

The Significance of Mate Choice: Exploring its Role in Captive Animal Welfare

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Layman's summary

Animals need to express normal behaviors to adapt to their environment. While welfare research often focuses on for example foraging as a normal behavior, we tend to overlook the importance of mate choice behavior for animals. Choosing a mate involves behaviors like courtship and copulation. Courtship behavior serves to attract and evaluate a potential mate, and copulation behavior leads to reproduction. Animals are motivated to perform both courtship and copulation because they are rewarding, and provide various benefits. For example, they can give animals a sense of control over their environment, provide access to resources bound to their partner and increase their chances of successful reproduction. However, in captivity, animals often cannot choose their mates freely, which may cause stress and other welfare problems. This review investigates how mate choice relates to animal welfare by examining the existing studies in birds and mammals. For courtship behavior, these studies showed that animals were still motivated to perform courtship, even when they could not copulate. Furthermore, animals experienced stress when they could not perform courtship with a preferred partner, which may reduce their welfare. Additionally, animals paired with non-preferred partners had less reproductive success, than animals that were paired with their preferred partners. Reproductive success was, for example, measured by the number of surviving offspring, or the time to egg-laying in birds. This higher reproductive success may indirectly indicate that animals had higher motivation to invest in offspring when they were paired with their preferred partner. For copulation behavior, animals of species that mate often and with multiple partners in the wild tended to face more welfare challenges than species that do not naturally mate often. This suggests that the captive environment does not adhere to the sexual needs of these animals, which negatively impacts their welfare. Furthermore, animals that were allowed to copulate, and monogamous animals, tended to live longer compared to animals that were not allowed to mate or were naturally promiscuous. In conclusion, mate choice likely influences the welfare of captive animals. To improve animal welfare, captive animals should be allowed to exhibit mate choice behavior. Monogamous species should be able to choose a compatible partner and be pair-housed with them for the long term. Polygamous species, on the other hand, should have access to a variety of potential mates to meet their natural needs. This review highlights the need to not only address current welfare challenges but also point out potential new welfare risks. Future research should include more behavioral and physiological welfare indicators to better understand how mate choice affects welfare within and across different species.

Abstract

The ability to express normal behavior is crucial for animal welfare. While behaviors such as foraging are often recognized as critical to animal welfare, reproductive behaviors – including mate choice – are generally overlooked. Mate choice behaviors, such as courtship and copulation, are not only highly motivated and rewarding but they also contribute to both proximate benefits, such as a sense of control, and ultimate benefits, such as access to resources, genetic fitness and reproductive success. However, captive environments often restrict the ability of animals to express mate choice, potentially leading to welfare issues. This review explores the relationship between mate choice and animal welfare through a review of the relevant literature. The findings demonstrated that courtship behaviors remained motivated even when copulation was not possible. Moreover, as courtship is important for evaluating partner quality and compatibility, the inability to court a preferred partner elicited stress which may ultimately result in reduced welfare. More indirectly, successful courtship with preferred partners correlated with higher reproductive success, suggesting that animals are more motivated to invest in offspring with preferred compared to non-preferred partners. In terms of copulation, species that naturally engage in frequent mating with several individuals often experienced lower welfare in captivity than species with a lower need for sexual behaviors. This difference may indicate that captive environments fail to meet the sexual needs of these animals, negatively impacting their welfare.

Additionally, the ability to perform copulation behaviors and mating system may influence lifespan, as animals that were allowed to copulate and animals in monogamous mating systems lived longer than animals deprived from copulation and polygamous animals. Survival is not necessarily indicative of welfare yet it may suggest whether the captive environment fits the animal's needs. Based on these findings, mate choice appears to be a key factor in shaping welfare outcomes for captive animals. Overall, this review highlights the need to integrate mate choice into welfare assessments in captive settings. For monogamous species, providing multiple potential partners may enhance welfare by enabling the selection of a compatible partner, and housing established pairs together may further support welfare outcomes. In contrast, promiscuous species should have sufficient mating options and variation in partners to align with their natural behaviors. This review underscores the importance of addressing existing welfare issues while remaining vigilant to other factors potentially influencing animal welfare. Future research should focus on incorporating direct welfare indicators, i.e. behavioral and physiological parameters, to further examine the link between mate choice and welfare within and across species.

1. Introduction

The dynamic animal welfare concept (DAWCon) states that an animal is in a positive welfare state when it can adapt to environmental changes by expressing normal behaviors, eventually leading to a positive affective state (Arndt et al., 2022). Consequently, a key aspect of animal welfare is the ability to perform normal behaviors, i.e. innate, intrinsic, and predictable behaviors reflecting an animal's biological functioning (Arndt et al., 2022). A commonly studied normal behavior is foraging, which is crucial for food acquisition and therefore, for survival. Foraging behavior is, at least partly, innately regulated (López-Cruz et al., 2019), and intrinsically motivated by hunger-related stress (Spruijt et al., 2001). The longer an animal does not eat, the higher the chance it will display foraging behavior, i.e. foraging is predictable within the context. Importantly, both food acquisition and food consumption are rewarding to animals, contributing to a positive affective state leading to a positive welfare state (Spruijt et al., 2001). Hence, when an animal is unable to perform its normal behavioral repertoire, welfare issues may arise.

Certain normal behaviors also qualify as behavioral needs: behaviors that animals are internally motivated to perform, regardless of their environment or its functional consequence (Duncan, 1998; Spruijt et al., 2001). Behavioral needs are often appetitive behaviors, which promote access to resources (Hughes & Duncan, 1988). For example, in birds, behaviors important to prepare reproduction such as nest building are considered behavioral needs (Greggor et al., 2018). The inability to perform such behaviors may lead to poor welfare (Duncan, 1998). Generally, appetitive behavior leads to consummatory behavior, which is the act of achieving the resource that appetitive behavior usually leads to. For example, foraging, i.e. appetitive behavior, leads to food ingestion, i.e. consummatory behavior (Hughes & Duncan, 1988). Both types of behavior are considered rewarding, though different parts of the reward system regulate them (Harst & Spruijt, 2007). Berridge et al. (2009) distinguished between two neural systems of reward; 'wanting', driven by dopamine and related to motivation and 'liking', driven by opioids and associated with obtaining the 'wanted' stimulus (Berridge & Robinson, 2016). Thus, normal behavior involves both appetitive ('wanting') and consummatory ('liking') actions, which are rewarding and may promote welfare (Figure 1).

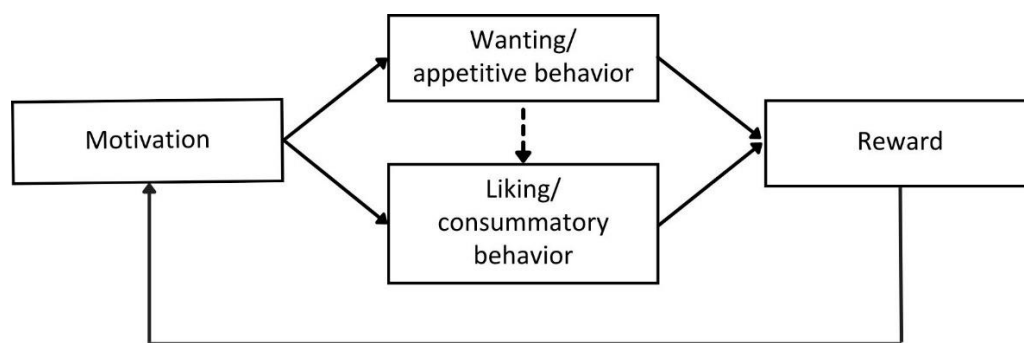


Figure 1. The dynamics between motivation, appetitive and consummatory behavior and reward. Arrows indicate the direction of the interaction and the broken arrow indicates that one phenomenon does not necessarily follow the other.

Although many people would agree that a lack of food is a serious welfare concern, not everybody would agree that this also applies to reproductive behaviors. However, one could argue that reproductive behaviors, including courtship and copulatory behaviors, also meet the criteria for normal behaviors outlined by Arndt et al. (2022). First, reproductive behavior is fundamental for biological functioning, as reproduction is a crucial part of fitness. Second, reproductive behaviors are initially innate but can be refined through learning and experience (Rodríguez-Manzo & Canseco-Alba, 2014). Third, the motivation for sexual behavior arises from both internal and

external stimuli (review: Singer & Toates, 1987), such as the presence of the opposite sex or seasonal changes, upregulating sex hormones to act in the brain (Rodríguez-Manzo & Canseco-Alba, 2014). Fourth, in the presence of these stimuli, sexual behavior is likely to occur, making the behavior predictable. Lastly, reproductive behaviors are social behaviors important for fitness that are intrinsically rewarding, contributing to a positive affective state (Paredes, 2009; Spruijt et al., 2001). Therefore, these behaviors are expected to have a strong influence on an individual's affective state and thereby welfare status.

In many species, reproductive behavior consists of courtship, known as the appetitive phase, and copulation, the consummatory phase. Usually, copulation is preceded by a mate selection process that involves courtship. This process can be referred to as mate choice (Martin-Wintle et al., 2019). Mate choice behavior is pivotal both on a proximate and ultimate level. Proximally, the presence of an attractive individual triggers hormonal changes that enhance motivation for sexual behavior (Hernández-González et al., 2007). Being able to act in alignment with this motivation by performing sexual behaviors is rewarding, causing a positive affective state crucial for welfare, according to the DAWCon (Arndt et al., 2022). Additionally, the ability to engage in mate choice may provide animals with a sense of control over their environment, which is a crucial requirement for good welfare as it enhances an animal's psychological state (Edgar et al., 2013; Englund & Cronin, 2023). From an ultimate perspective, mate choice behavior offers direct and indirect fitness benefits (Ihle et al., 2015). Direct benefits include access to resources, such as territory or parental care, quality and coordination (Ihle et al., 2015; Lindsay et al., 2019). Indirect benefits, on the other hand, are related to genetics, which can improve offspring health via genetic compatibility and fitness as supported by, for example, the good genes theory (survival) and sexy genes theory (reproduction) (Lindsay et al., 2019; Wedekind, 2002). According to evolutionary theory, behaviors that promote fitness, such as reproductive behavior, are rewarding and therefore highly motivated (Spruijt et al., 2001). Hence, both proximate and ultimate arguments highlight the motivation related to sexual behavior.

Despite animal's strong motivation for (free) mate choice behaviors, captivity often restricts this ability (Lewis et al., 2022). For example, farm breeding programs often strive to maximize reproductive output by keeping their lines of breeding pure, i.e. minimal genetic variation, often through artificial insemination (Ritter et al., 2019). These procedures leave no room for free mate choice or even any 'natural' reproductive behavior. For instance, in cattle, estrus is regulated by hormonal injection followed by artificial insemination (Ritter et al., 2019). This means that breeding cattle never encounter each other, causing no natural stimuli for sexual behavior to be present. Similarly, in horse breeding, mares are often confined, limiting the mare to take a receptive posture and preventing natural interactions between the mare and stallion (McDonnell, 2000). This management procedure often leads to resistance in mares, possibly leading to safety hazards, injury and reduced welfare. Problems regarding restricted mate choice also occur in zoos. Although zoos generally allow normal reproductive behavior, mate preferences are often not taken into account because breeding pairs are mostly assigned based on achieving maximum genetic variability and reproductive success (Schulte-Hostedde & Mastro Monaco, 2015). Nevertheless, the breeding advice of the Population Management Center of the Association of Zoos and Aquaria for achieving a viable population has a low success rate; only 20% of selected pairings lead to offspring (Faust et al., 2019). This may suggest that lack of mate choice may negatively impact animals' motivation to reproduce. Thus, breeding programs used in captivity generally do not consider the preferences and motivations of breeding individuals, which potentially has negative consequences for their welfare.

Currently, the potential existence of a link between welfare and mate choice has been largely overlooked in research. Nevertheless, Mellor & Mason (2023) recently hypothesized that welfare might be impaired in species that exhibit strong mate preferences that are unable to select their

mates or in promiscuous species that are unable to access multiple partners. In this review, I will explore the potential link between mate choice and welfare, based on the few studies that have addressed this topic as well as research on the motivational aspects of mate choice. To achieve this, I searched for relevant literature on mate choice, welfare, courtship and copulation behavior, sexual motivation, fitness, and compatibility in captive birds and mammals using Google Scholar and ScienceDirect. I based my review on a selection of the most relevant studies related to the subject and with a reliable source. In the following sections, I will start by defining and contextualizing mate choice behaviors, then I will discuss the potential welfare implications of restricted mate choice (behaviors), and finally, I will conclude with a discussion of whether there is indeed a link between mate choice and welfare. With this review, I aim to emphasize not only the importance of addressing and improving existing welfare issues but also staying alert to other potential factors that could impact welfare, which may not yet be fully recognized.

2. Mate choice behaviors

Mate choice behaviors can be categorized into two stages: courtship and copulation. Below, I will define both categories and discuss their causes and functions using some examples. I will also shortly examine how inter-individual and species differences influence these mate choice behaviors.

2.1. Courtship

Courtship behavior consists of behaviors attracting mates to initiate and sustain copulation (Ventura-Aquino et al., 2018). Other courtship functions include species and sex recognition, synchronizing copulation behavior, and enabling mate choice of either sex (Mitoyen et al., 2019). In some species, courtship is elaborate and consists of many repeated sequences. For example, Huxley (1914) described the complex and elaborate synchronized courtship rituals of the great crested grebe. Grebes repeatedly shake their heads near each other at the start, and between other courtship ceremonies, which take place in a random order. One of these ceremonies consists of the pair searching and finding each other again through a specialized call, whereafter the found individual dives and emerges around the initial searching individual, which is in a so-called cat-display where the head is close to the body and the wings are arched against the body, with the last emergence being back-to-back with the individual in cat-display. Another ceremony is when both individuals dive, extract weed from the lake, go up, find each other, and raise their bodies against each other's breasts in an upright position while stamping on the water's surface. Furthermore, a variety of different and incomplete outings of these ceremonies have been observed.

In contrast, courtship in some other species is far simpler. For example, the courtship behavior of female Japanese monkeys consists of three brief phases (McDonald, 1985). The first phase is showing her receptivity and choosing a potential mate, which usually involves vocalizations and estrous behaviors. The second phase includes increasing proximity by following and sometimes touching the male she chose in the first phase. The third phase of the female courtship sequence includes encouraging mounting from the chosen male by presenting her backside. This striking difference in courtship sequences between species is likely related to different mating systems. In monogamous species like Grebes, where long-term partner selection is crucial, more elaborate courtship rituals may allow for more careful selection for a good and compatible mate. In non-monogamous species, such as Japanese monkeys, where multiple mates are common, courtship may be less elaborate, reflecting the shorter-term investment in mate choice with less lasting consequences. Thus, courtship behavior is important for mate choice and is highly variable between species, likely depending on their mating system.

Courtship behavior is driven by the motivation for acquiring a resource: a partner to mate with, making it an appetitive behavior (Figure 2)(Duncan, 1998; Swaisgood, 2007). This motivation is driven by ‘wanting’ in the reward system, causing the expression of courtship behavior to be experienced as rewarding (Berridge et al., 2009; Ventura-Aquino et al., 2018). Appetitive behaviors are sometimes considered a behavioral need and one could argue that courtship qualifies as such because internal states are crucial for its expression; specifically, the upregulation of steroid hormones mediates brain regions responsible for sexual motivation and sexual behavior (Jennings & de Lecea, 2020). Nevertheless, courtship behavior is mainly triggered by external stimuli: a potential mate, often accompanied by the appropriate season-related environmental cues, such as photoperiod (Mitoyen et al., 2019). Thus, courtship behaviors are appetitive, rewarding and, potentially, a behavioral need.

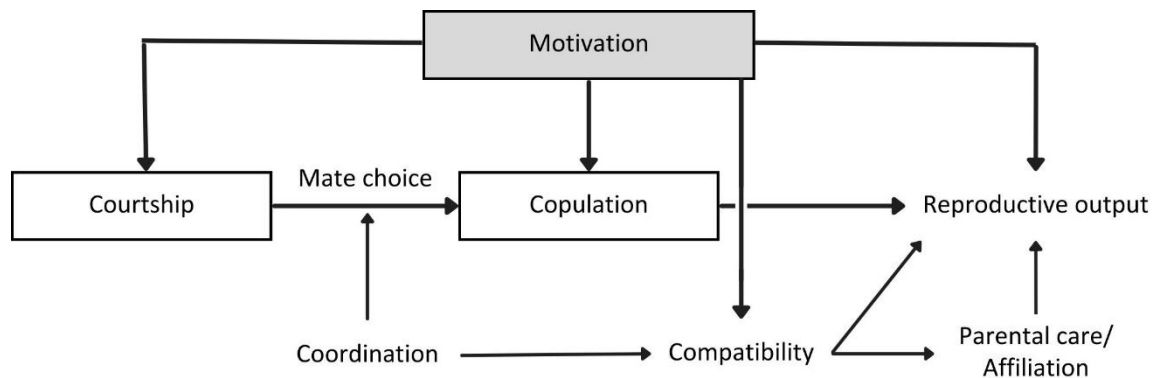


Figure 2. The dynamics between crucial elements of mate choice. Motivation is colored grey to emphasize its link with welfare. Terms in blocks are the main themes described in this review.

An important remark that should be made, is that there is not always consensus among the choosy sex on which potential mate is preferred (Widemo & Sæther, 1999). For example, in rats, it was shown that all females consistently preferred a certain male but the females did not prefer the same male (Lovell et al., 2007). Similarly, this variability in inter-individual preferences for mates was observed in fish and birds (Brooks & Endler, 2001; Forstmeier & Birkhead, 2004; Godin & Dugatkin, 1995; Lehtonen & Lindström, 2008). This suggests that mate choice is not purely based on universal traits of attractiveness but may also depend on genetic or behavioral compatibility. Nevertheless, some other species do show consensus on which is the most preferred mate, indicating that mate quality may be important for other species. This difference in agreement of mate choice may depend on the species' mating system. Monogamous species may prefer to pair with a mate with whom they have behavioral coordination and compatibility as they should provide parental care to their offspring and form a long-term pair bond (Figure 2)(e.g., Griffith, 2019; Ihle et al., 2015; Koeninger Ryan & Altmann, 2001; Roth et al., 2021). Here, courtship behavior may function as a measurement of inter-individual coordination (Figure 2)(Roth et al., 2021). In contrast, non-monogamous species may prefer a high-quality (good genes) and attractive (sexy genes) mate, to pass these characteristics on to their offspring (e.g. Andersson, 1982; Gibson & Bradbury, 1985; Hogan-Warburg, 1966; Méndez-Janovitz & Macías Garcia, 2017; Petrie et al., 1991; Setchell, 2005) and may therefore reach better agreement on their preferred partner. Thus, inter-individual and -species differences in partner preference may be dependent on the species mating system, where monogamous species prioritize compatibility in mate choice, leading to inter-individual variability in preferences, and non-monogamous species prioritize mate quality, leading to more uniform preferences.

In conclusion, courtship behavior is an appetitive and rewarding behavior essential for choosing a mate. The complexity and length of courtship rituals vary widely across species, likely

depending on their mating systems. In monogamous species, courtship is often more elaborate, as it involves testing coordination and establishing long-term bonds, whereas polygamous species exhibit simpler courtship behaviors that reflect a shorter-term investment in mate choice. These differences highlight the crucial role of courtship not only in attracting a partner but also in ensuring reproductive success through strategies suited to each species' needs.

2.2. Copulation

During copulation, the male usually mounts the female, while the female is in a receptive posture. Specific male copulatory behavior may vary among species. In male mammals, copulatory patterns differ in whether locking between genitalia is present, whether thrusting occurs, and the frequency of intromission and ejaculation (Dewsbury, 1972). In rats, for example, copulatory behavior consists of the male mounting the female, which causes the female to get into a receptive position called lordosis in which her back is arched, presenting her genitalia (Pfaff & Ågmo, 2002). The copulatory pattern of male rats typically contains repeated intromissions and ejaculations, without locking or thrusting (Dewsbury, 1972). Thus, copulation behavior generally consists of the male mounting the receptive female, in a species-specific manner.

The number of copulations differs tremendously between mating systems. Monogamous species generally engage in copulation with a single mate for the entire breeding season or for life, whereas polygamous species naturally mate with multiple individuals across a breeding season. Furthermore, in several bird species, the female copulation rate mainly depends on whether a male suspects that she had any copulation with another male, causing this male to copulate with her to increase his chances of producing offspring (Birkhead et al., 1987). If captive conditions restrict polygamous or naturally high-frequency copulating species from copulating often and with several individuals, this may pose a welfare problem (Mellor & Mason, 2023). Furthermore, total abstinence from copulation by prevention of access to members of the other sex or libido-inhibiting medication of animals may also affect animal welfare, as this prevents this normal behavior from taking place.

Copulation generally follows from appetitive behavior, i.e. courtship, and is therefore considered a consummatory behavior. Therefore, copulation is part of 'liking' in the reward system: the consumption of the 'wanted' stimulus (Hernández-González et al., 2007). Mate choice eventually leads to copulation and offspring with a preferred mate (Figure 2). According to evolutionary theory, behaviors that promote fitness, i.e. mating behaviors, are rewarding (Harst & Spruijt, 2007). As copulation does not have direct consequences, i.e. offspring, performing the behavior must be directly motivated through reward (Spruijt et al., 2001). Thus, during copulation, the brain is in a reward state for both males and females, causing a positive affective state, which is a key feature of positive welfare (Arndt et al., 2022; Paredes, 2009; Ventura-Aquino et al., 2018).

Note that preference for a partner to copulate with may also be subjected to confounding factors. First, the Coolidge effect – the phenomenon of the increase of an individual's sexual behavior when introduced to a new partner, where its initial sexual behavior stagnated because of habituation to its available partner (Vasconcelos, 2023; Wilson et al., 1963) – has been widely documented. In non-human animals, the Coolidge effect is almost exclusively studied and observed in males (e.g. rats: Bermant et al., 1968; guppies: Jordan & Brooks, 2010). However, some studies in human males (Koukounas & Over, 1993) and females (Meuwissen & Over, 1990) also provided some evidence for the presence of the Coolidge effect by showing that habituation took place after watching an erotic video multiple times, whereafter a different erotic stimulus increased sexual arousal again. Nevertheless, as arousal is not the same as copulation, results should be interpreted with caution. Thus, the Coolidge effect might be demonstrated in both sexes, although, relatively speaking, females appear less affected. This may be due to the high

costs of reproduction for females and the benefits of reproducing with multiple mates for males (Hughes et al., 2021). Second, mate choice copying, where individuals of the choosy sex are more likely to copulate with an individual of the other sex based on the number of previous copulations it had (Pruett-Jones, 1992), is an example of a social influence on mate choice (Galef & White, 2000). Mate-choice copying is hypothesized to be cost-efficient and reliable for mate quality, on the condition that the initiating individuals know what mates are high quality (Stöhr, 1998). Although it is a well-known biological concept, a lot of the empirical evidence provided (review: Galef & White, 2000) cannot be directly drawn to mate choice copying. For example, the tendency of females to be near each other may be due to reasons other than mate choice, e.g. safety, or males may signal that they copulated lately which attracts females (see review: Clutton-Brock & McAuliffe, 2009). Therefore, the occurrence of mate choice copying is dubious, but its possibility should be kept in mind. Overall, mate choice may be confounded by the Coolidge effect and mate choice copying, although the latter is not yet empirically substantiated.

In conclusion, copulation is a consummatory and rewarding behavior. The pattern and frequency of copulatory behavior vary widely across species, influenced by mating systems and factors such as the Coolidge effect and mate choice copying. Importantly, both courtship and copulation are driven by strong motivational and reward mechanisms. Therefore, restricting these natural behaviors in captive settings could raise welfare concerns. In the next chapter, I will explore the relationship between mate choice behaviors and animal welfare in more detail.

3. The link between mate choice and welfare

Mate choice behaviors encompass both courtship and copulation, each playing distinct yet interconnected roles in sexual behavior. Courtship facilitates mate choice, while copulation ensures reproduction. In this chapter, I will go into the potential relationship between these mate choice behaviors and welfare using the existing literature and studies on the motivational aspects of mate choice behavior.

3.1. Courtship

Courtship is an important behavior to assess partner preference based on either direct or indirect benefits. Below, I will first explore whether animals exhibit motivation to engage in courtship, despite being unable to copulate. Then, I will examine whether pairing with a non-preferred mate induces stress and whether free-choice pairs demonstrate greater behavioral compatibility, coordination and affiliation. Given the limited number of studies directly addressing courtship and welfare, I will also review indirect evidence to further explore the relationship between mate choice and animal welfare.

According to Berridge et al. (2009), ‘wanting’ (courtship) may occur without ‘liking’ (copulation). To directly measure an animal’s motivation to perform courtship behaviors at all, the prevalence of courtship behavior was examined in animals that were unable to copulate. Research showed that mice, rats, hamsters and goats with lesions in brain regions important for the copulatory reflex lose the ability to copulate but still express appetitive courtship behaviors (Bean et al., 1981; Edwards & Isaacs, 1991; Gianantonio et al., 1970; Hart, 1986; Powers et al., 1987). On the contrary, male cats with similar lesions lost both copulation and courtship behaviors (Hart et al., 1973), suggesting species-specific differences of the effect of this lesion. Overall, the majority of studies show that courtship behavior is motivated independently from copulation, implying its importance in the behavioral repertoire even when the consummatory act cannot be accomplished.

The inability to perform courtship, and ultimately copulation, with a preferred partner may have physiological impacts which potentially lead to negative welfare effects. For example, Griffith et

al. (2011) set up experiments with Gouldian finches in two settings; 1) an aviary where the only limitations were the social composition within the aviary and the number of still available individuals of the other sex, and 2) a forced pairing paradigm, in which preferred and non-preferred partners were paired in an isolated cage. Results showed that female finches of non-preferred pairs had a higher concentration of plasma corticosterone, a stress indicator, compared to free choice pairs after 12 hours of introduction in the forced pairing paradigm and, when she laid her second egg in both experiments (Figure 3). Unfortunately, no other studies directly measured proxies for stress related to preferred and non-preferred pairings. Nevertheless, this study suggests that pairing with a non-preferred partner elicits stress, which may eventually become long-term, posing a potential welfare issue.

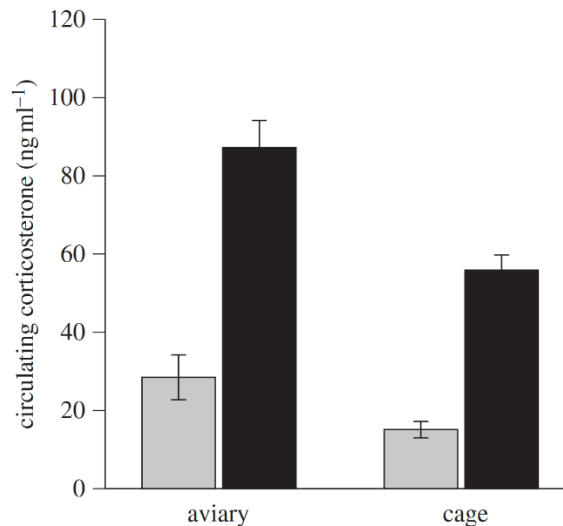


Figure 3. Mean concentration of plasma corticosterone in female Gouldian finches after they laid their second egg after pairing with a preferred partner (grey) and a non-preferred partner (black) in both the aviary and the forced pairing paradigm. Error bars represent the SEM. Differences in corticosterone concentration between preferred and non-preferred partners were significant in the aviary ($p = 0.005$) and the cage ($p < 0.001$). Reprinted from “Constrained mate choice in social monogamy and the stress of having an unattractive partner,” by Griffith, S. C., Pryke S. R., and Buttemer, W. A., 2011, *Proceedings of the Royal Society B: Biological Sciences*, 278(1719), p. 2798–2805.

In pair-forming or monogamous species, behavioral compatibility, coordination and affiliation may also be an important requirement for mate choice as these factors play an evident role in providing parental care and pair bonding. Courtship behavior may help to assess the presence of these elements, allowing for the evaluation of potential mates and eventually choosing a preferred mate. For example, the monogamous zebra finch chooses its mate based on behavioral compatibility as opposed to genetic compatibility, as embryo mortality did not differ between preferred and non-preferred partners but survival during rearing was higher within preferred (foster) pairs (Ihle et al., 2015). Similarly, Spoon et al. (2006) studied the influence of behavioral compatibility of cockatiel free-choice pairs, measured by their proximity, behavioral synchrony, copulatory rates, allopreening receptivity and aggression rates, on reproductive success and behavioral coordination. It was shown that pairs that laid eggs had a higher behavioral compatibility score than pairs that did not lay eggs. Furthermore, pairs with a higher behavioral compatibility score had better coordination of their parental care (incubation) and hatched more viable offspring compared to pairs with lower behavioral compatibility. These results suggest that behavioral compatibility is important for cooperation between parents and their reproductive success. Furthermore, a study in titi monkeys found that pairs of preferred mates displayed more affiliative behaviors together compared to pairs that were put together quasi-randomly (Baxter et al., 2023). This finding may suggest that allowing for mate choice may enhance pair bonding,

expressed through increased levels of affiliation, which is used as an indicator of positive welfare (Rault, 2019). In other species, species-typical courtship displays between partners seem to indicate relationship quality: in siamangs, Geissmann & Orgeldinger (2000) found a positive relationship between duet frequency and relationship quality, meaning that pairs that duetted more spent more time on affiliative behavior, had a higher level of behavioral synchronization and were in closer proximity to each other. Taken together, these studies suggest that courtship is important for assessing compatibility between mates in monogamous species which may enhance parental care and pair bonds, eventually benefitting their welfare.

A more indirect measure of the motivation for mate choice is reproductive success. Reproductive success is an ultimate measure related to fitness, whereas for welfare, proximate measures are usually used as indicators. Nevertheless, as previously mentioned, behaviors that are crucial for fitness tend to be driven by strong motivation, and hence important for welfare (Spruijt et al., 2001). Therefore, when an individual achieves higher reproductive success in a particular setting, it suggests a higher motivation to reproduce in that setting. Thus, reproductive success may be interpreted as an indirect measure of motivation, and therefore suggestive of enhanced welfare. In the studies I discuss below, reproductive success is assessed for preferred versus non-preferred or random partners, in which preferred partners were identified by a preference test or behavioral observations in a social group. A different setup that was often used is free versus forced pairing, which also tests the effect of mate choice on reproductive success.

Many studies on reproductive success with preferred partners compared to random or assigned partners were conducted with birds. For example, both female great tits and partridges laid their first clutch of eggs significantly earlier when paired with a preferred mate compared to a less-preferred mate according to a preference test (Delaitre et al., 2023; Prieto et al., 2018). These findings suggest that females may be more motivated to invest reproductive effort in the offspring of preferred partners. However, not all bird species exhibit the same pattern. In female zebra finches, the time to egg laying and brood mass did not differ between preferred and non-preferred pairings (Pogány et al., 2014). Yet, another study with zebra finches revealed that pairs formed through free mate choice had 37% higher relative fitness compared to individuals of assigned matings, with more offspring surviving until independence (Ihle et al., 2015). Similarly, female mallards had more offspring that survived until independence when paired with a preferred partner (Bluhm & Gowaty, 2004). These results suggest that, depending on the species, reproductive investment may either occur earlier (pre-laying) or later (post-breeding), indicating that mate choice may influence both reproductive effort and long-term offspring viability in birds.

In mammals, parallel trends have been observed. First, female dunnarts conceived faster and had more litters when allowed to choose their mate based on scent, although litter size remained unaffected (Parrott et al., 2019). However, litter size may not be the most reliable measure of reproductive success in this species, as it is limited by the mother's number of teats (Parrott et al., 2019). Second, studies in house mice provided further evidence that mate preference enhanced reproductive success. Preferred pairings consistently produced more offspring, with these offspring exhibiting greater fitness in their adult life (Drickamer et al., 2000, 2003; Gowaty et al., 2003). These results suggest that mate choice may have long-term benefits for offspring, possibly through genetic compatibility between preferred partners. Third, similar effects were found in giant pandas, where preferred matings resulted in more successful intromission and more offspring, even more so when there was mutual preference (Figure 4)(Martin-Wintle et al., 2015). These findings emphasize the critical role of mate choice in enhancing zoo breeding with endangered species. Lastly, in humans, a study comparing offspring outcomes in assigned and chosen partnerships across three tribes (two from Asia and one from South America) found no evidence in offspring quantity or mortality (Sorokowski et al., 2017). However, the complexities of arranged marriages and potential alignment between parental and individual mate preferences

may have confounded these results. Furthermore, social, cultural and ethical factors complicate the study of mate choice in humans. Taken together, these studies illustrate that mate choice positively influences reproductive success across various species, whereby reproductive success may serve as an indirect measure of motivation to invest in offspring with a preferred partner.

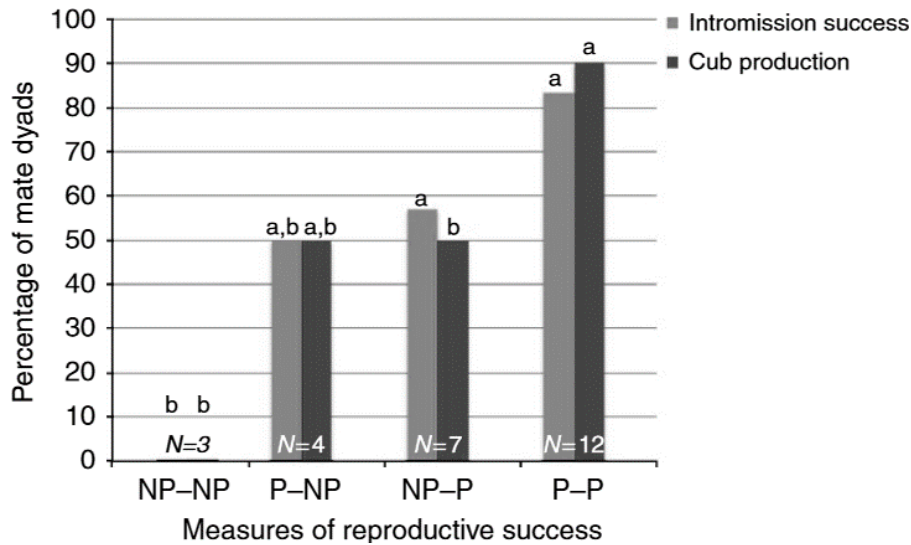


Figure 4. Percentage of dyads of combinations of preferred and non-preferred partners adhering to a measure of reproductive success. NP: non-preferred partner, P: preferred partner. Female preference is depicted in front of the hyphen, and male preference is behind the hyphen. Light bars represent intramission success, and dark bars show cub production. Different letters (a,b) indicate significant differences between groups. Reprinted from “Free mate choice enhances conservation breeding in the endangered giant panda,” by Martin-Wintle, M.S., et al., 2015, *Nature Communications*, 6(1), 10125.

In conclusion, courtship behavior is a highly motivated behavior, important for assessing partner compatibility, which is crucial for parental care, pair bonding and, eventually, reproductive success. The inability to perform courtship with a preferred partner can induce stress which could lead to reduced welfare. Based on the discussed findings, the ability to express mate choice through courtship behavior is highly motivated and seems to significantly impact welfare.

3.2. Copulation

Copulation is a natural behavior that elevates an individual’s fitness and is therefore highly motivated. The ability to express this behavior is important, especially for individuals of species that normally mate often. Restricting copulatory behavior may therefore pose a welfare issue.

Studies on sexual deprivation may indicate whether animals are more motivated to copulate after this period. I could identify only one study on sexual behavior after sexual deprivation. This study on rhesus macaques showed no significant differences in copulatory behaviors between 6-months deprived and non-deprived males (Phoenix & Chambers, 1984). This finding suggests that there is no rebound effect after sexual deprivation, indicating that copulation behavior is not motivated extra after its absence.

On the other hand, in species with high sexual motivation, the inability to engage in copulation may lead to frustration and diminished welfare. Lewis et al. (2022) found that captive ungulates from species with promiscuous mating systems performed more stereotypic behaviors, compared to species with polygynous mating systems (Figure 5). Promiscuous species, which typically mate frequently with multiple partners, may be especially vulnerable to welfare concerns

in environments where opportunities for sexual behavior are restricted. A study on promiscuous species found that more promiscuous species had more same-sex sexual interactions, which may confirm the presence of high sexual motivation within these species (MacFarlane & Vasey, 2016). Similarly, ejaculatory frequencies in promiscuous primate species are higher (0.88/h) compared to monogamous (0.08/h) and polygynous species (0.27) (Dixon, 1997). Thus, in species with a high motivation for sexual behavior, restricting this behavior may decrease their welfare.

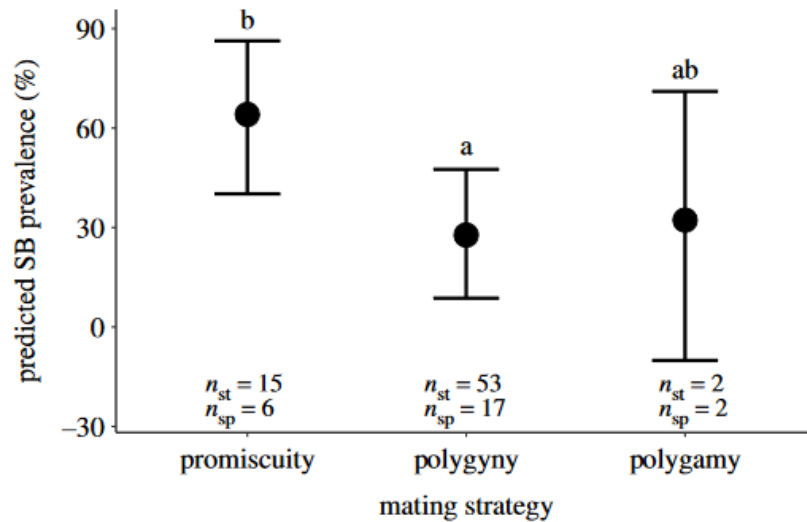


Figure 5. Predicted prevalence of stereotypic behavior of captive ungulates per mating system. Different letters (a,b) indicate significant differences between mating systems and error bars indicate 95% credible intervals. SB: Stereotypic behavior, n_{st} = number of studies, n_{sp} = number of species. Reprinted from “Risk factors for stereotypic behaviour in captive ungulates,” by Lewis, K., et al., 2022, *Proceedings of the Royal Society B: Biological Sciences*, 289(1983), 20221311.

While direct studies on the effects of restricted copulation on welfare are limited, some research has shown that copulatory behavior may have indirect benefits for health and longevity. Although survival is mostly important for fitness and not necessarily a component of welfare, it may be related to the quality of life. For example, male rats that were allowed to perform copulatory behaviors lived longer than rats that were deprived from copulating (Drori & Folman, 1969). From this result, the researchers suggest that the exercise coming with copulation may have resulted in a longer life span. As both exercise and sexual behaviors have rewarding properties (Heyse et al., 2015; Paredes, 2009), this may indirectly suggest that copulation may be beneficial for health and welfare. Furthermore, a study in captive ruminants found that the relative life expectancy of males of monogamous species was higher than that of polygamous species (Müller et al., 2010). These findings suggest that the management in captivity may be not adequately adapted to the sexual needs of polygamous animals. Thus, survival may not be indicative of welfare, yet it may indirectly indicate whether the captive environment fits the animal’s needs.

Overall, copulation is a natural, rewarding behavior that animals are motivated to perform. In contrast, sexual deprivation is not related to negative affect and did not cause a rebound effect. In species with frequent mating behaviors, the inability to copulate may lead to poor welfare outcomes and a shorter lifespan.

4. Discussion

This thesis aimed to explore the presence of a relationship between mate choice and welfare in captive animals, an area that has been largely overlooked in welfare research. While traditional welfare studies often focus on factors such as health and environmental enrichment, this review highlights the need to consider sexual behavior – particularly mate choice – as a potential contributor to animal welfare. Given the importance of mating for fitness and its rewarding value, incorporating mate choice into welfare assessments may lead to more comprehensive strategies for improving the lives of captive animals.

Courtship and copulation are mate choice behaviors that play a crucial role in fitness, making them highly motivated and rewarding. Courtship behavior, which corresponds to the ‘wanting’ component in the reward system, is an appetitive behavior important to assess potential partners. Through courtship, behavioral coordination, compatibility and, eventually, affection between partners may be predicted. The inability to engage in courtship behaviors with a preferred partner may lead to stress, which can negatively affect welfare. Additionally, successful courtship and subsequent copulation with a preferred mate often result in higher reproductive success, suggesting that animals are more motivated to invest in offspring with a preferred partner. Courtship behavior typically precedes copulation, a consummatory behavior that is associated with the ‘liking’ component of the reward system. This behavior is particularly important for animals that naturally mate frequently and the ability for performing copulation is shown to positively correlate with survival. This raises concerns that limiting opportunities for courtship and copulation may cause stress, reflected in physiology and behavior, potentially leading to welfare issues.

Based on these findings, mate choice appears to be a key factor in shaping welfare outcomes for captive animals. To enhance welfare in the context of mate choice, it is essential to adapt the captive environment to the specific mating system and associated needs per species. Mating systems seem to significantly influence the potential welfare effects of mate choice, as Mellor & Mason (2023) already proposed. For monogamous species, courtship rituals are often elaborate as coordination and compatibility are thoroughly tested before forming long-term pair bonds. Therefore, providing monogamous species with the opportunity to choose from multiple potential mates allows them to select the most compatible partner, which may improve their welfare. Once a pair is established, housing them together may further enhance welfare, as continued courtship behaviors help build, maintain and strengthen the pair bond (Baxter et al., 2023; Geissmann & Orgeldinger, 2000; Huxley, 1914). While copulation variation and frequency may be less important for monogamous species, copulation with preferred mates still appears to result in higher reproductive success. Thus, offering a range of potential mates supports welfare by the selection of a compatible partner, and keeping established pairs together may further enhance welfare.

On the other hand, in polygynous and polyandrous species, mate choice is particularly important for the choosier sex. Courtship behavior is often less elaborate in polygamous species, although not unimportant, as they still need to select high-quality mates. This is especially pivotal in species where no long-term bonds and no or limited parental care are established, as offspring must be of high quality to ensure survival and reproductive success, potentially through genetic traits like good genes or sexy genes. This was shown in polygamous species, which had more offspring and offspring with higher fitness (Drickamer et al., 2000, 2003; Gowaty et al., 2003; Martin-Wintle et al., 2015). Furthermore, copulation behaviors in polygamous species naturally occur frequently, and involve different mates throughout the breeding season. This makes copulation behavior an integral part of their behavioral repertoire. Preventing or limiting these natural behaviors may lead to frustration, expressed in stress-related or even stereotypical behavior, negatively impacting welfare. To meet the needs of polygamous species, it is crucial to

provide sufficient options and a variety of partners, mimicking their natural needs. In conclusion, allowing individuals across all mating systems to express mate choice through courtship and copulation provides them with more control over their environment and adapting the environment to their specific needs may enhance their welfare.

However, substantial gaps in our understanding of how mate choice affects welfare remain. Further research is necessary, particularly studies that focus on direct welfare indicators when comparing free mate choice with assigned pairings. Such welfare indicators include both behavioral parameters, such as affiliative and stereotypical behaviors, and physiological measures, such as oxytocin and cortisol levels. By taking into account positive and negative welfare indicators, a more holistic image of the welfare effects of mate choice will be achieved. Comparing these measures before and after being paired with preferred vs. non-preferred partners could help elucidate its welfare implications, which may also be studied across mating systems (Figure 6). Species that naturally demonstrate strong mate preferences, such as certain birds, rodents and primates, are particularly informative model species for such research. Additionally, comparing welfare measures across species with different mating systems would provide further insights into how the availability and variability of mate choice influence welfare (Figure 6). Birds provide good model species for these comparative studies, as they display a wide range of mating systems. While cross-species comparisons may introduce confounding factors, larger sample sizes across diverse species may reveal general trends in how mate choice affects welfare. Thus, further research incorporating direct welfare indicators within and between species may increase our understanding of the underlying affective state of individuals that are able to choose their mate and to express the accompanying behaviors.

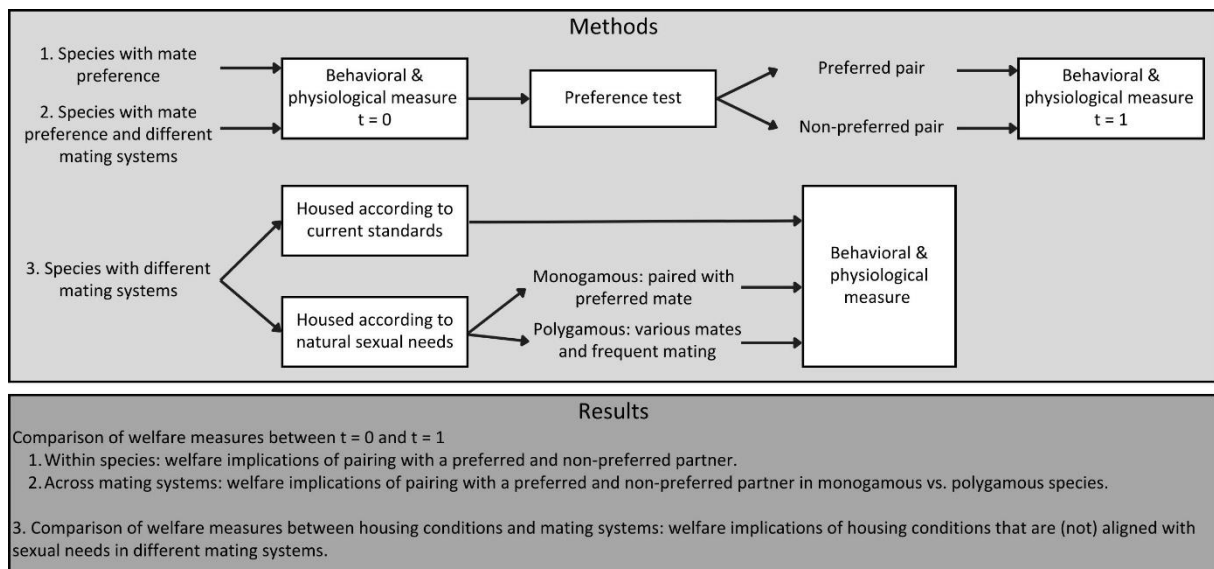


Figure 6. Proposed framework for future research on mate choice and welfare. Methods and potential results for three mate choice studies are shown. Terms in blocks represent experimental practices.

Despite the implications of the mentioned findings, several limitations and considerations must be acknowledged. First, mate choice is also not always possible in the wild due to factors such as restricted availability of potential mates, alpha monopolization, or forced mating (Griffith et al., 2011; McKinney et al., 1983). However, in the wild, animals generally have the opportunity to escape undesirable situations, which is rather challenging in captivity. Nevertheless, also in the wild animals have adapted to these challenges. For example, alpha monopolization by male primates is counteracted by females by secretly mating with subordinate males, followed by cryptic female choice, where physiological processes determine which sperm causes fertilization

(Carnes et al., 2011). These processes may also provide the females with some level of mate choice in captivity. Additionally, sexual conflict, in the forms of intimidation, harassment and coercion, is an evident phenomenon in several primate species, such as mandrills, orangutans and chimpanzees. Within sexual conflict, the sexual strategy of one sex reduces the fitness of the other (Palombit, 2014). Usually, males intimidate, harass and/or force copulation on females, who have developed counter-strategies, such as harm-inducing defense (Palombit, 2014). It is important to restrict opportunities for sexual conflicts in captivity to protect the welfare of the coerced animal. One possible solution is to provide hiding spots that only members of the coerced sex can access, allowing them to escape by limiting the aggressor's visual and physical access. Other solutions may include modifying social group compositions during the breeding season, allowing access only to preferred mates, or using hormonal interventions to reduce aggression. However, the latter should not be standard, as it also raises welfare concerns. Second, logistical and management constraints in captive environments – such as limited space, the need to transport animals, and the limited availability of individuals, particularly in endangered species – can complicate efforts to offer free mate choice (Asa et al., 2011). Although it is challenging to eliminate these constraints, Asa et al. (2011) suggest overcoming unnecessary practices regarding space and transport by implementing remote mate choice methods by providing cues such as odor, auditory or visual (video) signals. This approach facilitates mate choice while minimizing the associated costs and challenges. Lastly, introducing new individuals to enable mate choice poses its own welfare risks, including increased agonistic behaviors, stress and potential injury (e.g. Rox et al., 2018; Williams & Abee, 1988). Nevertheless, the practice of introducing new animals is common in many captive settings, where strategies are already in place to mitigate these risks.

In conclusion, this review emphasizes the importance of considering mate choice as a factor in animal welfare. Providing opportunities for mate choice in captivity could enhance welfare by allowing animals to engage in normal, highly motivated and rewarding behaviors. With this review, I want to highlight the need not only to address known welfare risks but also to beware for overlooking other potential factors that may impact animal welfare in captivity. Future studies that incorporate direct welfare indicators will be crucial in establishing a more pronounced link between mate choice and welfare within and across species, ultimately guiding improvements in animal care and management practices.

References

- Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. *Nature*, 299, 818–820. <https://doi.org/10.1038/299818a0>
- Arndt, S. S., Goerlich, V. C., & van der Staay, F. J. (2022). A dynamic concept of animal welfare: The role of appetitive and adverse internal and external factors and the animal's ability to adapt to them. *Frontiers in Animal Science*, 3. <https://www.frontiersin.org/articles/10.3389/fanim.2022.908513>
- Asa, C. S., Traylor-Holzer, K., & Lacy, R. C. (2011). Can conservation-breeding programmes be improved by incorporating mate choice? *International Zoo Yearbook*, 45(1), 203–212. <https://doi.org/10.1111/j.1748-1090.2010.00123.x>
- Baxter, A., Lau, A. R., Savidge, L. E., & Bales, K. L. (2023). Initial compatibility during a “Speed-Dating” test predicts postpairing affiliation in titi monkeys (*Plecturocebus cupreus*). *American Journal of Primatology*, 85(7), e23496. <https://doi.org/10.1002/ajp.23496>
- Bean, N. J., Nunez, A. A., & Conner, R. (1981). Effects of medial preoptic lesions on male mouse ultrasonic vocalizations and copulatory behavior. *Brain Research Bulletin*, 6(2), 109–112. [https://doi.org/10.1016/S0361-9230\(81\)80033-0](https://doi.org/10.1016/S0361-9230(81)80033-0)
- Bermant, G., Lott, D. F., & Anderson, L. (1968). Temporal characteristics of the coolidge effect in male rat copulatory behavior. *Journal of Comparative and Physiological Psychology*, 65(3, Pt.1), 447–452. <https://doi.org/10.1037/h0025841>
- Berridge, K. C., & Robinson, T. E. (2016). Liking, Wanting and the Incentive-Sensitization Theory of Addiction. *The American Psychologist*, 71(8), 670–679. <https://doi.org/10.1037/amp0000059>
- Berridge, K. C., Robinson, T. E., & Aldridge, J. W. (2009). Dissecting components of reward: ‘Liking’, ‘wanting’, and learning. *Current Opinion in Pharmacology*, 9(1), 65–73. <https://doi.org/10.1016/j.coph.2008.12.014>
- Birkhead, T. R., Atkin, L., & Moller, A. (1987). Copulation Behaviour of Birds. *Behaviour*, 101, 101–138. <https://doi.org/10.1163/156853987X00396>
- Bluhm, C. K., & Gowaty, P. A. (2004). Social constraints on female mate preferences in mallards, *Anas platyrhynchos*, decrease offspring viability and mother productivity. *Animal Behaviour*, 68(5), 977–983. <https://doi.org/10.1016/j.anbehav.2004.01.013>
- Brooks, R., & Endler, J. A. (2001). Female guppies agree to differ: Phenotypic and genetic variation in mate-choice behavior and the consequences for sexual selection. *Evolution; International Journal of Organic Evolution*, 55(8), 1644–1655. <https://doi.org/10.1111/j.0014-3820.2001.tb00684.x>
- Carnes, L. M., Nunn, C. L., & Lewis, R. J. (2011). Effects of the Distribution of Female Primates on the Number of Males. *PLOS ONE*, 6(5), e19853. <https://doi.org/10.1371/journal.pone.0019853>
- Clutton-Brock, T., & McAuliffe, K. (2009). Female Mate Choice in Mammals. *The Quarterly Review of Biology*, 84(1), 3–27. <https://doi.org/10.1086/596461>
- Delaitre, S., van Oers, K., Visser, M. E., & Caro, S. P. (2023). Female great tits (*Parus major*) reproduce earlier when paired with a male they prefer. *Ethology*, 129(9), 461–471. <https://doi.org/10.1111/eth.13381>

- Dewsbury, D. A. (1972). Patterns of Copulatory Behavior in Male Mammals. *The Quarterly Review of Biology*, 47(1), 1–33. <https://doi.org/10.1086/407097>
- Dixon, A. F. (1997). Evolutionary Perspectives on Primate Mating Systems and Behavior. *Annals of the New York Academy of Sciences*, 807(1), 42–61. <https://doi.org/10.1111/j.1749-6632.1997.tb51912.x>
- Drickamer, L. C., Gowaty, P. A., & Holmes, C. M. (2000). Free female mate choice in house mice affects reproductive success and offspring viability and performance. *Animal Behaviour*, 59(2), 371–378. <https://doi.org/10.1006/anbe.1999.1316>
- Drickamer, L. C., Gowaty, P. A., & Wagner, D. M. (2003). Free mutual mate preferences in house mice affect reproductive success and offspring performance. *Animal Behaviour*, 65(1), 105–114. <https://doi.org/10.1006/anbe.2002.2027>
- Drori, D., & Folman, Y. (1969). The effect of mating on the longevity of male rats. *Experimental Gerontology*, 4(4), 263–266. [https://doi.org/10.1016/0531-5565\(69\)90014-X](https://doi.org/10.1016/0531-5565(69)90014-X)
- Duncan, I. J. (1998). Behavior and behavioral needs. *Poultry Science*, 77(12), 1766–1772. <https://doi.org/10.1093/ps/77.12.1766>
- Edgar, J. L., Mullan, S. M., Pritchard, J. C., McFarlane, U. J. C., & Main, D. C. J. (2013). Towards a ‘Good Life’ for Farm Animals: Development of a Resource Tier Framework to Achieve Positive Welfare for Laying Hens. *Animals*, 3(3), Article 3. <https://doi.org/10.3390/ani3030584>
- Edwards, D. A., & Isaacs, S. (1991). Zona incerta lesions: Effects on copulation, partner-preference and other socio-sexual behaviors. *Behavioural Brain Research*, 44(2), 145–150. [https://doi.org/10.1016/S0166-4328\(05\)80019-1](https://doi.org/10.1016/S0166-4328(05)80019-1)
- Englund, M. D., & Cronin, K. A. (2023). Choice, control, and animal welfare: Definitions and essential inquiries to advance animal welfare science. *Frontiers in Veterinary Science*, 10. <https://doi.org/10.3389/fvets.2023.1250251>
- Faust, L. J., Long, S. T., Perišin, K., & Simonis, J. L. (2019). Uncovering challenges to sustainability of AZA Animal Programs by evaluating the outcomes of breeding and transfer recommendations with PMCTrack. *Zoo Biology*, 38(1), 24–35. <https://doi.org/10.1002/zoo.21470>
- Forstmeier, W., & Birkhead, T. R. (2004). Repeatability of mate choice in the zebra finch: Consistency within and between females. *Animal Behaviour*, 68(5), 1017–1028. <https://doi.org/10.1016/j.anbehav.2004.02.007>
- Galef, B. G., & White, D. J. (2000). Evidence of social effects on mate choice in vertebrates. *Behavioural Processes*, 51(1), 167–175. [https://doi.org/10.1016/S0376-6357\(00\)00126-1](https://doi.org/10.1016/S0376-6357(00)00126-1)
- Geissmann, T., & Orgeldinger, M. (2000). The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*. *Animal Behaviour*, 60(6), 805–809. <https://doi.org/10.1006/anbe.2000.1540>
- Giantonio, G. W., Lund, N. L., & Gerall, A. A. (1970). Effect of diencephalic and rhinencephalic lesions on the male rat’s sexual behavior. *Journal of Comparative and Physiological Psychology*, 73(1), 38–46. <https://doi.org/10.1037/h0030005>

- Gibson, R. M., & Bradbury, J. W. (1985). Sexual selection in lekking sage grouse: Phenotypic correlates of male mating success. *Behavioral Ecology and Sociobiology*, 18(2), 117–123. <https://doi.org/10.1007/BF00299040>
- Godin, J.-G. J., & Dugatkin, L. A. (1995). Variability and repeatability of female mating preference in the guppy. *Animal Behaviour*, 49(6), 1427–1433. [https://doi.org/10.1016/0003-3472\(95\)90063-2](https://doi.org/10.1016/0003-3472(95)90063-2)
- Gowaty, P. A., Drickamer, L. C., & Schmid-Holmes, S. (2003). Male house mice produce fewer offspring with lower viability and poorer performance when mated with females they do not prefer. *Animal Behaviour*, 65(1), 95–103. <https://doi.org/10.1006/anbe.2002.2026>
- Greggor, A. L., Vicino, G. A., Swaisgood, R. R., Fidgett, A., Brenner, D., Kinney, M. E., Farabaugh, S., Masuda, B., & Lamberski, N. (2018). Animal Welfare in Conservation Breeding: Applications and Challenges. *Frontiers in Veterinary Science*, 5. <https://doi.org/10.3389/fvets.2018.00323>
- Griffith, S. C. (2019). Cooperation and Coordination in Socially Monogamous Birds: Moving Away From a Focus on Sexual Conflict. *Frontiers in Ecology and Evolution*, 7. <https://doi.org/10.3389/fevo.2019.00455>
- Griffith, S. C., Pryke, S. R., & Buttemer, W. A. (2011). Constrained mate choice in social monogamy and the stress of having an unattractive partner. *Proceedings of the Royal Society B: Biological Sciences*, 278(1719), 2798–2805. <https://doi.org/10.1098/rspb.2010.2672>
- Harst, J. V. der, & Spruijt, B. M. (2007). Tools to measure and improve animal welfare: Reward-related behaviour. *Animal Welfare*, 16(S1), 67–73. <https://doi.org/10.1017/S0962728600031742>
- Hart, B. L. (1986). Medial preoptic-anterior hypothalamic lesions and sociosexual behavior of male goats. *Physiology & Behavior*, 36(2), 301–305. [https://doi.org/10.1016/0031-9384\(86\)90020-X](https://doi.org/10.1016/0031-9384(86)90020-X)
- Hart, B. L., Haugen, C. M., & Peterson, D. M. (1973). Effects of medial preoptic-anterior hypothalamic lesions on mating behavior of male cats. *Brain Research*, 54, 177–191. [https://doi.org/10.1016/0006-8993\(73\)90043-7](https://doi.org/10.1016/0006-8993(73)90043-7)
- Hernández-González, M., Prieto-Beracochea, C. A., Arteaga-Silva, M., & Guevara, M. A. (2007). Different functionality of the medial and orbital prefrontal cortex during a sexually motivated task in rats. *Physiology & Behavior*, 90(2–3), 450–458. <https://doi.org/10.1016/j.physbeh.2006.10.006>
- Heyse, N. C., Brenes, J. C., & Schwarting, R. K. W. (2015). Exercise reward induces appetitive 50-kHz calls in rats. *Physiology & Behavior*, 147, 131–140. <https://doi.org/10.1016/j.physbeh.2015.04.021>
- Hogan-Warburg, A. J. (1966). *Social behavior of the ruff, Philomachus pugnax (L.)*. 54, 109–229.
- Hughes, B. O., & Duncan, I. J. H. (1988). The notion of ethological ‘need’, models of motivation and animal welfare. *Animal Behaviour*, 36(6), 1696–1707. [https://doi.org/10.1016/S0003-3472\(88\)80110-6](https://doi.org/10.1016/S0003-3472(88)80110-6)
- Hughes, S. M., Aung, T., Harrison, M. A., LaFayette, J. N., & Gallup, G. G. (2021). Experimental Evidence for Sex Differences in Sexual Variety Preferences: Support for the Coolidge Effect in Humans. *Archives of Sexual Behavior*, 50(2), 495–509. <https://doi.org/10.1007/s10508-020-01730-x>

- Huxley, J. S. (1914). 33. The Courtship—Habits * of the Great Crested Grebe (*Podiceps cristatus*); with an addition to the Theory of Sexual Selection. *Proceedings of the Zoological Society of London*, 84(3), 491–562. <https://doi.org/10.1111/j.1469-7998.1914.tb07052.x>
- Ihle, M., Kempnaers, B., & Forstmeier, W. (2015). Fitness Benefits of Mate Choice for Compatibility in a Socially Monogamous Species. *PLOS Biology*, 13(9), e1002248. <https://doi.org/10.1371/journal.pbio.1002248>
- Jennings, K. J., & de Lecea, L. (2020). Neural and Hormonal Control of Sexual Behavior. *Endocrinology*, 161(10), bqaa150. <https://doi.org/10.1210/endo.cr/bqaa150>
- Jordan, L. A., & Brooks, R. C. (2010). The lifetime costs of increased male reproductive effort: Courtship, copulation and the Coolidge effect. *Journal of Evolutionary Biology*, 23(11), 2403–2409. <https://doi.org/10.1111/j.1420-9101.2010.02104.x>
- Koeninger Ryan, K., & Altmann, J. (2001). Selection for male choice based primarily on mate compatibility in the oldfield mouse, *Peromyscus polionotus rhoadsi*. *Behavioral Ecology and Sociobiology*, 50(5), 436–440. <https://doi.org/10.1007/s002650100385>
- Koukounas, E., & Over, R. (1993). Habituation and dishabituation of male sexual arousal. *Behaviour Research and Therapy*, 31(6), 575–585. [https://doi.org/10.1016/0005-7967\(93\)90109-8](https://doi.org/10.1016/0005-7967(93)90109-8)
- Lehtonen, T. K., & Lindström, K. (2008). Repeatability of mating preferences in the sand goby. *Animal Behaviour*, 75(1), 55–61. <https://doi.org/10.1016/j.anbehav.2007.04.011>
- Lewis, K., Parker, M. O., Proops, L., & McBride, S. D. (2022). Risk factors for stereotypic behaviour in captive ungulates. *Proceedings of the Royal Society B: Biological Sciences*, 289(1983), 20221311. <https://doi.org/10.1098/rspb.2022.1311>
- Lindsay, W. R., Andersson, S., Bererhi, B., Höglund, J., Johnsen, A., Kvarnemo, C., Leder, E. H., Lifjeld, J. T., Ninnis, C. E., Olsson, M., Parker, G. A., Pizzari, T., Qvarnström, A., Safran, R. J., Svensson, O., & Edwards, S. V. (2019). Endless forms of sexual selection. *PeerJ*, 7, e7988. <https://doi.org/10.7717/peerj.7988>
- López-Cruz, A., Sordillo, A., Pokala, N., Liu, Q., McGrath, P. T., & Bargmann, C. I. (2019). Parallel Multimodal Circuits Control an Innate Foraging Behavior. *Neuron*, 102(2), 407–419.e8. <https://doi.org/10.1016/j.neuron.2019.01.053>
- Lovell, J. L., Diehl, A., Joyce, E., Cohn, J., Lopez, J., & Guarraci, F. A. (2007). “Some guys have all the luck”: Mate preference influences paced-mating behavior in female rats. *Physiology & Behavior*, 90(4), 537–544. <https://doi.org/10.1016/j.physbeh.2006.11.002>
- MacFarlane, G. R., & Vasey, P. L. (2016). Promiscuous primates engage in same-sex genital interactions. *Behavioural Processes*, 126, 21–26. <https://doi.org/10.1016/j.beproc.2016.02.016>
- Martin-Wintle, M. S., Shepherdson, D., Zhang, G., Zhang, H., Li, D., Zhou, X., Li, R., & Swaisgood, R. R. (2015). Free mate choice enhances conservation breeding in the endangered giant panda. *Nature Communications*, 6(1), 10125. <https://doi.org/10.1038/ncomms10125>
- Martin-Wintle, M. S., Wintle, N. J. P., Díez-León, M., Swaisgood, R. R., & Asa, C. S. (2019). Improving the sustainability of ex situ populations with mate choice. *Zoo Biology*, 38(1), 119–132. <https://doi.org/10.1002/zoo.21450>

- McDonald, M. S. (1985). The Courtship Behaviour of Female Japanese Monkeys. *Canadian Review of Physical Anthropology*, 4, 67–75.
- McDonnell, S. M. (2000). Reproductive behavior of stallions and mares: Comparison of free-running and domestic in-hand breeding. *Animal Reproduction Science*, 60–61, 211–219. [https://doi.org/10.1016/S0378-4320\(00\)00136-6](https://doi.org/10.1016/S0378-4320(00)00136-6)
- McKinney, F., Derrickson, S. R., & Mineau, P. (1983). Forced Copulation in Waterfowl. *Behaviour*, 86(3/4), 250–294.
- Mellor, E. L., & Mason, G. J. (2023). Feeding, mating and animal wellbeing: New insights from phylogenetic comparative methods. *Proceedings of the Royal Society B: Biological Sciences*, 290(1994), 20222571. <https://doi.org/10.1098/rspb.2022.2571>
- Méndez-Janovitz, M., & Macías Garcia, C. (2017). Do male fish prefer them big and colourful? Non-random male courtship effort in a viviparous fish with negligible paternal investment. *Behavioral Ecology and Sociobiology*, 71(11), 160. <https://doi.org/10.1007/s00265-017-2385-2>
- Meuwissen, I., & Over, R. (1990). Habituation and dishabituation of female sexual arousal. *Behaviour Research and Therapy*, 28(3), 217–226. [https://doi.org/10.1016/0005-7967\(90\)90004-3](https://doi.org/10.1016/0005-7967(90)90004-3)
- Mitoyen, C., Quigley, C., & Fusani, L. (2019). Evolution and function of multimodal courtship displays. *Ethology*, 125(8), 503–515. <https://doi.org/10.1111/eth.12882>
- Müller, D. W. H., Lackey, L. B., Streich, W. J., Fickel, J., Hatt, J.-M., & Clauss, M. (2010). Mating system, feeding type and ex situ conservation effort determine life expectancy in captive ruminants. *Proceedings of the Royal Society B: Biological Sciences*, 278(1714), 2076–2080. <https://doi.org/10.1098/rspb.2010.2275>
- Palombit, R. A. (2014). Chapter Five—Sexual Conflict in Nonhuman Primates. In M. Naguib, L. Barrett, H. J. Brockmann, S. Healy, J. C. Mitani, T. J. Roper, & L. W. Simmons (Eds.), *Advances in the Study of Behavior* (Vol. 46, pp. 191–280). Academic Press. <https://doi.org/10.1016/B978-0-12-800286-5.00005-5>
- Paredes, R. G. (2009). Evaluating the Neurobiology of Sexual Reward. *ILAR Journal*, 50(1), 15–27. <https://doi.org/10.1093/ilar.50.1.15>
- Parrott, M. L., Nation, A., & Selwood, L. (2019). Female mate choice significantly increases captive breeding success, and scents can be frozen to determine choice, in the stripe-faced dunnart. *Applied Animal Behaviour Science*, 214, 95–101. <https://doi.org/10.1016/j.applanim.2019.03.006>
- Petrie, M., Tim, H., & Carolyn, S. (1991). Peahens prefer peacocks with elaborate trains. *Animal Behaviour*, 41(2), 323–331. [https://doi.org/10.1016/S0003-3472\(05\)80484-1](https://doi.org/10.1016/S0003-3472(05)80484-1)
- Pfaff, D. W., & Ågmo, A. (2002). Reproductive motivation. In *Steven's handbook of experimental psychology: Learning, motivation, and emotion*, Vol. 3, 3rd ed (pp. 709–736). John Wiley & Sons, Inc. <https://doi.org/10.1002/0471214426.pas0317>
- Phoenix, C. H., & Chambers, K. C. (1984). Sexual Deprivation and Its Influence on Testosterone Levels and Sexual Behavior of Old and Middle-Aged Rhesus Males. *Biology of Reproduction*, 31(3), 480–486. <https://doi.org/10.1095/biolreprod31.3.480>

- Pogány, Á., Szurovecz, Z., Vincze, E., Barta, Z., & Székely, T. (2014). *Mate preference does not influence reproductive motivation and parental cooperation in female zebra finches*. <https://doi.org/10.1163/1568539X-00003221>
- Powers, J. B., Newman, S. W., & Bergondy, M. L. (1987). MPOA and BNST lesions in male Syrian hamsters: Differential effects on copulatory and chemoinvestigatory behaviors. *Behavioural Brain Research*, 23(3), 181–195. [https://doi.org/10.1016/0166-4328\(87\)90019-2](https://doi.org/10.1016/0166-4328(87)90019-2)
- Prieto, R., Carlos Sánchez-García, Emilio J. Tizado, Marta E. Alonso, & Vicente R Gaudioso. (2018). Mate choice in red-legged partridges (*Alectoris rufa* L.) kept in commercial laying cages; does it affect laying output? *Applied Animal Behaviour Science*, 199, 84–88. <https://doi.org/10.1016/j.applanim.2017.10.007>
- Pruett-Jones, S. (1992). Independent Versus Nonindependent Mate Choice: Do Females Copy Each Other? *The American Naturalist*, 140(6), 1000–1009. <https://doi.org/10.1086/285452>
- Rault, J.-L. (2019). Be kind to others: Prosocial behaviours and their implications for animal welfare. *Applied Animal Behaviour Science*, 210, 113–123. <https://doi.org/10.1016/j.applanim.2018.10.015>
- Ritter, C., Beaver, A., & von Keyserlingk, M. A. G. (2019). The complex relationship between welfare and reproduction in cattle. *Reproduction in Domestic Animals*, 54(S3), 29–37. <https://doi.org/10.1111/rda.13464>
- Rodríguez-Manzo, G., & Canseco-Alba, A. (2014). 9 - A Role for Learning and Memory in the Expression of an Innate Behavior: The Case of Copulatory Behavior. In A. Meneses (Ed.), *Identification of Neural Markers Accompanying Memory* (pp. 135–147). Elsevier. <https://doi.org/10.1016/B978-0-12-408139-0.00009-2>
- Roth, T. S., Samara, I., Tan, J., Prochazkova, E., & Kret, M. E. (2021). A comparative framework of inter-individual coordination and pair-bonding. *Current Opinion in Behavioral Sciences*, 39, 98–105. <https://doi.org/10.1016/j.cobeha.2021.03.005>
- Rox, A., de Vries, H., Louwerse, A. L., & Sterck, E. H. M. (2018). Female social behaviour during three male introductions in captive groups of rhesus macaques. *Applied Animal Behaviour Science*, 207, 89–97. <https://doi.org/10.1016/j.applanim.2018.07.006>
- Schulte-Hostedde, A. I., & Mastro Monaco, G. F. (2015). Integrating evolution in the management of captive zoo populations. *Evolutionary Applications*, 8(5), 413–422. <https://doi.org/10.1111/eva.12258>
- Setchell, J. M. (2005). Do Female Mandrills Prefer Brightly Colored Males? *International Journal of Primatology*, 26(4), 715–735. <https://doi.org/10.1007/s10764-005-5305-7>
- Singer, B., & Toates, F. M. (1987). Sexual motivation. *The Journal of Sex Research*, 23(4), 481–501. <https://doi.org/10.1080/00224498709551386>
- Sorokowski, P., Groyecka, A., Karwowski, M., Manral, U., Kumar, A., Niemczyk, A., Marczak, M., Misiak, M., Sorokowska, A., Huanca, T., Conde, E., Wojciszke, B., & Pawłowski, B. (2017). Free mate choice does not influence reproductive success in humans. *Scientific Reports*, 7(1), 10127. <https://doi.org/10.1038/s41598-017-10484-x>

- Spoon, T. R., Millam, J. R., & Owings, D. H. (2006). The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Animal Behaviour*, *71*(2), 315–326. <https://doi.org/10.1016/j.anbehav.2005.03.034>
- Spruijt, B. M., van den Bos, R., & Pijlman, F. T. A. (2001). A concept of welfare based on reward evaluating mechanisms in the brain: Anticipatory behaviour as an indicator for the state of reward systems. *Applied Animal Behaviour Science*, *72*(2), 145–171. [https://doi.org/10.1016/S0168-1591\(00\)00204-5](https://doi.org/10.1016/S0168-1591(00)00204-5)
- Stöhr, S. (1998). Evolution of mate-choice copying: A dynamic model. *Animal Behaviour*, *55*(4), 893–903. <https://doi.org/10.1006/anbe.1997.0674>
- Swaisgood, R. R. (2007). Current status and future directions of applied behavioral research for animal welfare and conservation. *Applied Animal Behaviour Science*, *102*(3), 139–162. <https://doi.org/10.1016/j.applanim.2006.05.027>
- Vasconcelos, Í. G. (2023). Coolidge Effect. In T. K. Shackelford (Ed.), *Encyclopedia of Sexual Psychology and Behavior* (pp. 1–4). Springer International Publishing. https://doi.org/10.1007/978-3-031-08956-5_160-1
- Ventura-Aquino, E., Portillo, W., & Paredes, R. G. (2018). Sexual Motivation: A Comparative Approach in Vertebrate Species. *Current Sexual Health Reports*, *10*(3), 114–123. <https://doi.org/10.1007/s11930-018-0156-3>
- Wedekind, C. (2002). Sexual Selection and Life-History Decisions: Implications for Supportive Breeding and the Management of Captive Populations. *Conservation Biology*, *16*(5), 1204–1211. <https://doi.org/10.1046/j.1523-1739.2002.01217.x>
- Widemo, F., & Sæther, S. A. (1999). Beauty is in the eye of the beholder: Causes and consequences of variation in mating preferences. *Trends in Ecology & Evolution*, *14*(1), 26–31. [https://doi.org/10.1016/S0169-5347\(98\)01531-6](https://doi.org/10.1016/S0169-5347(98)01531-6)
- Williams, L. E., & Abee, C. R. (1988). Aggression with mixed age-sex groups of bolivian squirrel monkeys following single animal introductions and new group formations. *Zoo Biology*, *7*(2), 139–145. <https://doi.org/10.1002/zoo.1430070207>
- Wilson, J. R., Kuehn, R. E., & Beach, F. A. (1963). Modification in the sexual behavior of male rats produced by changing the stimulus female. *Journal of Comparative and Physiological Psychology*, *56*(3), 636–644. <https://doi.org/10.1037/h0042469>