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Social recognition and short-term memory in two taxa of striped mouse with differing social systems

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Abstract

The ability to distinguish between familiar and strange conspecifics is important in group-living animals and influences the types of interactions between conspecifics. Social systems differ in sister taxa of the striped mouse genus *Rhabdomys* originating from different environments. Xeric-adapted *R. pumilio* displays facultative group-living whereas the mesic-adapted *R. d. chakae* is solitary. We assessed social recognition and attraction to strangers in females of two populations each of *R. pumilio* and *R. d. chakae* by means of a social discrimination task. We used a three-chamber apparatus developed in an established protocol and measured the latency of test females to approach and the duration of their investigation of stimulus females. Differences in social recognition of and preference for unfamiliar conspecifics in group-living and solitary-living taxa occurred at the taxon-level, even though constituent populations occurring kilometers apart showed similar responses. Females differed in the latency (testing phase) and duration of investigation (familiarization and testing phases) inter-specifically but not intra-specifically. Female *R. pumilio* approached stimulus females faster than female *R. d. chakae*. Female *R. pumilio* also investigated stimulus females for longer, regardless of stimulus type compared to *R. d. chakae*, but both taxa spent more time investigating familiar females than novel females and approached the familiar females faster than novel females. Social recognition, short-term memory, and social preference do not appear to differ between closely related taxa and differences in behavior between the two taxa might be related to inherent personality and social proclivity.

KEYWORDS
recognition memory, *Rhabdomys*, social discrimination, social preference

1 | INTRODUCTION

Social systems reflect the way conspecifics interact (Hinde, 1976) and are underpinned by the social organization (i.e., group size and composition), social structure (i.e., how individuals interact with one another), mating system (i.e., which individuals reproduce and what are the reproductive tactics), and care system (i.e., who cares for the offspring) of a species (Kappeler & van Schaik, 2002; Kappeler, 2019). Social behavior in a species is thus driven by the interaction of the various components of the social system.

Variation in social systems in closely related taxa may result in variation in social behaviors because of different selection pressures

(Ward & Webster, 2016). Social groups form when the benefits (e.g., reduced predation risk) accrued by group-living outweigh the costs (e.g., competition for resources; Krause & Ruxton, 2002). The ability to recognize and remember familiar individuals is thus critical for animals that live in groups since the group has common incentives, such as defending resources (Choleris et al., 2009; Christensen & Radford, 2018). Studying closely related species with different social organizations could help to elucidate the underlying mechanisms of social recognition.

Social recognition is the ability of animals to distinguish between familiar and unknown conspecifics and is necessary for displaying appropriate behavioral responses during social encounters (Mateo, 2004). Social recognition is especially important in group-living animals where social interactions may be amicable, fostering group-cohesion when displayed toward a group-member, or aggressive and territorial, such as with an intruder (Madison & McShea, 1987). For example, female meadow voles (*Microtus pennsylvanicus*) are territorial during the reproductive season but form affiliative aggregates during winter when they display group defense of the territory, share nest sites and display reduced intra-group aggression (Madison & McShea, 1987). Additionally, social recognition can reduce mating with dispersed kin (Winn & Vestal, 1986). Such discrimination of kin is likely to be important in both solitary and group-living animals. For example, mature female bank voles (*Myodes glareolus*) prefer the scents of unrelated males over related males (Kruczek, 2007). In addition, female house mice (*Mus musculus*) prefer to associate with unrelated males rather than familiar or unfamiliar related males (Winn & Vestal, 1986).

In rodents, recognition of familiar conspecifics occurs through olfaction, predominantly via the accessory olfactory system (Insel & Fernald, 2004). Rodents show a preference for social novelty, showing greater investigation of novel conspecifics than they do familiar conspecifics (Wistar rats [*Rattus norvegicus*]: van Wimersma Greidanus & Maigret, 1996; C57BL/6J, DBA/2J, FVB/NJ, A/J and B6129PF2/J inbred strains: Moy et al., 2004; C57BL/6J: Crawley et al., 2007; but see Beery et al., 2018 [*Microtus ochrogaster* & *M. musculus*]; and C57BL/6J: Pearson et al., 2010). Yet, prairie voles (*M. ochrogaster*) and meadow voles prefer to huddle with familiar rather than unfamiliar same-sex conspecifics (Beery et al., 2018; Parker & Lee, 2003), but female degus (*Octodon degus*) huddle equally with familiar and unfamiliar same-sex conspecifics (Insel et al., 2020). During the initial encounter, the increased time spent investigating the unknown conspecific allows an individual to note olfactory cues that are associated with the conspecific and form a social memory (Young, 2002). Later encounters with the same conspecific produce shorter periods of investigation when the individual recalls the olfactory cues of a conspecific from memory (Young, 2002). The μ-opioid system has been linked to social novelty preference in Wistar rats in a motivational capacity (Smith et al., 2015), suggesting that preference for social novelty may be neurochemically rewarded. Preference for novelty may be driven by territoriality when it would promote the investigation of intruders or it might be a reproductive

mechanism allowing the recognition of novel mating opportunities while also avoiding mating with kin (Clark et al., 2020).

Recognition can occur mainly through phenotype matching or familiarity by prior association. In phenotype matching, individuals recognize kin via a phenotypic reference (e.g., odor) even if they have not made prior contact (reviewed in Mateo [2004]). For example, bank voles can recognize relatives by odor despite being raised separately, and females prefer the scent of unrelated males to close relatives they are unfamiliar with (Kruczek, 2007). In contrast, familiarity by association occurs when individuals have encountered a conspecific or their odor previously (reviewed in Mateo [2004]). For instance, in prairie voles, individuals are unable to recognize siblings without some degree of prior association (Paz y Miño & Tang-Martínez, 1999).

The ability to differentiate between group members and outsiders allows for context-specific behaviors with the potential for shared benefits (Christensen & Radford, 2018). For example, within territorial species where groups perform shared territory defense, an individual needs to differentiate kin or a group-member, where behaviors such as grooming or huddling would be appropriate, from an intruder, where an aggressive response might be needed (as in the meadow vole; Madison & McShea, 1987). Recognition can be the result of individual recognition where precise characteristics unique to an individual in a population are learned or because of class-level recognition where characteristics are learned and associated with a class of individual such as dominant or submissive (Dale et al., 2001). In the meerkat (*Suricata suricata*), for instance, individuals can differentiate vocal calls of individual group-members (Townsend et al., 2012), suggesting complex recognition of which specific individual is associated with an identifying vocal character. In contrast, all conspecifics, particularly unrelated ones, are potential competitors for valuable resources in solitary species. Thus, a highly developed social memory might be unnecessary for solitary species since responses to conspecifics are likely to be similar outside of breeding and parental-offspring bonds. For instance, the vlei rat (*Otomys irroratus*) is always aggressive to strangers (Pillay, Willan, & Cooke, 1995; Pillay, Willan, Meester, et al., 1995). We compared social recognition between two sister taxa of African striped mouse genus *Rhabdomys* with different social systems.

The African striped mouse (genus *Rhabdomys*) is a small (40–50 g), diurnal rodent with a widespread distribution throughout southern and eastern Africa (Monadjem et al., 2015). Members of the genus are opportunistic generalist omnivores, although the diet is specific to the environments within which each species occurs (Schradin, 2005). The genus was originally considered monotypic, although recent genetic analyses have putatively described four species, *R. pumilio*, *R. bechuanae*, *R. intermedius* and *R. dilectus*, which evolved in association with the establishment of specific biomes (Ganem et al., 2020; du Toit et al., 2012); however taxonomic revision
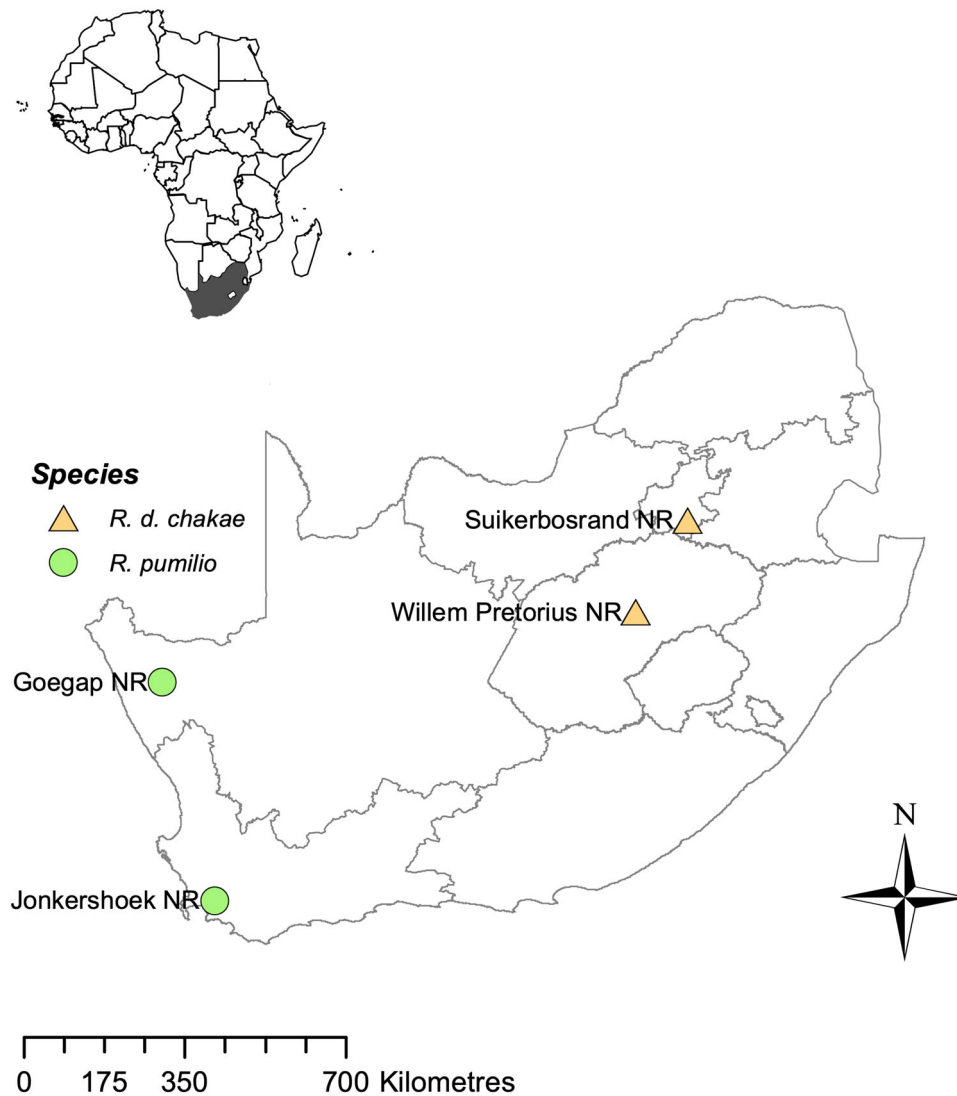
FIGURE 1 Populations of *Rhabdomys* taxa considered in this study. This study considered two populations of *R. d. chakae* (orange triangles) from Suikerbosrand Nature Reserve (Gauteng Province) and Willem Pretorius Nature Reserve (Free State Province) and *R. pumilio* (green circles) from Goegap Nature Reserve (Northern Cape Province) and Jonkershoek Nature Reserve (Western Cape Province)

is on-going. *Rhabdomys dilectus* consists of two subspecies: *R. d. dilectus* (2*n* = 46) and *R. d. chakae* (2*n* = 48) (Rambau et al., 2003). We focussed on the xeric-adapted *R. pumilio* and the mesic-adapted *R. d. chakae*. *R. pumilio* is distributed within the Fynbos and Succulent Karoo biomes which occur along the western coast of southern Africa (Monadjem et al., 2015). *R. d. chakae* occurs in the montane and submontane grasslands along the eastern part of southern Africa (Monadjem et al., 2015).

R. pumilio in the Succulent Karoo is facultatively group-living, with the social organization changing in response to habitat saturation (Schradin et al., 2010). Groups are composed of a breeding male, multiple breeding females, and their philopatric adult offspring (Schradin & Pillay, 2004). Group members share a territory and nest (Schradin, 2004), and males display paternal care when group-living (Schradin & Pillay, 2003), but individuals forage alone (Schradin & Pillay, 2003). Striped mice in the Succulent Karoo are highly

aggressive towards conspecifics from other groups, while displaying lower levels of aggression toward group-members (Schradin, 2004). Groups disband at lower population densities, and individuals of both sexes can become solitary (Schradin et al., 2012). Sociality in *R. pumilio* has only been studied in the Succulent Karoo population and, although less is known about sociality in *R. pumilio* in other populations, the Fynbos populations such as the Jonkershoek population considered in our study have been observed to form small groups (pers obs.). In contrast, *R. d. chakae* is solitary-living with home ranges of males overlapping home ranges of multiple females and association between the sexes is restricted to breeding, whereafter females raise offspring alone (Schradin & Pillay, 2005). Given this limited association, *R. d. chakae* males do not show paternal care in the field although they do in the laboratory (Schradin & Pillay, 2003).

Differences in the social systems of *Rhabdomys* taxa present an opportunity to compare social recognition and short-term memory in
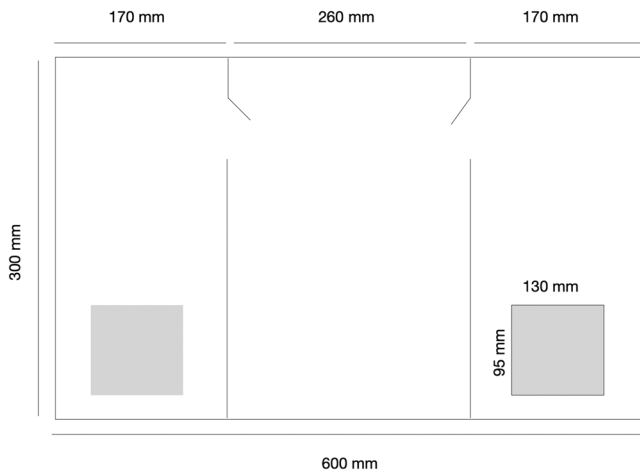
FIGURE 2 Dorsal view of the three-chambered apparatus (adapted from Moy et al. [2004] and Crawley et al. [2007]) used to test social recognition. The wire mesh cage is indicated by a gray rectangle and chamber entrances are indicated by open spaces with oblique lines at the top of the diagram

closely related taxa with differing social systems. We investigated the variation in social recognition in females for unfamiliar, unrelated female conspecifics in *R. pumilio* and *R. d. chakae*. We tested females in this study because groups in *R. pumilio* are usually made up of multiple females with one breeding male, such that females make up the core of the group (Schradin et al., 2012). In addition, we tested recognition for unrelated females since *R. pumilio* is always attracted to kin (pers. obs.), potentially biasing the outcome of experiments. We also studied two populations per taxon to assess whether the constituent populations show within-taxon responses. We predicted that both solitary-living *R. d. chakae* and group-living *R. pumilio* females would distinguish between unrelated familiar and novel females. We predicted that *R. pumilio* females would be attracted to familiar conspecifics, as shown in other group-living species (meadow voles; Parker & Lee, 2003), and that *R. d. chakae* populations would display similar responses to both familiar and novel females.

2 | MATERIALS AND METHODS

2.1 | Subjects

The subjects used in this study were F2 and F3 captive-born females (12 test and 24 stimulus females per population). Subjects were bred from individuals of *R. d. chakae* obtained from Suikerbosrand Nature Reserve (26°29′1″ S, 28°13′45″ E) and Willem Pretorius Nature Reserve (28°18′26″ S, 27°13′56″ E) in the Free State Province, and individuals of *R. pumilio* obtained from Goegap Nature Reserve (29°40′53″ S, 17°58′9″ E) in the Northern Cape Province and Jonkershoek Nature Reserve (33°55′51″ S, 18°51′16″ E) in the Western Cape Province (Figure 1). The original populations of *R. d. chakae* were located 356 km apart and *R. pumilio* populations were located 486 km apart.

2.2 | Husbandry

Striped mice were housed under partially controlled conditions at the Milner Park Animal Unit, University of the Witwatersrand. Environmental conditions included a 14:10 light:dark cycle with lights on at 0500 h, at a temperature of 22–24°C (relative humidity of 30%–50%). Mice were housed individually in standard lab-o-tec cages (15 cm × 42 cm × 15 cm) with wood-shavings at the bottom of the cage, dry grass, and a plastic nesting box (10 cm × 10 cm × 10 cm) and paper towel as nesting material. All *Rhabdomys* taxa are not stressed by solitary housing (Mackay et al., 2014). Each cage also had a cardboard roll as well as a wooden chew block for enrichment. Water and Epol™ mouse cubes were available ad libitum, and mice were fed 5 g of fresh vegetables and one teaspoon of millet per day. Experiments were approved by the University of the Witwatersrand Animal Ethics Screening Committee (2012/28/2A).

2.3 | Experimental design

Social recognition was tested by means of a social discrimination task (Crawley et al., 2007; Moy et al., 2004) conducted on anoestrous *R. pumilio* and *R. d. chakae* female striped mice. Vaginal smears were obtained to confirm that females were anoestrous. Twelve test females (see below) were used per population. We used a plexiglass box (600 mm × 400 mm × 300 mm), subdivided into three compartments by moveable clear plexiglass sheets (Figure 2). The plexiglass sheets contained openings on one side of the sheet (60 mm × 60 mm) to allow movement between compartments. The two outer compartments each contained a smaller wire mesh cage (130 mm × 105 mm × 95 mm) positioned at the end furthest from the chamber entrance (Figure 2). Cages were weighted down with a white ceramic tile which prevented interaction between the focal and stimulus mice from above the wire mesh cage. All experiments were undertaken during the active phases of striped mice between 0800 h and 1200 h (Rymer & Pillay, 2012). Testing sessions were video recorded for subsequent analysis.

Individuals in the colony were assigned pseudo-randomly to age- and size-matched groups of three unrelated females per population. They were all housed alone and never made contact before experiments. One of the females was randomly designated as the test female and the other two were stimulus females. Before each experiment, a test female was placed individually in the testing apparatus, facing toward the chamber openings, and was allowed to habituate to the testing apparatus for 15 min. The female was then returned to its home cage after the habituation session ended. Twenty-four hours after the habituation process, testing occurred in two phases: the familiarization and the testing phases, which occurred 30 min apart. During the familiarization phase, test subjects were restricted to the middle compartment with the movable barriers, which were locked shut. A conspecific stimulus female of the same population assigned to the test subject (see above) was placed in one of the smaller mesh cages in one of the side compartments,

which was randomly determined. The movable partitions were opened, and the behavior of the test female was recorded. After a 10-min period had elapsed, both the test and stimulus mouse were returned to their home cages. During the testing phase, the test female was again locked into the middle compartment and the familiar stimulus female (used in the familiarization phase) was returned to its original wire mesh cage and compartment. A second stimulus novel conspecific female of the same population (the third member of the group) was placed in the wire mesh cage in the second, previously vacant, compartment. The behavior of the test female was filmed for a period of 15 min and analyzed later. The test apparatus was thoroughly washed after each session to remove residual olfactory cues of test and stimulus females.

In the familiarization phase, we scored the latency of the test female to approach the unknown stimulus female and the duration of investigation of the unknown stimulus female. In the testing phase, we scored the latency of the test female to approach the familiar versus the novel stimulus female and the duration of investigation of the familiar versus novel stimulus female. The latency to approach was measured from the time the partition was opened to the time that the test female entered the compartment of one stimulus female. Investigation was defined as when the test female contacted the wire mesh cage of a stimulus female or when the test female was within 1 cm of the stimulus female's cage and with its head pointed toward the stimulus mouse.

2.4 | Data analysis

All statistical analyses were conducted in RStudio (R version 3.6.1 and RStudio version 1.2.1335, RStudio Team, 2018). We tested the data for normality using Shapiro–Wilk normality tests. Normality tests indicated latency to approach and duration of investigation were non-normally distributed. Both variables were transformed using the orderNorm function in the "bestNormalize" package (Peterson & Cavanaugh, 2019) and normality was confirmed with Shapiro–Wilk normality tests. Homogeneity of variance was confirmed for all variables using Levene's

test for homogeneity of variance ("car" package; Fox & Weisberg, 2019). All tests were two-tailed with alpha set at 0.05. All data are presented as the fitted values from repeated measures linear models.

We used restricted maximum likelihood linear mixed-effects models with a repeated measures design to test for variation in social recognition using the "lme4" package (Bates et al., 2015) and obtained p values with the "lmerTest" package (Kuznetsova et al., 2017). We included latency to approach and duration of investigation as response variables in separate models for both the familiarization and testing phase (Rimbach et al., 2021). Population was included as a fixed factor, stimulus type as the repeated measure, and individual as a random factor. Normality of model residuals was confirmed visually using quantile–quantile plots. Any significant statistical results were analyzed further using post hoc contrasts with the "emmeans" package (Lenth, 2019) to assess specific differences between fixed factors.

3 | RESULTS

3.1 | Familiarization phase

3.1.1 | Latency

Population ($F_{3,44} = 5.93$, $p = 0.002$) and stimulus female type ($F_{1,44} = 64.00$, $p < 0.001$) were significant predictors of the latency of test females to approach the first stimulus females. Test females from the Suikerbosrand (R. d. chakae) population took longer to approach stimulus females than Goegap and Jonkershoek (R. pumilio) females, regardless of familiarity (Figure 3a). Additionally, Willem Pretorius females (R. d. chakae) took longer to approach stimulus females than Jonkershoek females (Figure 3a), but no other comparisons reached statistical significance. Test females approached stimulus females faster in the test session than in the familiarization session, regardless of taxon (Figure 3b). The population*stimulus interaction ($F_{3,44} = 1.71$, $p = 0.179$; Figure S1a) was not a significant predictor of the latency to approach the stimulus female.
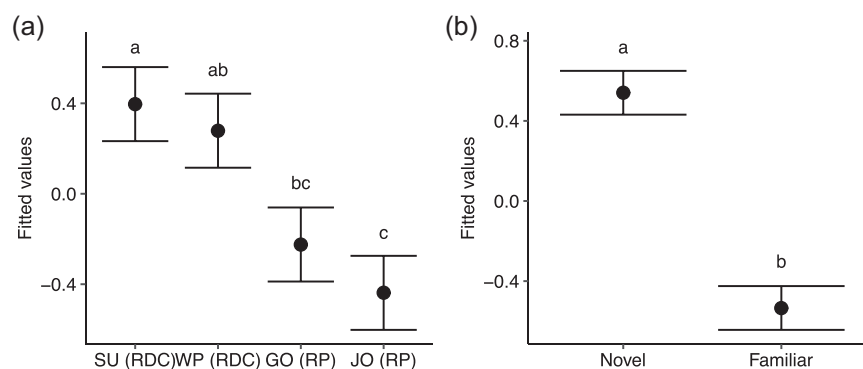

FIGURE 3 Fitted values of the latency to approach stimulus female 1 by Rhabdomys test females across (a) populations regardless of stimulus type, and (b) stimulus condition, regardless of population. Species have been abbreviated as *R. d. chakae* (RDC) and *R. pumilio* (RP). Populations have been abbreviated as Suikerbosrand NR (SU), Willem Pretorius NR (WP), Goegap NR (GO), and Jonkershoek NR (JO). Post hoc outcomes are shown by letters

3.1.2 | Investigation

Population ($F_{3,44}$ = 18.89, $p < 0.001$) and stimulus female type ($F_{1,44}$ = 36.00, $p < 0.001$) were significant predictors of the duration of investigation by test females of the stimulus female. Populations did not differ intra-specifically for both taxa. Goegap and Jonkershoek (both *R. pumilio*) females spent longer interacting with the stimulus female regardless of familiarity than the Suikerbosrand and Willem Pretorius (both *R. d. chakae*) females, suggesting that the difference in inter-specific responses occurs at the taxon level (Figure 4a). Regardless of population, test females spent longer investigating familiar versus novel stimulus females (Figure 4b). The population*stimulus interaction ($F_{3,44}$ = 2.47, $p = 0.075$) approached significance (Figure S1b).

3.2 | Testing phase

3.2.1 | Latency

Population ($F_{3,44}$ = 10.26, $p < 0.001$) was a significant predictor of the latency of test females to approach the stimulus females. Goegap and Jonkershoek females (both *R. pumilio*) approached the stimulus mice faster (Figure 5) than the Suikerbosrand and Willem Pretorius (both *R. d. chakae*) females. The similarity in responses within taxa indicate a taxon-level difference. Stimulus female type ($F_{1,44}$ = 3.92, $p = 0.054$) and the population*stimulus female type interaction ($F_{3,44}$ = 2.68, $p = 0.058$) approached significance (Figure S2a).

3.2.2 | Investigation

Population ($F_{3,44}$ = 48.43, $p < 0.001$) and stimulus female type ($F_{1,44}$ = 12.93, $p = 0.001$) were significant predictors of the duration of investigation by test females of the stimulus females. Goegap and Jonkershoek *R. pumilio* females spent longer interacting with the stimulus females, regardless of stimulus type, than the Suikerbosrand
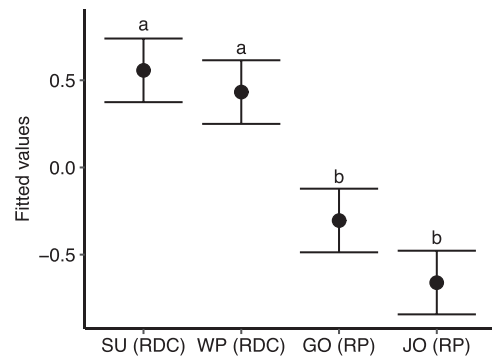
FIGURE 5 Fitted values of the latency to approach the stimulus females by Rhabdomys test females across populations regardless of stimulus type. Species have been abbreviated as *R. d. chakae* (RDC) and *R. pumilio* (RP). Populations have been abbreviated as Suikerbosrand NR (SU), Willem Pretorius NR (WP), Goegap NR (GO), and Jonkershoek NR (JO). Post hoc outcomes are shown by letters

and Willem Pretorius *R. d. chakae* females once more suggesting a taxon-level influence (Figure 6a). Test females investigated familiar stimulus females for longer than novel stimulus females, regardless of population (Figure 6b). The population*stimulus female type interaction ($F_{3,44}$ = 1.58, $p = 0.208$; Figure S2b) was not a significant predictor of the duration of investigation of the stimulus females by test females.

4 | DISCUSSION

We studied social recognition and short-term memory in *R. pumilio* and *R. d. chakae* females, to assess attraction to unrelated strangers. We predicted that both taxa would be able to distinguish between unrelated and novel females. Given the different social organizations of the taxa, we expected *R. pumilio* would be attracted to (short-term) familiar conspecifics and that *R. d. chakae* would display similar responses to familiar and novel females. Our prediction was not
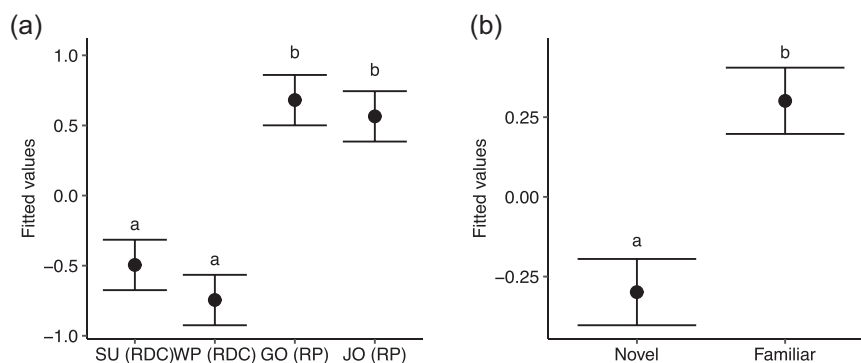
FIGURE 4 Fitted values of the duration of investigation of stimulus female 1 of Rhabdomys test females across (a) populations regardless of stimulus type, and (b) stimulus condition, regardless of population. Species have been abbreviated as *R. d. chakae* (RDC) and *R. pumilio* (RP). Populations have been abbreviated as Suikerbosrand NR (SU), Willem Pretorius NR (WP), Goegap NR (GO), and Jonkershoek NR (JO). Post hoc outcomes are shown by letters
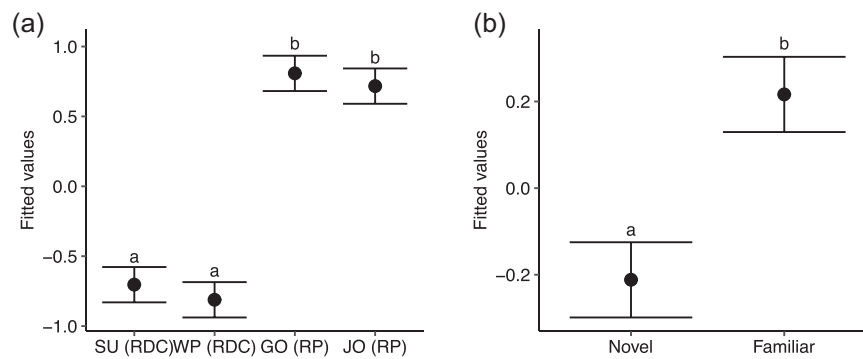
FIGURE 6 Fitted values of the duration of investigation of stimulus females of Rhabdomys test females across (a) populations regardless of stimulus type, and (b) stimulus condition, regardless of population. Species have been abbreviated as *R. d. chakae* (RDC) and *R. pumilio* (RP). Populations have been abbreviated as Suikerbosrand NR (SU), Willem Pretorius NR (WP), Goegap NR (GO), and Jonkershoek NR (JO). Post hoc outcomes are shown by letters

supported since *R. pumilio* and *R. d. chakae* females did not differ in their social preference, both preferring familiar rather than novel conspecifics. Regardless of stimulus type, *R. pumilio* approached stimulus females faster and spent longer investigating stimulus females than *R. d. chakae*. This difference in motivation may be related to personality differences between these taxa (see Mackay & Pillay, 2021; Rymer & Pillay, 2012). In contrast, the taxa did not differ statistically from one another in the time test females spent investigating familiar and novel females but regardless of population, test females spent longer investigating familiar females. This suggests that the taxa do not differ in their preference for familiar females.

Using the social discrimination paradigm, social recognition of conspecifics is measurable as a reduction in time spent investigating familiar compared to novel conspecifics (Engelmann et al., 1995). However, regardless of population, test females spent longer investigating familiar stimulus females and approached stimulus females faster. Previous studies have suggested that a lack of reduction in the investigation period provides evidence of an absence of social recognition memory (Engelmann et al., 1995; Moy et al., 2004). This conclusion is unlikely since the ability to form stable groups requires distinguishing group members from nongroup members (Ferguson et al., 2002). *R. pumilio* shows group territoriality and is aggressive to nongroup members in free-living populations (Schradin, 2004). Additionally, when arginine vasopressin (AVP) was experimentally elevated, *R. pumilio* and *R. d. dilectus* (a sister-subspecies of *R. d. chakae*, i.e., also solitary) did not show reduced investigation between familiar and novel (unrelated) females but were preferentially amicable toward familiar (*R. d. dilectus*) and novel (*R. pumilio*) females (Hartman, 2018). In contrast, while our results agree with Hartman (2018) regarding social preference in *R. d. chakae*, in our study *R. pumilio* preferred familiar females, suggesting that social preference may be phylogenetically constrained at the taxon level and modulated by the enhancement of AVP.

Social recognition and memory in rodents can be promoted by continued association between familiar conspecifics (Paz y Miño & Martinez, 1999). The continued association may act to re-enforce the initial memory. However, the duration of the investigation period as

well as the degree of possible interaction might also be important. Prairie voles showed a preference in longer partner preference tests only when they spent a significant period huddling with conspecifics, although the preference was for familiar conspecifics (Beery et al., 2018). An alternate explanation for the apparent lack of discrimination, as indicated by a failure to reduce investigation of familiar individuals, between familiar and novel females in our study may be that the initial exposure period between the focal mice and the 'familiar' stimulus mice was insufficient for both species to develop a social memory of the stimulus females. However, our results indicate that test females approached the familiar female faster in the test phase than they did in the familiarization phase and showed an increase in investigation of the same stimulus female used in the familiarization and test phases. In addition, an earlier study showed that, for both *R. pumilio* and *R. dilectus*, this period was sufficient for social memory to develop (Hartman, 2018). Our results indicate that *Rhabdomys* is more motivated to approach familiar females (in partial agreement with Hartman [2018]), suggesting they can in fact differentiate between the novel and familiar females.

In our experiment, social recognition and memory did not appear to be related to different social systems, but this may be the result of similar responses with different causes. Under an experimental AVP treatment, *R. pumilio* preferred unfamiliar females whereas *R. dilectus* was attracted to familiar females (Hartman, 2018). Yet, our results suggest that without AVP enhancement, *R. pumilio*, like *R. d. chakae* showed a similar preference for familiar individuals. Attraction to familiar conspecifics in *R. pumilio* would promote group cohesion while attraction to familiarity in *R. d. chakae* would promote the investigation of potential established competitors. We could not study social interactions between test and stimulus females in our study because stimulus females were housed in separate cages to reduce potential aggression between two or all three females. Yet, a laboratory experiment of sociability within the genus *Rhabdomys* indicated that *R. pumilio* was more amicable with conspecifics than *R. d. chakae* (Neves & Pillay, 2022). Prairie voles, that are monogamous, and live in family groups are more affiliative in their interactions with

novel and familiar conspecifics, whereas meadow voles, that form over-wintering groups, have low levels of aggression to unfamiliar conspecifics (Lee et al., 2019). Similarly, female degus huddled as frequently with stranger females as they did with familiar females although interactions with strangers were typically more agonistic (Insel et al., 2020). Differences in amicability between individuals of different *Rhabdomys* taxa suggest that the causal mechanism for social preference may differ in the genus.

Personality experiments in non-social contexts have shown that *R. pumilio* is comparatively less anxious and bolder than *R. d. chakae* (Mackay & Pillay, 2021; Rymer & Pillay, 2012) which is partially modulated by rearing environment and a result of phylogenetic differences between taxa (Mackay & Pillay, 2019). We found that *R. pumilio* approached stimulus females faster and investigated them for longer than *R. d. chakae*, regardless of stimulus type. This suggests that personality differences between the taxa may extend to social contexts. *R. d. dilectus* (a sister subspecies of *R. d. chakae*) forms social groups when group-housed, just like *R. pumilio* (Rimbach et al., 2022), but, in *R. d. dilectus*, corticosterone levels were significantly higher than in *R. pumilio*. A less bold personality and social anxiety in the naturally solitary *R. d. chakae* might thus explain why this taxon was less motivated to investigate stimulus females generally, and novel females in particular. In contrast, a bolder personality and greater tendency for social contact might explain the behavior of *R. pumilio* in our study.

Within-taxon populations showed similar social responses despite occurring many kilometers apart, suggesting that these are conserved traits. Populations have thus retained taxon-specific social recognition and memory abilities. However, whether populations showed similar taxon-specific patterns due to an attraction to group-formation or to investigate potential competitors is not readily apparent in our study. Detailed behavioral studies are required to understand the underlying motivation for the similarity in *within* taxon-level responses.

In conclusion, we found social recognition and short-term social memory were similar but social motivation differed in two taxa (two populations each), of striped mice with different social systems. The motivation to investigate stimulus females differed between taxa, most likely related to differences in personality between taxa. *R. pumilio* and *R. d. chakae* were more motivated to investigate familiar females than novel females but *R. pumilio* approached stimulus females faster and investigated stimulus females for longer than *R. d. chakae*. Personality and social proclivity may explain the taxon-level differences in motivation between *R. pumilio* and *R. d. chakae* but the influence of environment cannot be excluded. Further studies are needed to confirm the social organization of *Rhabdomys* from different environments, particularly in *R. pumilio*. Populations showed consistent within-taxon responses, indicating that these responses are likely to be conserved taxon-specific traits. Future studies should investigate the underlying driving motivation for investigation of familiar and novel conspecifics in *Rhabdomys* taxa to assess the reasons for social investigation preferences in group-living and solitary taxa.

REFERENCES
Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Beery, A. K., Christensen, J. D., Lee, N. S., & Blandino, K. L. (2018). Specificity in sociality: Mice and prairie voles exhibit different patterns of peer affiliation. *Frontiers in Behavioral Neuroscience, 12*, 50. https://doi.org/10.3389/fnbeh.2018.00050

Choleris, E., Clipperton-Allen, A. E., Phan, A., & Kavaliers, M. (2009). Neuroendocrinology of social information processing in rats and mice. *Frontiers in Neuroendocrinology, 30*, 442–459. https://doi.org/10.1016/j.yfrne.2009.05.003

Christensen, C., & Radford, A. N. (2018). Dear enemies or nasty neighbors? Causes and consequences of variation in the responses of group-living species to territorial intrusions. *Behavioral Ecology, 29*, 1004–1013. https://doi.org/10.1093/beheco/ary010

Clark, K. E., Messler, K. A., & Ferkin, M. H. (2020). Sex differences in olfactory social recognition memory in meadow voles, *Microtus pennsylvanicus. Ethology, 126*, 993–1003. https://doi.org/10.1111/eth.13074

Crawley, J. N., Chen, T., Puri, A., Washburn, R., Sullivan, T. L., Hill, J. M., Young, N. B., Nadler, J. J., Moy, S. S., Young, L. J., Caldwel, H. K., & Young, W. S. (2007). Social approach behaviours in oxytocin knockout mice: Comparisons of two independent lines tested in different laboratory environments. *Neuropeptides, 41*, 145–163. https://doi.org/10.1016/j.npep.2007.02.002

RStudio Team. (2018). *RStudio: Integrated development for R.* RStudio, Inc. http://www.rstudio.com

Dale, J., Lank, D. B., & Reeve, H. K. (2001). Signaling individual identity versus quality: A model and case studies with Ruffs, Queleas, and House Finches. *American Naturalist, 158*, 75–86. https://doi.org/10.1086/320861

Engelmann, M., Wotjak, C. T., & Landgraf, R. (1995). Social discrimination procedure: An alternative method to investigate juvenile recognition abilities in rats. *Physiology and Behavior, 58*, 315–321. https://doi.org/10.1016/0031-9384(95)00053-L

Ferguson, J. N., Young, L. J., Hearn, E. F., & Insel, T. R. (2002). The neuroendocrine basis of social recognition. *Frontiers in Neuroendocrinology, 23*, 200–224. https://doi.org/10.1006/frne.2002.0229

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Ganem, G., Dufour, C. M. S., Avenant, N. L., Caminade, P., Eiseb, S. J., Tougourd, C., & Pillay, N. (2020). An update on the distribution and diversification of *Rhabdomys* sp. (Muridae, Rodentia). *Journal of Vertebrate Biology, 69*, 20013. https://doi.org/10.25225/jvb.20013

Hartman, K.-J. (2018). *The behavioural and neuroendocrinological mechanisms affecting group formation in the African striped mouse,*

Rhabdomys. [Unpublished PhD thesis]. University of the Witwatersrand, Johannesburg. https://hdl.handle.net/10539/25740

Hinde, R. A. (1976). Interactions, relationships and social structure. *Man*, *11*, 1–17. https://doi.org/10.2307/2800384

Insel, N., Shambaugh, K. L., & Beery, A. K. (2020). Female degus show high sociability but no preference for familiar peers. *Behavioural Processes*, *174*, 104102. https://doi.org/10.1016/j.beproc.2020.104102

Insel, T. R., & Fernald, R. D. (2004). How the brain processes social information: searching for the social brain. *Annual Review of Neuroscience*, *27*, 697–722. https://doi.org/10.1146/annurev.neuro.27.070203.144148

Kappeler, P. M. (2019). A framework for studying social complexity. *Behavioral Ecology and Sociobiology*, *73*, 13. https://doi.org/10.1007/s00265-018-2601-8

Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, *23*, 707–740. https://doi.org/10.1023/A:1015520830318

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.

Kruczek, M. (2007). Recognition of kin in bank voles (*Clethrionomys glareolus*). *Physiology & Behavior*, *90*, 483–489. https://doi.org/10.1016/j.physbeh.2006.10.012

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26. https://doi.org/10.18637/jss.v082.i13

Lee, N. S., Goodwin, N. L., Freitas, K. E., & Beery, A. K. (2019). Affiliation, aggression, and selectivity of peer relationships in meadow and prairie voles. *Frontiers in Behavioral Neuroscience*, *13*, 52. https://doi.org/10.3389/fnbeh.2019.00052

Lenth, R. (2019). *Emmeans: Estimated marginal means, aka Least-Squares means. R package version 1.4.2*.

Mackay, M., & Pillay, N. (2019). Anxiety and exploratory behaviour in the African striped mouse, *Rhabdomys*, taxa are partially modified by the physical rearing environment. *Developmental Psychology*, *61*, 179–190. https://doi.org/10.1002/dev.21814

Mackay, M., & Pillay, N. (2021). Environmental correlates of exploratory behaviour and anxiety in three African striped mouse (*Rhabdomys*) taxa occurring in different habitats and contexts. *Journal of Comparative Psychology*, *135*, 304–314. https://doi.org/10.1037/com0000235

Mackay, M., Rymer, T. L., & Pillay, N. (2014). Separation at weaning from the family is stressful for naturally group-living, but not solitary-living, males African striped mice *Rhabdomys*. *Stress*, *17*, 266–274. https://doi.org/10.3109/10253890.2014.910762

Madison, D. M., & McShea, W. J. (1987). Seasonal changes in reproductive tolerance, spacing and social organisation in meadow voles: A microtine model. *American Zoologist*, *27*, 899–908. https://doi.org/10.1093/icb/27.3.899

Mateo, J. M. (2004). Recognition systems and biological organization: The perception component of social recognition. *Annales Zoologici Fennici*, *41*, 729–745. http://www.jstor.org/stable/23736140

Monadjem, A., Taylor, P. J., Denys, C., & Cotterill, F. P. D. (2015). *Rodents of Sub-Saharan Africa: A biogeographic and taxonomic synthesis*. De Gruyter.

Moy, S. S., Nadler, J. J., Perez, A., Barbaro, R. P., Johns, J. M., Magnuson, T. R., Piven, J., & Crawley, J. N. (2004). Sociability and preference for social novelty in five inbred strains: An approach to assess autistic-like behaviour in mice. *Genes, Brain and Behavior*, *3*, 287–302. https://doi.org/10.1111/j.1601-1848.2004.00076.x

Neves, C. N., & Pillay, N. (2022). Sociability, but not spatial memory, is correlated with regional brain volume variation in the striped mouse *Rhabdomys* spp. *Behavioural Brain Research*, *417*, 113567. https://doi.org/10.1016/j.bbr.2021.113567

Parker, K. J., & Lee, T. M. (2003). Female meadow voles (*Microtus pennsylvanicus*) demonstrate same-sex partner preference. *Journal of Comparative Psychology*, *117*, 283–289. https://doi.org/10.1037/0735-7036.117.3.283

Paz y Miño, C., & Tang-Martínez, Z. (1999). Effects of exposure to siblings or sibling odors on sibling recognition in prairie voles (*Microtus ochrogaster*). *Canadian Journal of Zoology*, *77*, 118–123. https://doi.org/10.1139/z98-190

Pearson, B. L., Defensor, E. B., Blanchard, D. C., & Blanchard, R. J. (2010). C57BL/6J mice fail to exhibit preference for social novelty in the three-chamber apparatus. *Behavioural Brain Research*, *213*, 189–194. https://doi.org/10.1016/j.bbr.2010.04.054

Peterson, R. A., & Cavanaugh, J. E. (2019). Ordered quantile normalization: A semiparametric transformation built for the cross-validation era. *Journal of Applied Statistics*, *47*, 2312–2327. https://doi.org/10.1080/02664763.2019.1630372

Pillay, N., Willan, K., & Cooke, J. (1995b). Evidence of pre-mating reproductive isolation in two allopatric populations of the vlei rat, *Otomys irroratus*: Experiments of intra-and interpopulation male-female encounters. *Zeitschrift für Säugetierkunde*, *60*, 352–360. http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail%26idt=2920912

Pillay, N., Willan, K., Meester, J., & Cooke, J. (1995a). Evidence of pre-mating reproductive isolation in two allopatric populations of the vlei rat, *Otomys irroratus*. *Ethology*, *100*, 61–71. https://doi.org/10.1111/j.1439-0310.1995.tb00315.x

Rambau, R. V., Robinson, T. J., & Stanyon, R. (2003). Molecular genetics of *Rhabdomys pumilio* subspecies boundaries: mtDNA phylogeography and karyotypic analysis by inflorescence in situ hybridisation. *Molecular Phylogenetics and Evolution*, *28*, 564–575. https://doi.org/10.1016/S1055-7903(03)00058-7

Rimbach, R., Pillay, N., & Schradin, C. (2021). Prolonged growth during the food-restricted dry season in a small African mammal. *Journal of Mammalogy*, *102*, 296–307. https://doi.org/10.1093/jmammal/gyaa169

Rimbach, R., Hartman, K.-J., Currin, C., Schradin, C., & Pillay, N. (2022). Females of solitary- and group-living sister species of African striped mice show a similar social structure following experimentally imposed group-living. *Behavioral Ecology and Sociobiology*, *76*, 29. https://doi.org/10.1007/s00265-022-03144-2

Rymer, T. L., & Pillay, N. (2012). The development of exploratory behaviour in the African striped mouse *Rhabdomys* reflects a gene x environment compromise. *Behavior Genetics*, *42*, 845–856. https://doi.org/10.1007/s10519-012-9555-9

Schradin, C. (2004). Territorial defense in a group-living solitary forager: Who, where, against whom? *Behavioral Ecology and Sociobiology*, *55*, 439–446. https://doi.org/10.1007/s00265-003-0733-x

Schradin, C. (2005). When to live alone and when to live in groups: Ecological determinants of sociality in the African striped mouse (*Rhabdomys pumilio*, Sparrman, 1784). *Belgian Journal of Zoology*, *135*(Suppl. 1), 77-82.

Schradin, C., & Pillay, N. (2003). Paternal care in the social and diurnal striped mouse (*Rhabdomys pumilio*): Laboratory and field evidence. *Journal of Comparative Psychology*, *117*, 317–324. https://doi.org/10.1037/0735-7036.117.3.317

Schradin, C., & Pillay, N. (2004). The striped mouse (*Rhabdomys pumilio*) from the Succulent Karoo, South Africa: A territorial group-living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology*, *118*, 37–47. https://doi.org/10.1037/0735-7036.118.1.37

Schradin, C., & Pillay, N. (2005). Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy*, *86*, 99–107. https://doi.org/10.1644/1545-1542(2005)086%3C0099:IVITSA%3E2.0.CO;2

Schradin, C., König, B., & Pillay, N. (2010). Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice. *Journal of Animal Ecology*, 79, 515–521. https://doi.org/10.1111/j.1365-2656.2009.01651.x

Schradin, C., Lindholm, A. K., Johannesen, J. E. S., Schoepf, I., Yuen, C. H., Koenig, B., & Pillay, N. (2012). Social flexibility and social evolution in mammals: A case study of the African striped mouse (*Rhabdomys pumilio*). *Molecular Ecology*, 21, 541–553. https://doi.org/10.1111/j.1365-294X.2011.05256.x

Smith, C. J. W., Wilkins, K. B., Mogavera, J. N., & Veenema, A. H. (2015). Social novelty investigation in the juvenile rat: Modulation by the μ-opioid system. *Journal of Neuroendocrinology*, 27, 752–764. https://doi.org/10.1111/jne.12301

du Toit, N., Jansen van Vuuren, B., Matthee, S., & Matthee, C. A. (2012). Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys pumilio* (Rodentia: Muridae) from southern Africa with implications for taxonomy. *Molecular Phylogenetics and Evolution*, 65, 75–86. https://doi.org/10.1016/j.ympev.2012.05.036

Townsend, S. W., Allen, C., & Manser, M. B. (2012). A simple test of vocal individual recognition in wild meerkats. *Animal Behavior*, 8, 179–182. https://doi.org/10.1098/rsbl.2011.0844

Ward, A., & Webster, A. (2016). Sociality, *Sociality: The behaviour of group-living animals*. Springer International Publishing. https://doi.org/10.1007/978-3-319-28585-6

van Wimersma Greidanus, T. J. B., & Maigret, C. (1996). The role of limbic vasopressin and oxytocin in social recognition. *Brain Research*, 713, 153–159. https://doi.org/10.1016/0006-8993(95)01505-1

Winn, B. E., & Vestal, B. M. (1986). Kin recognition and choice of males by wild female house mice (*Mus musculus*). *Journal of Comparative Psychology*, 100, 72–75. https://doi.org/10.1037/0735-7036.100.1.72

Young, L. J. (2002). The neurobiology of social recognition, approach, and avoidance. *Society of Biological Psychiatry*, 51, 18–26. https://doi.org/10.1016/S0006-3223(01)01268-9

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