PREPRINT

A new perspective on Squamate social cognition – the use of semiochemicals

Birgit Szabo [a] *

[a] Centre for Research on Ecology, Cognition and Behaviour of Birds, University of Gent, Belgium

*Correspond to: Birgit Szabo, Sint-Pietersnieuwstraat 33, 9000 Gent, Belgium, email: birgit.szabo@gmx.at

BS ORCID: 0000-0002-3226-8621

Abstract

The Social Intelligence Hypothesis suggests that cognition might be key to enable animals to live in social groups. Especially social cognition is important as it allows animals to respond appropriately to conspecifics and ensure group cohesion. Social cognition is extensively studied in mammals and birds but to gain a broad understanding of the benefits of social cognitive processes in social interactions we need a broader phylogenetic approach. In this opinion paper, I suggest Squamates (lizards, snakes, and worm lizards) as promising models due to their diverse but facultative sociality and reliance on semiochemical communication in social contexts. Squamates possess a highly developed vomeronasal system to detect semiochemicals for social recognition and discrimination. Similar to the well-studied rodents, squamates detect a wide range of information within chemical cues but research on the associated decision-making processes, individual differences and development of these abilities is still scarce. Comparative approaches leveraging Squamates' semiochemical communication and sociobiological diversity could provide important new insights into the evolution of social cognition. Future research should further focus on individual abilities, their link to environmental and social demands, and consequences for fitness, advancing our understanding of adaptive social cognitive skills across taxa.

Keywords: chemical communication, chemical ecology, discrimination, lizard, recognition, reptile, snake, social evolution, vomerolfaction, worm lizards

Introduction

Social cognition involves all neural processes by which individuals collect, retain, process and use information that are beneficial in a social context to avoid competition and conflict or aid cooperation and group cohesion (Seyfarth and Cheney, 2015; Shettleworth, 2009). As such, social cognition plays a crucial role in recognition and memory of specific individuals which forms the basis of any social aggregation, may it be mate guarding, pair formation, parent-offspring aggregation, and at its extreme, long-term group living (Rubenstein and Abbot, 2017; Ward and Webster, 2016). The role that cognition plays in social group living was first highlighted by Chance and Mead (1953), Humphrey (1976) and Jolly (1966) on the basis of observations in primates which demonstrated that species living in social groups possess better cognitive abilities which led to the formulation of the Social Intelligence Hypothesis (Byrne and Whiten, 1988; Chance and Mead, 1953; Humphrey, 1976; Jolly, 1966). It suggests that having to discriminate, track and remember specific individuals and their relationships poses a challenge that can be overcome by developing enhanced cognitive skills. Consequently, individuals with better cognitive skill fare better in their social environment and produce more offspring (Zuberbühler and Byrne, 2006). The Social Intelligence Hypothesis has been tested widely across mammal and bird species confirming the link between sociality and cognition across taxa (Speechley et al., 2024). However, most studies have focused on more general cognitive skills such as associative learning and flexibility (e.g. Ashton et al., 2018; Berhane and Gazes, 2020; Borrego and Gaines, 2016). One might argue that a stronger focus on social cognition is warranted as we would expect the largest effects of sociality to be found in the social cognitive domain (e.g. MacLean et al., 2013).

Even though the link between sociality and cognition has received much attention, most studies have been conducted in mammals and birds with investigations in other taxa lacking, including reptiles (Speechley et al., 2024). This gap might be linked to the still prevailing, but shown to be incorrect, view of reptiles being asocial and cognitively limited (Font et al., 2023; Szabo et al. 2021). Social cognition involves not just widely studied phenomena such as social learning or highly complex processes such as knowledge attribution (i.e. “theory of mind”), but more subtle phenomena such as recognising and remembering specific individuals, detecting specific social information and responding appropriately to the gathered information (Kavaliers and Choleris, 2017; Seyfarth and Cheney, 2015; Shettleworth, 2009). A growing body of literature has demonstrated that reptiles possess good cognitive abilities (Burghardt, 2013; Szabo et al., 2021) and even (seemingly) “non-social” reptiles are capable of social learning (e.g. Damas-Moreira et al., 2018; Wilkinson et al., 2010). Furthermore, especially Squamates (lizards, snakes and worm lizards) express a large diversity in social complexity (Doody et al., 2021; Whiting and While, 2017). Consequently, Squamates provide an exciting opportunity to study the evolution of social cognition in relation to social complexity using a comparative approach.

Squamates rely heavily on semiochemicals (one or more chemicals that influence the behaviour of conspecifics) for intra-specific social communication (Martín and López, 2024; Mason and Parker, 2010). The use of semiochemicals for such communication is beneficial because they can be deposited without the receiver present, last for a long time and can be detected without the sender present (Norris and Lopez, 2011). Squamates have a highly developed vomeronasal system with which they process both volatile and non-volatile compounds collected with their tongue (Norris and Lopez, 2011). As such, recognition, discrimination and interest in a chemical can be easily quantified by recording the frequency of sampling, also called tongue-flicking (Cooper, 1994; 1998). This quantification method has been used widely to gain insights into Squamate intra-specific social chemical ecology. For example, self-other discrimination based on chemicals has been demonstrated in a range of squamate species (lizards: Aguilar et al., 2009; Szabo and Ringler, 2023; snakes: Burghardt et al, 2021; Chiszar et al., 1991; Freiburger et al., 2024; worm lizards: Martín et al., 2020). Furthermore, different squamate species can discriminate familiar versus unfamiliar individuals in a territorial (e.g. Aragón et al., 2001), and a mating context (e.g. Cooper, 1996; Martín et al., 2020; Verger et al., 2024) as well as in the context of parental care (e.g. Bull et al., 1994; Martín et al., 2021). Moreover, chemical secretions might carry information about sex (e.g. Cooper and Pèrez-Mellado, 2002; Martín et al., 2020), size (e.g. Labra, 2006; Martín et al., 2024; Shine et al., 2003), age (e.g. Gabirot et al., 2012; López et al., 2003), kinship (e.g. Bull et al., 2001; Lena and de Fraipont, 1998; O'Connor and Shine, 2006; Pernetta et al., 2009), group membership (e.g. Bull et al., 2000), reproductive status (e.g. Cooper and Pèrez-Mellado, 2002), health (e.g. Martín et al., 2024), dominance status (e.g. Martín et al., 2007) and even individual identity (e.g. Bull et al., 1999; Carazo et al., 2008; Mangiacotti et al., 2019). A recent phylogenetic analysis highlighted the potential important role of this social chemical communication in lizard social evolution linking the presence of signalling glands to the evolution of social aggregations (Baeckens and Whiting, 2021). Given the diversity in information content within the chemical signals of Squamates and their diverse social expression it is surprising that chemical social communication has not yet been considered from a social cognitive perspective.

Therefore, the aim of this paper is to highlight the potential benefits of utilising chemical communication to better understand social cognitive skills and their relationship to social expression in Squamates, and hopefully, inspire future work into this fascinating topic. I first performed a systematic literature search in order to highlight some studies which provide excellent foundational work on which future investigation with a more social cognitive focus can build upon. Then, I will shortly provide some knowledge gaps that need to be filled to produce a complete picture of social cognition based on chemicals in Squamates. And finally, I will provide some broader future directions that can produce novel insights into the evolution of adaptive social cognitive skills to deal with social challenges.

A solid foundation - model studies in Squamates

I performed a systematic literature search in August 2024 to evaluate the number of studies in Squamates that focus on intra-specific chemical communication (for details on the search results see Szabo, 2024). In total I identified 152 studies focusing on 97 species (30 snakes, 65 lizards and 2 worm lizards; for more details on the search and a full list of the selected literature see Szabo, 2024). Given the vast diversity of Squamates which include about 12,386 extant species (as of January 2025; Uetz et al., 2025), our understanding of their use of chemicals for social communication is still limited. Nonetheless, though small, the literature is diverse. In the following sections, I present some selected studies that provide a solid foundation from which to delve deeper into Squamate chemical-based social cognition.

Selected studies on intra-specific chemical communication based on tongue-flicks in Squamates

Lizards

An interesting model species is the Tokay gecko (*Gekko gecko*), which I have used in my research. This is a social lizard species that forms pairs, shows biparental care and family group living (Grossmann, 2007), with natural variation in pair association (in the lab, unpublished data) and family group size (Grossmann, 2007). In our research, we have demonstrated that these lizards can discriminate their own chemicals from those of same-sex unfamiliar conspecifics. They also show self-directed behaviour and increase the sampling rate (tongue-flicks) of their own chemicals in response to the chemicals of same-sex unfamiliar conspecifics. Importantly, Tokay geckos can use both skin derived and faecal chemicals to make the discrimination (Figure 1; Szabo and Ringler, 2023). Self-recognition is an important ability especially in a social context to be able to recognize one’s own home range or territory as well as recognise chemicals left by conspecifics such as territory neighbours or intruders to make appropriate decisions regarding territory defence (Freiburger et al., 2024).

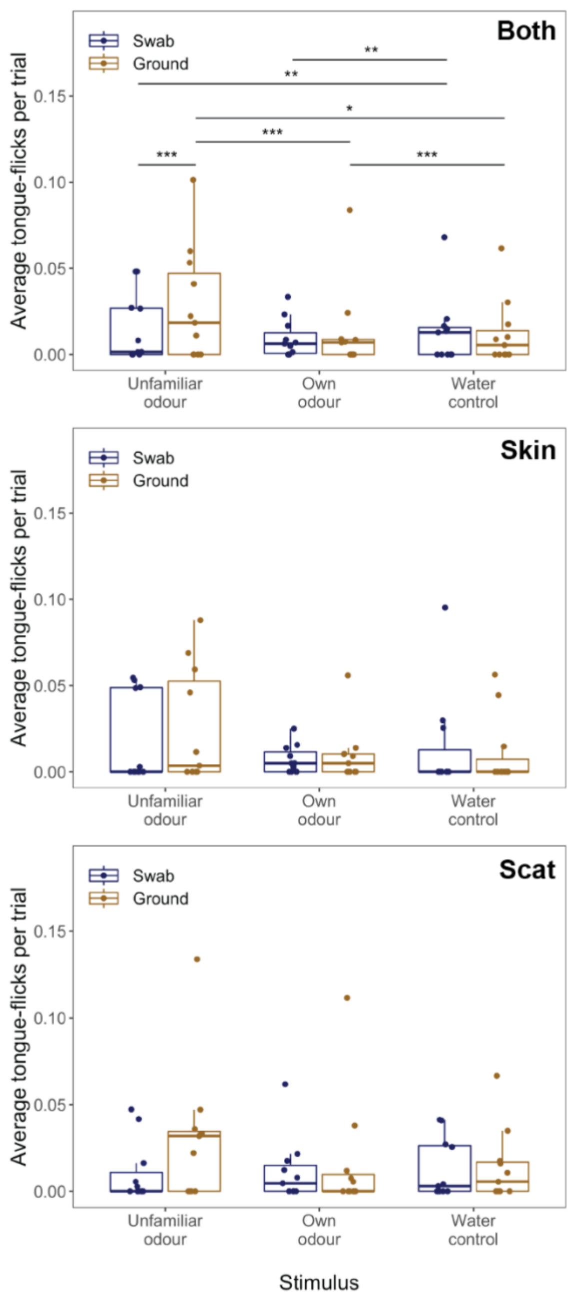

Figure 1. Boxplots of average tongue flick responses towards different stimuli presented on swabs within the lizards' home enclosure. Swab-directed tongue flicks are defined as the tip of the tongue pointing towards the swab during tongue flicking. Ground-directed tongue flicks are defines as the head and tongue tip pointing towards the substrate (e.g. ground, wall) during tongue flicking. The bold line indicates the median, the upper edge of the box represents the upper quartile, the lower edge the lower quartile, the whisker the maximum and minimum, dots represent individual data. Top panel shows all data (responses towards skin and faecal chemicals) while the bottom two show data for responses to skin and scat (faecal) chemicals separated. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Figures were taken and modified from Szabo and Ringler, 2023.

After establishing these lizards' ability to discriminate different chemical stimuli, we proceeded to investigate their ability to discriminate familiar from potential new mates and remember familiar mates. Tokay geckos form pairs that perform biparental care in the form of protection of eggs and hatchlings from predators which might be unfamiliar conspecific individuals (Grossmann, 2007). Therefore, recognizing a familiar mates' chemicals to make appropriate decisions regarding offspring protection is important in this species. We found that both male and female geckos can discriminate between familiar and potential new mates but they showed sex specific responses. Females showed more interest (higher tongue flick rate) towards the chemical of an unfamiliar male, while males showed more interest in the chemical of a familiar female. Interestingly, males also discriminated their own chemicals from that of their familiar female, showing that they do not just simply label the female with their own chemicals to make the discrimination. Finally, discrimination ability vanishes four to six weeks after separation from the partner indicating that constant reinforcement is needed for geckos to continue to recognize their mating partner (Verger et al., 2024; Figure 2).

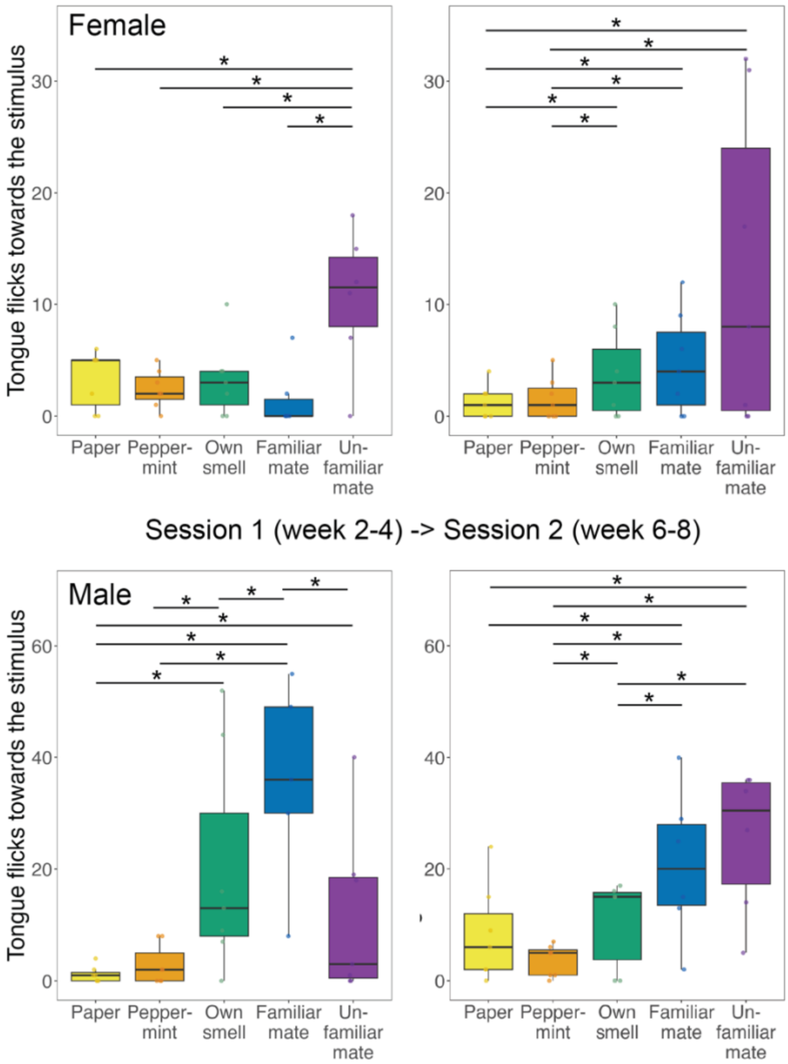

Figure 2. Boxplots of tongue flick responses towards different stimuli presented on a piece of filter paper within a glass enclosure. Dots indicate individual responses. The bold line indicates the median, the upper edge of the box represents the upper quartile, the lower edge the lower

quartile, the whisker the maximum and minimum, dots represent individual data. The top two figures show females responses in the first and second session of the experiment, while the bottom two figures show males responses. * $p < 0.05$, **. Figures were taken and modified from Verger and colleagues (2024).

Snakes

The vast majority of studies in snakes focuses on scent trailing behaviour in males which occurs in the mating season and aims at finding mates (Ford, 1986). However, more recent studies have started to link chemical recognition and discrimination to the sociobiology of different species, especially focusing on differences in self-recognition. These studies show interesting results. For example, social Eastern gartersnakes (*Thamnophis sirtalis sirtalis*) aggregate frequently across the year with conspecifics (Skinner and Miller, 2020), while more solitary ball pythons (*Python regius*) do not aggregate into groups (Gardner et al., 2016). While gartersnakes show increased interest (tongue-flicks) in their marked own scent compared to their own scent, the mark alone and the marked scent of a familiar conspecific, ball pythons show no such discrimination (Freiburger et al., 2024). This difference could be attributed to a range of differences in the species ecology, including their feeding ecology, habitat and sociobiology. However, interestingly, both species, but especially ball pythons, show great individual variation in their responses (Figure 3). Furthermore, both gartersnakes and ball pythons show large variation in responses in those conditions including the scent of a familiar individual. Even though the authors state that snakes were familiar, only garter snakes were housed in groups, and memory of a familiar scent can be limited without constant reinforcement (in geckos; Verger et al., 2024). Therefore, some individuals might have not recognised the scent of familiar individuals as “familiar” which could have increased variation.

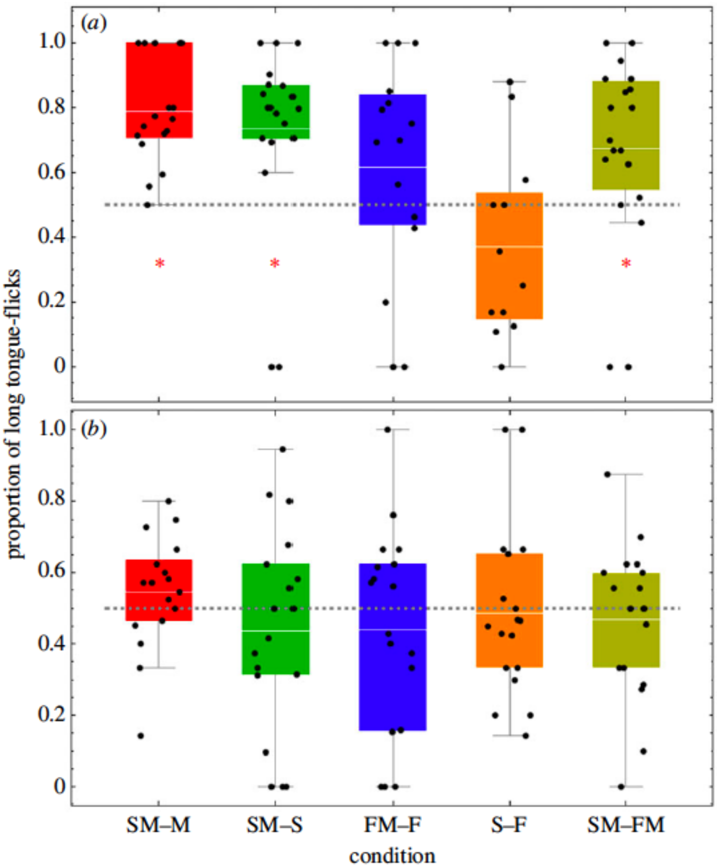

Figure 3. Proportion of tongue-flicks directed to the stimulus of interest (listed first) for gartersnakes (a) and ball pythons (b). Black dots indicate individual data; white lines inside the bars give means; the bars extend from the 25th to the 75th quantiles, and error bars show 95% confidence intervals. Red asterisks indicate conditions in which the evidence indicated a very strong preference for the stimulus of interest: S, self; M, mark; SM, self + mark; F, familiar conspecific; FM, familiar conspecific + mark. Figure taken from Freiburger et al., 2024.

As a social species, gartersnakes have been the focus of a large number of studies on the use of intra-specific chemicals (Szabo, 2024). A study in juvenile Eastern gartersnakes without previous experience with conspecific chemicals revealed only weak evidence for self-recognition. Females did not differentiate between their own and chemicals of conspecifics but could differentiate individuals based on what diet they were fed. While males could discriminate their own chemicals from those of a sibling on the same diet as well as discriminate individuals based on diet (Burghardt et al., 2021). These results together with the findings of Freiburger and colleagues (2024) suggest that experience with chemicals might be important for the development of chemical recognition and discrimination, however, research on the development of such skills is almost entirely missing from the literature (but see Léna et al., 2000 in a lizard species).

Worm lizards

Worm lizards are fossorial animals and our knowledge about their social behaviour is limited due to the difficulty of studying these animals under natural conditions. Nonetheless, two studies focus on social chemical communication in *Trogonophis wiegmanni*, a species that is frequently observed in social aggregations (Martín et al., 2011). More specifically, they are often found in pairs (more frequently so in the breeding season) and juveniles are often found with adults, most often with a female (Martín et al., 2011). Similar to Tokay geckos (Verger et al., 2024), male *T. wiegmanni* respond stronger to the chemicals of a familiar compared to an unfamiliar female mate, while females respond stronger to an unfamiliar male compared to their familiar mate (Figure 4). Martín and colleagues' hypothesis that chemosensory discrimination of female scent marks by males might facilitate pair bonding and mate guarding but might not be related to parental care as another study showed that only females, but not males, discriminate between familiar and unfamiliar juveniles (Martín et al., 2021). However, about 50% of males did show an ability to discriminate between familiar and unfamiliar juveniles but what causes this variation is unclear (Martín et al., 2021). Male *T. wiegmanni* also respond stronger to the chemicals of an unfamiliar same-sex conspecific compared to their own odour while females do not (Martín et al., 2020; Figure 4). This finding is contrary to Tokay geckos (Szabo and Ringler, 2023) in which females showed the same responses as *T. wiegmanni* males. Female Tokay geckos are aggressive towards other females while it is unclear if this is also the case for *T. wiegmanni* females, which could potentially explain the difference in ability. Finally, juvenile *T. wiegmanni* tongue flick more towards the chemicals of familiar adults (male and female) compared to an unfamiliar male which points towards an influence of experience on discrimination ability (Martín et al., 2021) similar to gartersnakes described above.

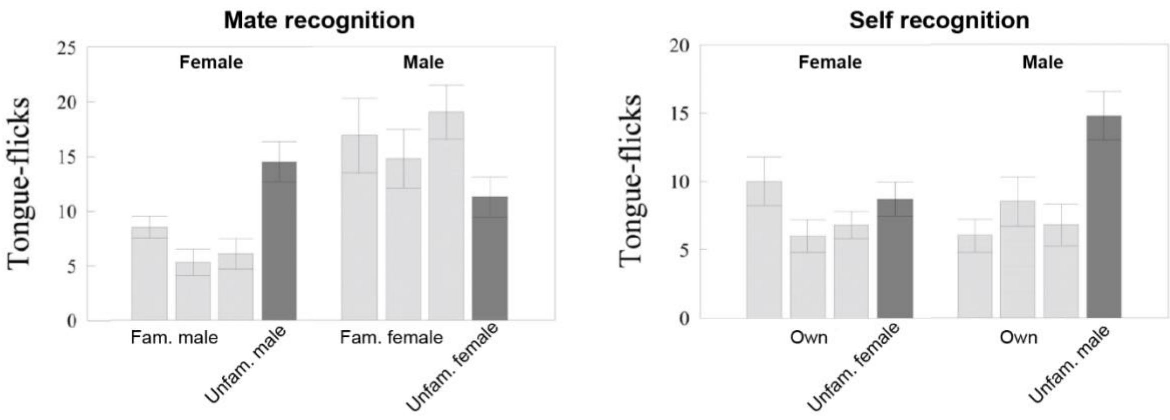

Figure 4. Average (± SE) number of tongue flicks towards different chemical stimuli emitted by male and female *T. wiegmanni*. A habituation-dishabituation methods was used to quantify discrimination ability across stimuli (habituation trials in light grey and dishabituation trials in dark grey). Data for mate- as well as self-recognition are shown. Fam., familiar; unfam., unfamiliar. Figures were taken and modified from Martín and colleagues (2020).

All these examples take the sociobiology of the tested species into account to better understand their chemical recognition and discrimination abilities. However, so far, individual differences and their consequences or how decision making is related to recognition and discrimination ability has not been well studied. In the next section, I will describe research methods to study social cognition in a very well-studied taxa that also rely heavily on chemicals to communicate in a social context: rodents. This knowledge will help to delve deeper into squamate social semiochemical cognition.

Liking well-established social cognitive research on rodents to Squamates

Mate choice in rodents has been considered the outcome of a social cognitive process. It involves decisions regarding who to mate with and when, a process in which the recognition and discrimination of olfactory cues plays a crucial role (Beach 1942; Kavaliers and Choleris, 2017). Similar to Squamates (see above), rodents detect information regarding age, sex, kinship, familiarity, dominance status, reproductive state and body condition as well as individual identity based on chemicals (reviewed in Johnston, 2003). Mate choice is reliant on the detection and processing of this information leading to social decision making and consequently appropriate social behaviour and mating (Kavaliers and Choleris, 2017). Considering the parallels between rodent and Squamate social recognition ability, researchers can utilise similar techniques to better understand social cognition in Squamates. The habituation/ dishabituation paradigm is one method used to understand social recognition in rodents. First, an animal is repeatedly presented with a social stimulus (an animal or their odour) to which it habituates (shown in a gradual decrease in responses). Thereafter, a new social stimulus is presented. If the test animal can recognise the new stimulus as different from the stimulus it was habituated to, then it will show increased responses. This paradigm can be used to address a broad range of questions from category discrimination, to individual recognition with the possibility to take different environmental context into account (Paletta et al., 2023). For example, a recent study in male *Psammodromus algirus* lizards used the habituation/ dishabituation paradigm to link age dependent reproductive strategies (territorial, dominant older males and younger sneaker males) to the ability to discriminate individuals. Older males could discriminate between individual older males but not younger males, while younger males could not discriminate individual males of any age class (Martín et al., 2024). This makes sense as territory holders need to defend against all young sneaker males (no discrimination required) but only against unfamiliar dominant males. Young males, however, need to avoid any other male to be successful (Martín et al., 2024).

Another paradigm used in rodents is the social recognition test. Here, two social stimuli are repeatedly presented at the same time. Test animals are allowed to investigate both across trials. In the test phase, one stimulus is replaced with a new stimulus and if the new stimulus is investigated more, then it shows the test animal can recognise the familiar stimulus and discriminate it from the new stimulus (Paletta et al., 2023). Furthermore, the duration between training and test can be varied to study recognition memory. A memory of familiar individuals is important in the establishment of social hierarchies, mate choice decisions and parental care (Jacobs et al., 2016). Together, the habituation/ dishabituation and social recognition paradigm are excellent methods to answer questions regarding what information animals can detect and discriminate.

For a comprehensive understanding, it is important to also consider the subsequent use of the information gathered from recognition and discrimination in decision making, but this is far less well studied in Squamates (Mason and Parker, 2010). Nonetheless, social information is used during mate choice (e.g. Bruinjé et al., 2022), settlement (e.g. Léna et al., 2000), retreat site (e.g. Scott et al., 2013; Thompson et al., 2020), and foraging decisions (e.g. Clark, 2007) as well as in agonistic encounters (e.g. López and Martín, 2002). However, much research still needs to be done to understand the chemically mediated social decisions in these animals (e.g. utilising choice tests). For example, studies focus on group average ability rather than individual differences even though results can show considerable individual variation (e.g. Martín et al., 2021). Furthermore, the causes (e.g. genetic or environmental based developmental plasticity) and consequences of this variation especially under natural conditions in the wild (relationship between decision making and fitness; Thornton and Lukas, 2012) are poorly understood. For example, dispersal in juvenile common lizards (*Zootoca vivipara*) is associated with attraction and aversion to maternal chemical cues. These differences are already present at birth (common lizards are a viviparous species) and are not influenced by early experience of being raised with or without their mother (Léna et al., 2000). Unfortunately, this study did not link individual ability to choice and dispersal decisions. For future research, it will be important to move beyond studies testing if a species can recognise or discriminate conspecific chemicals or not, towards quantifying individual ability and the source of individual variation such as past experiences, the demands of the social environment, and importantly, if individual variation has consequences for social interactions, decision making and consequently individual fitness under natural conditions. Only then will we be able to grasp the full extent of social cognition in Squamates.

A bright future: semiochemical-based social cognition in Squamates

Heritable individual phenotypic variation is the basis on which selections acts upon (Darwin, 1859; Thornton and Lukas, 2012). Therefore, understanding the full extent and variation of chemical-based social cognitive abilities within species is of great interest to link species-specific environmental and sociobiological characteristics to the information content of the chemical signals, detection ability of this information and the decision outcomes and fitness consequences based on the collected information. Such detailed information provides the substrate for comparative studies that focus rather on broader questions regarding the selective pressures driving the evolution of social cognitive abilities (Völter et al., 2018). I believe that Squamates are a powerful comparative model system in this regard, because (1) a wide range of information is encoded reliably in the chemical signals of Squamates, (2) the detection of and preference for this information can be measured through a combination of test on tongue-flick rates and choice tests across species (Szabo, 2024), and (3) Squamates express a large diversity in sociality including parthenogenetic species, parental care level (no care to short-term care to long-term care until offspring reach sexual maturity) and facultative sociality (from no group living to long-term stable family groups) (Doody et al., 2021; Gardner et al., 2015; Rheubert et al., 2014; Somma, 2003; Whiting and While, 2017). Some lizard species have already been successfully used to understand potential environmental factors driving the evolution of cognition. For example, a study on 13 lacertid species showed a link between behavioural flexibility (reversal learning) and environmental variability (De Meester et al., 2022). Similarly, by testing semiochemical social cognition across species, we can answer broad evolutionary questions about what information might be relevant, and therefore detected, and how this information is used for decision making under different social conditions. For example, depending on the mating system, species should express appropriate social semiochemical cognitive abilities that will help them select the most appropriate mating partner. If females choose, they need to be able to reliably detect male quality and be able to discriminate across males. If females mate multiple times, they should be able to discriminate and remember specific males to avoid remating. On the other hand, if female do not choose, then they would not need to discriminate and remember males. The facultative social nature of Squamates also provides a new perspective on the importance of social cognition when species naturally experience variation in sociality that exceeds what is possible in more obligate social species. For instance, even in species that show parental care, not all offspring might receive care (e.g. some siblings disperse while others stay; While et al., 2009) which can be related to semiochemical social cognitive abilities (e.g. Léna et al., 2000). A broader phylogenetic approach to the study of the evolution of cognition in relation to sociality (Social Intelligence Hypothesis) will provide a novel perspective on what types of social aggregations exert selective pressure on which social cognitive abilities.

Conclusion

Social behaviour and cognition might not be what we readily associate with lizards, snakes and worm lizards. Their social interactions can be inconspicuous, especially when strongly relying on channels other than visual communication with its obvious colours and elaborate display behaviour. However, those who dare to venture into the unknown with a keen eye and an open mind, will discover a new world, not as flashy but surely as captivating. I believe that there is much to learn about Squamate sociality and the evolution of social behaviour through the study of Squamate semiochemical-based social cognition.

Acknowledgements

This work was supported by the University of Bern and Gent University Methusalem Project (01M00221). I would like to thank Charlène Gémard and Isabel Damas-Moreira for their comments on an early draft of this paper.

References

Aguilar, P. M., Labra, A., & Niemeyer, H. M. (2009). Chemical self-recognition in the lizard *Liolaemus fitzgeraldi*. Journal of Ethology, 27(1), 181-184. doi:10.1007/s10164-008-0088-x

Aragón, P., López, P., & Martín, J. (2001). Discrimination of femoral gland secretions from familiar and unfamiliar conspecifics by male Iberian rock-lizards, Lacerta monticola. Journal of Herpetology, 35(2), 346-350.

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. Nature, 554(7692), 364-367. https://doi.org/10.1038/nature25503

Baeckens, S., & Whiting, M. J. (2021). Investment in chemical signalling glands facilitates the evolution of sociality in lizards. Proceedings of the Royal Society B - Biological Sciences, 288(1945), 20202438.

Beach, F. A. (1942). Analysis of the stimuli adequate to elicit mating behavior in the sexually inexperienced rat. Journal of Comparative Psychology, 33(2), 163.

Berhane, J. F., & Gazes, R. P. (2020). Social monkeys learn more slowly: Social network centrality and age are positively related to learning errors by capuchin monkeys (*Cebus [Sapajus] apella*). Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale, 74(3), 228.

Borrego, N., & Gaines, M. (2016). Social carnivores outperform asocial carnivores on an innovative problem. Animal Behaviour, 114, 21-26.

Bruinjé, A. C., Paiva, T. M. D., & Costa, G. C. (2022). Multimodal female mate choice in a polymorphic flat rock lizard. Behavioral Ecology and Sociobiology, 76(6). doi:10.1007/s00265-022-03181-x

Bull, C. M., Doherty, M., Schulze, L. R., & Pamula, Y. (1994). Recognition of offspring by females of the Australian skink, Tiliqua rugosa. Journal of Herpetology, 28(1), 117-120.

Bull, C. M., Griffin, C. L., Bonnett, M., Gardner, M. G., & Cooper, S. J. B. (2001). Discrimination between related and unrelated individuals in the Australian lizard *Egernia striolata*. Behavioral Ecology and Sociobiology, 50(2), 173-179.

Bull, C. M., Griffin, C. L., Lanham, E. J., & Johnston, G. R. (2000). Recognition of pheromones from group members in a gregarious lizard, *Egernia stokesii*. Journal of Herpetology, 34(1), 92-99. doi:10.2307/1565244

Bull, C. M., Griffin, C. L., & Perkins, M. V. (1999). Some properties of a pheromone allowing individual recognition, from the scats of an Australian lizard, Egernia striolata. Acta Ethologica, 2(1), 35-42.

Burghardt, G. M. (2013). Environmental enrichment and cognitive complexity in reptiles and amphibians: Concepts, review, and implications for captive populations. Applied Animal Behaviour Science, 147(3-4), 286-298.

Burghardt, G. M., Partin, A. M., Pepper, H. E., Steele, J. M., Liske, S. M., Stokes, A. E., Lathan, A. N., Springer, C. M., Jenkins, M. S. (2021). Chemically mediated self-recognition in sibling juvenile common gartersnakes (*Thamnophis sirtalis*) reared on same or different diets: evidence for a chemical mirror? Behaviour, 158(12-13), 1169-1191. doi:10.1163/1568539X-bja10131

Byrne, R. W., & Whiten, A. (1988). Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes, and humans. Behavior and Philosophy, 18(1), 73-75.

Carazo, P., Font, E., & Desfilis, E. (2008). Beyond 'nasty neighbours' and 'dear enemies'? Individual recognition by scent marks in a lizard (*Podarcis hispanica*). Animal Behaviour, 76, 1953-1963. doi:10.1016/j.anbehav.2008.08.018

Chance, M. R. A., & Mead, A. P. (1953). Social behaviour and primate evolution. Symposium of the Society for Experimental Biology and Evolution, 7, 395-439.

Chiszar, D., Smith, H. M., Bogert, C. M., & Vidaurri, J. (1991). A chemical sense of self in timber and prairie rattlesnakes. Bulletin of the Psychonomic Society, 29(2), 153-154. doi:10.3758/BF03335221

Cooper, W. E. (1996). Chemosensory recognition of familiar and unfamiliar conspecifics by the scincid lizard Eumeces laticeps. Ethology, 102(6), 454-464. doi:10.1111/j.1439-0310.1996.tb01139.x

Cooper, W. E. (1994). Chemical discrimination by tongue-flicking in lizards: a review with hypotheses on its origin and its ecological and phylogenetic relationships. Journal of Chemical Ecology 20, 439-487.

Cooper, W. E. (1998). Evaluation of swab and related tests as a bioassay for assessing responses by squamate reptiles to chemical stimuli. Journal of Chemical Ecology 24, 841-866. DOI 10.1023/A:1022373517653.

Cooper, W. E., & Pèrez-Mellado, V. (2002). Pheromonal discriminations of sex, reproductive condition, and species by the lacertid lizard <i>Podarcis hispanica</i>. Journal of Experimental Zoology, 292(6), 523-527. doi:10.1002/jez.10089

Damas-Moreira, I., Oliveira, D., Santos, J. L., Riley, J. L., Harris, D. J., & Whiting, M. J. (2018). Learning from others: an invasive lizard uses social information from both conspecifics and heterospecifics. Biology letters, 14(10), 20180532.

Darwin, C. (1859). On the origin of species by means of natural selection (Vol. 167). John Murray, London.

De Meester, G., Van Linden, L., Torfs, J., Pafilis, P., Šunje, E., Steenssens, D., Zulčić, T., Sassalos, A., & Van Damme, R. (2022). Learning with lacertids: Studying the link between ecology and cognition within a comparative framework. Evolution, 76(11), 2531-2552.

Doody, J. S., Dinets, V., & Burghardt, G. M. (2021). The secret social lives of reptiles. JHU Press.

Font, E., Burghardt, G. M., & Leal, M. (2023). Brains, behaviour, and cognition: Multiple misconceptions. In Health and welfare of captive reptiles (pp. 211-238). Cham: Springer International Publishing.

Ford, N. B. (1986). The role of pheromone trails in the sociobiology of snakes. In Chemical Signals in Vertebrates 4: Ecology, Evolution, and Comparative Biology (pp. 261-278). Boston, MA: Springer US.

Freiburger, T., Miller, N., & Skinner, M. (2024). Olfactory self-recognition in two species of snake. Proceedings of the Royal Society B-Biological Sciences, 291(2020). doi:10.1098/rspb.2024.0125

Gabirot, M., Picerno, P., Valencia, J., Lopez, P., & Martin, J. (2012). Chemosensory age discrimination in the snake *Boa constrictor* (Serpentes: Boidae). Revista De Biologia Tropical, 60(4), 1603-1611.

Gardner, M. G., Pearson, S. K., Johnston, G. R., & Schwarz, M. P. (2016). Group living in squamate reptiles: a review of evidence for stable aggregations. Biological Reviews, 91(4), 925-936.

Humphrey, N. K. (1976). The social function of intellect. In Growing Points in Ethology (eds Bateson, P. P. G., and Hinde, R. A.), pp. 303-317. Cambridge University Press, Oxford.

Jacobs, S. A., Huang, F., Tsien, J. Z., & Wei, W. (2016). Social recognition memory test in rodents. Bio-protocol, 6(9), e1804-e1804.

Jolly, A. (1966). Lemur Social Behavior and Primate Intelligence: The step from prosimian to monkey intelligence probably took place in a social context. Science, 153(3735), 501-506.

Kavaliers, M., & Choleris, E. (2017). Social cognition and the neurobiology of rodent mate choice. Integrative and Comparative Biology, 57(4), 846-856.

Labra, A. (2006). Chemoreception and the assessment of fighting abilities in the lizard *Liolaemus monticola*. Ethology, 112(10), 993-999. doi:10.1111/j.1439-0310.2006.01256.x

Léna, J. P., & de Fraipont, M. (1998). Kin recognition in the common lizard. Behavioral Ecology and Sociobiology, 42(5), 341-347. doi:10.1007/s002650050446

Léna, J. P., De Fraipont, M., & Clobert, J. (2000). Affinity towards maternal odour and offspring dispersal in the common lizard. Ecology Letters, 3(4), 300-308. doi:10.1046/j.1461-0248.2000.00155.x

López, P., Aragón, P., & Martín, J. (2003). Responses of female lizards, Lacerta monticola, to males' chemical cues reflect their mating preference for older males. Behavioral Ecology and Sociobiology, 55, 73-79.

López, P., & Martín, J. (2002). Chemical rival recognition decreases aggression levels in male Iberian wall lizards, <i>Podarcis hispanica</i>. Behavioral Ecology and Sociobiology, 51(5), 461-465. doi:10.1007/s00265-001-0447-x

MacLean, E. L., Sandel, A. A., Bray, J., Oldenkamp, R. E., Reddy, R. B., & Hare, B. A. (2013). Group size predicts social but not nonsocial cognition in lemurs. PLoS One, 8(6), e66359. https://doi.org/10.1371/journal.pone.0066359

Mangiacotti, M., Gaggiani, S., Coladonato, A. J., Scali, S., Zuffi, M. A. L., & Sacchi, R. (2019). First experimental evidence that proteins from femoral glands convey identity-related information in a lizard. Acta Ethologica, 22, 57-65.

Martín, J., García, E. R., Ortega, J., & López, P. (2020). How to maintain underground social relationships? Chemosensory sex, partner and self recognition in a fossorial amphisbaenian. PLoS One, 15(8). doi:10.1371/journal.pone.0237188

Martín, J., & López, P. (2024). Pheromones and reproduction in reptiles. In Hormones and Reproduction of Vertebrates, Volume 3 (pp. 135-163). Academic Press.

Martín, J., López, P., Rodríguez-Ruiz, G., Cuervo, J. J., Sacchi, R., & Mangiacotti, M. (2024). Age-dependent self-and individual chemosensory discrimination in male Psammodromus algirus lizards is based on lipids and proteins from their scent. Behavioral Ecology and Sociobiology, 78(12), 125.

Martín, J., Moreira, P. L., & López, P. (2007). Status-signalling chemical badges in male Iberian rock lizards. Functional Ecology, 21(3), 568-576.

Martín, J., Polo-Cavia, N., Gonzalo, A., López, P., & Civantos, E. (2011). Social aggregation behaviour in the North African amphisbaenian Trogonophis wiegmanni. African Journal of Herpetology, 60(2), 171-176.

Martín, J., Raya-García, E., Ortega, J., & López, P. (2021). Offspring and adult chemosensory recognition by an amphisbaenian reptile may allow maintaining familiar links in the fossorial environment. PeerJ, 9. doi:10.7717/peerj.10780

Martín, J., Rodríguez-Ruiz, G., Navarro-Castilla, A., Barja, I., & López, P. (2024). Blind date: female fossorial amphisbaenians prefer scent marks of large and healthy males. Integrative Zoology. doi:10.1111/1749-4877.12802

Mason, R. T., & Parker, M. R. (2010). Social behavior and pheromonal communication in reptiles. Journal of Comparative Physiology A, 196, 729-749.

Miller, G. F., & Todd, P. M. (1998). Mate choice turns cognitive. Trends in cognitive sciences, 2(5), 190-198.

Norris, D. O., & Lopez, K. H. (Eds.). (2011). Hormones and Reproduction of Vertebrates, Volume 3: Reptiles. Elsevier.

O'Connor, D. E., & Shine, R. (2006). Kin discrimination in the social lizard *Egernia saxatilis* (Scincidae). Behavioral Ecology, 17(2), 206-211. doi:10.1093/beheco/arj019

Paletta, P., Aspesi, D., Bass, N., & Choleris, E. (2023). The Study of Social Cognition: Social Recognition and Social Learning in Laboratory Rats and Mice. In Animal Models of Reproductive Behavior (pp. 1-31). New York, NY: Springer US.

Pernetta, A. P., Reading, C. J., & Allen, J. A. (2009). Chemoreception and kin discrimination by neonate smooth snakes, Coronella austriaca. Animal Behaviour, 77(2), 363-368.

Rheubert, J. L., Siegel, D. S., & Trauth, S. E. (Eds.). (2014). Reproductive biology and phylogeny of lizards and tuatara. CRC Press.

Rubenstein, D. R., & Abbot, P. (Eds.). (2017). Comparative social evolution. Cambridge University Press.

Scott, M. L., Whiting, M. J., Webb, J. K., & Shine, R. (2013). Chemosensory discrimination of social cues mediates space use in snakes, Cryptophis nigrescens (Elapidae). Animal Behaviour, 85(6), 1493-1500.

Servedio, M. R., & Dukas, R. (2013). Effects on population divergence of within-generational learning about prospective mates. Evolution, 67(8), 2363-2375.

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. Animal Behaviour, 103, 191-202.

Shettleworth, S. J. (2009). Cognition, Evolution, and Behavior. Oxford University Press.

Shine, R., Phillips, B., Waye, H., LeMaster, M., & Mason, R. T. (2003). Chemosensory cues allow courting male garter snakes to assess body length and body condition of potential mates. Behavioral Ecology and Sociobiology, 54(2), 162-166. doi:10.1007/s00265-003-0620-5

Skinner, M., & Miller, N. (2020). Aggregation and social interaction in garter snakes (Thamnophis sirtalis sirtalis). Behavioral Ecology and Sociobiology, 74(5), 51.

Somma, L. A. (2003). Parental Behavior in Lepidosaurian and Testudinian Reptiles: A Literature Survey. Malabar, US: Krieger Publishing Company.

Speechley, E. M., Ashton, B. J., Foo, Y. Z., Simmons, L. W., & Ridley, A. R. (2024). Meta-analyses reveal support for the Social Intelligence Hypothesis. Biological Reviews. https://doi.org/10.1111/brv.13103

Szabo, B. (2024). Literature list on intraspecific chemical communication in Squalates. Retrieved from https:/doi.org/10.17605/OSF.IO/J9RXN

Szabo, B., Noble, D. W., & Whiting, M. J. (2021). Learning in non-avian reptiles 40 years on: advances and promising new directions. Biological Reviews, 96(2), 331-356.

Szabo, B., & Ringler, E. (2023). Geckos differentiate self from other using both skin and faecal chemicals: evidence towards self-recognition? Animal Cognition, 26(3), 1011-1019. doi:10.1007/s10071-023-01751-8

Thompson, S. A., Pearson, S. K., While, G. M., Chapple, D. G., & Gardner, M. G. (2020). Scat on the doorstep: Refuge choice in a group-living lizard is influenced by the presence of scat piles. Austral ecology, 45(4), 426-434.

Thornton, A., & Lukas, D. (2012). Individual variation in cognitive performance: developmental and evolutionary perspectives. Philosophical Transactions of the Royal Society B: Biological Sciences, 367(1603), 2773-2783.

Toor, I., Clement, D., Carlson, E. N., & Holmes, M. M. (2015). Olfaction and social cognition in eusocial naked mole-rats, *Heterocephalus glaber*. Animal Behaviour, 107, 175-181.

Uetz, P., Freed, P, Aguilar, R., Reyes, F., Kudera, J. & Hošek, J. (eds.) (2025) The Reptile Database, http://www.reptile-database.org, accessed [06/02/25]

Verger, M. O., Devillebichot, M., Ringler, E., & Szabo, B. (2024). Sex-specific discrimination of familiar and unfamiliar mates in the Tokay gecko. Animal Cognition, 27(1), 55.

Völter, C. J., Tinklenberg, B., Call, J., & Seed, A. M. (2018). Comparative psychometrics: establishing what differs is central to understanding what evolves. Philosophical Transactions of the Royal Society B: Biological Sciences, 373(1756), 20170283.

Ward, A., & Webster, M. (2016). Sociality: the behaviour of group-living animals (Vol. 407). Berlin, Germany: Springer.

While, G. M., Uller, T., & Wapstra, E. (2009). Within-population variation in social strategies characterize the social and mating system of an Australian lizard, Egernia whitii. Austral Ecology, 34(8), 938-949.

Whiting, M. J., & While, G. M. (2017). Sociality in Lizards. Comparative social evolution, 390.

Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). Biology letters, 6(5), 614-616.

Zuberbühler, K., & Byrne, R. W. (2006). Social cognition. Current Biology, 16(18), R786-R790.