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RESEARCH ARTICLE

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Experience of social density during early life is associated with attraction to conspecific odour in the common vole (*Microtus arvalis*)

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Abstract

Social organisation in species with fluctuating population sizes can change with density. Therefore, information on (future) density obtained during early life stages may be associated with social behaviour. Olfactory cues may carry important social information. We investigated whether early life experience of different experimental densities was subsequently associated with differences in attraction to adult conspecific odours. We used common voles (*Microtus arvalis*), a rodent species undergoing extreme density fluctuations. We found that individuals originating from high experimental density populations kept in large outdoor enclosures invested more time in inspecting conspecific olfactory cues than individuals from low-density populations. Generally, voles from both treatments spent more time with the olfactory cues than expected by chance and did not differ in their latency to approach the odour samples. Our findings indicate either that early experience affects odour sensitivity or that animals evaluate the social information contained in conspecific odours differently, depending on their early life experience of conspecific density.

KEYWORDS
early experience, olfactory, population cycles, priming, rodents

1 | INTRODUCTION

Olfactory cues are important and reliable cues used by animals, both as repellent and as attractant (Li & Liberles, 2015). For example, small mammals avoid predator odours (e.g. Calder & Gorman, 1991), and mice use odour cues of the opposite sex to find and choose partners (e.g. Kavaliers & Colwell, 1995; Nyby et al., 1985). Although the information transmitted by olfactory cues can be universal for a species, the behavioural response may differ depending on the state or functional group of an individual. While predator cues should be avoided by all individuals, the information provided by conspecific odour may lead to changes in behaviour depending on the motivation of the receiver. Wild mice, for example, are attracted to conspecific, same-sex odours in autumn to form wintering aggregations, but repelled in spring when competing for mates (Simeonovska-Nikolova, 2007). Thus, the social and seasonal context can shape an individual's interest in conspecific odour as well as its behavioural response towards such cues.

The use of olfactory cues for social communication is well known in rodents (Schultz & Tapp, 1973). Bank voles (*Myodes glareolus*), for example, increase foraging activity when conspecific scent is present (Verplancke et al., 2010). Generally, olfaction plays an important role during mate choice (Ferkin, 2018), offspring rearing (e.g. Moore, 1981) and development (Alberts, 1976)

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in rodents. The social rearing environment has a strong impact on the processing of olfactory information (Sanchez-Andrade and Kendrick, 2009. The frequency of social interactions increases with population density in some rodents, including meadow voles, *Microtus pennsylvanicus* (Reich & Tamarin, 1980). High social density can enhance physiological stress due to depletion of resources, competition and higher predation risk (Creel et al., 2013; but see Parrish & Edelstein-Keshet, 1999). Thus, behaviour of individuals and interactions with conspecifics may depend on the population density they live in. For example, female striped mice (*Rhabdomys pumilio*) reduce their home range with increasing number of female neighbours (Schoepf et al., 2015). Furthermore, higher population density in fluctuating rodent populations may lead to higher infanticide in bank voles (Korpela et al., 2011), lower probability of pregnancy failure (Eccard et al., 2017) and a change from mostly monogamous to mostly polygynous mating systems (Lucia et al., 2008; Schradin & Pillay, 2005; Streatfeild et al., 2011). Thus, density may be the most important factor influencing the social environment of small rodents (Korpela et al., 2011). Information gathering from conspecific density (and potentially also identity of conspecifics and relatedness) may be pivotal for the expression of social behaviour towards conspecifics. More specifically, density experienced during pre- and postnatal development is known to prime adult behavioural strategies (Eccard & Rödel, 2011; Sachser & Kaiser, 1996; Sachser et al., 2020).

Here, we ask whether social density conditions experienced in early life influence how individuals gather information from conspecific odours as adults. We used females of the common vole (*Microtus arvalis*) as a study system, as these short-lived, iteroparous rodents undergo typical annual and interannual variations in population dynamics (Frank, 1957; Boyce & Boyce, 1988a). Densities during these fluctuations vary strongly, and densities from about 24 per ha in winter to 2000 individuals per ha in summer were reported (Boyce & Boyce, 1988a, Jacob et al., 2013). During winter, when overall density populations are low, common voles live in clusters of isolated groups of mixed sex and ages (Chełkowska, 1978. During summer, females live in groups of 2–6 individuals that share large burrows (Boyce & Boyce, 1988b) and even visit each other when breeding solitarily (Liesenjohann et al., 2013). For this, burrows are connected by a network surface runways (Pelikán, 1982. Females use urine to mark their territory (Dobly, 2005), but do not use their own scent markings for remembering the path back to their burrow (Dobly, 2001). Thus, scent marks mainly contain information for conspecifics on identity and number of conspecifics producing the scent mark, and voles might be attracted to the odour of conspecifics to associate in shared burrows.

The social system and seasonal fluctuation in population density leads to two predictions considering the reaction of voles to conspecific odour cues:

- Individuals born in high density will be more sociable than voles born under low density conditions and may therefore exhibit a stronger attraction to conspecific odour to obtain information. On the one hand, high density may result in higher competition for food, shelter and mates, which may result in animals born in such conditions investing more time in gaining information about conspecifics. Alternatively, since many rodent species are promiscuous in high densities, odour cues may provide information on mating partners or opportunities.
- Individuals born under low density will show a stronger attraction to conspecific odours of unknown individuals, since they need to associate in small breeding groups or pairs. Alternatively, individuals born in high social densities may avoid odours of unknown conspecifics since they already experience social exchange and may avoid competitors. In order to assess the influence of density per se on the behaviour of voles to conspecific olfactory cues, we experimentally manipulated population densities at the same season. We then collected pups from both high and low population densities and tested their reaction as adults to conspecific odour.

2 | METHODS

2.1 | Individuals and housing

We caught 36 adult common voles in spring 2019 around Potsdam, Germany, serving as the parental generation in the density treatments. For individual identification, each animal was injected with a passive integrated transponder tag (PIT; Trovan ID-100, 2.12 mm × 11.5 mm, 0.1 g). After capture, we transferred the parental generation into 8 grassland outdoor enclosures with a size of 15 × 15 m, surrounded by galvanised metal walls extending 1 m below and 0.5 above the ground. The experimental facility was protected from ground predators with an electrical veterinary fence and from avian predators with a mesh net covering the experimental fields. Four live traps (Ugglan Special No. 2, Grahnab, Sweden) were permanently installed in each enclosure to ease recapture.

Two enclosures were stocked with 10 males and 10 females (890 voles per hectare) from different capture sites to ensure unrelatedness, while 6 enclosures were stocked with one male–female pair (89 voles per ha). The expression of these treatments as density per hectare may not capture the essence of the treatment: Mobility of common vole allows them to reach each part of the enclosure (Jakob & Hempel, 2003; Briner et al., 2005) and interact with every individual in the enclosure. Thus, individuals may experience contacts to other individuals, not density per se. In the high contact treatment, each parental individual potentially experienced contacts with 19 different individuals (55 potential dyads), while in the low contract treatment, there was only one potential contact.

Parental males were removed from the enclosures after 20 days to prevent breeding with the focal offspring. Thus, treatments differed by contacts and relatedness: in the high-density treatments, females and their offspring experienced contacts to other families, while in the low-density females, all contacts were restricted within a family (mother and siblings). After another 20 days, parental females and their weaned offspring were removed from the enclosures by live trapping. Offspring, the test animals, had experienced close contact with their nestling siblings and their mothers, but in the high contact treatments potentially had contacts to other adult females and other juveniles since vole females can nest communally (Boyce & Boyce, 1988b), can visit each other's nests (Boyce & Boyce, 1988b; Liesenjohann et al., 2013) or may meet at their first days of leaving the nest and experiencing the environment.

As enclosures were limited, we performed this outdoor breeding experiments in two rounds. In July 2019, we run one high-density enclosure and 5 low-density enclosure, while in September 2019, we repeated the procedure by mixing up the distribution of parental animals and densities in the enclosures, ending up with one additional high-density enclosure and 5 low-density enclosures. Parental animals that have previously been put into high-density treatments were used for low-density enclosures in the second round and vice versa.

After capture, offspring were housed individually in standard makrolon cages (Ehret GmbH, Germany, Type III: 42 cm × 27 cm × 16 cm) equipped with wooden bedding, hay for food and nest building, and a paper roll. Conventional food pellets and water were provided *ad libitum*. Housing rooms had natural light conditions and an ambient temperature ranging from 12°C to 24°C. Offspring were tested for their reaction to conspecific odour at the age of 4 months, that is as adults.

2.2 | Experimental set-up

We observed reactions of voles to odour of unknown conspecifics using a semi-transparent plastic box (45 × 22 × 22 cm) which was visually divided into six compartments, including the starting zone, a neutral zone in the centre and the odour zone (Figure 1). The box's ground was covered with wooden shavings, and a tablespoon of bedding including urine and faeces from three same-sex, unknown individuals (from different enclosures than the test subject) placed in one of the box corners, the odour zone. Immediately after preparation of the box with the sample, the test individual was then placed under a cover at the corner opposite of this odour sample. After one minute of acclimatisation, the cover was carefully removed to start the test. The behaviour of each test subject was recorded with a camera (Logitech®WebCam, Software Version 12.10.1113.0000) attached vertically above the arena and controlled from an adjacent room in order not to disturb the animal. From the videos, we noted the latency of the test subject to enter the neutral centre, the latency to enter the odour zone and the total amount of time spent with the odour. After a total of six minutes, the test was stopped, the individual removed and placed back in its home cage, and the test set-up was cleaned with alcohol.

In total, we tested 12 (5 males and 7 females) from high and 26 (9 males and 17 females) from low-density populations three months after capture (December).

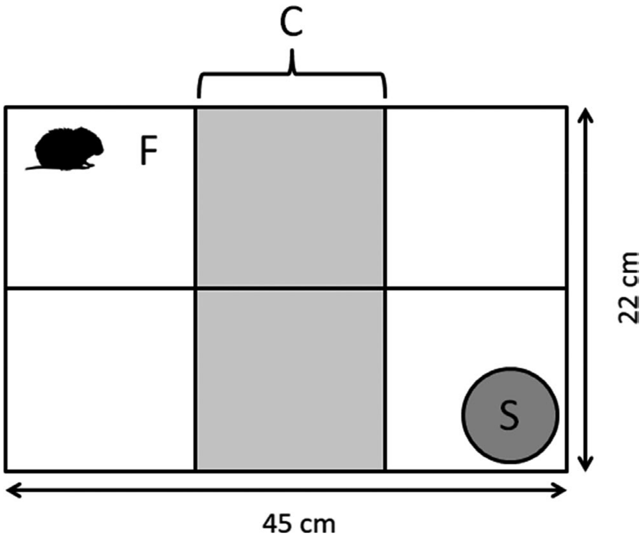

FIGURE 1 Experimental set-up. The focal animal (F) was placed in a box, with the olfactory sample (S) consisting of bedding from cages of three unknown same-sex conspecifics being placed in the opposite corner. Latency to enter the centre zone (C), latency to enter the compartment with the sample and amount of time spent with the sample were measured

2.3 | Statistical analyses

First, we tested whether the voles spend more time in the compartment with the odour sample than by chance (60 s) using a one-sample Wilcoxon signed-rank test. We then tested for differences in the latency to approach the odour and the total time spent in the odour zone between voles born in high- and low-density populations using a mixed-effect model with enclosure as random factor to account dependencies within enclosures (e.g. sibling effects, dominance hierarchies). Density, sex and latency to enter the centre zone were potentially explanatory factors. Males and females may differ in their motivation to investigate conspecific odour, while the latency to enter the centre zone may affect the detectability of the odour sample. Latency to enter the odour zone was square-root-transformed in order to meet normal distribution.

2.4 | Ethical note

Animals were housed and bred in the enclosures and indoor facilities of the University of Potsdam according to permit 3854-1-132 by the City Council (Stadtverwaltung Potsdam). Behavioural observations were conducted under the permits 2347-A-16-2-2018 and 2347-42-2017 by the County Brandenburg (Landesamt für Verbraucherschutz und Gesundheit) We minimised stress experienced by the animals through maintaining regular trapping intervals (8 h), short transport times (enclosures and holding facilities were <1 km apart), and through minimising their handling (test animals were transferred from their cages into the test arena, and back, in a tube). Offspring were removed from the enclosures at the age 20+

days, which is after weaning and at a subadult age where dispersal can occur.

3 | RESULTS

All animals examined spent more time in the compartment with the odour sample than expected by chance ($V = 616.5$; $p < .001$). Latency to enter the centre and the odour zone were positively correlated ($X^2 = 53.90$; $p < .001$), with no differences between males and females ($X^2 = 0.58$; $p = .25$) or between individuals from high or low population densities ($X^2 = 0.32$; $p = .57$; Figure 2).

Males and individuals that entered the centre earlier spent more time in the odour zone (sex: $X^2 = 7.12$; $p = .008$; latency to enter centre: $X^2 = 5.90$; $p = .015$). When including both parameters into the mixed model, voles from high-density populations spent more time investigating the odour of conspecifics than individuals from low-density populations ($X^2 = 7.11$; $p = .008$; Figure 3).

4 | DISCUSSION

In this study, common voles were generally attracted rather than repelled by conspecific odours. Individuals from both high and low social density populations spent more time close to the odour samples than expected by chance. This may be explained either by the general interest of common voles in odours or by an attraction of common voles to conspecifics and their cues. As the experimental animals have been kept individually for three months before starting the test, they might have been seeking company the presence of conspecifics (see Tokumaru et al., 2015). An alternative in which voles were attracted to potential mating opportunities (Eccard et al., 2018) may be discarded because only same-sex odours were provided.

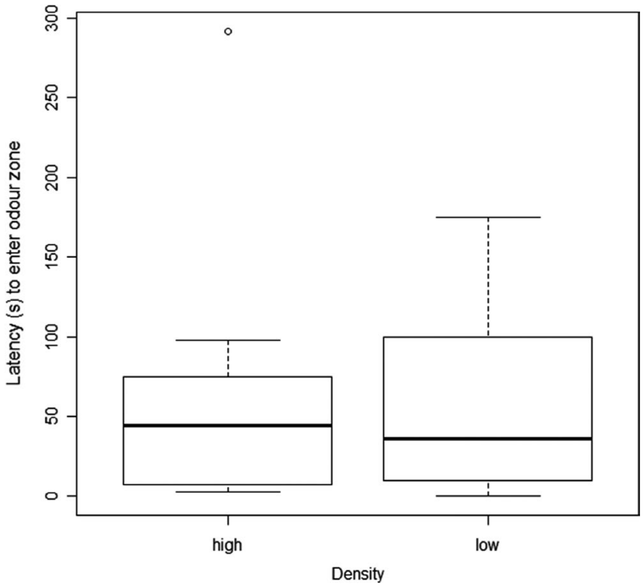

FIGURE 2 Latency (s) to enter odour zone: There was no difference between animals from high-density ($N = 12$) or low-density ($N = 26$) populations ($p = .57$)

In line with these results, there was no difference in the latency to enter the area with bedding from conspecifics between individuals raised under high- and low-density populations. Thus, the motivation to approach and invest the odour appeared independent from the social environment an individual grew up in. However, voles from high population densities spent more time investigating the odours than individuals from low-density populations. These results remain relatively more consistent with our first hypothesis, which predicts this difference as a response to the early social environment experienced. The social environment under high-density populations was probably more complex than under low population density, meaning that individuals encountered conspecifics more often than in low-density populations. The social environment an individual grows up in may shape behaviour later in life (e.g. Kaiser et al., 2015 for cavies; Eccard & Rödel, 2011 for European rabbits), and social information may thus vary in value between animals with different social experiences in early life. Alternatively, social experience may affect ontogenetic development in reactivity to social cues, as observed in locusts (Despland, 2001, Ochieng′ and Hansson, 1999, a possibility that needs to be investigated during follow-up experiments.

Alternatively, voles from high population densities may invest substantially more time inspecting conspecific odour than average. As individuals in high population densities face increased competition for food, shelter and mates, spending more time in gaining information from conspecific olfactory cues may have important fitness consequences. Indeed, scents from urine can inform individuals about the competitive ability of conspecifics (through its activity level or its weight; Dobly, 2005). As female common voles scent mark their territory, information gained from such urine marks may modify individual behaviour leading to a reduced home range in the presence of same-sex conspecifics (Dobly, 2005). We found that males spend more time with the odour samples than females, which may reflect the generally higher intrasexual competition among males than among females (Bateman, 1948).

Our second hypothesis predicted that individuals from low-density populations, which are usually experienced in winter, could be attracted to conspecifics since in nature aggregations are formed during winter. Since both high and low population densities were experimentally created in summer, there was no seasonal need for voles from low densities to aggregate. Our results showed that if population densities are low in summer, which can be the case in multiannual density fluctuations, common voles are not more attracted to conspecific odours than voles from high population density. Therefore, season itself (temperature or photoperiod) rather than population density may represent a cue for voles to form social aggregations in winter (Nelson et al., 1990).

Growing up in a specific population density may predict the subsequent social environment of a short-lived animal, as revealed in *Octodon degus* (Ebensperger et al., 2021). Thereby, cues detected by the mother can shape the behavioural phenotype of the

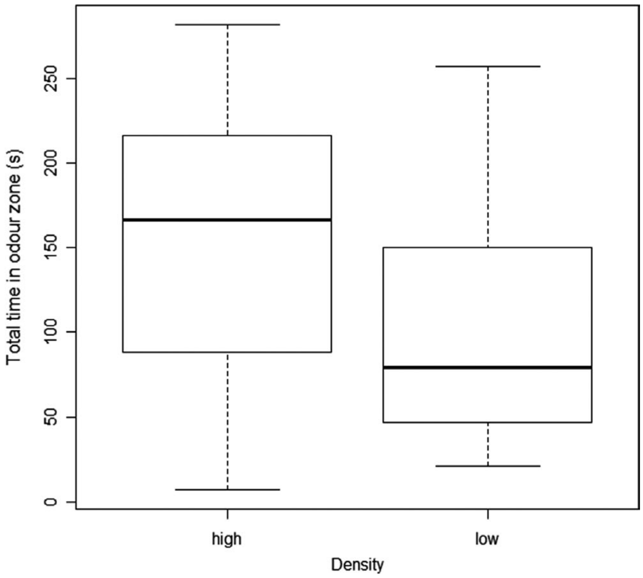

FIGURE 3 Total time (s) spent in the odour zone: Individuals from high-density populations ($N = 12$) spent more time in the compartment with the conspecific odour sample than voles from low-density populations ($N = 26$; $p = .015$)

offspring, both prenatally and through maternal behaviour (Sachser et al., 2018). Thus, early experience may form the basis of hormonal, neurological and behavioural patterns later in life and individuals primed for a life in a complex social environment may be more variable in behaviour (Kemme et al., 2007; Sachser et al., 2018, 2020).

Individually consistent behaviour across time and context, referred to as behavioural type or personality, is well known in the common vole (Herde & Eccard, 2013; Lantova et al., 2011). While classic personality traits such as boldness, activity and exploration directly affect survival and overall fitness (Smith & Blumstein, 2008), social behaviour is a lesser-known personality trait, which can have fitness consequences. For example, social and asocial lizards (*Lacerta vivipara*) display different fitness outcomes in populations of different densities (Cote et al., 2008). Asocial animals survived better in low-density populations, while social females reproduced better. Spatiotemporal variation in environmental conditions might thus be the process underlying the maintenance of these personality traits within a population. While it is known that vole personality changes with season (Gracceva et al., 2014), it is yet to be determine whether these changes are mediated by density or by other environmental cues. It has previously been found that animal personality differed between bank voles from naturally high and low population density (Korpela et al., 2011). Here, we have shown that the behaviour towards conspecific scents was associated with the individuals' social experience early in life, indicating that the value of social information or the individual's sensitivity to odours may have been affected by early experience. Subsequent experiments are needed to disentangle the proximate mechanisms of odour attraction and ultimate value of information gathering for cohorts with different early experience in animals with fluctuating density populations.

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REFERENCES

Alberts, J. R. (1976). Olfactory contributions to behavioral development in rodents. In R. L. Doty (ed.), *Mammalian olfaction, reproductive processes and behavior* (pp. 67–94). Academic Press.

Bateman, A. J. (1948). Intra-sexual selection in Drosophila. *Heredity*, *2*(3), 349–368. https://doi.org/10.1038/hdy.1948.21

Briner, T., Nentwig, W., & Airoldi, J. P. (2005). Habitat quality of wildflower strips for common voles (Microtus arvalis) and its relevance for agriculture. *Agriculture, ecosystems & environment*, *105*(1-2), 173–179.

Boyce, C. C., & Boyce, J. L. (1988a). Population biology of *Microtus arvalis*. III. Regulation of numbers and breeding dispersion of females. *The Journal of Animal Ecology*, 737–754. https://doi.org/10.2307/5090

Boyce, C. C., & Boyce, J. L. (1988b). Population biology of *Microtus arvalis*. I. Lifetime reproductive success of solitary and grouped breeding females. *The Journal of Animal Ecology*, 711–722. https://doi.org/10.2307/5088

Calder, C. J., & Gorman, M. L. (1991). The effects of red fox *Vulpes vulpes* faecal odours on the feeding behaviour of Orkney voles *Microtus arvalis*. *Journal of Zoology*, *224*(4), 599–606.

Chełkowska, H. (1978). Variations in number and social factors in a population of field voles. *Acta Theriologica*, *23*, 213–238.

Cote, J., Dreiss, A., & Clobert, J. (2008). Social personality trait and fitness. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1653), 2851–2858.

Creel, S., Dantzer, B., Goymann, W., & Rubenstein, D. R. (2013). The ecology of stress: Effects of the social environment. *Functional Ecology*, *27*, 66–80.

Despland, E. (2001). Role of olfactory and visual cues in the attraction/repulsion responses to conspecifics by gregarious and solitarious desert locusts. *Journal of Insect Behavior*, *14*(1), 35–46.

Dobly, A. (2001). Movement patterns of male common voles (*Microtus arvalis*) in a network of Y junctions: Role of distant visual cues and scent marks. *Canadian Journal of Zoology*, *79*(12), 2228–2238.

Dobly, A. (2005). Scent marking by common voles *Microtus arvalis* in the presence of a same-sex neighbour. *Acta Theriologica*, *50*(3), 343–356. https://doi.org/10.1007/BF03192630

Ebensperger, L. A., Abades, S., Riquelme, J., Correa, L. A., & Hayes, L. D. (2021). Socioecological conditions predict degu social instability and provide limited cues to forecast subsequent breeding conditions. *Behavioral Ecology and Sociobiology*, *75*(77), 1–15.

Eccard, J. A., Dammhahn, M., & Ylönen, H. (2017). The Bruce effect revisited: is pregnancy termination in female rodents an adaptation to ensure breeding success after male turnover in low densities? *Oecologia*, *185*(1), 81–94. https://doi.org/10.1007/s00442-017-3904-6

Eccard, J. A., Reil, D., Folkertsma, R., & Schirmer, A. (2018). The scent of infanticide risk? Behavioural allocation to current and future reproduction in response to mating opportunity and familiarity with intruder. *Behavioral Ecology and Sociobiology*, *72*(11), 1–11. https://doi.org/10.1007/s00265-018-2585-4

Eccard, J. A., & Rödel, H. G. (2011). Optimizing temperament through litter size in short-lived, iteroparous mammals in seasonal environments. *Developmental Psychobiology*, *53*(6), 585–591.

Ferkin, M. H. (2018). Odor communication and mate choice in rodents. *Biology*, *7*(1), 13. https://doi.org/10.3390/biology7010013

Frank, F. (1957). The causality of Microtine cycles in Germany (second preliminary research report). *The Journal of Wildlife Management*, *21*(2), 113–121.

Gracceva, G., Herde, A., Groothuis, T. G., Koolhaas, J. M., Palme, R., & Eccard, J. A. (2014). Turning shy on a winter's day: effects of season on personality and stress response in *Microtus arvalis*. *Ethology*, *120*(8), 753–767.

Herde, A., & Eccard, J. A. (2013). Consistency in boldness, activity and exploration at different stages of life. *BMC Ecology*, *13*, 49.

Jacob, J. (2013). Vertebrate pest management: Science and application. *Pest management science*, *3*(69), 321–322.

Jacob, J., & Hempel, N. (2003). Effects of farming practices on spatial behaviour of common voles. *Journal of Ethology*, *21*(1), 45–50.

Kaiser, S., Schwerdt, B., Siegeler, K., & Sachser, N. (2015). Social instability during pregnancy and lactation alters female wild cavy offsprings' endocrine status and behaviour later in life. *Behaviour*, *152*(7–8), 837–859. https://doi.org/10.1163/1568539X-00003256

Kavaliers, M., & Colwell, D. D. (1995). Discrimination by female mice between the odours of parasitized and non-parasitized males. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *261*(1360), 31–35.

Kemme, K., Kaiser, S., & Sachser, N. (2007). Prenatal maternal programming determines testosterone response during social challenge. *Hormones and Behavior*, *51*(3), 387–394. https://doi.org/10.1016/j.yhbeh.2006.12.009

Korpela, K., Sundell, J., & Ylönen, H. (2011). Does personality in small rodents vary depending on population density? *Oecologia*, *165*(1), 67–77. https://doi.org/10.1007/s00442-010-1810-2

Lantova, P., Sichova, K., Sedlacek, F., & Lanta, V. (2011). Determining behavioural syndromes in voles – the effects of social environment. *Ethology*, *117*, 124–132.

Li, Q., & Liberles, S. D. (2015). Aversion and attraction through olfaction. *Current Biology*, *25*(3), R120–R129. https://doi.org/10.1016/j.cub.2014.11.044

Liesenjohann, M., Liesenjohann, T., Palme, R., & Eccard, J. A. (2013). Differential behavioural and endocrine responses of common voles (*Microtus arvalis*) to nest predators and resource competitors. *BMC Ecology*, *13*(1), 1–10. https://doi.org/10.1186/1472-6785-13-33

Lucia, K. E., Keane, B., Hayes, L. D., Lin, Y. K., Schaefer, R. L., & Solomon, N. G. (2008). Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. *Behavioural Ecology*, *19*, 774–783. https://doi.org/10.1093/beheco/arn028

Moore, C. L. (1981). An olfactory basis for maternal discrimination of sex of offspring in rats (*Rattus norvegicus*). *Animal Behaviour*, *29*(2), 383–386. https://doi.org/10.1016/S0003-3472(81)80097-8

Nelson, R. J., Badura, L. L., & Goldman, B. D. (1990). Mechanisms of seasonal cycles of behavior. *Annual Review of Psychology*, *41*(1), 81–108. https://doi.org/10.1146/annurev.ps.41.020190.000501

Nyby, J., Kay, E., Bean, N. J., Dahinden, Z., & Kerchner, M. (1985). Male mouse (Mus musculus) attraction to airborne urinary odors of conspecifics and to food odors: Effects of food deprivation. *Journal of Comparative Psychology*, *99*(4), 479. https://doi.org/10.1037/0735-7036.99.4.479

Ochieng', S. A., & Hansson, B. S. (1999). Responses of olfactory receptor neurones to behaviourally important odours in gregarious and solitarious desert locust. *Schistocerca Gregaria. Physiological Entomology*, *24*(1), 28–36.

Parrish, J. K., & Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary tradeoffs in animal aggregation. *Science*, *284*, 99–101.

Pelikán, J. (1982). *Microtus arvalis* on mown and unmown meadow. *Acta Scientiarum Naturalium, Brno*, *16*, 1–36.

Reich, L. M., & Tamarin, R. H. (1980). Trap use as an indicator of social behavior in mainland and island voles. *Acta Theriologica*, *25*, 295–307. https://doi.org/10.4098/AT.arch.80-26

Sachser, N., Hennessy, M. B., & Kaiser, S. (2018). The adaptive shaping of social behavioural phenotypes during adolescence. *Biology Letters*, *14*(11), 20180536. https://doi.org/10.1098/rsbl.2018.0536

Sachser, N., & Kaiser, S. (1996). Prenatal social stress masculinizes the females' behaviour in guinea pigs. *Physiology & Behavior*, *60*(2), 589–594. https://doi.org/10.1016/S0031-9384(96)80036-9

Sachser, N., Zimmermann, T. D., Hennessy, M. B., & Kaiser, S. (2020). Sensitive phases in the development of rodent social behavior. *Current Opinion in Behavioral Sciences*, *36*, 63–70. https://doi.org/10.1016/j.cobeha.2020.07.014

Sanchez-Andrade, G., & Kendrick, K. M. (2009). The main olfactory system and social learning in mammals. *Behavioural Brain Research*, *200*(2), 323–335. https://doi.org/10.1016/j.bbr.2008.12.021

Schoepf, I., Schmohl, G., König, B., Pillay, N., & Schradin, C. (2015). Manipulation of population density and food availability affects home range sizes of African striped mouse females. *Animal Behaviour*, *99*, 53–60. https://doi.org/10.1016/j.anbehav.2014.10.002

Schradin, D., & Pillay, N. (2005). Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy*, *86*, 99–107.

Schultz, E. F., & Tapp, J. T. (1973). Olfactory control of behavior in rodents. *Psychological Bulletin*, *79*(1), 21. https://doi.org/10.1037/h0033817

Simeonovska-Nikolova, D. M. (2007). Interspecific social interactions and behavioral responses of *Apodemus agrarius* and *Apodemus flavicollis* to conspecific and heterospecific odors. *Journal of Ethology*, *25*(1), 41–48. https://doi.org/10.1007/s10164-006-0203-9

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, *19*(2), 448–455. https://doi.org/10.1093/beheco/arm144

Streatfeild, C. A., Mabry, K. E., Keane, B., Crist, T. O., & Solomon, N. G. (2011). Intraspecific variability in the social and genetic mating systems of prairie voles, *Microtus ochrogaster. Animal Behavior*, *82*, 1387–1398. https://doi.org/10.1016/j.anbehav.2011.09.023

Tokumaru, R. S., Ades, C., & Monticelli, P. F. (2015). Social support does not require attachment: Any conspecific tranquilizes isolated guinea-pig pups. *Applied Animal Behaviour Science*, *171*, 197–203. https://doi.org/10.1016/j.applanim.2015.08.027

Verplancke, G., Le Boulengé, É., & Diederich, C. (2010). Differential foraging in presence of predator and conspecific odors in bank voles: A field enclosure study. *Ecological Research*, *25*(5), 973–981. https://doi.org/10.1007/s11284-010-0721-3

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