INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

2015, 28
José E. Burgos
Special Issue Editor
Peer-reviewed

From Biological Constraints to Flexible Behavior Systems: Extending Our Knowledge of Sexual Conditioning in Japanese Quail

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The traditional learning view involves the general process theory of learning that focuses on identifying universal principles that apply to all species capable of learning from experience. Examples of behavior that contradict general-process conceptions of learning have been in the past referred to as *biological constraints* and as exceptions to otherwise universal principles of learning. In the present paper, we suggest that ethology and animal learning can both benefit from more in-depth study of each other, and that collectively, our understanding of animal behavior would greatly benefit from the integration of these two well-established disciplines. Perhaps the most successful attempt at a theoretical and methodological integration of animal learning and ethology has been the development of the behavior systems approach. Behavior systems conceptualize experiential learning not as a set of universal principles, but as species-typical processes that reflect the specific demands of the ecological niche in which the species evolved. Behavior systems have been developed for the analysis of learned defensive and feeding behaviors in rats, the development of pecking behavior and dustbathing in jungle fowl, and the sexual behavior of male domesticated quail. The latter example is the focus of the current presentation. Male Japanese quail display a wide range of behaviors prior to, during, and after mating. A behavior system has been developed that describes both unconditioned and Pavlovian conditioned effects of sexual behavior. Conditioned effects are of particular interest because what an animal learns about predictive relationships between stimuli and responses ultimately reflects the potential demands of the particular ecological niche in which it has evolved. The paper brings to date the sexual behavior system in male quail and describes data that support the system. Future directions are suggested that include the study of other behavior systems in different species, and more importantly, the study of behavior systems in female animals.

Animal Learning versus Ethology

The fields of animal learning and ethology have traditionally moved in separate directions. Learning theorists have typically used laboratory preparations to examine the mechanisms of learning that apply equally to all animal species. These investigations have attempted to uncover the universal features, or general

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https://doi.org/10.46867/ijcp.2015.28.01.05

processes, of learned behavior. The typical ethologist, on the other hand, is interested in both learned and unlearned behaviors and is more likely to be concerned with how specific behaviors may have evolved. Toward this end, ethologists have been more interested in an animal's species typical responses to stimuli they are likely to encounter in their natural environment (Domjan, 1998).

For the most part, animal learning and ethology continue to progress in separate directions despite the discovery of instances in which general-process learning theories fall short of explaining laboratory findings. Perhaps the most familiar example of this shortcoming is Garcia and Koelling's (1966) demonstration that, in rats, taste stimuli are more easily associated with sickness than are audio-visual cues, whereas audio-visual cues are more easily associated with cutaneous pain than are taste stimuli. LoLordo and his associates have demonstrated that in pigeons, auditory cues are more effective than visual cues in avoidance conditioning, whereas visual cues are more effective than auditory cues in conditioning reinforced with food (e.g. Foree & LoLordo, 1973). Instances of behavior that contradict general-process conceptions of learning have been in the past referred to as *misbehavior*, *selective associations*, *biological constraints*, or *adaptive specializations in learning* (Breland & Breland, 1961; Hinde & Stevenson-Hinde, 1973; Rozin & Kalat, 1971; Seligman & Hager, 1972; Shettleworth, 1972; see also, Krause, 2015 for further discussion on selective associations). Rather than relinquishing claims of generality (or embracing ethological explanations for these findings), traditional learning theorists choose to consider these results as exceptions to otherwise universal principles of learning.

Integration of the results of laboratory investigations of animal learning into the theoretical framework of ethology has not been well accomplished. For example, traditional ethological views (Lorenz, 1981; Tinbergen, 1951) describe species typical behavior sequences as consisting of appetitive responses and consummatory responses. The terminal responses at the end of behavior sequences that appear to *satisfy* the animal are labeled *consummatory* (Craig, 1918). Responses at the beginning of behavior sequences are labeled *appetitive*. Traditional ethological conceptions of the appetitive-consummatory distinction have described appetitive responses as being inherently more variable in form, while consummatory responses are presumed to be fixed, rigid, or unchanging (Baerends, 1988; Eibl-Eibesfeldt, 1970; Tinbergen, 1951). However, ethologists rarely conceptualize the variability of appetitive behaviors using the fundamental principles of animal learning theory, and much research, including some described in the current paper, has demonstrated that there is a great deal of plasticity to what we once thought as rigid and fixed consummatory behaviors. In the present paper we suggest that ethology and animal learning can both benefit from more in-depth study of each other, and that collectively, our understanding of animal behavior would greatly benefit from the integration of these two well-established, tenaciously independent disciplines. One way to achieve this is for animal learning theories to move away from assumptions of ubiquity and find ways to better explain learning phenomena that are unique to individual species or specific ecological conditions. Perhaps the most successful attempt at a theoretical and methodological integration of this sort has been the development of the behavior systems theory of learning (Timberlake, 1983, 1994, 2001; Timberlake & Lucas, 1989).

Behavior Systems Theory

Behavior systems have been developed for the analysis of learned defensive and feeding behaviors in rats (Fanselow, 1994, 1997; Timberlake, 1994), the development of pecking behavior and dustbathing in jungle fowl (Hogan, 1994), and the sexual behavior of domesticated quail (Domjan, 1994). In contrast to the general–process view of animal learning, the behavior systems approach emphasizes the contribution of the animal's ecology to learned behavior. Unlike more traditional learning investigations, behavior systems are studied with reference to the stimuli that animals encounter in their natural environment and to the naturalistic challenges they must overcome to survive and reproduce. From this perspective, what an animal learns about predictive relationships between stimuli and responses ultimately reflects the potential demands of the particular ecological niche in which it has evolved (Timberlake, 1983). More importantly, the behavior systems approach has been successful in combining the theoretical frameworks of ethology and animal learning.

Behavior systems are unique to the motivational states of a specific species. They are organized as a series of modules arranged in a temporal-spatial sequence with general search behavior on one end, a consummatory response module on the other end, and a focal search module in the middle of the continuum (Timberlake & Lucas, 1989). In appetitive situations, presentations of biologically relevant stimuli activate the behavior system relevant to that reinforcer. For example, presentations of small portions of food to a hungry animal presumably activate the feeding system. Once food has been located, the focal search module is activated, keeping the animal near the location of the food. When food is close enough for the animal to handle it, food handling and consummatory modules are activated. The effects of experiential learning may also be understood from this perspective by observing how the preexisting behavior system is altered by naturally occurring learning trials. The conditioned response that develops depends on which module is activated. In this way, behavior systems accurately account for the flexible and dynamic nature of naturally-occurring behavior modifications.

The Sexual Behavior System

In their natural setting, male Japanese quail (*Coturnix japonica*) typically live on the ground in areas covered with grass and shrubs (Schwartz & Schwartz, 1949). In this environment, males may see the head and neck of a female sticking out of the grass before approaching her. The sight of the female's head above the grass may elicit approach followed by a courtship-like response during which the male walks on its toes, stiff legged, with its feathers fluffed out, and its head and neck extended in a horizontal position (Farris, 1967; see also Mills, Crawford, Domjan, & Faure, 1997 for review). Males typically attempt to copulate with a female through a sequence of behaviors. The male grabs the female neck feathers in its beak, mounts the female's back with both feet, and then makes a series of cloacal thrusts (Wilson & Bermant, 1972). Pavlovian conditioning may occur in this setting if an environmental cue or stimulus reliably precedes the copulatory interaction, or if the male comes to associate the visual cues of the female he perceives at a distance with the reinforcement he experiences during copulation. In this way, male birds can accurately predict future occurrences of a mating opportunity.

Over two decades ago, Domjan (1994) formulated a behavior system for male quail sexual behavior and used it to help explain how the sexual responses of male quail were modulated by Pavlovian conditioning. Like the formation of other behavior systems, Domjan's approach was synthetic, including elements in the system only if they were discovered empirically via observational study or laboratory experimentation. The resulting behavior system for unconditioned male sexual behavior is a 3 x 3 matrix of nine cells that includes a stimulus dimension and a response dimension (see Domjan, 1994, Figure 2). The stimulus dimension consists of species typical cues, local cues, and contextual cues. The response dimension consists of general search, focal search, and copulatory behavior. There are small circles within each cell and the density of the circles in each cell represents the presumed degree of control of a given response category by the various types of stimuli.

Prior to conditioning, contextual cues are capable of eliciting general search behavior but not focal search or copulatory behavior. For example, a male quail may wander around a grassy area where a female may later be present. Arbitrary local cues, much like contextual cues, are capable of eliciting focal search behavior, but not general search or copulatory behavior. Movement of blades of a small patch of grass might elicit approach behavior in a male seeking out a female partner. However, species typical cues may elicit all three response components unconditionally.

After conditioning, the sexual behavior system is changed to reflect both conditioned and unconditioned behavior (see Domjan, Figure 3). As before, there are circles in cells that represent unconditioned effects but the flexibility of the system is now illustrated by stars that indicate the effects of conditioning. For example, species typical cues may be conditioned to elicit general search, focal search, and copulatory behavior. There are also arrows present that represent modulatory effects that may occur between stimuli. For example, conditioned contextual cues might increase the effectiveness of species typical cues in eliciting copulatory behavior or local cues in eliciting focal search behavior. It is evident from this model that Pavlovian manipulations increase the range of environmental stimuli that are effective in eliciting sexual responses.

In sum, the sexual behavior system for male quail integrates the concepts of ethology and animal learning, the former by including unconditioned, innate behaviors and species typical cues, and the latter by illustrating how the behavior system is flexible and may undergo dramatic alterations as a result of conditioning. The result is a true integration of both perspectives that in theory, better explains animal behavior compared to traditional ethological and animal learning approaches in isolation. Below, we present sexual conditioning data that support the behavior systems approach and highlight the role of Pavlovian conditioning in eliciting sexual responses.

Species-Typical Cues as Conditioned Stimuli

Early laboratory investigations confirmed that the visual features of a female's head and neck, more so than auditory or olfactory cues, were important to the regulation of sexual interactions in domesticated quail. Domjan and Nash (1988; see also Domjan & Hall, 1986; Nash, Domjan, & Askins, 1989) measured the percentage of time sexually experienced male birds spent viewing a variety of different stimuli through a narrow window. The stimuli presented to the males included live male and female birds, taxidermically prepared full-body models of male and female birds, and various combinations of taxidermic body parts presented alone. Male birds spent significantly more time viewing the taxidermic model of a female than they did viewing either another male bird or a taxidermic model of a male bird. But of primary interest is that males spent a similar amount of time viewing the taxidermic model of a female as they did the live female.

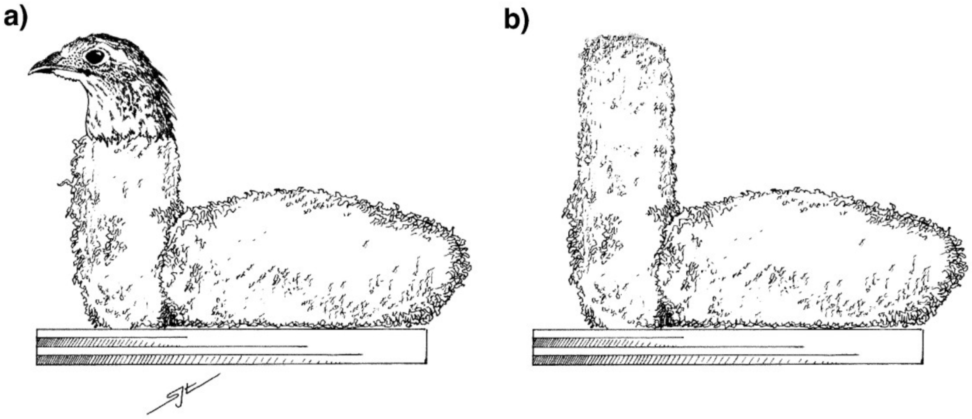

Figure 1. The head (a) and no head (b) CS objects used during conditioning trials. Both objects were made of terrycloth filled with soft polyester fiber and consisted of a vertical section positioned in front of a horizontal mounting pad. (From Cusato & Domjan, 1998, with permission).

Cusato and Domjan (1998) compared the effectiveness of terry cloth CS objects with and without female head and neck cues and found that the presence of female head and neck cues facilitated the acquisition of some, but not all, types of conditioned sexual responses. Some males received a CS with female cues (see Figure 1a) paired with opportunity to copulate with a live female (the US). Others were given the same paired presentations, but their CS lacked female head and neck cues (see Figure 1b).

Each of the 32 males in the experiment received one trial a day for 15 days with a nonreinforced test trial presented after every two conditioning trials. Unpaired control groups received the same CS and US exposure, but the CS and US were separated by at least 45 min.

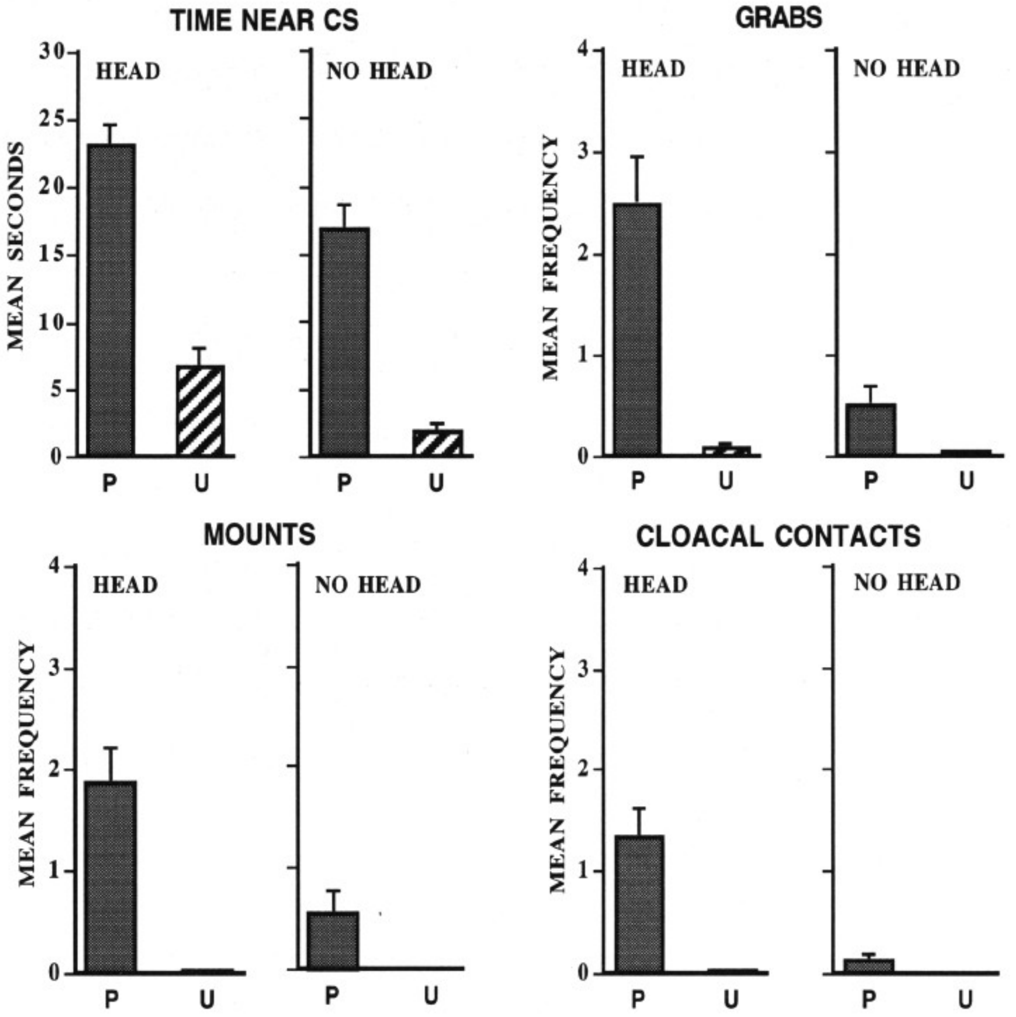

Figure 2. Mean seconds (+ SEM) of time spent near the CS object (upper left panel) and mean frequency (+ SEM) of grabs, mounts, and cloacal contacts directed toward the CS object (remaining panels) during the 5 conditioning trials. P = paired, U = unpaired (From Domjan, Cusato, & Krause, 2004; based on Cusato & Domjan, 1998 with permission).

Figure 2 represents the results from the test trials. Four different responses to the CS objects were measured: time spent near the CS (approach responding), and the frequency of grabs, mounts, and cloacal contact responses (copulatory responses). Results showed that conditioned approach behavior developed at the same rate whether or not the CS object contained cues of a female's head and neck. However, the conditioning of copulatory responses was facilitated by the presence of female cues on the CS object. The CS with a female head and neck elicited more conditioned grabs, mounts and cloacal contacts than did the CS without female cues. Domjan, O'Vary, and Green (1988) reported similar findings. They presented males with a small stuffed toy dog paired with copulatory opportunity and found that this CS, much like the terry cloth only CS used by Cusato and Domjan (1998), elicited approach responding, but not conditioned copulatory responding. Thus, the development of conditioned copulatory responding appears to require the presence of female cues on the CS object, and also, that the object be paired with sexual reinforcement.

According to the sexual behavior system of male quail (Domjan, 1994), conditioning of copulatory responding is only evident through modulatory influences of local and contextual cues. Relatively new findings (Cusato & Domjan, 1998) indicate that conditioned copulatory responding may also develop in the presence of female species typical cues. From a behavior systems perspective, species typical cues that are presented relatively close in time to a copulatory event may become conditioned to elicit copulatory behavior and focal search behavior.

Interestingly, when species typical cues are presented as a CS with a long delay between the CS and copulatory opportunity (US), the effectiveness of these cues in eliciting conditioned copulatory responding is altered. Akins (2000) gave male quail conditioning trials in which a CS was presented for either 1 or 20 min followed by copulation with a female quail. For some males, the CS consisted of a terrycloth model (similar to Cusato & Domjan, 1998; see Figure 1) and for others, the terrycloth model included of a taxidermically prepared head and neck of a female quail. Unpaired control groups received similar models and CS-US intervals except that their copulatory access was given 2 hours before the CS was presented, in an unpaired fashion.

Figure 3 shows the percentage of time paired and unpaired groups spent near the terrycloth model that did not contain the head and neck features of a female (top panel) and the terrycloth model that contained the head and neck features of a female quail (bottom panel). There was very little approach from any of the groups when no female cues were present except when the terrycloth CS was presented for 1 min. In addition, the terrycloth CS came to elicit conditioned general search behavior when it was presented for 20 min. This was consistent with previous findings (e.g., Akins, Domjan, & Gutiérrez, 1994) and the latter is represented in the male quail behavior system (Figure 2; Domjan; 1994) as stars in the square at the intersection of local cues and general search. In contrast to conditioned general search behavior, when the female head and neck cue was present, males that received the model for 20 min increased their focal search behavior. Thus, from the behavior systems view, the CS that contained species-specific cues may have shifted the conditioned response toward copulatory responding, from general search to focal search. Based on these findings, it appears as though female head and neck cues are especially salient to male quail and thus, occupy a special place in the sexual behavior system of male quail. The results from other experiments comparing the effectiveness of CSs with and without species typical cues further support this assertion. The visual features of a female’s head and neck also have been shown to facilitate conditioning to a food US (Cusato & Domjan, 1998) and to disrupt traditional blocking and extinction effects (Köksal, Domjan, & Weisman, 1994; Krause, Cusato, & Domjan, 2003).

Local Cues as Conditioned Stimuli

Several studies have demonstrated that male quail elicit strong and persistent approach behavior to an arbitrary localized cue that reliably predicts a female bird (e.g., Domjan, Lyons, North, & Bruell, 1986). Numerous learning phenomena have also been documented with male Japanese quail using the sexually conditioned approach procedure, including acquisition, extinction, and retention (Domjan et al., 1986), blocking (Köksal et al., 1994), discrimination learning (Nash et al., 1989), second-order conditioning (Crawford & Domjan, 1995), conditioned inhibition (Crawford & Domjan, 1996), and sign tracking (Burns & Domjan, 1996, 2001).

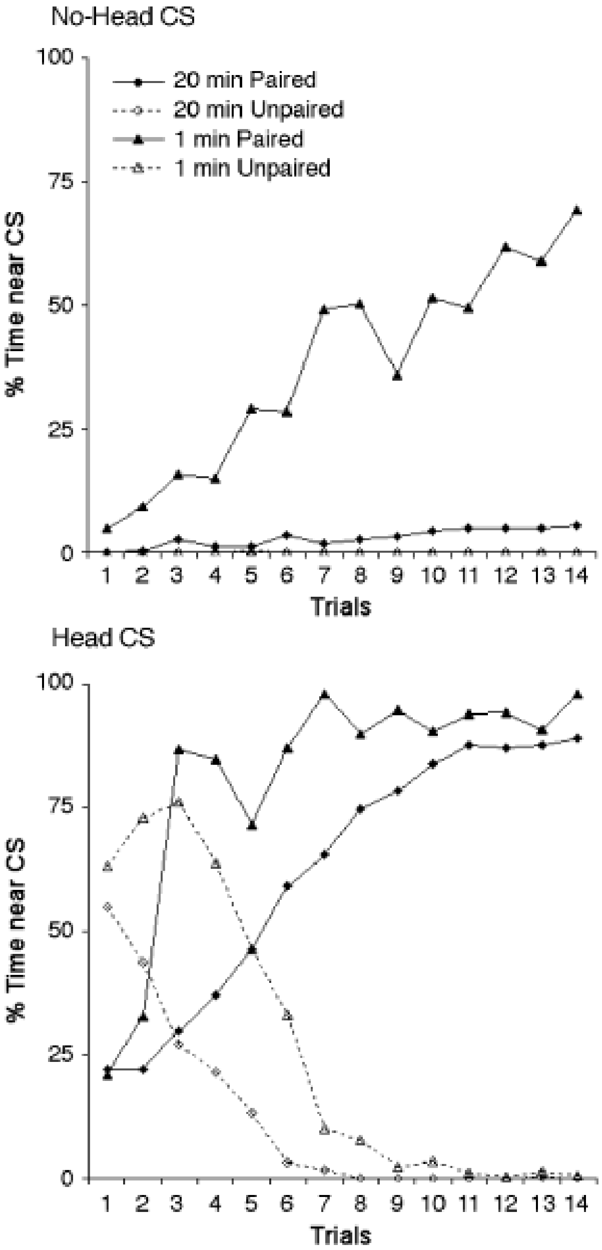

Figure 3. Time (sec) spent near a CS object that contained no head and neck features of a female quail (upper panel) and one that contained head and neck features (lower panel) in males that

received a 1 or 20 min CS-US interval for 14 conditioning trials. Unpaired subjects received the US 2 hr prior to CS exposure. (From Domjan et al., 2004; Based on Akins, 2000 with permission).

In general, sexual conditioning to local cues appears to have clear biological significance. In blue gourami fish, sexual conditioning of males and females dramatically facilitates reproductive behavior and results in an increase in the number of offspring produced (Hollis, Cadieux, & Colbert, 1989). Zamble, Mitchell, and Findley (1986) found that male rats were faster to ejaculate with female rats if they were presented with a CS paired with exposure to a female rat. Similar results have been found in male quail that have been sexually conditioned to an arbitrary local cue. Sexually conditioned males initiate copulation sooner than nonconditioned males (Domjan et al., 1986), release greater quantities of sperm (Domjan, Blebois, & Williams, 1998), and have enhanced copulatory efficiency (Mahometa & Domjan, 2005).

More recently, Domjan, Mahometa, and Matthews (2012) conducted an experiment to investigate the effect of conditioning on fertility by measuring how many fertilized eggs were evident as a result of prior conditioning. During conditioning, both male and female quail were presented with a CS light followed by copulatory opportunity (signaled groups). For male quail, the CS duration was 30 sec before a door was opened that gave males access to the female. For female quail, the CS duration was 10, 20, or 30 min before copulatory opportunity. A nonsignaled control group that did not receive the CS light prior to copulation was included. Both signaled and unsignaled groups received a separate copulation test and eggs were collected from the females for 10 days after the test and examined for evidence of fertilization.

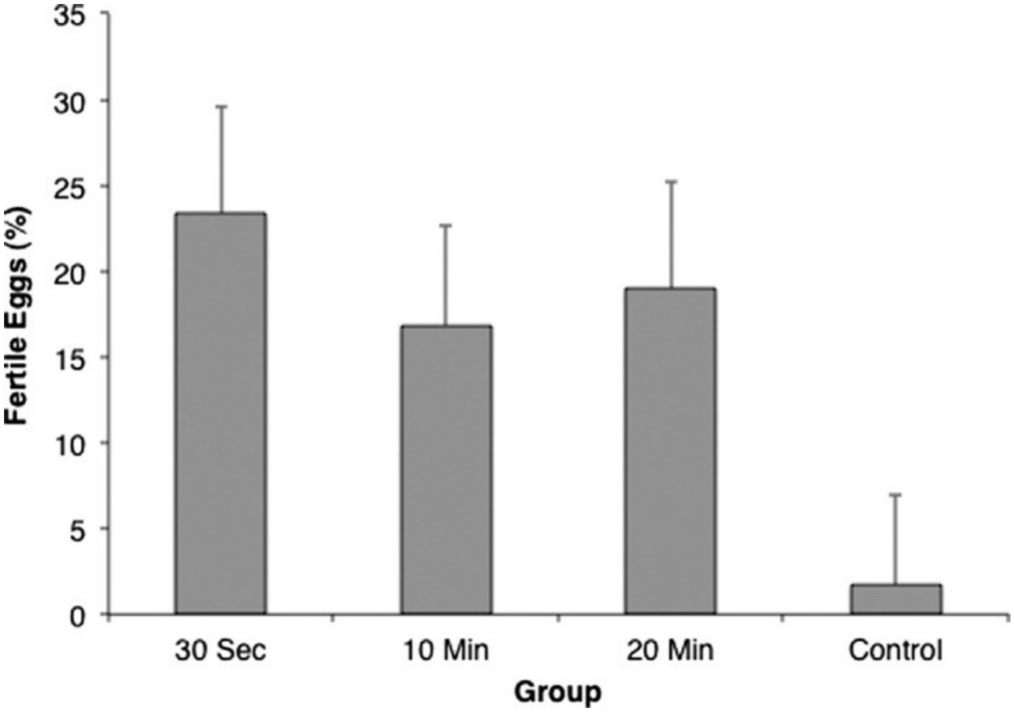

Figure 4. Rate of fertilization of eggs in female quail (mean + S.E.M.) as a function of the CS duration used during conditioning. (From Domjan, Mahometa, & Matthews, 2012 with permission.)

Figure 4 illustrates the rate of fertilization of eggs laid by female quail as a function of CS duration during conditioning for female quail. All of the groups that received the CS prior to copulatory opportunity had much higher rates of fertilization compared to the control group that did not receive the CS prior to copulatory opportunity. The rate of fertilization was not affected by exposing females to longer CS durations, even as long as 20 min. The findings support and extend the previous findings that indicate that Pavlovian conditioning enhances reproductive success. Conditioning of local cues that signal a potential mating opportunity may therefore be of particular biological relevance.

The majority of research on the sexual behavior system has been conducted with male quail because the unconditioned and conditioned responses of female quail are more subtle and difficult to identify relative to those of male quail. However, Gutiérrez and Domjan (1997) investigated whether female quail would also demonstrate sexually conditioned approach behavior to a local cue. They found that, unlike males, female quail did not display sexually conditioned approach behavior elicited by a local cue that signaled a conspecific. Rather, female quail increased responding in the presence of a male that was presented after a CS. The CS did not elicit squatting directly but presentation of the CS enhanced squatting behavior once a male was released. This conditioned squatting response in female quail may have ecological relevance. In their natural environment, male quail establish territories and female quail arrive later to select a nest and a potential mate (Kawahara, 1967). Once a female has *selected* a territory, the male remains in close proximity to her and engages in mate-guarding behavior. Therefore, female approach and maintenance of proximity to a male is not likely to occur during male-female interactions. Instead, female quail display receptivity by squatting and remaining immobile. Squatting behavior by female quail in the presence of a male copulation partner has been considered evidence of female sexual receptivity (e.g., Noble, 1972). Given these natural parameters of unconditioned female sexual receptivity, the results of Gutiérrez and Domjan (1997) suggest that, like male quail, the naturally-occurring sexual behavior of female quail may be enhanced by Pavlovian conditioning (see also Gutiérrez & Domjan, 2011). Despite these provocative findings, relatively few experiments have been specifically designed to investigate the effects of sexual conditioning in female quail.

It should be noted that the sexual behavior system of male quail (Domjan, 1994) indicates that local cues can elicit conditioned copulatory behaviors. While this is typically not the case, Domjan, Huber-McDonald, and Holloway (1992) used a fading procedure consisting of first establishing copulation with a female head and neck model and then gradually covered up the female quail features with terrycloth material over successive conditioning trials. After conditioning, all subjects were tested with the entirely covered terrycloth model. Male quail that received the fading procedure grabbed, mounted, and made more cloacal contact movements toward the model. Therefore, conditioned copulatory behavior to a local cue is evident when species typical cues were initially present and paired with copulation and gradually removed.

Contextual Cues as Conditioned Stimuli

As expected, contextual cues can influence sexual behavior by modulating responses elicited by other conditioned stimuli (see “modulatory effects between stimuli” below). Conditioned contextual cues facilitate conditioned copulatory behavior elicited by species typical cues (Domjan, Greene, & North, 1989) and conditioned approach or focal search behavior elicited by local cues (Akins, 1998; Domjan, Akins, & Vandergriff, 1992). To date, there are a scant number of experiments that demonstrate conditioning of contextual cues on sexual responding via a direct context-US association, rather than a modulatory role of context on responses elicited by other stimuli. In one experiment (Zamble et al., 1986), male rats were carried to a holding room and placed in a plastic tub with wood shavings (the putative contextual CS). After 10 min in the tubs, they were exposed to a receptive female rat (US) located behind a wire mesh screen. Subjects in a control group were given both contextual CS and US presentations in a random order. Rats that received context-US pairings showed a decrease in latency to ejaculate with a female rat after conditioning trials. The findings suggest that contextual cues may become directly associated with a sexual US to facilitate sexual responding.

Other rodent research refers to the preference for a context that has been paired with access to a mate over a context that has not, as a conditioned place preference (CPP; see Pfaus, Kippen, & Centeno, 2001 for review). Male rats demonstrate a CPP for a distinct context in which copulation to ejaculation is allowed to occur over one in which it is not (e.g., Agmo & Berenfeld, 1990; Everitt, 1990; Hughes, Everitt, & Herbert., 1990). Interestingly, female rats demonstrate a robust CPP for a distinct context in which they are able to pace the rate of copulation (referred to as *paced* copulation) but not when copulation was unpaced (Paredes & Alonso, 1997; Paredes & Vazquez, 1999). Female quail show a similar CPP for an area where male quail had previously been presented (Gutiérrez & Domjan, 2011).

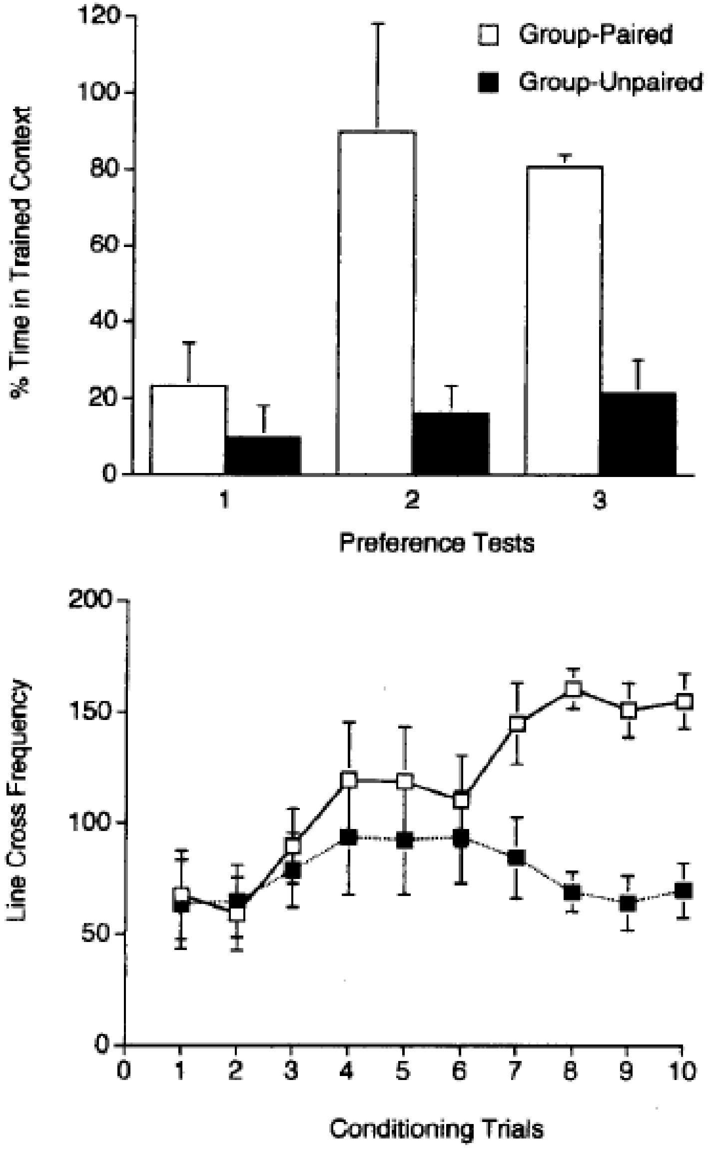

Figure 5. Mean (+ SEM) percent time groups paired and unpaired spent in the trained context during 3 preference tests in which subjects had access to both contexts (upper panel) and the frequency of line crosses made during conditioning (bottom panel; From Akins, 1998 with permission).

Using a similar procedure as CPP, Akins (1998) measured contextual conditioning in male Japanese quail in two ways. First, acquisition of context-US association was assessed in a context preference test procedure. A context preference test was conducted before any conditioning trials began and subsequently after every fifth conditioning trial. Second, locomotor activity was recorded during each conditioning trial. Group Paired received copulatory opportunity (US) after 5 min in the trained context whereas Group Unpaired received the same amount of time in the trained context but was given copulatory opportunity in the home cage 2 hr prior to exposure to the trained context.

Figure 5 shows the percent time paired and unpaired males spent in the trained context (top) and the frequency of locomotor activity (bottom). After five conditioning trials, Group Paired increased their time spent in the trained context relative to Group Unpaired and this preference for the trained context was maintained after an additional five trials. In addition (Figure 5 bottom), during the 5 min prior to introducing a female quail, Group Paired showed an increase in locomotor activity during the last few conditioning trials whereas Group Unpaired did not. In the current experiment, conditioned responding was in the form of approach behavior to an area where a mating event occurred. Males also increased their activity just prior to the introduction of a female into the context. This increase in activity is consistent with other observations of general search behavior within the sexual behavior system of male quail (e.g., Akins et al., 1994). The current findings further extend the sexual behavior system of male quail (Domjan, 1994).

Modulatory Effects between Stimuli

Because conditioning allows for increased flexibility of responding within the sexual behavior system of male quail, responses elicited by species-specific cues and local cues can also be modulated by contextual cues. Domjan et al. (1989) conducted an experiment in which two groups of male quail received extensive sexual experience in a distinct test arena (Group Test Cage) whereas the other group received its sexual experience in the colony cages (Group Home Cage). Males received equal exposure to the test arenas. During a test session, all males were presented with a head and neck terrycloth model of a female quail. The results indicated that Group Test Cage made more sexual responses to the head and neck model and were much more likely to copulate with the model than Group Home Cage. Thus, sexual experience facilitates copulation with a model if the same contextual cues are present during sexual experience and testing with the model. Contextual cues can also facilitate focal search behavior elicited by female species specific cues (Domjan et al., 1989). Both of these effects are represented in the male quail behavior system (Domjan, 1994).

Similar to species typical cues that elicit copulatory behavior, the effectiveness of local cues to elicit focal search behavior can also be modified by contextual cues. In one experiment (Domjan et al., 1992), a holding box served as the localized cue and was raised to release a female into one context (sexual context) or was raised with no female present in a different context (nonsexual context). Therefore, the copulatory opportunity that was provided in the sexual context was signaled by the presence of the localized cue (holding box). As a result, male quail exhibited greater conditioned approach behavior to the holding box in the sexual context compared to the nonsexual context. The findings indicate that contextual cues may serve to modulate the effectiveness of local cues to elicit focal search.

Akins (1998) further investigated the modulatory role of contextual cues on local cue-elicited responses. Her design was similar to Domjan et al. (1992), except the local CS was a small wooden cylinder block and female quail were not released into the context. Rather, male quail received copulatory opportunity with a female bird (the US) after entering a side cage. During discrimination training, male quail were presented with the CS in one context (CTX+) followed by the US in the side cage and the CS in the other context (CTX-) followed by no US in the side cage. The amount of time they spent near the CS (conditioned approach) was measured. Following discrimination training, subjects were given simultaneous access to CTX+ and CTX- and a preference for each context was assessed to measure context excitation.

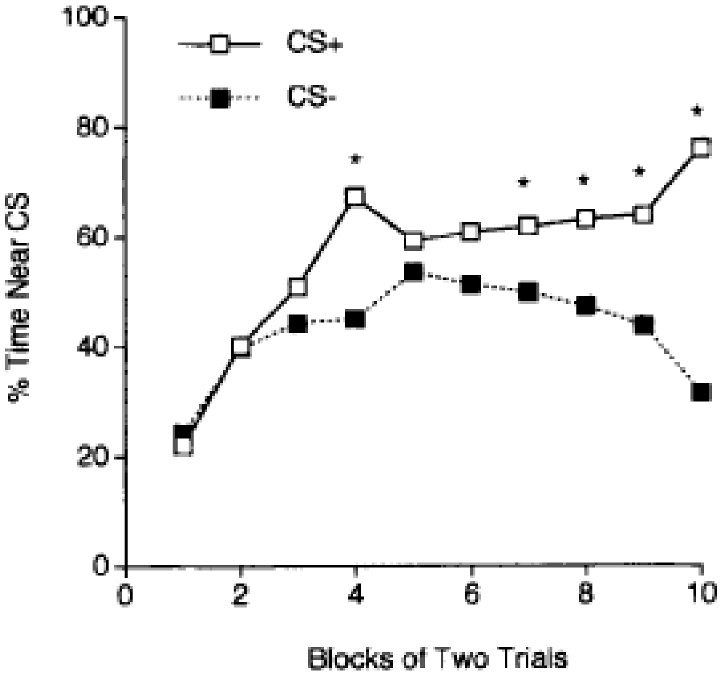

Figure 6. Mean percent time (sec) that subjects spent in the CS zone during discrimination training as a function of two-trial blocks. CS+ represents presentation of the CS that was followed by a copulatory opportunity with a female. CS- represents presentation of the CS followed by no female. (From Akins, 1998 with permission).

Figure 6 represents the percent time males spent near the block CS during discrimination training. Male quail increased the amount of time spent near the CS when the CS was followed by copulation (in the side cage) but not when the CS was not followed by copulation. However, male quail did not show a preference for CTX+ over CTX- and CTX+ did not appear to acquire excitatory conditioned properties. The findings suggest that context may have served as a modulator or occasion setter to facilitate focal search toward a local cue that signaled copulation.

Updating the Sexual Behavior System

Domjan formulated a sexual behavior system that encompassed both unconditioned and conditioned effects of male sexual behavior (Domjan, 1994).

The system includes a stimulus dimension consisting of species typical cues, local cues, and contextual cues, and a response dimension consisting of general search, focal search, and copulatory behavior. The inclusion of conditioning to the system increases potential stimulus and response variation, thereby increasing the flexibility of the system as it evolves in reaction to the results of continuing observation and experimentation. Some of the findings presented in the current paper represent an extension in the flexibility of the sexual conditioning model even more so.

Figure 7 represents our attempt to extend and update the male quail behavior system (Domjan, 1994) for sexual conditioning. Relative to Domjan's original version, open stars representing more recent evidence for sexual conditioning have been added to three additional squares. New stars in the upper-most right hand square (intersection of species typical cues and copulatory behavior) indicate that species specific cues can elicit conditioned copulatory responses. Previous research on the role of species typical cues in eliciting responding has consistently demonstrated that the presence of species specific head and neck features of the female quail elicit conditioned focal search.

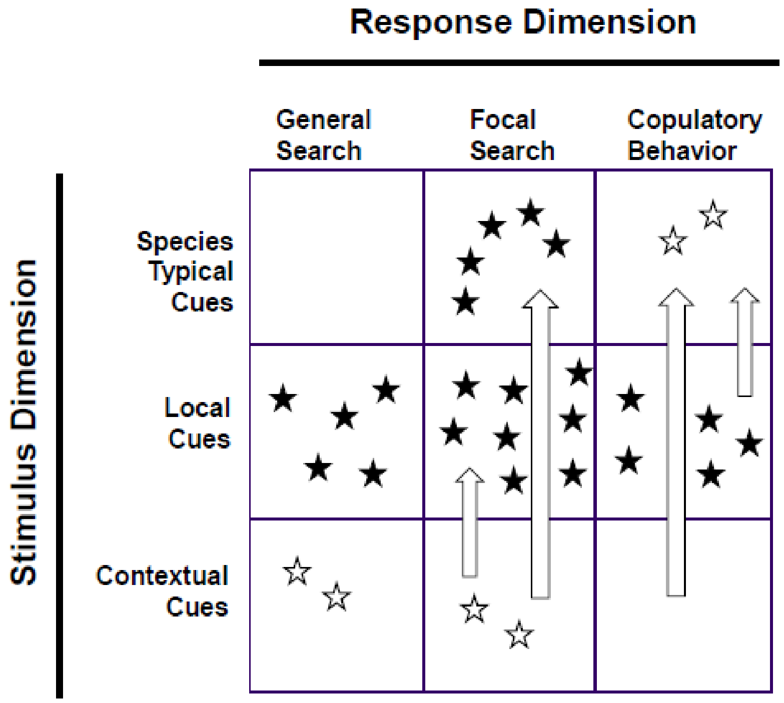

Figure 7. Stimulus and response dimensions of the modified sexual behavior system after conditioning. The stars (conditioned effects) represent the degree of control of each type of stimulus over each type of response. The open stars represent more recently found conditioned effects. Arrows represent conditioned modulatory effects. Unconditioned effects (open circles in Domjan, 1994) are not presented. (New figure based on Domjan, 1994 with permission).

There are no new stars with regard to the type of conditioned responses that local cues can elicit because prior research on the conditioning of local cues to elicit conditioned responding is abundant and the procedure has been used to demonstrate numerous learning phenomena. Sexual conditioning with a local cue has also been investigated in female quail and rather than demonstrate approach behavior, female quail engage in preparatory squatting behavior. More recent research involving sexual conditioning of a local cue has focused on whether it affords a reproductive advantage. The findings indicate that sexual conditioning has a myriad of reproductive advantages including release of greater sperm, enhanced copulatory efficiency, and a greater rate fertilization of eggs.

New open stars have been added to the bottom left two squares in the sexual behavior system of male quail (Figure 7) to represent conditioning of general search and focal search by contextual cues, respectively. Using a conditioned place preference procedure, male quail demonstrate approach behavior to a distinct chamber where they had a mating opportunity with a female quail. When placed a distinct chamber for 5 min prior to the mating opportunity, male quail show increased activity or general search behavior in anticipation of the female's arrival. Therefore, in addition to the modulatory effects that contextual cues have on conditioned responding elicited by local cues and species specific cues, they can have a direct conditioning effect on focal and general search behaviors.

General Discussion

The general process theory of learning focuses on identifying universal principles that apply to all species capable of learning from experience, and that operate across a wide variety of situations (e.g., Darwin, 1897; Morgan, 1903; Thorndike, 1911). The theory does not account for how animals learn about species specific, differentially-relevant environmental stimuli they encounter in their natural environment. Very often the conditioned behaviors elicited by these stimuli do not resemble, either in form or intensity, the conditioned responses elicited by more arbitrary stimuli. For this reason, traditional learning theories have categorized these conditioned responses as *biologically constrained*, a phrase that ironically, suggests an animal's sensory and behavioral predispositions should be considered inconvenient or limiting instead of ecologically sound. Further, general process theory assumes that general principles hold true across a broad range of stimuli and responses.

Timberlake's behavior systems theory (Timberlake, 1983, 2001; Timberlake & Lucas, 1989) represents an effort to integrate response and stimulus factors into a general theory of learning. The theory conceptualizes experiential learning not as a set of universal principles, but as species typical processes that reflect the specific demands of the ecological niche in which the species evolved. (For a review of how hypotheses of adaptive specializations of learning may be tested, see Krause, 2015). The behavior systems approach to investigating animal learning assumes that species specific mechanisms, honed by an animal's evolutionary history, guide an animal's learned and unlearned behaviors in both naturalistic and laboratory environments. Relative to general process conceptions, behavior systems are constructed. By definition, they assume non-equivalence across species and are built from the bottom up. Elements and parameters of each system are the culminating result of both naturalistic observation and experimentation. The former helps construct the system as it operates innately, the latter investigates how the system is affected and/or enhanced by experiential learning. Though the process of system design is more time consuming and less universal, the end result is arguably more accurate ¬since all system elements are derived from observation of, and experimentation with, each individual species.

Behavior systems have been developed for various learned behaviors including defensive behaviors (Fanselow, 1994), feeding behaviors (Timberlake, 1994, Silva & Timberlake, 2005), pecking and dustbathing behavior (Hogan, 1994), and sexual behavior (Domjan, 1994), the latter of which has been updated in the current paper. Relatively recent research has also contributed toward the development of a socially-acquired predator avoidance behavior system that incorporates Pavlovian conditioning (Griffin, 2008; Dunlap & Stephens, 2014). The basic premise of these behavior systems is that the determinants of behavior have been shaped by evolutionary pressure but that learning can be incorporated to increase flexibility within each system. This increased flexibility may ultimately result in increased survival and reproductive success (see Krause, 2015, for further discussion).

It is evident that, with some exception, a limited amount of work has been done in the field of learning to continue to apply laboratory data to the naturalistic behavior systems of animals. There are numerous behavior systems that could be developed in a variety of animal species. For example, researchers have collected a plethora of data on parental care in various species of animals. It would be of interest in determining whether/how those data would support a behavior systems. Furthermore, with the exception of the female rat feeding system, studies on behavior systems have been limited to studying male behavior. It should be noted that Timberlake’s studies on the feeding behavior system (e.g., Timberlake, 1983; Silva & Timberlake, 1998, 2005) typically used female rats. In contrast, the sexual behavior system in quail is specific to male quail. However, research on female sexual behavior (Gutiérrez & Domjan, 1997, 2011) is a step closer to the development of a well needed behavior system in female quail.

Finally, it is important to note that the successes of the behavior system approach do not discount the existence of universal learning principles. In fact, similar mechanisms may be responsible for the learning that occurs in multiple species. But the existence of such general learning principles should not be assumed. The results from multiple learning paradigms have revealed such assumptions to be inaccurate. Instead, if general learning processes exist they need to be discovered, by comparing the elements and parameters of multiple behavior systems and identifying common features. Only in this way can similarities among species, and thus general processes of learning, be identified.

Acknowledgments

We would like to thank Dr. Michael Domjan whose ideas were the impetus for this paper.

References

Agmo, A., & Berenfeld, R. (1990). Reinforcing properties of ejaculation in the male rat: The role of opioids and dopamine. *Behavioral Neuroscience*, *104*, 177-182.

Akins, C. K. (1998). Context excitation and modulation of conditioned sexual behavior. *Animal Learning and Behavior*, *26*, 416-426.

Akins, C. K. (2000). Effects of species-specific cues and the CS-US interval on the topography of the sexually conditioned response. *Learning and Motivation*, *31*, 211-235.

Akins, C. K., Domjan, M., & Gutiérrez, G. (1994). Topography of sexually conditioned behavior in male Japanese quail (*Coturnix japonica*) depends on the CS-US interval. *Journal of Experimental Psychology: Animal Behavior Processes*, *20*, 199-209.

Baerends, G. P. (1988). Ethology. In R. C. Atkinson, R. J. Herrnstein, G. Lindsey, & R. D. Luce (Eds.), *Stevens' Handbook of Experimental Psychology* (Vol. 1, pp. 765-830). New York, NY: Wiley.

Breland, K., & Breland, M. (1961). The misbehavior of organisms. *American Psychologist*, *16,* 681-684.

Burns, M., & Domjan, M. (1996). Sign tracking versus goal tracking in the sexual conditioning of male Japanese quail (*Coturnix japonica*). *Journal of Experimental Psychology: Animal Behavior Processes, 22*, 297-306.

Burns, M., & Domjan, M. (2001). Topography of spatially directed conditioned responding: effects of context and trial duration. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*, 269-278.

Craig, W. (1918). Appetites and aversions as constituents of instincts. *Biological Bulletin of the Marine Biological Laboratory, Woods Hole*, *MA*, *34*, 91-107.

Crawford, L. L., & Domjan, M. (1995). Second-order sexual conditioning in male Japanese quail (*Coturnix japonica*). *Animal Learning & Behavior*, *23*, 327-334.

Crawford, L. L., & Domjan, M. (1996). Conditioned inhibition of social approach in male Japanese quail (*Coturnix japonica*) using visual exposure to a female. *Behavioral Processes*, *36*, 163-169.

Cusato, B., & Domjan, M. (1998). Special properties of species typical cues in sexual conditioning: Tests with a conditioned stimuli preexposure design. *Learning and Motivation*, *29*, 152-167.

Darwin, C. (1897). *The descent of man and selection in relation to sex*. New York, NY: Appletone-Century-Crofts.

Domjan, M. (1994). Formulation of a behavior system for sexual conditioning. *Psychonomic Bulletin & Review*, *1*, 421-428.

Domjan, M. (1998). Going wild in the laboratory: Learning about species typical cues. In D. L. Medin (Ed.), *The Psychology of Learning and Motivation* (Vol. 38). San Diego, CA: Academic Press.

Domjan, M., Akins, C., & Vandergriff, D. H. (1992). Increased responding to female stimuli as a result of sexual experience: Tests of mechanisms of learning. *Quarterly Journal of Experimental Psychology*, *45B*, 139-157.

Domjan, M., Blebois, E., & Williams, J. (1998). The adaptive significance of sexual conditioning: Pavlovian control of sperm release. *Psychological Science*, *9*, 411-415.

Domjan, M., Cusato, B., & Krause, M. (2004). Learning with arbitrary versus ecological conditioned stimuli: Evidence from sexual conditioning. *Psychonomic Bulletin and Review*, *11*, 232-246.

Domjan, M., Greene, P., & North, N.C. (1989). Contextual conditioning and the control of copulatory behavior by species-specific sign stimuli in male Japanese quail. *Journal of Experimental Psychology: Animal Behavior Processes*, *15*, 147-153.

Domjan, M., & Hall, S. (1986). Determinants of social proximity behavior in Japanese quail (*Coturnix coturnix japonica*): Male behavior. *Journal of Comparative Psychology*, *100*, 59-67.

Domjan, M., Huber-McDonald, M., & Holloway, K. S. (1992). Conditioning copulatory behavior to an artificial object: Efficacy of stimulus fading. *Animal Learning & Behavior, 20*, 350-362.

Domjan, M., Lyons, R., North, N.C., & Bruell, J. (1986). Sexual Pavlovian conditioned approach behavior in male Japanese quail (*Coturnix japonica*), *Journal of Comparative Psychology*, *100*, 413-421.

Domjan M., Mahometa, M. J., & Matthews, R. N. (2012). Learning in intimate connections: Conditioned fertility and its role in sexual competition._*Socioaffective Neuroscience and Psychology*, *2*, 17233.

Domjan M., Mahometa, M. J., & Mills, A. D. (2003). Relative contributions of the male and the female to sexual behavior and reproductive success in the Japanese quail *(Coturnix japonica). Journal of Comparative Psychology*, *117*, 391-399.

Domjan, M., & Nash, S. (1988). Stimulus control of social behavior in male Japanese quail, *Coturnix coturnix japonica*. *Animal Behaviour*, *36*, 1006-1015.

Domjan, M., O'Vary, D., & Greene, P. (1988). Conditioning of appetitive and consummatory sexual behavior in male Japanese quail. *Journal of the Experimental Analysis of Behavior*, *50*, 505-519.

Dunlap, A. S., & Stephens, D. W. (2014). Experimental evolution of prepared learning. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 11750-11755.

Eibl-Eibesfeldt, I. (1970). *Ethology: The Biology of Behavior*. New York, NY: Holt, Rinehart and Winston.

Everitt, B. J. (1990). Sexual motivation: A neural and behavioral analysis of the mechanisms underlying appetitive and copulatory responses of male rats. *Neuroscience and Biobehavioral Reviews*, *14*, 217-232.

Fanselow, M. S. (1994). Neural organization of the defensive behavior system responsible for fear. *Psychonomic Bulletin & Review*, *1*, 429-438.

Fanselow, M. S. (1997). Species-specific defensive reactions: Retrospect and prospect. In M. E. Bouton and M. S. Fanselow (Eds.), *Learning, Motivation, and Cognition*. (pp. 321-341). Washington, D. C.: American Psychological Association.

Farris, H. E. (1967). Classical conditioning of courting behavior in the Japanese quail, *Coturnix coturnix japonica*. *Journal of the Experimental Analysis of Behavior*, *10*, 213-217.

Foree, D. D., & LoLordo, V. M. (1973). Attention in the pigeon: the differential effects of food-getting vs. shock-avoidance procedures. *Journal of Comparative and Physiological Psychology*, *85*, 551-558.

Garcia, J., & Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychonomic Science*, *4*, 123-124.

Griffin, A. S. (2008). Socially acquired predator avoidance: Is it just classical conditioning? *Brain Research Bulletin*, *76*, 264-271.

Gutiérrez, G., & Domjan, M. (1997). Differences in the sexual conditioned behavior of male and female Japanese quail (*Coturnix japonica*). *Journal of Comparative Psychology*, *111*, 135-142.

Gutiérrez, G. & Domjan, M. (2011). Conditioning of sexual proceptivity in female quail: Measures of conditioned place preference. *Behavioural Processes, 87*, 268-283.

Hinde, R. A., & Stevenson-Hinde, J. (Eds.) (1973). *Constraints on learning*. New York, NY: Academic Press.

Hogan, J. A. (1994). Structure and development of behavior systems. *Psychonomic Bulletin & Review*, *1*, 439-450.

Hollis, K. L., Cadieux, E. L., & Colbert, M. M. (1989). The biological function of Pavlovian conditioning: A mechanism for mating success in the blue gourami (*Trichogaster trichopterus*). *Journal of Comparative Psychology, 103*, 115-121.

Hughes, A. M., Everitt, B. J., & Herbert, J. (1990). Comparative effects of preoptic area infusions of opioid peptides, lesions, and castration of sexual behavior in male rats: Studies of instrumental behavior, conditioned place preference and partner preference. *Psychopharmacology*, *102*, 243-256.

Kawahara, T. (1967). Wild Coturnix quail in Japan. *Quail Quarterly*, *4*, 62-63.

Köksal, F., Domjan, M., & Weisman, G. (1994). Blocking of the sexual conditioning of differentially effective conditioned stimulus objects. *Animal Learning & Behavior*, *22*, 103-111.

Krause, M. (2015). Evolutionary perspectives on learning: conceptual and methodological issues in the study of adaptive specializations. *Animal Cognition*, DOI 10.1007/s10071-015-0854-4.

Krause, M., Cusato, B., & Domjan, M. (2003). Extinction of conditioned sexual responses in male Japanese quail (*Coturnix japonica*): role of species-typical cues. *Journal of Comparative Psychology*, *117*, 76-86.

Lorenz, K. (1981). *The Foundations of Ethology*. New York, NY: Springer-Verlag.

Mahometa, M. J., & Domjan, M. (2005). Classical conditioning increases reproductive success in Japanese quail, *Coturnix japonica*. *Animal Behaviour, 69*, 983-989.

Mills, A. D., Crawford, L. L., Domjan, M., & Faure, J. M. (1997). The behavior of the Japanese of domestic quail *Coturnix japonica*. *Neuroscience and Biobehavioral Review*, *21*, 261-281.

Nash, S., Domjan, M., & Askins, M. (1989). Sexual-discrimination learning in male Japanese quail (*Coturnix coturnix japonica*). *Journal of Comparative Psychology*, *52*, 415-419.

Noble, R. (1972). The effects of estrogen and progesterone on copulation in female quail (*Coturnix coturnix japonica*) housed in continuous dark. *Hormones and Behavior*, *3*, 199-204.

Paredes, R., & Alonso, A. (1997). Sexual behavior regulated (paced) by female induces conditioned place preference. *Behavioral Neuroscience*, *111*, 123-128.

Paredes, R., & Vazquez, B. (1999). What do female rats like about sex? Paced mating. *Behavioural Brain Research*, *105*, 117-127.

Pfaus, J. G., Kippin, T. E., & Centeno, S. (2001). Conditioning and sexual behavior: A Review. *Hormones and Behavior*, *40*(2), 291-321.

Rozin, P., & Kalat, J. W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychological Review*, *78*, 459-486.

Schwartz, C. W., & Schwartz, E. R. (1949). *A reconnaissance of the game birds in Hawaii*. Hilo: Hawaii Board of Commissioners of Agriculture and Forestry.

Seligman, M. E. P., & Hager, J. L. (Eds.) (1972). *Biological boundaries of learning*. New York, NY: Appleton-Century-Crofts.

Shettleworth, S. J. (1972). Constraints on learning. *Advances in the study of behavior*, *4*, 1-68.

Silva, K. M., & Timberlake, W. (1998). A behavior systems view of responding to probe stimuli during an interfood clock. *Animal Learning & Behavior*, *26*, 313-325.

Silva, K. M., & Timberlake, W. (2005). A behavior systems view of the organization of multiple responses during a partially or continuously reinforced interfood clock. *Learning & Behavior*, *33*, 99-110.

Timberlake, W. (1983). The functional organization of appetitive behavior. Behavior systems and learning. In M. D. Zeiler and P. Harzem (Eds.), *Advances in Analysis of Behaviour. Vol. 3: Biological Factors in Learning*. (pp. 177-221). Chichester, England: Wiley.

Timberlake, W. (1994). Behavior systems, associationism, and Pavlovian conditioning. *Psychonomic Bulletin & Review*, *1*, 405-420.

Timberlake, W. (2001). Motivational modes in behavior systems. In R. R. Mowrer & S. J. Klein (Eds.), *Handbook of contemporary learning theories*, pp.155-209. Mahwah, NJ: Erlbaum.

Timberlake, W., & Lucas, G. A. (1989). Behavior systems and learning: From misbehavior to general principles. In S. B. Klein and R. R. Mowrer (Eds.), *Contemporary learning theories: Instrumental conditioning theory and the impact of biological constraints on learning*. (pp. 237-275). Hillsdale, NJ: Erlbaum.

Tinbergen, N. (1951). *The Study of Instinct*. London, UK: Oxford University Press.

Thorndike, E. L. (1911). *Animal intelligence: Experimental studies*. New York: Macmillan.

Wilson, M. I., & Bermant, G. (1972). An analysis of social interactions in Japanese quail (*Coturnix coturnix japonica*). *Animal Behaviour*, *20*, 252-258

Zamble, E., Mitchell, J. B., & Findlay, J. B. (1986). Pavlovian conditioning of sexual arousal: Parametric and background manipulations. *Journal of Experimental Psychology: Animal Behavior Processes*, *12*, 403-411.

Financial conflict of interest: No stated conflicts.
Conflict of interest: No stated conflicts.

Submitted: *March 8th, 2015*
Revision submitted: *June 9th, 2015*
Accepted: *June 10th, 2015*