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THE AUGRABIES FLAT LIZARD

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Most visitors to Augrabies, especially in the main viewing area of the falls, are stunned by the technicoloured lizards scurrying about their feet. From rushing head-first down a vertical precipice 100 m above the snake-like Orange River, to doing 360° flips to catch an aerial insect, their acrobatic antics are likely to impress even Olympic gymnasts! What most visitors fail to recognise, is the myriad of extraordinary social interactions unfolding at their feet. These range from male dominance contests to courtship and sexual harassment. And because the Augrabies population is one of the densest lizard populations on earth, social interactions are frequent and easily observed by visitors to the park.



83. *A male Augrabies flat lizard. Males are adorned in a multitude of primary colours that include yellow, orange and various shades of blue and turquoise.*

Lizard tails and crevices

The Augrabies flat lizard is a rock specialist designed to squeeze into tight crevices. The banks of the Orange River provide a myriad of hiding places in the form of peeling granite and deep crevices. The river banks are therefore where the

majority of lizards may be found. Flat lizards generally sleep tightly wedged into crevices, often communally. Some crevices are shared by more than 100 lizards!



84. *Female Augrabies flat lizard. Females lack the bright colours. Young males can look like females*

While sleeping, flat lizards wrap their tail around their body. In so doing, they can avoid predation by dropping their tail if seized by a predator. During daily activity, the ability to drop their tail also acts as insurance against predators such as snakes and birds. If the tail is seized, the lizard releases it at the point of contact and makes good its escape, while the predator consumes the thrashing tail. Crevices are also where the female lays her eggs. Two eggs are laid during midsummer and most hatchlings appear in January.

The rainbow lizard

Adult males are brightly coloured, while females are a drab brown and may appear to be a different species to the untrained eye. Males are also larger than females. During the breeding season, males court females using a series of push-ups while approaching or circling them. Males are territorial and engage in intense rivalry in competition for females. These social behaviours are described below.

Sexual conflict

Competition for mates occurs through a process called sexual selection, which was described by

Charles Darwin in 1871. Sexual selection occurs on two levels: within a sex (normally between males), and by mate choice (normally female choice). Sexual selection arises from sexual conflict. In other words, the stakes for males and females differ considerably. Males can afford to mate with multiple females because they can produce enough sperm to do so. In reproductive terms, the male's only contribution is sperm (compared to some other animals in which males also contribute parental care). Females, especially those that produce only a few young, may have an entire season's reproduction riding on a single mating and are therefore likely to be choosy. If a female makes the wrong choice, her offspring may not survive to reproduce and an entire season may be wasted.



85. The flat lizard population at Augrabies is among the densest in the world.

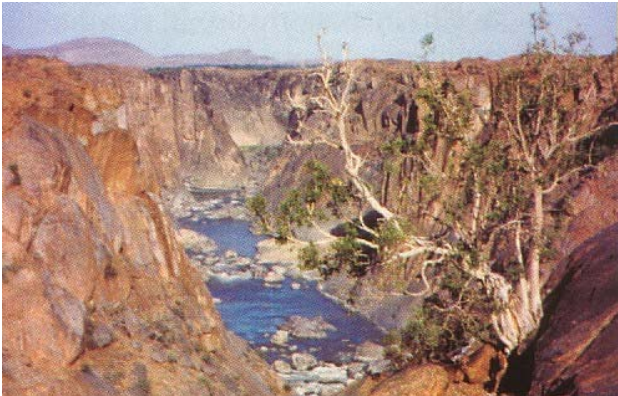
Under natural selection (originally coined by Darwin), the name of the game is to pass on your genes and because of selective pressures, reproduction has strayed far from merely mating with the nearest available mate. Therefore, a mistake in mate choice for a female could greatly reduce life-time reproductive success and the probability of successfully passing on her genes. Thus, the onus is on the male to convince the female that his genes are worthy. How do males demonstrate their superior quality? One means is through bright coloration. Brightness can demonstrate quality through vigour (e.g. parasite resistance) and therefore good genes. Females selecting the brightest males will pass on good genes to their offspring. However, bright colours may also make a lizard more conspicuous to a

predator. Females choose which males they mate with and therefore have no need for bright colour, which comes at the price of increased predation risk. This explains why females are drab. To deal with this dilemma, natural selection has cleverly distributed colour pigments on male flat lizards. Consider that the lizard's primary predator is the common kestrel, an aerial predator viewing lizards from above. Also consider that the bright colours on a male are important for signalling to other lizards on ground level. The brightest colours occur where they are visible to other lizards: sides of the body (including head), sides of the tail, the chin and the front and underside of the fore-legs. Also, males have bright venters (the lizard's underside) which are flashed at rival males and are therefore invisible to kestrels.

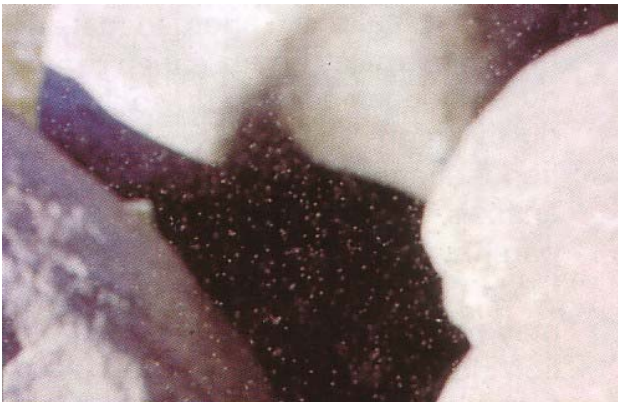
The importance of resources: black flies and mating success

As was discussed above, there is intense competition for mates. Flat lizards are territorial, which means they exclude all other males from a given area during the breeding season. The quality of their territory can influence their reproductive success. For example, if a male's territory has abundant food, more females may visit his territory. At Augrabies, the lizards' primary prey is the black fly (locally referred to as a muggie). Black flies occur in greatest abundance in the rocky, fast-flowing sections of the Orange River. It is here that conditions are most suitable for breeding. Female flies metamorphose from their aquatic larval stage and emerge from the river before dispersing in search of a blood meal. Male flies on the other hand, rarely (if ever) feed and congregate where the female flies emerge, waiting for a mating opportunity. This results in a situation where, under ideal conditions, large plumes of flies occur in the rocky stretches of the river. Consequently, male flat lizards that are able to establish territories in these areas have access to large numbers of female lizards. That is to say, they may court large numbers of females. At Augrabies, it is clear that it is the location, not the size, of your territory that counts. Once a male secures a territory, the old proverb of 'ownership is nine-tenths of the law' applies. Territorial males are extremely difficult to displace from territories

and frequently occupy the same territories year after year.



86. Black flies occur in large plumes above the rocky, fast flowing sections of the river.



87. Close-up of a plume of black flies.

Rogue males

The large number of lizards at Augrabies means that good territories are at a premium. Defending a low quality territory may not be a viable strategy. Consequently, some males adopt a 'sneaker' strategy. This is a common phenomenon among territorial animals. Sneaking involves trying to secure matings using alternative means. In flat lizards, sneaker males intercept travelling females. However, compared to territorial males, their treatment of females is far from gentlemanly.

Sexual harassment

Persistent advances on females, physical biting and attempted rape constitute sexual harassment. Sneaker males are the primary perpetrators. Under normal circumstances, males (normally territorial mates) court females without physical contact.

Compared to territorial males, courtship by sneaker males is brief or dispensed with and they frequently grab a female by a limb or the neck and attempt copulation. This activity often attracts the attention of other sneaker mates that attempt to get in on the action! In high-density areas, it is not uncommon to see two or three males pulling a female from different directions and climbing on her back. During such pandemonium, mates rarely succeed in mating with the female. Males will also attempt to displace rivals from a female; copulating pairs are sometimes disrupted in this manner. Females can reduce the effect of sexual harassment by spending much of their time in a single male's territory. The territorial male will keep sneaker (and other) males at bay and all the female will have to put up with is his occasional courtship.

She-males

Juvenile flat lizards closely resemble females in appearance. As males approach adulthood, colour development must take place. The first visible colour to appear is generally, on the male's lips. The appearance of any bright colour identifies the bearer as male and invites attack from rival males, especially adults. This effect is reduced as initial colour development is on the lizard's underside and is therefore concealed. It is common to see males that are large enough to be adult, but appear to be females from above. Their colourful venters give them away, as does their scent, the result of pheromones. It is therefore important that they avoid physical contact with adult males that can identify their sex with the flick of a tongue (lizards use their tongues to detect chemical scents). It is possible that males that are sexually mature but female-like in appearance are securing some matings. This may therefore constitute another reproductive strategy (as it does in some other animals), although this remains to be verified.

Male rivalry and badges of status

Some of the most spectacular lizard behaviour occurs when rival males meet. The extraordinary concentration of lizards at Augrabies results in frequent male contact. During the breeding

season, these interactions stem from aggression related to reproductive behaviour. Aggression and fighting in any animal species may be costly; first, the energy expended can be significant; second, there is an increase in the risk of injury and in extreme cases, death; finally, while heavily engaged in a fight, males may make themselves more vulnerable to predation. It therefore makes sense to have a mechanism to reduce risky and costly behaviour. Males make use of status signalling badges to signal levels of aggression and/or fighting ability. These badges occur on the lizard's abdomen and are orange, yellow, or a combination of the two. Generally, better fighters have larger badges. By signalling fighting ability, males can determine the superior fighter in a matter of seconds, without having to engage in a fight. The 'loser' can therefore back down without any risk of injury. This behaviour, termed a 'ventral display', consists of a male raising his side and thereby exposing his abdominal badge. Occasionally, males are closely matched in fighting ability or dispute a resource of high value, for example territory ownership. Under such circumstances, the badges may be ineffective and the two males may engage in a fight. Besides biting, fights still involve various forms of displays in which males attempt to intimidate their opponents. The degree of male-male competition has also resulted in natural selection for larger male body size such that males have significantly larger heads and bodies than females.



88. Male flat lizards have an orange, yellow or orange-yellow status signalling badge on their abdomens.

Lizard neighbours

Male territories frequently abut each other, especially near the river where fly plumes occur. Under such circumstances, neighbouring males are often in continual visual contact. Because lizards can identify each other individually (as opposed to merely seeing another male), males can discriminate among neighbours and strangers. Given that continued aggression between individuals can be energetically taxing and costly in terms of injury and predation risk, neighbouring males 'strike a deal' in which they recognise each other's turf and are less aggressive towards each other than to strangers. Scientists call this the 'dear enemy phenomenon', as it occurs in a wide variety of territorial animals, including birds and mammals. Male flat lizards, through the dear enemy phenomenon, are therefore able to focus their energies on keeping unfamiliar males at bay.



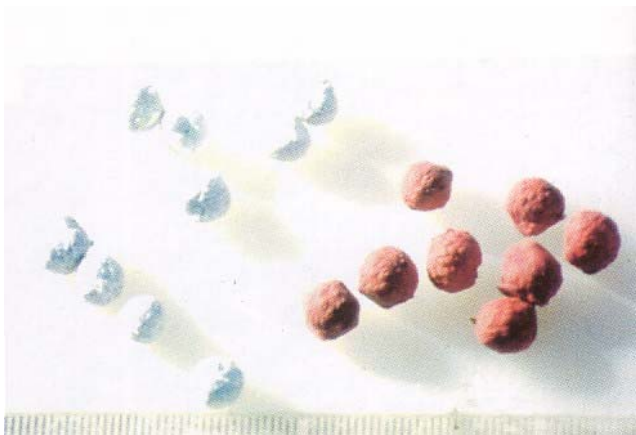
89. A male flashing his badge at a rival male that has ventured too close to his territory.



90. Males "square-off" and perform a behaviour known as back arching - the prelude to a fight.

Lizards on a diet of figs and flies

Flat lizards are primarily carnivorous and much of their diet at Augrabies consists of black flies. This will no doubt cheer any visitor that is troubled by the swarms of flies inhabiting the park! However, flies constitute a small food item and large numbers must therefore be consumed. Nevertheless, because the flies occur in such large concentrations, lizards can sit in one place and consume one after the next. As ambush foragers (an animal that remains stationary and awaits its prey), this is an ideal situation. They may also feed on larger insects that stray across their path. Lizards feeding on flies represent a spectacular sight. They frequently leave the ground as they snap flies from the air and some even perform a complete somersault to this end.



91. In an experiment to determine how lizards select figs (a valuable food item), scientists painted figs different colours. In the wild, lizards select red, ripe figs (unripe figs are white and hard.)-Photo: J.M. Greeff.

One of the more interesting aspects of the lizard's biology is its fig-feeding behaviour. Namaqua fig trees *Ficus cordata* are common in the park and their figs are very nutritionally rewarding to lizards. When lizards discover a fruiting fig tree, they will return daily until all ripe figs on the ground have been eaten. However, they experience stiff competition from birds such as starlings and bulbuls that also feed on figs. Rock dassies are another animal that feeds on figs and are therefore also a source of competition, albeit to a lesser degree.

The way figs are selected and eaten by lizards has

been studied in detail by scientists. For example, males have larger heads than females and eat the entire fig in much shorter time. Juveniles, with their smaller heads, are forced to break off pieces of fig or consume pieces broken off by birds or other lizards. They almost never eat an entire fig and frequently eat individual seeds from broken figs. Because figs are so nutritionally valuable, lizards sometimes attempt to steal ripe figs from the mouths of other flat lizards. To reduce this threat, when lizards discover an edible fig, they normally pick it up and run to an area free of other flat lizards that may attempt to steal it.

Lizards use colour and/or brightness to select figs for consumption. To determine how lizards select figs for consumption, scientists performed an experiment in which unripe white figs were painted red, while red ripe figs were painted white and offered to lizards. (All figs were of similar size.) Flat lizards avoided the figs painted white in favour of the red figs. However, once the lizards determined that the figs were in fact unripe, they ceased any further feeding! A further experiment showed that they have a sensory bias for movement. That is, movement quickly attracts their attention. When lizards were given a choice between moving unripe figs and stationary ripe figs, they went for the moving unripe figs.

Unfortunately for lizards, not all fig trees fruit at the same time. Therefore, it is very difficult to predict when an individual tree is in fruit. Systematically searching for figs and travelling from one tree to the next is an energetically costly exercise and may also increase predation risk. So how do lizards determine when ripe figs are available? Undoubtedly it occurs by chance in many instances. However, recent experiments showed that lizards also use bird activity as cues to locate fig trees in fruit.

Lizards, birds and figs: a unique relationship

When fig trees are in fruit, large numbers of birds congregate to feed. The flapping action of birds concentrated in a tree may serve to attract lizards given that they have a sensory bias for movement. To test this idea, a large cage containing birds was

placed in a tree devoid of figs. Lizards arriving at the tree in a set time interval were then counted and compared to how many lizards arrived when just an empty cage was placed in the same tree. This experiment was repeated in five different trees and showed that flat lizards are attracted to trees containing congregations of birds, as would occur during fruiting. The use of cues from a different species to locate food is rare among animals. A classic example is lions and spotted hyaenas using circling vultures to locate kills. The use of birds by lizards to locate figs is truly unique among animals.

Fig seeds eaten by lizards, birds and dassies are all able to germinate and demonstrate that all three animals serve as seed dispersers. In other words, seeds eaten by any of the three will still germinate and have the added advantage of being dispersed to areas where fewer competing seeds occur. Namaqua fig trees therefore benefit from the dispersal action of lizards, birds and dassies, while this trio gains nutritional benefits from eating figs.

Lizards and tourists

Flat lizards in the tourist areas are habituated to people and allow close approach. In some areas near the falls, lizards will ignore people until they are only a few metres away. This makes for perfect lizard viewing! Flat lizards are active throughout the year, but for shorter periods during winter and only if it is sufficiently warm. During summer, they are most active during morning hours and stick to the shade during the heat of the day. The best time to observe social behaviour is during the breeding season. Males are most aggressive from August to December, although aggressive behaviour will persist to some degree until autumn. Most copulations occur during September and October and hatchlings begin appearing from late December to January.

Flat lizards have learnt that humans occasionally drop morsels of food and are quick to seize an unattended sandwich! Feeding of animals changes their natural behaviour and this should therefore be avoided.