RESEARCH ARTICLE

ethology *International journal of behavioural biology* WILEY

Characterization of social behavior in the spiny mouse, *Acomys cahirinus*

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Abstract

While there are many species that are commonly used for the study of mammalian social behavior, there remains a need for lab-suitable organisms that are appropriate for examining sociality specifically in non-reproductive contexts (i.e., social behavior not in the context of mating or parenting). The spiny mouse, *Acomys cahirinus*, is a cooperatively breeding rodent that lives in large groups and is a species that holds great potential for studying a wide range of social behaviors in reproductive *and* non-reproductive contexts. Here, we characterize the basic social behaviors in male and female *A. cahirinus* to obtain a foundation for future study. We tested adult *A. cahirinus* in social approach, social preference, social interaction, social recognition, and group size preference paradigms. Regardless of sex, novelty, or familiarity, we found that both males and females rapidly approach conspecifics demonstrating high social boldness. Additionally, both sexes are significantly more prosocial than aggressive when freely interacting with conspecifics. However, we observed effects of sex on social preferences, such that males exhibit a preference to affiliate with same-sex conspecifics, whereas females exhibit a preference for affiliating with opposite-sex conspecifics. We discuss how this preference may relate to the cooperative breeding system of spiny mice. Lastly, both sexes show a robust preference for affiliating with large over small groups, indicating they may be an ideal species for the study of mammalian gregariousness. These data lay a basic foundation for future studies that seek to assess complex group dynamics and the mechanisms underlying reproductive and non-reproductive social behaviors in a highly social mammal.

KEYWORDS
affiliation, behavior, gregariousness, non-reproductive sociality, prosocial

1 | INTRODUCTION

Examining the evolution of social behavior using a comparative approach across species provides valuable insight into important selection pressures as well as mechanistic commonalities and differences underlying behavior across organisms. However, to utilize comparative strategies, it is necessary to have several species in multiple mammalian families available that exhibit a particular behavioral phenotype of interest. Obtaining a variety of species can be a challenge when searching for species amenable to experimental manipulation in a laboratory setting, especially when the behavioral phenotype of interest is mammalian grouping behavior. Importantly, social behavior is a broad term that encompasses many distinct types of behavior that may not have evolved in a linked manner (Goodson, 2013). For example, a species that is excellent for studying the behavior between bonded mates may not be the

ideal species for studying large group behavior. In order to understand the factors that influence mechanisms underlying grouping behavior, it is crucial to use an organism for which their natural history reflects large, social group living. Studies have identified several species of birds, fishes, and insects that are highly social and suitable for studying grouping behavior (Bazazi et al., 2008; Brandl & Bellwood, 2015; Breed et al., 1990; Kasper et al., 2017; Keller, 1998; Remeš et al., 2015; van Dijk et al., 2014; Voelkl et al., 2015). However, many mammals that live in large groups, such as primates, herding ungulates, and mongooses (i.e., meerkats) simply are not suitable for maintaining large colonies in laboratory settings. Arguably, mammals most tractable for laboratory experiments are in the Order Rodentia. Frequently used rodents for studying grouping behaviors include African striped mice (*Rhabdomys pumilio*), Ansell's mole-rats (*Fukomys anselli*), naked mole-rats (*Heterocephalus glaber*), seasonally grouping female meadow voles (*Microtus pennsylvanicus*), Norway rats, and degus (*Octodon degus*; Bappert et al., 2012; Braude et al., 2021; Ebensperger et al., 2021; Insel et al., 2020; Lee et al., 2019; Quirici et al., 2011; Schoepf & Schradin, 2012; Schradin & Pillay, 2004; Schweinfurth, 2020). In the present study, we sought to expand the number of highly social rodents available for laboratory and field study by characterizing the basic social behaviors of the spiny mouse, *Acomys cahirinus*.

Spiny mice are native to Africa, the Middle East, and southern Asia where they preferentially live in rocky outcroppings (Deacon, 2009; Frynta et al., 2011; Nowak, 1999). Spiny mice were historically used for studying obesity due to their propensity to overeat and develop Type II diabetes (Gonet et al., 1966; Shafrir, 2000). However, more recently, they have emerged as a powerful model for studying complex tissue regeneration (Gawriluk et al., 2016; Seifert et al., 2012), and as a model for human-like reproductive biology given that at least one species of spiny mouse exhibits a menstrual cycle in captivity (Bellofiore et al., 2017, 2018). In captivity, spiny mice exhibit cooperative breeding and are stable in large groups (~30 individuals per group), traits that suggest these rodents hold great potential for lab-based social behavior studies (Haughton et al., 2016). Indeed, studies during the 1980s explored some of the social components of their cooperative breeding tactics and kin recognition abilities. Porter and colleagues identified that spiny mouse mothers would nurse unfamiliar neonates as frequently as their own pups, suggesting a high degree of sociality regardless of genetic relation (Porter et al., 1980). This study also proposed the hypothesis that a primary strategy for kin recognition in spiny mice may be phenotype matching based on odors identified during nursing (Porter, 1988; Porter et al., 1983). Recently, there has been a resurgence in spiny mouse behavioral research, and studies have explored both their cooperative breeding strategy (Tučková et al., 2016) and their behavior in standard non-social laboratory paradigms such as the elevated plus-maze and open field test (Ratnayake et al., 2014). In order to build upon this growing literature, and to lay a basic foundation for studying highly social behaviors, here we examine *A. cahirinus* behavior in a variety of ethologically relevant social behavioral paradigms.

The genus *Acomys* collectively refers to many species of "spiny mice." However, the most commonly used *Acomys* species for laboratory studies is *A. cahirinus* (Bellofiore et al., 2018; Haughton et al., 2016; Ratnayake et al., 2014; Tučková et al., 2016), of which we have an established breeding colony in our lab and describe the behavior of it in this paper. To characterize the adult social behaviors and preferences, we ran male and female *A. cahirinus* through tests in both reproductive (i.e., potential for the motivation to mate) and non-reproductive contexts. Animals underwent variations of social approach, social interaction, social recognition, social preference, and group-size preference tests. Both sexes rapidly approached all stimulus conspecifics and displayed high levels of prosocial behavior, as well as robust gregariousness (i.e., a preference to affiliate with large groups). However, we observed the effects of sex on behavioral preferences when animals were given a choice between investigating and affiliating with either a same-sex or opposite-sex conspecific. The findings presented here are suitable for behavioral comparison with other rodents typically used for social behavior studies, and highlight the gregarious nature of *A. cahirinus*, suggesting they are an excellent species for examining mammalian grouping behavior.

2 | MATERIALS AND METHODS

2.1 | Animals

Fifteen adult female *A. cahirinus* (post-natal day (PND) 60–200) were used for all behavioral tests in this experiment. Sixteen adult male *A. cahirinus* (PND 60–200) were used for the social approach, social preference, and social recognition tests, and 15 additional adult males (PND 60–200) were used for the group size preference and social interaction tests. All animals were obtained from our breeding colony and breeders were obtained from the captive-bred colony of Dr. Ashley W. Seifert (University of Kentucky), which has been maintained for 10 years. All animals were group-housed (2–5) in either standard rat polycarbonate cages (40.64 × 20.32 × 20.32 cm) or larger two-level polycarbonate cages (32 × 38 × 40 cm) lined with Sani-Chips bedding and were provided with nesting material, rodent igloos, and shepherd shacks. Animals were able to obtain food and water ad libitum and were kept on a 14-h light: 10-h dark cycle. An ambient temperature was maintained at 24 ± 2°C. All procedures were approved by the Institutional Animal Care and Use Committee of Emory University (PROTO201900126).

2.2 | Experimental design

To obtain a profile of basic *A. cahirinus* social behavior, we ran males and females (PND 60–200) through variations of five common social behavior tests: social approach, social interaction, social preference, social recognition, and group size preference. All behavioral tests were video recorded using Sony Handycam HDR-CX405

1080p Camcorders (Sony) for subsequent scoring using Behavioral Observation Research Interactive Software (BORIS; Friard & Gamba, 2016). Most tests lasted no more than 10 min because similar to many rodents in lab studies, spiny mice exhibit a burst of behavior at the beginning of the test. In the absence of the ability to freely interact with conspecifics, behavior tapers off after about 10 min and animals choose to sleep or rest. The order of tests for all subjects was randomized. The results were analyzed to identify both species-wide patterns in social behavior as well as potential sex effects.

2.3 | Social approach test

To assess general social attraction/aversion, subjects underwent three social approach tests with three different types of stimuli: familiar same-sex, novel same-sex, and novel opposite-sex individuals. Subjects were placed in a large Plexiglas testing chamber (81.28 × 40.64 × 38.1 cm) and allowed to acclimate for 3 min. After acclimation, subjects were contained under a plastic beaker on one end of the chamber, while a stimulus animal was placed under a wire mesh container on the opposite side of the chamber. The subjects were then released and the latency to approach the stimulus animal, time spent within the one-body length of the stimulus animal, and time spent investigating the stimulus animal (defined as nose inserted into or rearing up on the stimulus tube) were recorded during a 5-min test (Table 1).

2.4 | Social interaction test

In order to quantify behavior during freely behaving social interactions, subjects were run in two tests where they were allowed to freely interact with a novel opposite-sex stimulus animal in one test and a novel same-sex stimulus animal in the other test. The order subjects were exposed to the types of stimulus animals and were randomized. In a testing chamber (40.64 × 20.32 × 20.32 cm), subjects were allowed to acclimate for 3 min. After acclimation, the stimulus animal was released into the chamber, and the interactions were recorded for 8 min. Behaviors scored (Table 2) included the subject's overt prosocial behavior (positive investigation, allogrooming, huddling, and positive side-by-side contact), overt aggressive behavior (biting, chasing, pinning, lunging/attacking, rearing, and aggressive

side-by-side contact), and non-interactive social behaviors (all other behaviors not considered overtly prosocial or aggressive, including grooming, jumping, sitting alone, and nonsocial exploration).

2.5 | Social preference test

To examine social preferences, subjects were run in two social choice tests: novel versus familiar and same-sex versus opposite-sex. In a large testing chamber (81.28 × 40.64 × 38.1 cm), subjects were acclimated for 3 min. After acclimation, subjects were contained in the middle of the chamber while the 2 stimuli (a novel, same-sex conspecific and a familiar, same-sex cagemate or a novel, same-sex conspecific and a novel, opposite-sex conspecific) were placed under-wire mesh containers at opposite ends of the chamber. Upon release, the percentage of the total time spent within one body length of the stimuli, time spent investigating the stimuli (defined as nose inserted into or rearing up on the stimulus tube), and jumping was recorded during a 5 min test (Table 3).

2.6 | Social recognition test

In order to examine the ability to discriminate between different conspecifics, subjects were run in a standard habituation-dishabituation paradigm. After a 3 min acclimation period in a large testing chamber (81.28 × 40.64 × 38.1 cm), subjects were contained under a plastic beaker to one end of the chamber. During the first novel, the same-sex stimulus animal was placed under a wire mesh container on the opposite side. The subject was then released and the latency to approach the stimulus, time spent within one body length of the stimulus, and time spent investigating the stimulus (defined as nose inserted into or rearing up on the stimulus tube) were recorded for 5 min (Table 4). This 5-min trial was repeated four times at 15-min intervals with the same stimulus animal. On the fifth and final trial, a new novel, same-sex stimulus was presented with the same measures for 5 min. The first, fourth, and fifth trials were compared. Discrimination between the "old" and "new" stimulus animals is determined by the observation of decreased time engaging in social investigation from Trial 1 to Trial 4, and a reinvigoration of investigative behavior in Trial 5 when the new animal is presented (Choleris et al., 2003).

TABLE 1 Social approach ethogram

Behavior	Description
Approach latency	Latency for subject to approach the stimulus animal. Active from the moment the subject is released from the beaker to the point when the subject reaches the stimulus animal
Social investigation	Time subject spends poking nose through or rearing up on the stimulus animal's container. Time when the subject is on the top of stimulus container is not included
Jumping	Time subject spends jumping

TABLE 2 Social interaction ethogram

	Behavior	Description
Prosocial	Positive investigation	Subject sniffing or positively investigating the stimulus animal
	Allogrooming	Subject grooms the stimulus animal
	Huddling	Subject and stimulus are either touching flanks or criss-crossed on top of each other
	Positive side-by-side contact	Subject showing positive, prosocial contact side-by-side with the stimulus that is not specifically huddling
Aggressive	Biting	Subject biting at the stimulus animal, mouth making contact with the stimulus animal's body
	Chasing	Subject aggressively chasing the stimulus animal. Initiator is chaser for entire event
	Pinning	Pinning the stimulus down
	Rearing	Subject rearing up on hind paws for either offense or defense
	Aggressive side-by-side contact	Subject and stimulus are touching flanks but in an aggressive manner. May be between aggression bouts
Non-interactive	All behavior instances not included in prosocial or aggressive	Subject is not making contact with or exhibiting behavior direct toward stimulus animal

TABLE 3 Social preference ethogram

Behavior	Description
Social investigation	Time subject spends poking nose through or rearing up on the stimulus animal's container. Time when the subject is on the top of the stimulus container is not included
In zone	Time subject spends within one body length (approximately 1/3 of the chamber) from the stimulus container
Jumping	Time subject spends on jumping

TABLE 4 Social recognition ethogram

Behavior	Description
Social approach (Trials 1–5)	Latency for subject to approach the stimulus animal. Includes moment the subject is released from the beaker to the point when the subject reaches the stimulus animal. Trial 5 is a new stimulus animal
Social investigation (Trials 1–5)	Time subject spends poking nose through or rearing up on the stimulus animal's container. Time when the subject is on the top of the stimulus container is not included. Trial 5 is new stimulus animal
Jumping (Trials 1–5)	Time subject spends on jumping

2.7 | Group size preference test

Subjects underwent a group size preference test where they were given the choice to affiliate with either a small (2) or large (8) group of novel, same-sex conspecifics. In a large testing chamber (60.96 × 45.72 × 38.1 cm), stimulus groups were placed on the opposite sides of the chamber under individual wire mesh containers and were allowed to acclimate for 3 min. After acclimation, the subjects were placed under a plastic beaker in the middle of the chamber between the large and small groups and were then released. Upon release, the time spent within one body length of the stimulus groups and time spent investigating the stimulus groups (defined as nose inserted into or rearing up on one of the stimulus tubes) were recorded during an 8-min test (Table 5). This test is used to determine the degree of gregariousness (a preference to affiliate with large groups) that a species or individual exhibits (Kelly & Goodson, 2013, 2014).

2.8 | Statistical analysis

Behavioral measurements for each test were analyzed using SPSS 26 (IBM Analytics). The use of parametric or non-parametric tests was based on the distribution of the data. In behavioral tests in which no sex effects were identified for any of the variables quantified, the data were combined to include males and females in the analysis in order to increase the statistical power. Outliers for the individual

TABLE 5 Group size preference ethogram

Behavior	Description
Social investigation	Time subject spends poking nose through or rearing up on the stimulus animal/group's container. Time when the subject is on the top of the stimulus container is not included
In zone	Time subject spends on the stimulus animal/group's side (approximately 1/3 of the chamber)
Jumping	Time subject spends on jumping

behavioral tests that were three standard deviations outside the mean were removed from analyses. Effect sizes for normally distributed data were calculated and reported as Cohen's *d*, whereas effect sizes for nonparametric analyses were reported as *r* where $r = \frac{Z}{\sqrt{n}}$.

3 | RESULTS

Here, we aimed to characterize the basic social behaviors of *A. cahirinus* to lay a foundation for future social behavior and social neuroscience studies. For this characterization, we ran males and females through five common social paradigms: a social approach test, a social interaction test, a social preference test, a social recognition test, and a group-size preference test. Behavioral analyses were used to identify both species-wide and sex-specific trends in social behavior. For behavioral tests, examining differences in subjects' behavior with stimulus animals that were same-sex or opposite-sex, we did not combine male and female data for analyses because the sex of the stimulus animal is confounded with the sex of the focal animal. However, for all other behavioral tests, where no sex effects were identified, male and female data were combined for analyses.

3.1 | Social approach test

In order for an animal to engage in social interaction, they must first exhibit approach behavior. Aversion or attraction to conspecifics can be influenced by factors such as novelty, familiarity, and/or the sex of the conspecific. To determine whether *A. cahirinus* exhibit differences in the readiness to approach and investigate different types of individuals, subjects were exposed to novel opposite-sex, novel same-sex, and familiar same-sex conspecifics during social approach tests. Friedman's analysis suggested neither males ($\chi^2(2) = 2$, $p = .37$) nor females ($\chi^2(2) = 1.08$, $p = .58$) displayed a difference in approach latency based on stimulus type, and rather subjects rapidly approached all conspecifics (see Figure S1). Similarly, there was no difference in time spent investigating novel opposite-sex, novel same-sex, or familiar same-sex conspecifics in males ($\chi^2(2) = 3.35$, $p = .15$) or females ($\chi^2(2) = 1.73$, $p = .42$; Figure 1). We did identify an effect of sex, however, such that female *A. cahirinus* spent significantly more time than males investigating a novel, opposite-sex conspecific (Mann Whitney *U* (n1 = 16, n2 = 15) = 66, $Z = -2.14$, $p = .03$; $r = .38$; Figure 1). Thus, whereas males and females readily approached and investigated all types of stimulus animals tested here, females spend more time investigating the opposite-sex individuals.
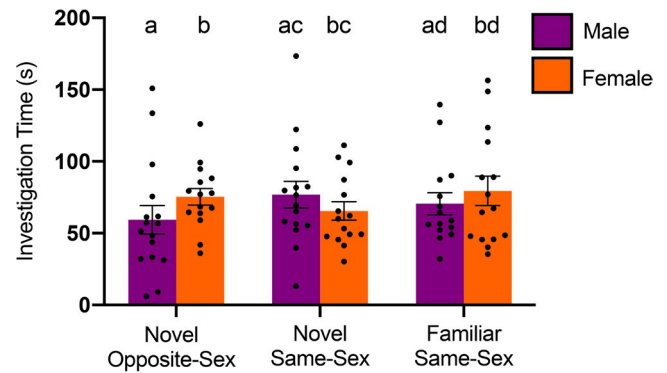

FIGURE 1 *Acomys cahirinus* exhibit an effect of sex on the investigation of conspecifics during social approaches. Mean (±SEM) time in seconds both male (magenta) and female (orange) *A. cahirinus* spent investigating novel opposite-sex, novel same-sex, and familiar same-sex conspecifics. Male and female *A. cahirinus* investigated all conspecific equally, but females investigated novel opposite-sex conspecifics longer than males. Dots represent individual data. Letters (a–d) denote significant post hoc comparisons ($p \leq .05$), with shared letters indicating statistical similarity between groups; bars that do not share a letter were significantly different

3.2 | Social interaction test

Approach behavior may not necessarily be indicative of the valence of how an animal will interact with a conspecific. Thus, we also conducted social interaction tests where subjects freely interacted with novel, same-sex and novel, and opposite-sex conspecifics in order to determine the composition of time *A. cahirinus* spend engaging in overtly prosocial, overtly aggressive, and non-interactive behaviors. We scored the interactions for overt prosocial (positive investigation, allogrooming, huddling, and positive side-by-side contact), overt aggressive (biting, chasing, pinning, lunging/attacking, rearing, and aggressive side-by-side contact), and non-interactive behaviors (self-grooming, solitary sitting, jumping, cage exploration) and compared the total time spent engaging in each of these types of behavior. Overall, both males and females spent significantly more time engaged in non-interactive behaviors than prosocial (all $p < .01$) and aggressive (all $p < .01$) behaviors when interacting with either a novel, same-sex or novel, and opposite-sex animal (Table 6; Figure 2a). However, between the interactive behaviors, *A. cahirinus* were more prosocial than aggressive (all $p < .01$) (Table 6; Figure 2a). Notably, very little aggressive behavior was observed for all subjects in either stimulus condition. These results suggest that *A. cahirinus* are, generally, highly prosocial.

TABLE 6 Breakdown of behavior during the social interaction tests

Sex	Conspecific	Comparison	Test	χ^2/Z	p	r
Male	Same-sex	Overall	Friedman's test	25.20	<.01*	
		Prosocial* vs aggression	Wilcoxon	−3.41	<.01*	.62
		Prosocial vs non-interactive*	Wilcoxon	−2.61	<.01*	.67
		Aggression vs non-interactive*	Wilcoxon	−3.308	<.01*	.88
	Opposite-sex	Overall	Friedman's test	25.20	<.01*	
		Prosocial* vs aggression	Wilcoxon	−3.41	<.01*	.62
		Prosocial vs non-interactive*	Wilcoxon	−3.00	<.01*	.76
		Aggression vs non-interactive*	Wilcoxon	−3.41	<.01*	.88
Female	Same-sex	Overall	Friedman's test	28.13	<.01*	
		Prosocial* vs aggression	Wilcoxon	−3.25	<.01*	.59
		Prosocial vs non-interactive*	Wilcoxon	−3.41	<.01*	.88
		Aggression vs non-interactive*	Wilcoxon	−3.41	<.01*	.88
	Opposite-sex	Overall	Friedman's test	28.13	<.01*	
		Prosocial* vs aggression	Wilcoxon	−3.41	<.01*	.88
		Prosocial vs non-interactive*	Wilcoxon	−3.35	<.01*	.87
		Aggression vs non-interactive*	Wilcoxon	−3.41	<.01*	.88

Note: Under the column Comparison * greater time. Under the Column *p* * indicates statistical significance.
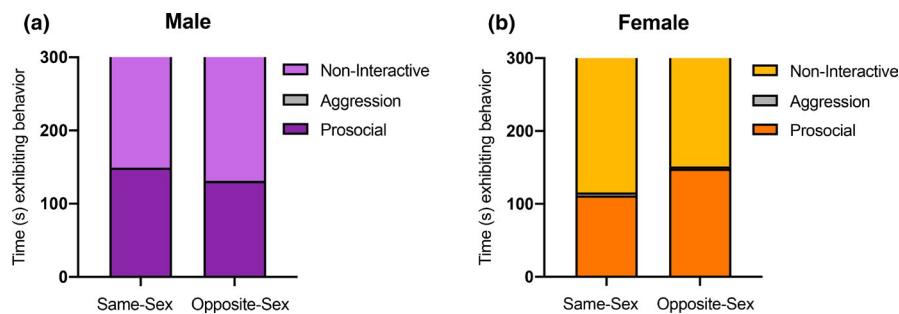

FIGURE 2 *Acomys cahirinus* engage in high levels of non-interactive and prosocial behavior in social interactions. Breakdown of time male (a) and female (b) *A. cahirinus* spent engaging in non-interactive (light purple; yellow), prosocial (dark purple; orange), and aggressive (gray) behavior during a 5-min social interaction test with same- and opposite-sex, novel conspecifics. Both male and female *A. cahirinus* spent significantly more time exhibiting non-interactive behavior than prosocial and aggressive behaviors and more time engaged in prosocial behavior than aggressive behavior. Females spent more time interacting prosocially with novel opposite-sex conspecifics than same-sex conspecifics

Next, within each sex, we examined whether *A. cahirinus* exhibit differences in behavior when interacting with a novel, same-sex conspecific and a novel, and opposite-sex individual. A general linear model analysis indicated a significant difference in the time males and females spent engaged in prosocial and non-interactive behaviors with same versus opposite-sex conspecifics (all $p < .01$; Table 7), but not for aggression ($F = 0.89$, $p = .36$; Table 7). *Wilcoxon* signed ranks for males revealed no difference in prosocial, aggressive, or non-interactive behavior between interactions with a same- and opposite-sex conspecific (all $p > .36$; Table 7). Similarly, we observed no difference in aggressive behavior with the same- versus opposite-sex stimuli for females (all $p = .06$; Table 7). However, we did find that females spent more time exhibiting prosocial behavior toward opposite-sex stimulus animals than they did toward same-sex stimuli ($Z = −2.67$, $p = .01$; $r = .69$; Figure 2b), as well as more time engaged in non-interactive behaviors when with

a same-sex individual than an opposite-sex stimulus ($Z = 2.67$, $p = .01$, $r = −.69$). Together, these findings suggest that although both males and females are highly prosocial, female *A. cahirinus* exhibit different degrees of prosociality and non-interactive behavior, which may be primarily dependent on the sex of the conspecific.

3.3 | Social preference test

To determine if *A. cahirinus* exhibit a preference to affiliate with specific types of conspecifics, we performed two social preference choice tests: novel versus familiar and same-sex versus opposite-sex. For the novel versus familiar choice test, a combined analysis for males and females yielded no significant difference in the time spent investigating each stimulus ($Z = −0.26$, $p = .80$) or the percentage

TABLE 7 Differences in time engaged in behavior based on stimulus sex during the social interaction tests

Behavior	Comparison	Test	F/Z	p	r
Prosocial	Overall	GLM	4.63	.04*	
	Male same vs opposite-sex	Wilcoxon	−1.02	.31	
	Female same vs opposite-sex*	Wilcoxon	−2.70	<.01*	.69
Aggression	Overall	GLM	0.89	.36	
Non-interactive	Overall	GLM	4.48	.04*	
	Male same vs opposite-sex	Wilcoxon	−0.97	.33	
	Female same* vs opposite-sex	Wilcoxon	−2.67	<.01*	.69

Note: Under the column Comparison * indicates greater time. Under the column *p* * indicates statistical significance.

of total time spent in a stimulus zone ($Z = −0.32$, $p = .75$), suggesting that *A. cahirinus* do not exhibit a preference for investigating or affiliating with novel or familiar conspecifics during a 5-min test (Figure 3a).

For the novel, same-sex versus novel, opposite-sex choice test, a paired t-test revealed that males spent significantly more time investigating a same-sex conspecific than an opposite-sex individual ($t(14) = 2.3$, $p = .04$; $d = 0.92$; Figure 3b). Similarly, a Wilcoxon-signed ranks test showed that males also spent a larger percentage of total contact time in the stimulus zone of the same-sex conspecific ($Z = −2.10$, $p = .04$; $r = .38$; Figure 3b). Females, on the contrary, displayed the opposite preference and spent more time investigating the opposite-sex stimulus animal ($Z = −2.22$, $p = .03$; $r = .40$; Figure 3c). However, females did not exhibit a significant difference in the percentage of total contact time spent in the zones of either stimulus ($Z = −1.59$, $p > .05$; Figure 3c). Despite the lack of preference for female time spent affiliating with the same- or opposite-sex individuals, the female investigation preference observed in this choice test mirrors the results presented above, such that females spend more time investigating novel opposite-sex individuals in a social approach test, and females spend more time engaging in prosocial behavior with opposite-sex conspecifics than with same-sex ones in a social interaction test. Together, these results suggest that, while *A. cahirinus* do not display a preference for social novelty or familiarity, males prefer investigating and affiliating with same-sex individuals, whereas females exhibit a preference for investigating opposite-sex conspecifics.

3.4 | Social recognition test

Most animals are presumably capable of discriminating between different individuals. However, *A. cahirinus* indiscriminately provides parental care (including female nursing) to pups regardless of genetic relation (Tučková et al., 2016). *A. cahirinus* may not need to identify specific individuals due to their large groups and generalized parental behavior. In order to validate the efficacy of a standard social recognition paradigm and confirm social discrimination abilities in *A. cahirinus*, subjects were run in a habituation-dishabituation test. Briefly, this test consisted of five trials of same-sex social exposure, with the same stimulus animal used in Trials 1–4, and a new stimulus was used in Trial 5. We compared the difference in time spent

investigating the stimulus animal across Trials 1, 2, and 5. We observed no statistically significant differences between males and females, and so proceeded with combining male and female data. Friedman's analysis revealed a difference in investigation time across the three trials ($\chi^2(2) = 22.50$, $p < .001$). Post hoc analyses indicated that the subjects spent more time investigating the stimulus animal in Trial 1 than in Trial 4 ($Z = −2.17$, $p = .03$; $r = .28$), suggesting a decrease in interest due to repeated exposure to the same stimulus animal. However, subjects spent more time investigating the novel stimulus animal in Trial 5 compared to Trial 4 ($Z = −4.21$, $p < .001$; $r = .54$; Figure 4), suggesting a renewed interest in the social investigation due to the exposure of a new stimulus animal. These findings reflect the expected results of a habituation-dishabituation test, demonstrating that an animal exhibits social discrimination. However, subjects also spent more time investigating the stimulus animal in Trial 5 compared to Trial 1 ($Z = −3.38$, $p = .001$; $r = .58$; Figure 4). Typically, results for this test in other species do not report a difference in investigation time between the first trial exposure of the initial stimulus animal and the first (and only) trial exposure of the new stimulus animal. The increase in the investigation of the second stimulus animal in *A. cahirinus* may be a byproduct of their highly prosocial nature in both reproductive and non-reproductive contexts (see Section 4). Regardless, *A. cahirinus* do indeed recognize different conspecifics and largely exhibit the expected behavior of an animal tested in a habituation-dishabituation paradigm.

3.5 | Group size preference test

Lastly, because *A. cahirinus* live in large groups, they may exhibit higher degrees of gregariousness (a preference to affiliate with large groups). To both confirm this possibility as well as identify whether rodent group size preferences can be accurately captured in the lab, *A. cahirinus* were tested in a group size choice test to determine whether they prefer affiliating with smaller (2) or larger (8) groups (see (Kelly et al., 2011) for group size choice tests in birds). We found no statistically significant differences in males and females, and thus we combined these data. Wilcoxon-signed ranks tests revealed that animals spent more time investigating the large group than the small group ($Z = −4.78$, $p < .001$; $r = .62$; Figure 5a) and also spent a significantly larger percentage of total contact time in the stimulus zone
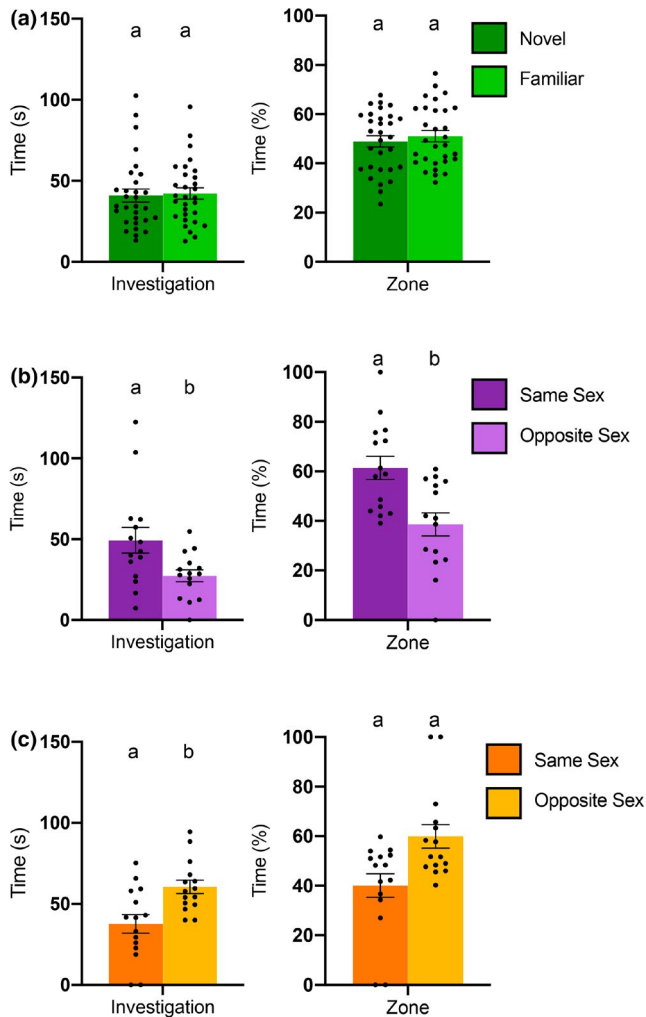
(a)
(b)
(c)

Novel / Familiar

Same Sex / Opposite Sex

Same Sex / Opposite Sex

FIGURE 3 *Acomys cahirinus* exhibit social preferences based on sex. (a) Combined male and female *A. cahirinus* mean (±SEM) time in seconds for investigation (left) and percentage of total time spent in a stimulus zone (right) during the novel (dark green) vs familiar (light green) conspecific social preference test. Animals did not display a significant preference for a novel or familiar conspecifics. (b) Male mean (±SEM) time in seconds for investigation (left) and percentage of total time spent in a stimulus zone (right) during the same- (dark purple) versus opposite-sex (light purple) conspecific social preference test. Males spent significantly more in the zone of and investigating same-sex than opposite-sex conspecifics. (c) Female mean (±SEM) time in seconds for investigation (left) and percentage of total time spent in a stimulus zone (right) during the same- (orange) versus opposite-sex (yellow) conspecific social preference test. Females spent more time investigating, but not more time in the zone of, opposite-sex than same-sex conspecifics. Dots represent individual data. Letters (a, b) denote significant post hoc comparisons ($p \leq .05$), with shared letters indicating statistical similarity between groups; bars that do not share a letter were significantly different

of the large group ($Z = -4.78$, $p < .001$; $r = .62$; Figure 5b). These results reflect the gregariousness observed in the field studies and laboratory colonies of *A. cahirinus* and demonstrate that we can accurately measure group size preferences in spiny mice in a laboratory setting. Together, these findings demonstrate that the male and
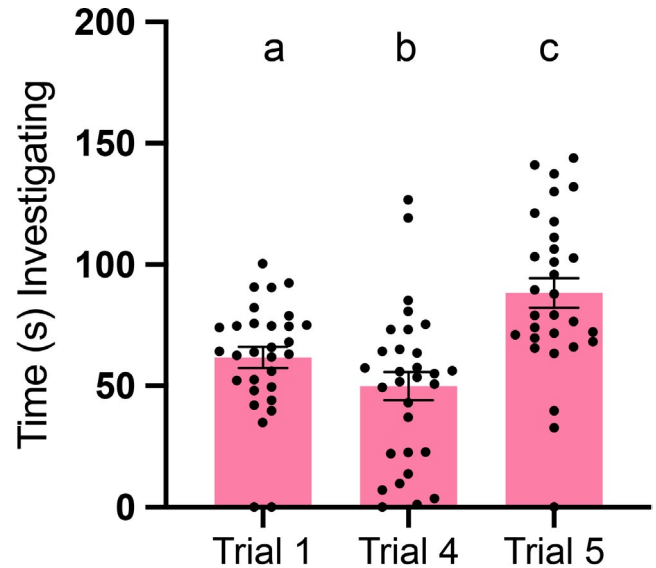

FIGURE 4 *Acomys cahirinus* display social discrimination in the social recognition test. Combined male and female *A. cahirinus* mean (±SEM) time in seconds for investigation of novel, same-sex conspecifics during the social recognition test. Animals show significantly decreased interest after repeated exposure to the same novel conspecific (Trial 1 vs Trial 4), but renewed interest upon exposure to a new, novel conspecific (Trial 4 vs Trial 5). Dots represent individual data. Different letters indicate $p \leq .05$

female *A. cahirinus* are not only highly prosocial but are also highly gregarious.

4 | DISCUSSION

In the present study, we characterized basic social behaviors of male and female *A. cahirinus* using five common social paradigms. Generally, we found that both sexes were highly prosocial in all paradigms. Here, we discuss how *A. cahirinus* behavior compares to other rodents commonly used in studies of social behavior and consider potential functions of behavioral sex effects.

4.1 | Characterization of *A. cahirinus* social behavior

All social interactions begin with an initial approach. Examination of social approach can be indicative of social characteristics of a species, including levels of boldness, sociability, and neophobia. Social approach tests are frequently used to determine levels of sociability in mouse models of autism (Yang et al., 2011). In the social approach tests in the present study, spiny mice of both sexes rapidly approached and investigated all stimulus animals at similar rates. Female *A. cahirinus*, however, spent significantly more time investigating novel, opposite-sex conspecifics, whereas males showed no difference in the investigation based on stimulus type. This sex effect underscores the importance of distinguishing affiliation time
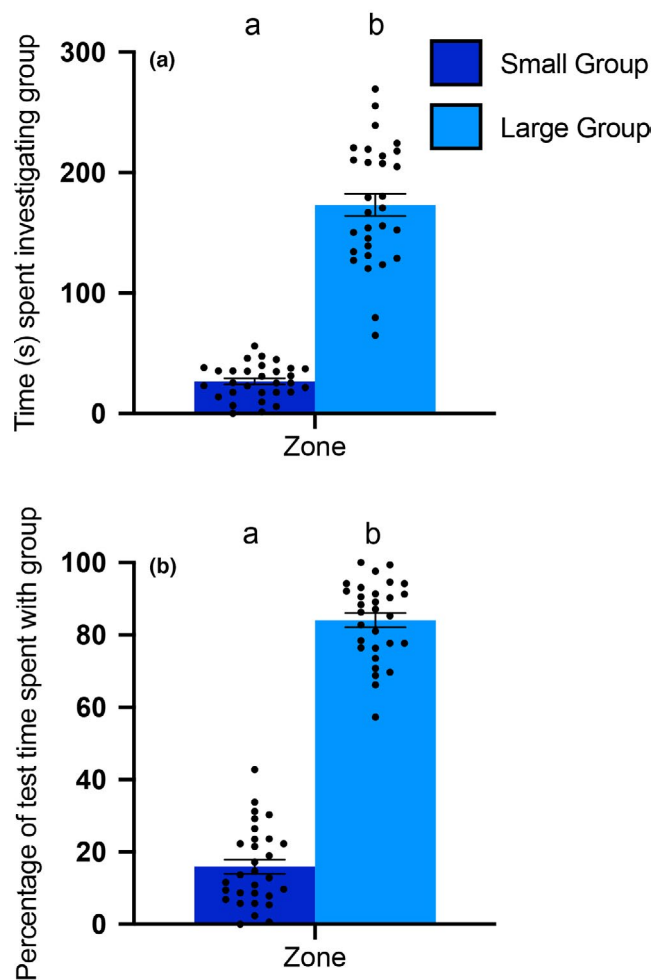
FIGURE 5 *Acomys cahirinus* prefer larger groups over smaller groups. Combined male and female *A. cahirinus* mean (±SEM) time in seconds for investigation (a) and percentage of total time spent in a stimulus zone (b) during a group size preference test. Animals spent significantly more in the zone of and investigating large groups (8; light blue) over small groups (2; dark blue). Dots represent individual data. Different letters indicate *p* ≤ .05

other rodents highlights this high level of sociability. While it can take some species, such as standardly reared prairie voles (*Microtus ochrogaster*), an average of 82 s (Kelly et al., 2020) and Mongolian gerbils (*Meriones unguiculates*), an average of 29 s (A. Kelly et al. unpubl. obs.) to approach a novel, same-sex conspecific, *A. cahirinus* approached novel, same-sex conspecifics, on average, in 7 s (note that the Mongolian gerbils and *A. cahirinus* had the same distance to travel in these studies, whereas the prairie voles had a shorter distance to travel to reach the stimulus animal). The swift social approach and high sociability of *A. cahirinus* may be particularly appealing for studies interested in using approach latency as an important metric of social boldness, social attraction, or social avoidance.

While social approach tests may capture initial social attraction or avoidance, a social interaction test in which animals are allowed to freely interact can provide a fine-grained evaluation of social responses to conspecifics. Such tests can also be used to identify the degree to which a species is prosocial and/or aggressive. In the social interaction tests used in the present study, we grouped behaviors into three major categories: prosocial, aggressive, and noninteractive (i.e., presumably nonsocial behaviors; Ahern et al., 2019; Kelly et al., 2018; McGuire & Novak, 1984). When comparing these three types of behavior, we found that male and female *A. cahirinus* spent significantly more time engaged in non-interactive behaviors regardless of the type of stimulus animal (i.e., novel, opposite-sex or novel, same-sex) with which they interacted. Notably, this abundance of non-interactive behavior may, at times, communicate important social information that we were unable to detect and/or interpret. For example, self-grooming, which was categorized under non-interactive behavior here, may be indicative of stress or anxiety, parasite loads, social signals, or body temperature regulation in rodents (Ferkin & Leonard, 2005; Kalueff & Tuohimaa, 2005). As non-interactive prosocial and aggressive behaviors are difficult to interpret, we cannot explain why *A. cahirinus* spend more time engaged in non-interactive behaviors. This finding, however, has also been shown in prairie voles when they interact with a novel, same-sex conspecific (Kelly et al., 2018), suggesting that it may be common for rodents to choose to spend time alone even when in a social context. In order to understand the potential social signals embedded within these seemingly non-interactive behaviors, future studies could examine non-behavioral social signals including scent marking and ultrasonic vocalizations.

Considering the interactive behaviors displayed in the social interaction tests, we can place *A. cahirinus* as a predominantly prosocial species given that males and females spent significantly more time engaged in prosocial than aggressive behavior. Generally, very low levels of aggression were observed in all subjects, and we did not find that stimulus type (novel, same-sex or novel, opposite-sex) influenced aggressive behavior for either males or females. Males exhibited similar behavior profiles when interacting with male and female conspecifics. However, we found that females displayed different levels of prosocial behavior depending on the sex of the conspecific, such that females spent significantly more time engaged in prosocial behaviors with opposite-sex stimulus animals.

and investigation time as only investigation time differed between males and females. Together, these variables may be more indicative of a preference for one stimulus type over another, however, the investigation may largely reflect information-seeking to determine whether the conspecific is a threat, potential mate, or familiar kin. Our findings here are consistent with previous studies in spiny mice showing that female spiny mice are more aggressive and dominant toward opposite-sex intruders than males (Porter, 1976), and that if given a choice between sexually experienced or inexperienced males, females display more aggression toward the sexually inexperienced male (Andres & Deni, 1982). These previous findings and the effects of sex on the social investigation in the present study suggest that female *A. cahirinus* may be significantly more choosey than males.

In addition, the rapid approach times for all stimulus animals demonstrate that *A. cahirinus* have a high degree of social boldness and/or interest in conspecifics. Comparing these approach times to

This difference in prosociality is consistent with the results from the social approach test and suggests that not only do females more thoroughly investigate an opposite-sex conspecific, but they also exhibit more prosocial behavior toward males than other females when freely interacting. Notably, previous studies demonstrated that female spiny mice are more dominant and aggressive than males and that more aggression is observed in all-female cages than in all-male cages (Porter, 1976). Together, these findings suggest that female *A. cahirinus* may prefer affiliating with opposite-sex over same-sex conspecifics, while males are less socially discriminate. This may be a unique social feature about male *A. cahirinus* given that studies in other species show patterns similar to the females in our study—typically an animal modifies its behavior based on the sex of the conspecific. For example, both male and female Mongolian gerbils, prairie voles, and Sprague-Dawley rats exhibit differential prosocial and aggressive behavior dependent on the sex of the conspecific they are interacting with (Argue & McCarthy, 2015; DeVries et al., 1997; Swanson, 1974). Why male *A. cahirinus* behave similarly with same- and opposite-sex conspecifics warrants further study but may suggest males of this species are more socially tolerant. Interestingly, this stands in contrast to Norway rats, which are also a large group living species in the wild, such that male Norway rats are less socially tolerant and more territorial than females (Brain, 1976; Calhoun, 1979).

The high proportion of prosocial behavior exhibited by *A. cahirinus* in both novel, same-sex and novel, and opposite-sex interactions sets this species apart from many rodents as being highly social in multiple social contexts. The lack of aggression exhibited by *A. cahirinus* stands in contrast to mice (e.g. Falkner et al., 2016; Golden et al., 2017, 2019; van Heukelum et al., 2019), hamsters (e.g. Grieb et al., 2021; McDonald et al., 2012; Olvera-Ramos et al., 2020), and Sprague-Dawley rats, which will engage in lethal aggression toward novel conspecifics (Blanchard et al., 1975). Meanwhile, prairie voles are highly prosocial in reproductive contexts with pairbond partners and family members but can be very aggressive toward novel, same-sex conspecifics (Kelly & Ophir, 2015; Lee et al., 2019). In contrast to prairie voles, female meadow voles are prosocial in both non-reproductive and reproductive contexts, which is demonstrated by high levels of intrasexual female sociality and low levels of intersexual aggression (Kelly & Ophir, 2015; Lee et al., 2019). However, unlike *A. cahirinus*, female meadow vole prosociality is seasonally dependent, with group sizes consisting of roughly eight individuals (Ferkin & Gorman, 1992; Leonard & Ferkin, 2005; Ondrasek et al., 2015). Together, our findings in *A. cahirinus* demonstrate that they are well-suited for the study of both male and female reproductive and non-reproductive prosociality in a year-round, group-living species.

Although social interaction tests evaluate social responses to conspecifics, they do not indicate which type of conspecifics may be preferred over others. Social preference tests allow for a direct comparison between conspecifics to identify any such preferences. In the present study, we exposed *A. cahirinus* to either novel and familiar same-sex conspecifics or to same-sex and opposite-sex novel individuals for 5 min and evaluated subject preference based on how they

divided affiliation and investigation time with the two social choices. When choosing between interacting with novel or familiar conspecifics, both male and female *A. cahirinus* showed no preference for either individual. While lack of preference for a novel or familiar conspecifics in short-duration tests is not uncommon in rodents, the lack of preference observed here might be a function of this species' sociality. More colonial species, including spiny mice, degus in a 3-h partner preference test (Insel et al., 2020) and adult mice (*Mus musculus*) in both a 3-h partner preference test and 5-min social preference test (Beery et al., 2018), tend to show no preference for a novel or familiar conspecifics. However, juvenile inbred mice strains do prefer novel conspecifics (Moy et al., 2004). Territorial species, on the contrary, typically prefer familiar individuals. In a similar 5 min social preference paradigm to the one in this study, Mongolian gerbils show a preference for familiar same-sex individuals (A. Kelly et al. pers. obs.), as do prairie voles (Beery et al., 2018) and meadow voles (*M. pennsylvanicus*; Anacker et al., 2016) during a 3-h partner preference tests. Non-territorial, large group living may allow for more freedom in social interactions, while territorial, small group living species may benefit from more stringent interactions with familiar over novel conspecifics. Alternatively, the high levels of prosociality we described in the social interaction tests may mask any preference that *A. cahirinus* possess. From our findings, we can conclude that *A. cahirinus* exhibit no immediate preference, however, future studies may utilize significantly longer tests in order to determine if novel versus familiar social preferences emerge.

In the same-sex versus opposite-sex preference test, we found that *A. cahirinus* preferences differed based on sex. Males preferred investigating and affiliating with same-sex conspecifics, whereas females preferred investigating the opposite-sex individuals. This sex effect is in line with our social approach test results indicates a difference in affiliation and investigation time between the sexes, as well as previous studies, show that females are more aggressive toward the opposite-sex individuals than males (Porter, 1976). Together, our findings suggest not only that female *A. cahirinus* may be more selective in mate choice than males, but they may also be the primary driver of these reproductive behaviors. Furthermore, this effect of sex on social preference stands in contrast to other rodents often studied for their sociality. For example, while both prairie and meadow vole females successfully form same-sex preferences, male voles of either species engage in high levels of aggression toward novel same-sex individuals (Lee et al., 2019). The significant preference to affiliate and investigate same-sex individuals in male *A. cahirinus* reinforces their potential as a lab-tractable mammalian organism for studying non-reproductive prosociality. Indeed, several non-reproductive social behaviors, such as coordinated cooperation (Avital et al., 2016), juvenile play (Berg et al., 1999; Panksepp, 1981), and sentinel behavior (Dr. Ashley Seifert, pers. comm.), along with their neural underpinnings, could be elucidated through the studies utilizing male spiny mice.

Social recognition is critical for the structure and stability of groups and informs decision-making processes that promote context-appropriate behaviors in relation to established social hierarchies

(Kaidanovich-Beilin et al., 2011; Lee et al., 2018). Even though we observed no preference for the novel over familiar conspecifics in the spiny mice, trajectories of social interactions likely differ based on whether or not an individual recognizes a conspecific. A social recognition test is commonly used in rodent behavioral testing (Kercmar et al., 2011; Thor et al., 1982) and evaluates whether animals can distinguish between a repeatedly introduced conspecific and subsequently introduced novel conspecific. Typically, the subject habituates to the increasingly familiar first stimulus animal as it becomes familiar and exhibits a decrease in investigation time; upon introduction of the novel stimulus animal, investigation time increases, confirming that the subject is capable of social discrimination (Hölter et al., 2015). Here, we found that *A. cahirinus* were successful at discriminating between two separate novels, same-sex conspecifics. This is consistent with the previous studies suggesting spiny mouse weanlings are able to differentiate between kin and non-kin based on olfactory cues (Porter et al., 1983, 1986). Interestingly, male and female *A. cahirinus* spent more time investigating the second novel conspecific presented in Trial 5 than they did for the first novel conspecific in Trial 1. While it is not uncommon to find the slight behavioral variations in a social habituation-dishabituation paradigm (Zheng et al., 2013), our findings may indicate increasing interest as more conspecifics are presented. Such increased interest could act as a mechanism that promotes affiliation with, and potentially the formation and/or maintenance of, large group sizes.

Social recognition capabilities may be especially important in large group-living species, where there are more individuals to differentiate between and greater complexity in social hierarchies (Pusey & Packer, 1997). To our knowledge, extremely little is known about spiny mouse social hierarchies, and thus the extent of social memory in spiny mice remains unknown. However, in sciurid rodents (i.e., squirrels, marmots, prairie dogs), variation between individual animal alarm vocalizations increases as group size increases (Pollard & Blumstein, 2011); this may act as a way to better discriminate between the individuals for species that frequently encounter novel conspecifics and/or live in large groups. Because spiny mice emit ultrasonic vocalizations (pers. obs.), future studies could seek to elucidate whether *A. cahirinus* identify individuals through vocalization in addition to olfactory cues.

While gregariousness (a preference to affiliate with large groups) is well characterized in avian species (Goodson et al., 2009; Kelly et al., 2011), it is surprisingly understudied in mammals—particularly the mechanisms of gregariousness. This is especially true in a laboratory setting. As *A. cahirinus* live in especially large groups and are lab-tractable, they offer the opportunity for the study of mammalian gregariousness and can contribute to our understanding of group living. Thus, we aimed to develop a group-size preference test that would allow us to capture gregarious behavior in *A. cahirinus* in a lab setting. This test was modeled after a group size preference test previously used in several species of Estrildid finches (Kelly & Goodson, 2013; Kelly et al., 2011). When presented with 2 or 8 novels, same-sex conspecifics, *A. cahirinus* preferred to affiliate with and investigate the larger group. To our knowledge, group size preference has

not been directly tested in other highly social rodents, however, it is worth noting that other rodents do exhibit gregarious behaviors including rats (Latané, 1969), CD-1 mice (Lee et al., 2018), meadow voles (Ondrasek et al., 2015), and African striped mice (Schradin et al., 2010). Performance in a group size preference test and the degree of gregariousness in the lab presumably reflect the behavioral ecology and species-typical group size of a species. For example, the Mongolian gerbil, a relative of the spiny mouse (Alhajeri et al., 2015; Fabre et al., 2012; Steppan & Schenk, 2017), may exhibit a preference for the smaller group over the larger group due to their small group sizes and high territory defense in the wild (Deng et al., 2017). Additional studies could compare these closely related species to identify any potential differences in gregariousness and their underlying mechanisms to better understand the evolution of grouping behaviors.

It remains unclear what aspect of spiny mouse behavioral ecology may drive gregariousness. Breeding strategy and mating systems likely relate to gregariousness, but whether one precedes the other is unknown and difficult to disentangle. Importantly, the breeding strategy does not always predict gregariousness given that Estrildid finches are socially monogamous, yet flock in large groups and are highly gregarious (Goodson et al., 2012). However, for spiny mice, the group care for offspring involved in their communal breeding strategy may indeed encourage gregarious behavior. Increased alloparental care for offspring can decrease the amount of time individuals spend parenting, thus allowing more time for resource acquisition for mates, food, or territories, which is particularly beneficial in unpredictable environments (Guindre-Parker & Rubenstein, 2018). Indeed, some mammalian species form groups specifically when they are young are most vulnerable in order to take advantage of communal-rearing benefits (White et al., 2010). However, our group size preference test used novel, same-sex stimulus animals, so any motivation to interact with the larger group is unlikely to stem exclusively from their breeding strategy and motivations to mate. This test design does not negate the possibility that gregariousness could still be a byproduct of communal breeding. Given the high levels of prosociality, we observed in the social interaction tests, it is also feasible that spiny mice generally find social interactions rewarding, which may facilitate a preference to affiliate with the larger group. Future studies could examine the reward circuitry of spiny mice interacting with small versus large groups in order to address proximate questions about spiny mouse gregariousness. Together, these findings demonstrate that *A. cahirinus* are an ideal species for examining gregariousness, grouping behavior, and inter-group dynamics due to their high levels of sociality and communal breeding (Porter et al., 1980; Tučková et al., 2016).

4.2 | Adjustments of social behavior tests in *A. cahirinus*

When testing *A. cahirinus*, we discovered that modifications of existing rodent behavioral tests were needed to properly test social behavior in *A. cahirinus* as compared to other species, including prairie

voles or Mongolian gerbils (Kelly et al. pers. obs.). For most species, social approach/investigation/recognition tests using stimulus chambers with 1-cm diameter holes in one wall are sufficient to maintain the subject's interest in the stimulus animals (Castro et al., 2020; Kelly et al., 2020). In *A. cahirinus*, however, we required access holes surrounding the entire stimulus container that were at least 2 cm in diameter in order for the animals to engage in the social investigation for more than a few seconds. It is clear that, while spiny mice may learn olfactory cues quickly (Janus, 1993) and form preferences based on them (Janus, 1988; Porter et al., 1983, 1986; 1986), olfactory cues alone are not the sufficient motivation for social interactions. This preference for physical contact during an interaction may explain some differences across studies where spiny mouse behavior is examined. For example, Ratnayake et al. (2014) designed their social interaction paradigm with two chambers that allowed the subject to remain separated from the stimulus animal and also restrained the stimulus animal in a cylinder. Our study, in contrast, allowed for free interactions in a single chamber. This methodological difference may account for the larger interest in the investigation that we report here compared to the findings presented by Ratnayake et al. (2014).

We also noted that extensive acclimation times appeared to decrease interest in the behavioral tests. While it is common to allow other rodent species acclimation periods as long as 30 min for behavioral tests in novel apparatuses (Kelly et al., 2020), 3-minute acclimations were more than sufficient for *A. cahirinus* in all of the current paradigms. In our experience, prairie voles are an easily stressed rodent, where longer periods to acclimate to new surroundings are necessary, whereas *A. cahirinus* are quite bold and readily explore new environments. Additionally, we found that *A. cahirinus* frequently succeed at jumping out of 2 ft. tall testing chambers (by, rather impressively, doing backflips), so chambers with high walls and lids are recommended for testing.

4.3 | A consideration of *A. cahirinus* social phenotype from the perspective of cooperative breeding

The sex effects identified in our study—in the social approach, social interaction, and social preference tests—may be related to the breeding strategy of spiny mice. Notably, field studies are needed to accurately characterize breeding and offspring rearing in spiny mice in the wild. While it is currently unknown how spiny mice parse breeding dominance among female spiny mice, mammalian cooperative breeders often have a single-dominant female engaging in the majority of breeding relations (Lukas & Clutton-Brock, 2012). The greater interest in opposite-sex individuals exhibited by female *A. cahirinus* here may serve as a mechanism to maintain breeding dominance through consistently searching for mating opportunities. However, within our colony, females in the same breeding cage appear to all reproduce (pers. obs.). Rather, there may be no dominant female and all females compete for access to the available males. Consistent competition seems unlikely, though, as

high reproductive competition tends to favor solitary living, not cooperative communities, in other rodents (Schradin et al., 2010). Therefore, it may be more likely that there are dominant females that drive a potentially matrilineal system in spiny mice. If female spiny mice drive a matrilineal reproductive system, then several factors would be expected within their groups. Three of these factors include large groups, small litter sizes, and male-biased dispersal rates (Holekamp & Sawdy, 2019). While spiny mice do live in large groups and produce small litters in the field (Haughton et al., 2016), it is yet unknown whether they have a male-biased dispersal rate. Given that subordinate females sometimes receive higher inclusive fitness benefits than males in cooperatively breeding species (Richardson et al., 2002), it seems plausible that spiny mice could display this biased dispersal. Future field and lab studies in spiny mice are required to further characterize their cooperative breeding system and hierarchy.

5 | CONCLUSION

In this study, we characterized the basic social behavior of *A. cahirinus* through social approach, social interaction, social preference, social recognition, and group size preference tests. We identified a high propensity for prosocial behaviors in all of our behavioral paradigms. We also noted several sex effects that indicate that male *A. cahirinus* prefer engaging in non-reproductive prosocial behaviors with same-sex conspecifics, whereas females prefer interacting with opposite-sex conspecifics. These preferences highlight the value of *A. cahirinus* as being suitable for studies of *both* reproductive and non-reproductive prosociality. Further, the preference for males and females to affiliate with large groups demonstrates that *A. cahirinus* are an ideal, lab-tractable organism for studying mammalian gregariousness. Together, this study lays a basic foundation for future exploration of mechanisms underlying social behaviors in a group-living mammal and for the study of complex group dynamics.

CONFLICT OF INTEREST
The authors have no conflicts of interest.

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