Trends in
Ecology & Evolution

CellPress

Opinion

The prenatal foundations of kin recognition

Yorick Lambreghts [1,2,*], Martin J. Whiting [2], Tobias Uller [3], Camilla M. Whittington [4], and Geoffrey M. While [1]

Kin recognition, the ability to identify genetic relatives, relies on familiarisation for the creation of recognition templates. During development, parent and embryo(s) are exposed to chemical, auditory, and tactile cues that can communicate reliable genetic information. We discuss how these cues can have organisational effects during a time of heightened phenotypic sensitivity, creating postnatal kin preferences. As familiarisation is often determined by the prenatal social environment, we argue that reproductive traits that alter the social context of the prenatal environment, such as reproductive mode, could facilitate the evolution of kin recognition. Furthermore, we outline how these effects of prenatal familiarisation can extend beyond kin recognition and play a pivotal role in the emergence and evolution of complex social behaviours.

Highlights

Kin recognition is central to social evolution, influencing cooperation, parental care, inbreeding avoidance, and group cohesion, yet we lack a clear understanding of how recognition systems originate and evolve.

Research on kin recognition has focused largely on postnatal cues, overlooking the prenatal environment where parents and embryos are intimately associated. We argue that this association can bias postnatal kin preferences.

Reproductive traits – including reproductive mode, clutch or litter size, gestation length, and gestational position – should shape opportunities for prenatal and early postnatal communication, influencing when and how kin recognition can arise.

Integrating prenatal social environments into models of kin recognition offers a new framework for understanding the emergence of recognition systems and their broader role in the evolution of social behaviour.

Kin recognition throughout the tree of life

Kin recognition is the ability of an organism to distinguish its genetic relatives from unrelated conspecifics [1]. Being able to distinguish related from unrelated individuals can have significant benefits through increased **inclusive fitness** (see Glossary) [2], for instance by allowing parents to care for their offspring (e.g., providing nourishment and protection) or preferential cooperation among relatives (e.g., nepotism). While kin recognition has been found in a wide range of organisms, including microorganisms, plants and mammals [3], there are also counter-examples where kin recognition is absent, even in contexts where recognising kin would provide substantial fitness benefits [4–6]. One potential explanation is that the evolution of kin recognition requires not just a selective environment within which recognising kin is functional, but also a developmental and ecological context that creates opportunities for kin recognition to emerge in the first place. The social interactions within those contexts are the building blocks of kin recognition that natural selection can modify and refine over time.

Kin recognition requires a period of prior familiarisation, either for recognition of specific relatives (recognition by familiarity or **direct familiarisation**) or to construct a generalised **kin template** from which a broader group of relatives can be recognised (phenotypic matching or **indirect familiarisation**) [1]. This familiarisation is typically assumed to take place in the postnatal environment, such as in a nest, where related individuals can freely interact. While postnatal familiarisation is undoubtedly important and may, in some systems, be sufficient for kin recognition to develop, individuals also regularly interact during earlier periods of development, for example, when in the womb [7]. Recent molecular, neural, and behavioural research suggests that this prenatal period may provide comparable or even more favourable conditions for familiarisation, yet its role in the emergence and evolution of kin recognition remains unknown [3].

Here, we argue that the prenatal embryonic environment constitutes a critical social context that facilitates kin familiarisation, even without selection for recognition mechanisms. Reproductive traits influence the developmental environment, thereby shaping recognition pathways to favour kin bias. These traits often co-occur with ecological and social conditions that favour kin

[1]School of Natural Sciences, University of Tasmania, Hobart, Tasmania 7001, Australia
[2]School of Natural Sciences, Macquarie University, Sydney, New South Wales 2109, Australia
[3]Department of Biology, Lund University, Lund 223 62, Sweden
[4]School of Life and Environmental Sciences, The University of Sydney, Sydney, New South Wales 2050, Australia

*Correspondence:
yorick.lambreghts@mq.edu.au
(Y. Lambreghts).

recognition after birth, suggesting that prenatal development and postnatal sociality may co-evolve in an adaptively integrated manner (Figure 1).

The developmental biology of kin recognition templates

Kin recognition requires a period of familiarisation during which individuals memorise social cues (e.g., odour profile, song characteristics, or colour patterns) from relatives and form kin templates – either individual-specific or generalised [1]. These templates, embedded in neural substrates such as the mammalian hippocampal CA2 region or lateral septum [8–10], are built from sensory cues – most commonly olfactory and/or auditory, but also visual [11–13] – encountered during a **sensitive developmental window**. Outside this window, kin recognition templates can continue to be created and updated, for example to account for ageing [14]. Despite recent advances in identifying the neural circuits involved, our understanding of how these templates are formed remains limited [15–18]. Moreover, most studies investigating the developmental basis of kin recognition rely on postnatal cross-fostering or manipulate early-life social environments to examine the role of familiarity and relatedness in kin recognition [19]. This focus on the postnatal environment overlooks a potentially more critical and underappreciated period of development: the prenatal period [20].

The prenatal environment, characterised by a combination of a high reliability of kin cues and phenotypic malleability, is ideally suited for the development of kin templates. Parent–embryo and embryo–embryo associations – particularly in species with prolonged internal development – enable consistent exposure to social cues (Box 1), including those from close kin [21–23]. Cues can be auditory [24], chemical [7], tactile [25], or even visual [26]. We expect the prenatal chemical environment to be especially well suited for the development of kin templates, given that chemosensory systems mature earlier than auditory or visual systems [27]. The prenatal environment, therefore, provides both the cues and neural plasticity necessary to bias familiarisation towards kin before postnatal interactions can take place. Kin selection can then reinforce these biases during postnatal interactions, resulting in kin recognition.

Prenatal chemical communication

During pregnancy – a collective term for oviparous brooding and viviparity [28] (Box 1) – embryonic development is characterised by an intimate association between parental (typically maternal, but in some species paternal [29]) and embryonic tissues, often involving the exchange of chemical substances. Specialised structures or substances such as a placenta or amniotic fluid play a key role in facilitating chemical communication [30,31]. For example, water, amino acids, glucose, small fatty acids, and bile salts are exchanged for embryonic metabolism [32–34]; signalling molecules such as growth factors, hormones and cytokines are excreted by the embryo in the uterus, for example causing changes to the endometrial cells required for mammalian implantation [35]; and, immune cells are exchanged to prepare embryonic immunity to the postnatal environment [36]. This prenatal chemical exposure is crucial for behavioural development and for providing opportunities for offspring to learn about their (social) environment. For instance, newborn human babies preferentially orientate towards their mother's nipple based on odour cues [37]. Similarly, maternal exposure to specific food items in rats, dogs, and humans leads to a preference towards these items in newborns [38–40]. Exposure to chemical social cues *in ovo* can also bias social behaviour – for example after hatching in birds, where chemical interactions are limited to what is deposited in the egg before shell formation, and in oviparous fishes and amphibians, where chemical interactions can take place through permeable eggs [41–43]. These studies show a clear precedence for embryonic learning of cues to which individuals can respond postnatally. If these cues reflect both shared familial identity and are sufficiently distinct across individuals to allow for familiarisation, they can be co-opted for kin recognition.

Glossary

Direct familiarisation: also known as familiarisation or association, a kin recognition mechanism based on individual recognition where familiar relatives can be recognised after a previous period of association.
Inclusive fitness: the sum of an individual's own reproductive success (direct fitness) and the reproductive success gained by helping related individuals (indirect fitness).
Indirect familiarisation: also known as phenotypic matching, a kin recognition mechanism in which familiar and unfamiliar relatives can be recognised through generalisation of a kin-level recognition template constructed during a period of familiarisation with relatives and/or one's own phenotype.
Kin templates: a metaphor for the representation of the kin phenotype in the brain.
Oviparity: spawning or laying of (un) fertilised eggs with external embryonic development.
Sensitive developmental windows: a specific developmental time period of heightened responsiveness to certain environmental stimuli or experiences.
Social evolution: an evolutionary change in the structure, organisation and/or behaviour involved in animal interactions.
Viviparity: live birth of embryos after a period of incubation inside the female reproductive tract.

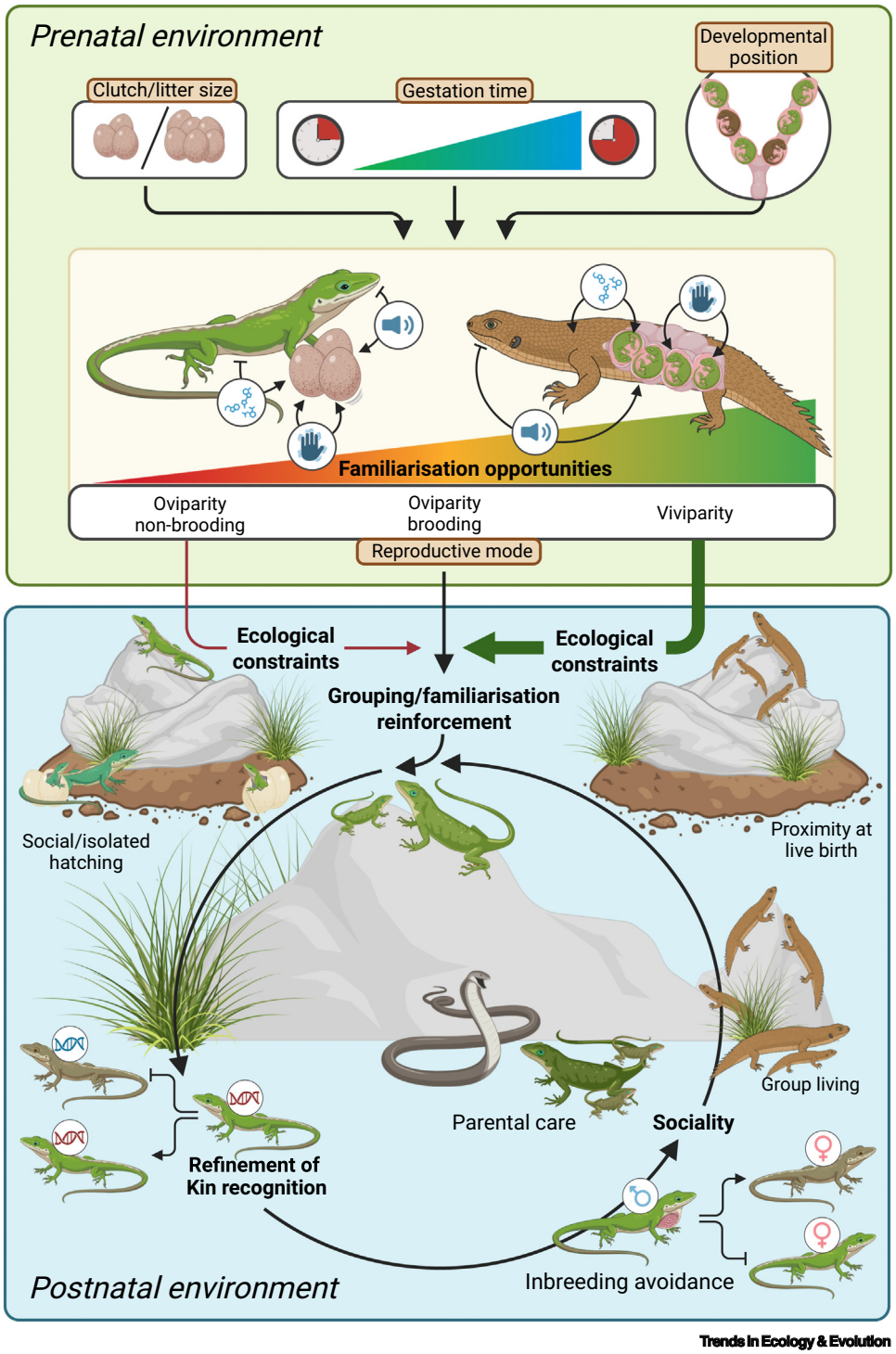

Figure 1. Framework outlining how prenatal familiarisation can affect postnatal kin recognition and sociality. Reproductive traits such as clutch/litter size, gestation period, developmental position, intimacy of parent–embryo association (e.g., via placenta versus through egg shell in uterus; not shown), and especially reproductive mode (continuum from oviparous non-brooding to viviparity) determine opportunities for familiarisation during development (green upper box).

(Figure legend continued at the bottom of the next page.)

Box 1. Parental care facilitates prenatal communication

In many species, communication between parent and offspring is crucial for successful embryo development, from ensuring an optimal microenvironment and nutrient provisioning [86] to preparing the offspring phenotype for external threats [36] or foraging opportunities [26]. Parental care affects the extent to which the developmental environment allows such communication.

In broadcast spawning species, where gametes are expelled and usually no additional care is provided, the exchange of social cues is limited to chemical compounds deposited in gametes prior to their release [87]. A certain level of conspecific interaction in other externally fertilizing species is possible, for example if embryos clump together, as is the case in many amphibians [88]. Some externally fertilising species provide parental care where developing embryos are incubated on or in the body of the parent, at sites other than the female reproductive tract. This form of parental care is referred to as oviparous brooding and can take a variety of forms. For example, females of the now extinct frog genus *Rheobatrachus* exhibited gastric brooding, where fertilised eggs are swallowed for internal incubation in the stomach [89]; the fishes *Platystacus* spp. and *Solenostomus* spp. use skin brooding to incubate embryos attached on their skin [90]; and, in seahorses (*Hippocampus* spp.), males have specialised brood pouches for embryo incubation [29,67]. In these species, communication most likely occurs via chemical cues, and a placenta may be present. Non-brooding **oviparous** species, such as birds, may also have specialised structures for embryo incubation (e.g., brood patches). Although these structures do not provide the same level of close association, communication in these systems is well documented, particularly for auditory cues [22,24,71,72,91,92]. Finally, in **viviparous** species, where embryos develop inside the female reproductive tract, parent and embryo are very closely associated, often via a placenta [30], as evidenced in many mammals.

Two key recognition cue candidates have thus far been identified, the vertebrate major histocompatibility complex (MHC) and rodent major urinary proteins (MUPs) [44,45]. Both gene complexes are highly polymorphic, contributing to individually unique scent profiles [16], and are linked to kin recognition in fishes [46–48] and mice [49]. Importantly, embryonic MHC peptides are already present before mammalian implantation [50,51], suggesting that incubating parents have access to these cues for the entire duration of embryonic development. Furthermore, in mice, MHC peptides activate the same olfactory pathways as other social cues [52], suggesting that kin recognition does not require entirely new neural machinery to develop but can instead co-opt existing chemosensory pathways.

The chemosensory pathways that mediate chemical cue detection, and consequently template construction, emerge early in embryonic development. In most vertebrates, chemical cues are detected by olfactory sensory neurons (OSNs) located in the main olfactory epithelium and/or vomeronasal organ in the mouth or nasal cavity. These OSNs project signals to the olfactory bulb (OB), where OSN axons converge into distinct glomeruli based on the type of olfactory receptor (OR) proteins they carry on their cell surface [53]. All three structures – the main olfactory epithelium, vomeronasal organ, and olfactory bulb – reach functional maturity either before birth [54–56] or soon after birth [57–59], depending on taxon. However, full maturity of olfactory machinery may not be required for early cue detection. In zebrafish (*Danio rerio*), for example, the olfactory bulb already shows patterns of activation within three days of fertilisation [60], despite maturing only after hatching [61].

While the mechanism remains poorly understood, these sensory functions likely facilitate familiarisation through feedback between cue exposure and receptivity. Receptivity to a given

Communication among parent and embryo(s) can utilise vocal, tactile, or chemical cues. In the postnatal environment (blue lower box) this familiarity can be reinforced via prolonged kin associations in the form of simple grouping. Even postnatally, certain reproductive traits – especially reproductive mode – can directly influence postnatal associations by increasing the opportunity for ecological constraints to keep closely related individuals together. For example, eggs can hatch in isolation or in the presence of parents, while close proximity is inherent in live birth. The reinforcement of initial grouping and familiarisation can lead to the emergence of kin recognition. Kin recognition may then facilitate the evolution of more complex social behaviours – such as parental care, inbreeding avoidance, or group living. In turn, increasing social complexity can further refine kin recognition abilities in a feedback loop. Figure created in BioRender. Lambreghts, Y. (2025; https://BioRender.com/c194uoc).

chemical cue is determined by the OSNs, which each express a single OR type [53]. Prior exposure to cues can have organisational effects on the neuronal topography, thus influencing neural activation patterns. For example, exposure to chemical compounds can increase chemical sensitivity through OB glomeruli enlargement or increased OR expression [62,63]. Such effects have been observed specifically in a kin recognition context in zebrafish [64]. However, prior exposure can also decrease OR transcription, or have no effect, as observed in different OR-carrying OSNs [16,63,65,66]. This observation suggests that exposure effects may depend on the specific cue–OR pair [63]. The resulting neuronal topography will then determine how cues are processed going forward, thus acting as cue-recognition templates.

The timing of the exposure to cues also matters. The earlier in development the exposure occurs, the larger the resulting changes [62]. This observation suggests that the prenatal chemical environment may potentially be more influential than the postnatal environment, for early familiarisation of cues that may later be involved in recognition. While dependent on the level of parental care provided (Box 1), the cues to which embryos are exposed overwhelmingly originate from related individuals – mother, (half-)sibling(s), or father [36,67,68]. Therefore, these cues convey highly reliable and informative genetic information [69]. This, combined with the highly malleable nature of the neuronal machinery, biases familiarisation towards kin. Selection can then act on this initial kin bias in the postnatal environment, resulting in further biases in recognition (see subsequent text).

Prenatal communication through other mechanisms

Chemical communication is arguably universal across taxa, yet most vertebrates also rely on other sensory modalities. While evidence for prenatal visual or tactile communication in vertebrates is limited, there are notable exceptions. For instance, prenatally experienced visual prey cues influence cuttlefish (*Sepia officinalis*) food preferences [26], and close physical contact between eggs allows yellow-legged gull (*Larus michahellis*) embryos to communicate predation risk to neighbours [70] and results in more sociable neonates in water snakes (*Natrix maura*) [71]. However, prenatal vocal communication has received extensive support, particularly in birds [18]. For example, chicken and duck embryos increase bill-clapping and vocalisations in response to maternal calls [72], superb fairy wren (*Malurus cyaneus*) embryos learn maternal calls *in ovo* to enable post-hatching recognition and parasite rejection [73], and male zebra finch (*Taeniopygia guttata*) chicks select song tutors based on prenatally experienced songs [22]. Similar prenatal auditory learning occurs in humans, where maternal sounds enlarge the auditory cortex [74], and newborns – but not foetuses – discriminate their mother's voice from that of an unrelated female [75]. These examples suggest that the effect of the prenatal environment on kin familiarisation is not just restricted to olfactory communication but likely traverses multiple sensory modalities.

Reproductive traits shape prenatal familiarisation

Given the potential of the prenatal environment for familiarisation, any trait that alters the social context of the prenatal environment also has the potential to influence the opportunities for familiarisation and, thus, bias the emergence of kin recognition. For instance, clutch or litter size determines how many related individuals are available for familiarisation; gestation time determines the duration of familiarisation; and positional effects cause inequality in accessibility of cues between individuals (e.g., neighbouring embryo versus sibling in a separate uterine horn) [68]. One trait that is potentially most influential in this context is reproductive mode (oviparity to viviparity continuum) (Figure 1). This is because viviparity results in a more prolonged intimate connection between embryo and parent compared to oviparity. The transition from ancestral oviparity, without brooding on or in the body of the parent, to pregnancy, brings related individuals together and is associated with major morphological, physiological and immunological

changes to the developmental environment (e.g., formation of placenta instead of egg shell) that drastically affect opportunities for communication [28,76]. Indeed, viviparous amniotes transfer more glucocorticoid-mediated maternal effects compared to oviparous amniotes [77] and viviparous reptiles produce signalling molecules that are absent in oviparous reptiles [78]. These studies show that reproductive mode can have measurable impacts on prenatal communication with potentially significant implications for familiarisation. This generates testable predictions regarding when and where kin recognition might evolve (see Outstanding questions). Nevertheless, their influence on the evolution of kin recognition remains unknown.

Consequences for social evolution

We argue that familiarisation within the prenatal social environment is not only important for the emergence of kin recognition itself but can also shape postnatal **social evolution** in other ways. For instance, the process of live birth can also promote sustained social and/or physical contact between parent and offspring at birth, and between (half-)siblings – something that occurs only under specific circumstances when young hatch in isolation. This dual effect, biasing the social environment towards kin and enabling their discrimination, may lay the foundation for the stabilisation of postnatal social groups. While such groups likely begin as simple aggregations, they create new substrates for selection, opening pathways to more complex behaviours such as parental care and inbreeding avoidance. Thus, reproductive mode and its associated traits would not merely enable kin recognition; they may act as critical catalysts for broader social evolution. As social systems grow more complex, we expect social evolution to, in turn, further refine kin recognition mechanisms in a coevolutionary feedback loop (Figure 1) [79]. These cascading effects of reproductive traits on the evolution of social behaviour remain largely unexplored (see Outstanding questions), although preliminary evidence in reptiles suggest that the evolution of complex social systems is associated with the transition to viviparity [80].

Future research investigating the evolutionary consequences of prenatal familiarisation on sociality should target model systems that exhibit high variation in intimacy of prenatal parent–offspring associations. While birds and mammals dominate the current kin recognition and sociality literature in vertebrates, much could be learned by research on fishes and non-avian reptiles. Both groups exhibit high diversity in reproductive traits, having independently transitioned from oviparity to pregnancy multiple times independently [81]. These taxa also have multiple origins of placental structures [30]. The degree of molecular transport and intimacy of placental connection also varies greatly, including between closely related species [82,83]. Furthermore, both fishes and reptiles include species that exhibit intraspecific variation in reproductive mode (e.g., European common lizard, *Zootoca vivipara*) [28], or maternal versus paternal recognition in skin brooding fishes (e.g., seahorses, *Hippocampus* spp.) [84] allowing for more targeted, within-species, case studies (see Outstanding questions). Finally, both taxa also show substantial lability in social evolution, with each group having evolved (simple) parent–offspring associations over 20 times [80,85]. Therefore, reptiles and fishes not only allow for within- and between-species comparisons of the development and evolution of kin recognition but also offer an opportunity to directly explore how this has shaped social evolution.

Concluding remarks

Our current understanding of the emergence of social behaviours, such as kin recognition, is almost entirely based on postnatal social interactions. As a result, biases in neonate behaviours that remain even after cross-fostering within moments of birth – for example recognition of unfamiliar kin – are often attributed to genetically determined preferences. We argue that at least some of these biases may be due to the social environment in which prenatal development takes place. Developmental traits heavily influence the foundation (e.g., neuronal machinery) upon

Outstanding questions

What are the mechanisms of early prenatal familiarisation?

How does prenatal familiarisation affect morphological, neurological, physiological, and gene regulatory changes to facilitate postnatal kin bias?

How does variation in reproductive traits (e.g., gestation time, reproductive mode, and opportunities for parental care) affect prenatal familiarisation? Does this predispose certain taxonomic groups to develop kin recognition over others? For example, is kin recognition more likely to evolve in viviparous compared to non-brooding oviparous species – or populations for species with intraspecific variation in reproductive mode? Does male pregnancy bias kin recognition towards the father over the mother?

How does the development of siblings together, or in separate reproductive structures (e.g., uterine horns), alter kin recognition abilities? Do individuals show higher discrimination towards siblings who developed in close proximity?

How does variation in cue relatedness (e.g., presence of half-siblings due to sperm competition) during prenatal familiarisation affect recognition templates? Does it reduce recognition accuracy by introducing template variation, or does it broaden the range of relatives that can be recognised?

How do different reproductive traits affect social evolution in the postnatal environment? For example, is complex sociality more likely to emerge in species with more intimate prenatal parent-offspring associations?

How are kin recognition and social complexity linked? Once basic kin recognition and social structure have coevolved, do kin recognition mechanisms themselves become increasingly refined as social systems grow in complexity?

which postnatal interactions rely, yet precisely how prenatal conditions affect social behaviour immediately after hatching or birth remains largely unknown (see Outstanding questions). Understanding how the prenatal environment shapes early social cues will be pivotal for explaining not only the evolution of kin recognition but the developmental foundations of social evolution itself.

Acknowledgments

We thank Ingo Schlupp and two additional anonymous reviewers for their generous and constructive feedback. We were supported by an Australian Research Council grant (DP180102615) awarded to G.M.W., M.J.W., and T.U., a Holsworth Wildlife Research Endowment and Ecological Society of Australia grant awarded to Y.L., and an Australian Research Council grant (DP210101738) to C.M.W.

Declaration of interests

The authors declare no competing interests.

References

1. Tang-Martinez, Z. (2001) The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. *Behav. Process.* 53, 21–40
2. Hamilton, W.D. (1964) The genetical evolution of social behaviour. I & II. *J. Theor. Biol.* 7, 1–52
3. Green, J.P. *et al.* (2024) The evolution of kin discrimination across the tree of life. *Annu. Rev. Ecol. Evol. Syst.* 55, 347–367
4. Lattore, M. *et al.* (2019) No evidence for kin recognition in a passerine bird. *PLoS One* 14, e0213486
5. Trujillo-García, M. *et al.* (2025) Female filial cannibalism in the red-head goby (*Elacatinus puncticulatus*) in captivity. *Diversity* 17, 365
6. Grieves, L.A. *et al.* (2025) Offspring provisioning is affected by begging and hatch order but not relatedness in a communally breeding bird. *Anim. Behav.* 228, 123311
7. Fazeli, A. and Godakumara, K. (2024) The evolving roles of extracellular vesicles in embryo-maternal communication. *Commun. Biol.* 7, 1–7
8. Clemens, A.M. *et al.* (2020) The lateral septum mediates kinship behavior in the rat. *Nat. Commun.* 11, 3161
9. Laham, B.J. *et al.* (2021) Newborn mice form lasting CA2-dependent memories of their mothers. *Cell Rep.* 34, 108668
10. Diethorn, E.J. and Gould, E. (2023) Development of the hippocampal CA2 region and the emergence of social recognition. *Dev. Neurobiol.* 83, 143–156
11. Akcay, C. *et al.* (2013) Vocal kin recognition in kin neighborhoods of western bluebirds. *Behav. Ecol.* 24, 898–905
12. Kazem, A.J.N. and Widdig, A. (2013) Visual phenotype matching: cues to paternity are present in rhesus macaque faces. *PLoS One* 8, e55846
13. Daniel, M.J. and Rodd, F.H. (2021) Kin recognition in guppies uses self-referencing based on olfactory cues. *Am. Nat.* 197, 176–189
14. Tumulty, J.P. and Sheehan, M.J. (2020) What drives diversity in social recognition mechanisms? *Front. Ecol. Evol.* 7, 517
15. Bolhuis, J.J. and Moorman, S. (2015) Birdsong memory and the brain: in search of the template. *Neurosci. Biobehav. Rev.* 50, 41–55
16. Gerlach, G. *et al.* (2019) Behavioural and neuronal basis of olfactory imprinting and kin recognition in larval fish. *J. Exp. Biol.* 222, jeb189746
17. Rossi, N. and Derégnaucourt, S. (2020) Mechanisms of recognition in birds and social Hymenoptera: from detection to information processing. *Proc. R. Soc. B Biol. Sci.* 375, 20190483
18. Mariette, M.M. (2024) Developmental programming by prenatal sounds: insights into possible mechanisms. *J. Exp. Biol.* 227, jeb246696
19. Mateo, J.M. and Holmes, W.G. (2004) Cross-fostering as a means to study kin recognition. *Anim. Behav.* 68, 1451–1459
20. Robinson, S.R. and Smotherman, W.P. (1991) Fetal learning: implications for the development of kin recognition. In *Kin Recognition* (Hepper, P.G., ed.), pp. 308–334, Cambridge University Press
21. Mariette, M.M. *et al.* (2021) Acoustic developmental programming: a mechanistic and evolutionary framework. *Trends Ecol. Evol.* 36, 722–736
22. Ruiz-Raya, F. and Velando, A. (2024) Lasting benefits of embryonic eavesdropping on parent-parent communication. *Sci. Adv.* 10, eadn8542
23. Carrillo, J.F.C. *et al.* (2024) Mother-offspring chemical communication and tadpole aggregation in a neotropical foam-nesting frog. *Behav. Ecol. Sociobiol.* 78, 53
24. Kleindorfer, S. *et al.* (2024) Nestling begging calls resemble maternal vocal signatures when mothers call slowly to embryos. *Am. Nat.* 203, 267–283
25. Aubret, F. *et al.* (2016) Heartbeat, embryo communication and hatching synchrony in snake eggs. *Sci. Rep.* 6, 23519
26. Darmaillacq, A.-S. *et al.* (2008) Embryonic visual learning in the cuttlefish, *Sepia officinalis*. *Anim. Behav.* 76, 131–134
27. Browne, J.V. (2008) Chemosensory development in the fetus and newborn. *Newborn Infant Nurs Rev* 8, 180–186
28. Whittington, C.M. *et al.* (2022) Understanding the evolution of viviparity using intraspecific variation in reproductive mode and transitional forms of pregnancy. *Biol. Rev.* 97, 1179–1192
29. Skalkos, Z.M.G. *et al.* (2020) Paternal nutrient provisioning during male pregnancy in the seahorse *Hippocampus abdominalis*. *J. Comp. Physiol. B.* 190, 547–556
30. Whittington, C.M. *et al.* (2022) Embryonic specializations for vertebrate placentation. *Phil. Trans. R. Soc. B, Biol. Sci.* 377, 20210261
31. Schaal, B. *et al.* (2020) Olfaction scaffolds the developing human from neonate to adolescent and beyond. *Proc. R. Soc. B Biol. Sci.* 375, 20190261
32. Sewell, R.B. *et al.* (1982) Fetal bile salt metabolism: placental transfer of dihydroxy bile salts in sheep. *Am. J. Physiol. Gastrointest. Liver Physiol.* 243, G172–G175
33. Van Winkle, L.J. (2021) Amino acid transport and metabolism regulate early embryo development: species differences, clinical significance, and evolutionary implications. *Cells* 10, 3154
34. Buddle, A.L. *et al.* (2022) Structure and permeability of the egg capsule of the placental Australian sharpnose shark, *Rhizoprionodon taylori*. *J. Comp. Physiol. B.* 192, 263–273
35. Wang, H.-Q. *et al.* (2023) Maternal and embryonic signals cause functional differentiation of luminal epithelial cells and receptivity establishment. *Dev. Cell* 58, 2376–2392.e6
36. Stelzer, I.A. *et al.* (2021) Vertically transferred maternal immune cells promote neonatal immunity against early life infections. *Nat. Commun.* 12, 4706
37. Porter, R.H. and Winberg, J. (1999) Unique salience of maternal breast odors for newborn infants. *Neurosci. Biobehav. Rev.* 23, 439–449
38. Hepper, P.G. *et al.* (2013) Long-term flavor recognition in humans with prenatal garlic experience. *Dev. Psychobiol.* 55, 568–574
39. Hepper, P.G. (1988) Adaptive fetal learning: prenatal exposure to garlic affects postnatal preferences. *Anim. Behav.* 36, 935–936

40. Wells, D.L. and Hepper, P.G. (2006) Prenatal olfactory learning in the domestic dog. *Anim. Behav.* 72, 681–686
41. Caspers, B.A. *et al.* (2017) Zebra Finch chicks recognise parental scent, and retain chemosensory knowledge of their genetic mother, even after egg cross-fostering. *Sci. Rep.* 7, 12859
42. Crane, A.L. *et al.* (2018) Learning to find food: evidence for embryonic sensitization and juvenile social learning in a salamander. *Anim. Behav.* 142, 199–206
43. Karasch, B. and Ward, J. (2025) Social influences on embryonic behaviour and the developmental onset of embryonic acquired predator recognition in minnows. *Anim. Behav.* 219, 123017
44. Green, J.P. *et al.* (2015) The genetic basis of kin recognition in a cooperatively breeding mammal. *Curr. Biol.* 25, 2631–2641
45. Chung, M. *et al.* (2020) Diverse sensory cues for individual recognition. *Develop. Growth Differ.* 62, 507–515
46. Rajakaruna, R.S. *et al.* (2006) Major histocompatibility complex and kin discrimination in Atlantic salmon and brook trout. *Mol. Ecol.* 15, 4569–4575
47. O'Farrell, B. *et al.* (2012) MHC-mediated spatial distribution in brown trout (*Salmo trutta*) fry. *Heredity* 108, 403–409
48. Hinz, C. *et al.* (2013) Olfactory imprinting is triggered by MHC peptide ligands. *Sci. Rep.* 3, 2800
49. Yamazaki, K. *et al.* (2000) Parent–progeny recognition as a function of MHC odortype identity. *Proc. Natl. Acad. Sci.* 97, 10500–10502
50. Warner, C.M. *et al.* (1988) Why aren't embryos immunologically rejected by their mothers? *Biol. Reprod.* 38, 17–29
51. Sprinks, M.T. *et al.* (1993) Preimplantation mouse embryos express MHC class I genes before the first cleavage division. *Immunogenetics* 38, 35–40
52. Leinders-Zufall, T. *et al.* (2004) MHC Class I peptides as chemosensory signals in the vomeronasal organ. *Science* 306, 1033–1037
53. Firestein, S. (2001) How the olfactory system makes sense of scents. *Nature* 413, 211–218
54. Holtzman, D.A. and Halpern, M. (1990) Embryonic and neonatal development of the vomeronasal and olfactory systems in garter snakes (*Thamnophis* spp.). *J. Morphol.* 203, 123–140
55. Salazar, I. *et al.* (2003) Development of the vomeronasal receptor epithelium and the accessory olfactory bulb in sheep. *Microsc. Res. Tech.* 61, 438–447
56. Salazar, I. *et al.* (2004) The prenatal maturity of the accessory olfactory bulb in pigs. *Chem. Senses* 29, 3–11
57. Hudson, R. and Distel, H. (1986) Pheromonal release of suckling in rabbits does not depend on the vomeronasal organ. *Physiol. Behav.* 37, 123–128
58. Coppola, D.M. *et al.* (1993) The vomeronasal duct has a protracted postnatal development in the mouse. *J. Morphol.* 218, 59–64
59. Matsuoka, M. *et al.* (2002) A comparative immunocytochemical study of development and regeneration of chemosensory neurons in the rat vomeronasal system. *Brain Res.* 946, 52–63
60. Li, J. *et al.* (2005) Early development of functional spatial maps in the zebrafish olfactory bulb. *J. Neurosci.* 25, 5784–5795
61. Mack-Bucher, J.A. *et al.* (2007) Early functional development of interneurons in the zebrafish olfactory bulb. *Eur. J. Neurosci.* 25, 460–470
62. Todrank, J. *et al.* (2011) Effects of *in utero* odorant exposure on neuroanatomical development of the olfactory bulb and odour preferences. *Proc. R. Soc. B Biol. Sci.* 278, 1949–1955
63. Cadiou, H. *et al.* (2014) Postnatal odorant exposure induces peripheral olfactory plasticity at the cellular level. *J. Neurosci.* 34, 4857–4870
64. Biechl, D. *et al.* (2016) Crypt cells are involved in kin recognition in larval zebrafish. *Sci. Rep.* 6, 24590
65. Zhao, S. *et al.* (2013) Activity-dependent modulation of odorant receptor gene expression in the mouse olfactory epithelium. *PLoS One* 8, e69862
66. Calfún, C. *et al.* (2016) Changes in olfactory receptor expression are correlated with odor exposure during early development in the zebrafish (*Danio rerio*). *Chem. Senses* 41, 301–312
67. Dudley, J.S. *et al.* (2021) Structural changes to the brood pouch of male pregnant seahorses (*Hippocampus abdominalis*) facilitate exchange between father and embryos. *Placenta* 114, 115–123
68. Ryan, B.C. and Vandenbergh, J.G. (2002) Intrauterine position effects. *Neurosci. Biobehav. Rev.* 26, 665–678
69. Hepper, P.G. (1987) The amniotic fluid: an important priming role in kin recognition. *Anim. Behav.* 35, 1343–1346
70. Noguera, J.C. and Velando, A. (2019) Bird embryos perceive vibratory cues of predation risk from clutch mates. *Nat. Ecol. Evol.* 3, 1225–1232
71. Aubret, F. *et al.* (2016) Only child syndrome in snakes: eggs incubated alone produce asocial individuals. *Sci. Rep.* 6, 35752
72. Gottlieb, G. (1965) Prenatal auditory sensitivity in chickens and ducks. *Science* 147, 1596–1598
73. Colombelli-Négrel, D. *et al.* (2012) Embryonic learning of vocal passwords in superb fairy-wrens reveals intruder cuckoo nestlings. *Curr. Biol.* 22, 2155–2160
74. Webb, A.R. *et al.* (2015) Mother's voice and heartbeat sounds elicit auditory plasticity in the human brain before full gestation. *Proc. Natl. Acad. Sci. U. S. A.* 112, 3152–3157
75. Hepper, P.G. *et al.* (1993) Newborn and fetal response to maternal voice. *J. Reprod. Infant Psychol.* 11, 147–153
76. Foster, C.S.P. *et al.* (2020) Emergence of an evolutionary innovation: gene expression differences associated with the transition between oviparity and viviparity. *Mol. Ecol.* 29, 1315–1327
77. Macleod, K.J. *et al.* (2021) Viviparous mothers impose stronger glucocorticoid-mediated maternal stress effects on their offspring than oviparous mothers. *Ecol. Evol.* 11, 17238–17259
78. Wen, J. *et al.* (2022) Comparing the potential for maternal-fetal signalling in oviparous and viviparous lizards. *Phil. Trans. R. Soc. B, Biol. Sci.* 377, 20210262
79. Tumulty, J.P. *et al.* (2023) Evidence for a selective link between cooperation and individual recognition. *Curr. Biol.* 33, 5478–5487.e5
80. Halliwell, B. *et al.* (2017) Live bearing promotes the evolution of sociality in reptiles. *Nat. Commun.* 8, 2030
81. Blackburn, D.G. (2015) Evolution of vertebrate viviparity and specializations for fetal nutrition: a quantitative and qualitative analysis. *J. Morphol.* 276, 961–990
82. Thompson, M.B. *et al.* (2000) Comparison of nutrient transport across the placenta of lizards differing in placental complexity. *Comp. Biochem. Physiol.* 127, 469–479
83. Pollux, B.J.A. *et al.* (2009) Evolution of placentas in the fish family Poeciliidae: an empirical study of macroevolution. *Annu. Rev. Ecol. Evol. Syst.* 40, 271–289
84. Whittington, C.M. and Friesen, C.R. (2020) The evolution and physiology of male pregnancy in syngnathid fishes. *Biol. Rev.* 95, 1252–1272
85. Goodwin, N.B. *et al.* (1998) Evolutionary transitions in parental care in cichlid fish. *Proc. R. Soc. B Biol. Sci.* 265, 2265–2272
86. Kölle, S. *et al.* (2009) Ciliary transport, gamete interaction, and effects of the early embryo in the oviduct: ex vivo analyses using a new digital videomicroscopic system in the cow. *Biol. Reprod.* 81, 267–274
87. McGhee, K.E. *et al.* (2020) Effects of predation risk on egg steroid profiles across multiple populations of threespine stickleback. *Sci. Rep.* 10, 5239
88. Jung, J. *et al.* (2022) Frog embryos use multiple levels of temporal pattern in risk assessment for vibration-cued escape hatching. *Anim. Cogn.* 25, 1527–1544
89. Corben, C.J. *et al.* (1974) Gastric brooding: unique form of parental care in an Australian frog. *Science* 186, 946–947
90. Wetzel, J. *et al.* (1997) Comparative morphology of cotylephores in *Platystacus* and *Solenostomus*: modifications of the integument for egg attachment in skin-brooding fishes. *Environ. Biol. Fish* 50, 13–25
91. Colombelli-Négrel, D. *et al.* (2021) Prenatal auditory learning in avian vocal learners and non-learners. *Phil. Trans. R. Soc. B, Biol. Sci.* 376, 20200247
92. Katsis, A.C. *et al.* (2023) Prenatal sound experience affects song preferences in male zebra finches. *Anim. Behav.* 199, 1–9