CHAPTER 1

General introduction

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Background

Social relationships and habitat utilisation are closely intertwined with life history characteristics. These features provide a framework that enables survival under fluctuating ecological conditions, especially unpredictable weather patterns like those experienced in Australia. Effective conservation biology practice is dependent upon an understanding of behavioural ecology, or the way organisms respond behaviourally to ecological challenges in both the short term and the longer, or evolutionary, term (Calow 1999). As a ‘sixth wave of mass extinction looms’ (May 2004) it is critical to discover more about our unique fauna if Natural Resource Management strategies are to succeed in their conservation effort during the emergence of climate change.

This thesis reports the results of investigations into the life history and chemosensory communication of a social Australian skink, *Egernia whitii*, using a range of techniques involving field populations from Wedge Island in South Australia’s Spencer Gulf, laboratory colonies captured for experimental work, and preserved specimens from the South Australian Museum, Adelaide (SAMA).

Study model: genus and species characteristics

The Scincidae family comprises 57% of Australian lizard species and members fill almost every niche in Australia, showing a huge variety of body form, size and behaviours (Cogger 2000). Within the *Egernia* genus 30 species are currently recognised with all but one being endemic to Australia (Chapple 2003). The *Egernia* genus is distinguished by one morphological character, in which the palatines curl partially around the nasal passage anteriorly above the secondary palate and the vomers send back long posterior processes along the medial edge of the open palatine scroll (Hutchinson 1983 *op cit*. Greer 1989).

Egernia species are unusual among lizard species in forming stable social aggregations (Greer 1989, Hutchinson 1993, Gardener *et al*. 2001, Fuller *et al*. 2005), with reports of social complexity in 23 of the 30 described species (Chapple 2003). Greer (1989) notes an additional behavioural characteristic for the genus in the strong attachment to a permanent retreat or shelter site around which all activities are centred, and he comments that this is unique amongst Australian skinks.

Egernia species are medium to large in size and may be terrestrial, saxicolous, or semi-arboreal. Most Australian terrestrial habitats support at least one species (Greer 1989), and scat piling has been described in twelve species.

Egernia whitii species group

The *E. whitii* species group is described by Cogger (2000) as a highly variable species complex. Varying numbers of species have been attributed to the species group by Storr (1968), Horton (1972), Donnellan *et al.* (2002) and Chapple and Keough (2004). Taxonomic relationships are in a state of flux. In recent research Donnellan *et al.* (2002) differentiated at least six major, genetically differentiated, groups within and between populations in south-eastern Australia when they used allozyme electrophoresis to assess the taxonomic significance of colour pattern variation and morphological data. Two new species, *Egernia guthega* and *Egernia montana,* were formally described at this time, and the remaining four species recognised were *E. margaretae, E. modesta, E. multiscutata* and *E. whitii (*Donnellan *et al.* 2002).

Two years later Chapple & Keough (2004) conducted a more extensive search by including arid zone species, and obtained sequence data from ten of the 11 species within the species group (*E. slateri* are critically endangered and no tissue samples were available). Their aim was to test biogeographical hypotheses regarding the origin of Australian arid zone fauna. Using mitochondrial DNA they conducted phylogenetic analyses and they report results strongly supporting two major clades within the species group: temperate-adapted rock-dwelling species and arid-adapted, obligate burrowing species.

In addition to the species listed by Donnellan *et al*. (2002), Chapple & Keough (2004) included a sub-species *of E. margaretae* (*E. m. personata*), and the arid dwelling species *E. inornata, E. kintorei,* and *E. striata* in the *E. whitii* species group.

Egernia whitii

E. whitii (White's skink) is a common and widespread species within the species group. It demonstrates marked clines in morphology along its distributional range (Donnellan *et al.* 2002). Like others skinks in the genus, *E. whitii* are viviparous throughout their range (Hickman 1960, Milton 1987, Greer 1989). They are found in a variety of habitats between the subtropical regions of southern Queensland, and the cool temperate regions of southern and eastern Tasmania, and are characteristically associated with loose rocky areas (Milton 1986) with friable top soil (Hickman 1960) or substrate suitable for burrowing (Ehmann 1976, Green 1984).

E. whitii are essentially social animals (Rawlinson 1974), with the majority living in small groups of two to six individuals which include closely related juveniles (Chapple & Keough 2006). They were first reported anecdotally as scat piling over forty years ago (Hickman 1960). This secretive and cryptic species is polymorphic in colour pattern, with three pattern morphs represented. Fully patterned individuals, like those found on Wedge Island, display dorsal and lateral patterning, and comprise the most abundant morph (Milton 1990, Donnellan *et al.* 2002, Chapple 2005).

Distribution of *E. whitii*

The *E. whitii* species is distributed from the extreme south-eastern zone of Queensland, south through New South Wales and Victoria to the islands of Bass Strait and Tasmania, and as far west as Eyre Peninsula in SA, including islands in the Spencer Gulf (Figure 1).

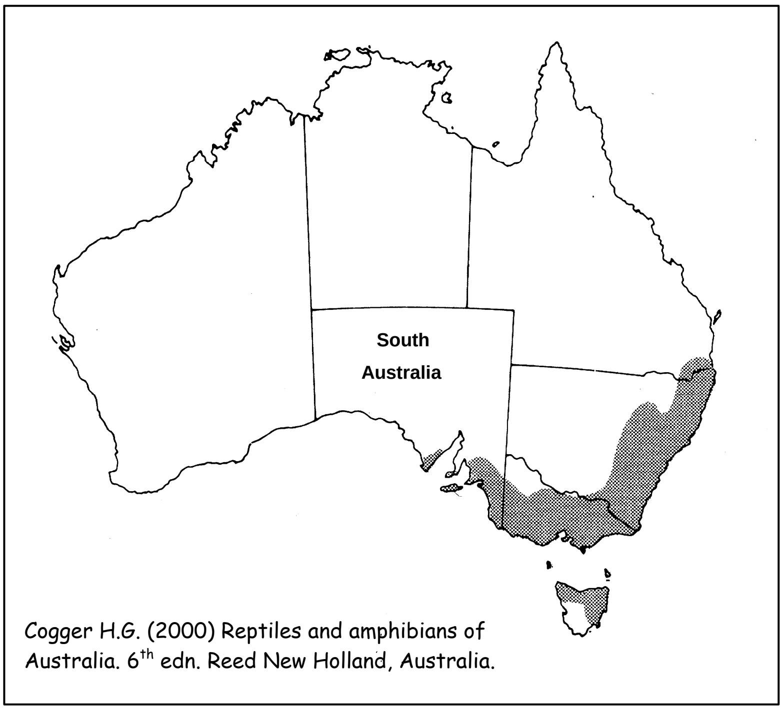

Figure 1: The distribution of the *E. whitii* species in south-eastern Australia

Donnellan *et al.* (2002) found no support for the recognition of a subspecies within *E. whitii (sensu stricto*) from morphological evidence, or genetic data gained by allozyme electrophoresis. However Chapple *et al.* (2005) sampled *E. whitii* across its distributional range using 700 base pairs of the mitochondrial gene *ND4,* reporting a deep phylogeographical break between a 'northern' population in Queensland, New South Wales, the Australian Capital Territory and extreme south-eastern Victoria, and a 'southern' population in the reminder of Victoria, Tasmania and SA.

Genetic divergence at ND4 between these populations was calculated at 12.3-12.6%, with a number of clades identified within each group (Chapple *et al*. 2005). Figures 2 and 3 show the map and clade diagram figures for the southern population. Note that all major clades identified by Chapple *et al.* (2005) form a polytomy, but that the Wedge Island and Kangaroo Island clades were recovered as a single clade, and that within this the two Kangaroo Island clades were sister groups to each other. All study specimens in this thesis originate in SA and have been drawn from Clades 2 and 3 for the SA mainland, and Clade 4 for SA off-shore islands.

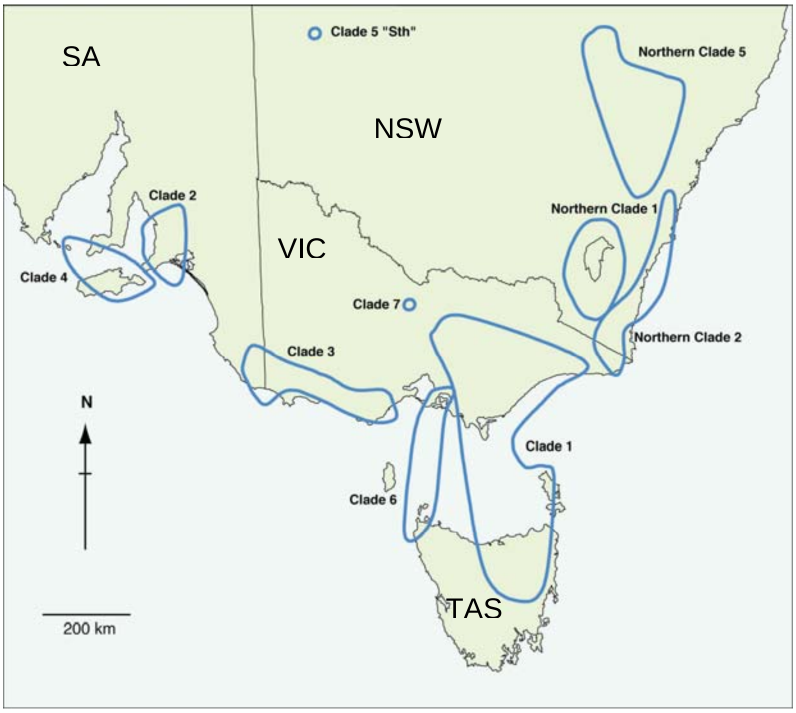

Figure 2: Clade map of the southern population of *Egernia whitii*, showing the SA population composed of Clades 2, 3 and 4. The off-shore islands encircled in Clade 4 are Kangaroo Island to the south, and Wedge Island to the north-east. Modified from Chapple *et al*. (2005)

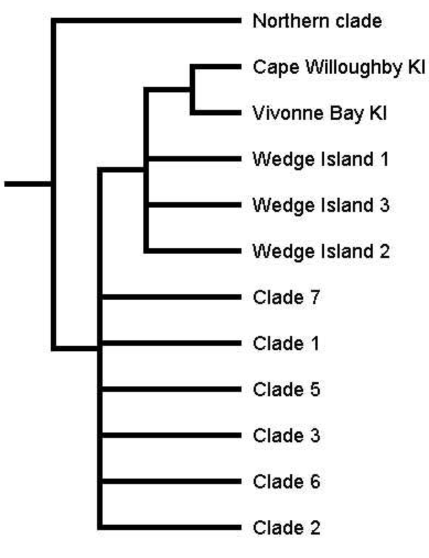

Figure 3: Cladogram of the southern population of *Egernia whitii*, using mitochondrial DNA sequence data. Specimens are derived from South Australia, Victoria, Tasmania, the Islands of Bass Strait, and the mid-west of New South Wales (Clade 5). Specimens from SA's off-shore islands and the SA mainland are treated in greater detail. Modified from Chapple *et al*. (2005)

Life history strategies in the major ‘northern’ and ‘southern’ clades and between the clades nested within these are likely to vary, given the differences in climate and ecology that these ranges encompass. A range of biotic and abiotic habitat characteristics can be distinguished along the distributional range of *E. whitii* between the subtropical regions of southern Queensland, and the cool temperate regions of southern and eastern Tasmania.

The most westerly populations occur in SA. The populations sampled from SA comprised those from the drier, western off shore islands (Kangaroo Island and Wedge Island), constituting clade 4, the Mount Lofty Ranges and environs, constituting clade 2, and regions from the wetter south-eastern mainland region and the south-west of Victoria, constituting clade 3 (Chapple *et al*. 2005).

Information gained by examining the *E. whitii* collection in SAMA, provided a background for the field and laboratory research in this thesis, which is focussed on the *E. whitii* population from Wedge Island (Clade 4). Skinks from Kangaroo Island form the majority of the off-shore island specimens from SAMA (Clade 4). The mainland specimens from SAMA were derived from Clades 2 and 3.

Study scope

Species persistence in challenging environments is dependent on sufficient genetic variation to facilitate maximisation of some components of fitness (Roff 1992). The objectives in this study were to investigate and document information relating to communication using *E. whitii* as a model system for social lizards. It would not be possible to understand chemical communication in lizards outside of the context of life history. The dynamics involved in social living depend upon the common features which characterise the individuals that comprise the group. As a consequence, life history components such as age to sexual maturity, sexual dimorphism, reproductive patterns, litter size, longevity, morphological plasticity and juvenile survival rates may all influence group activity and motivate interactions within the group. Data targeting these aspects of life history development in *E. whitii* are examined and presented in this thesis prior to an investigation of scat piling behaviour and chemical communication.

Habitat and morphology

An examination of habitat characteristics on Wedge Island is treated separately from analytical sections and presented early in the thesis. Pattern morphology is briefly described prior to an analysis for morphological differences in geographic populations on the mainland, Kangaroo Island and Wedge Island. Island populations are analysed for sexually dimorphic differences, and compared for divergences, but sexual dimorphism is not examined in the mainland population because specimens were not available for dissection.

Difficulty experienced in determining gender in many Wedge Island captures based on direct observation of genital morphology, led to the use of Discriminant Analysis to predict sex for animals in which sexual category was initially in doubt. Results of these investigations are reported in Chapter 2.

Growth and reproduction

E. whitii located in other areas produce no more than one (Chapple 2003) small litter of well formed offspring per year, females do not reproduce every year (Chapple 2005) and previous research has shown that at other latitudes this species takes a varying number of years to reach sexual maturity (Hickman 1960, Milton 1987).

Skeletochronology studies have been lacking from the available research data to date. In this study sections were examined to establish a lifespan patterns for this species. Developmental measurements using live field captures from Wedge Island have been combined with the results of skeletochronology analysis to estimate age/size at sexual maturity in the mid-latitude zone of South Australia.

Gonad measurements from preserved off-shore island specimens are analysed. Although the largest sample size came from KI, some preserved specimens originated on the smaller islands. An examination of gonad activity was important to discover when reproduction occurs during the year.

The occurrence of *E. whitii* over a geographically and climatically extensive area in Australia allowed a comparison of variations in birth size, growth patterns, size at reproduction and maximum size attained of my data with data from earlier publications. Adaptation to climate, vegetation and the presence of other species can be inferred in latitudinal differences.

There is a paucity of research on juvenile survival in lizard taxa in general, and in *Egernia* species in particular (Chapple 2003). Multiple threats to immature reptiles have not been thoroughly investigated and little is known about lizard dispersal patterns. However there is general agreement that tail loss leads to an increased risk of death in other juvenile lizard species (Civantos & Forsman 2000, Fox & McCoy 2000, Blomberg & Shine 2001). The relationship between caudal autotomy and juvenile survival in *E. whitii* is explored using available data from field trips and laboratory births. Results of these investigations are reported in Chapter 3.

Data collected from juveniles born and reared in the laboratory were used to compare growth rates of free-living field populations with those reared in laboratory conditions. Information concerning the extent of morphological plasticity in a social species underpins the effects of competition on social cohesion when sociality is examined. Noë (2006) suggests that cooperation and conflict are two sides of the same coin with only what he describes as 'taste' prescribing which side receives more attention. In theory a larger lizard 'out competes' a smaller lizard. However a smaller animal may choose to fight only when evenly matched, thus conserving resources through conflict avoidance. Size, competitive interactions and morphological plasticity are intimately interwoven when applied to social cohesion, especially in juveniles.

Scat piling

Hypotheses on the existence of communal latrines have developed along three main themes: allelomimetic behaviour (Leuthold 1977), parasite avoidance (Apio *et al*. 2006), and social functions (Chame 2003, Stewart *et al*. 2001, Begg *et al*. 2003). Species using communal latrines possess well-developed chemosensory abilities (eg. Sneddon 1991), and the localised deposition of faeces suggests the existence of some kind of social function.

Scat piling is a descriptive term for the multiple depositions of faeces or scats by either individuals, or groups of individuals, at a specific site, where they accumulate to form clusters or piles. Gekkonids are the only other lizard species demonstrated as scat piling (Carpenter & Duvall 1995, Shah *et al*. 2006). However, the occurrence of scat piling in the *Egernia* genus has not previously been quantified, and no studies have been undertaken specifically to investigate its behavioural and ecological significance. Scat piling behaviour is investigated for singletons, and small groups of related *E. whitii*. The occurrence of two scat piling species occupying the territory on Wedge Island is investigated from field records and suggestions are made concerning social uses these species may be utilising within and between species. Results of these investigations are reported in Chapter 4.

Chemosensory communication

Crozier (1999) defines a society as a group of cooperating individuals of the same species involving reciprocal communication and going beyond sexual behaviour. Communication is therefore an important aspect of social behaviour. Moore (1999) defines communication as "the transfer of information between animals using visual, audible or chemical means". Social organisation then, according to these definitions, necessarily involves associations of interacting individual conspecifics, whose behavioural repertoires include cooperation and reciprocal communication. Scat piling is strongly linked with social function and communication.

Numerous lizard behaviours are influenced by chemosensory cues. They encompass recognition behaviours (Main & Bull 1996, Léna & de Fraipont 1998, Cooper *et al.* 1999, Hanley *et al.* 1999, Bull *et al*. 2000, Bull *et al.* 2001, Aragón *et al.* 2001, Font & Desfilis 2002, O'Connor & Shine 2005), competition and territorial interactions, (López & Martín 2002), sexual choice (Olsson & Shine 1998, López *et al*. 2003, López *et al*. 2002, López & Martín 2005, Head *et al*. 2005), and predation avoidance (Amo *et al*. 2004, Labra & Niemeyer 2004, Stapley 2003, Downes 2002, Downes & Bauwens 2002). This is the first time the role of scats in *E. whitii* communication has been investigated, and these results including a new behaviour, scent marking, are reported in Chapter 5.

Photographic identification

During the research project the need for individual identification became acute. The most popular form of permanently identifying small lizards in Australia is toe clipping (Ferner 1979). Although measurements were not taken, the behaviour of the animals initially toe-clipped for skeletochronology appeared to be modified following the procedure. I considered that this would negatively impact on behavioural observations and future research outcomes. As there were few alternatives available I developed a system of photographic identification, testing it for persistence, reliability and individual discrimination.

Photographic identification requires minimal handling time, it is non-invasive, and if carefully implemented can avoid the misidentification problems that could arise with toe clipping. In this study field captures are analysed for toe damage to provide an accurate context against which to examine an alternative identification method. Pattern persistence and individuality in a sample group is investigated, a technique for pattern identification is presented, and the reliability of the method is rigorously assessed using a sample of laboratory reared *E. whitii* individuals photographed over developmental time from birth to adult size. Results of these investigations are reported in Chapter 6.

References

Apio A., Plath M. & Wronski T. (2006) Localised defecation sites: a tactic to avoid re-infection by gastro-intestinal tract parasites in bushbuck, *Tragelaphus scriptus*? *Journal of Ethology* **24**, 85-90.

Amo L., Lopez P. & Martin J. (2004) Chemosensory recognition and behavioural responses of wall lizards, Podarcis muralis, to scents of snakes that pose different risks of predation. *Copeia* **2004**, 691-696.

Aragón P., López P. & Martín J. (2001) Chemosensory discrimination of familiar and unfamiliar conspecifics by lizards: implications of field spatial relationships between males. *Behavioural Ecology and Sociobiology* **50**, 128-133.

Begg C.M., Begg K.S., Du Toit J.T. & Mills G.L. (2003) Scent-marking behaviour of the honey badger, *Mellivora capensis* (Mustelidae), in the southern Kalahari. *Animal Behaviour* **66**, 917-929.

Blomberg S.P. & Shine R. (2001) Modelling life history strategies with capture-recapture data: Evolutionary demography of the water skink *Eulamprus tympanum*. *Austral Ecology* **26**, 349-359.

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

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

Calow P. (1999) *Blackwell's Concise Encyclopedia of Ecology* (ed. P. Calow). Blackwell Science, Melbourne, Australia.

Carpenter G.C. & Duvall D. (1995) Fecal scent marking in the Western banded gecko (*Coleonyx variegatus*). *Herpetologica* **51**, 33-38.

Chame M. (2003) Terrestrial mammal feces: a morphometric summary and description. *Memórias do Instituto Oswaldo Cruz* 98, 71-94.

Chapple D.G. (2003) Ecology, life-history, and Behaviour in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs* **17**, 145-180.

Chapple D.G. (2005) Life history and reproductive ecology of White's skink, *Egernia whitii*. *Australian Journal of Zoology* **53**, 353-360.

Chapple D.G. & Keough J.S. (2004) Parallel adaptive radiations in arid and temperate Australia: molecular phylogeography and systematics of the *Egernia whitii* (Lacertilia: Scincidae) species group. *Biological Journal of the Linnean Society*. **83**, 157-173.

Chapple D.G.**,** Keogh J.S. & Hutchinson M.N. (2005) Substantial genetic substructuring in southeastern and alpine Australia revealed by molecular phylogeography of the *Egernia whitii* (Lacertilia: Scincidae) species group. *Molecular Ecology*, 14: 1279-1292.

Chapple D.G. & Keough J.S. (2006) Group structure and stability in social aggregations of White's Skink, *Egernia whitii*. *Ethology* **112**, 247-257.

Civantos E. & Forsman A. (2000) Determinants of survival in juvenile *Psammodromus algirus* lizards. *Oecologia* **124**, 64-72.

Cogger H.G. (2000) *Reptiles and amphibians of Australia.* Reed New Holland, Sydney, Australia.

Cooper W.E., Wyk J.H. & Mouton P.L.F.N. (1999) Discrimination between self-produced pheromones and those produced by individuals of the same sex in the lizard *Cordylus cordylus*. *Journal of Chemical Ecology* **25**, 197-208.

Crozier R.H. (1999) *Blackwell's Concise Encyclopedia of Ecology* (ed. P. Calow). Blackwell Science, Melbourne, Australia.

Dodd, C.K. & Cade B.S. (1998) Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. *Conservation Biology* **12**, 331-339.

Donnellan S.C., Hutchinson M.N., Dempsey P. & Osbourne W. (2002) Systematics of the *Egernia whitii* species group (Lacertilia: Scincidae) in south-eastern Australia. *Australian Journal of Zoology* **50**, 439-459.

Downes S.J. (2002) Does responsiveness to predator scents affect lizard survivorship ? *Behavioural Ecology and Sociobiology* **52**, 38-42.

Downes S.J. & Bauwens D. (2002) Does reproductive state affect a lizard's behavior toward predator chemical cues? *Behavioural Ecology and Sociobiology* **52**, 444-450.

Ehmann H.F.W. (1976) Reptiles of the Mt. Lofty Ranges, South Australia. Part 1. *Herpetofauna* **8**, 2-5.

Ferner J.W. (1979) *A review of marking techniques for amphibians and reptiles*. SSAR Herpetological Circular No. 9.

Horton D.R. (1972) Evolution in the genus *Egernia* (Lacertilia: Scincidae). *Journal of Herpetology*, **6**, 101-109.

Font E. & Desfilis E. (2002) Chemosensory recognition of familiar and unfamiliar conspecifics by juveniles of the Iberian wall lizards *Podarcis hispanica*. *Ethology* **108**, 319 330.

Fox S.F. & McCoy J.K. (2000) The effect of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana* in the field. *Oecologia* **122**, 327-334.

Fuller S.J., Bull C.M., Murray K. & Spencer R.J. (2005) Clustering of related individuals in a population of the Australian lizard, *Egernia frerei*. *Molecular Ecology* **14**, 1207-1213.

Gardner M.G., Bull C.M., Cooper S.J.B. & Duffield G.A. (2001) Genetic evidence for a family structure in stable social aggregations of the Australian lizard *Egernia stokesii*. *Molecular Ecology* **10**, 175-183.

Green R.H. (1984) The vegetation, fauna and archaeology of Ordnance Point, north-western Tasmania. *Records of the Queen Victoria Museum* **84,** Launceston**,** Tasmania.

Greer A.E. (1989) *The Biology and Evolution of Australian Lizards*. Surrey Beatty & Sons, Sydney.

Hanley K.A. Elliot M.L. & Stamps J.A. (1999) Chemical recognition of familiar vs. unfamiliar conspecifics by juvenile Iguanid lizards, *Ctenodaura similis*. *Ethology* **105**, 641-650.

Head M.L., Keough J.S. & Doughty P. (2005) Male southern water skinks (*Eulamprus heatwolei*) use both visual and chemical cues to detect female sexual receptivity. *Acta ethologica* **8**, 79-85.

Hickman J.L. (1960) Observations of the skink lizard *Egernia whitii* (Lacepede). *Papers and Proceedings of the Royal Society of Tasmania* **94**, 111-118.

Hudson S. (1996) Natural toe loss in southeastern Australian skinks: implications for marking lizards by toe-clipping. Journal of Herpetology, 30, 106-110.

Hutchinson M.N. (1983) The generic relationships of the Australian lizards of the family Scincidae. A review and immunological reassessment. PhD Thesis, La Trobe University, Bundoora, Victoria.

Hutchinson M.N. (1993) Family Scincidae. In: *Fauna of Australia, Vol. 2A*: *Amphibia and Reptilia* (eds Glasby CJ, Ross GJB, Beesley BL), pp.261-279. Australian Government Publishing Service, Canberra.

Labra A. & Niemeyer H.M. (2004) Variability in the assessment of snake predation risk by *Liolaemus* lizards. *Ethology* **110**, 649-662.

Lena J.P. & de Fraipont M. (1998) Kin recognition in the common lizard. *Behavioural Ecology and Socio*biology **42**, 341-347.

Leuthold W. (1977) *African ungulates: A comparative review of their ethology and behavioral ecology*. New York: Springer-Verlag.

López P. & Martín J. (2002) Chemical rival recognition decreases aggression levels in male Iberian wall lizards, *Podarcis hispanica. Behavioural Ecology and Sociobiology* **51**, 461-465.

López P., Martín J. & Cuadrado M. (2002) Pheromone-mediated intrasexual aggression in male lizards, *Podarcis hispanicus. Aggressive Behaviour* 28, 154-163.

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

López P. & Martín J. (2005) Intersexual differences in chemical composition of precloacal gland secretions of the Amphisbaenian *Blanus cinereus*. *Journal of Chemical Ecology* **31**, 2913-2921.

Main A.R. & Bull C.M. (1996) Mother-offspring recognition in two Australian lizards, *Tiliqua rugosa* and *Egernia stokesii*. *Animal Behaviour* **52**, 193-200.

May R.M. (2004) Ethics and amphibians. Nature 431, 403.

Milton D.A. (1986) Habitat selection by two closely related skinks, *Egernia modesta* Storr and *Egernia whitii* Lacepede (Lacertilia: Scincidae). *Australian Wildlife Research* **13**, 295-300.

Milton D.A. (1987) Reproduction of two closely related skinks, *Egernia modesta* and *E. whitii* (Lacertilia: Scincidae) in south-east Queensland. *Australian Journal of Zoology* **35**, 35-41.

Milton D.R. (1990) Genetic evidence for sympatric differentiation between two colour morphs of the skink Egernia whitii. Australian Journal of Zoology 38, 117-130.

Moore B. (1999) *The Australian Oxford Dictionary*. Oxford University Press, Melbourne, Australia.

Noë R. (2006) Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour* **71**, 1-18.

O'Connor D.E. & Shine R. (2005) Kin discrimination in the social lizard *Egernia saxatilis* (Scincidae). *Behavioural Ecology* **17**, 206-211.

Olsson M. & Shine R. (1998) Chemosensory mate recognition may facilitate prolonged mate guarding by male snow skinks, *Niveoscincus microlepidotus*. *Behavioural Ecology and Sociobiology* **43**, 359-363.

Rawlinson P.A. (1974) Biogeography and ecology of the reptiles of Tasmania and the Bass Strait area. In: *Biogeography and Ecology in Tasmania* (ed. W.D. Williams). 291-338. The Hague: Dr W. Junk.

Roff D.A. (1992) *The evolution of life histories: Theory and analysis*. Chapman & Hall, New York, NY USA.

Shah B., Hudson S. & Shine R. (2006) Social aggregation by thick-tailed geckos (*Nephrurus milii*, Gekkonidae): does scat piling play a role? *Australian Journal of Zoology*, **54**, 271-275.

Sneddon I.A. (1991) Latrine use in the European rabbit (*Oryctolagus cuniculus*). *Journal of Mammalogy* **72**, 769-745.

Stapley J. (2003) Differential avoidance of snake odours by a lizard: evidence for prioritized avoidance based on risk. Ethology 109, 785-796.

Stewart P.D., Macdonald D.W., Newman C., Cheeseman C.L. (2001) Boundary faeces and matched advertisement in the European badger (Meles meles): a potential role in range exclusion. *Journal of Zoology* **255**, 191-198.

Storr G.M. (1968) Revision of the *Egernia whitei* species-group (Lacertilia, Scincidae). *Journal of the Royal society of Western Australia*, **51**, 51-62.