

## Female guinea pigs prefer familiar opposite-sex individuals but not familiar same-sex peers

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While some species show a preference for familiar individuals when choosing a social or sexual partner, this tendency is not universal and varies across species. However, the association between partner preference and social system is still not clear, and partner preference needs to be studied in species with different social systems from those already studied. Here we evaluated familiarity preference in nonreproductive (same-sex) and reproductive (opposite-sex) social contexts in female guinea pigs, *Cavia porcellus*, a species that forms stable groups of two to three females and one male. We used a three-chamber apparatus that allowed the focal females to freely interact and choose between a familiar or novel individual or to remain in a solitary space. Females showed a strong preference for social over nonsocial chambers, indicating a preference for a social companion. Females also exhibited a clear preference for familiar males but exhibited no marked preference between familiar or novel females, suggesting context-dependence preference. This result is consistent with familiarity preference in other species of rodents exhibiting stable social groups, indicating that familiarity is key for the stability of social groups. Our study provides key evidence of opposite-sex partner preference in one Ctenohystrica rodent species and demonstrates partner preference in a mate (opposite-sex) but not a peer (same-sex) context, a novel finding among rodent species.

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Group-living species, including humans, form selective social relationships (Alexander, 1974), likely because of their associated fitness benefits (Archie et al., 2014). However, not all group-living species exhibit such selectivity (Lee & Beery, 2022). Selective social relationships, such as friendships, involve individuals preferentially interacting with other individuals based on specific behavioural or morphological traits (e.g. assort by kin, behavioural similarity, sex or age; Lusseau & Newman, 2004; Massen & Koski, 2014; Silk, 2002). These relationships can enhance individual fitness (Archie et al., 2014; Silk et al., 2003; Stanton & Mann, 2012), particularly in same-sex relationships (Cameron et al., 2009; Riehl & Strong, 2018; Schülke et al., 2010; Silk et al., 2003, 2009, 2010). In opposite-sex social relationships, the benefits are associated with increased recruitment (Dunning et al., 2023), biparental offspring

care and reduced harassment (Cheney & Seyfarth, 1982; Schülke et al., 2013). Moreover, selective social relationships can vary across contexts (e.g. nonreproductive versus reproductive) (Henley et al., 2011) and be driven by factors such as familiarity (Jordan et al., 2010). However, understanding how preferences for familiar individuals may change across nonreproductive (same-sex) and reproductive (opposite-sex) social contexts remain largely unexplored.

Familiarity among individuals, the degree to which kin or nonkin individuals know each other (Godin et al., 2003), can influence the formation of peer social relationships (Fernandez-Duque et al., 2000). However, the tendency to engage and form preferred associations with familiar individuals may vary across species based on characteristics of their social system (Gobrogge & Wang, 2016), such as group stability and mating patterns (Beery & Shambaugh, 2021). For example, in monogamous species, individuals display exclusive and long-lasting preferences towards particular opposite-sex partners (Fuentes, 2002), whereas in polygamous species, such preferences are not expected

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(Buchanan-Smith & Jordan, 1992). Moreover, in species with stable social groups, where social relationships between individuals endure over time, individuals may form selective relationships with familiar individuals (Insel et al., 2020; Lee et al., 2019), while in fluid groups, where social interactions and group membership change over time, individuals do not exhibit such selectivity (Ebensperger et al., 2009). These studies suggest that both familiarity and social system characteristics are key factors shaping partner choice preferences.

Different components of the social system, such as social organization and mating system, are associated with partner preference. For example, species such as prairie voles, *Microtus ochrogaster*, and eastern meadow voles, *Microtus pennsylvanicus* (Getz et al., 1981; Madison et al., 1984), which form stable groups part of the year, exhibit selective preferences for familiar opposite-sex individuals (Beery, 2019; DeVries et al., 1997; Parker et al., 2001; Williams, Catania, et al., 1992; Wu et al., 2020; Yang et al., 2016) and familiar same-sex individuals (Beery, 2019; Beery et al., 2009; Beery & Shambaugh, 2021; DeVries et al., 1997; Lee et al., 2019; Parker & Lee, 2003). However, despite their similar social organization, they exhibit different mating systems; *M. ochrogaster* is monogamous, whereas *M. pennsylvanicus* is promiscuous (Wolff & Sherman, 2007). A monogamous mating system may not be essential for emergence of partner preferences but it can facilitate it (Williams, Carter, et al., 1992). In contrast, species that form fluid groups of unrelated individuals, such as the brown rat, *Rattus norvegicus* (Berdoy & Drickamer, 2007), house mouse, *Mus musculus* (Lore & Flannelly, 1977), and degus, *Octodon degus* (Ebensperger et al., 2009), do not exhibit same-sex preferences for familiar individuals (Beery et al., 2018; Beery & Shambaugh, 2021; Insel et al., 2020; Schweinfurth et al., 2017). These species, too, exhibit diverse mating systems. Brown rats, for example, are polygamous (both sexes mate with multiple partners) (McClintock et al., 1982); house mice are polygynous (multiple females per male) (König & Lindholm, 2012); and degus can alternate between polygynous and monogamous breeding depending on the number of females present (Hayes et al., 2009). These examples highlight an association between the social organization and partner preference, regardless of the mating system. Individuals in stable social groups, but not in fluid social groups, show a preference for familiar individuals.

In this study, we investigate the influence of social context on partner preference in guinea pigs, *Cavia porcellus*, a rodent species of the Caviidae family, and the Ctenohystrica lineage (Blanga-Kanfi et al., 2009). Guinea pigs were domesticated 5000 years ago (Kleven, 2021). *Cavia aparea*, the wild ancestral species, is a polygynous species from South America that lives in stable harems of one male with two to three females (Asher et al., 2008). Domestic guinea pigs exhibit a similar social structure; they form linear dominance hierarchies, and males and females form social bonds (Sachser, 1998). Given that preference for familiar individuals may be associated with stable (less flexible) groups and the presence of social bonds, we hypothesized that female guinea pigs would exhibit a social preference for familiar individuals in both same-sex and opposite-sex contexts.

## METHODS

### Study System

For this experiment, we used 30 adult (~2 years old with no previous reproduction) individuals bought from commercial breeders in Bogotá, Colombia. Guinea pigs were maintained in same-sex groups of four individuals in an outdoor enclosure on the north campus of Universidad del Rosario. Female groups were kept

in a 1.2 × 1.5 m pen, ensuring their individual space requirements (Willis et al., 1977), while males were temporarily kept in a smaller mesh cage (0.6 × 0.75 m) within the pen to avoid aggression (Supplementary Fig. S1). Every enclosure was enriched with a house, a tube for hiding and sticks for chewing. Additionally, food (hay and pellets, Premium Alduque) and water were provided daily and supplemented with vegetables (broccoli and carrot, among others) on a weekly basis.

To ensure familiarity between males and females, we introduced a male in the female enclosure 2 weeks prior to the partner preference test. Females were allowed to freely interact within the enclosure. However, because we could not castrate males, we placed the novel male in a smaller mesh pen (0.6 × 0.3 m) within the female enclosure (Supplementary Fig. S2) to prevent pregnancies that may alter the female social behaviour. The mesh holes allowed social recognition through chemical signals (Winslow & Insel, 2004) as well as physical contact between males and females but prevented copulatory behaviours (Supplementary Fig. S2), thus ensuring the familiarization process.

### Data Collection

#### Peer partner preference test

We evaluated peer partner preference using the peer partner preference test described by Beery (2021) and adapted the size of the experimental apparatus for guinea pigs (0.6 × 1.2 m; Fig. 1). The apparatus consisted of a three-chamber structure with transparent acrylic walls and open passages to allow for movement between chambers. The central chamber was designated as the nonsocial chamber, where the focal individual was initially placed, and the lateral chambers were designated as social chambers, where familiar and novel individuals were placed.

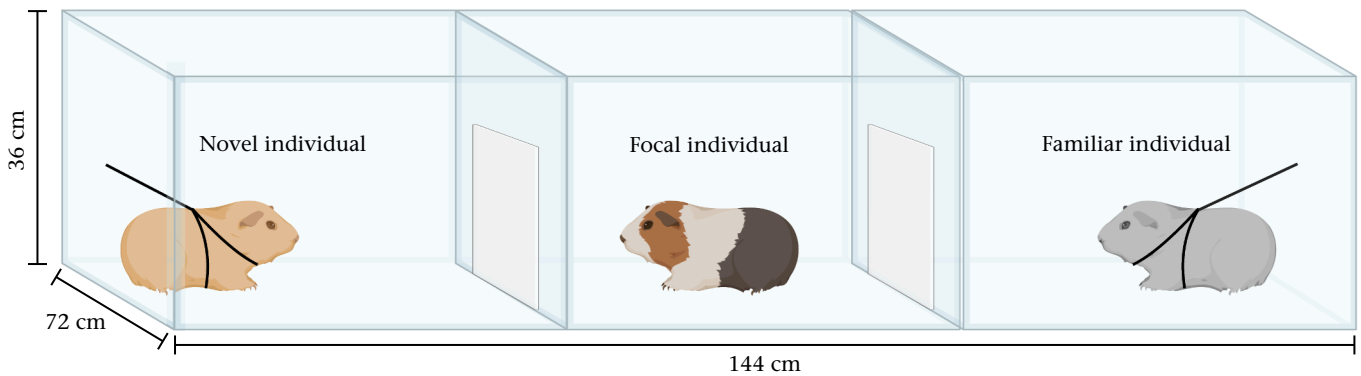
The test was performed in two different contexts: (1) same-sex test, where a focal female chose between two females; (2) opposite-sex test, where a focal female chose between two males. At the beginning of each test, the familiar and novel individuals were placed in the lateral chambers and tethered with a harness to the wall (Fig. 1). The position of the familiar and novel individual within the social chambers was assigned randomly to avoid lateral preferences of the focal individual. After 10 min of acclimatization, we introduced the focal individual to the central chamber and started the test. The trial lasted 180 min and was recorded with a camera above the apparatus. At the end of the trial, individuals were returned to their respective enclosure. Males and females were used multiple times in the rotation. However, individuals were only placed in the experimental apparatus after a minimum of 1 day between trials. Females were used as focal and novel/familiar individuals, whereas males were only used as novel/familiar individuals.

#### Video analysis

We scored all videos in Boris version 7 (Friard & Gamba, 2016). For each video, we quantified the time that the focal individual spent in each chamber (neutral, familiar and novel) and the length of the behaviours exhibited by the focal individual towards the familiar or the novel individual (following Beery & Zucker, 2010). We followed the ethogram by Cardona-Restrepo (2023) and recorded grooming, huddling, anogenital investigation, face-to-body investigation and aggression (boxing or biting) (social behaviours) and walking and remaining still (nonsocial behaviours). All the videos were renamed to ensure the scorer was blind to the position of the familiar and novel individual.

#### Behaviour measures

First, we quantified the sociability score that measures the preference for being with another individual instead of alone. It



**Figure 1.** Partner preference test apparatus. Familiar (grey) and novel (light brown) individuals are leashed to the lateral chambers of the apparatus (i.e. the social chambers), and the focal female (multicolour) individual is initially placed in the central chamber (i.e. nonsocial chamber) with no movement restriction. Guinea pigs have different colours to indicate that individuals had different colour patterns in the experiment.

was defined as the time spent in the social chambers compared to the neutral chamber. Second, we quantified the partner and stranger preference score that measures the preference for being in physical contact with a familiar individual and novel individual, respectively. It was calculated by dividing the time spent huddling with the familiar or novel individual over the total time spent huddling (following Beery & Zucker, 2010). We also calculated partner preference in two additional ways: (1) adding time spent huddling and time spent grooming (physical contact); (2) adding time spent huddling, time spent grooming and time spent in chamber (close proximity).

#### Statistical Analyses

First, to evaluate sociability, we used a Kruskal–Wallis test with the duration of time spent in each chamber as the response variable and the chamber type (familiar/neutral/novel) as a factor. Second, to evaluate partner preference, we used a Mann–Whitney  $U$  test comparing the time spent huddling with the familiar versus the novel individual. We also ran this comparison for the variables physical contact and close proximity. Finally, to compare the behaviours exhibited towards the familiar or novel individual, we performed a two-way ANOVA with the log-transformed duration ( $\log(d + 1)$ ) of each behaviour in each chamber as the response variable and the behavioural category (behaviour displayed by the focal individual) and familiarity (familiar/novel) of the nonfocal individual as factors. Note that courtship and mounting behaviours were only used in the opposite-sex analysis. All analyses were done in R version 4.2.1. (R Core Team, 2022).

#### Ethical Note

This project was conducted under the permit DVO005 2269-CV1691 approved by the Research Ethics Committee of the Universidad del Rosario, in accordance with Colombian government ethical and legal requirements. The guinea pigs used in this study came from commercial breeders and were housed in outdoor enclosures of the Universidad del Rosario (Bogota, Colombia) They were regularly monitored by the researchers to identify any signs of distress or abnormal conditions. To minimize stress, only one test was conducted per day, with each animal receiving at least 1 day of rest between trials. During testing, guinea pigs were transported in secure crates and fitted with specially designed fabric harnesses to reduce stress.

## RESULTS

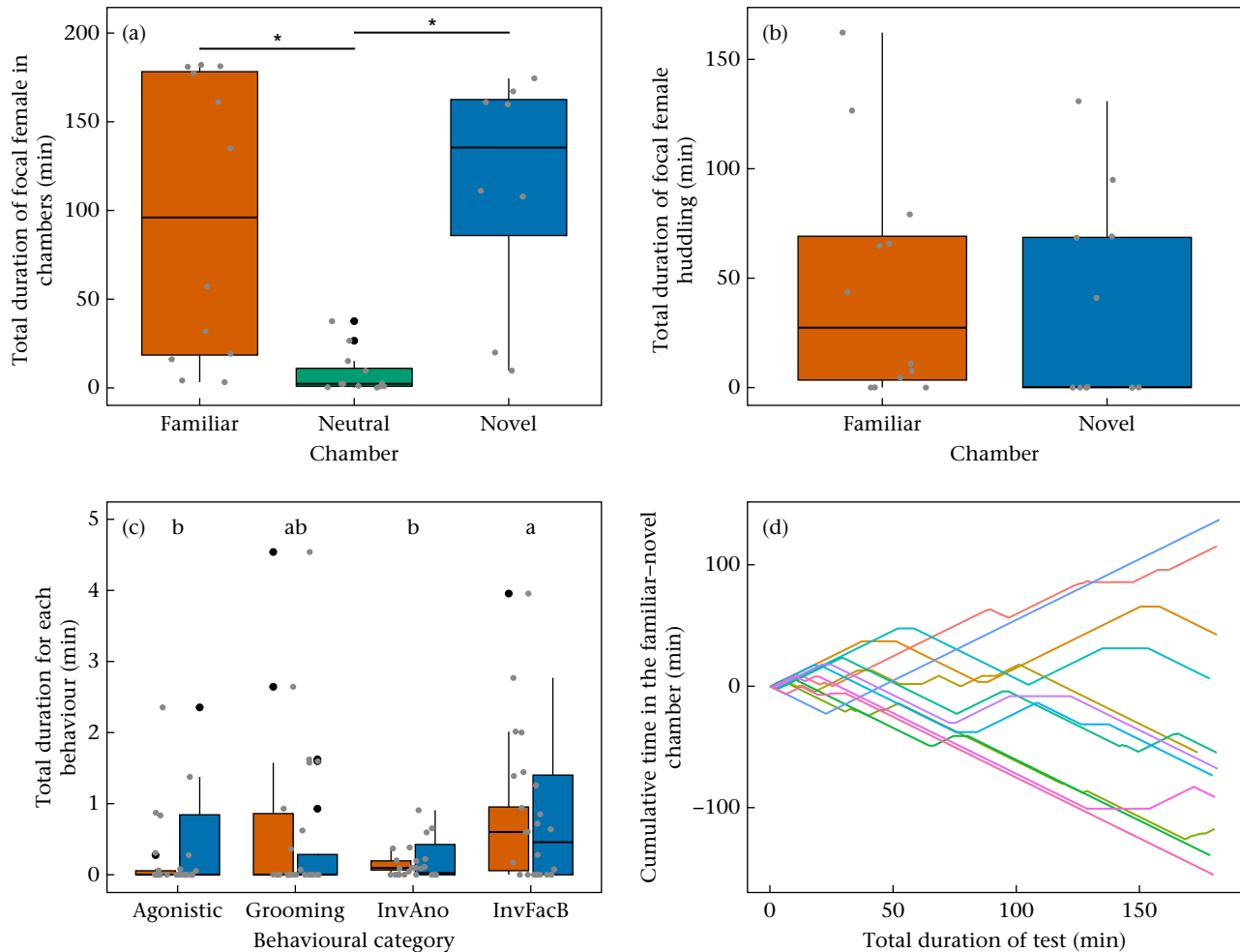
We ran 12 same-sex trials with females and 12 opposite-sex trials (all with focal females) during 15 May 2023–3 June 2023 and 24 November 2023–6 December 2023, respectively, and recorded 3 h videos of each trial.

#### Sociability and Partner Preference in Same-sex Trials

Female guinea pigs exhibited a strong preference for social over nonsocial chambers. Focal females spent an average ( $\pm$  SE) of  $171.7 \pm 1.825$  min (95.4% of their time) in a social chamber compared to  $8.3 \pm 0.705$  min in the neutral chamber. Within the social chambers, focal females spent an average of  $95.8 \pm 1.26$  min (53.2% of the time) in the familiar female chamber and  $75.9 \pm 1.32$  min (42.2% of the time) in the novel female chamber. The Kruskal–Wallis test showed that the time the focal female spent in the chambers was significantly affected by the chamber type ( $H_2 = 15.775$ ,  $P = 0.0004$ ). Focal females spent significantly more time in the familiar ( $P = 0.0007$ ) and the novel ( $P = 0.0018$ ) chambers compared to the neutral chamber, but there was no significant difference in time spent in familiar and novel chambers ( $P = 1.000$ ) (Fig. 2a). The familiar preference score, which considered only the time spent huddling within the trial, showed no significant difference in the time focal females spent huddling with familiar females (0.583) compared to novel females (stranger preference score: 0.417) ( $V = 46$ ,  $P = 0.622$ ; Fig. 2b). This indicates that female guinea pigs did not exhibit preferences for familiar or novel females. We also ran this comparison for the variables physical contact and close proximity but the results did not differ (Supplementary Fig. S3). The two-way ANOVA indicated that focal females allocated different amounts of time to different behaviours ( $F_{3,88} = 3.617$ ,  $P = 0.0163$ ), spending significantly more time engaged in face-to-body investigation compared to other behaviours. However, there was no significant effect of familiarity ( $F_{1,88} = 0.151$ ,  $P = 0.6983$ ) and no interaction between familiarity and behavioural category ( $F_{3,88} = 1.266$ ,  $P = 0.2910$ ) in the time allocated to specific behaviours towards familiar or novel females (Fig. 2c, Supplementary Table S1). Finally, focal females investigated all chambers and only showed a preference for the novel or the familiar individual around the second hour of the test (Fig. 2d).

#### Sociability and Partner Preference in Opposite-sex Trials

Female guinea pigs exhibited a strong preference for social over nonsocial chambers. Focal females spent an average ( $\pm$  SE) of  $156 \pm$



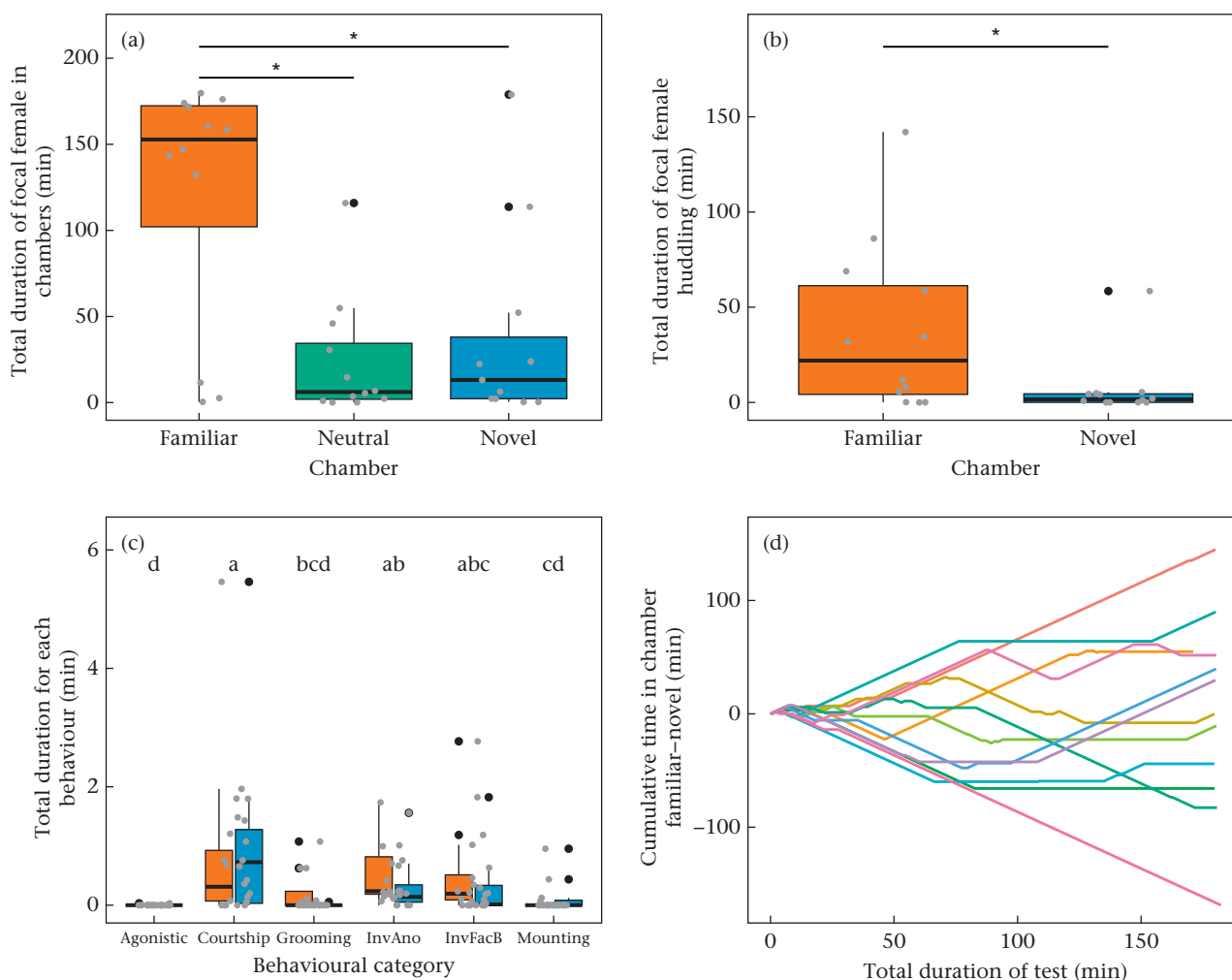
**Figure 2.** Results of partner preference tests in same-sex trials. (a) Total time focal females spent in social chambers (with familiar or novel females) versus the neutral chamber. (b) Total time focal females spent huddling with the familiar versus the novel female. (c) Total time focal females engaged in each behaviour with familiar (orange) and novel (blue) females. InvAno = anogenital investigation; InvFacB = face-to-body investigation. Box plots show the medians (line in the boxes), 25% and 75% quartiles (box boundaries), outermost values within the range of 1.5 times the respective quartiles (whiskers), outliers (black dots) and raw data (grey dots). Letters above bars indicate significant differences between behavioural categories. (d) Cumulative time the focal female spent in the familiar and novel chambers during each 3 h trial (each line corresponds to one trial); positive values correspond to occupancy in the familiar female's chamber, while negative values correspond to occupancy in the novel female's chamber.

3.12 min (87% of their time) in a social chamber compared to  $23.4 \pm 1.17$  min in the neutral chamber, and within the social chambers, females spent an average ( $\pm$  SD) of  $122 \pm 2.57$  min (67.7% of their time) in the familiar male chamber and  $34.6 \pm 1.76$  min (19.3%) in the novel male chamber. The Kruskal–Wallis test showed that the time focal females spent in different chambers was significantly affected by the chamber type ( $H_2 = 8.951$ ,  $P = 0.01138$ ). Focal females spent significantly more time in the familiar male chamber than in the neutral chamber ( $P = 0.0075$ ) or the novel male chamber ( $P = 0.0346$ ), but there was no significant difference in time spent in the neutral chamber and the novel male chamber ( $P = 0.9525$ ) (Fig. 3a). The familiar preference score, which considered only the time spent huddling, indicated that focal females spent significantly more time huddling with the familiar male (0.84) than with the novel male (novel preference score: 0.153) ( $V = 66$ ,  $P = 0.0342$ ; Fig. 3b), indicating a female preference for familiar males. We also ran this comparison for the variables physical contact and close proximity but the results did not differ (Supplementary Fig. S4). The two-way ANOVA indicated a significant effect of behavioural category ( $F_{5,132} = 9.693$ ,  $P = 6.66e-08$ ), but there was no significant effect of familiarity ( $F_{1,132} = 0.283$ ,  $P = 0.596$ ) and no interaction between familiarity and behavioural

category ( $F_{5,132} = 1.246$ ,  $P = 0.291$ ) in the time allocated to specific behaviours towards familiar or novel male individuals. Focal females spent significantly more time investigating (anogenital and face-to-body) and performing courtship behaviours compared to other behaviours (Fig. 3c, Supplementary Table S2). Focal females also tended to spend more time grooming and investigating the familiar male but more time in courtship and mounting the novel male (Fig. 3c, Supplementary Table S2). Finally, focal females investigated all chambers and only showed a preference for a social chamber 30 min after the test started (Fig. 3d).

## DISCUSSION

Our study reveals that female guinea pigs prefer being in social proximity than alone and that they have a clear preference for familiar opposite-sex partners and no preference for familiar or novel same-sex individuals. In both same-sex and opposite-sex tests, the focal female spent almost all the time in the social (occupied) chambers compared to the neutral (unoccupied) chamber. More importantly, our results partially support our prediction based on the known stability of the social organization of guinea pigs that they would prefer familiar same-sex



**Figure 3.** Results of partner preference tests in opposite-sex trials. (a) Total time focal females spent in social chambers (with familiar or novel males) or in the neutral chamber. (b) Total time focal females spent huddling with the familiar male compared to the novel male. (c) Total time focal females spent engaged in each behaviour with familiar (orange) and novel (blue) males. InvAno = anogenital investigation; InvFacB = face-to-body investigation. Box plots show the medians (line in the boxes), 25% and 75% quartiles (box boundaries), outermost values within the range of 1.5 times the respective quartiles (whiskers), outliers (black dots) and raw data (grey dots). Letters above bars indicate significant differences between behavioural categories. (d) Cumulative time the focal female spent in the familiar and novel chambers during each 3 h trial (each line corresponds to one trial); positive values correspond to occupancy in the familiar male's chamber, while negative values correspond to occupancy in the novel male's chamber.

and opposite-sex individuals. Females in opposite-sex trials showed a clear preference for familiar male individuals, as evidenced by high partner preference scores for familiar males and increased huddling with familiar males compared to novel males. These findings suggest that preference for familiar individuals was not consistent in same-sex and opposite-sex contexts.

Similar to other social species, guinea pigs displayed a preference for spending time in spatial proximity with a conspecific over being solitary (Anacker et al., 2016; Insel et al., 2020; Lee et al., 2019). Importantly, focal female guinea pigs investigated and huddled with familiar and novel females but displayed agonistic behaviour towards novel females, suggesting that they showed an interest in novel individuals but discriminated against them. However, in opposite-sex trials, focal females mostly interacted with familiar males and did not display agonistic interactions towards familiar or novel males, indicating a higher tolerance for opposite-sex conspecifics. Social tolerance has been suggested to influence the evolution of cooperation (Hare et al., 2007; Kaigaishi et al., 2019) and other social traits such as prosocial behaviour

(Burkart et al., 2014) and patterns of aggression and affiliation (Ciani et al., 2012), and thus, the development of social interactions among the individuals (Illenberger et al., 2013). However, the preference for occupied spaces could also indicate avoidance of solitary spaces, attraction to social environments (White et al., 1989) and a potential stress response towards novelty (Kaiser et al., 2003).

The lack of partner preference for familiar or novel same-sex individuals may be a factor influencing the social organization of a species. For example, degus (Insel et al., 2020; Lidhar et al., 2021), house mice (Beery et al., 2018), spiny mice, *Acomys cahirinus* (Fricker et al., 2022) and brown rats (Beery & Shambaugh, 2021) exhibit a lack of familiarity preference and live in fluid groups where individuals constantly change their patterns of interactions (Beery & Shambaugh, 2021). This indicates that the absence of preference is a component of flexible and gregarious social groups (Lee & Beery, 2022). However, female guinea pigs maintain stable territories (Asher et al., 2008; Sachser, 1998), which suggests that other factors may be at play. In the sable antelope, *Hippotragus niger*, calves select same-sex social partners during play

(playmates) based on age, size and similarity rather than familiarity (Thompson, 1996). Antelopes and guinea pigs both live in female-biased groups; thus, the lack of familiarity preference may be associated with other characteristics of the social organization such as group composition. Finally, the agonistic behaviours exhibited between female guinea pigs may be used to regulate group composition, exclude nongroup members and promote stability within the social group (Lee & Beery, 2022). Therefore, group stability could come from familiarity preference or novelty avoidance or aggression.

Partner preference for familiar opposite-sex individuals has been described in species with stable social groups. For example, meadow voles and prairie voles show a preference for familiar opposite-sex individuals and exhibit stability in their social groups, which may explain this preference (Asher et al., 2008; Lee et al., 2019). Similarly, Kenyan blue monkeys, *Cercopithecus mitis*, live in stable social groups and exhibit opposite-sex partner preferences for familiar individuals (Schembari et al., 2024). Both Kenyan blue monkeys and guinea pigs exhibit polygynous mating systems, suggesting that the mating system may be a factor influencing partner preference. However, the mating system alone may not fully explain this behaviour, as polygynous species have shown both the presence (Schembari et al., 2024; this study) and absence (Beery & Shambaugh, 2021) of partner preferences for familiar individuals in opposite-sex social relationships. This suggests that group stability plays a more significant role, as it has been suggested in monogamous European siskins, *Carduelis spinus* (Senar et al., 2013).

Our finding that female guinea pigs preferred familiar opposite-sex individuals but had no familiarity preference for same-sex peers highlights the role of these preferences in shaping the social organization and group stability of a species. Our results also reveal for the first time in the Ctenohystrica suborder a preference for familiar individuals, thus contributing to the understanding of the evolution of sociality. The preference for a social environment over solitary space underscores the importance of social interactions for affiliative behaviour and stress reduction. Future research should aim to quantify the relative contribution of different components of the social system and other factors that may influence partner preference, such as ecological and social contexts as well as the effect of nonfocal individuals' behaviours on the decision making of focal individuals.

## Author Contributions

**Ana M. Romero-Chacón:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Formal analysis, Data curation. **Manuela Cardona-Restrepo:** Writing – review & editing, Investigation, Conceptualization. **Gabriela Pena-Bello:** Writing – review & editing, Investigation, Conceptualization. **Adriana A. Maldonado-Chaparro:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

## Data Availability

Data and code are available at [https://osf.io/v4sde/?view\\_only=1ff5c3efe95146d8a0feede6453833c0](https://osf.io/v4sde/?view_only=1ff5c3efe95146d8a0feede6453833c0).

## Declaration of Interest

The authors have no competing interests.

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## Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2025.123384>.

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