COMPARATIVE PSYCHOLOGY BY ANIMAL

NO.2 - CRICKETS

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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**

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.

	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.

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

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

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).

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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 → 1 survive = 2 offspring


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

1 offspring - 2 survive = 4 offspring → 4 survive = 8 offspring

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

There are 35 orders of insects, and crickets are part of the order: orthoptera (grasshoppers, locusts, katydids and crickets). There are 17000 species in this order (Chinery 1993). Table 4 lists some of the main families of crickets, while table 5 gives the key differences between crickets and other insects.

FAMILY	EXAMPLE	NUMBER OF SPECIES (Daly et al 1998)
Cone-heads (Copiphorinae)	short-winged cone-head	
Bush crickets (Tettigoniidae) (known as katydids in USA)	great green bushcricket wart-bites Mormon cricket	5000
Ephippigeridae	saddle-backed bushcricket	
Wingless camel cricket (also known as cave crickets) (Raphidophoridae)	greenhouse camel cricket	600
True crickets (Gryllidae)	field cricket house cricket wood cricket	12000
Ant-loving cricket (Myrmecophilidae)		50
Tree cricket (Oecanthinae)	Italian cricket	
Mole cricket (Gryllotalpidae)		50
Pigmy mole cricket (Tridactylidae)		75
Jerusalem crickets/ potato bugs (Stenopelmatidae)		200

Table 4 - Examples of families of crickets.

- Average length: 3 cms
- 2 pairs of wings (where have them)
- Can fold wings back
- Incomplete or simple metamorphosis: egg-nymph-adult (no larva or pupa stages)

Table 5 - Key facts about crickets compared to other insects.

COMMUNICATION

Crickets communicate by sound exclusively, though other orthoptera, like locusts, do use chemical communication (Daly et al 1998). Auditory communication has strengths and weaknesses compared to other forms of communication (table 6).

	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

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

Table 6 - Three main types of communication used by non-human animals and their advantages and disadvantages.

Alexander (1968) lists eleven different functions of orthoptera sound communication (those marked with * are relevant to crickets):

i) food directives; ie: where to find food;

ii) nest site directives;

iii) disturbance and alarm signals (predator repelling and alarming);

iv) calling signals (pair forming and congregation)*;

v) aggression signals (rival separating and dominance establishment)*:

vi) courtship signals *;

vii) courtship interruption signals; eg: when courtship rebuffed*;

viii) copulatory signals*;

ix) post-copulation and inter-copulation signals;

x) recognition signals;

xi) mimicry signals (prey attraction by production of their courtship calls by predator).

Table 7 outlines the main characteristics of the male cricket's song.

- "window of hearing"; ie: specific frequency (4-5kHZ)
- interval between calls (rate of emission); eg: 10ms gap
- song automatic; ie: genetically programmed
- song is species-specific

- calling signals quality of male and their genes:
    - length of calling
    - volume of song
    - method of producing call is clue to quality of specialised wings and their symmetry

Table 7 - Characteristics of male cricket's song.

The male produces a song by stridulation - much of which is ultrasonic, while the female is usually silent (ie: does not call). Usually during singing, the left wing with its "stridulatory file" (row of teeth-like formations) is scratched over a raised vein on the right forewing (Rust et al 1999). This is stridulation.

This process does not make much sound, so a system of amplification is required. One method used is by the tegmina (modified fore wing), while mole crickets have a horn-shaped burrow which acts as a sound enhancer (Gullan and Cranston 2000).

The song serves the function of repelling male competitors, and attracting receptive females. The song is usually species-specific.

CIRCADIAN RHYTHMS IN CALLING

Male crickets call to attract males at roughly the same time every day - early evening. Experiments keeping crickets in a controlled environment of 12 hours light and 12 hours darkness found that after a period of adjustment, the crickets would start to call two hours before darkness and continue until two and half hours before light.

While those kept in constant darkness, singing begins at intervals of 23.5 hours and lasts the normal period. In constant light, the interval is 25.3 hours (Loher 1972). This is an endogenous rhythm; ie: partly independent of environmental signals.

Calling at night occurs because this is the time when females move around.

It appears that visual signals help the cricket to keep their calling in rhythm. If the optic nerve is cut, the calling period changes each day (Johnson and Hasting 1986).

LENGTH OF CALLING

There are differences in the length of calls of male crickets: some call for many hours through to others who rarely sing. Cade (1981) selectively bred long and short callers over four generations. The difference in length of calls was found to be genetic, as shown by the results summarised in table 8.

APPROXIMATE PERCENTAGE OF OFFSPRING

MEAN CALLING TIME (hrs)	SHORT CALL OFFSPRING		LONG CALL OFFSPRING	
Generation:	1st	4th	1st	4th
0.5	30	0	56	0
1.5	20	4	28	10
2.5	4	6	10	0
3.5	8	12	0	15
4.5	28	10	4	15
5.5	4	12	2	8
6.5	6	15	0	8
7.5	0	12	0	4
8.5	0	25	0	30
9.5	0	4	0	10
10.5	0	0	0	0

(Data from Cade 1981)

Table 8 - Summary of results from breeding studies by Cade (1981).

The length of song has been found to be a key for female attraction. Hedrick (1986) used a common experimental technique of two speakers in opposite parts of the room, each playing a different call. One speaker played a long running call, the other played short bouts of song. In 23 of 25 trials, females moved towards the long-running call, suggesting female preference for this attribute.

To call continuously shows evidence of evolutionary fitness and thus "good quality" genes in the male.

OTHER CHARACTERISTICS OF COMMUNICATION

It is the volume and rate of emission that is key, and a number of different messages can be thus communicated. Alexander (1962) recorded five different calls by one type of cricket (Teleogryllus commodus) (as described in table 9).

Though the cricket is able to communicate different messages, it would be wrong to class it as a language. Table 10 compares cricket communication with human verbal language using the criteria of a language from Hockett (1960).

The quality of song is also linked to the symmetry of the male's body (McGavin 2001), and symmetry is seen as a key signal of "good genes".

TYPE OF CALL	kHZ	DESCRIPTION IN ONE SECOND OF TIME
CALLING	4	equal distance longer calls
ENCOUNTER	3-4	individual call similar in length to above but grouped as short bursts, pause, longer burst, pause, short burst
FIGHTING	6/4-5	initially at higher kHZ, then steady bursts of equal distance at lower frequency
TRANSITION TO COURTSHIP	4	short bursts build up, and even then steady song
COURTSHIP	4	short steady calls

(After Alexander 1962)

Table 9 - Different cricket calls recorded by Alexander (1962).

CRITERIA OF LANGUAGE (from Hockett 1960)	CRICKET COMMUNICATION
1. vocal-auditory channel	auditory, but not vocal
2. broadcast transmission and directional reception - direction of communication controllable	yes
3. rapid fading of message	yes
4. interchangeability - both transmitter and receiver both use same system (female of species rarely sing)	partial
5. complete feedback - "speaker" able to perceive own signal	yes
6. specialisation - energy produced by sound not as important as effect of sound	yes?
7. semanticity - different signals have different meanings	partial
8. arbitrariness - symbols have abstract meanings	?
9. discreteness - each sound separate	yes
10. displacement - can refer to objects not physically present	-
11. openness - new messages created	no
12. tradition - passed on by learning	no
13. duality of patterning - individual elements meaningless until combined	?
14. prevarication - ability to lie or talk nonsense	no
15. reflectiveness - ability to talk about talk	no
16. learnability - speaker of one language to learn another	no?

(After Thorpe 1972, 1974)

Table 10 - Characteristics of human verbal language compared to cricket communication.

GENETIC CONTROL OF BEHAVIOUR

Selective breeding and cross-breeding of species (eg: Teleogrillus commodus with Teleogrillus oceanus; Bentley 1971) show that individual song characteristics are determined by specific genes.

Other such studies have found many behaviours to be controlled genetically (eg: fighting in the juvenile period in Gryllus campestris; von Hormann-Heck 1957 quoted in Eibl-Eibesfeldt 1975).

Further evidence that the mechanism of control of the call is genetic comes from isolation studies. Here animals are kept separate from their species from birth, and thus cannot hear the normal call. Male crickets kept in isolation sing a normal song at the appropriate time (Bentley and Hoy 1974).

Also crickets deafened at birth still make stridulation even though unable to hear the call. Severing the wings does not effect the male's call. It seems to be resistant to environmental modification (Alexander 1968).

The rate of calling tends to be automatic also. Heiligenberg (1966 quoted in Hinde 1970) has shown how the call response is a stimulus-response relationship; ie: the rate of calling affected by the calls heard by the cricket. This would make sense as calling is a key means of male competition and signalling who is best to the female. Captive house crickets were played calls at a rate of every 2.5 or 0.625 seconds, or none at all (control group). The captive crickets rate of calling was then recorded. Table 11 shows that the more frequent the calls heard, the faster the reply.

It can be seen that singing is ritualised aggression and competition between males where tympanal organs (hearing mechanisms) are destroyed (ie: the cricket can no longer hear its own singing).

AVERAGE NUMBER OF CHIRPS IN ONE SECOND INTERVAL	
no stimulation	15
2.5 second stimulation	29
0.625 second stimulation	33

(After Hinde 1970)

Table 11 - Summary of findings from Heiligenberg (1966).

In this situation, Gryllus pennsilvanicus starts to show aggression not normally shown (Phillips and Konishi 1972). Aggression has costs to the animal (ie: risk of injury or death) and so ritualised forms are a less risky way of males showing the female is best.

PREDATOR-PREY RELATIONS

Night activity by the cricket allows avoidance of visual-hunting predators, but exposes them to specialist nocturnal predators.

Crickets are predated by bats. Bats hunt by the use of ultrasonic cries in the range of 40-50 kHZ. Researchers have found that crickets are sensitive when flying to this range of sound, and automatically turn away from the source. Furthermore, crickets turn towards sounds of 5kHZ, which is the range of its own call.

Moiseff et al (1978) held a cricket suspended in the air, as if flying, while playing different frequency sounds from speakers in different directions. The movement of the cricket confirmed its flight towards and away from certain frequency ranges.

The response of the cricket here is a reflex, which occurs within milliseconds of hearing the bat's call, and before the detection of the prey by the bat.

The evolution of sensitivity to the predator's sound range is an example of the "evolutionary arms race", where predator and prey co-evolve strategies to capture and survive.

It is believed that the response to certain frequency ranges related to finding a mate evolved in crickets long before bats evolved, and then the detection of ultrasound came later. This is classed as exaptation - a morphological-physiological [2] predisposition to evolve into a new function (Gulland and Cranston 2000). A particular behaviour which initially evolved for one purpose later evolves to include another purpose: detecting mates in one frequency and then predators at another frequency.

The male's song is also detected by parasitoid flies who lay their eggs on or near the cricket at night. The larvae burrow into the host for 7-10 days, emerge from the dying host and pupariate in the ground (Gullan and Cranston 2000). For example, parasitic tachinid fly and North American cricket. However, this risk is less than the need to reproduce, and if it does happen, the male will probably have mated at least once (O'Toole 1995).

The problem for the flies after detecting the call of the cricket is to localise the source. Because the ears are too close together (less than 1.5mm apart), this limits the normal means of localisation - the difference in timing and intensity between each ear. These type of

[2] Morph = genetic form or variation.

flies have special hearing apparatus on the neck, and it is more highly developed in the female, who lays the eggs in the host.

An interesting method of defence shown by katydids is to cause blood to flow out through the joint membranes of the thorax ("reflexive bleeding") (Rietschel 1975).

MATING STRATEGIES

NUPTIAL GIFT

The "nuptial feeding" of females by males in insects takes three forms (bold type is the form taken with crickets):

i) food collected and regurgitated by males;

ii) glandular product (eg: spermatophore) of male;

iii) cannibalisation of male during or after copulation [3].

One way in which males show their quality of genes is through a "nuptial gift" to the female. For example, the male of decorated crickets gives the female a two-part spermatophore (jelly-like substance) during copulation.

The first part of the "gift" (spermatophylax) is eaten, while the second part (sperm ampulla), containing the sperm, is left in the female genital opening. While eating the first part, the sperm have time to fertilise the eggs. But as soon as the female finishes the first part of the spermatophore, she will eat the second part including the sperm (Sakaluk 1984) [4].

Thus the larger the first part of the "gift", the longer the sperm has to fertilise the eggs, and more reproductive success. Males who produce large spermatophore will have more evolutionary success. The size of the spermatophore will depend upon the male's ability to collect the nutrients needed. It contains proteins and rare traces elements needed for pregnancy.

The "nuptial gift" usually weigh up to 25% of the male's body weight, and leave them unable to mate for several days afterwards. Where environmental conditions are poor, there can be a reversal of typical sex roles,

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[3] In North American sagebush crickets, the female eats the male's hind wing during copulation, while in the Bradyporus (type of Bush cricket), the female bites the partner's back and drinks the "blood" (haemolymph) (McGavin 2001).

[4] In many species of crickets, there is not really a penis (Rietschel 1975).

and females compete with each other for the choosy males.

In Mormon crickets, whose "nuptial gift" can weigh up to one-third of body weight of the male, females compete to mount the male who weighs them. The weight is a signal of the number of eggs. Gwynne (1981) found the average number of eggs was 48 for females accepted by the male, but only 30 for those rejected.

However, there are some cases where the spermatophylax contains enough amino acid to persuade the female to eat it, but not so much that the male is depleted. It may use up more energy for the female in eating it (McGavin 2001). This allows the male to distribute more sperm at less cost to itself.

The sperm contained in some "nuptial gifts", like the Mormon cricket, include substances that "turn-off" female receptivity to further males. Insemination also stimulates ovulation and increases the chances of fertilisation (Gwynne 1981). These processes have evolved as part of sperm competition [5].

Thus the "nuptial gift" has two functions (Gwynne 1990):

i) as a sperm-protection device against male competitors;

ii) as a parental investment by the male to help the female survive and bring up offspring by herself.

OTHER BEHAVIOURS

Traditionally insects lay eggs which over-winter and hatch the next year, but crickets have flexible egg biology. If conditions are poor, eggs can enter diapause (a form of suspended animation), and hatch years later (Ritchie 2002).

Male crickets have a general memory of what happened in past fights. Alexander (1961) used a modal cricket to fight, and noticed a "pseudo-dominance hierarchy"; ie: males had knowledge of their position in relation to others. But they do not recognise each other (thus not "true" dominance hierarchy).

Burk (1980) noticed that male crickets who had recently won a fight were more likely to court a female.

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[5] Sperm competition is the competition among sperm for egg fertilisation of more than one male (Alcock 1993).

Other strategies in sperm competition include removal of rival sperm after copulation which is eaten (eg: 87% of sperm removed by Truljalia hibinonis type of cricket; McGavin 2001), or simply hanging on to the back of the female until she lays the eggs. Where females are in short supply, males will fight.

This is known as the "Duke of Marlborough Effect" (sex after fighting), and may be due to the increase in testosterone from fighting.

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