A test of spatial proximity as a driver for social bond formation

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ABSTRACT

Spatial proximity is a factor that facilitates the formation of social relationships. Here, I evaluated whether spatial proximity promotes the development of low-cost relationships and whether these favor the formation of cooperative relationships (high-cost relationships). To do this, I used 23 guinea pigs distributed in six enclosures controlling for familiarity between group members. The experiment consisted of three treatments that were evaluated in three phases. In treatment A individuals could freely interact in a shared foraging arena; In treatment B individuals were forced to share the foraging arena and in the control group, individuals were not allowed to share. The results suggest that spatial proximity facilitates the development of low-cost foraging relationships. The strength of foraging relationships increased over time, a phenomenon that was more evident when individuals were allowed to freely decide whether to share space with other individuals. Additionally, pairs that form strong foraging relationships were more likely to develop high-cost relationships. In conclusion, spatial proximity, especially voluntary proximity, promotes the formation of low-cost social relationships, and these in turn favor the formation of cooperative relationships.

RESUMEN

La proximidad espacial es un factor que puede promover la formación de relaciones sociales. En esta investigación plantee un experimento en el que se evaluó si la proximidad espacial puede promover la formación de relaciones sociales de bajo costo, y favorecer la formación de relaciones de cooperación (relaciones de alto costo). Para esto se usaron 23 curíes divididos en grupos de cuatro individuos en seis encierros diferentes, en los cuales controlé la familiaridad entre ellos. El experimento consistió en tres tratamientos que fueron evaluados en tres fases. En el tratamiento A los individuos podían interactuar libremente, En el tratamiento B los individuos fueron forzados a compartir un espacio y en el control, los individuos no tenían oportunidad de compartir. Los resultados sugieren que la proximidad espacial promueve la formación de relaciones sociales. Este fenómeno es más evidente cuando los individuos pueden decidir libremente si compartir el espacio con otros. Adicionalmente, las parejas de individuos que forman relaciones de forrajeo tienen mayor opción de desarrollar relaciones de alto costo. En conclusión, la proximidad espacial, especialmente la voluntaria, promueve la formación de relaciones sociales de bajo costo, y estas a su vez favorecen la formación de relaciones de cooperación.

KEYWORDS

Cooperative relationships, Foraging relationships, Greeting, Guinea Pigs, Social networks

PALABRAS CLAVE

Acicalamiento, Cuys, Relaciones Cooperativas, Relaciones de Forrajeo, Redes Sociales, Saludos

INTRODUCTION

Social relationships are characterized by the content, quality, and pattern of the interactions among individuals in a group and are influenced by the history and course of these interactions (Hinde, 1976). Social bonds are a type of social relationships among individuals of the same or opposite sex, characterized by their stability and endurance (Ostner & Schülke, 2014). Social bonds are stronger between some individuals in a group than between others (Silk, Alberts, & Altmann, 2003; Lee, 2022). Moreover, social bonds may be adaptive and often entail fitness benefits to individuals (Silk et al., 2009). For example, in baboons, females with stronger social bonds live longer than others, and also the offspring of females with stronger and more stable relationships are more likely to survive (Silk et al., 2003; Silk et al., 2010). Social bonds can also promote cooperation among individuals in a group (Berghänel, Ostner, Schröder, & Schülke, 2011) which can further enhance the benefits of group living. Although social bonds have fitness advantages, the process by which they are formed is still not well understood. However,the drivers that promote cooperative relationships in humans (e.g., Barclay & Willer, 2007) and non-human species (e.g., Carter et al., 2020) can also provide insight into the ontogeny of social bonds.

A key factor that explains the stability of cooperative relationships in humans and other primates is reciprocity, i.e., the act of providing benefits to an individual in response to those benefits that have been received (Molm, 2010). For example, in macaque(*Macaca fascicularis*) individuals appear to exchange benefits such as defense against predators, social grooming or food sharing (Majolo, Schino, & Aureli, 2012). In vampire bats *(Desmodus rotundus*) reciprocity of food sharing emerges via establishment of reciprocal grooming relationships (Carter et al., 2020), consistent with strategies such as “Raise the Stakes" (RS), where individuals escalate their investment depending on the investment done by their partner, thus increasing the trust and the stability of the relationships (Roberts & Sherratt, 1998). Another example occurs in patterns of social grooming in male chimpanzees (*Pan troglodytes*) under conditions of social instability (Kaburu & Newton- Fisher, 2013). Although reciprocity can stabilize cooperative relationships that exist, the mechanisms by which such relationships form initially are still unclear.

Spatial proximity is a simple mechanism that can lead to spatial tolerance thus facilitating the development of social relationships (Di Bitetti, 1997). Spatial proximity allows and promotes for frequent interactions among individuals (Byrne, Heinonen, & Jussila, 2015), thus facilitating the development of a preference for their closest partners (Razik, Brown, & Carter, 2022). Close individuals are more likely to engage in low-cost social interactions and progressively developcostly interactions such as cooperative relationships (Razik et al., 2022). For example, in vampire bats (*Desmodus rotundus*), individuals establish long-lasting relationships when being forced to share a space (Razik et al., 2022). Spatial proximity can directly promote survival by improving social thermoregulation and vigilance (Ancillotto, Serangeli, & Russo, 2012). For example, female capuchin monkeys *(Cebus capucinus)* have a higher survival rate when they experience more social interactions and longer time of foraging together (Kajokaite, 2022), and in male macaques (*Macaca assamensis*) strong social bonds are associated with a higher dominance rank and siring success (Schülke, 2010).

Here, I tested whether spatial proximity promotes the establishment of low-cost social relationships (e.g., foraging) among individuals and whether they may further facilitate the formation of cooperative relationships (Figure 1). I tested two scenarios, one in which individuals can freely interact and a second in which individuals are forced to share the space. I expected individuals that freely interact to form stronger low-cost relationships compared to those that were forced to share a space. I focused on two types of social behaviors from which social relationships can emerge: foraging (low cost) and greeting (high cost), where the cost of the relationship is related to a potential fitness cost to the interacting individuals that are investing in the relationship (Roberts & Sherratt, 1998). In this way, sharing a space requires a low investment and thus, a low-cost, as opposed to a cooperative relationship that requires a higher investment. Social foraging requires spatial proximity and tolerance among individuals (Ottoni, Izar, & Resende, 2004) and thus facilitates the interaction among the individuals in a group favoring the emergence of foraging relationships. Once foraging relationships are formed, we expect them to facilitate the development of cooperative relationships, in the form of greetings. Greeting is an exchange of non-aggressive signals, that can be expressed with behaviors such as genital touch, sniff, and nose touch (Kutsukake et al., 2006; Nishida, 1970; Dal Pesco & Fischer, 2018). This behavior facilitates social proximity and physical contact among individuals (Colmenares, 1990). Thus, individuals that establish strong foraging relationships are expected to develop high-cost relationships (i.e., greetings).

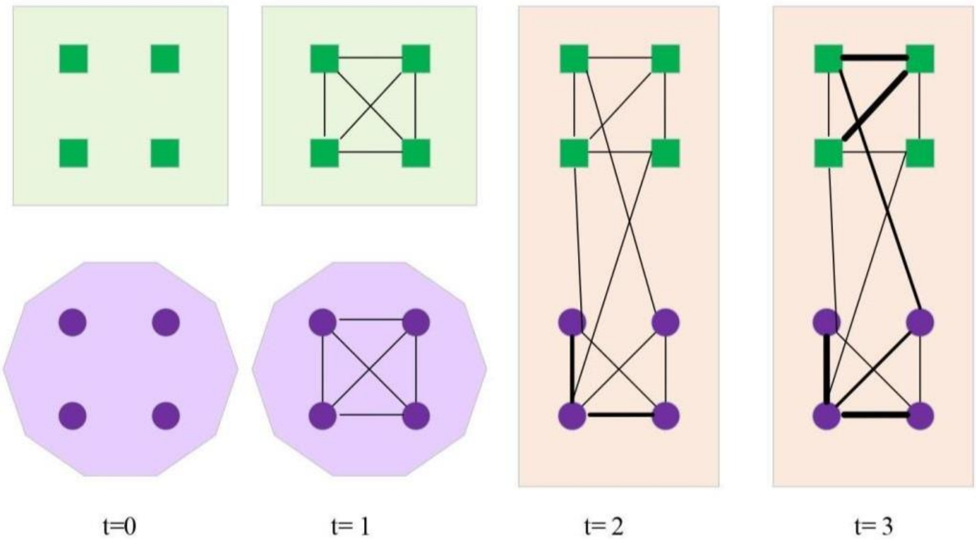

Figure 1. Expected social networks. At the beginning of the experiment (t=0) individuals

within groups have not developed social relationships among them. As they interact (e.g., t=1), social relationships start to develop among individuals within groups. At the beginning of the experiment (t=2) individuals between groups start to develop social relationships. At the end of the experiment (t=3), individuals within groups have further developed differentiated social relationships.Some of the dyads developed stronger social bonds (thicker lines) compared to other dyads (thinner lines). Dots and squares indicate individuals from group 1 (purple dots) and 2 (green squares) within a treatment.

Methodology

Study system

Guinea pigs (*Cavia porcellus*) is a rodent species that live mainly in meadows (Salvador & Fernandez, 2008) in groups generally composed of 2 to 3 individuals, e.g., one male and two females (Asher, De Oliveira, & Sachser, 2004). They spend most of the time foraging together, feeding mainly on grass (Willis, Levinson, & Buchanan, 1977).

Experimental design

I used 24 captive breed adult females sourced from a breeder in Bogota, Colombia. Females came from six different breeding pens, had previous breeding experience and were between 6-8 months old to avoid developmental changes in social behavior occurring between juvenile and adulthood stages in females (Trillmich, Sötemann, & Clara, 2007). Upon arrival, I created six experimental groups composed by four unknown individuals. To control for familiarity among individuals, females in each group came from each of the breeding pens. Each group was housed in a pen of 1.2 x 1.5 m made of mesh, following suggested space requirements (Willis et al., 1977). One side of the pen had a wall (made of drywall) to ensure that groups from contiguous pens could not see or smell each other (Figure 2). Each pen was enriched with a house, a tube for hiding, and sticks for chewing. Food hay and pellets; Alimentos Alduque S.A. and water were provided *ad libitum*, and vegetables were provided three days a week. Before the start of the experiment, individuals were allowed to acclimate for three weeks. This period was also used to ensure that individuals within the group had known each other for the same amount of time. All individuals were measured and uniquely marked with hair dye (Figure 2).

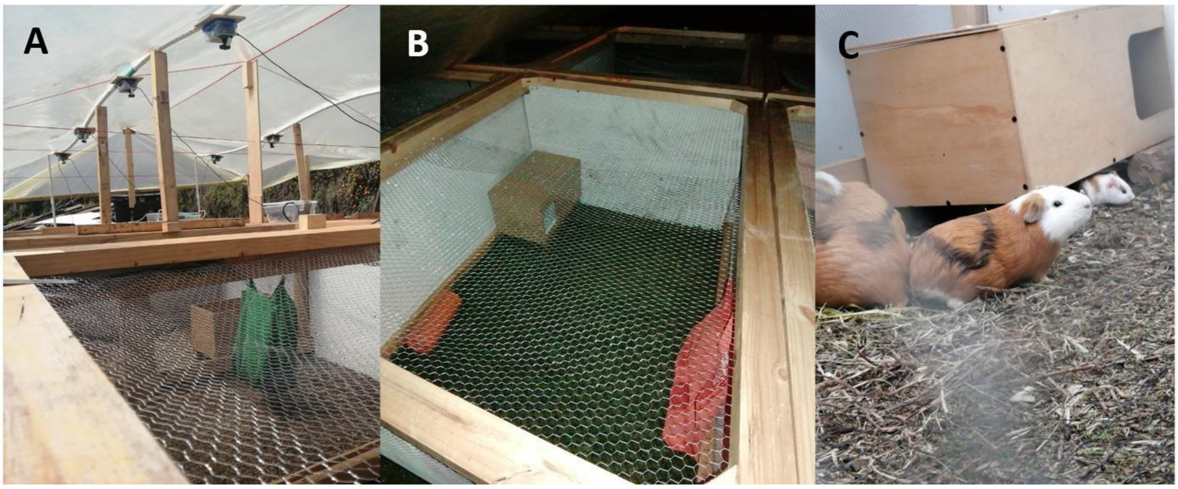

Figure 2. Overview of the experimental set up. A. The enclosure with the camera disposition above each pen. B. Close up of one of the pens of the enclosure showing its organization (a house, a feeding bag and a hiding tube, water bowls are not shown). C. Guinea pigs showing the hair dye mark.

Groups were assigned to one of the three treatments for a total of two groups per treatment. In treatment A, the doors from the pens were opened into a foraging arena and individuals from group 1 and 2 were allowed to freely move between pens (their own and the foraging pen) and freely interact (Figure 3A). In treatment B, individuals were forced to share the foraging pen (Figure 3B). Treatment C corresponds to the control where pens were separated by a wall and individuals were not allowed to see or interact with the members of the other group.

Groups experienced three phases: Pre-treatment (tThree weeks), treatment (four weeks) and post-treatment (three weeks). In the pre-treatment, individuals within each initial group were allowed to freely interact (i.e., the baseline). In the treatment phase, fresh grass (highly palatable food) was provided in a foraging arena (middle area with a bowl in Figure 2) for groups in treatments A and B and in their own pen for control groups. During this period, two groups were allowed to freely interact in a shared foraging arena (Treatment A), two groups were forced to share the foraging arena for a period of four hours per day (Treatment B), and two groups were not allowed to interact (Control). Finally, in the post-treatment, the walls between the pens were removed allowing the two groups of each treatment to freely interact.

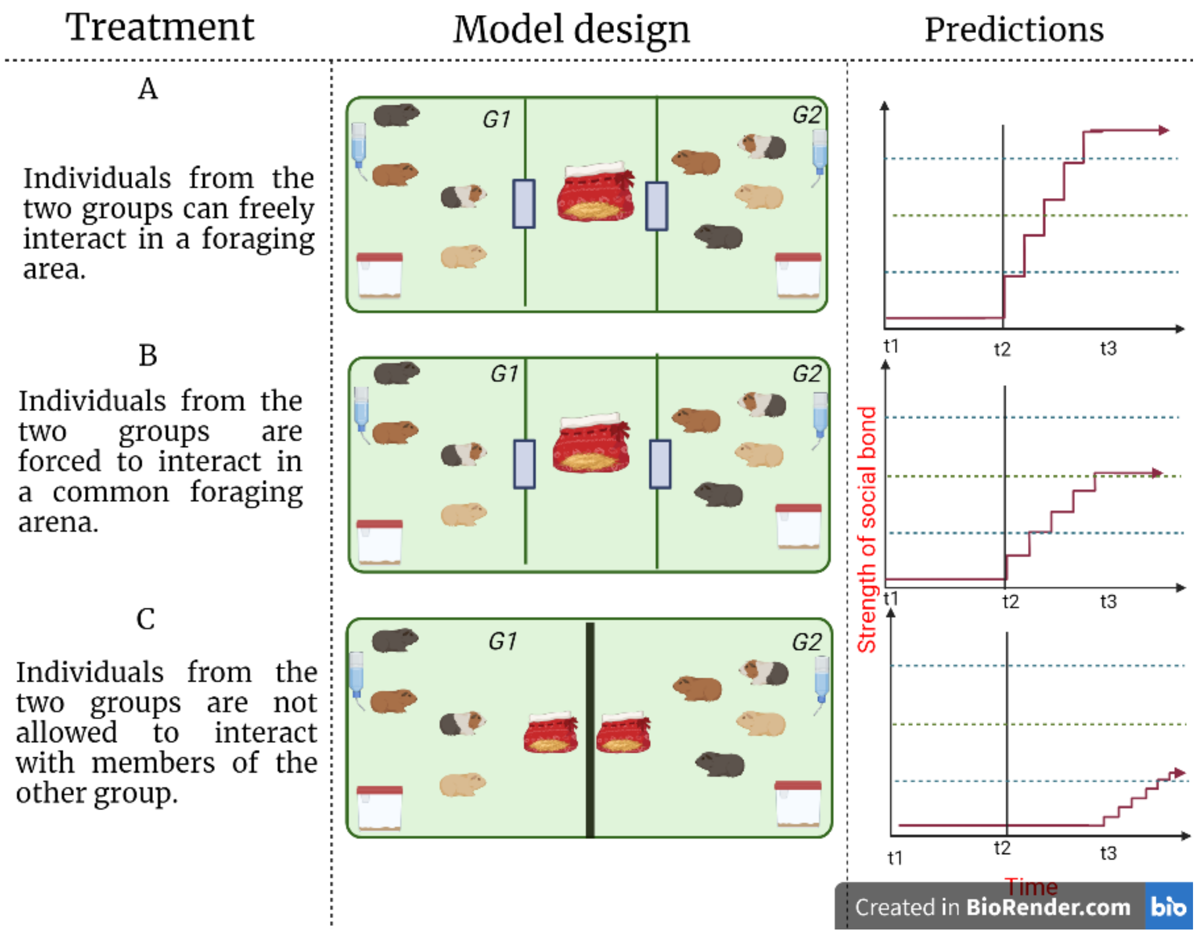

Figure 3. Scheme of the treatments evaluated in the experiment, and the predicted strength of the foraging relationships. **A.** Individuals freely interact at the foraging arena, doors (gray rectangles) are always open allowing individuals interact in the foraging arena. This group is expected to develop stronger relationships starting at time t=2 (indicated by the black vertical lines in the right panel). **B.** Individuals are only allowed to interact in the foraging arena during foraging time. Once individuals are in the foraging arena, doors (gray rectangles), are closed, thus restricting the space in which the individuals. This group is expected to develop relationships starting at time t=2 (black vertical lines in the right panel indicated in the right panel) and these relationships are weaker compared to the treatment A (as indicated by the horizontal solid line in the right panel). **C.** Individuals from the two groups are not allowed to see or interact with each other. This group is expected to develop their social relationships only after they are allowed to interact in time t=3 (indicated by the vertical line in the right panel).

They are expected to develop weaker relationships compared to the treatments A and B (as indicated by the horizontal solid line in the right panel).

4.3 Monitoring and scoring of social relationships

Each pen had a camera (Raspberry Pi Module 2 NoIR 8MP) controlled by a Raspberry Pi (Raspberry Pi 4 Model B) to monitor the social interactions within each group for a period of four hours a day throughout all the experiment. Two types of interactions were recorded from videos: 1) foraging together, defined as the shared activity of consuming food, and 2) greeting, defined as a nonaggressive signal where two individuals touch their noses. I decided to focus on these behaviors because foraging requires spatial tolerance between individuals and greeting requires physical contact (in addition to spatial tolerance) implying the need for trust between individuals (Nishida, 1970). Foraging together was measured as the time that any two individuals are seen foraging in the foraging area, whereas greeting was measured the number of times that any two individuals are seen greeting.

Videos were stored and scored by four trained observers that trained until achieving an inter-observer reliability of at least 85% before starting video scoring. For behavioral scoring, videos were analyzed using the VLC media player v. 3.0.18 (VideoLand) and played at a speed between 0.2X and 0.6X. For each of the focal behaviors, we registered the date, the enclosure, the type of interaction (forage together or greeting), the identity of the initiator and receiver of the interaction, the start and end time of the interaction.

4.3 Social Analyses

To construct foraging and greeting networks, I first estimated the length of the foraging association and the number of greeting interactions between any two dyads for each of the treatments in each phase of the experiment. The length of the foraging association corresponds to the amount of time (estimated from the videos) that any two individuals spent foraging together at the food source during the observation period. The number of greeting interactions corresponds to the number of times any two individuals greet during the observation period. Then, I calculated the strength of the associations for every dyad in each treatment and phase of the experiment using the Simple Ratio Index (SRI) (Whitehead, 2008). I generated weighted and undirected social networks for foraging and for greeting for each group at each phase of the experiment. In each network, nodes correspond to individuals and edges to the sri calculated from foraging (sri_{forage}) and greeting (sri_{greet}).

4.4 Statistical Analyses

To test if spatial proximity facilitates the formation of foraging relationships, I evaluated the structure of foraging networks during the pre-treatment phase and compared their similarity against the foraging networks of the pos-treatment phase using a Mantel in the package Vegan v 2.6-4 (Oksanen, et.al., 2022). I used Pearson correlation method with 499 permutations and calculated 95% confidence levels (all other parameters of the function were kept as defaults). To test if foraging relationships facilitated the emergence of cooperative relationships, I used a regression approach. I fit a linear regression model using the strength of greeting (sri_{greet}) as the response variable, and the strength of foraging (sri_{forage}), the type of dyad (old/new) and the treatment (A, B, C) as factors.

Results

I tested a total of 23 individuals distributed in three treatments (one individual died during the experiment) and recorded a total 3875 foraging associations and 192 greeting interactions. Four data points were eliminated because of misidentification of the individuals during the video scoring. I had a total of 30 dyads (4 individuals per treatment, except in treatment A where I had 3 individuals), for which I calculated the strength of the relationships (sri_{forage} and sri_{greet}) and built the corresponding social networks (Figure 4). The mean strength of foraging relationships formed during the pre-treatment phase had the lowest strength values (sri_{fora}ge-mean=0.174±0.033) and kept increasing during the treatment ($sri_{forage-mean}$= 0.792± 0.407) and the post-treatment phases ($sri_{forage-mean}$= 0.987±0.114). The strength of the greeting relationships increased from the pre-treatment to the treatment phase ($sri_{pretreatment-mean}$=0.183± 0.040; $sri_{treatment-mean}$=0.441±0.498) but then decreased during post-treatment ($sri_{post-treatment-mean}$= 0.285±0.498).

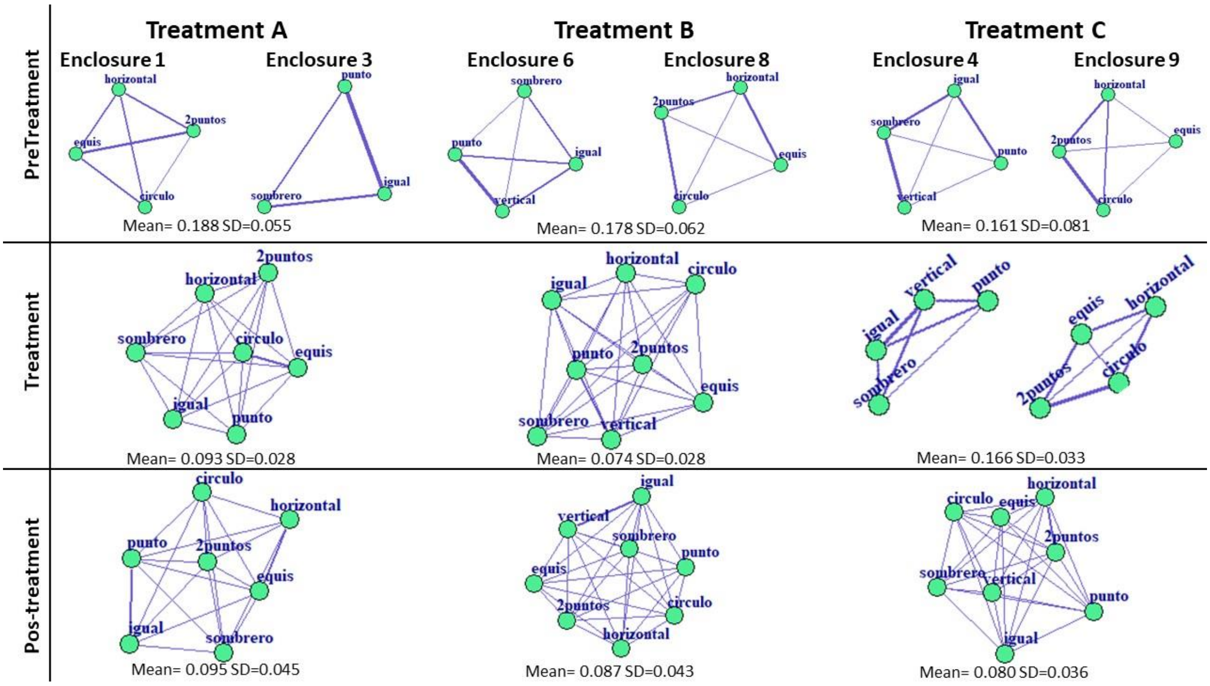

Figure 4. Foraging networks for each phase of the treatment. Dots represent individuals in each treatment, edges represent the strength of foraging relationships based on the simple ratio index (sri).

The Mantel tests suggest that spatial proximity may allow for the formation of foraging relationships, although any of these relationships were statistically significant. Individuals that were allowed to freely interact in a shared foraging arena (Treatment A) developed the strongest foraging relationships (Mantel=0.75, p =0.125; Mantel= 0.99, p =0.166), followed by individuals in the control group (Control C) (Mantel=0.583, p=0.208; Mantel=0.6842, p=0.125). Individuals that were forced to share the foraging arena (Treatment B) developed foraging relationships, but this were not as strong as in treatment A and control (Mantel= -0.192, p=0.666; Mantel= 0.302, p=0.25).

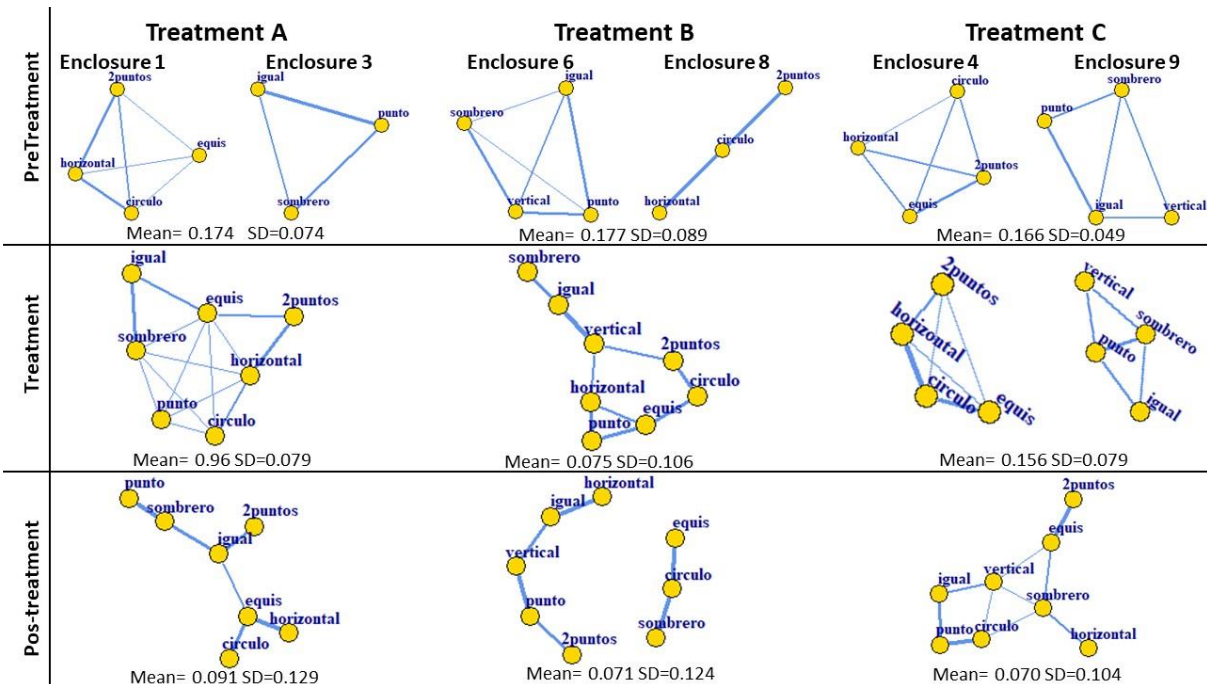

Figure 5. Greeting networks for each phase of the treatment. Dots represent individuals in each treatment, edges represent the strength of greeting relationships based on the simple ratio index (sri).

The regression analysis indicated that dyads that developed stronger foraging relationships were more likely to develop strong greeting relationships (Table 1). There was a significant difference between old (those formed during the pre-treatment) and new dyads (those formed during the treatment), new dyads developed weaker greeting relationships compared to old dyads. Also, individuals in treatment A (Free interaction) and B (forced interaction), developed weaker greeting relationships compared to control individuals.

Table 1. Regression coefficients for the courtship model evaluating the relationship between foraging and the formation of greeting relationships. Bold values denote statistical significance at the P<0.005 level. N=4037 observations.

Predictors	Estimates	t- value	SE	P
Intercept	0.091	15.293	0.006	**< 2e-16**
SRIForage	0.310	9.706	0.032	**< 2e-16**
Treatment [A]	-0.004	-1.191	0.004	0.2338
Treatment [B]	-0.014	-3.465	0.004	**0.0005**
New dyad [1]	-0.041	-10.349	0.004	**< 2e-16**

Discussion

My results show that spatial proximity may facilitate the formation of foraging relationships, and these relations are stronger when individuals are free to socially interact. Foraging relationships are a good predictor of greeting relationships, suggesting that costly relationships can develop from low-cost social relationships such as foraging. Overall, my data support the hypothesis that spatial proximity can lead to the development of low-cost relationships, and that these can favor the development of cooperative relationships.

Spatial proximity may facilitate the formation of social relationships sharing spaces, especially when decisions to whether sharing a space are freely made. First, I showed that the strength of foraging relationships increased over time in both free and forced sharing scenarios. This increment in the strength of social relationships can result from an increased familiarity among individuals, which in turn decreases the novelty factor, the stress levels and the foraging competition and improves access to new information (Kern & Radford, 2021). Second, similarly to what has been shown in vampire bats (Razik et al., 2022), my results indicated that when individuals were forced to physically share a space unfamiliar individuals developed new social relationships. Moreover, I have further demonstrated that when individuals are free to share a space and engage in social interactions, individuals developed not only new relationships with unfamiliar individuals, but they build stronger social relationships. This can result from the fact that the movements that individuals make within a space reflect their social preferences by approaching or attracting other individuals (Ramos et al., 2021). This suggests that even though forced interactions allowed for the formation of social relationships, when individuals freely interact, they can develop preferential relationships.

High-cost relationships such as greetings, can be formed among group members that already established low-cost relationship (i.e., foraging). Greeting requires a trust factor between individuals that exhibit this behavior, generating a sense of security and confidence between the members around (Mercier et al., 2017). I propose that this trust element can be developed during the formation of low-cost relationships in a rise-the-stakes fashion (Roberts & Sherratt, 1998). Greeting generates a possible high cost for individuals (e.g., physical contact enables aggressive interactions), thus foraging a way to test the relationship potentially measuring the willingness to engage in cooperative behaviors. For example, in spotted hyenas greeting mainly occurs among individuals belonging to the same hunting pack that spend most of their time offoraging together (Smith et al., 2011). These results lead to more open questions such as the which factors affect an individual's decision of to whom socialize with or the process by the mechanisms that facilitate the integration of a new individual.

In conclusion, spatial proximity facilitates the formation of low-cost behaviors (i.e., foraging) and these, foster the formation of high-cost relationships (i.e., greeting). Such process seems to be affected by individual decisions of whether to allow or engage in spatial proximity and on the space available for interacting. There are still a lot of questions about how individuals choose whom they relate with and how these decisions affect the formation and strength of social bonds.

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