



Naturalistic learning and reproduction in ring neck doves (*Streptopelia risoria*)

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Abstract

Successful reproduction in avian species requires considerable parental care, and for most species the efforts of both parents are necessary for the survival of offspring. Here we make the case that in these species reproductive interactions are enhanced when neurochemical activity reinforces critical stimuli and behaviors through associative learning. Drawing from research on several different species, we describe evidence for the role of associative learning in the reproductive behaviors of ring neck doves (*Streptopelia risoria*). A hypothetical mechanism involving a combination of classical and operant conditioning is proposed to explain the formation and maintenance of the pair bond, nest fidelity, and incubation behavior. The role of the opiate system in reinforcing various aspects of reproductive behavior in this and other species is discussed.

Keywords Naturalistic learning · Incubation · Contact reward · Opioids · Ring neck dove

Introduction

For most birds, successful reproduction requires considerable parental care. In fact, in over 80% of avian species the efforts of both parents are necessary for the survival of offspring (Cockburn, 2006). Based on available evidence we herein make the case that the naturally occurring reproductive behavior of ring neck doves is enhanced through a series of conditioning events in which critical stimuli and behaviors are reinforced via neurochemical activity.

Between the 1950s and early 1990s, researchers such as Daniel Lehrman, John Buntin, Rae Silver, and Mei-Fang Cheng advanced understanding of avian reproductive behavior using ring neck doves (*Streptopelia risoria*) as a model species (e.g., Buntin et al., 1996; Cheng, 1979; Lehrman, 1955; Silver et al., 1973). Ring neck doves were a much better model for avian reproduction than other avian species common to laboratories at the time (e.g., domestic chickens (*Gallus gallus*)). Chickens belong to a minority of bird species that do not engage in biparental care. Ring neck doves, in contrast, expressed forms of reproductive behaviors seen in the majority of birds: courtship from both the male and

female, pair bonding, nest attachment, shared incubation with a predictable schedule, and biparental care for young chicks. This intense research attention yielded a wealth of information regarding the neuroendocrine underpinnings of ring neck doves' reproductive and parental behavior, including the hormonal profiles necessary to mediate each stage of the reproductive cycle. However, hormonal systems alone were rarely used as the sole explanatory mechanisms of complex behaviors such as the formation and maintenance of the pair bond or the emergence of shared incubation schedules, or even the relatively simple reproductive behavior of incubation itself. Rather, these early researchers correctly surmised that hormones serve a permissive or modulatory role (Beach, 1948) in avian reproduction, initiating a cascade of neuronal activity that underlies the different behavioral components. It was Beach (1948) who also concluded that most reproductive behavior is overdetermined, regulated by redundant physiological mechanisms, and that this redundancy includes learning processes that complement the neurological circuitry responsible for correct behavioral responses under appropriate stimulus conditions. Given the redundancy supporting avian reproductive behavior, a number of important questions emerge. What are the learning mechanisms regulating avian reproductive behavior? Do associative learning mechanisms serve a major or supporting role, and if so, what conditioning parameters regulate the specific behaviors during each reproductive

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stage? Finally, how might physiological, neurological, and behavioral mechanisms interact in the initiation and regulation of parental behavior of ring neck doves?

We explore these questions here, some of which have been addressed in research and some that still need to be explored. We have adopted the same principled thinking applied by Michael Domjan in his study of the conditioning of sexual behavior in male and female Japanese quail (*Coturnix japonica*) (Burns & Domjan, 1996; Crawford et al., 1993; Domjan et al., 1986; Domjan & Gutiérrez, 2019; Krause et al., 2003). These thorough investigations have produced a wealth of information regarding the role of learning in the regulation of male and female sexual responding (Akins & Cusato, 2015). Much of this work has focused on the plasticity of male sexual behavior and how Pavlovian conditioning serves to improve the efficiency of male-female sexual interactions (Domjan et al., 1998; Domjan et al., 2000). Among its most impressive outcomes, Domjan's 40 plus years of disciplined research in this area has produced a detailed behavior system for male quail sexual behavior that organizes the specific stimulus and response parameters regulating reproductive success in this species (Crawford et al., 1993; Domjan, 1994; Domjan & Gutiérrez, 2019; Hilliard et al., 1997). We recognize similar interplay among the stimuli and responses that regulate the complex reproductive behavior of ring neck doves.

Courtship and mating in ring neck doves

When a male dove is paired with another dove, it will engage in aggressive courtship (Lovari & Hutchison, 1975), energetically lowering the rostral portion of the body till the beak nearly touches the floor as he emits a “coo.” He then stands tall as he inhales and repeats the movement while maintaining close proximity to the other bird. This behavior is referred to as bow-cooing. If the introduced bird is a male, it will likely respond with its own aggressive courtship, leading to antagonistic behavior between the two males. The aggressive courtship interaction may last for several minutes and escalate to include pecks directed towards the head, “kah” vocalizations, hop charges, and wing boxing (Miller & Miller, 1958) until the conflict eventually appears to resolve. If the introduced bird is a receptive female, however, she responds to the male's aggressive courtship by producing her own vocalizations (Lehrman, 1965) and tail quivers (Mitoyen et al., 2021), a signal to the male that the reproductive interaction is progressing. These behavioral signals trigger an increase in the male's plasma testosterone, an effect that only occurs when he is paired with a female and not with another male (Feder et al., 1977). By the second day, the male shifts from aggressive to nest-oriented courtship in which a less vigorous form of the bow-coo is performed as

he stands on or near the potential nest site (“nest-coo”). The nest-coo differs from the bow-coo of aggressive courtship both in its location (with the former always performed at the nest and the later occurring at any location in the cage) but also with the addition of a “wing flip,” twitching of the tips of the wings when the head is in the lowered position. If the female accepts the chosen nest site, she will also perform nest-coos and wing-flips. Interestingly, it is the female's vocalizations at this point in courtship that activate the oviducts leading to ovulation (M.-F. Cheng, 1992).

During this period, a critical change occurs that underlies the formation of a bond between the male and female, and as a result of this change, each bird acquires reinforcement value for the other bird in the pair (Burns-Cusato & Cusato, 2013). We found evidence for this change in ring neck doves using a conditioned place-preference paradigm. In a series of experiments, individual ring neck dove spent time with their bonded mate in one cage (Mate Context) and with an unfamiliar bird of the opposite sex in a different cage (Stranger Context). Then, when given a choice, both males and females showed a preference for the Mate Context over the Stranger Context even though neither stimulus birds were present at the time of testing (Burns-Cusato & Cusato, 2013). Presumably, interactions with the mate engendered a positive affective state (reinforcement) to a greater degree than interactions with the stranger. Because the positive experience occurred in the Mate Context, the unique features of this environment (e.g., color of the walls) became associated with the rewarding state and, hence, elicit conditioned approach. This suggests that the pair bond, which has been described as a psychological adhesive bond that keeps the birds together (Bales et al., 2021), may be formed and/or maintained as a function of Pavlovian conditioning. Each bird of the pair becomes attached to distinctive stimuli, the specific visual and/or behavioral characteristics of the other bird – its pair-bonded mate, and these previously neutral stimuli acquire reinforcement value, presumably because of their temporal pairing with pleasurable sensation (Burns-Cusato et al., 2005). As seen in the conditioned place-preference experiments (Burns-Cusato & Cusato, 2013), these distinctive stimuli will elicit conditioned approach.

Other associative mechanisms, in addition to Pavlovian condition, may also play a role in the formation and maintenance of the pair bond in this species. Drawing on a model proposed by Lauren Ritters (2011) to explain the role of negative reinforcement within the bird song system (Ritters, 2011), we hypothesize that a similar mechanism may govern the interactions of male and female ring neck doves during courtship. In this hypothetical paradigm, the nest-coo and/or wing flip acts as an unconditioned stimulus that triggers the release of endorphins. Opioids are known to underlie reward-seeking behavior: agonists decreased, and antagonists increased, reward seeking such as courtship in

European starlings (*Sturnis vulgaris*) (Schroeder & Ritters, 2006) and white-throated sparrows (*Zonotrichia albicollis*) (Maney & Wingfield, 1998). Opioids within the ventral tegmental area (VTA) stimulate dopamine neuronal firing rate and release, and associated sexually motivated behaviors, presumably by inhibiting GABA, which then disinhibits dopamine neuronal firing and release (Kalivas, 1993; van Furth et al., 1995). Although it remains unclear whether dopamine underlies seeking or anticipation of reward (Berridge & Kringelbach, 2008) or reinforcement and incentive salience functions (Wang et al., 2020), dopaminergic activity in the VTA is associated with courtship behavior in European starlings (Heimovics & Ritters, 2005) and zebra finch (*Taeniopygia guttata*) (Hara et al., 2007), and dopamine is released in the medial pre-optic area (mPOA) in association with sexually motivated behavior in Japanese quail (Kleitz-Nelson et al., 2010). Moreover, consistent with the prediction that dopamine is critical for sexually motivated courtship behavior, peripherally administered dopamine agonists stimulate whereas antagonists inhibit female-directed song in both zebra finches (Rauceo et al., 2008) and European starlings (Schroeder & Ritters, 2006).

Ritters (2011) describes a negative reinforcement system by which opioid activity can maintain the conditioned response (courtship directed towards a specific individual) in song birds via negative feedback. In the absence of social contact, opioid levels drop, resulting in an unpleasant affective state that can be remedied through social contact-induced opioid release. Thus, a drop in opioid levels may trigger dopamine-mediated reward-seeking behaviors (such as female-directed singing). Once a male has attracted a female, opioids are released during physical contact, and dopamine-triggered seeking behavior is inhibited (Ritters, 2011). In a similar way, the lack of social contact from a female dove may cause a decrease in opioid levels and corresponding aversive drive state in the male, and this, in turn, may trigger dopamine-mediated reward-seeking behaviors such as bow cooing and nest cooing. If the courtship is successful, the resulting physical contact releases opioids that reduces the drive state. Moreover, any net increase in opioid levels during male-female interactions may also explain why specific characteristics of the pair-bonded mate acquire reinforcing value as conditioned stimuli. Similar feedback and feed-forward mechanisms have been shown to regulate a wide variety of social interactions in birds and other species (see Domjan et al., 2000, for a review).

Nonapeptides, such as mesotocin, may further strengthen the association between specific characteristics of the stimulus bird (now a conditioned stimulus) and the internal reinforcement. There is some evidence that mesotocin, the avian oxytocin-analog, may play a selective role in social but not general reward (Ritters et al., 2019). In zebra finches, for example, activation of midbrain receptors by mesotocin is

necessary for the formation of pair bond (Goodson et al., 2009; Klatt & Goodson, 2013). The same neuropeptide underlies social bonding in pinyon jays (*Gymnorhinus cyanocephalus*) (Duque et al., 2020). In rats, oxytocin has been found to enhance conditioned place preference for a context previously paired with a mu opioid receptor agonist (Moadab et al., 2015). This indicates that oxytocin may increase the salience of stimuli that release opioids (Moaddab et al., 2015). If the same holds true for birds, then the difference between courtship directed towards a potential mate and courtship directed towards an acquiescent mate (one that has signaled acceptance/consent with wing flip) is that the wing flip stimulates secretion of mesotocin, which makes the reward circuit more sensitive to opioids. Henceforth, that specific bird engenders stronger reinforcement than other birds and, thus, becomes a conditioned stimulus eliciting a conditioned approach. Therefore, the pair bond observed between a breeding male and female is the conditioned approach mediated by acquired reinforcement value of a specific bird. Our lab aims to test these ideas in the future but as of this writing, this model is hypothetical.

After the birds have exchanged bow coos, nest coos, and wing flips as described above, the pair begins nest building in earnest. Typically, the male will bring nest material to the site, which the female then tucks into place. Throughout the nest-building process, the male will continue to court the female with bow-coos while standing in the nest. Copulation then takes place at the nest over a 2- to 3-day period and the female will sit in the nest for several hours prior to the appearance of the first egg. The second of the two-egg clutch is usually laid 24 h later initiating a shift from courtship to parental care behavior in the form of cooperative incubation of the eggs (Lehrman, 1965).

Nest fidelity and incubation

As demonstrated during the stages of courtship, nest building, and copulation, early elements of the reproductive cycle in ring neck doves are dynamic, cooperative, and likely regulated by a complex interplay of behavioral and neuroendocrine mechanisms. Later elements of the cycle include incubation and parental care, and these too are best characterized in the same way. Following nest building, copulation, and laying eggs, parents will begin to incubate the eggs. In ring neck doves, the breeding pair incubates in a fairly reliable fashion: the male sits on the nest for several hours during the middle of the day (e.g., Craig, 1909; Ramos & Silver, 1992; Wallman et al., 1979) and the female typically leaves the vicinity to forage, engage in self-care such as bathing, and avoid drawing potential predators' attention to the location of the nest (McFarland, 1977). In the late afternoon, the female returns to the nest and takes over as nest sitter as

the male flies away. Evidence suggests that although sexually dimorphic endogenous circadian factors are probably responsible for the gross sitting patterns, the precise timing of incubation and brooding by the male and female may be affected by environmental, behavioral, and experiential factors (Wallman et al., 1979). For example, in ring neck doves the number of nest exchanges tended to decrease after the second day of incubation, indicating that at the onset of incubation, the drive to sit on the nest but not necessarily the timing of cooperative incubation, is in place (Ball & Silver, 1983). Typically, by the third day of incubation, a reliable nesting schedule is established in which the male and female take predictable turns on the nest (nesting session) and away from the nest (recess). Other species that share incubation duties have also been reported to show an initial period of arrhythmicity before the emergence of a predictable schedule of nest exchanges between the male and female emerges (Coulson, 1970). An initial period of behavioral flexibility is beneficial for bird species with a serial monogamous mating system, such as ring neck doves. In serial monogamy, a male and female form short-term pair bonds for the duration of a single breeding cycle or season. Subsequent breeding attempts are then made with new bonded partners, likely exhibiting nesting patterns that are somewhat different from the previous mate.

Even though sitting schedules are fairly predictable by the third day of incubation, there is a degree of variability in the schedule both within and between pairs of ring neck doves. For example, for one breeding pair, the first nest switch of the day may typically occur any time between 900 h and 1100 h (mid-morning), whereas a different breeding pair does not typically shift sitters until early afternoon (between 1200 h and 1400 h) (see Ramos & Silver, 1992, Fig. 3A, for timing of incubation bouts in a representative pair). Wallman et al. (1979) found that some ring neck dove males were observed to be on the nest for as little 23% (short sitters) and others as much as 76% (long sitters) of observations made between 900 h and 1700 h each day of the incubation period. Pairing short sitters and long sitters with new breeding partners in subsequent breeding cycles revealed that the male and female both make adjustments to sitting duration to ensure the eggs are continuously covered.

During the early days of incubation, the partners may be learning how the idiosyncratic nesting pattern of the mate fits with their own nesting drive in order to form a cooperative and predictable schedule. Plasticity in the incubation schedule allows the birds to experience their new partner's unique pattern of behavior and make necessary adjustments to their own behavior to facilitate successful biparental care. Further evidence that ring neck doves adjust the timing of their incubation behavior to that of their mate comes from reports of extended incubation sessions when a partner fails to show up at the nest at the predicted time (Silver & Gibson,

1980). If a bird is taken off the nest during while incubating, its mate will reliably move to the nest to cover the eggs (personal observation). This suggests that the birds may be responding to external cues (mate's behavior and/or exposed eggs) and not exclusively to circadian rhythms.

During the 14-day incubation period, both the mate and the nest serve as natural reinforcers for doves. The male and female spend little time together during this phase of the reproductive cycle. Yet, the strength of the pair bond appears to increase during incubation relative to the courtship phase. In one study (Burns-Cusato & Cusato, 2013), both male and female doves showed stronger evidence of conditioned place preference for a context that was paired with a bonded mate during the incubation phase of the reproductive cycle than with a different context that had been paired with the same mate during courtship (see Fig. 1).

The conditioned place preference tests suggest that a breeding ring neck dove is strongly attracted to its mate during the incubation phase of reproduction. However, at the beginning of each nesting session, one bird settles on the nest while its mate leaves the vicinity. This separation conflicts with expected approach to high-valued reinforcers. Unless, of course, the reinforcement value of the eggs and nest exceed that of the mate. Burns-Cusato and colleagues found this to be the case in a more recent study. When male ring neck doves had visual access to their nest on one side of a test chamber and visual access to their mate on the other side of the test chamber, they spent significantly more time near the window through which they could see the nest, or "nest zone" (see Fig. 2, Burns-Cusato et al., 2021). The fact that the nest site elicited a strong approach indicates that this previously neutral location in which the pair have engaged in courtship, copulation, and deposited eggs acquired reinforcement value that was greater than reward associated with the mate alone.

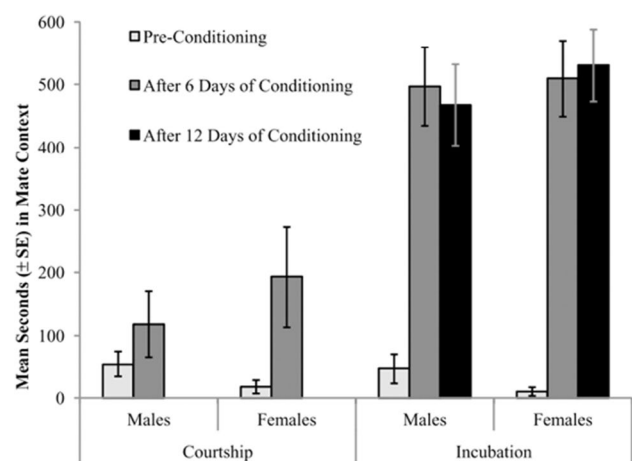


Fig. 1 From Burns-Cusato and Cusato (2013)

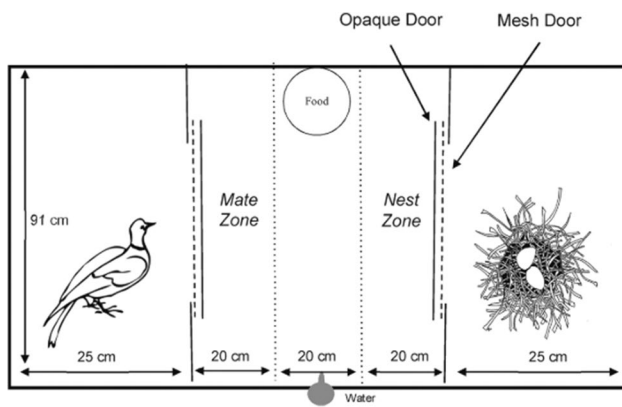


Fig. 2 Apparatus used in Burns-Cusato et al. (2021)

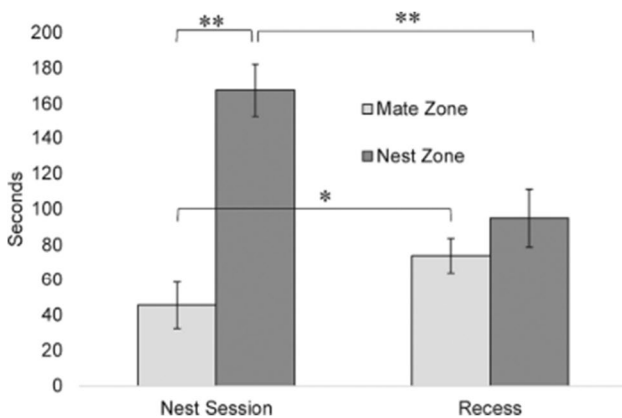


Fig. 3 From Burns-Cusato et al. (2021)

Interestingly, the marked preference for the nest over the mate was only observed when testing occurred at a time when subjects were scheduled to be on the nest (nest session), mid-day for male ring neck doves (Fig. 3). In tests that were conducted in the evening, when the female was scheduled to be on the nest (the male's "recess"), males showed no preference for the mate (behind one window) or the uncovered nest (behind the other) (Burns-Cusato et al., 2021). Presumably, the same is true for female doves but this is yet to be tested. These results suggest that for ring neck doves, and possibly other bird species that share incubation responsibilities, acquired reinforcement value of the nest waxes and wanes in a sexually dimorphic circadian pattern that complements that of their mate, resulting in alternating nest-sitting turns in the incubation schedule. This would explain why one parent stays on the nest and its bonded mate flies away. The powerful attraction of the nest increases and decreases in conjunction with each bird's nesting session and recess, respectively.

The alternating-nest sitting behavior characteristic of shared incubation in ring neck doves has led us to consider

what it is about the nest or eggs that overrides the reinforcing elements of the pair-bonded mate. Physical contact with warm stimuli is reinforcing for numerous species including birds (Panksepp et al., 1980a), rats (Blumberg et al., 1992), pigs (Baldwin & Meese, 1977), and primates (Harlow, 1958). This phenomenon, known as *contact comfort* (Harlow, 1958), typically occurs with taction between parents and offspring, siblings, and mates, but is also evident in the somnolent behavior of domestic chicks cupped in warm human hands (Panksepp et al., 1980a). Similarly, physical contact between warm eggs and the parent's belly may engender contact comfort in incubating birds. Like Panksepp's hand-warmed chicks, birds incubating eggs spend the vast majority of nest sessions resting and sleeping (Deeming, 2002). The hypothesis that contact with eggs is reinforcing is further supported by observations of wild birds pushing reluctant mates off the nest during an exchange (Murton & Isaacson, 1962; Skutch, 1976). Eventually, drives to eat, drink, and engage in self-care override the drive to sit on the nest, and this results in the sitter giving up its position (Hogan, 1989). Ball and Silver (1983) suggested that the term "nest take-over" was a more apt description of the nest changeover than the more commonly used term, "nest relief."

What might be the neuroendocrine mechanism responsible for the contact comfort documented in so many species? Endogenous opiates have been identified as the reinforcing factor in several socially motivated behaviors, such as pair bonding (Resendez et al., 2013), copulation (Ågmo & Berenfeld, 1990), mother-infant bonding (Shayit et al., 2003), grooming (Keverne et al., 1989; Martel et al., 1995), and social affiliation (Panksepp et al., 1980b; Riters et al., 2019). The opiate system may also reinforce incubation behavior.

Opiate-mediated reinforcement resulting from physical contact with eggs could support two separate but complementary conditioning mechanisms that facilitate the maintenance of incubation. Through instrumental conditioning processes, the act of sitting on the eggs may be reinforced by the release of endorphins and subsequent pleasure. Egg-sitting becomes an operant response that the bird performs in order to derive the pleasurable outcome. Evidence for this learning mechanism was reported by Burns-Cusato et al. (2021). Blocking opiate receptors with naloxone produced a disruption in incubation behavior of ring neck doves. In addition to spending less time on the nest overall, subjects tended to leave and return to the nest, unlike their saline-treated counterparts. Movement towards and away from the nest may be indicative of conditioned nest sitting followed by discontinuation of the behavior when the expected reward does not occur. Administration of a non-sedating dose of morphine, an opiate receptor agonist, also decreased time spent nesting, possibly because during the test, subjects experienced the desired reinforcement without needing to engage in the

conditioned behavior. It is important to note that neither treatment with an opiate antagonist nor agonist completely eliminated nesting behavior during the tests. Rather less time was spent on the nest when the opiate system was compromised compared to controls. This supports Beach's assertion that redundant mechanisms underlie reproductive behavior (Beach, 1948) and that learning mechanisms alone cannot explain incubation behavior.

A second form of conditioning may coincide with the operant processes described above. The positive effects of opioids are easily associated with locations and objects (Bardo & Neisewander, 1986; Schuster & Woods, 1968; Wise, 1989). Thus, the visual stimuli that surround the parent bird as it sits on the nest, such as the trunk of a tree, likely become associated with the pleasurable experience via Pavlovian mechanisms. Electromagnetic cues used by birds to navigate the environment (Able, 1994) may also become associated with the location of reinforcement. Through such associations, the nest and other environmental elements of the nest site become predictive, or conditioned, stimuli that signal the location where pleasure is experienced. As a result of this association, the bird expresses a conditioned response in the form of approach to the nest. Therefore, activation of the opiate system during incubation would simultaneously assign associative value to stimuli related to important "what" and "where" elements of each bird's reproductive behavior: what specific behaviors need to occur at this particular point in the incubation cycle and where the behaviors should occur. When a parent bird has been away from the eggs for a period of time, an opiate-mediated drive-state may become activated, motivating the bird to return to the nest and bring its belly in contact with the warm eggs. The efficacy of endogenous opiates to serve as a reward substrate in learning ensures not only that the parent bird engages in the critical behavior, incubation, but does so at the proper location, its own nest. Nest-site fidelity, the tendency of some birds to return to the same nest sites for multiple breeding attempts within a single breeding season or across many breeding seasons, may represent persistence of a conditioned approach to the nest location. This process has not yet been thoroughly explored.

In addition to facilitating the identity of important incubation stimuli and locations, an opiate-based hedonic system may also play a role in the gross pattern and/or fine-tuning of incubation schedules. Sex-specific differences in opiate levels and/or sensitivity may be responsible for observed differences in incubation bout durations. Female shifts tend to be longer than male shifts (Craig, 1909) and male approaches to the nest more often end in non-exchanges (Ball & Silver, 1983). Both of these findings suggest that females may experience stronger reinforcement from the nest and/or eggs, and, hence, stronger attachment. Both findings are also compatible with Trivers' "ultimate" functional explanations of

sex-specific parental-care investment. He suggested that in the absence of other factors, females are selected initially to show greater amounts of care because they contribute gametes to the offspring that are more expensive to produce (Trivers, 1972). Differences in the intensity of the opiate-mediated drive (and subsequent behaviors that lead to drive reduction) may be the proximate mechanism that supports the ultimate functional differences between the incubation behavior of males and females.

Conclusions

We have described several instances in which learning processes may serve as redundant systems or fine-tuning mechanisms within the reproductive cycle of ring neck doves. During courtship, behavior of potential mates induces neurohormonal changes resulting in the mate acquiring reinforcement value. This reinforcement becomes associated with the physical and behavioral characteristics of the mate, which now serves as a conditioned stimulus that elicits a conditioned approach that is typically labeled as a pair bond. Likewise, incubation behavior may be reinforced through both classical and operant conditioning processes as both the physical attributes of the nest as well as the behavior of sitting on the nest are paired with the release of pleasure-stimulating endorphins triggered by physical contact with the warm eggs. While this proposed model for reproductive behavior in ring neck doves is supported by the findings of ourselves and other researchers, several aspects remain to be addressed by future investigations.

Declarations

Conflict of interests None

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None of the data or materials for the experiments reported here are available, and none of the experiments was preregistered.

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