COMPARATIVE PSYCHOLOGY BY ANIMAL

NO.5 - STICKLEBACKS

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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

1. Co-operation
   - group foraging
   - communal care
   - co-operative males

2. Mating strategies
   - infanticide

3. Communication

No.2 Crickets

1. Communication

2. Genetic control of behaviour

3. Predator-prey relations

4. Mating strategies
   - "nuptial gifts"

No.3 Frogs

1. Mating behaviour

2. Auditory Communication
   - Satellite Behaviour
   - Costs of auditory communication

3. Territoriality

4. Predator behaviour

No.4 Robins

1. Territoriality

2. Communication

3. Mating strategy

4. Other behaviours
    - predator-prey relations
    - foraging behaviour
    - migratory behaviour

No.5 Sticklebacks

1. Foraging Behaviour

2. Courtship Behaviour

3. Parental Care

4. Fighting Behaviour

5. Ethology - Explaining Instinctive 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:

i) survival from predators;
ii) obtaining food/prey;
iii) 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: 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).

	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.

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

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 STICKLEBACKS

Sticklebacks are from the family of fish, Gasterosteidae, and the order, Gasterosteiformes. The main characteristic of this order are fish with several erectile spines in front of the dorsal fin (Frank 1969). Table 4 lists three main types of sticklebacks.

NAME	LATIN NAME	LIVES IN FRESH OR SALTWATER	LENGTH
Three-spined stickleback	Gasterosteus aculeatus	both	5-10cms
Ten-spined stickleback	Pygosteus pungitius	fresh	5-10cms
Fifteen-spined stickleback	Spinachia spinachia	salt	20cms

Table 4 - Three main types of sticklebacks.

Sticklebacks vary in the number of spines on their backs. The Ten-spined stickleback has that number of spines, but they are small and little protection against predators. This causes the fish to be less bold in behaviour and colouration. While the Three-spined variety has three large spines, which are good protection against predators. This fish is bolder (Tinbergen 1974).

The Three-spined stickleback has been studied extensively, particularly by ethologists. Daly and Wilson (1983) go as far as to call it: "the laboratory rat of ethology" (1).

FORAGING BEHAVIOUR

When an animal seeks food it has to make two decisions: where to find the food, and which food to choose. There is a term used here: "optimal foraging", which means the maximum net rate of food/energy intake for the minimum expenditure of energy, and risk (of predation).

For predators, the decisions in optimal foraging are (Krebs 1978):

i) which type of prey to eat;
ii) where to hunt for prey;
iii) what type of search strategy to use in hunting prey.

The upshot is that predators will aim to choose "profitable prey". The profitability of a prey can be seen as an equation in figure 2.

```
PROFITABILITY           NET FOOD VALUE *
OF PREY       =        -------------------
                        HANDLING TIME **
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* = gross energy value of food minus energy costs of capture and digestion (Krebs 1978)
** = time to capture, subdue and digest

Figure 2 - Equation for profitability of prey.

Kislalioglu and Gibson (1976) applied this model to the capture of Neomysis integer by Fifteen-spined sticklebacks. The larger the fish, the larger the prey taken. For example, sticklebacks 120mm long preferred prey 15mm in length, while smaller sticklebacks (70mm long) captured smaller prey (8mm long). The relationship of prey chosen by size of predator is close to the optimum.

Smaller fish trying to capture longer prey takes more energy and handling time, and gives a lower net food value than shorter prey. While for larger sticklebacks, short prey are not profitable relative to the effort to capture. Table 5 is a hypothetical example of optimal foraging.

stickleback/ prey	HANDLING TIME (a)	ENERGY GAINED (b)	PROFITABILITY (b-a)
large/small	+2 units*	+3	+1
small/small	+3	+3	0
large/large	+4	+6	+2
small/large	+9	+6	-3

* units are arbitrary measure for model; normally use kCals.

Table 5 - Hypothetical example of optimal foraging.

For the larger fish, it is more profitable to choose larger prey (+2 vs +1), while for smaller fish, the opposite is true (+1 vs -3).

Much of the research into foraging behaviour has applied mathematical modelling to animal behaviour. For example, Beukema (1968) calculated the optimal foraging value to be 0.17 for an experiment with sticklebacks, but the fish did not achieve this value in their search strategy for prey. There are limitations to the usefulness of such mathematical modelling with artificial experiments.

Outside the breeding season, sticklebacks live in schools, and forage together. When one stickleback finds prey, it starts to eat it, which stimulates other sticklebacks to try and get some of it. Usually they do not succeed, and start searching nearby for other prey. This encourages the exploitation of groups of prey. This stimulation to eat in all sticklebacks at the sight of one eating is an example of "sympathetic induction" (Tinbergen 1965).

COURTSHIP BEHAVIOUR

At the beginning of the breeding season, males isolate themselves and set up territories. Their skin colour changes from dull to bright with the appearance of the red underbelly in particular. Other males showing this red underbelly are attacked if they enter the owner's territory. The confrontation between males is very ritualised, and rarely involves actual fighting.

Within their territory, the male builds a nest of a shallow pit covered with algae. The fish secretes a sticky glue which sticks the material together to produce a tunnel for the female to place the eggs inside.

After the nest is finished, the male's appearance becomes even brighter, and his movements around the territory become jerky. Thereby making him more visible to the females.

The females, meanwhile, are swimming around and assessing the territories of the males. If the male's nest is finished, he will perform a "zigzag mating dance" towards the female (figure 3).

The female leaves after depositing the eggs in the nest, and it is the job of the male to care for the eggs and the offspring. This includes "fanning" water through the nest to aerates the eggs (Tinbergen 1965).

The stages of the courtship dance are quite complicated, and require synchronisation between the male and female. Each action is a trigger for the next action of the partner; eg: the male's "zigzag dance" releases the approach behaviour of the female and so on.

MALE		**FEMALE**
		APPEARS
	↓	
ZIGZAG DANCE		
	↓	
		COURTS
	↓	
LEADS		
	↓	
		FOLLOWS
	↓	
SHOWS NEST ENTRANCE		
	↓	
		ENTERS NEST
	↓	
TREMBLES		
	↓	
		SPAWNS
	↓	
FERTILISES		

(After Tinbergen 1965)

Figure 3 - Stages of courtship dance of sticklebacks.

Tinbergen (1965) has shown this process of action and reaction using model stickleback males and females which act as triggers. It is not only the movements that produce the timing of the responses, but aspects of the appearance of the fish - the female must have a swollen abdomen to stimulate the "zigzag dance", and the male must show the red underbelly. Also the female swimming in an upright position in the water is a trigger (Ter Pelkwijk and Tinbergen 1937 quoted in Hinde 1970).

Figure 3 shows the general pattern of the courtship behaviour, but detailed observations by Morris (1958) found that some stages can be skipped if the fishes are highly motivated, and the action of one fish can trigger more than one reaction in the partner. In other words, there are multiple triggers for each behaviour (figure 4).

Finally, there will be tactile stimulation by the male as the female enters the nest, and thus she releases the eggs there. This stimulation does not need the presence of the male, but can be created in experiments with a glass rod (Tinbergen 1974).

FEMALE TRIGGERS		**MALE BEHAVIOUR**
Appearance OR Presentation	→	Zig-zag dance
Appearance OR Presentation OR Orientation towards male OR Following behaviour	→	Leading behaviour
Following behaviour OR Swim beneath male to nest entrance OR Buries head in nest	→	Ritualised fanning
MALE TRIGGERS		**FEMALE BEHAVIOUR**
Appearance OR Zig-zag dance OR Leading behaviour	→	Presentation behaviour
Appearance OR Zig-zag dance OR Leading behaviour	→	Orientation towards male
Leading behaviour OR Shows entrance OR Ritualised fanning	→	Swims beneath male to nest entrance

(After Morris 1958)

Figure 4 - Multiple triggers in the courtship dance.

Another species of fish, looking similar to the female stickleback, entering the male's territory can produce the "zigzag dance", but when there is no reaction, the sequences of courtship do not continue. The appearance of the female shape is a sign stimulus (2).

The courtship dance (and male fighting reaction) are instinctive behaviours. Sticklebacks raised in isolation show the responses in the appropriate situations without any learning (Cullen 1960).

PARENTAL CARE

The patterns of parental care vary between species based on the amount of parental investment by each sex. "Investment" is seen as anything done by a parent to increase the chances of the survival of that particular offspring, which is at the expense of the parent's ability to invest in future offspring (Trivers 1972). Thus the parent who has invested more tends to care for that offspring, while the parent with the least investment may desert.

Maynard Smith (1977) views the relationship between the parents as a "game" (as in "game theory") - an assessment of costs and benefits of staying or deserting (table 6).

AMOUNT OF INVESTMENT	FEMALE MORE THAN MALE	MALE MORE THAN FEMALE	EQUAL
WHO CARES FOR YOUNG	MALE	FEMALE	JOINT/BOTH DESERT

Table 6 - Strategies for parental care based on parental investment.

The decision to desert or stay and care for the offspring depends on a number of factors (Maynard Smith 1978):

i) Effectiveness of parental care by one vs two parents.

ii) The chances of the deserter being able to mate again.

iii) The security of paternity for the male.

iv) The age of the offspring - male sticklebacks will take greater risks to defend older eggs because more investment has been made in those eggs (eg: time spent fanning and consequent energy loss for the male). A greater risk is also taken for a larger brood by the male stickleback (Pressley 1981).

v) Whether fertilisation is internal or external. Sticklebacks have external fertilisation, and like many other species of fish (table 7), males will care for the eggs.

FERTILISATION INTERNAL			FERTILISATION EXTERNAL		
MALE	FEMALE	BOTH	MALE	FEMALE	BOTH
28	6	8	2	10	0

(After Breder and Rosen 1966)

Table 7 - Number of species of bony fishes where different parents care for offspring based on type of fertilisation.

The male stickleback constructs a nest for the eggs before the courtship begins. It is one of many activities that the males do. The male sticklebacks fight for territory, build nests, court females, stimulate them to lay the eggs in that nest, guard the eggs, and care for the offspring. The female investment is the production of the "egg biomass".

The male is also the suitor and must prove to the female his worth in terms of the nest and territory quality. But this does allow the male to be polygymous. Encouraging many females to lay their eggs in the nest requires little extra effort for the male compared to one set of eggs. The investment for the female stickleback is in egg production ("individual investment"), and for the male, it is the guarding of the eggs ("whole-brood investment") (Power 1980 quoted in Daly and Wilson 1983).

Fanning behaviour is a key part of the care by the male. The eggs are ventilated by the fanning movements of the pectoral fins, which increases until the eggs hatch. The fanning behaviour is linked to the oxygen consumption of the eggs as determined by the carbon dioxide content of the water around the nest (van Iersel 1953).

Where there is one set of eggs, fanning peaks at six-seven days after laying. Where there is multiple laying of eggs at different times, fanning is less on each subsequent occasion (table 8). This decline may be due to a reduction in that particular drive (van Iersel quoted in Tinbergen 1951).

	MAXIMUM AMOUNT OF NUMBER OF SECONDS OF FANNING IN 30 MINUTES OF OBSERVATION
1st set of eggs	600
2nd set	450
3rd set	300
4th set	250

(After Tinbergen 1951)

Table 8 - Amount of fanning behaviour by the male based on number of sets of eggs in the nest.

The quality of the nest and the male's territory are important indicators to the female of his quality, and thus an encouragement for her to lay the eggs there. Males can also signal their quality in other ways.

For example, Semler (1971) notes a preference of females for males with red colouration among Three-spined sticklebacks found in Lake Wapata, USA. These males are better at defending their territory. However, there are also more visible to predators (like trout). Thus brightly coloured animals are saying: "look my genes are good because I have survived easy predation".

But this bright colouration only appears during the breeding season. There is too much risk to maintain it for the whole year. The red colour is "quite clearly of service in the competition to fertilize" (Daly and Wilson 1983).

Larger male territories also give greater reproductive success; ie: less risk of predation of eggs by other males. So it is important for the male to signal this to the female. Furthermore, males unable to claim territories, cannot make nests, and thus do not breed (Van den Assem 1967).

FIGHTING BEHAVIOUR

The tendency of the male to attack another male in the breeding season depends on who owns the territory. The resident is usually the attacker. Tinbergen (1965) showed this in a series of experiments in an aquarium that contained two male territories. When the two sticklebacks were placed in separate glass tubes in territory A, the resident tried to attack and the intruder to flee. The opposite was true when the two fish were placed in territory B (figure 5).

TERRITORY A		TERRITORY B	
→	→	←	←
A attacks	B flees	A flees	B attacks

(After Tinbergen 1951)

Figure 5 - Behaviour of two male sticklebacks in different territories.

The aggression response in the breeding season is due to hormonal changes in the fish. The pituitary gland, which responds to daylight and seasonal rhythms, triggers the gonadal growth in the fish, which makes them prone to fight.

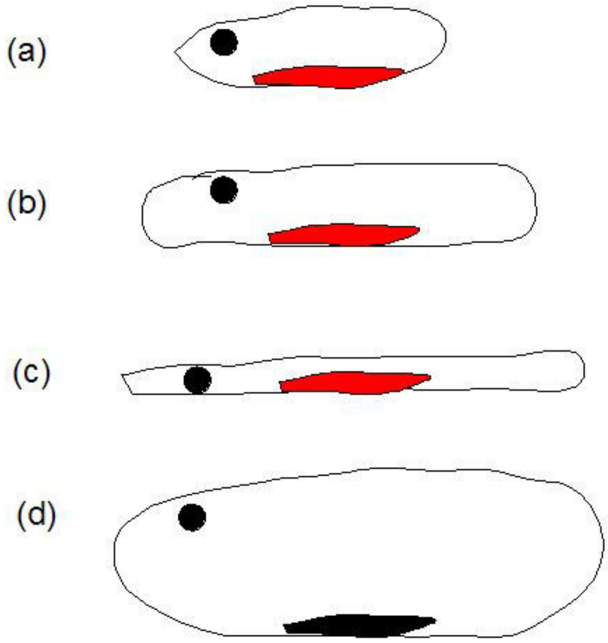
Hormonal changes had been responsible for the male Three-spined stickleback leaving the sea and migrating upriver to the breeding ground. While migrating, they do not show aggression towards other males. When the male has found a suitable site for nest-building, their behaviour then becomes territorial. The discovery of a suitable site brings migration to an end, and is classed as a "consummatory stimulus" (hinde 1970). A stimulus that inhibits a sequence of behaviour. Stimuli can start and stop particular behaviours.

If a group of males are kept in a bare tank without vegetation, they do not form territories nor change to a brighter colour (Eibl-Eibesfeldt 1975).

The male is primed to fight in their own territory (or flee if in another's territory), but needs a trigger to produce these reactions. For the Three-spined stickleback, it is the red underbelly that is the trigger, not the size of the fish. Ter Pelkwijk and Tinbergen (1937 quoted in Hinde 1970) found that even crude models of sticklebacks could produce aggression if they had the red underbelly, and an accurate model without red did not elicit a response (figure 6). Furthermore, the red had to be on the underside of the fish not the upper to produce a response (Baerends 1957).

Tinbergen (1965) reports the males showing an aggressive response to a red van passing the aquarium.

VARIETY OF MODELS USED



(Attack response elicited from models a, b, and c)

(Redrawn from Tinbergen 1951)

Figure 6 - Models used to elicit aggressive responses.

The attack response is also enhanced by the threat posture taken by a male. Interestingly, models of male sticklebacks without the red underbelly can still trigger the fighting response if in a threat posture (Tinbergen 1951). The red underbelly and threat posture together produce the strongest aggression response. The eliciting of the same behaviour by different stimuli is known as the "law of heterogeneous summation" (Seitz 1940 quoted in Eibl-Eibesfeldt 1975).

ETHOLOGY - EXPLAINING INSTINCTIVE BEHAVIOUR

Ethologists have been interested to explain these behaviours. Key to ethologists is the concept of instinct, which is the basis of most animal behaviour. An instinct is an inherited behaviour pattern common to all members of a species (Tinbergen 1951) (3). Instincts show themselves in units of behaviour known as "Fixed Action Patterns" (FAPs) (4).

FAPs have a number of charactersitics (Lea 1984):

i) stereotyped - the behaviour always occurs in the some order and way;

ii) universal - the behaviour is the same in all members of the species;

iii) independent of individual experience - the behaviour is entirely innate and there is no learning involved;

iv) ballistic - once triggered, the FAP must run the whole course and cannot be changed or stopped;

v) specific triggers - each FAP will have a particular trigger(s), known as a "sign stimulus".

For male sticklebacks, the aggressive response to the red underbelly of another male, and the courtship dance are FAPs. The courtship dance is a combination of FAPs to produce a complex behaviour between two fishes.

Some behaviours are a combination of drives - leading to displacement behaviour (5). The arrival of an invader in the territory activates the drive (6) to attack and the drive to escape. This tension needs release, which comes in the form of a third action (displacement) (Tinbergen 1952).

For example, the displacement of attack and escape is sand-digging (the first phase of nest-building), which is similar to the threat posture. If the territory owner is faced with a model that does not flee, the resident will hide themselves between plants. After a while, the resident will attack again (as the aggression drive becomes stronger), but before attacking he will show displacement digging (Tinbergen 1952).

While the male "zigzag dance" of courtship can be seen as the displacement of the sex drive and the attack drive (Tinbergen and Van Iersel quoted in Tinbergen 1965). Put another way, fertilisation occurs because the sex drive has over-ridden hostility. The "zig-zag dance" involves a movement away from the female and then towards her. After fertilisation, the attack drive dominates again and the female is driven off. The lack of a swollen abdomen after laying the eggs produces the attack response in the male.

Displacement occurs when aggressive drives are activated, but also when the goal of a behaviour has been reached too quickly; eg: a rival male leaves the territory quickly or a female does not follow the male in the courtship dance. Such a situation leaves an energy surplus ("central excitatory potential") which spills over to produce the other (displaced) behaviour (Tinbergen 1952).

Displacement fanning when a female does not respond to the "zig-zag dance" can be taken as a measure of the male's sexual motivation (Tinbergen and van Iersel 1947).

The concept of energy and drives are fundamental in ethologist's explanations of animal behaviour. Each FAP has a reservoir of "action-specific-energy" (ASE) (7) that builds up. The appropriate sign stimulus causes the "innate releasing mechanism" (IRM) (8) to release this energy and the animal shows the FAP. After performing the FAP, the reservoir of ASE is empty. Thus the behaviour cannot be repeated until the ASE has built up again. This is sometimes called the "hydraulic model of instinctive behaviour" (Lorenz 1950) (figure 7).

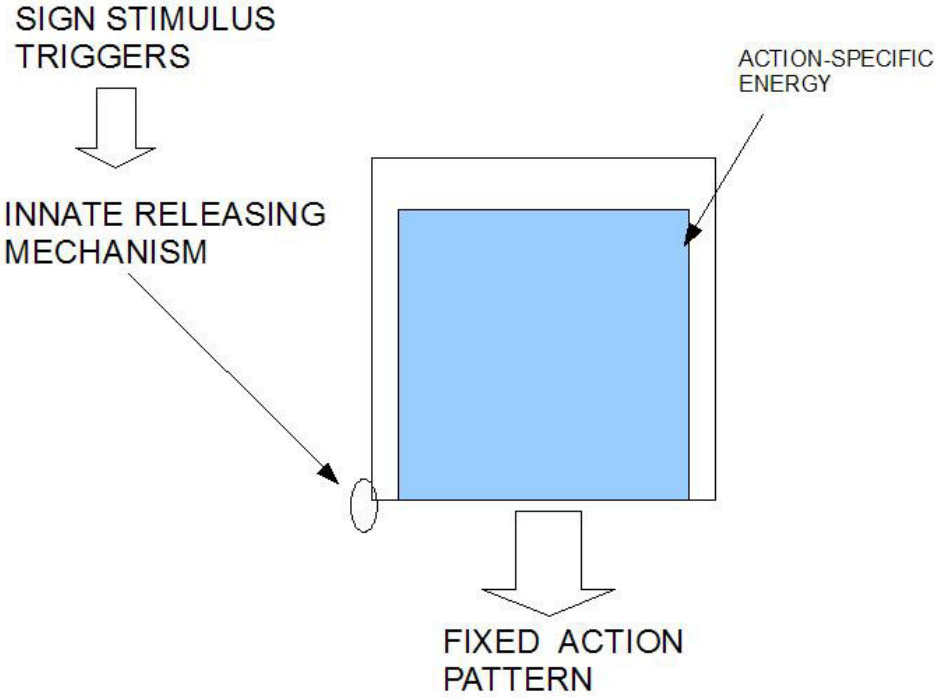


Figure 7 - Hydraulic model of instinctive behaviour.

FOOTNOTES

1. Ethology concentrates upon studying animal behaviour, and particularly the mechanisms of instinctive behaviour. It is sometimes viewed as a bridge between zoology and psychology.

2. Sign stimulus - this is the trigger for a response of an instinctive behaviour that depends upon a certain characteristic (Russell 1943); eg: red underbelly for aggressive response in male sticklebacks.

3. Characteristics of instinctive behaviour (Lorenz and Tinbergen 1938 quoted in Hayes 1994):

a) behaviour always appears in the same form;
b) it is species-specific;
c) it appears even in animals reared in isolation;
d) the behaviour appears fully developed.

4. Fixed Action Pattern (FAP) - This is a complicated pattern of muscle movements which produce an action (or reaction) that cannot be split up into separate parts (Tinbergen 1942).

5. Displacement - behaviours that appear during conflict and seem irrelevant to the conflict. Such activities evolved from the conflict of drives (Zeigler 1964).

6. Drive - the motivation to perform a particular behaviour; eg: the hunger drive motivates the animals to eat.

7. Action-specific-energy - energy for specific behaviour linked to a particular drive.

8. Innate Releasing Mechanism - "A hypothetical 'trigger' which activates fixed action patterns when the appropriate environmental stimulus is present" (Hayes 1994).

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