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Assessment of same-sex and opposite-sex partner preferences in guinea pigs (*Cavia porcellus*)

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ABSTRACT

Selective social relationships are non-fundamental relationships occurring in group living species probably due to the benefits they entail. Partner preference is the selective social relationships for familiar individuals and has been evidenced in different species across the animal kingdom. In this study, I evaluated the partner preference in same-sex female and opposite-sex social relationships in guinea pigs (*Cavia porcellus*). I used a partner preference test with a three-chamber experimental apparatus in which the focal individual can freely interact and choose between a familiar, a novel individual or neither of them. My results showed a high sociality and preference for a familiar partner in opposite-sex relationships. Partner preference seems to be determined by the ecological and social conditions that the species is exposed to rather than to an evolutionary context.

KEYWORDS

Selective social relationship, social behavior, social structure, sociality.

RESUMEN

Las relaciones sociales selectivas son relaciones no fundamentales que se dan en las especies que viven en grupo, probablemente debido a los beneficios que conllevan. La preferencia de pareja son las relaciones sociales selectivas para individuos familiares y se ha evidenciado en diferentes especies a lo largo del reino animal. En este estudio, evalué la preferencia de pareja en relaciones sociales entre hembras del mismo sexo y de sexo opuesto en cobayas (*Cavia porcellus*). Utilicé un test de preferencia de pareja con un aparato experimental de tres

cámaras en el que el individuo focal puede interactuar libremente y elegir entre un individuo familiar, uno nuevo o ninguno de ellos. Mis resultados mostraron una alta socialidad y preferencia por una pareja conocida en relaciones de sexo opuesto. La preferencia de pareja parece estar determinada por las condiciones ecológicas y sociales a las que está expuesta la especie más que a un contexto evolutivo.

PALABRAS CLAVE

Relación social selectiva, comportamiento social, estructura social, socialidad.

1. INTRODUCTION

In group living species, including humans, individuals may form selective social relationships with other individuals within their social groups (Alexander, 1974). Although these selective social relationships are not fundamental for group living (Lee & Beery, 2022); some species form them probably because they provide fitness benefits (Archie et al., 2014). Selective social relationships can be defined as a type of relationship, such as friendships, in which individuals choose to interact with certain individuals based on specific behavioral or morphological traits (i.e. assort by kin, behavioral similarity, sex or age; Lusseau & Newman, 2004; Massen & Koski, 2014; Silk, 2002). Selective social relationships can improve individual fitness and survival (Archie et al., 2014; J. Silk et al., 2013) for both same-sex (Cameron et al., 2009; Riehl & Strong, 2018; Schülke et al., 2010; J. B. Silk et al., 2003, 2009, 2010) and opposite-sex (Dunning et al., 2023) relationships. Moreover, selective social relationships can be driven by factors such as familiarity between individuals (Bateson, 1973) which indicates that they may emerge from individual preferences. Preferred partners can vary across contexts (e.g. non-reproductive vs reproductive) (Henley et al., 2011) and have been suggested to be related to the stability of the size and composition of the social group and the nature of the mating patterns of each species (i.e., social organization and the mating system, *sensu* Kappeler, 2019) (Beery & Shambaugh, 2021) indicating that social preferences are influenced by a diversity of biotic factors. However, how factors such as familiarity with conspecifics, shape the decision of individuals to choose with whom they associate remains challenging.

The formation of peer-social relationships can be influenced by the familiarity among individuals (i.e. the degree to which kin or non-kin individuals know each other) (Godin

et al., 2003). However, the tendency to engage and form preferred associations with familiar individuals may vary with characteristics of the social system of the species (Gobrogge & Wang, 2016). For example, in monogamous species it is expected that individuals display exclusive and long-lasting preferences toward one particular partner whereas in polygamous species such preferences are not expected. Thus, in a reproductive context, a preference can be viewed as selectivity in courtship and copulation towards a particular individual. However, individuals also interact in non-reproductive context forming other types of selective social relationships with preferred partners. Thus, more broadly social preference can be regarded as selectivity in social contacts towards a particular individual, or a disproportionate amount of time that two individuals spent together (Coria-Avila, 2012).

Species that live in stable social groups are expected to form selective social relationships. This has been widely studied in rodents where it has been suggested that the variation in partner preference is related to the variation in the stability of the social group rather than their mating system (Beery & Shambaugh, 2021). This suggests that stable groups, where social relationships between individuals endure over time, form selective relationships with familiar individuals (Lee et al., 2019), whereas more fluid groups, where social interactions and group membership change over time tend not to display selective relationships towards familiar individuals (Ebensperger et al., 2009). For example, *Microtus ochrogaster* and *Microtus pennsylvanicus*, species living in stable groups during part of the year (Getz et al., 1981; Madison et al., 1984), exhibit selective preference for familiar individuals (Lee et al., 2019) but have different mating systems: *M. ochrogaster* is monogamous whereas *M. pennsylvanicus* is promiscuous (Wolff & Sherman, 2007). Furthermore, *Rattus norvegicus*, *Mus musculus* and *Octodon degus* exhibit highly fluid social groups (Berdy & Drickamer,

2007; Ebensperger et al., 2009; Lore & Flannelly, 1977) usually composed of multimale/multifemale clans of unrelated individuals (Berdoy & Drickamer, 2007; Hayes et al., 2009). Unlike *Microtus* species, these species do not exhibit preference for familiar individuals (Beery et al., 2018; Beery & Shambaugh, 2021; Insel et al., 2020) but similarly they have different mating systems. *R. norvegicus* and *M. musculus* are polygynous (Berdoy & Drickamer, 2007) and *O. degus* mating system changes according to female density (Hayes et al., 2009). These examples reveal a noteworthy association between three components of the social system (*sensu* Kappeler, 2019) and the emergence of partner preference: the social structure (e.g., the tendency to form selective relationships), the social organization (group size and composition) and the mating system (who breeds with whom).

In this study, I used a three-chamber test to evaluate social preference (sociability) and social novelty preference in guinea pigs (*Cavia porcellus*). Guinea pigs belong to the Caviidae family and the Ctenohystrica lineage and are a suitable system to address this question because is highly social species that lives in stable social groups of 2-3 females and a male (Asher et al., 2008) and exhibit a polygynous mating system (Sachser, 1998). Thus, I expect them to exhibit a social preference for familiar partners, in both same and opposite-sex scenarios. Analyzing social preferences allows us to better understand the factors shaping social relationships in different social context and give us insights on the evolution of sociality in rodents, and in group living species, in general.

2. MATERIALS AND METHODS

2.1 Study system

In this study I used *Cavia porcellus*, a rodent species from the Caviidae family domesticated 5.000 years ago (Kleven, 2021). These rodents are highly social, they exhibit a polygynous mating system and females form a linear hierarchy of dominance (Sachser, 1998). *C. aparea*, the ancestral species, is commonly found in south America; it exhibits polygynous societies, one male with 2 to 3 females (Asher et al., 2008). Groups are territorial, females hold restricted territories whereas males hold larger territories that overlap with those of the females (Asher et al., 2008).

For this experiment, I used 30 individuals bought from a commercial breeder in Bogotá, Colombia. Twenty-six individuals that were previously bought and four males that were acquired for this study. Guinea pigs were maintained in same-sex groups of four individuals in an outdoor enclosure in the north campus at Universidad del Rosario. Each group was kept in a pen (1.2 x 1.5 m) following the space requirements (Willis et al., 1977) (Figure S1). To avoid aggression between males, male pens were further divided in four, therefore each male was kept in a smaller pen (0.6 x 0.75 m) but with the option to interact through the mesh. Every enclosure was enriched with a house, a tube for hiding, and sticks for chewing. Additionally, food (hay and pellets) and water were provided on a daily base and their diet was supplemented with vegetables (corn, broccoli, cabbage, among others) on a weekly base.

To ensure that males and females were familiar with each other before the experiment started, I introduced a male in the female enclosure two weeks prior to the partner preference test. However, to prevent pregnancies that would change social decision making due to hormones, the male was placed in a smaller mesh pen (0.6 x 0.3 m) within the female pen. This

arrangement allows individuals to interact, see and smell each other without being able to engage in sexual behaviors (Figure S2).

2.2 Data collection

2.2.1 Peer partner preference test

The peer partner preference test was developed following Beery (2021). This test has been used in different rodent species (*Rattus norvegicus* (Beery & Shambaugh, 2021), *Mus musculus* (Beery et al., 2018), *Microtus ochrogaster* (Beery et al., 2018; Lee et al., 2019), *Microtus pennsylvanicus* (Anacker et al., 2016; Beery & Shambaugh, 2021; Lee et al., 2019) and *Octodon degus* (Insel et al., 2020)) but for this study, the size of the experimental apparatus was adapted for the guinea pigs. The apparatus consisted of a three-chamber structure (two laterals and a central), where the chambers are separated by transparent acrylic walls (Figure 1). The walls have open holes to allow the movement of the individual between chambers. The lateral chambers correspond to the social chambers and the central to the non-social chamber.

At the beginning of the test, the familiar and unfamiliar individuals were fasten to one of the lateral chambers with a harness (Figure 1). The position of each individual within the apparatus was assigned randomly to avoid lateral preferences of the focal individual. After 10 minutes of acclimatization, I introduced the focal individual and placed it in the central chamber. At this point the test begun and was recorded for 180 minutes. Once the test finished, all individuals were returned to their corresponding group in the big enclosure. This

study was performed in two different tests: the same-sex test consisted of a focal female who chose between two females, and the opposite-sex test consisted of a focal female who chose between two males.

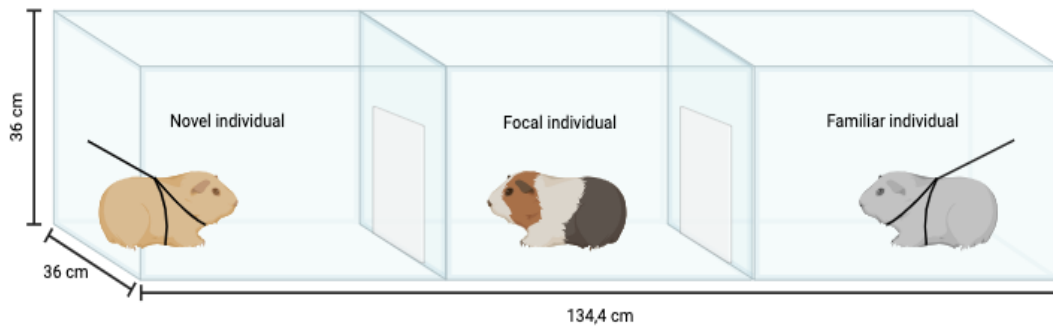


Figure 1. Partner preference test apparatus. Familiar and novel individuals are leashed to the chambers on the opposite sides of the apparatus (i.e., the social chambers) and the focal individual is initially placed in the central chamber (i.e., non-social chamber) with no movement restriction.

2.2.2 Video analysis

I scored the video recordings of each trial in Boris V7 (Friard & Gamba, 2016). For each video, I quantified the time that the focal individual spent in each chamber and the behaviors exhibited by the focal individual either when being alone or towards another individual. Thus, I recorded: aggression, grooming, huddling, ano-genital investigation, face-to-body investigation, walking and remaining still. The behaviors were previously described in an ethogram built by Cardona-Restrepo (2023). All the videos were renamed to prevent any bias (i.e., they were blind to the scorer).

2.3 Statistical Analyses

To evaluate chamber preference (sociability), I used a Kruskal-Wallis, with the duration of the time spent on each chamber as the response variable and the chamber (familiar/neutral/novel) as a factor (Beery, 2021). Second, to quantify partner preference, I calculated the partner preference score by dividing the time adjacent to the familiar individual over the total time adjacent to familiar and novel individual (Beery & Zucker, 2010). To evaluate partner preference, I used a U Mann-Whitney test comparing the time spent huddling with the familiar individual versus the novel individual. Furthermore, to compare the behaviors exhibited towards the familiar or novel individual, I performed a 2-way ANOVA with the duration of each behavior in each chamber (log-transformed) as the response variable and the behavior and familiarity of the individual as factors. Note that courtship and mounting behaviors were only used to evaluate the opposite-sex test. All analyzes were done in R v4.2.1. (R Core Team, 2022).

3. RESULTS

I run a total of 12 female same-sex trials and 12 opposite sex-trials between 05/15/2023 - 06/03/2023 and 11/24/2023 - 12/06/2023, respectively, and recorded a total of 24 three-hour long videos.

Sociability and Partner preference in same-sex trials

During the same-sex test, the focal female guinea pigs spent on average $95.4 \pm 0.75\%$ of the time in a social chamber ($53.2 \pm 0.379\%$ with familiar and $42.2 \pm 0.502\%$ with novel)

compared to the central chamber. When comparing the time spent in each chamber, there were significant differences between all chambers: social chambers were preferred over the non-social chamber (Kruskal-Wallis $H(2) = 119.59$, $p = < 2.2e-16$, Fig. 2A).

The partner preference score for the familiar individual ($58.3 \pm 1.21\%$) was numerically larger than for the novel individual ($41.7 \pm 2.11\%$). However, there are no significant differences in the time spent huddling with the novel or the familiar individual (U Mann-Whitney $W = 89$, $p = 0.3348$, Fig. 2B) indicating no preferences for familiar or novel individuals. Furthermore, there were no differences in the behaviors exhibited towards the familiar or novel individual (i.e., the time spent between chambers in each behavioral category did not differ) nor between the behaviors (two-way ANOVA $F(3, 88) = 0.603$, $p\text{-value} = 0.61$) (Fig. 2C). Finally, there was not a clear pattern of the movement between the chambers, all individuals investigated both social chambers (novel and familiar). Social preference was only evident around the second hour of the experiment (Fig. 2D).

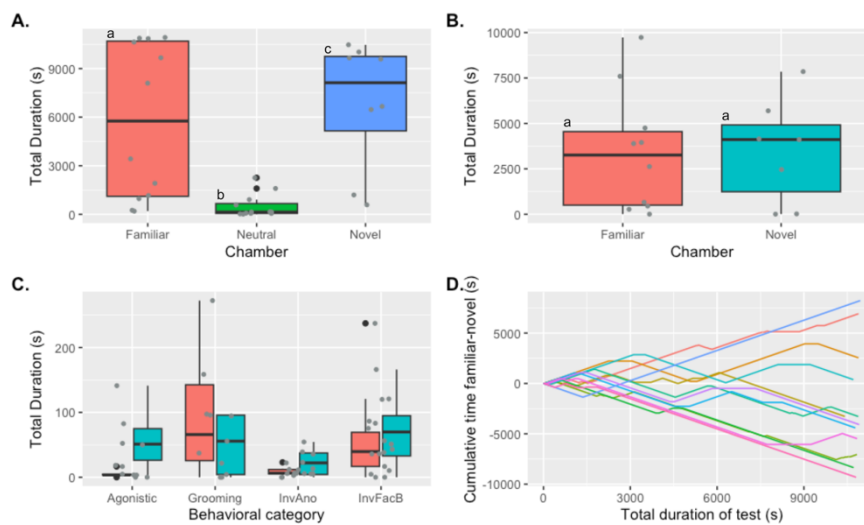


Figure 2. Partner preference test behavior in same-sex experiment. **A.** Guinea pigs spent significantly more time in the familiar and NOVEL chamber compared to the neutral one. **B.** Guinea pigs did not differ in the time huddling with the familiar and the NOVEL individual. **C.** Comparison between the behaviors exhibited towards the familiar or novel individual. There were no differences between the behaviors exhibited towards the familiar and novel individual. **D.** Cumulative time distribution of the 12 trials (each line corresponds to one trial) along the 3-hour trial. In A, B and C, pink bars indicate familiar and blue bars indicate NOVEL chamber, both representing the social chambers, and in A. the green bar indicates the neutral chamber.

Sociability and Partner preference in opposite-sex trials

During the opposite sex trial, the focal female guinea pigs spent $87 \pm 1.59\%$ of time in a social chamber ($67.7 \pm 0.611\%$ with familiar and $19.3 \pm 1.47\%$ with novel) compared to the central chamber. When comparing the time spent in each chamber, there were significant differences between all chambers: the familiar chamber was preferred over the others (Kruskal-Wallis $H(2) = 81.059$, $p < 0.0001$, Fig. 3A).

The partner preference score for the familiar individual ($84.7 \pm 3.82\%$) was larger than for the novel individual (15.3 ± 6.70). The focal individual spent significantly more time huddling with familiar than with the novel individual (U Mann-Whitney $W = 111$, $p = 0.0251$, Fig. 3B), indicating partner preferences for familiar individuals. Furthermore, when comparing the behaviors exhibited towards the familiar or novel individual, there were no significant differences in the time spend between chambers; however, there were differences

between behavioral categories and in the behaviors exhibited towards the familiar or novel individual (two-way ANOVA $F_{(5, 132)} = 2.508$, $p\text{-value} = 0.0333$). Overall, agonistic interactions, grooming and mounting had less duration than courtship and ano-genital and face-to-body investigation (Table S1; Fig. 3C). Moreover, the focal individual spent more time grooming and investigating the familiar individual but displayed more courtship and mounting the novel individual (Table S1; Fig. 3C). Finally, there was not a clear pattern of the movement between the chambers, all individuals investigated all chambers (novel and familiar). A preference for the social chamber was evident 30 minutes after the test started (Fig. 3D).

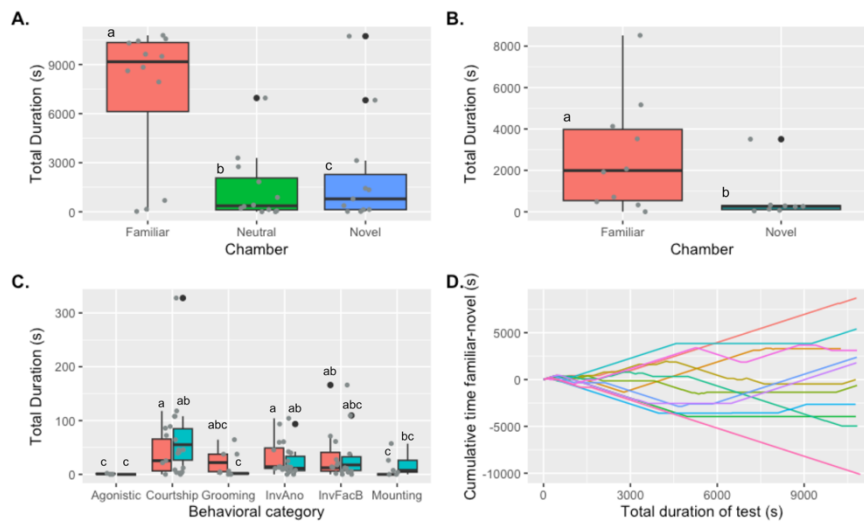


Figure 3. Partner preference test behavior in opposite sex trials. **A.** Guinea pigs spent significantly more time in the familiar chamber rather than on the neutral and the novel one. **B.** Guinea pigs spent significantly more time huddling with the familiar individual rather than to the NOVEL one. **C.** Time spent in each behavioral category differ by chambers. **D.** Cumulative time distribution of the 12 trials (each line) along 3-hour trial.

4. DISCUSSION

My results indicate there is an opposite-sex partner but not a same-sex partner preference for familiar individuals in guinea pigs. In both, same-sex and opposite-sex tests, the focal individual spent less time in the neutral chamber and explored every chamber indicating high sociality and the avoidance of solitary spaces (White et al., 1989). However, only opposite-sex trials showed a high partner preference score and spent more time huddling with the familiar individual. Usually, partner preference in same-sex and opposite-sex scenarios show the same general preference, however, in this study I showed how partner preference can vary according to the sex of the partner evaluated.

Female guinea pigs do not seem to prefer novel or familiar same-sex individuals. This absence of same-sex partner preference may occur because female guinea pigs maintain stable territories and avoid invading other female territories, this behavior may lead to a general avoidance to any individual, both familiar and novel individuals (Asher et al., 2008; Sachser, 1998). The lack of partner preference in same-sex trials has been also observed in *Octodon degus* (Insel et al., 2020), another rodent species from the Ctenohystrica lineage as the guinea pig. *C. porcellus* and *O. degus*, have the same polygynous mating system; however, in the case of *O. degus* the absence of same-sex partner preference may be explained by the fluidity of the group structure (Beery & Shambaugh, 2021). In other species such as guppies (*Poecilia reticulata*) from a Trinidadian population where same-sex partner preference between females has been reported, the preference emerges regardless of the familiarity between the individuals (Godin et al., 2003). Although female guinea pigs within the same harem form social relationships that are necessary to maintain security and support under challenging ecological conditions (Sachser, 1998), the benefits that emerge from this same-sex social relationships do not depend on the familiarity of the individuals. This might

be the reason for the absence of same-sex partner preference. This indicates that the lack of same-sex partner preference in guinea pigs may be driven by the mating system.

Female guinea pigs prefer familiar opposite-sex individuals. These results are similar to what has been found in *Microtus* species (Lee et al., 2019) from the Myodonta lineage. Both *Microtus* and *Cavia* share stability in their social structure but differ in their mating systems, thus indicating that social stability can be an important predictor of opposite-sex selective social relationships. Moreover, *Microtus* and *Cavia* are distant in the rodent phylogenetic tree (Blanga-Kanfi et al., 2009), suggesting that the similarities between these two groups may not have an evolutionary explanation. Opposite-sex partner preference has been evidenced in other species such as marmosets (Cavanaugh et al., 2014) and golden lion tamarins (Inglett et al., 1990), both species live in highly familiar social groups (Digby & Barreto, 1993; Inglett et al., 1990) as guinea pigs, but exhibited monogamy. However, in general, the preference for familiar opposite-sex individuals is consistent with the polygynous social groups, and high site and partner fidelity that females exhibit for the harem male. Moreover, in opposite-sex relationships in guinea pigs, both individuals are fundamental to enhance reproductive fitness and to avoid resource competition (Asher et al., 2008), thus both individuals may benefit of exhibiting preference for the familiar male.

Partner preference has emerged in response to the ecological and social context that the species experienced rather than to their evolutionary history (Ecoffet et al., 2021). It has been proposed that partner preference occurs when the individuals have the ability to compare and choose the most advantageous social interaction and when the partner constitutes a resource

that can provide benefits (Campenni & Schino, 2014). However, the social and ecological factors that influence partner preference are not clear and need to be further explored.

This study shows, for the first-time, the existence of partner preference in the *Ctenohystrica* lineage. Guinea pigs exhibit high sociality and a preference for opposite-sex familiar individuals, which can be driven by the stability of the social system, specifically of the social organization and mating system. Moreover, this study demonstrates that partner preference can vary according to the sex of the evaluated partner. However, further studies evaluating a wider diversity of species are needed to better understand the role of the sex of the individuals in partner preference and its relation to the different components of the social system. Likewise, future research should explore other factors that may influence partner preference such as ecological factors (e.g. resource availability) and social conditions (e.g. parental care and dominance).

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