CHAPTER 7

General discussion

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Background

Social relationships, habitat utilisation and life history characteristics provide a framework which enables species persistence in fluctuating ecological conditions. An understanding of behavioural ecology is critical to the implementation of Natural Resource Management strategies if they are to succeed in their conservation efforts during the emergence of climate change. The objectives in this study were to investigate and document life history features and chemosensory communication using a social lizard species as a model system.

Study scope

Analyses showed morphological differences not only between the mainland and offshore island populations of *E. whitii* but also between Kangaroo Island and Wedge Island populations. Mainland skinks had greater mass per unit SVL, shorter hind leg and foot measurements and deeper heads than island skinks. Differences in sexual dimorphism between Kangaroo Island and Wedge Island were also apparent. On Kangaroo Island males had wider and deeper heads than females, while on Wedge Island males had wider and longer heads than females. Difficulties in determining the sex of these skinks led to the use of discriminant analysis to predict sex.

Duffield & Bull (2002) predict the development of social relationships between conspecifics sharing rock crevices from their work with *E. stokesii*, extended to include *E. cunninghami* and *E. saxatilis* by Chapple (2003). However *E. whitii* does not share the same habitat limitations as saxicolous species. It has been described as a temperate-adapted, rock associated (Chapple *et al.* 2005) facultative burrower in suitable habitat and saxicolous in others (Chapple 2003), but it burrows in all known habitats on Wedge Island. Habitats with some potential for burrowing, plus loose rock, appear to be essential habitat requirements for *E. whitii*.

An examination of gut contents shows that *E. whitii* consumes a generalist diet with a preference for animal rather than vegetative content (Appendix A). The flexibility and opportunism exhibited by ingesting a broad range of items indicates a link

between diet and their wide range of habitat choices. The high vegetative constituent found in some individuals is probably seasonal as a large component of the *E. whitii* diet during summer on Wedge Island consists of small fruits or berries found on three native and one exotic species of vegetation. Habitat requirements and morphology are discussed in Chapter 2.

James & Shine (1988) suggest that rapid growth and earlier maturation in warmer climates may be phenotypic responses to environmental conditions rather than genetically based life history adaptations. Data demonstrating rapid growth in laboratory conditions and field data on body size in *E. whitii* showing an increase in SVL with a decrease in latitude supports this hypothesis. Body size data combined with skeletochronology data compiled to estimate age and developmental rates showed a minimum of two juvenile years before sexual maturity could be reached under natural conditions, and skeletochronology data suggest a lifespan of \geq 13 years.

Low survival rates for juveniles in their first year of life was evident and the loss of proximal tail sections in juveniles suggests that extensive tail loss at an early stage of development imposes severe costs on immature lizards. Juveniles with toe loss are also less likely to survive (Chapter 6). Vulnerability caused by tail or toe loss is compounded by the use of tail tips for social signalling. Growth, longevity, tail loss and juvenile survival are discussed in Chapter 3.

Individuals and small related groups deposited scat piles in their enclosures. Anecdotatal observations record that *Egernia* scat piles are generally located near the entrance to a permanent home site (Chapple 2003), and it has been suggested that scat piles may indicate species' presence in an area (Wilson & Knowles 1988 *op. cit.* Chapple 2003). Chapple (2003) suggests that scat piling may be necessary to renew the signal so that it can retain a social function. These hypotheses were supported by *E. whitii* research.

Social benefits arising from signalling could confer both cooperative and competitive benefits. Permanent territorial markers have the potential to benefit conspecifics, congenerics and other species. The high incidence of a skink species (E. whitii) refuging with a gecko species (N. milii) on Wedge Island provides an example of interspecific cooperation. The diurnal refuge of the nocturnal gecko is a useful transient shelter for the diurnal skink. Scat piling may release a species 'signature'

for each group that allows mutual recognition. Scat piling also facilitates intraspecific scent marking by individual members which has the potential to indicate relatedness, or social or sexual status within the group. The practice also makes information concerning the social environment available to dispersing transient and potential immigrant conspecifics, enabling settlement choices to be made. In terms of population dynamics it may be adaptive for recruitment and would allow the newcomers and other species to avoid agonistic encounters. Scat piling is discussed in Chapter 4.

E. whitii are essentially social animals (Rawlinson 1974, Chapple & Keough 2006). Resident skinks demonstrated differentiation between their own and unknown conspecific scent in scats, and their own and congeneric scent in scats. Response differences between the sexes may imply different roles for the sexes and ultimately highlights the complex nature of communication in retiles, and the need to separate and test both sexes to obtain accurate chemosensory communication data. Higher levels of relatedness have been shown in group females than males (Chapple & Keough 2006) which may in turn indicate that dispersal is male biased. Where sex biased dispersal can be demonstrated, it is also likely that the philopatric sex will be the one in which dispersal would cause the greatest delay in breeding (Johnson & Gaines 1990). Further testing would be required to test the hypothesis that female responses differ because they are the sex that remains philopatric.

The discovery of cloacal scent marking activity is new to the *Egernia* genus. By their scent marking patterns *E. whitii* demonstrated both recognition of conspecifics as different from congenerics, and a predisposition for chemosensory communication with their own kind. It is very likely that individuals convey socially relevant information about themselves in this way. Cooperation in group scat piling, allows individual members of the group to leave chemical cues with scats that may indicate relatedness or social or sexual status within the group. By their practice of scat piling, individuals belonging to groups may reinforce their group membership by providing individual scent cues, and also provide interspecific recognition cues. Chemosensory communication is discussed on Chapter 5.

An alternative method for permanently marking lizards was developed. Persistence, reliability and individual discrimination were demonstrated using photographic identification and the method was shown to be reliable for broad-scale application by

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researchers. Naturally occurring toe loss in the field provided a context against which to examine this alternative identification method and revealed the need to further investigate the consequences of routine toe clipping, as this practice appears to diminish survivorship. Photographic identification as an alternative to toe clipping in patterned lizards is discussed in Chapter 6.

Study Model

E. whitii cover an extensive area in Australia but have only recently attracted research attention. They share common characteristics with many of the other species in the *Egernia* genus including vomerolfactory structures (Hutchinson 1983 *op cit.* Greer 1989), strong attachment to a permanent retreat or shelter site (Greer 1989), the establishment of stable social aggregations (Greer 1989, Hutchinson 1993, Gardener *et al.* 2001, Fuller *et al.* 2005), and viviparity (Greer 1989, Cogger 2000).

Twelve *Egernia* species are now described as scat piling, and although the level of sociality is still unknown for five species, only two of the remaining 25 species are thought to be solitary (Chapple 2003). The prevalence of scat piling and sociality in *Egernia* species may be higher than available records indicate at present, as prior to this study no *Egernia* species had been researched for scat piling, and social and chemosensory studies have been restricted to several of the larger species.

Chapple (2006) describes *E. whitii* social groups as stable. According to some views of life history theory, in stable populations maturation should be delayed, and a few large young, parental care and small reproductive efforts should be favoured. In addition brood size should maximise the number of young surviving to maturity over the lifetime of the parent (Stearns 1976). These hypotheses are supported by present research on *E. whitii*.

A prolonged period of juvenile growth and adult longevity may be prerequisite to the development of parental care. Parental care may, in turn, be the determining factor that facilitates the formation of small family groups. In *E. whitii* parental care takes the form of foetal and neonatal provisioning, and tolerance of juveniles by small family or social groups within established resource areas. Presumably resident juveniles also benefit from adult territorialism. Arnold and Owens (1998) suggest that low (adult) mortality predisposes cooperative breeding (social grouping) in birds. Hatchwell and Komdeur (2000) extend this line of thinking by suggesting that

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life history traits and ecological factors act together to facilitate cooperative systems. Recent research on social insects has highlighted the importance of prolonged offspring dependency and long periods of time before offspring become reproductively mature for understanding social evolution (Field & Brace 2004, Field 2005). This needs to be examined in reptiles.

The practice of scat piling may enhance sociality in small groups, by providing individual information about group members. Communication between the individuals that form a group facilitates the establishment of orderly spatial relationships. Orderly spatial relationships within a group are governed by consistent and recognised behaviours displayed by individuals. In these ways survivorship is influenced by group membership. Some of these behaviours have been identified in *E. whitii* during scat piling and chemosensory experiments but a great deal more information is likely to be forthcoming with more extensive scent tests.

For solitary and social groups scat piles may function as territorial markers identifying the group to conspecifics and other lizard species. Information derived from chemosensory cues in scats is likely to elicit different responses depending on the identity of the recipient. Many behaviours are associated with lizard chemosensory signals. They can facilitate relationships with kin (Léna & de Fraipont 1998, Main & Bull 1996, O'Connor & Shine 2005), group members (Glinski & Krekorian 1985, Graves & Halpern 1991, Hanley *et al.* 1999, Bull *et al.* 2000), and potential or actual reproductive partners (Olsson & Shine 1998, López *et al.* 2003, Head *et al.* 2005), provide information about the size of potential competitors (Aragón *et al.* 2000, Aragón *et al.* 2001, López *et al.* 2002, López & Martín 2002), and can be used by lizards to adjust activity patterns and location to limit and avoid risks associated with known predators (Stapley 2003, Downes 2002, Amo *et al.* 2004).

This thesis has explored some of the behavioural strategies employed by *E. whitii* to reduce risks to individuals within groups and between groups. Scents eliciting a range of behavioural responses relevant to the formation of adaptive social groupings, reproductive activity, and juvenile protection until maturity and dispersal are likely to be present in this species. Tests confirming chemosensory cues that differentiate sex, kin and age would be an interesting addition to current knowledge.

The interaction of delayed maturity, parental care, sociality, chemosensory communication and scat piling highlights the emerging sophistication of this species behaviour. Ongoing natural selection pressures are punctuated with stochastic environmental events to ensure a wealth of interesting components in animal behaviour studies and these studies demonstrate the versatility and tenacity of native wildlife.

References

- 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.
- Arnold K.E. & Owens I.P.F. (1998) Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society, London B* 265, 739-745.
- 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.
- 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., Keough 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.
- Chapple D.G. (2006) Group structure and stability in social aggregations of White's skink, *Egernia whitii*. *Ethology* **112**, 274-257.
- Cogger H.G. (2000) *Reptiles and amphibians of Australia*. Reed New Holland, Sydney, Australia.
- Downes S.J. (2002) Does responsiveness to predator scents affect lizard survivorship? *Behavioural Ecology and Sociobiology* **52**, 38-42.
- Duffield G.A. & Bull C.M. (2002) Stable social aggregations in an Australian lizard, *Egernia stokesii. Naturwissenschaften* **89**, 424-427.
- Field J. & Brace S. (2004) Pre-social benefits of extended parental care. *Nature* **428**, 650-652.
- Field J. (2005) The evolution of progressive provisioning. *Behavioural Ecology* **16**, 770-778.
- 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.
- Glinski T.H. & Krekorian C.O. (1985) Individual recognition in free-living adult male desert iguanas, *Dipsosaurus dorsalis*. *Journal of Herpetology* **19**, 541-544.

- Graves B.M. & Halpern M. (1991) Discrimination of self from conspecific chemical cues in *Tiliqua scincoides* (Sauria: Scincidae). *Journal of Herpetology* 25, 125-126.
- Greer A.E. (1989) *The Biology and Evolution of Australian Lizards*. Surrey Beatty & Sons, Sydney, NSW, Australia.
- 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.
- Hatchwell B.J. & Komdeur J. (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour* **59**, 1079-1086.
- 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.
- 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). Australian Government Publishing Service, Canberra, Australia.
- James C. & Shine R. (1988) Life history strategies of Australian lizards: a comparison between the tropics and the temperate zone. *Oecologia* **75**, 307-316.
- Johnson M. L. & Gaines M. S. (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and* systematics **21**, 449-480
- Lena J.P. & de Fraipont M. (1998) Kin recognition in the common lizard. *Behavioural Ecology and Socio*biology **42**, 341-347.
- 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.
- Main A.R. & Bull C.M. (1996) Mother-offspring recognition in two Australian lizards, *Tiliqua rugosa* and *Egernia stokesii*. *Animal Behaviour* **52**, 193-200.
- 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.
- Stapley J. (2003) Differential avoidance of snake odours by a lizard: evidence for prioritized avoidance based on risk. Ethology 109, 785-796.
- Stearns S.C. (1976) Life-history tactics: a review of the ideas. *The Quarterly Review of Biology* **51**, 3-47.
- Wilson S.K. & Knowles D.G. (1988) Australia's Reptiles. Angus and Robertson, Sydney, Australia.