the context of answering questions relevant to animal welfare. Finally, I started addressing questions that I really cared about, my motivation recovered, I started getting grants and my career was reinvigorated. Animal welfare research has suffered from having rather low status within biology — it is perceived by some as applied and therefore dull. However, I believe that it actually poses some extremely challenging and interesting biological questions. My research in animal welfare got me interested in emotions, and I now ask fundamental questions about the nature and origin of emotions in parallel with my more applied work.

Do you believe that there is a need for more crosstalk between biological disciplines? Absolutely yes, but the problem is how this is to be achieved. Everyone pays lip service to the value of cross-disciplinary collaboration, but we still don't have mechanisms for funding such research effectively. This is a particular problem in the behavioural sciences, where the gulfs between different sub-disciplines are huge in terms of the general philosophies and theoretical approaches adopted, yet to the outsider the research might not even seem cross-disciplinary and thus might not qualify for schemes designed to promote it. Communication is also a huge problem; cognition and emotion are two concepts defined and understood very differently depending on your background, making the writing of cross-disciplinary papers and research grants in this area a minefield of potential confusion.

Despite these problems, I have stubbornly persisted in trying to do cross-disciplinary research. I do this because my most important contributions have come from taking ideas from one area and applying them in another. One of my current projects is to understand whether we can use results from ageing biology to develop novel measures of the cumulative impact of experimental procedures on laboratory animals.

Do you think ethology has a future? When I got my chair, I was confronted by a Dutch colleague who questioned why I would want to associate myself with an outdated discipline. I was somewhat taken aback because I imagined that the Dutch might be proud of their strong ethological tradition, but clearly some people think ethology has had its day. I had family reasons for wanting to call myself an ethologist, but I also strongly believe that there are two central tenets of ethology that remain important in modern biology. These are, first, the conviction that we need to understand the behaviour of animals in their natural environments, or more specifically the environments in which they have evolved, and second, that to understand behaviour fully we need to answer questions about causation, development, function and evolution. Much of modern biomedicine is concerned with understanding the phenotypes that animals develop in specific environments. However, there is often no consideration of whether the phenotype in question is an adaptive response to that environment, or whether it is the product of a malfunctioning mechanism operating outside the range of conditions in which it has evolved. In some cases, it will matter which of these is the case because blocking adaptive plasticity could carry fitness costs.

In our recent work investigating the behavioural consequences of early-life adversity in starlings, we have been keen to stress that our manipulations of early-life experience are based on the range of natural experience in the wild population from which our birds come. This allows us to make the claim that the behavioural phenotypes developed by the adult birds are likely to be adaptive. For example, we interpret increased impulsivity in starlings from high-competition nests as an adaptive behavioural response to poor somatic state as opposed to a pathological consequence of impaired executive control. This may seem like a subtle distinction, but it potentially has implications when we are thinking about prevention and treatment of behavioural problems in humans or other animals.

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Quick guide

Egernia lizards

Geoffrey M. While[1,2,*], David G. Chapple[3], Michael G. Gardner[4], Tobias Uller[2,5], and Martin J. Whiting[6]

What are* Egernia *lizards? *Egernia* are a group of family-living lizards that occur throughout Australasia (Figure 1). The group comprises approximately 60 species from seven different genera. They contain a number of iconic Australian lizards like the bluetongue lizard (*Tiliqua scincoides*), the sleepy lizard (*Tiliqua rugosa*) and the wonderfully named 'land mullet' (*Egernia major*). Here, we will refer to *Egernia* as a collective group encompassing all seven genera.

Hang on, did you say family living? Yes. One of the most striking features of *Egernia* is that they include highly social lizards that form stable social aggregations based around kin. While some species are largely solitary, in others males and females form long-term pair-bonds sometimes holding territories where juveniles can remain with their parents. In the most extreme cases this can lead to large communal groups of up to 30 related individuals, including non-breeding adults who stay within their parent's social group.

How stable are these pair bonds? Stable social monogamy is a hallmark of *Egernia* family living, so pair bonds are extremely stable. In the sleepy lizard, which can live for more than 50 years, the record for a male–female pair is 27 years and counting. In the White's skink (*Liopholis whitii*), which live for up to 15 years, the record duration is 10 years. And divorce is uncommon: only 15% of pairs separate, a level of pair stability that puts many human societies to shame.

Are males and females faithful to each other? For the most part, yes. Lizards in general are highly promiscuous and multiple paternity seems to be the norm for almost all species studied. But in social *Egernia* species, multiple and extra-pair mating is very rare. For example, in

Figure 1. Representative *Egernia* lizards.
Top panel: White's skink lives in stable 'nuclear' family groups. Pairs are mostly monogamous and rarely divorce. Bottom left: the sleepy lizard is long lived and forms life-long pair bonds but pairs separate outside the breeding season and there is no parental care. Bottom middle: the black rock skink (*Egernia saxatilis*) also lives in family groups and parent–offspring associations are thought to reduce the likelihood of infanticide. Bottom right: the gidgee skink lives in large communal groups containing multiple adults and multiple cohorts of young. (Photos: Geoff While, Dave O'Connor, Dale Burzacott.)

the communal living Cunningham's skink (*Egernia cunninhamii*), only 2% of offspring are sired by males outside the social pair. These levels are higher in other *Egernia* species, but still much lower than most non-social lizards where females typically mate with several males. Indeed, levels of multiple mating in solitary *Egernia* species, such as the pygmy bluetongue (*Tiliqua adelaidensis*), can be as high as 75%.

Do these lizards really care for their young? Yes, they do. In fact, lizards in general exhibit a surprising diversity in parental care, ranging from simple nest and egg attendance to prolonged parent–offspring association following birth or hatching. In the *Egernia*, care extends to parents tolerating offspring within their burrow/crevice system. In some species, parents tolerate a single offspring or a single cohort of offspring, while in others offspring delay dispersal for years, sometimes even into adulthood, and parents tolerate multiple cohorts of young. In its extreme, this results in the large social groups mentioned above. While parental care is relatively simple compared to, say, birds and mammals, it is exactly the kind of care that one would expect in the early stages of the evolution of more complex forms of family living.

What do the offspring gain from staying with their parents? Because care is simple, the benefits are simple too. Offspring gain access to resources associated with the parental burrow/crevice system, like food and shelter, but so far there has been no evidence of direct parental provisioning. Offspring also get protection from hungry neighbours. Infanticide is common in *Egernia* and the presence of the mother can virtually eliminate this threat. In fact, female *Egernia* become far more aggressive following birth, presumably to defend their young. There is even anecdotal evidence that mothers protect their offspring from predators.

How do the siblings get along? Not particularly well. In White's skink only a single offspring typically gets to stay with the parents, which creates huge competition between the siblings. Bullying tactics result in the formation of large sibling size-hierarchies. The mother appears to facilitate this by giving birth to offspring one at a time, over a period of up to 10 days. This birthing asynchrony is analogous to hatching asynchrony in birds. It is a completely unique behaviour for lizards but common across the *Egernia*. All is not conflict, however; in gidgee skinks (*Egernia stokesii*) up to five cohorts of young live within groups seemingly without aggression.

Is it common for lizards to live in family groups? Lizards have traditionally been assumed to have a simple social life. That is not to say it's boring — in fact lizards have been extensively studied with respect to territoriality, social communication, alternative reproductive tactics and sexual selection. It is just that they

have not been thought to live in family groups. But there is now increasing evidence that this may not be as rare as previously thought. Kin-based family living similar to that of *Egernia* has been observed in the desert night lizard (*Xantusia vigilis*). And there are probably several more cases of family living in lizards, as there is evidence of group aggregations also in cordylids, agamids and geckos. But to show that these are kin groups we need genetic confirmation. One of the reasons for the uncertainty is that group living is often more cryptic than it is in other animals. Even for *Egernia*, social associations are often only identified by long-term field studies and molecular assignment of kinship. A growing appreciation that lizards can help us understand the early steps in the evolution of animal societies and recent technological advances may encourage biologists to pay greater attention to the diversity of lizard social life.

Why is family living so common in* Egernia *if it is rare in other lizards? Several reasons: first, *Egernia* take several years to reach maturity and have low turnover of breeding adults. Second, many species rely heavily on crevice and burrow sites that are limited but long-lasting. In extreme cases these consist of small rocky outcrops separated by tens or hundreds of metres of unsuitable habitat. This promotes a sedentary life, makes natal dispersal costly, and thus makes it possible to gain inclusive fitness benefits from relatives (i.e., kin selection). Third, *Egernia* are live-bearing, which allows parents to recognize and interact with their offspring. It may in fact be a small evolutionary step for live-bearing territorial species to evolve parental care, particularly in long-lived species where competition for space is intense. Interestingly, most other lizard species that are suspected to live in family groups share these basic characteristics.

Habitat constraints, life history traits, kin selection… this all sounds very similar to other family living taxa? Yes, it is. Evolution is often convergent. Ranging from bacteria to large mammals, complex social organisation tends to emerge when ecological conditions impose constraints that make close kin interact. *Egernia* are no different. However, the *Egernia*, with their large diversity in social behaviour, can really help us to understand the early stages in the evolution of family living. Complex social behaviours, such as parental provisioning and cooperative breeding, have their origins in relatively simple traits, such as long-term monogamous male–female pair bonds, territoriality or guarding of offspring. The *Egernia* provides us with an opportunity to address how these simple social traits may have influenced the initial origins of kin-based sociality.

Horses come in herds, fish in schools, birds in flocks… what should I call a group of* Egernia *if I ever see one? There is currently no collective noun for a group of *Egernia*. However, given their highly aggressive nature we propose that a group of *Egernia* should be called a 'fury'.

Where can I find out more?

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Competition drives sophisticated hunting skills of archerfish in the wild

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Several animals are renowned for their cognitive skills, such as tool use, metacognition or social learning. However, it remains puzzling why some species excel whereas others — sometimes even closely related ones — do not [1,2]. Archerfish show a remarkable assembly of skills in the context of their unique hunting behavior in which they down aerial prey with shots of water [3,4]. Hoping to find ecological factors behind these skills, we have over the past years regularly traveled to archerfish mangrove habitats in Thailand (Figure 1A). One of our most consistent findings was the presence of other surface-feeding fish, particularly the similar-sized halfbeak *Zenarchopterus buffonis*, wherever we spotted groups of archerfish (Figure 1A; Supplemental movie S1). We describe here that *Zenarchopterus* is superbly equipped with water-wave detectors, rapidly detects the impact of prey even in the dark, is active at all times, is usually more numerous than archerfish and supplements its capabilities with visual skills. Without sophisticated additions to their hunting technique archerfish would thus lose most of their downed prey to halfbeaks. We suggest that the evolution of several skills of archerfish may have thus been influenced not only by intraspecific competition [5] but also by competition with other surface-feeding fish species.

Remarkably, *Zenarchopterus* fed on all food items that archerfish shot down in our experiments, e.g. crickets, flies, beetles or pieces of bread. By nightfall, archerfish quickly ceased to catch food, whereas *Zenarchopterus* remained active (Figure 1B). However, when tested

