COMPARATIVE PSYCHOLOGY BY ANIMAL

NO.3 - FROGS

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CONTENTS

INTRODUCTION TO SERIES

"Comparative Psychology By Animal" is a series of booklets which aims to cover the topics within comparative psychology by focusing on specific animals. Each booklet will concentrate on specific issues that are relevant to that species, whether mammal, bird, amphibian/reptile, insect, or fish.

There will also be general discussions of the topics and different strategies available to the animals. All of the information is assessed from the point of evolutionary costs and benefits of a particular behaviour.

No.1 Lions

Topics

1. Co-operation
2. Mating strategies
3. Communication

No.2 Crickets

Topics

1. Communication
2. Genetic control of behaviour
3. Predator-prey relations
4. Mating strategies

No.3 Frogs

Topics

1. **Mating behaviour**
2. **Auditory Communication**
3. **Territoriality**
4. **Predator behaviour**

COMPARATIVE PSYCHOLOGY

Comparative psychology is the study of non-human animal behaviour, usually, but not necessarily, to apply the results to understanding human behaviour. Thus everything revolves around the evolution of behaviour.

Evolution can be reduced to three key aspects, and all other behaviour is an offshoot of these:

- Survival from predators;
- Obtaining food/prey;
- Reproduction.

Different species will have evolved different strategies in order to do these three key things. In many cases, it is a delicate balance between getting food, and surviving in order to reproduce and pass the genes to the next generation without being eaten.

It could be better to hide and eat less because predators won't find them, yet there is a need to advertise their presence to mates.

Table 1 shows some of the main topics in comparative psychology and how they relate to the three aspects of evolution.

EVOLUTION

Evolution is the cornerstone of understanding non-human behaviour (and human behaviour, according to Evolutionary Psychologists). It is based around two central concepts, proposed by Charles Darwin [1]: natural selection and sexual selection.

NATURAL SELECTION

This is the idea of the survival of animals within a species with particular traits that give them an advantage compared to others. This behaviour is "adapted", and is well suited to the environment that the animal lives in. These "fit" animals will survive and leave more offspring, which means the spread of "adaptive traits" in that species.

For example, running faster is an adaptive trait for prey being chased by fast predators (figure 1).

[1] Complete works of Darwin at http://darwin-online.org.uk/

	SURVIVAL FROM PREDATORS	OBTAINING FOOD/PREY	REPRODUCTION
SEXUAL SELECTION			Advertising good quality of genes; different strategy for males and females of species
PREY-PREDATOR RELATIONS	Evolution of strategies to stay ahead of predator or catch the prey		
FORAGING		Optimal input of energy for less output and risk of predation	
TERRITORIALITY		Resources to survive	To attract females and discourage competitors
MATING STRATEGIES			Mating with one partner or more, or not at all
GROUP BEHAVIOUR	"Selfish herd"	"Group hunting"	Ease of availability of mates
COMMUNICATION	"Illegitimate receivers" ie: predators		Locating mates

Table 1 - Main behaviours in comparative psychology and how they relate to the key aspects of evolution.

EXAMPLE - Each animal has two offspring:

CURRENT SITUATION — FUTURE SITUATION

Majority - animal A: Runs slow**; Few offspring in subsequent generations

2 offspring - 1 survive = 2 offspring $\rightarrow$ 1 survive = 2 offspring

Minority - animal B: Runs fast*: Many offspring in subsequent generations

1 offspring - 2 survive = 4 offspring $\rightarrow$ 4 survive = 8 offspring

KEY: * adaptive trait = run fast; ** non-adapt = run slow; each animal has 2 offspring

Figure 1 - Example of natural selection for adaptive traits.

More formally, natural selection depends on three principles (Dowling 1994):

i) Principle of diversity - there are a large number of variant forms of the same species (known as members of the population).

ii) Principle of interaction - these variant forms interact with the environment to see which "fit"; eg: animals that breathe air will not "fit" a permanent underwater environment.

iii) Principle of differential amplification - the variants that "fit" will spread at the expense of those who don't "fit"; ie: more offspring.

In terms of leaving offspring, animals will have evolved different strategies in relation to fecundity and viability. The first term relates to the number of fertilised eggs, and viability is the fertilised egg's chances of surviving (table 2).

	FECUNDITY	VIABILITY	EVOLUTIONARY STRATEGY
FISH	High	Low	Many eggs laid but few survive
MAMMAL	Low	High	Few or single eggs fertilised but most survive

Table 2 - Examples of fecundity and viability.

SEXUAL SELECTION

The best strategy for passing the genes into the next generation will vary between the male and female of the species. The male is able to produce many sperm, and so can theoretically have as many offspring as mates found.

But the female is restricted, in most species, by giving birth to the offspring. Thus she has more invested in its survival (table 3).

Different species behave in different ways depending upon their environments, but generally the example in table 3 is the common strategy of sexual selection. "Female choosiness" has led to the evolution of males who compete, in some way, to show the female that their genes are best for mating. This competition involves fights, "shows of quality" (eg: ornaments like a peacock's tail), or the collection of scare resources to give to the female ("resource-holding power"; RHP).

EXAMPLE - Male mates with ten females, who have one offspring each in the breeding season

	OFFSPRING	STRATEGY
MALE	10 fathered; can afford some not to survive	Find many female mates ie: indiscriminate; little concern for post-natal care
FEMALE	Each female has one offspring and thus survival important	Female invests time and effort in survival, but must exercise choosiness about male ie only mate with male who has "best genes"

Table 3 - Sexual selection and strategies for males and females.

The ideas of evolution from Charles Darwin are based upon the survival of the individual. But Dawkins (1976), more recently, has suggested that it is the survival of the genes that matter. For example, a mother who sacrifices herself for her three offspring will guarantee three copies of half of her genes survive. This has an evolutionary advantage over the survival of the mother at the expenses of her offspring. This has led to the focus on "inclusive fitness" (the survival of the individual and their biological relatives).

INTRODUCTION TO FROGS

There are three orders of amphibian, of which Anura ("without tail") includes frogs (Rana) and toads. Anura includes 3680 species divided into 22 families (Raven and Johnson 2002). The families are often divided between three sub-orders: primitive, transitional, and advanced frogs (Zug 1993). The main characteristics of frogs are described in table 4.

- compact tail-less body
- large head fused to trunk
- rear limbs specialised for jumping
- large eyes
- smooth or warty moist, glandular skin
- carnivores
- live in/near water
- lay eggs in water and fertilisation externally
- length ranges from 1cm to 30cm

Table 4 - Main characteristics of frogs

MATING BEHAVIOUR

As with many species, females choose the males. Mate selection by females is influenced by:

a) nature of call - ie: pitch and/or duration;

b) body size of male as communicated by frequency of calls;

c) quality of territory;

d) number of nights that male occupied the same site (Jacobson 1985).

The usual means of courting in frogs is by the male giving "advertisement calls". There are exceptions, though:

i) the use of visual display - eg: male Neotropical dendrobatid frogs (colostethus palmatus) turn black and jump up and down to gain the female's attention (Wells 1980);

ii) courtship dance by the male - eg: Neotropical dendrobatid frogs (colostethus collaris) (Dole 1974);

iii) female actively courts the male - eg: Green Poison-Arrow frog (Wells 1978).

Mating behaviour is characterised after copulation by amplexus (the male grasps the female around the middle until the eggs are released) for several hours to weeks. Thus the male can be confident that his sperm fertilised the eggs (Purves et al 1997).

Certain female qualities will encourage the male to maintain amplexus - silence; firmness (ie: body distended with eggs); and receptiveness to the male's clasp. Females can produce release by the "release call" or vibrating her body after laying the eggs. The soft abdomen now produced is a "turn-off" for the male (Stebbins and Cohen 1995).

The clasping response is very strong during breeding, and frogs have been observed clasping to inanimate objects, like floating apples.

AUDITORY COMMUNICATION

Frogs communicate by sound primarily (auditory communication), and there are advantages and disadvantages to this method compared to other forms of communication (table 5).

	AUDITORY	CHEMICAL	VISUAL
EXAMPLE	**call**	scent	plumage
RANGE/DISTANCE	**low**	low	medium
RATE OF CHANGE OF SIGNAL	**fast**	slow	fast
ABILITY TO GO PAST OBSTACLES	**good**	good	poor
RAPID EXCHANGE	**fast**	slow	fast
LOCATABILITY	**medium**	variable	high
COMPLEXITY	**high**	low	high
ENERGY COST OF COMMUNICATION	**high**	low	high
DURABILITY	**low**	high	variable

(Bold = auditory communication used primarily by frogs)

(After Krebs and Davies 1993; Goodenough et al 1993)

Table 5 - Three types of communication used by non-human animals and their advantages and disadvantages.

Frogs tend to call for mating (advertising presence), warning, distress, territorial ownership (more than one type of call in some species), release (male gives when clasped by another male or given by a female not sexually receptive), and a rain call (McFarland 1981).

Slater (1999) reports "dialects" in the calls of cricket frogs - with frequency differences in Kansas, New Jersey, and South Dakota.

The inflation of the throat sac is used to amplify the sound. Puncturing this sac reduces the sound by two to five times (Martin 1971). The volume of the call varies in the distance over which it can be heard: from 12 feet among some Australian frogs (Loftus-Hill and Littlejohn 1971) to half a mile in Green frogs (Martoff 1953).

When studying auditory communication among frogs, there are three key questions asked (Halliday 1992):

i) how do females identify their species-specific call?
ii) how do females locate a particular male?
iii) do females discriminate among the males?

1. How do females identify their species-specific call?

The answer is that different species have various dominant frequencies for calling, and different durations of the call. Females tend to be deaf to sounds outside that frequency.

This is evidence of peripheral tuning of the ear; ie: the ear is designed to receive stimuli from particular sound waves (frequencies) only. This is not present in birds of mammals (Bradbury and Vehrencamp 1998).

Because the male is almost always calling, there are evolutionary differences between the males and females in terms of acoustics; ie: the female ear is different to the male's. These differences are a result of the pressures of sexual selection, and Balaban (1994) sees this as the product of the "neurally amplified morphological evolution (NAME)" model. Female ears as a group are more sensitive than males to frequencies slightly lower.

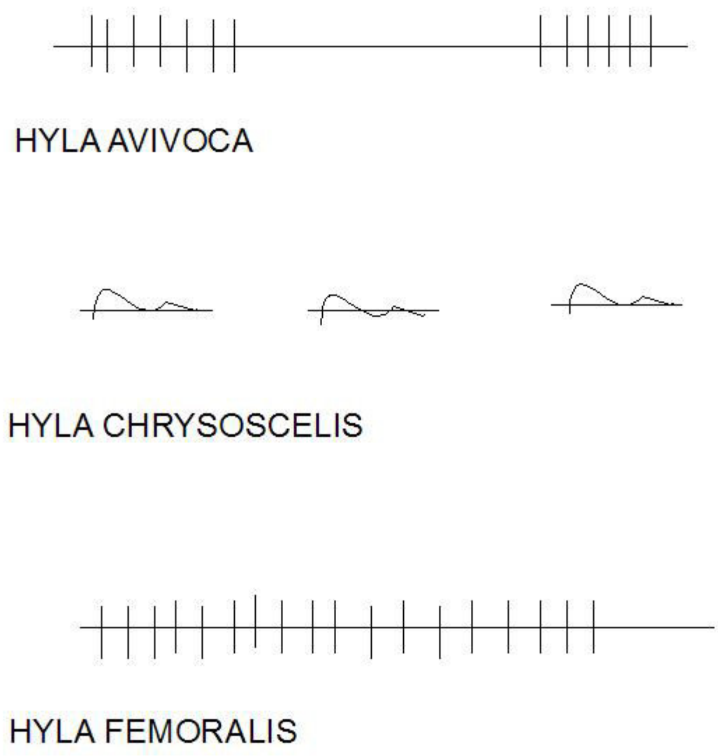
However, African clawed frogs do have the same ear physiology in males and females. But features of the female larynx prevent her from producing male calls (Kelley 1986).

Examples of frequency and duration (temporal structure) of calling of four Australian frogs are given in table 6 (Littlejohn 1977). Figure 2 also shows the differences in call between three species of Tree frogs.

TYPE OF AUSTRALIAN FROG	FREQUENCY kHz	DURATION millisecs
Limnodynastes dumerili	0.75	150
Limnodynastes peroni	1.00	50
Ranidella signifera	3.25	150
Litoria verreauxi	2.00	200

(After Halliday 1992)

Table 6 - Differences in frequency and duration of calls of four Australian frogs.



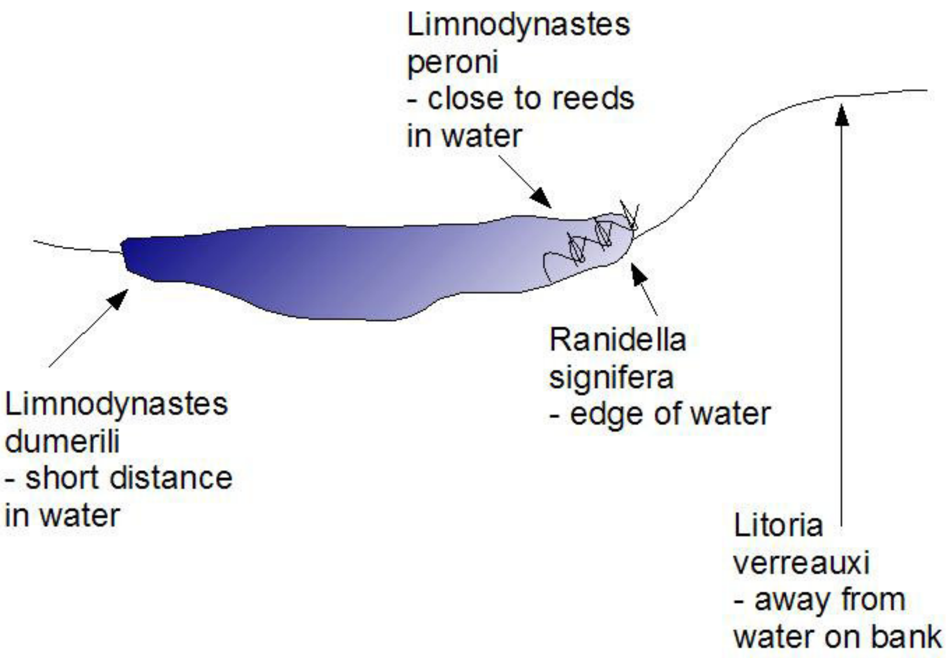
(Redrawn from Krebs and Davies 1993)

Figure 2 - Oscillogram traces of calls of three Tree frogs (approximately 5 seconds).

The timing of the call can also be influenced by the temperature of the frog because frogs are ectotherms (ie: their body heat comes from external sources). In other words, cold frogs will have a slowed down call. Females compensate for this potential problem by assessing their own body temperature (temperature-coupling). Gerhardt (1978) tested this experimentally with two loud-speakers and temperature changed female Gray Treefrogs. Females preferred the slower call when cold themselves.

2. How do females locate a particular male?

Different species will also have different positions in or close to the water (known as micro-habitats). Figure 3 shows the different positions around the pond of four types of Australian frogs.



(After Halliday 1992)

Figure 3 - Position around a pond of four species of Australian frog when calling.

Duellman (1967a) noted ten different species of frogs in a small lowland Costa Rican pond with each preferring a different area in or out of the water (see figure 4).

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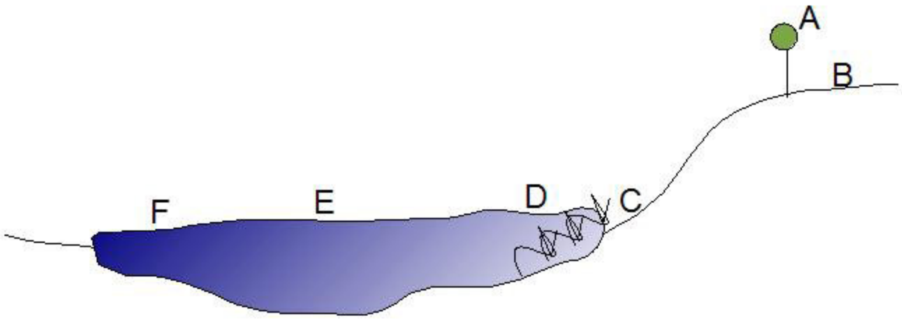

(Each letter = different species and preferred position)

(After Duellman 1967)

Figure 4 - Position around a pond of different frogs in Costa Rica.

3. Do females discriminate among the males?

There may be 50 males to one female in certain situations, so it is crucial for her to choose the best male.

Female choice can be seen in the evolution of calls by males. Generally the ability to produce the monotonous song is the sign of the quality of the genes (Blair 1968).

Calling requires a lot of energy, particularly to produce the loudest sound, and the ability to use up the energy is taken as a sign of a "good individual". Male Gray Treefrogs use more energy (as measured by oxygen consumption) at the fastest calling rate (eg: 1500 calls per hour) than forced exercise (Taigen and Wells 1985).

Male Tungara frogs produce whining calls which end with "chucks". Ryan (1985) compared sonograms of five calls of increasing complexity, and found females prefer males giving "chucks" as well as whines.

But the characteristic of the call that matters is the frequency of the "chuck". Ryan (1980) using a choice of two calls, from speakers in opposite parts of a pond, found that females went towards the lower-pitched "chucks". This type of "chuck" requires more energy to produce (up to 20 times more), and so is a signal of the size of the frog. The complex call is also easier for the female to locate, but so can bats.

Large frogs produce lower-pitched "chucks", and thus can be found by females as males aggregate together in the pond. The frequency of the call decreases with increasing body size (Ryan 1985).

Large frogs have a greater probability of mating. Research has found that a large body size is important. For example, in the Wood frog, larger animals produce more sperm, and thus greater fertilisation success (Smith-Gill and Berven 1980).

SATELLITE BEHAVIOUR

It has been noticed in Green treefrogs, for example, that males call on some nights and not others. On the silent nights, individuals remain near the chorus hoping to intercept approaching females ("satellite behaviour"). This is "eavesdropping" of a manner different to predators (Halliday 1992).

However, this strategy only works if a minority of frogs are "satellites" or "satellites" on some night only. Otherwise, the chorus would fall silent. Varying between calling and "satelliting" is evidence of an "evolutionary stable strategy" (ESS) (Maynard Smith 1976). "Satelliting" is a good strategy, though, for smaller, and for younger males.

"Satellite" behaviour (or parasitic behaviour) has been found in many species of frogs. Usually silent males close to the chorus waiting to intercept approaching females. There are variations on this behaviour:

a) medium-sized Bullfrog males will infiltrate the territory of larger males, who are mating, in order to call (Mauger 1988);

b) "satellite" males calling in unison to interfere with the female's ability to find the chosen male (Ovaska and Hunte 1992);

c) "satellites" chase amplexing pairs and attempting to remove the male, with limited success in African leaf-folding frogs (Blackwell and Passmore 1991);

d) silent "satellite" behaviour has also been observed in larger males in order to save energy or avoid predators who hunt by sound (Perrill and Magier 1988).

COSTS OF AUDITORY COMMUNICATION

There is a trade-off for the males between conserving energy, beating the competitors to a female, and avoiding predators.

Obvious communication like calling has the downside of "illegitimate receivers" or "eavesdroppers" - ie:

predators - Fringe-lipped bats for Tungara frogs.

The key is to attract mates but not predators. Certain strategies have evolved to deal with this dilemma.

i) Stop calling when detect flying bat, or cardboard model in the case of experiments (Tuttle et al 1982). But this would not happen on cloudy nights among Mud-puddle rain forest frogs, who suffered high levels of predation on such nights (Tuttle and Ryan 1981).

ii) Males can adapt their calls to narrow-frequency whines only when alone. Fringe-lipped bats respond to calls with "chucks" at the end in speaker experiments (Ryan 1983). Thus when alone, it is more important to survive than to mate. Females with no other choices will mate with frogs that produce whines only.

iii) Calling while in large choruses is safer for the individual because there is less chance of being the chosen victim.

TERRITORIALITY

ADVANTAGES	DISADVANTAGES
- signal to attract mate	- easy for predators to find
- access to food	- conflict over territory and consequent risks from fights, or energy wasting in displays

Table 7 - Advantages and disadvantages of territorial behaviour.

REASON FOR TERRITORY	NUMBER OF ANIMALS (from 40; Wilson 1975)
1. control food supply	14
2. retreat; shelter; nest	8
3. access to females; space for sexual display; courtship	18

Table 8 - Main reasons for territories among non-human animals.

Territoriality is very important (tables 7 and 8), and at dusk, male Bullfrogs take up their position to call for mates. The process of calling exposes a colourful area of the throat which acts as a visual signal as well. The protection of the territory is paramount to allow space for sexual display primarily.

This has been shown in Pipid frogs (Rabb and Rabb 1963), Bullfrogs (Capranica 1968), and Green frogs (Martof 1953).

If another male approaches the territory, a "vocalisation battle" occurs. If the intruder does not withdraw, the two males will wrestle until one is forced onto his back (Emlen 1968). Wells (1981) reports observing a fight of over two hours in Trinidad. Residents tend to do better in fights, and win over 90% of contests (Stewart and Rand 1991).

After disputes between neighbours are resolved, the residents only respond aggressively to strangers. This is known as the "dear-enemy truce-relationship" (Jaeger 1981), and saves energy and reduces the risk of endless fights.

TERRITORIALITY AND CALLING

Bullfrog males call from their territory where water temperature and vegetation is suitable for egg development. Females move around and choose the larger males, usually because they have the best territory. This is similar to a lek used by some species of birds.

Evidence to back up this idea comes from studies which show males calling in harmony, and the existence of small dominance hierarchies. Males may duet by alternating notes, and the removal of one of the frogs causes disruption to the singing of the other (Lemon 1971). Frogs may call in groups of three or four also, and removal of the loudest male of Central American chorusing frog causes the others in the group to fall silent (Duellman 1967b). When the quieter members are removed, this does not happen. This suggests a form of dominance hierarchy in the small groups [2]. The loudest male may also control the calling of the whole chorus.

From an evolutionary point of view, it is not clear why the males would call in harmony. Unless it is a way that smaller males can gain from the louder calls of the bigger males. A way of cheating females, possibly, by the smaller males.

In another situation, Coe (1967) reports a case of African rhacophorid frog males co-operating to build an egg nest for a female. Only one of the four males was in the amplexus position throughout the nest-building. All the males may have believed that they had fertilised the

[2] Dominance hierarchies have been reported in crowded colonies of Leopard frogs (Boice and Witter 1969) and African clawed frogs (Haubrich 1961).

eggs.

The territory's characteristics are important because of embryo mortality, which is linked to overheating and leech predation. Howard (1978) found a negative correlation between male size and embryo mortality. For example, males of 120mm or less body length (small) had nearly total embryo mortality compared to less than one third for males of 150mm or longer.

The call of the male frog can vary over the night because it has different purposes. Puerto-Rican tree frogs make a two-note sound "co-qui" ("ko-kee") (Narins and Capranica 1980). The first part of the sound establishes territory, appears earlier in the night, and is a fequency aimed at other males. The second part of the call dominates later in the night to attract females at another particular frequency.

The "co" at 1 kHz is received by both males and females, but the "qui" is heard only by females (at 2 kHz) (Narins and Capranica 1976). Females do not respond to just the "co" sound in loudspeaker tests.

VARIATIONS IN BEHAVIOUR

Female Wood frogs are receptive for one night a year. Thus the best strategy for males is to hurry around the pond to find as many females as possible rather than maintaining a territory and waiting (Bervan 1981).

The different species of frogs show a range of behaviours that include territories on land and water. For example, the male Primitive tailed frog has no voice and hunts for passive females (Wilson 1975). While other species wait on their territory for the female. However, there is a variety here too: some males pursue any female as soon as spotted, while other males must be touched by a female before they begin courtship.

In one particular type of frog (Dendrobates), females pursue the moving males. In this species, males receive the eggs of females on land and carry the tadpoles to water (Wilson 1975).

PREDATOR BEHAVIOUR

Frogs are solitary hunters. There are varied strategies for catching prey. For example, among Leaf-litter frogs in Panama, these strategies vary from "sit and wait" for mobile prey (eg: flies) to those frogs who "hunt" slow prey (like worms) (Toft 1981).

African clawed frogs have pit-like organs on the side of their body which responds to water movement along the skin. This allows the frogs to detect the movement of prey (insects) in water, which can be caught even when frogs blindfolded (Tinbergen 1974).

Another aspect of evolution is vision. Because of the need for speed to catch flying insects, most of the visual information is processed in the retina and linked to the reflex centre in the brain. Visual information in humans tends to be processed in the visual cortex. Frogs are also extra sensitive to certain visual stimuli - ie: those that appear "bug-shaped".

Thus named "bug-detectors". Measurement of cell firing in the retina occurs when a small rounded object passes into the field of view, even if the object then becomes stationary. The cells do not fire if the object suddenly appears or a large dark bar moved in front of the eye (Lettvin et al 1959) (table 9).

But sudden shadows cause firing and the reflex response to escape. The other response to small rounded objects is for the tongue to fire out at it (feeding response). The responsiveness of the frog's eye to a limited number of stimuli is known as stimulus filtering.

RESPONSIVE	NOT RESPONSIVE
- single moving dot especially irregular movement	- field of dots

Table 9 - What shapes frogs respond and do not respond to.

For example, Green Treefrogs respond very fast to objects crawling at a certain speed and having a certain length/width - ie: worms (their main prey) (Freed 1982).

A number of species of frog feed on ants and termites, which are formidable defenders of their colony. Through the use of chemical signals, it is presumed, a South American frog (lithodytes lineatus) lives in the nest of the ants, and an Australian frog (myobatrachus gouldi) with termites (Zug 1993).

REFERENCES

Backwell, P & Passmore, N (1991) Satellite behaviour in the leaf-folding frog, Afrixalis delicatus, Journal of Herpetology, 25, 497-498

Balaban, E (1994) Sex differences in sounds and their causes. In Short, R & Balaban, E (eds) The Differences Between the Sexes, Cambridge: Cambridge University Press

Berven, K (1981) Mate choice in the wood frog Rana sylvatica, Evolution, 35, 707-722

Blair, W (1968) Amphibians and reptiles. In Sebeok, T (ed) Animal Communication: Techniques of Study and Results of Research, Bloomington: Indiana University Press

Boice, R & Witter, D (1969) Hierarchical feeding behaviour in the leopard forg (Rana pipiens), Animal Behaviour, 17, 3, 474-479

Bradbury, J & Vehrencamp, S (1998) Principles of Animal Communication, Sunderland, MA: Sinauer Associates

Coe, M (1967) Co-operation of three males in nest construction by Chiromantis rufescens Gunther (Amphibia: Rhacophoridae), Nature, 214, 112-113

Capranica, R (1968) The vocal repertoire of the bullfrog (Rana catesbeiana), Behaviour, 31, 3, 302-325

Dole, J (1974) Home range in the canyon tree frog (Hyla cadaverina), Southwestern Naturalist, 19, 105-107

Duellman, W (1967a) Courtship isolating mechanisms in Costa Rican hylid frogs, Herpetologica, 23, 169-183

Duellman, W (1967b) Social organisation in the mating calls of some Neotropical anurans, American Midland Naturalist, 77, 1, 156-163

Emlen, S.T (1968) Territoriality in the bullfrog, Rana catesbeiana, Copeia, 2, 240-243

Freed, A (1982) A treefrog's menu: selection for an evening meal, Oecologia, 53, 20-26

Gerhardt, H (1978) Temperature coupling in the vocal communication system of the gray tree frog, Hyla versicolor, Science, 199, 992-994

Goodenough, J; McGuire, B & Wallace, R (1993) Perspective on Animal Behaviour, New York: John Wiley & Sons

Halliday, T (1992) (ed) Brain, Biology and Behaviour: 3 - Senses and Communication, Milton Keynes: Open University

Haubrich, R (1961) Hierarchical behaviour in the South African clawed frog, Xenopus laevis Daudin, Animal Behaviour, 9, 1&2, 71-76

Howard, R (1978) The evolution of mating strategies in bullfrogs Rana catesbiana, Evolution, 32, 850-871

Jacobsen, S (1985) Reproductive behaviour and male mating success in two species of glass frogs (Centrolenidae), Herpetologica, 31, 425-429

Jaeger, R (1981) Dear enemy recognition and the costs of aggression between salamanders, American Naturalist, 117, 962-974

Kelley, D (1986) Neuro-effectors for vocalisation in Xenopus laevis: hormonal regulation of sexual dimorphism, Journal of Neurobiology, 17, 231-248

Krebs, J & Davies, N (1993) An Introduction to Behavioural Ecology (3rd ed), Oxford: Blackwell

Lemon, R (1971) Vocal communication by the frog Eleutherodactylus martinicensis, Canadian Journal of Zoology, 49, 2, 211-217

Lettvin, J; Maturana, H; McCulloch, W & Pitts, W (1959) What the frogs eye tells the frogs brain, Proceedings of the I.R.E, 47, 1940-1951

Littlejohn, M (1977) Long-range acoustic communication in anurans: an integrated and evolutionary approach. In Taylor, D & Guttman, S (eds) The Reproductive Biology of Amphibians, New York: Plenuim Press

Loftus-Hill, J & Littlejohn, M (1971) Mating-call sound intensities of anuran amphibians, Journal of Acoustical Society of America, 49, 1327-1329

Martin, W (1971) Mechanisms of sound production in toads of the genus Bufo; passive elements, Journal of Experimental Zoology, 176, 273-294

Martof, B (1953) Territoriality in the green frog, Rana clamitans, Ecology, 34, 1, 165-174

Mauger, D (1988) Observations on calling behaviour of bullfrogs in relation to male mating strategy, Bulletin of Chicago Herpetological Society, 23, 57-59

Maynard Smith, J (1976) Evolution and the theory of games, American Scientist, 64, 41-45

McFarland, D (1981) (ed) The Oxford Companion to Animal Behaviour, Oxford: Oxford University Press

Narins, P & Capranica, R (1976) Sexual differences in the auditory system of the tree frog Eleutherodactylus coqui, Science, 192, 378-380

Narins, P & Capranica, R (1980) Neural adaptations for processing the two-note call of Puerto-Rican tree frog Elentherodactylus coqui, Brain and Behaviour, 17, 48-66

Ovaska, K & Hunte, W (1992) Male mating behaviour of frog Eleutherodactylus johnstonei (Leptodacxtylidae) in Barbados, West Indies, Herpetologica, 48, 40-49

Perrill, S & Magier, M (1988) Male mating behaviour in Acris crepitans, Copeia, 1988, 245-248

Purves, W.K et al (1997) Life: The Science of Biology (5th ed), Sunderland,MA: Sinauer Associates

Rabb, G & Rabb, M (1963) On the behaviour and breeding biology of the African pipid frog Hymenochirus boettigeri, Zeitschrift fur Tierpsychologie, 20, 2, 215-241

Raven, P.H & Johnson, G.B (2002) Biology (6th ed), New York: McGrawHill

Ryan, M (1980) Female mate choice in a neo-tropical frog, Science, 209, 523-525

Ryan, M (1983) Sexual selection and communication in a neo-tropical frog Physalaemus pustulosus, Evolution, 37, 261-272

Ryan, M (1985) The Tungara Frog, Chicago: University of Chicago Press

Slater, P (1999) Essentials of Animal Behaviour, Cambridge: Cambridge University Press

Smith-Gill, S & Berven, K (1980) In vitro fertilisation and assessment of male reproduction potential using mammalian gonadotropin-releasing hormone to induce spermiation in Rana sylvatica, Copeia, 1980, 723-728

Stebbins, R & Cohen, N (1995) A Natural History of Amphibians, Princeton, NJ: Princeton University Press

Stewart, M & Rand, A (1991) Vocalisations and the defence of retreat sites by male and female frogs, Eleutherodactylus coqui, Copeia, 1991, 1013-1024

Taigen, T & Wells, K (1985) Energetics of vocalisations by an anuran amphibia (Hyla versicolor), Journal of Comparative Physiology and Biology, 155, 163-170

Tinbergen, N (1974) Animal Behaviour, Time-Life Books

Toft, C (1981) Feeding ecology of Panamanian litter anurans: patterns in the diet and foraging mode, Journal of Herpatology, 15, 139-144

Tuttle, M & Ryan, M (1981) Bat predation and the evolution of frog vocalisations in neo-tropics, Science, 214, 677-678

Tuttle, M; Taft, L & Ryan, M (1982) Evasive behaviour of a frog in response to bat predation, Animal Behaviour, 30, 393-397

Wells, K (1978) Courtship and parental behaviour in a Panamanian poison-arrow frog (Dendrobates auratus), Herpetologica, 34, 148-155

Wells, K (1980) Social behaviour and communication of a denbrobatid frog (Colostethus trinitatis), Herpetologica, 36, 189-199

Wells, K (1981) Territorial behaviour of the frog, Eleutherodactylus urichi in Trinidad, Copeia, 1981, 726-728

Wilson, E.O (1975) Sociobiology: The New Synthesis, Cambridge, MA: Belknap Press

Zug, G (1993) Herpetology, San Diego: Academic Press