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Tiliquin lizards as a model vertebrate system for understanding the emergence of societies

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The Tiliquini skinks are a clade of lizards that include multiple species that live in long-lasting, territorial groups. Memberships among group-living species range from simple nuclear families to larger, more complex groups containing multiple generations of offspring and sometimes, unrelated adults. We detail the factors that favour the formation of societies in one model species, the White's skink, *Liopholis whitii*, in which groups typically consist simply of a nuclear family (parents plus one generation of offspring), although some groups expand into what can be called incipient societies in that they can contain multiple generations of offspring and unrelated adults. Conversely, two other species (Cunningham's skink, *Egernia cunninghami*, and the gidgee skink, *Egernia stokesii*) live in much larger groups and their behaviour is more consistent with being societal. We suggest that the mechanism whereby individuals can gain entrance into a new group is through repeated exposure at the periphery of the group's territory, which in turn generates familiarity and tolerance. We argue that lizards provide a valuable model for understanding the origins and maintenance of societal formation in vertebrates.

Among reptiles, the 62 species of Australo-Melanesian Tiliquini skinks (Brennan et al., 2024), formerly referred to as the '*Egernia* group', stand out for their unusually high incidence of stable groupings (Chapple, 2003; Gardner et al., 2016; While et al., 2019; Whiting & While, 2017). Most of these species (77%, or 48) are endemic to Australia, and members of three genera (*Bellatorias*, *Egernia* and *Liopholis*) typically form enduring family groups that may span multiple generations and sometimes include unrelated individuals. Globally, such long-lasting memberships are considered rare among lizards, although this perception may be shaped by a paucity of detailed studies on lizard social organization (Doody et al., 2013, 2021; Gardner et al., 2016; While et al., 2019; Whiting & While, 2017). A key question is whether any lizards that live in aggregations maintain a group identity through the generations, consistent with living in a society as spelled out for this issue of *Animal Behaviour* (i.e. can they distinguish group from nongroup members and do they defend a group space or territory)? We begin by examining the behaviour of one particularly well-studied tiliquin skink, White's skink, *Liopholis whitii*, which forms flexible groups that occasionally extend beyond the immediate family. We then broaden our focus to include several other group-living tiliquins, which exhibit more complex systems involving multiple adults and overlapping generations of offspring. We end by discussing whether these groups adhere to the broad definition of a society outlined in this theme issue and discuss the ways in which lizards can contribute to our understanding of how such vertebrate societies initially evolve, become established and later, become refined.

WHITE'S SKINK: AN INCIPIENT SOCIETY DWELLER

White's skink (Fig. 1) is a low-elevation (<1200 m), group-living Australian skink, with detailed studies of sociality conducted in populations from Tasmania and the Australian Capital Territory. Notably, one Tasmanian population has been monitored continuously for 21 years (as of April 2025). Group sizes in White's skink are relatively small compared to some other tiliquins. The adult make-up of the group most commonly consists of a single pair of adults, although some include additional (typically 2–3) adult females (Chapple & Keogh, 2005, 2006; While et al., 2009),

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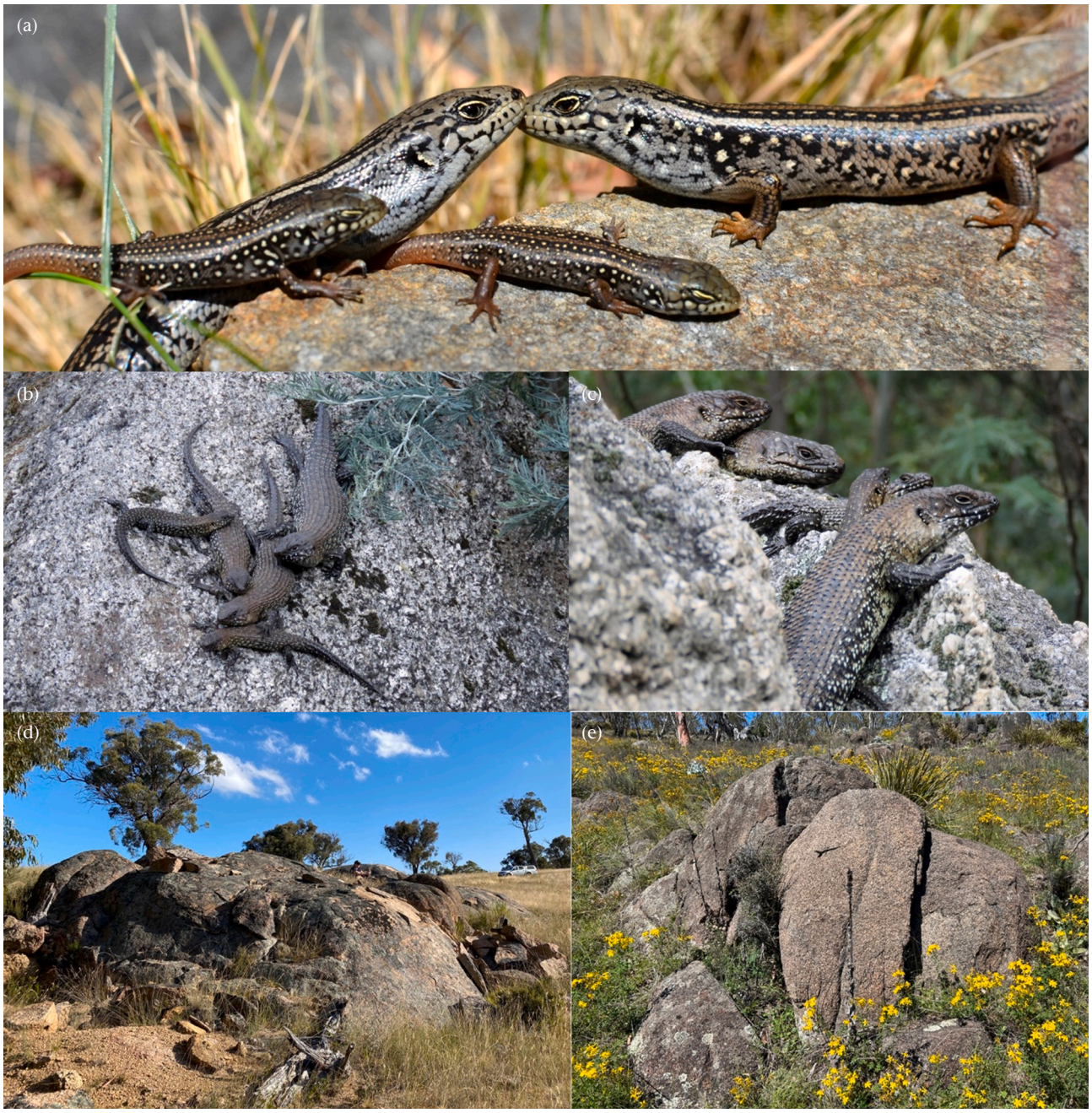

Figure 1. (a) White's skinks commonly live in nuclear families, sometimes with more than one generation of offspring and occasionally with unrelated individuals, making them an example of an incipient society. (b–c) Cunningham's skinks live in multigenerational groups of mostly kin, but also unrelated individuals, and more consistently meet the definition of a society. (d) Typical habitat for Cunningham's skink consisting of isolated rock outcrops with boulders and crevices for refuge. (e) White's skinks frequently live in smaller rock complexes, often associated with a burrow or crevice. Note the lizard basking in the centre. Photo credits: (a) Geoff While; (b–c) Deb Ralph; (d–e) Martin Whiting.

particularly when a male is in a high-quality territory (typically a rocky outcrop with refuges, Fig. 1; Halliwell, Uller, Wapstra, et al., 2017). However, around 10% of observed adult groupings contain multiple adults of both sexes (with up to 6 adults; Chapple & Keogh, 2006). Seventy per cent of pairs remain together from one year to the next (While et al., 2009), with some pairs staying together for up to 9 years (While & Wapstra, 2025a). Pair separation is primarily driven by mortality, with separations between living partners rarely occurring (While & Wapstra, 2025a). Yet, groups can add additional female partners over time (While et al., 2009). Where multiple females occur in a group, the resident male typically sires offspring in the litters of all female group members (Chapple & Keogh, 2005; While et al., 2009). Females can also birth young that are not the progeny of the group's male, presumably fathered by a male from a neighbouring group (While et al., 2014), but these comprise a small minority of litters (10–30%; Chapple & Keogh, 2005; While et al., 2009, 2011). In the small number of groups in which multiple adult males also occur, reproduction appears to be shared among the males (Chapple & Keogh, 2005). This suggests an absence of breeding hierarchies between males within White's skink groups. In theory, as breeding individuals (of either sex) die, others can replace them, permitting the groups to continue through the generations. Almost invariably in this species, however, the groups tend to revert to having a single

reproductive pair, and the death of one of them (most commonly, the male) will cause its members to disband, such that nearly all the groups of this species probably last just one or two generations, to be replaced by an entirely new set of lizards who locate the site.

Offspring membership is more ephemeral than that of adults. Most offspring only remain in a group for their first year of life, although some stay into their second year, but rarely beyond that (offspring usually do not mature until their third year), creating multicohort groups (While et al., 2009). Because of this delayed dispersal, most offspring typically reside with one or both parents (Botterill-James et al., 2016; Halliwell, Uller, Chapple, et al., 2017). However, about 25% of first-year offspring are unrelated to any adult in their group (Chapple & Keogh, 2006; While et al., 2009), suggesting their immigration and acceptance into an established group, although the process by which this occurs has as not yet been documented.

The number of offspring in groups varies considerably across years due to variation in rates of dispersal from the groups (While et al., 2009). In some years, all the offspring depart, leaving many groups without them, while in other years, at least a few stay (While & Wapstra, 2025b). The drivers of this variation and the roles family members play in shaping dispersal remain unclear, including whether this represents an active decision of the offspring to disperse or parental eviction. Adult female aggression towards conspecifics in general, increases during the early stages of gestation (Sinn et al., 2008) and may force older offspring out. Another potential explanation for juvenile departure is that the dynamics of membership is primarily shaped by offspring–offspring aggression. Intralitter conflict, whereby offspring actively fight one another, is common in this species (Botterill-James et al., 2017). Conflict in the laboratory varies from litters in which fights between offspring are ubiquitous to litters in which there are no such fights (Bouffet-Halle et al., 2024). This conflict results in the emergence of hierarchies where one offspring, usually the first born, becomes dominant and is able to stay relatively closer to, and therefore likely gain greater protection from, their mother (Bouffet-Halle et al., 2024; While & Wapstra, 2008). In the field, these dominance hierarchies potentially dictate which offspring stay or leave. We hypothesize that variation between litters in the level of conflict may also dictate which groups accept unrelated individuals.

The memberships outlined above primarily form through occupation and control of a group space, typically a suitable burrow system located in a rocky outcrop, maintained by adults. This group control is mediated by high levels of aggression towards conspecific intruders (see Chapple, 2003 for information on aggression within and between tiliquins), as shown in laboratory assays of White's skinks (McEvoy et al., 2015; Sinn et al., 2008). Both males and females exhibit similar levels of aggression (McEvoy et al., 2015), but whether territorial defence is coordinated between adults or simply done individually on an ad hoc basis is currently unknown. Offspring are unlikely to contribute to territorial defence, as they are substantially smaller than adults in both their first and second years and body size is an important predictor of contest outcome in lizards (Whiting et al., 2003). Nonetheless, offspring benefit from the adults' territorial behaviour because adults that are not members of the group represent a mortality risk to young lizards. Infanticide by neighbouring conspecifics is a major risk of offspring mortality in tiliquin skinks if they leave the protection of their core home range (Lanham & Bull, 2000; O'Connor & Shine, 2004). Within the core home range, adults likely deter nongroup adults from cannibalizing their young (O'Connor & Shine, 2004; Sinn et al., 2008). The heightened aggression females show towards conspecifics postpartum is when offspring are most vulnerable, and more aggressive mothers have higher offspring survival rates (Sinn et al., 2008). Similar protective effects are seen in other tiliquins, where adult presence reduces aggression from conspecifics (O'Connor & Shine, 2004) or may even deter predators (Watson et al., 2019). While the offspring are precocial and forage independently from birth, those associated with adults also gain better access to foraging resources (invertebrate prey and plant materials) and grow faster (Botterill-James et al., 2016). This is potentially because, in the presence of adults, offspring increase their activity and exploratory behaviour (Munch et al., 2018). Associations with older siblings or unrelated adults may also amplify these benefits via enhanced group vigilance (Lanham & Bull, 2004).

We argue that White's skinks are best described as living in incipient societies. That is, while they typically form territorial groups centred around a refuge that contain both parents and a single cohort of offspring, those family groups may expand to include multiple cohorts of offspring and unrelated individuals. This group structure may represent an early, transitionary stage in the evolution of larger and more complex group living that is more consistent with the definition of a society (Moffett, 2025).

BEYOND WHITE'S SKINKS: MORE COMPLEX TILIQUIN SKINK SOCIETIES

Several other tiliquin skinks exhibit similar incipient societies to Whites skinks (e.g. tree skinks, *Egernia striolata*: Riley et al., 2021; black rock skinks, *Egernia saxatilis*: O'Connor & Shine, 2003). However, two tiliquin species, the Cunningham's skink, *Egernia cunninghami*, and the gidgee skink, *Egernia stokesii*, stand out as living in groups that are perhaps more often in line with a 'society' in that they contain multiple adult group members and multiple cohorts of young. For example, Cunningham's skinks (Fig. 1), which do not breed more than once per year, form groups that initially involve a single adult pair, expanding to multiple adult males or females that accumulate up to 23 offspring in up to five cohorts (i.e. 5 years of offspring; Stow & Sunnucks, 2004a; Stow et al., 2001) without disbanding as readily as the White's skink groups do at the death of a breeding individual. Importantly, these groups can include both unrelated (presumably immigrant) individuals and (usually related) nonbreeding adults, the latter potentially representing the offspring of the breeding pair (Stow & Sunnucks, 2004a, 2004b). The groups are maintained through the generations, with limited dispersal and strong site fidelity. However, we do not yet know whether any group members spend their entire lives in the same group, and we also have a poor understanding of the social interactions and reproductive constraints of unrelated and nonbreeding adults.

Cunningham's skinks' territories are centred around a discrete rocky outcrop with suitable crevices that provide safe refuge (Fig. 1), which are sparsely distributed across the landscape. Adults are territorial and chase away nongroup members (A. Stow, personal observation). Similarly, gidgee skinks control discrete rock outcrops in groups of up to 17 individuals that likewise contain multiple adults, including one or occasionally more breeding pairs, with multiple additional adult males (2–6) or multiple adult females (2–5) (Duffield & Bull, 2002; Gardner et al., 2001, 2002, 2007). Compared to White's skinks and other family-living tiliquins, Cunningham's skinks and gidgee skinks live on larger rock outcrops, which in turn may support larger groups. Indeed, habitat constraints have been shown to be a major factor that influences both within- and between-population variation in social structure (Halliwell, Uller, Chapple, et al., 2017; Michael et al., 2010) and may thus explain part of the variance in social organization among these species. As in the Cunningham's skink, limited dispersal

promotes multigenerational kin groups, although unrelated adults also frequently occur within them (Gardner et al., 2007). This social organization facilitates the persistence of groups through the generations.

DO TILIQUIN SKINKS FORM SOCIETIES?

As outlined above, tiliquins live in groups centred on defence of a territory with a shared resource (e.g. a burrow system/rocky outcrop containing crevices) and may consist of multiple generations of related individuals, with unrelated members also present. Thus, two of the three criteria for a society are clearly met. Can individuals distinguish group members from outsiders? In tiliquins, social recognition is primarily chemosensory and appears to be based on familiarity. For instance, sleepy lizards, *Tiliqua rugosa*, gidgee skinks and black rock skinks discriminate their own offspring based on prior association (Bull et al., 1994; Main & Bull, 1996; O'Connor & Shine, 2006). This familiarity appears to rely on ongoing reinforcement. For example, in tree skinks, offspring removed at birth and later reintroduced are attacked and cannibalized by their mothers (Riley & Whiting, 2017), which supports the assertion that recognition is not based on relatedness per se (but see Bull et al., 2001). The role of familiarity potentially extends beyond parent–offspring recognition to group membership more broadly. Gidgee skinks, for example, respond differently to chemosensory cues (pheromones, scats) from group members versus nonmembers, regardless of relatedness (Bull et al., 2000). Such recognition also underpins group defence in tiliquins, as adults are aggressive towards unfamiliar conspecifics (O'Connor & Shine, 2004). These studies collectively suggest that tiliquins recognize group members at a minimum, a precondition for societal living.

How do these societies form? The tiliquin skink societies documented here consist largely of close relatives. Such a pattern likely arises from a combination of life-history traits and ecological constraints. Tiliquins are livebearing. This results in a physical association between parents and offspring following birth, which has the potential to promote selection for extended periods of tolerance (Halliwell, Uller, Holland, et al., 2017). This is especially advantageous in species where the costs of tolerating offspring that stay within adult territories are low. Ecology also plays a critical role. As outlined above, most social tiliquins inhabit spatially discrete and defensible rock outcrops or burrow systems. These resources provide secure refuges but restrict dispersal, particularly for offspring, due to the risks associated with crossing open ground (O'Connor & Shine, 2004) and because available habitat/resources are saturated (Botterill-James et al., 2016; Halliwell, Uller, Chapple, et al., 2017; see also Halliwell et al., 2024) for broader implications for the emergence of sociality across lizards. This combination of life-history traits and ecology may encourage the formation of group territoriality. The fact that recognition of group membership is based largely on familiarity may further bias the emergence of largely kin-based societies as the group members that are most likely to be 'familiar' are those close kin they grow up with.

Given the above, how do nonrelatives gain access to established groups? We argue that in systems where group membership is determined primarily by familiarity rather than genetic relatedness, nonkin individuals have the potential to be accepted, particularly if familiarity develops during key developmental windows (Tang-Martinez, 2001). For example, unrelated offspring present in the natal environment during early postnatal periods, when recognition cues are first learned and reinforced, may be perceived and treated as kin. Experimental manipulations of adult–offspring associations, including the creation of artificial kin and nonkin pairings, show that strong bonds can form between parents and unrelated offspring as well as between parents and their biological offspring (Russell et al., 2025). This principle may extend beyond parent–offspring interactions to shape adult relationships as well. In gidgee skinks, the home ranges of neighbouring groups overlap by approximately 14%, including peripheral refuges such as crevices, while each maintains exclusive use of its core refuges (Duffield & Bull, 2002). These shared peripheral areas may act as neutral zones, allowing for repeated exposure, through visual and chemical cues, without immediately provoking territorial aggression, notably during the nonbreeding season. While data on how individuals transfer between societies are needed, we hypothesize that such low-risk encounters could promote the development of familiarity, increasing the likelihood of tolerance and eventual group acceptance of a persistent immigrant.

Dispersal patterns further reinforce this dynamic: individuals typically relocate only short distances from their natal group, often settling in adjacent territories (Gardner et al., 2001), where they may already be familiar to resident individuals. Thus, limited dispersal combined with partial space sharing creates a framework through which nonkin can integrate into groups via familiarity rather than kinship. Critically, if increased group size yields augmentation benefits, it could drive the emergence and stability of mixed-kin societies through the incorporation of these unrelated individuals (Shah & Rubenstein, 2023). On the other hand, if the fitness costs of interacting with nonkin become too high, selection may favour the refinement of recognition mechanisms, ultimately reinforcing the formation of strictly kin-based groups.

In summary, tiliquin skinks form enduring group memberships ranging from simple parent–offspring associations to larger communal groups comprising multiple generations and, at times, unrelated individuals. White's skink, and many others not covered in detail in this piece (e.g. tree skinks: Riley et al., 2021; black rock skinks: O'Connor & Shine, 2003) live in simple family groups, or occasionally, multigenerational groups. Conversely, the Cunningham's skink and the gidgee skink more consistently meet the definition of being societal because they often live in multiadult groups, sometimes including unrelated individuals, defend exclusive spaces from extragroup members, show evidence of recognition based on learnt familiarity and have long-term cohesion. We still have only a rudimentary understanding of the dynamics of dispersal, recognition and group membership. As social systems mature, and the fitness stakes of interacting with kin versus nonkin rise, we expect such mechanisms to become more refined. Whether this occurs in tiliquins is yet to be determined, but their variation in societal structure and tractability in both field and laboratory settings make them an exceptional system for understanding how and why societies evolve, not just in lizards, but in animals more broadly.

Author Contributions

Martin J. Whiting: Writing – review & editing, Writing – original draft, Conceptualization. **Geoffrey M. While:** Writing – review & editing, Writing – original draft, Conceptualization.

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