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Social Instability effects on courting receptivity and aggressive behaviors

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ABSTRACT

Social instability has negative effects on various social behaviors and social traits, but some are still understudied and the way they are affected is still not well understood. This is the case for courting behavior and social bonding, which are understudied when the exposure is during adulthood. Here, I studied the effects of social instability (SI) on aggressive behaviors and female courting receptivity. To do this, 12 female adult guinea pigs were separated into four groups: two were socially stable and two were exposed to social instability. Social instability was induced by changing group composition every three days for a month. Once the treatment finished, I created 4 groups with different behavioral phenotypic compositions. Then, I introduced a male during the first two days (acute effects) and days 8-9 (medium-term effects). The results suggest that SI significantly increases aggression rates, but not courting rates; meanwhile, group composition significantly affects courting rates, but not aggressive rates. Individuals exposed to SI had overall less successful courting rates and higher aggression rates, the latter being related to a lower capacity to form and maintain social bonds. In conclusion, exposure to SI led to an increase in aggression rates and possibly to a lower capacity to form social bonds, but doesn't directly lower female receptivity, although changes in group composition do. These results show how social instability may affect social bond formation through increased aggressive behaviors and how exposure to social instability affects courting receptiveness through changes in group behavioral dynamics.

RESUMEN

La inestabilidad social tiene efectos negativos sobre gran variedad comportamientos y rasgos sociales, pero aún falta saber más sobre algunos. Este es el caso del cortejo y la formación de lazos sociales, entonces se evaluó los efectos de la inestabilidad social sobre los comportamientos agresivos y la receptividad al cortejo. Para ello, se separaron 12 cobayas hembras adultas en cuatro grupos: dos de inestabilidad social y dos de estabilidad social. En los grupos inestables se cambió la composición del grupo cada tres días, durante un mes. Después, se crearon 4 grupos con diferentes composiciones comportamentales y se introdujo un macho los dos primeros y los dos últimos días. Los resultados sugieren que la IS aumenta

significativamente la agresión, pero no el cortejo; mientras que la composición del grupo afecta significativamente el cortejo, pero no la agresión. Los individuos expuestos a IS presentaban en general menores tasas de cortejo y mayores tasas de agresión, estando esta asociada con una menor capacidad para formar lazos sociales. En conclusión, la exposición a la IS genera un aumento de las tasas de agresión y posiblemente una menor capacidad para formar vínculos sociales, pero no tiene un efecto directo en la receptividad, aunque cambios en la composición del grupo sí la afectan. Estos resultados son importantes porque muestran cómo la inestabilidad social puede afectar a la formación de vínculos sociales mediante un aumento en comportamientos agresivos y cómo esta afecta a la receptividad del cortejo a través de cambios en la dinámica comportamentales del grupo.

KEYWORDS: Courtship, receptivity, aggression, unstable social environment, behavioral profile group composition.

PALABRAS CLAVE: Cortejo, receptividad, agresión, ambiente social inestable, composición comportamental del grupo.

1. INTRODUCCIÓN (INTRODUCTION)

Social instability (SI) is a natural phenomenon in group-living animals consisting in sudden or constant changes to the group composition, leading to group uncertainty (Wooddell et al., 2021). It can be produced by changes in dominance hierarchies (Sapolsky, 1983), mortality (Ebensperger et al., 2017), emigration (Bateman et al., 2013; Christal et al., 1998), immigration (Christal et al., 1998; Port & Johnstone, 2013) or by human disturbance (Shannon et al., 2013) that result in variations of group composition. When the group composition is highly variable and its uncertainty is high, it can result in chronic social stress (Koert et al., 2021). SI can negatively affect reproductive-related behaviors, it can increase the aggression of mothers toward their offspring (Pittet et al., 2017), decrease parental care (Ebensperger et al., 2017), lower courtship behavior if exposed from an early age (Sachser et al., 2011), masculinization of courting behavior in females (Kaiser et al., 2015), a deficit in male sexual behavior (McCormick et al., 2013), a decreased sociality during adulthood when animals are exposed at an early age (McCormick et al., 2015), increase aggressive interactions (Maslova et al., 2010; Sachser et al., 2011), and can also negatively affect reproductive success (Wingfield & Sapolsky, 2003). Although numerous scientific studies have addressed the effects of SI, these are mostly focused on understanding the early life effects on physiological traits (Jarcho et al., 2016; Kaiser et al., 2015; Maslova et al., 2010), meanwhile, the effects of SI on adult individuals that developed in stable social environments is still understudied, which lead to a lack of knowledge about the effects of SI exposure during adulthood.

Social bonds convey survival and fitness benefits to individuals in group-living species (Ancillotto et al., 2015; Silk et al., 2010). Strong social bonds enhanced the longevity of *Papio hamadryas* female adults (Silk et al., 2010) and the survival of *P. cynocephalus* offspring (Silk et al., 2009). The strength of social bonds, which can be weakened or reshaped by continuous exposure to SI (Maldonado-Chaparro et al., 2018; Silk et al., 2006), can affect other factors of fitness, such as longevity and survival of offspring (Silk et al., 2009, 2010) and reproductive success (McCormick et al., 2013; Wingfield & Sapolsky, 2003). Social bonds can also buffer the negative effects of low dominance ranks and can promote the formation of stable social groups (Waal, 1986). SI can negatively impact the dynamics of social interactions (Maslova et al., 2010;

McCormick et al., 2015; Sachser et al., 2011) which are fundamental for social bonding (Ancillotto et al., 2015; Silk et al., 2010). It can also have negative effects on the early social and behavioral development of infants, leading to weaker mother-offspring bonds, which are fundamental for the behavioral development of social skills (Ebensperger et al., 2017; Pittet et al., 2017; Sachser et al., 1998), resulting in lower fitness and survival capabilities. Although social bonding can buffer negative early life effects through enhanced survival by having strong social bonds (Lange et al., 2022, 2023), social bonding can be affected by SIS and other social stressors. Given the importance of social bonding as a buffer of these harmful effects, it is relevant to study more about its role on social interactions and social bonding on the life of social species, and how it can be negatively affected by social stressors.

SI negatively affects courting behavior when females are exposed from an early age (Kaiser et al., 2015; Sachser et al., 2011), but it's still not understood how it can affect courting receptivity when females are exposed during adulthood. Courtship refers to a social behavior where a series of multimodal signals are emitted by the competitive sex, usually, the male, to increase its chances of obtaining a mate for reproduction by turning the non-competitive sex receptive to copulation (Gwynne, 1991; Verzola-Olivio et al., 2021). Courtship is a social behavior directly related to reproductive success and most of the time to sexual selection too (Jacobs, 1976; Schneider & Lesmono, 2009). Although courtship is of utter importance in the reproductive behavior of social species, the environmental and social factors that can affect it are little studied and there is still a lot we do not know about it (Ancel et al., 2013; Cole & Endler, 2016). The strength of social bonds, which can be weakened or reshaped by continuous exposure to SI (Maldonado-Chaparro et al., 2018; Silk et al., 2006), can affect other factors of fitness, such as longevity and survival of offspring (Silk et al., 2009, 2010) and reproductive success (McCormick et al., 2013; Wingfield & Sapolsky, 2003), which implies that there is a high chance that behaviors directly related to it, such as courtship, are also affected (Schneider & Lesmono, 2009; Wingfield & Sapolsky, 2003) even in adulthood.

In this study, I explored the effects of SI on aggressive behavior and courtship receptivity in adult guinea pigs (*Cavia porcellus*) who grew up in socially stable environments. Guinea pigs are a suitable system to study these effects because they live in usually stable social groups (Sachser et al., 1999), have a complex system of courtship

behavior (Verzola-Olivio et al., 2021; Wagner et al., 1976), and are a well-known system to study the effects of sociality in physiological and mental health (Morrison et al., 2018). I conducted an experiment in which groups of adult female guinea pigs were exposed to either stable or unstable social environments (i.e. SI). To induce social instability, I used the social instability stress (SIS) paradigm, an experimental process to generate long-lasting stress effects on individuals that consists of the introduction of one or multiple unfamiliar same-sex partners which leads to the concurrent formation of new relationships, thus resulting in great and unpredictable physical and social stress (Koert et al., 2021). This paradigm has been proven to be a valid chronic stress paradigm for both female and male rodents (Yohn et al., 2019).

I proposed two hypotheses by which SI can affect aggressive behavior, social bond formation and courtship receptivity. First, the *hyper-aggression hypothesis* which states that if SI can alter or weaken existent social bonds (Maldonado-Chaparro et al., 2018) and can increase aggressiveness when exposed during early life (Maslova et al., 2010; Silk et al., 2006), the exposure of adult individuals to SI will result in individuals also becoming more aggressive with others and therefore, affecting the formation and maintenance of social bonds. Second, the *hypo-receptivity hypothesis* which states that if SI can lead to a deficit in male sexual behavior and a masculinization of female courting behavior (Kaiser et al., 2015; McCormick et al., 2013), the exposure of adult females to this stress will lead to females being less receptive to courting bouts compared to non-exposed females.

2. MÉTODOS Y MATERIALES (MATERIALS AND METHODS)

Study system and experimental manipulations

This study was conducted at the north campus of the Universidad del Rosario in Bogotá, Colombia. The study subjects (n=21 individuals) were bought at least three months before the experiment from breeding farms around the city. Subjects were individually marked using hair dye. Upon arrival, individuals were housed in five groups of four in outdoor enclosures (1.2 x 1.5 m), following natural day and night cycles, and

ambient temperature and humidity. Commercial guinea pig diet (Rodent commercial food, “Alduque”) and hay were given every day, tap water was available *ad libitum*. The diet was complemented weekly with vegetables and supplemented with vitamin C.

I used 17 female individuals: 6 assigned to the SS control groups (SS individuals), 6 to the SI exposed groups (SI individuals) and 5 individuals were used to generate the SU environment. The experiment consisted of two phases (figure 1): (i) Treatment lasted 31 days (figure 1A) and (ii) Post-treatment took 9 days and started immediately after the treatment phase ended (figure 1b). The treatment phase consisted of four groups: two control groups of three individuals each, experiencing a socially stable environment (6 SS individuals) and two treatment groups of three individuals exposed to a socially unstable environment (6 SI Individuals) (figure 2A). I used five additional individuals to rotate in the social unstable environment (total of 17 individuals). For each group, I randomly chose a focal individual at the beginning of the experiment that were not manipulated during SI or not handled in the SS groups. To generate a socially unstable environment I changed the composition of the group (alternations of group members) every three days until the end of the phase (figure 1B), following other SIS protocols (Koert et al., 2021; Pittet et al., 2017). To avoid handling bias in the control groups, an individual of the SS groups (not the focal) was extracted from the enclosure and stored in a cage for one minute before being put inside again.

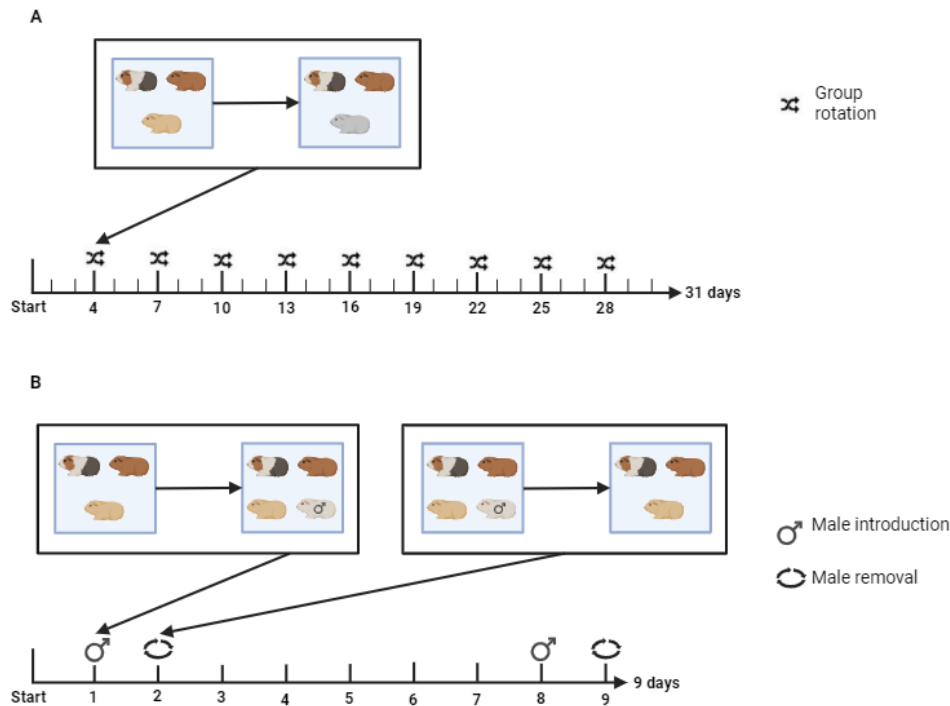


Figure 1. Experimental timeline of SIS protocol and male exposure for courtship behavior. (A) The timeline of the SI protocol (31 days), in which the cage composition (three guinea pigs per cage) is changed every third day. (B) The post-treatment phase (9 days), where males were introduced on days 1 and 8, and removed on days 2 and 9.

During the post-treatment phase (figure 1b) I created four groups with different behavioral phenotype composition, meaning that each group had a different number of SI and SS individuals: (SSS) all SS, (SSI) 2 SS and 1 SI, (IIS) 2 SI and 1 SS, and (III) 3 SI (figure 2b). Note that the four focal individuals from the treatment phase were introduced into different groups in the post-treatment phase. These different groups were exposed for one day to a male at 1) the beginning of the phase (days 1 and 2) to evaluate acute effects, and 2) eight days later (days 8 and 9), to evaluate medium term effects of SI exposure on courting receptivity of females. The males were introduced and removed, before and after data collection. In this phase, 16 individuals were used, 12 females from the treatment experimental groups and 4 males.

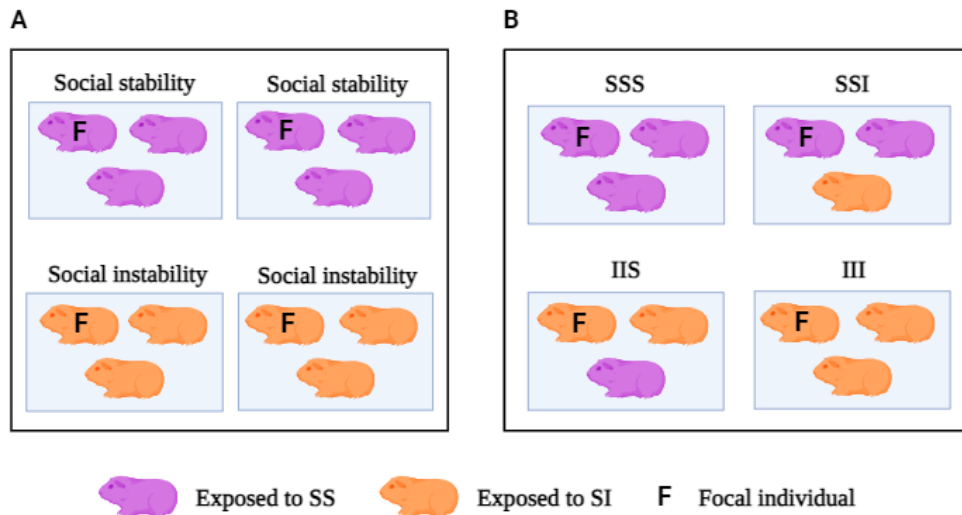


Figure 2. Experimental enclosures used in the treatment and post-treatment phases. (A) Groups from the treatment phase: 2 control (SS) and two treatments (SI). (B) Post-treatment groups created with different behavioral phenotypic compositions.

Behavioral measures

For both phases of the experiment, the groups were recorded every day from 07:00 h to 11:00 h (4 hours of recording per day) using a Raspberry Pi 3 camera set to take 1 picture every 1.5 seconds. The photos were processed and converted into a 5-minute video. The videos were scored by three trained researchers with an interobserver reliability of at least 95%. The researchers scored the duration of affiliative behaviors and the frequency of aggressive behaviors (Supplementary table 1). In the post-treatment, we also scored the courting behaviors (Supplementary table 1). The definition and categorization of the behavioral patterns are based on previous work by Kaiser et al., (2015) and Verzola-Olivio et al., (2021), and complemented by Cardona-Restrepo, (2023) and Garrido-Villegas, (2024), and personal observations. Courting behavior was classified as fail when the female ran away from the male or responded on an aggressive manner, otherwise it was classified as successful.

Quantification of behavior

To quantify aggressive and courtship behaviors, I estimated the aggression rate and successful courting rate. The aggression rate corresponds to the total amount of aggressive interactions started by an individual i on a day j , divided by the total number

of hours recorded. The successful courting rate corresponds to the amount of successful courting bouts divided by the total amount of courting bouts directed toward that individual i on a day j . It was calculated for each female in the enclosure. When no courting or aggressive behavior was recorded, the data for that individual was eliminated for the day to ensure no bias was made in the statistical analysis.

Statistical analysis

To test the *hyper-aggression hypothesis*, I compared the aggression rate of SI individuals and SS individuals (i.e., individuals that were exposed or not to social instability) in days 1 and 9 in the post-treatment phase. First, I performed a Shapiro test to check the normality of the data. Then, I performed an ANOVA test to compare the values of aggression rate between SI and SS individuals, using aggression rate as the response variable and treatment group as the explanatory variable. To evaluate differences in aggression rate between the groups with different behavioral composition, I performed an ANOVA using the focal individual's aggression rate as the response variable and each group focal as the explanatory one, in case of there being significant differences, a Tukey test must be done. To visualize the changes in aggression rate during the post-treatment, I plotted the average aggression rate for individuals from SI and SS groups.

To test the *hypo-receptivity hypothesis*, I compared the successful courting rates of individuals from SS with individuals from SI groups. First, I performed a Shapiro test to check for normality. Then, I performed an ANOVA with successful courting rates as the response variable and treatment group as the explanatory variable. To check if the behavioral composition of the group influenced the courting rate, I performed an ANOVA with successful courting rate as the response variable and behavioral composition of the group as the explanatory variable. Then I ran a post-hoc comparison. To check for acute and medium effects on courting rates, I performed an ANOVA with successful courting rates as the response variable and period after treatment ended as the explanatory variable. All statistical analyses were performed in R ver.4.3.2 (R Team, 2024).

3. RESULTADOS (RESULTS)

During the experiment, I tested a total of 13 individuals. The extra individual, had previously experienced an unstable social environment, replaced an individual that died during

the pos-treatment phase. During the pos-treatment I recorded a total of 278 aggressive interactions and a total of 413 courting interactions.

SI exposure increases aggressive rates of individuals.

The ANOVA test indicated that guinea pigs exposed to SI were significantly more aggressive (1.14 ± 0.85 ; $n=16$) than individuals from stable social environments (0.47 ± 0.42 ; $n=9$) ($F_{(1,23)} = 4.8$, $p = 0.038$), as they exhibited higher aggression rates (figure 3).

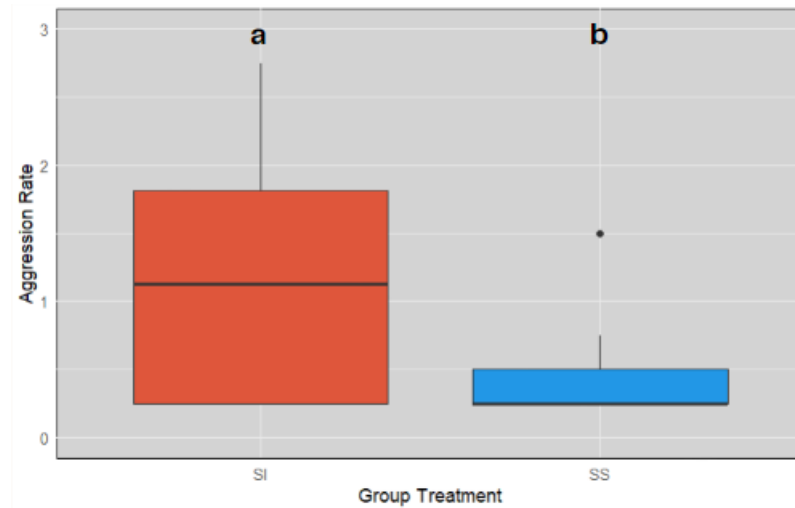


Figure 3. Aggression rate values for individuals exposed to SI and SS.

The aggression rate of SS individuals was lower than that of the SI individuals throughout the posttreatment phase (figure 4) and has more consistent values compared to SI aggression rates where the aggression rate does not have a distinctive pattern and has inconsistent values, showing no signs of recovery during the pos-treatment phase, even having one of its highest values towards the end of it.

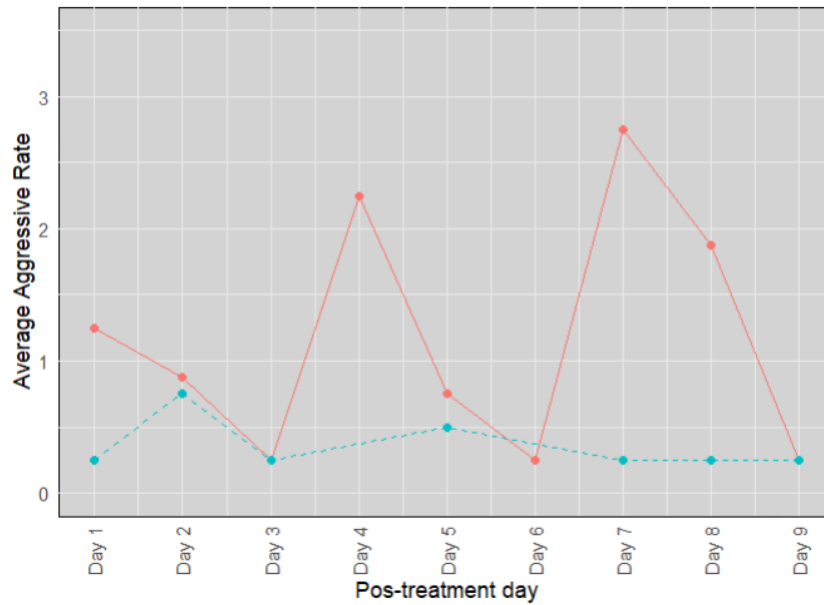


Figure 4. Aggression rate timeline for the post-treatment phase of the experiment. Red line represents the SI individuals, and the blue line represents the SS individuals.

The behavioral phenotype composition of the group did not have an impact on the aggressive rates of the focal individuals ($F_{(3, 21)} = 1.68$, $p = 0.202$), although there were overall lower values for groups where SS individuals were majority (figure 5). The group with two stable individuals had the lowest aggressive rate (0.33 ± 0.14 ; $n=3$) followed by the group with all stable individuals (0.54 ± 0.51 ; $n= 6$), and the group with two SI individuals (1.05 ± 0.97 ; $n=10$). Lastly, the group with the higher aggression rate had all SI individuals (1.29 ± 0.66 ; $n=6$).

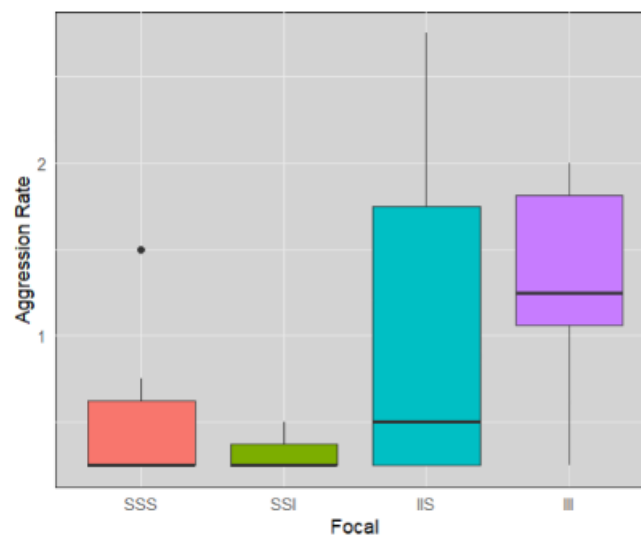


Figure 5. Aggression rate for each focal individual in the pos-treatment groups.

SI does not significantly lower successful courting rates, but group composition does.

SI exposure had no significant impacts on successful courting rates ($F_{(1, 39)} = 3.15$, $p = 0.084$), meaning that courting behaviors of SI individuals and SS individuals had not significant differences. However, SS individuals exhibited a higher overall courting rate (0.46 ± 0.21 ; $n=21$) compared to SI individuals (0.36 ± 0.17 ; $n=20$) (figure 6).

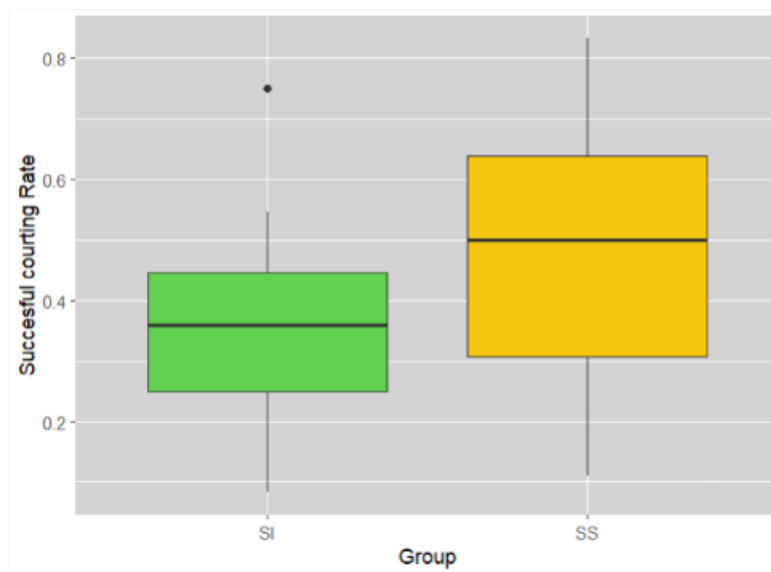


Figure 6. Successful courting rate for individuals exposed to SI and non-exposed individuals.

The behavioral phenotype composition of the groups had significant impacts on the successful courting rate ($F_{(3, 37)} = 2.89$, $p = 0.048$). The only groups that had significant differences were groups SSS (0.51 ± 0.14 ; $n=12$) and III (0.32 ± 0.14 ; $n=11$) ($p = 0.024$), which were groups entirely composed by SS individuals and SI individuals respectively (figure 7). This result suggests that group composition could have a moderate impact on female courting receptivity, since groups SSI (0.33 ± 0.24 ; $n=9$) and IIS (0.48 ± 0.21 ; $n=9$) had no differences with other groups. Additionally, successful courting rate between the acute period and medium period was not significantly different ($F_{(1, 39)} = 0.86$, $p = 0.36$) (figure 7). However, there was

a trend that showed signs of recovery since mean successful courting rates for all groups increased from the acute (0.39 ± 0.21 ; $n=23$) to the medium period (0.44 ± 0.17 ; $n=18$)

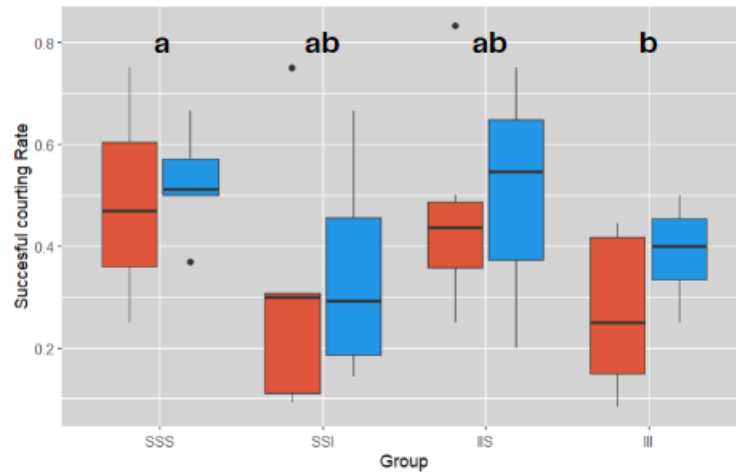


Figure 7. Successful courting rate for each behavioral profile group in each period. Red colors represent the acute period and blue represents the medium period.

4. DISCUSIÓN (DISCUSSION)

My results showed that exposure to social instability during adulthood does increase the aggressiveness of individuals, but the group behavioral phenotype composition does not. Meanwhile, courting receptivity is not significantly altered by SI, although group behavioral composition does affect it, meaning that SI exposure could have indirect negative effects on female courting receptivity. The negative effects caused by SI exposure during adulthood are not as strong as exposure during early life and social development, meaning that adults have a higher resilience and tolerance towards this social stressor. These results support *the hyper-aggression hypothesis* that exposure to SI during adulthood will cause increments in aggressiveness of individuals. Previous studies have shown that exposure to SI can lead to increased aggressiveness (Maslova et al., 2010; Sachser et al., 2011); however, these studies focused in adolescence (a fundamental stage in social development) exposure and chronic changes in behavioral profiles of individuals. My study shows that even during adulthood exposure to SI can lead to an increase in the amount of exhibited aggressive behaviors and not a quick recovery from these changes in behavior. However, my results did not support the hypo-receptivity hypothesis, which stated that exposure to SI will have a negative impact on

female receptivity to courtship. Other studies have shown that exposure to SI during early life would have negative effects on reproductive behaviors (Kaiser et al., 2015; McCormick et al., 2013; Sachser et al., 2011), however my results showed that when this exposure occurred during adulthood, courting behavior would not be directly affected and instead, has an indirect effect on lowering courting receptivity through changes in the behavioral phenotype composition of the group.

SI exposure has a significant impact on the increment of aggression rates, meaning it directly affects aggressive behavior (Koert et al., 2021). However, this relationship may not be as strong as expected in adult individuals that grew in a stable social environment. This could happen because developing in stable social environments, is fundamental for the correct neurodevelopment of resilience traits in individuals (Clinton et al., 2022; Shinohara & Furuyashiki, 2022). For example, in *Mus musculus*, it has been shown that individuals that developed in stable conditions tend to have a higher resistance to socially induced stress when exposed to it (Branchi et al., 2013), which may explain the lack of a strong effect caused by SI exposure. Moreover, in general, rodents have high tolerance to social chronic social stressors (Cathomas et al., 2019). The absence of a consistent pattern in the aggression rate of SI individuals is probably related to the fact that resilience and tolerance towards social stressors is not linear and can change even on a daily basis (Branchi et al., 2013; Dagnino-Subiabre, 2022), meaning that aggression caused by social stress can be increasing and decreasing by these changes in resilience.

Increments in aggression between individuals generates important impacts on the social dynamics of a group. Other studies have shown that an increase in rodent female-female aggression leads to a decline in affiliative behaviors (Bowler et al., 2002), in primates it was shown that females tend to avoid highly aggressive individuals, leading to a difficulty in forming social bonds with them (Lehmann & Boesch, 2009) and that high levels of aggressive behaviors lead to social challenges for individuals (Haller et al., 2014). This means that the increased rates of aggressiveness generated by SI exposure may have negative effects on the formation and maintenance of social bonds, supporting the hyper-aggression theory.

SI did not affect courtship rates. However, my results showed that individuals in socially stable environments exhibited a slightly higher courting rate. This is unexpected and does not support the *hypo-receptivity hypothesis*, but it could be explained by the fact that the individuals tested were all in adulthood, while the other studies where social instability affects directly

sexual behavior and courting all worked with individuals during development stages (Kaiser et al., 2007; McCormick et al., 2015; Sachser et al., 2011). Adult individuals show a higher resilience to social stress and although social stress can have a direct impact on sexual performance (McCormick et al., 2015), it may have been not be enough to reduce receptivity. In other studies, it was shown that social instability may not be a great social stressor for female guinea pigs, since it also did not have a significant impact on pregnant females and their daughter's behavior (Sachser & Kaiser, 1996); yet, the SI paradigm is the most recommended for female rodents (Beery & Kaufer, 2015). On the other hand, the behavioral profile of the group had a significant impact on the successful courting rates of individuals, suggesting that the composition of the group itself and the behavioral profiles of its members have a higher impact on the receptivity of females than the exposure to SI alone. Composition of the group having an important impact on courtship behavior is also reported for pigs, where courting receptivity is highly affected by other individuals behavioral phenotype within the group (Pedersen, 2007). It is also important to mention that group SSI has similar courting rate values to group III, this could be explained by the death of an individual, which is a natural light way of SI (Ebensperger et al., 2017). This suggest that this group may have been exposed to a mild form of social instability when the dead individual was replaced, therefore affecting this group and the results from it.

In conclusion, SI can increase the aggressive interactions individuals can exhibit, thus, it can affect the formation and maintenance of social bonds by decreasing the capacity of individuals to perform affiliative behaviors. The behavioral composition of the group plays a key role in courting bouts receptivity. These results are, to my knowledge, the first to showcase the importance of the behavioral phenotypic composition for courtship behavior in social rodents. Additionally, my results give insights of SI as a social stressor during adulthood, which at least for guinea pigs, may not be as strong as it is to individuals in early stages of their life. There are still a lot of questions about the direct relationship between social instability and social bond formation, the extent of the direct effect of SI in courtship behavior and the effect of time after exposure to SI on the negative effects it causes and how much time it takes for individuals and groups to go back to normal.

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