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Species-specific behavioural responses to peripheral arginine vasopressin in two African striped mice (genus *Rhabdomys*)

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ABSTRACT

Peripheral arginine vasopressin (AVP) administration modulates social behaviour in several mammalian species, although its effects are inconsistent and can be species- and context-specific. We investigated whether peripheral AVP modulates behavioural responses in females of two closely related African striped mouse species that differ in social organisation: group-living *Rhabdomys pumilio* and solitary-living *R. dilectus dilectus*. Using a three-chamber sociability and social novelty test, we investigated the behavioural responses of focal females, following saline, low-dose or high-dose subcutaneous AVP injections, to either familiar or novel stimulus females. We recorded the duration of time spent in the chambers of each stimulus female, the number of approaches, and the duration of affiliative and aggressive behaviours. Under high AVP, both species spent more time with, and made more approaches to, stimulus females, suggesting enhanced activity or investigatory behaviour. Specifically, under high AVP, *R. d. dilectus* showed increased affiliative behaviour toward familiar females, while *R. pumilio* generally showed greater aggression overall and more affiliative behaviour towards the novel female under high AVP. Our findings suggest that peripheral AVP can modulate certain aspects of social behaviour in *Rhabdomys*, although the underlying mechanisms (social, arousal-based or locomotor) remain untested. These results highlight the importance of considering species differences and peripheral neuropeptide effects when evaluating the associations between AVP expression and behaviour.

1. Introduction

Social recognition involves the ability to distinguish between individuals and is crucial for how conspecifics interact, influencing behaviours such as approaches, avoidance, affiliation and aggression (Winslow and Insel, 2004). Social recognition involves distinguishing conspecifics based on factors such as familiarity, sex, social rank and kinship (Bluthé and Dantzer, 1990; Song et al., 2016). While most studies on social behaviours and recognition have focused on social species, both social and solitary species benefit from recognising known and unknown conspecifics, although their motivations for doing so differ. Solitary species may investigate conspecifics as potential kin or competitors, eliciting aggressive behaviours (Madison and McShea, 1987). Social species may form and maintain groups through affiliative interactions, enhancing group cohesion (Ebensperger et al., 2009; Insel et al., 2020). For example, female degus (*Octodon degus*) form unstable groups and are highly affiliative toward both familiar and unknown conspecifics (Insel et al., 2020). Similarly, gregarious species like the house mouse (*Mus musculus*) and Long-Evans rat (*Rattus norvegicus*) may not show a preference for social novelty or familiarity (Beery et al., 2018; Beery and Shambaugh, 2021). Yet, in contrast to promiscuous meadow voles, communally living prairie vole females show greater aggression toward unknown same sex conspecifics, suggesting a selectivity in preference that may promote aggression toward unknown conspecific and maintain the pair bond with a housing partner (Lee, et al., 2019).

Social behaviour relies on both memory and motivation systems in the brain. For example, the memory of previous interactions creates social familiarity, which is crucial for recognising individuals and forming stable social relationships (Winslow and Insel, 2004; Choleris et al., 2009). These processes and social behaviours are generally coordinated by a collection of different brain regions known as the social behaviour network (SBN), which includes the bed nucleus of the stria terminalis (BNST) and hypothalamus (Hawthorn et al., 1980; Bradford, 1986; Bielsky et al., 2004; Veenema and Neumann, 2008; Leng et al., 2012; Dumais and Veenema, 2016). The SBN modulates many social

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behaviours, including social recognition and social bonding (Young, 2002; Winslow and Insel, 2004; Lim and Young, 2006; Carter et al., 2008; Albers, 2012), as well as affiliative behaviour (Winslow et al., 1993) and aggression (Albers et al., 2006).

The nonapeptide arginine vasopressin (AVP) performs several key physiological functions, including modulation of circadian rhythms (Rohr et al., 2021), osmoregulation and blood pressure regulation (Leng et al., 2012; Nelson, 2005), and is also critical for the modulation of social behaviours (Insel and Young, 2000). AVP and many of its receptors (V1a) are expressed in most parts of this SBN (Veenema and Neumann, 2008) and play significant roles in several social behaviours (Insel and Young, 2000), including social recognition, bonding, affiliation and aggression (Goodson, 2005; Winslow and Insel, 2004). For example, the Brattleboro rat, a naturally vasopressin-deficient strain of Long-Evans rat, lacks the ability to exhibit social recognition, but restores its capacity for social recognition after AVP is administered to the brain (Van Wimersma Greidanus, 1982; Engelmann and Landgraf, 1994). Additionally, AVP injected into the anterior hypothalamus reduced the duration of aggressive behaviour in female Syrian hamsters (*Mesocricetus auratus*; Gutzler et al., 2010). While Lukas and Neumann (2014) found that AVP does not appear to be involved in naturally occurring social preference behaviours in gregarious female Wistar rats, AVP administration increased the duration of social engagement, olfactory investigation and amount of time spent huddling with conspecifics in laboratory rats (Dantzer et al., 1987; Bluthé and Dantzer, 1990; Winslow and Insel, 2004; Albers, 2012), and peripheral administration of AVP prolonged social recognition in castrated male rats (Bluthé et al., 1990).

The effect of AVP and its receptors on social behaviours varies with social organisation (Insel and Young, 2000), and species that differ in their social organisations also show differences in neuropeptide synthesis and release, as well as in receptor distribution in the SBN (Insel and Young, 2000; Veenema and Neumann, 2008). Differences in AVP receptor distribution and synthesis between species suggest a physiological basis for social preference/avoidance and motivation (Insel and Young, 2000; Carter et al., 2008; Veenema and Neumann, 2008). For example, AVP has greater binding within the lateral septum of monogamous social prairie voles (*Microtus ochrogaster*) than in promiscuous montane voles (*M. montanus*; Insel et al., 1994), and prairie voles also show increased interactions under enhanced AVP, unlike solitary montane voles (Young et al., 1999). An artificial increase of AVP in male prairie voles, which typically display mate guarding and territorial defence, increased aggression toward other males and increased affiliative behaviour toward females, but this effect was absent in male montane voles (Winslow et al., 1993; Stribley and Carter, 1999; Choleris et al., 2004). When administered centrally to specific brain regions (Cho et al., 1999; Young et al., 1999), AVP facilitated social approach in prairie voles, and increased the duration of social engagement, olfactory investigation and amount of time spent huddling with conspecifics (Cho et al., 1999; Young et al., 1999). The colonial tuco-tuco (*Ctenomys sociabilis*) had reduced V1aR binding in the ventral pallidum compared to the solitary Patagonian tuco-tuco (*C. haigi*; Beery et al., 2008).

While AVP is important in the expression of socially motivated behaviours, either affiliative or aggressive, the direction of its influence appears to vary by sex (De Vries et al., 1984) and social organisation (Insel and Young, 2000), with some species demonstrating no observable response to changes in AVP expression (reviewed by Rigney et al., 2023). Moreover, AVP and its influence on social behaviour have been largely studied in laboratory rats and mice, as well as some species of voles (Rigney et al., 2023).

The use of laboratory bred mice has served as an important foundation to scientific advancement, but there is a pressing need for the inclusion of a broader range of naturally occurring, and non-standard, models. Recent studies have seen the emergence of new model species in the field of social behaviour such as the spiny mouse (*Acomys cahirinus*) (reproductive and non-reproductive social behaviour, Fricker, et al., 2021; precocial social behaviour, Ratnayake et al., 2014) and the Mongolian gerbil (*Meriones unguiculatus*) (OT and AVP modulation of juvenile social behaviour, Taylor, et al., 2017). The striped mouse (genus *Rhabdomys*) is an emerging model differing in social organizations that may expand our understanding of hormonal modulation of social behaviour in naturally occurring rodents.

Most studies examining the behavioural effects of AVP focus on central administration to target specific brain regions involved in social behaviour regulation (e.g., Gutzler et al., 2010). However, peripherally administered AVP also influences behaviour, likely through indirect modulation of central processes via the blood–brain barrier or through peripheral receptors affecting autonomic and hormonal systems. While less direct than intracerebral delivery, peripheral administration is more ecologically and translationally relevant, particularly for comparative studies and non-invasive applications. Moreover, some behavioural effects observed after central AVP manipulation have also been reported following peripheral administration, suggesting at least partially overlapping mechanisms of action (e.g., Appenrodt et al., 1998). By using peripheral delivery, we aimed to test whether exogenous AVP can modulate social behaviour under physiologically relevant conditions without the confounding effects of invasive neurosurgical procedures.

In this study, we focused on two closely related species of African striped mice. Striped mice are widespread, generalist murid rodents that are distributed throughout southern and eastern Africa (Monadjem et al., 2015). These species differ in their social organisation: *R. pumilio* is facultatively group-living, occurring either as solitary individuals or in small social groups consisting of one breeding male, two to four breeding females and their philopatric offspring that provide alloparental care (Schradin and Pillay, 2003, 2004). Group members share a nest and defend a shared territory, interact amicably and bask together at dawn and dusk, but forage alone (Schradin, 2005). Male *R. pumilio* display alternative reproductive tactics (group-living vs roaming), and group-living males show paternal care (Schradin and Pillay, 2003). In contrast, *R. d. dilectus* is generally solitary living (Schradin and Pillay, 2005a). Females interact with males only during the breeding season and raise offspring alone (Schradin and Pillay, 2003). However, some *R. d. dilectus* populations form groups because of interference competition with syntopic *R. bechuanae* (Dufour et al., 2019). In addition, *R. d. dilectus* males will show paternal care towards offspring in captivity (Schradin and Pillay, 2003), but this has not been seen in the wild.

Under laboratory conditions, *R. d. dilectus* has smaller relative amygdala and hippocampal volumes and is less affiliative towards conspecifics than *R. pumilio*. Hippocampus volume was positively associated with heightened amicability in *R. pumilio* but not in *R. d. dilectus* (Neves and Pillay, 2022a). Additionally, social preference did not differ between *R. pumilio* and *R. dilectus* because females of both species are capable of social recognition and show a preference for social familiarity over social novelty (Neves and Pillay, 2022b). Similarly, while *R. pumilio* females exhibited more initial aggression in imposed non-kin groups than *R. d. dilectus* females, females of both species became more affiliative toward group members the longer the imposed groups were maintained (Rimbach et al., 2022). While variation in naturally-occurring AVP levels in *R. d. dilectus* remains unknown, AVP levels are similar between *R. pumilio* individuals displaying alternative reproductive tactics, differing only between the wet and dry seasons (Schoepf and Schradin, 2014), as would be expected, given the role of AVP in osmoregulation (Schwimmer and Haim, 2009). Central AVP concentrations and immunoreactive cells also differ between individuals displaying alternative reproductive tactics in *R. pumilio* (Schoepf et al., 2015). However, the association between AVP and social behaviour across different *Rhabdomys* species requires further investigation.

We assessed whether peripherally administered AVP modified the social behavioural responses in the two closely related *Rhabdomys* species with different social tendencies. We tested whether peripheral AVP is a potential modulator of behaviour, while acknowledging that outcomes may reflect changes in arousal, anxiety or locomotion rather than

social motivation specifically. We examined whether peripherally administered AVP alters investigatory behaviour and affiliative or aggressive responses in females of each species, using a three-chamber assay to examine sociability and social novelty preference (Engelmann et al., 1995; Ferguson et al., 2002; Choleris et al., 2009). Given that *R. pumilio* is group-living and has shown higher exploratory behaviour than *R. d. dilectus* in previous studies (Rymer and Pillay, 2012; Mackay and Pillay, 2021), we expected *R. pumilio* to display more investigatory activity in the three-chamber test. We hypothesised that AVP might modulate social behaviours differently between species depending on their baseline activity levels and social tendencies, such that *R. pumilio* will engage in more social interactions than *R. d. dilectus*.

2. Materials and methods

2.1. Study species

We used F2 and F3 captive-born individuals from each species that originated from a colony maintained at the Milner Park Animal Unit at the University of the Witwatersrand, Johannesburg, South Africa. *R. pumilio* mice originated from the arid Succulent Karoo (160 mm rainfall per annum; Schradin and Pillay, 2005b), and *R. d. dilectus* mice originated from Sandveld Nature Reserve of South Africa (500 mm of rainfall per annum; Fick and Hijmans, 2017).

2.2. Husbandry

Subjects were housed and reared under partially controlled environmental conditions, with a light:dark cycle of 14:10. A total of 60 virgin adult (> 75 days of age) female striped mice were used, comprising of 30 *R. pumilio* and 30 *R. d. dilectus* individuals. Females were sexed by visual inspection of the external genitalia. All mice were housed singly in Lab-o-tec home cages (L × H × W: 425 mm×150 mm × 240 mm) from 25 days of age and throughout the study; individual housing does not affect the behaviour of both species (Mackay et al., 2014). Home cages included ≈ 1 cm wood shavings for bedding, and ≈ 20 g of *Eragrostis* grass and ≈ 5 g of tissue paper provided as nesting material. A cardboard tube (Length x Diameter: 99 mm×38 mm) and a small piece of wood for gnawing were provided as enrichment. All home cages were cleaned weekly with F10®SC disinfectant soap (Health and Hygiene (Pty) Ltd) and water, and air dried. Mice were provided with 5 g Epol mouse cubes, 5 g fresh vegetables and 2 g millet daily, with water available *ad libitum*.

Ten females of each species were randomly selected to be the focal individuals, while the remaining 20 individuals per species were used as stimuli. Two novel stimulus females were assigned to each focal female for each treatment, such that the stimulus females used differed for each AVP treatment (see below). Focal animals were housed in a separate room from stimulus animals throughout the study period. All stimulus females were unrelated and unfamiliar to the focal individuals. Stimulus animals were weight-matched for use in experiments to avoid variation in body size of a stimulus female affecting the responses of the focal female. This study was approved by the animal ethics screening committee of the University of the Witwatersrand, AESC number: 2014/34/B.

2.3. Experimental design

We used a three-chambered testing apparatus adapted from Moy et al. (2004) and Crawley et al. (2007). The testing apparatus consisted of a glass tank (L × H × W: 600 mm×400 mm × 300 mm) with wood shavings on the floor, divided into three chambers (central chamber: 260 mm wide; side chambers: 170 mm wide) by two clear flexiglass barriers with two 60 mm×60 mm archways (hereafter chamber entrances) allowing the focal animal to move freely between the three areas (Fig. 1). The chamber entrances were positioned in the front of the tank and could be opened or closed by the experimenter. The two test areas (unfamiliar zones) each contained a mesh holding cage (L × H × W: 130 mm×105 mm × 95 mm) that was covered on top with a small white tile to block interactions between the mice from above the cage, as well as to weigh the cage down. The holding cages were positioned in the sections of the chambers furthest from the chamber entrances. The mesh holding cages were used to house stimulus females during trials to avoid the risk of damaging fights between individuals and to allow only the focal animal to initiate interactions.

The focal animal was placed in the experimental tank between 13h00 and 15h00 the day before experiments to allow it to habituate to the tank. It was provided with 5 g mouse cubes, 2 g sunflower seeds, water, and a nest box. During the habituation period, the two empty mesh holding cages were present in their respective zones. This habituation period was included to ensure that the social stimulus was the only novel stimulus in the set up during the experimental trial, avoiding the

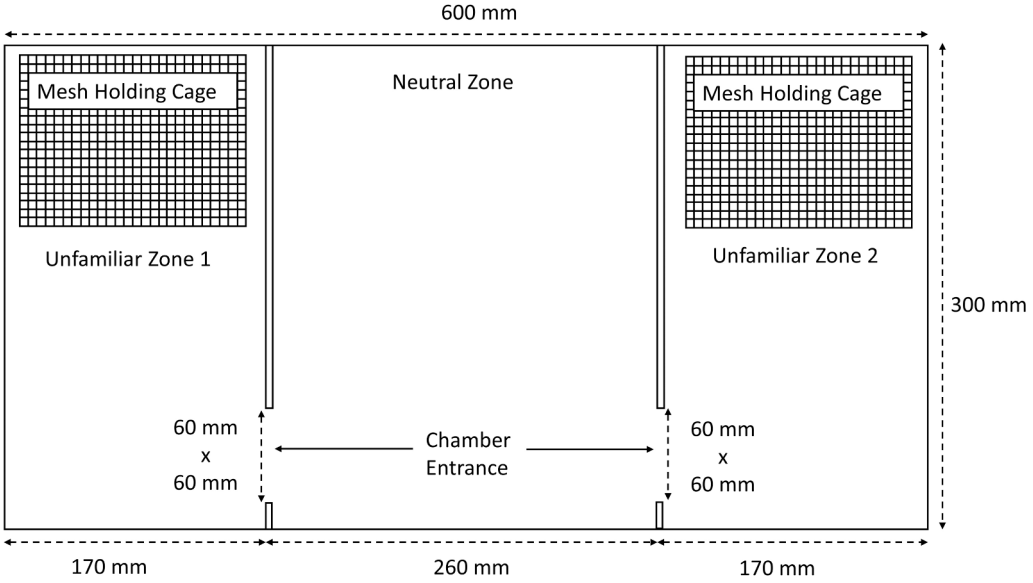

Fig. 1. The three-chambered test apparatus as viewed from above. The unfamiliar zones are the test area/chambers that contained the stimulus mice within mesh holding cages. White tiles above the holding cages are omitted from this image. Zones were divided by 3 mm thick clear flexiglass barriers.

potential for behavioural measures being confounded by the focal mouse's investigation of a novel set-up. All experimental trials were run between 09h00 – 12h00 when striped mice are most active (Pillay, 2000). The behaviour of the focal mouse was filmed from above the tank through a clear flexiglass lid using a Sony Handycam® video camera. No human observers were in the room during recording.

Each focal female underwent three treatments over a 5-day period. On Day 1, Day 3, and Day 5, individuals were injected subcutaneously into the scruff with 20 µl saline, 1 µg/g synthetic AVP (referred to as low AVP), or 1.5 µg/g synthetic AVP (referred to as high AVP), respectively. The treatments were administered in this sequence as a precaution against exposing individuals to high doses of AVP too soon, particularly since AVP had never been administered to *Rhabdomys* females previously. This allowed us to establish whether any dose responses or threshold concentration of AVP existed without jeopardizing the data collection for this study. These dosages were selected based on Schaller et al. (2010) for laboratory mice and naturally occurring plasma AVP levels recorded in field studies of *R. pumilio* (Schoepf and Schradin, 2014). Each focal female was rested for 48 h between each treatment/test period (see below). AVP injected subcutaneously has a half-life of 6–20 min (Glavaš et al., 2022) and was assumed to be fully eliminated from the mice before the subsequent experimental day. Animals were restrained and not anesthetized before injections were administered because this type of injection is only mildly painful for the animal and a small dose volume was used (as per guidelines of Boston University IACUC, 2019). Subcutaneous injection of AVP has elicited behavioural responses in previous studies on other species (reviewed by Ferguson et al., 2002) but the responses were mixed.

To account for potential oestrous stage effects on behavioural responses (Mora et al., 1996), vaginal swabs were taken from the focal and stimulus individuals after experiments were completed on each day of testing (between 11h30 and 12h30). Cotton swabs were inserted into the vagina with a rolling motion, and the swabs were then smeared on clean glass slides and allowed to dry. The oestrous cycle phase was ascertained microscopically and classified based on the proportions of leukocytes, nucleated epithelial cells, and anucleated cornified epithelial cells present to one of four stages: 1) oestrus; 2) met-oestrus; 3) di-oestrus; and 4) pro-oestrus (Bennett, 1999, Marcondes et al., 2002, Byers et al., 2012).

2.3.1. Sociability and social novelty preference

The three-chambered testing arena allowed us to measure sociability and social novelty. Sociability is used to quantify social motivation by comparing the duration of time the focal animal spends with a stimulus animal rather than in an empty chamber (Engelmann et al., 1995; Young, 2002; Moy et al., 2004; Choleris et al., 2009). Social novelty is measured using the social discrimination paradigm (Choleris et al., 2009), where the focal animal's ability to recognize conspecifics is tested by simultaneously introducing a novel stimulus animal into a previously empty chamber (in the prior sociability test) alongside the now known (but previously unfamiliar) stimulus animal, giving the focal animal the choice between the two (Engelmann et al., 1995; Ferguson et al., 2002; Bielsky and Young, 2004; Moy et al., 2004). This type of test has been used in several studies on different rodent species to test the effects of administered neuropeptides and hormones on sociability and social recognition (reviewed by Bielsky and Young, 2004; Choleris et al., 2009). We included measures of aggression and affiliative behaviour as recommended by Pearson et al. (2010) to better assess the motivation of the focal animal to investigate the stimulus animals.

2.3.2. Sociability test

On each experimental day, the focal females were tested as follows: following a 5-minute habituation to the lighting and the presence of the video camera in the filming room, the female was injected with either saline or low or high AVP (described in 2.3). The focal female was returned to the experimental tank (food, water bottle and nest box removed) and was allowed 10 min to settle after the injection and handling. Plasma AVP peaks within 10 min of exogenous injection (Engel et al., 1984). The focal female was then contained in the middle neutral zone by blocking off the chamber entrances. The novel stimulus animal was added to a holding cage in one of the side chambers, which was randomly selected for each trial. The other side chamber remained empty. The entrances were opened and the behavioural responses of the focal female to the empty chamber and stimulus female were video recorded for 10 min.

The following behaviours were scored by a single person (KJH) from the video footage using The Observer XT® software (version 9.0, Noldus, Netherlands); we measured: 1) the duration of time spent in each chamber, measured from the instant the focal female's head and forelimbs crossed the chamber entrance leading into the chamber to the point when the focal mouse entered an adjoining chamber; 2) the frequency of approaches to the stimulus animal or empty cage, when the focal female was within less than half a body length of the holding cage and facing the holding cage's direction; 3) the duration in affiliative contact with the stimulus mouse, when the focal female was in body contact with the holding cage, with no aggression displayed (this included resting against the cage, sniffing the stimulus mouse), and any other notable affiliative behaviours (e.g. sitting in close proximity, attempts at grooming stimulus female through the cage) to the stimulus mouse through the cage; and 4) the duration of aggression toward the stimulus animal (e.g., the focal female lunged toward, lifted, bit or pulled on the holding cage containing the stimulus mouse).

2.3.3. Social novelty preference test

Directly after the 10-minute sociability test, each focal mouse was tested for social novelty preference, or the preference to interact with an unknown conspecific, as a measure of social recognition (i.e., social discrimination; Engelmann et al., 1995). The focal female was gently coaxed back into the central chamber after the sociability test and all entrances were blocked. A second, novel stimulus female was then added to the empty holding cage. The chamber entrances were then opened simultaneously, allowing the focal female access to both stimulus mice, and the behaviours of the focal female were recoded for a further 10 min. The duration of time spent in each chamber, the frequency of approaches toward each stimulus animal, and duration of time spent in affiliative and aggressive contact with each stimulus animal were scored. Following this 10-minute trial, all three females were returned to their respective home cages and rested for 48 h. Between trials, the experimental equipment was cleaned with F10®SC disinfectant soap and water and then air dried to remove the scent of all other mice from the apparatus.

2.4. Statistical analyses

Data were analysed using RStudio (version 2024.06.14; https://www.rproject.org; R version 4.4.1, R Core Team, 2022). All response variables were not normally distributed (confirmed using Shapiro-Wilk tests) and were zero-inflated (performance package; Lüdecke et al., 2021). Therefore, we ran zero-inflation generalized linear mixed model (GLMM) ANOVAs (glmmTMB package; Brooks et al., 2017; car package; Fox and Weisberg, 2011). A Spearman's Rank Order correlation indicated that behaviours displayed, and duration of time spent, in the chambers were not affected by the oestrous stage or body mass of the focal or stimulus mice, and the side of the chamber (i.e., randomly assigned chamber) containing the stimulus mice for both the sociability and social novelty preference tests. Therefore, none of these effects were included in our final models.

We ran separate models for the response variables (frequency of approaches to the stimulus animal's holding cage; duration of time spent in each chamber, and duration of time spent in affiliative or aggressive contact with the stimulus animals) for both the sociability and social novelty tests, with individual focal female identity (ID) as a random effect. We used negative binomial GLMM models for the frequency of

approaches, and gamma GLMM models for the three duration measures. In the sociability test, we included chamber (unfamiliar mouse or empty), treatment (saline, low AVP, or high AVP), and species as categorical predictors. For the models of the duration of affiliative and aggressive contact in the sociability test, we only considered the occupied chamber, so only treatment and species were included as fixed effects. The social novelty test models included the same factors as in the sociability test analysis, but we also included the stimulus female chamber condition (known vs novel females) as a factor in the models assessing the duration of affiliative and aggressive behaviour.

Models were validated by comparing the residuals to the fitted values using qqnorm plots in the R Stats package (Crawley, 2009) and dispersion was tested using the DHARMa package (Hartig, 2022). Model significance was set at $p = 0.05$ for all tests. Effect sizes could not be calculated for individual factors in the models because generalized linear models were calculated using Wald statistics. Instead, Cohen's f calculated from R^2 are presented for each model. Where significant predictors were indicated, *post hoc* tests were run using pairwise comparisons (comparing estimated marginal means) with a Tukey adjustment using the emmeans package (Lenth, 2023). All data are presented as bar plots of mean ± standard error.

3. Results

3.1. Sociability test

3.1.1. Duration in chamber and frequency of approaches to stimulus animal

Neither species, treatment, nor chamber were significant predictors of the total duration (Cohen's $f = 0.01$) of time spent in the chambers nor the frequency of approaches (Cohen's $f = 1.15$; Table 1).

Species x treatment ($p = 0.035$) was a significant predictor of the frequency of approaches to the stimulus mouse. Post hoc comparisons showed that *R. pumilio* approached the stimulus mouse significantly more often under both AVP treatments than under saline, while *R. d. dilectus* approached the stimulus mouse more often under high AVP than *R. pumilio* under saline (Fig. 2).

Species x chamber, treatment x chamber and the three-way interaction between species x treatment x chamber were not significant predictors of the total duration of time spent in the chambers nor the frequency of approaches to the stimulus mouse or the empty cage in each chamber. Species x treatment did not significantly predict the duration of time spent in the chambers (Table 1).

Table 1
Results for the zero-inflated generalized linear mixed model ANOVAs with Wald chi-square statistics for the conditional and zero-inflated components of the models for the sociability test. Significant effects are noted in bold.

Model	Factor	Conditional component	Zero-inflated component
Total duration (s)	Species	$\chi^2 = 0.00$, d.f. = 1, p = 0.993	$\chi^2 = 0.28$, d.f. = 1, p = 0.762
	Treatment	$\chi^2 = 0.59$, d.f. = 2, p = 0.744	$\chi^2 = 4.87$, d.f. = 2, p = 0.080
	Chamber	$\chi^2 = 1.24$, d.f. = 1, p = 0.266	$\chi^2 = 1.26$, d.f. = 1, p = 0.369
	Species x Treatment	$\chi^2 = 0.10$, d.f. = 2, p = 0.949	
	Species x Chamber	$\chi^2 = 0.08$, d.f. = 1, p = 0.777	
	Treatment x Chamber	$\chi^2 = 0.87$, d.f. = 2, p = 0.647	
	Species x Treatment x Chamber	$\chi^2 = 0.72$, d.f. = 2, p = 0.699	
Frequency of approaches	Species	$\chi^2 = 0.30$, d.f. = 1, p = 0.587	$\chi^2 = 2.04$, d.f. = 1, p = 0.997
	Treatment	$\chi^2 = 0.43$, d.f. = 2, p = 0.808	$\chi^2 = 0.14$, d.f. = 2, p = 0.931
	Chamber	$\chi^2 = 3.60$, d.f. = 1, p = 0.058	$\chi^2 = 0.83$, d.f. = 1, p = 0.362
	Species x Treatment	**$\chi^2 = 6.70$, d.f. = 2, p = 0.035**	
	Species x Chamber	$\chi^2 = 0.85$, d.f. = 1, p = 0.356	
	Treatment x Chamber	$\chi^2 = 2.45$, d.f. = 2, p = 0.293	
	Species x Treatment x Chamber	$\chi^2 = 1.63$, d.f. = 2, p = 0.443	

3.2. Social novelty preference tests

3.2.1. Duration in chamber and frequency of approaches to stimulus mice

Neither species showed a preference for social novelty. Species, treatment, chamber (familiar or novel mouse's chamber; Table 3), or any interactions of the three categorical predictors were significant predictors of the duration of time spent in each chamber (Cohen's $f = 0.07$), nor the frequency of approaches (Cohen's $f = 1.01$).

3.2.2. Behaviour in the social novelty preference test

Species ($p = 0.003$) was a significant predictor of the duration of affiliative contact (Cohen's $f = 0.43$) with the stimulus mouse (Table 4). In general, *R. d. dilectus* displayed affiliative behaviour for longer than *R. pumilio* (Fig. 4). The interaction between species x treatment ($p = 0.006$; Table 4) was also a significant predictor of the duration of affiliative behaviour, with *R. pumilio* females displaying affiliative behaviour for a shorter duration under both AVP treatments than *R. d. dilectus* females under the high AVP treatment (Fig. 4). Species x chamber ($p = 0.020$; Table 4) was also a significant predictor of the

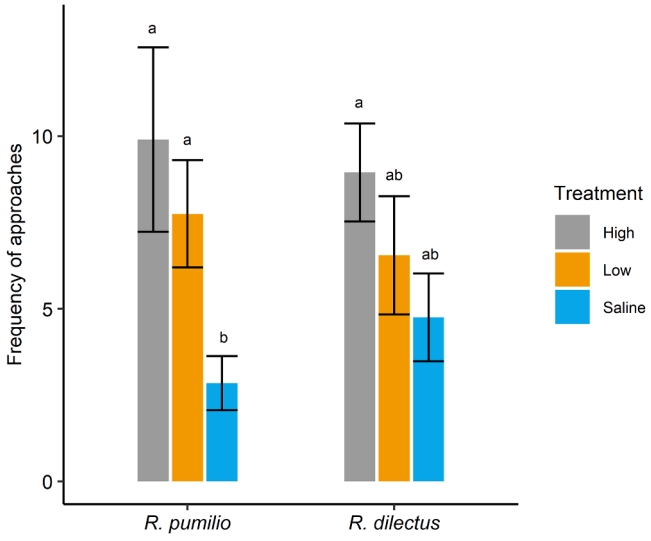

Fig. 2. Mean ± SE frequency of approaches toward the stimulus females in the sociability experiment across AVP treatments, grouped by species. Significant post hoc comparisons within groups are indicated by different letters.

Table 2
Results for the zero-inflated generalized linear mixed model ANOVAs for the duration (s) of affiliative and aggressive behaviours displayed toward the novel stimulus female during the sociability test. Significant effects are noted in bold.

Model	Factor	Conditional component	Zero-inflated component
Affiliative behaviours	Species	$\chi^2 = 1.57$, d.f. $= 1$, $p = 0.210$	$\chi^2 = 0.00$, d.f. $= 1$, $p = 1.000$
	Treatment	$\chi^2 = 2.45$, d.f. $= 2$, $p = 0.294$	$\chi^2 = 3.26$, d.f. $= 2$, $p = 0.195$
	Species x Treatment	$\chi^2 = 1.38$, d.f. $= 2$, $p = 0.502$	
Aggressive behaviours	**Species**	**$\chi^2 = 4.40$, d.f. $= 1$, $p = 0.033$**	$\chi^2 = 0.60$, d.f. $= 1$, $p = 0.438$
	Treatment	$\chi^2 = 1.17$, d.f. $= 2$, $p = 0.557$	$\chi^2 = 5.14$, d.f. $= 2$, $p = 0.076$
	Species x Treatment	$\chi^2 = 2.62$, d.f. $= 2$, $p = 0.270$	

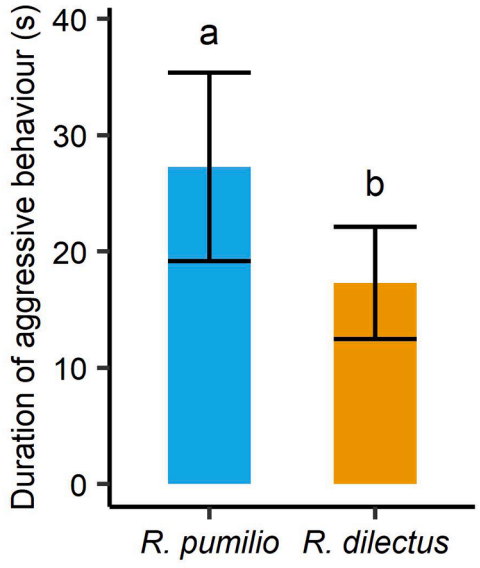

Fig. 3. Mean ± SE duration (s) of aggressive behaviours displayed by *R. dilectus* and *R. pumilio* focal females toward conspecific novel stimulus females in the sociability test. Significant post hoc comparisons within groups are indicated by different letters.

duration of affiliative behaviour, with *R. d. dilectus* females showing greater affiliative behaviour towards the familiar mouse than *R. pumilio* towards the novel mouse (Fig. 4). Finally, we also found that the interaction between species x treatment x chamber was a significant predictor of the duration of affiliative contact with the stimulus mouse ($p = 0.031$; Table 4). While *Post hoc* comparisons did not reveal statistically significant differences, plots showed that *R. d. dilectus* females were more affiliative toward the familiar stimulus mouse under high AVP than under saline and were also more affiliative towards the familiar stimulus mouse than the novel mouse under high AVP (Fig. 4). In contrast, *R. pumilio* females were less affiliative toward the familiar stimulus mouse under high AVP than under saline (Fig. 4). Additionally, under high AVP, *R. pumilio* females were less affiliative toward the familiar stimulus mouse than *R. d. dilectus* females (Fig. 4). Treatment, chamber and the interaction between treatment x chamber were not significant predictors of the duration of affiliative contact (Table 4).

We found no significant effects of species, treatment, chamber or any of the interactions on aggressive behaviour toward either stimulus mouse (Cohen's $f = 0.03$).

Table 3
Statistical results for the zero-inflated generalized linear mixed models for the social novelty test.

Model	Factor	Conditional component	Zero-inflated component
Total duration (s)	Species	$\chi^2 = 1.60$, d.f. $= 1$, $p = 0.206$	$\chi^2 = 0.00$, d.f. $= 1$, $p = 1.000$
	Treatment	$\chi^2 = 1.65$, d.f. $= 2$, $p = 0.439$	$\chi^2 = 1.61$, d.f. $= 2$, $p = 0.447$
	Chamber	$\chi^2 = 0.92$, d.f. $= 1$, $p = 0.339$	$\chi^2 = 0.37$, d.f. $= 1$, $p = 0.542$
	Species x Treatment	$\chi^2 = 2.94$, d.f. $= 2$, $p = 0.230$	
	Species x Chamber	$\chi^2 = 1.57$, d.f. $= 1$, $p = 0.211$	
	Treatment x Chamber	$\chi^2 = 1.23$, d.f. $= 2$, $p = 0.541$	
	Species x Treatment x Chamber	$\chi^2 = 3.53$, d.f. $= 2$, $p = 0.172$	
Frequency of approaches	Species	$\chi^2 = 1.11$, d.f. $= 1$, $p = 0.291$	$\chi^2 = 0.06$, d.f. $= 1$, $p = 0.813$
	Treatment	$\chi^2 = 0.68$, d.f. $= 2$, $p = 0.713$	$\chi^2 = 0.99$, d.f. $= 2$, $p = 0.608$
	Chamber	$\chi^2 = 2.05$, d.f. $= 1$, $p = 0.113$	$\chi^2 = 0.92$, d.f. $= 1$, $p = 0.337$
	Species x Treatment	$\chi^2 = 1.27$, d.f. $= 2$, $p = 0.422$	
	Species x Chamber	$\chi^2 = 0.04$, d.f. $= 1$, $p = 0.845$	
	Treatment x Chamber	$\chi^2 = 1.71$, d.f. $= 2$, $p = 0.425$	
	Species x Treatment x Chamber	$\chi^2 = 0.05$, d.f. $= 2$, $p = 0.977$	

Table 4
Results for zero-inflated generalized linear mixed model ANOVAs for the duration (s) of amicable and aggressive behaviours displayed during the social novelty test. Significant effects are noted in bold.

Model	Factor	Conditional component	Zero-inflated component
Affiliative behaviours	**Species**	**$\chi^2 = 8.65$, d.f. $= 1$, $p = 0.003$**	$\chi^2 = 0.77$, d.f. $= 1$, $p = 0.767$
	Treatment	$\chi^2 = 3.52$, d.f. $= 2$, $p = 0.172$	$\chi^2 = 0.55$, d.f. $= 2$, $p = 0.553$
	Chamber	$\chi^2 = 2.17$, d.f. $= 1$, $p = 0.141$	$\chi^2 = 0.38$, d.f. $= 1$, $p = 0.380$
	Species x Treatment	**$\chi^2 = 10.22$, d.f. $= 2$, $p = 0.006$**	
	Species x Chamber	**$\chi^2 = 5.42$, d.f. $= 1$, $p = 0.020$**	
	Treatment x Chamber	$\chi^2 = 3.46$, d.f. $= 2$, $p = 0.177$	
	Species x Treatment x Chamber	**$\chi^2 = 6.98$, d.f. $= 2$, $p = 0.031$**	
Aggressive behaviours	Species	$\chi^2 = 1.32$, d.f. $= 1$, $p = 0.251$	$\chi^2 = 0.91$, d.f. $= 1$, $p = 0.341$
	Treatment	$\chi^2 = 0.64$, d.f. $= 2$, $p = 0.725$	$\chi^2 = 3.61$, d.f. $= 2$, $p = 0.164$
	Chamber	$\chi^2 = 2.62$, d.f. $= 1$, $p = 0.105$	$\chi^2 = 0.91$, d.f. $= 1$, $p = 0.341$
	Species x Treatment	$\chi^2 = 0.51$, d.f. $= 2$, $p = 0.776$	
	Species x Chamber	$\chi^2 = 1.21$, d.f. $= 1$, $p = 0.271$	
	Treatment x Chamber	$\chi^2 = 0.63$, d.f. $= 2$, $p = 0.730$	
	Species x Treatment x Chamber	$\chi^2 = 0.91$, d.f. $= 2$, $p = 0.634$	

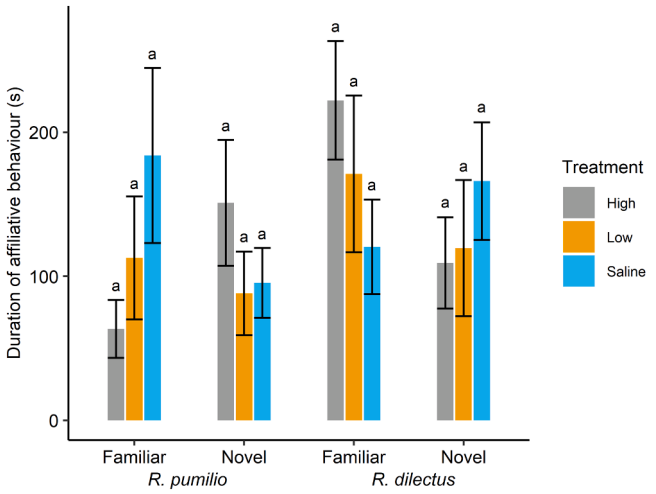

Fig. 4. Mean ± SE duration (s) of affiliative behaviors displayed by focal females toward novel and familiar stimulus females across AVP treatments, grouped by species in the social novelty test. Post hoc comparisons failed to detect statistical differences between groups, indicated by the same letter above each bar.

4. Discussion

We investigated whether peripherally administered AVP modulated social interactions and investigatory behaviours in two African striped mouse species. While social recognition is likely to be beneficial for both social and solitary species, social motivation and affinity for familiarity may differ between species with different social organisations (Lee and Beery, 2022). Based on prior studies, we know that group-living *R. pumilio* are more exploratory than *R. d. dilectus* (Rymer and Pillay, 2012; Mackay and Pillay, 2021). As such, we expected *R. pumilio* to show greater investigatory activity overall and hypothesised that AVP might differentially modulate social responses between the two species. In the sociability test, both species showed an increased frequency of approaches toward the stimulus mouse under AVP administration, but neither species exhibited a clear chamber preference. Similarly, in the social novelty test, neither species showed a preference for either the familiar or novel mouse. These findings suggest that the increase in approaches may reflect AVP-induced changes in arousal, exploration or anxiety, rather than greater social motivation or social discrimination. We acknowledge that the social discrimination paradigm does not fully dissociate recognition from preference, because increased investigation of an unfamiliar conspecific may reflect either successful discrimination or an underlying novelty bias. Nonetheless, this paradigm remains a widely used tool to assess social recognition capabilities in rodents and provides a consistent framework for comparative analyses. The lack of strong chamber or novelty preference, despite increased approach behaviours, suggests that peripherally administered AVP modulates general responsiveness rather than social responses *per se*.

Species differences emerged in aggressive responses in the sociability test, and affiliative responses in the social novelty test, which is consistent with findings by Schatz et al. (2018), who suggested that AVP modulates the type of social behaviour shown rather than the tendency to approach other individuals. *R. pumilio* was more aggressive towards the stimulus mouse in the sociability test than *R. d. dilectus*. Previous studies have also shown that *R. pumilio* is more aggressive towards conspecifics than *R. d. dilectus* (Rimbach et al., 2022; Neves and Pillay, 2022b). These species differences may reflect interacting modulation of oxytocin (OT) and AVP. In female Wistar rats, aggression is enhanced by increased OT release in the ventral lateral septum in conjunction with reduced AVP release in the dorsal lateral septum (Oliveira et al., 2021). While variation in AVP receptor density in striped mice species is currently unknown, OT receptor density is higher in both lobes of the lateral septum, as well as in the anterior BNST, of female *R. pumilio* than in female *R. d. dilectus* (Olazabal et al., 2023). The BNST has been linked to the onset of aggression in other species (reviewed in Riegler et al., 2022) and, due to the structural similarity between OT and AVP, both of these neuropeptides can bind to each other's receptors (Riegler et al., 2022). However, because peripheral AVP is unlikely to cross the blood–brain barrier (Wacker and Ludwig, 2019), the behavioural differences observed may reflect indirect modulation of central pathways or peripheral receptor activity rather than direct action within the SBN. A higher density of OT receptors in aggression-related brain areas, such as the BNST, may underlie the elevated aggression observed in *R. pumilio*, and the combined modulation of OT and AVP may help explain species-specific behavioural responses.

Social tolerance is frequently seen in animals with less stable grouping, in which groups may be prone to dissolution and reformation (reviewed in Lee and Beery, 2019). For example, degus showed social tolerance of conspecifics irrespective of familiarity (Insel et al., 2020), and meadow voles (*M. pennsylvanicus*) formed over-wintering groups and were more tolerant of conspecifics irrespective of familiarity during this period than at other times (Madison and McShea, 1987). *R. d. dilectus* is generally solitary, but under high AVP, females showed increased affiliative behaviour towards a familiar stimulus mouse, although these effects should be interpreted cautiously, given the lack of consistent significance in *post hoc* comparisons. This suggests that, during winter months when water is limited and AVP might be highest, free-living *R. d. dilectus* might respond similarly to meadow voles.

Although we interpret the observed differences in affiliation as treatment-related changes in social preference, we acknowledge that the social discrimination paradigm cannot fully disentangle social preference from social recognition. This limitation has been highlighted previously (e.g., Ferguson et al., 2002), and without complementary tests such as habituation–dishabituation trials, we cannot exclude the possibility that the effects reflect impairments in social recognition rather than preference alone. However, the consistent direction of the effect across groups, and the absence of generalised reduction in sociability, support our interpretation that AVP primarily modulated social motivation rather than recognition capacity

Rhabdomys pumilio is facultatively group-living, and although groups may disband when population densities are low (Schradin et al., 2010; Schoepf and Schradin, 2012), solitary living during the non-breeding season is uncommon (Schoepf and Schradin, 2014). The non-breeding season coincides with drier conditions, during which peripheral AVP levels are elevated (Schoepf and Schradin, 2014). Given the dual role of AVP in water regulation and social behaviour, we might expect that high circulating AVP during dry periods promotes social tolerance and group cohesion, particularly because females are more likely to occur in groups during this season (Schoepf and Schradin, 2014). However, *R. pumilio* displayed reduced affiliative behaviour toward the familiar stimulus mouse under high peripheral AVP in the social novelty test. This decrease in prosocial interaction was not associated with increased aggression, suggesting that AVP may modulate social engagement by dampening affiliative motivation rather than promoting antagonism. Taken together with the low overall sociability observed under AVP, these findings may reflect a form of selective social engagement, whereby individuals show reduced responsiveness to conspecifics they recognise but do not share social bonds with. This pattern may serve to maintain group integrity by narrowing social focus to established affiliative partners, particularly under conditions that simulate stress or heightened arousal.

Animals living in arid environments face limitations in water availability and have adapted to restrict water loss, such as by increasing water reabsorption from the kidneys (e.g., degu; Bozinovic et al., 2003), by producing hyperosmotic urine (e.g., bush karoo rat (*Otomys unisulcatus*); Jackson et al., 2004), and by limiting the amount of urine produced (e.g., spinifex hopping mouse (*Notomys alexis*); MacMillen and

Lee, 1969). *R. pumilio* lives in a semi-desert environment where water availability is limited. It feeds on water-rich plants (Schradin and Pillay, 2005b) and produces hyperosmotic urine (Buffenstein, 1984; Neves and Pillay, 2025) to overcome water restriction. Schoepf and Schradin (2014) hypothesized that the primary role of AVP in *R. pumilio* likely lies in its role as an osmoregulatory hormone, with baseline levels being environmentally determined based on water availability, not social organisation. It is possible, however, that water availability in the dry season (Schoepf and Schradin, 2014) could have a secondary effect on social behaviour, independently of AVP expression. Competition for water-rich plants in the dry season could explain a reduction in affiliative behaviour. *R. pumilio* is a solitary forager and competes for access to the same resources as round-eared sengis (*Macroscelides proboscideus*), bush karoo rats and whistling rats (*Parotomys brantsii*; Schradin and Pillay, 2004). While species within the genus *Rhabdomys* occur along a distinct aridity gradient, how they may differ in osmoregulatory capacity is unknown. No studies have been conducted on the variation of baseline peripheral AVP levels in *R. d. dilectus*, which occurs in less water-restricted environments, and so this presents an interesting avenue for future study.

Our findings demonstrate that peripheral AVP administration modulates behaviour in both *Rhabdomys* species, but the effects differ in direction and form. High doses of AVP increased approaches in both species, but affiliative behaviour increased only in *R. d. dilectus*, while aggression was higher in *R. pumilio* than *R. d. dilectus*. These patterns suggest that peripheral AVP modulates arousal or general social responsiveness, rather than specifically enhancing social motivation. Importantly, we do not interpret these effects as evidence of central modulation via the SBN, given that peripheral AVP does not cross the blood–brain barrier (Wacker and Ludwig, 2019). Instead, these behavioural changes may arise from indirect systemic mechanisms, such as altered autonomic or hormonal states, which influence how animals respond to social stimuli. Our study serves as an initial assessment of the significance of AVP in the modulation of social behaviour in species of the African striped mouse. Future studies using central administration, receptor antagonists or combined OT–AVP approaches, could clarify the pathways involved. These results reinforce the importance of comparative studies when examining peripheral neuropeptide effects and highlight how species differences in social structure may shape behavioural sensitivity to systemic neuroendocrine modulators.

CRediT authorship contribution statement

Candice Nikita Neves: Writing – original draft, Visualization, Formal analysis. **Tasmin Lee Rymer:** Writing – review & editing. **Neville Pillay:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Kirsty-Jane Hartman:** Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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Data availability

The data that support this study can be found on 'Figshare' at https://doi.org/10.6084/m9.figshare.29037386.

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