussion

Prior to statistical analyses, data from sequential pairs of CS- trials were averaged to equate the number of CS- data points with CS+ data points. Time spent in the CS zone and orientation toward the viewing window during discrimination training were analyzed separately with two-way repeated measures ANOVAs. Trials (1-14) and CS Type (CS+ and CS-) were within subject variables. The top panel of figure 5 represents the average amount of time subjects spent in the zone near the CS window during the 5 min period when the female was visible. The males initially spent more time looking at the CS- female than the CS+ female but this trend reversed with training. During the last 5 training trials, males showed a clear preference for the CS+ female over the CS- female. This change in preference across trials was reflected in the results of the analyses: the main effect of CS type was not significant, $F(1,11) < 1.0$, but the CS Type X Trials interaction was significant, $F(13, 143) = 5.99$, $p <0 .0001$. The main effect of Trials also was statistically reliable, $F(13, 143) = 4.85$, $p< 0.0001$, indicating a substantial increase in time spent in the CS zone across trials.

The pattern of orientation behavior was very similar to time spent in the CS zone (figure 5, bottom panel). Subjects looked at the CS- more often than the CS+ at the beginning of training but spent more time looking at the CS+ than the CS- at the end of the experiment. As a result, the main effect of CS type failed to reach significance, $F < 1.0$, but the main effect of Trials and the Trials X CS Type interactions were both significant, $F(13, 143) = 9.56$ and 4.84, respectively, p's < 0.0001.

Analysis of behavior during the transfer test failed to show any evidence of discrimination between the novel CS+ and CS- females (see figure 5). Both behaviors were evaluated using separate paired t-tests yet neither time in zone ($t(11) = 0.50$, $p = 0.630$) nor orientation ($t(11) = 0.52$, $p = 0.617$) were significant.

The behavior of the male subjects during the training phase confirmed that male quail are capable of discriminating between females with which they have and have not copulated. However, the males spent similar amounts of time near and orienting towards the novel CS+ and CS- females during the transfer test. These results suggest that social categorization based on sexual anticipation alone is insufficient for males to discriminate between individual females.
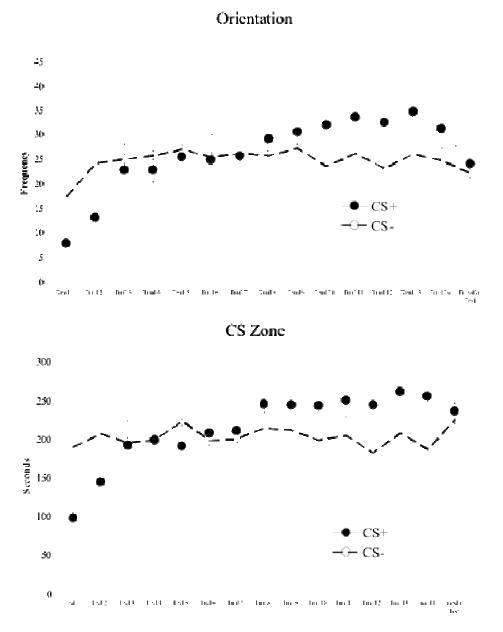
Orientation

CS Zone

Figure 5. Mean time (±SE) spent in the CS zone (top panel) and number of orientations towards the CS window (bottom panel). Subjects were allowed to copulate with CS+ females after the 5 min CS period but were not allowed to copulate with CS- females. On the first 14 trials, CS+ data represents single trials and the CS- data represents blocks of two trials. During the transfer test, subjects were exposed to unfamiliar females that had served as either CS+ or CS- females to other males.

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General Discussion

Individual recognition and social categorization represent two different ways animals draw on their past experiences with conspecifics to help determine their behavior during social interactions. Both mechanisms are pervasive throughout the animal kingdom and have obvious adaptive value (Seyfarth & Cheney, 2009), but only individual recognition requires that the unique traits of individuals be remembered in association with each individual's identity. In contrast, social categorization is a simpler task requiring only the recognition of the defining characteristics of two or more distinct social groups (e.g., receptive vs. non-receptive females). Only a relatively few distinguishing characteristics need be remembered, and no previous interactions with the target conspecific are necessary for categorizations to be swift and accurate.

There is evidence that some bird species are capable of true individual recognition (e.g., D'Eath & Keeling, 2003; Lovell & Lein, 2005; Watanabe & Ito, 1991). But even in these species it is possible that individuals utilize social categorization to narrow the possible identities of a conspecific. Since the two strategies may be used concurrently, experimental findings that have the appearance of individual recognition may actually represent social categorization (Riters & Balthazart, 1998).

The present experiments were conducted to identify the mechanisms by which male Japanese quail discriminate between individual females. The results of Experiment 1 indicated that male quail are capable of discriminating between female quail with which they have and have not copulated. The results of the subsequent experiments helped clarify the extent to which the males in Experiment 1 discriminated the females using their unique physical cues (Experiment 2), non-sexual behaviors (Experiment 3), or sexual anticipatory responding (Experiment 4). Unlike Experiment 1, the males in these subsequent experiments were unable to discriminate between the female stimulus birds using the limited physical and behavioral cues they were provided.

The fact that the males in Experiment 2 failed to recognize the differences between the 2 female models was somewhat surprising since the results of a pilot study indicated that human observers performed well on a similar task. However, poor performance on a discrimination task using taxidermic CSs is not without precedence. Ryan and Lea (1994) found that pigeons were unable to discriminate between two taxidermically prepared pigeon models when one model predicted food and the other did not. Perhaps the artificial nature of the taxidermic females in the present study prohibited the males from processing the relevant distinctions between the two models. This seems unlikely since male quail in a previous experiment responded to the visual aspects of live females and taxidermic females in a similar way (Hilliard, Nguyen, & Domjan, 1997).

Moreover, the failure of the males to discriminate between the two taxidermic models does not mean that the visual features of females are unimportant to male quail. Instead, these results suggest that visual features alone,

in the absence of other cues, are insufficient for males to make accurate female identifications. In fact, numerous sexual conditioning experiments with male quail have shown that the visual characteristics of live birds contribute substantially to conspecific and sex recognition (Domjan & Hall, 1986; Nash & Domjan, 1991; Nash, Domjan, & Askins, 1989;). But in all of these studies, the discrimination tasks were far less subtle (e.g., discriminating between different color strains of quail, recognizing males vs. females) and live stimulus birds provided the males with distinguishing behavioral cues to complement their static visual features.

The combined results of Experiments 1 and 2 suggest that male quail rely on behavioral cues to successfully discriminate between individual females. However, the results of Experiments 3 and 4 indicate that males are incapable of discriminating between individual females using non-sexual and sexual female behaviors when they are presented independent of one another.

How do these results clarify the extent to which male quail use either social categorization or individual recognition to discriminate female conspecifics? The inability of the males to discriminate between the taxidermic models in Experiment 2 suggests that unique physical cues alone are insufficient for individual recognition to occur. Likewise, individual recognition did not occur when the males in Experiment 3 were limited to using idiosyncratic physical and non-sexual behaviors. This suggest that male quail are incapable of discriminating individual females in the absence of differing levels of sexual receptivity responding. However, the males during the transfer test in Experiment 4 also failed to discriminate between individual females when sexual receptivity behaviors were provided as distinctive female cues. This latter finding suggests that, much like the physical and non-sexual behavioral cues of females, the social categorization cues of female receptivity are, at least by themselves, insufficient for males to use as discriminative stimuli.

The failure of the males to discriminate between the two stimulus females during the transfer test in Experiment 4 suggests that the male discrimination behavior observed in Experiment 1 and in the experiment conducted by Riters and Balthazart (1998) represents true individual recognition. This is of particular importance since quail are a polygynous species that lack biparental care (Tibbetts & Dale, 2007). Given the cognitive complexity that individual recognition requires (Beecher, 1989), identifying and remembering previous mating partners is likely to be important for the reproductive success of male quail in their natural environment. Why this is the case has yet to be empirically determined, but males would certainly benefit from avoiding females that were consistently nonreceptive. At the same time, males that consistently returned to females that were receptive to their previous mating attempts would have difficulty competing with males attracted to novel females. Perhaps male quail are capable of balancing between these two strategies to optimize their reproductive success. Future experiments should address this possibility.

The present findings also suggest that male recognition of individual females in this species is not accomplished by focusing on physical, non-sexual, or sexual receptivity behaviors in isolation. Instead, individual recognition is likely to

occur only when males are able to utilize all of these potentially distinctive female attributes at the same time. Such was the case in Experiment 1 and in the training phase of Experiment 4, as well as the experiment conducted by Riters and Balthazart (1998).

Another potential explanation for the present findings is that female Japanese quail receptivity responses are themselves unique and idiosyncratic, varying along one or more dimensions from one female to the next. One female may squat while looking toward the male, while another female may squat while looking away. Or perhaps individual female squatting responses vary in frequency and duration. Guttiérez and Domjan (1997) observed group differences in the duration of female squatting as a result of sexual conditioning. If this occurred in the present set of experiments, it is not surprising that males were unable to discriminate between the CS+ and CS− females they observed during the transfer test of Experiment 4. During this test the stimulus females no doubt displayed species-typical behaviors that were generally indicative of receptivity, but the idiosyncratic female receptivity responses the males were able to use during their previous discrimination training were absent. Thus, the lack of male discrimination during the transfer test suggests that each female's receptivity responses are unique, and these unique features are important for males to recognize one female as being distinct from another. The design of future experiments should directly investigate this possibility. Future experiments also need to further explore the cognitive and behavioral differences between social categorization and true individual recognition. It is likely that some species utilize both forms of recognition. Thus, distinguishing between these two forms of social learning in future experiments will be both challenging and important to the understanding of what regulates animal social interactions.

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