COMPARATIVE PSYCHOLOGY BY ANIMAL

NO.1 - LIONS

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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

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 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

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

traits" in that species.

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

EXAMPLE - Each animal has two offspring:

CURRENT SITUATION	FUTURE SITUATION
MAJORITY - animal A: Runs slow**; 2 offspring - 1 survive = 2 offspring	Few offspring in subsequent generations → 1 survive = 2 offspring
MINORITY - animal B: Runs fast*: 1 offspring - 2 survive = 4 offspring	Many offspring in subsequent generations → 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).

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

	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.

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 LIONS

There are nineteen orders of living species of mammals, and lions are of the order Canivora (meat-eaters). Lions, known as the species "Panthera leo", are part of the Family Felidae (cats).

There are four main sub-species that inhabit Africa south of the Sahara (Grzimek 1975):

i) Masai lion (Panthera leo massaicus);
ii) Sengalese lion (Panthera leo sengalensis);
iii) Angolan or Rhodesian lion (Panthera leo bleyenberghi);
iv) Transvaal lion (Panthera leo krugeri).

Other sub-species are the Asian lion (Panthera leo persica) and the North African Berber lion (Panthera leo leo) (Leyhausen et al 1990).

Adult male lions are larger than females (table 4). Females reach sexual maturity by three years old, but males not until 5-6 years old (Kat 2000).

	LENGTH	HEIGHT AT SHOULDER	WEIGHT
male	6-7 feet	4 feet	370-500 pounds
female	5 feet	3-3.5 feet	265-390 pounds

(Data from New Encyclopaedia Britannica 1997)

Table 4 - Physical differences between male and female lions.

As carnivores, their main prey are gnu, zebra or Thomson gazelle. The Okavango lion project recorded the prey taken by two prides. The most popular prey in order were warthog, impala (type of antelope), and zebra, but twelve different types of animals were caught. This diversity of prey is due to environmental conditions and seasonal availability of prey in that area (Kat 2000).

The average consumption per meal for adults may be 18 kg, but they will eat once every 3-4 days.

Lions are social animals, thus not nervous of others because they know each other. Mating can be affectionate compared to other big cats, except with a new male. The average pride size is fifteen (ranging from 4-37). The adult males are "partial parasites" (Wilson 1975) as they rarely participate in group hunting (Scheel and Packer 1991), nor care for the young.

Lionesses are key to the pride; ie: female leader and female offspring ("matrifocal packs"). The females raise the offspring together, even evidence of one sister hunting for another which is injured ("Survival: Lion Queen"; ITV). This is evidence of benefiting the genes (shared by sisters) rather than the individual ("inclusive fitness").

ORGANISATION OF PRIDE

There will be variations in the species' behaviour, but lion behaviour follows a basic pattern (Leyhausen et al 1990) (figure 2):

1. Females form group with shared territory.

2. If members are lost, daughters fill the spot.

3. Between two to five males control the pride. Occasionally it will be a single male or a male may hold two prides simultaneously.

4. All males and some females leave the pride around 2-3 years old.

5. Most territories have been established, so many males are nomads following the wandering herds. Territorial size can vary from 11 to 144 square miles; the average being 43-54 square miles (Schaller 1972).

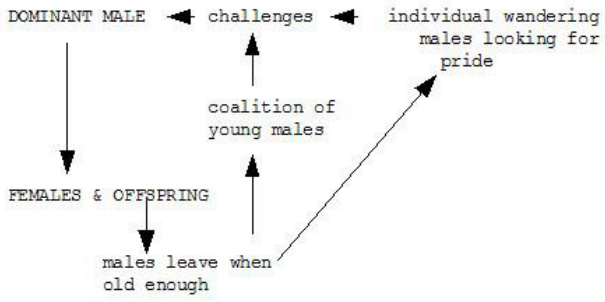


Figure 2 - Organisation of pride.

Most current research on lions in the wild comes from the Serengeti Research Institute began in 1966, and specifically today the Okavango lion project in Botswana (Kat 2000). Schaller (1972) carried out nearly 3000 hours of observation following the Serengeti lions over 100 000 miles, then Bertram (1978a) followed the same prides for four years.

CO-OPERATION

GROUP FORAGING

PREDATORS	PREY
1. Detection of prey - perceptual skills	1. Anti-detection responses - cyptic appearance - immobility
2. Attack prey - stealth - avoidance of certain patterns/colours	2. Anti-attack reponses - vigilance/alarm calls - advertising of poison - mimicry
3. Capture of prey **- group hunting** **- speed** - specific victims	**3. Anti-capture responses** **- herd** **- rapid acceleration**
4. Consumption of prey - begin at head - avoidance of dangerous foods - steal captured prey	4. Anti-consumption responses - misdirect attack - concentration of toxins in vulnerable body parts - fear screams

(After Alcock 1993)

KEY: bold = lion and prey strategies.

Table 5 - Strategies by predators and prey.

1. Conserve energy
2. Capture larger or dangerous prey
3. Use different skills
4. Increase food intake when food scarce
5. Protect kill from scavengers

Table 6 - Advantages of group foraging.

A meat diet of a carnivore provides more energy than a vegetarian one, but requires a greater expenditure of energy to catch the meal. Hunting together helps in resolving this dilemma.

Certain lions run around potential victims and chase them back to where other lions lay in wait (Stander 1992). Lions are strong but cannot run for long, and may easily be outrun by lighter, faster prey (Riley 1995). The chase is often limited to 100 metres, though they can achieve a maximum speed of 30 mph (Server 1998).

Working together also allows them to bring down prey that weighs much more than a single hunter could catch. Possibly up to twelve times heavier than a single animal could capture (Schaller 1972). Group foraging allows the capture of prey that are dangerous to the single

predator. For example, one kick from a giraffe could kill an adult lion.

Hunting in groups also conserves energy for individual animals. It allows the combination of different skills: certain lions may be better at perceiving prey, and others at chasing (Bailey 1995).

Schaller (1972) noted that lions on the Serengeti Plains are not that successful in their hunts. When hunting alone, only 15% of the time were the lions successful compared to 30% for group hunting. Thus there is a lot of energy expended when food is not gained.

These are the benefits to group hunting, but does the lion gain more calories per individual than hunting alone. Research has found that this is not the case for larger groups of five or six adults. Occasionally lions hunting in pairs had a higher food intake per day than loners. Approximately 10% more food intake per individual, whereas individuals in a group of six adults had 50% less intake per individual than individual hunters (Caraco and Wolf 1975).

The relationship between food intake and group size is also affected by the availability of prey. Packer et al (1990), after many hours of observation, noted that group foraging was an advantage when prey was scarce. The average food intake per adult female was eight kilograms per day when hunting alone in times of scarcity, but over 11 kgs when in groups of five or six adults.

In times of abundance, there was no advantage - average intake 10 kgs per day when alone compared to eight when in group of four.

Furthermore, individual animals would not be able to consume their whole kill before competition arrives (eg: hyena). Having genetic relatives around both protects the kill, and gives them food. Thus female adults clearly tolerate female relatives. More than that, any female may suckle the young because the actual mother may be out hunting.

But there are cases where the pride is made up of non-genetic relatives. What are the benefits in such situations?

i) Defence of territory - females without territory have limited opportunities to reproduce.

ii) Protection against infanticide - arriving males can kill the cubs of the pride to bring the females back to reproductive susceptibility. A group of lionesses can protect the cubs from a single male.

iii) Cubs grow slowly and need baby-sitting while the mother hunts. Death by disappearance from the nest is a risk.

COMMUNAL CARE

There are four types of communal care (CC) (Gittelman 1985):

i) Nuclear family with reproductive pair and offspring from previous seasons - eg: beaver.

ii) Matriarchy with reproductive female only - eg: little brown bat.

iii) Harem - eg: Northern elephant seal.

iv) Multi-male/multi-female group containing both related and unrelated individuals - lions (Packer and Pusey 1983b).

CC is beneficial where there is later sexual maturity of the young, and synchronised breeding. The average age of female first reproduction of lions is later than maternal (cared for by mother only) or bi-parental (cared for by both parents) carnivores.

CC has both advantages and disadvantages (table 7).

BENEFITS	COSTS
1. predator defence (not relevant for lions)	1. attract predators (not relevant for lions)
2. territority shared	**2. increased aggression**
3. communal suckling	**3. mix-up of litters**
4. acquisition of food easier	**4. disease spreads quickly**
	5. infanticide possible
	6. increased competition

Table 7 - Costs and benefits of communal care.

CO-OPERATING MALES

There are cases where non-genetic males will unite to oust the dominant male from the pride. Subsequently, these males rarely fight over the females even though reproductive success may not be equally shared.

Males usually pair with two females, and this leaves some males without mates. These "non-reproductive helpers" are useful in repelling rivals, but they do not mate. DNA fingerprinting of prides, by Packer et al

(1990), has clearly shown that the helpers are not genetically related.

If they were genetic relatives, then it would seem obvious that defending your relatives will help your own genes indirectly. Bertram (1978b) calls this "reproducing by proxy through his companions".

The presence of helpers in the pride increases the survival rate by 0.64 cubs (Packer et al 1991), but only for those mating.

What are the advantages for the "non-reproductive helpers"? The simplest answer is their continued survival while in the group, which allows them the opportunity to mate later. This is not a convincing answer, though, in terms of evolution.

Emlen (1991) talks of the coalition formation hypothesis. The females in the pride come into oestrus simultaneously, and there are benefits to male coalition in terms of lifetime reproductive success.

Packer et al (1988) estimated the approximate lifetime reproductive success (ie: number of offspring fathered) of different size coalitions: one male can father five offspring, whereas with three males it becomes 20, and for six males, 35.

Overall, the advantages of the coalition is to make the pride take-over easier, and to increase the tenure time of controlling the pride.

Respect of ownership

Males respect their companions' temporary ownership of females, and fighting only occurs when ownership is unclear or two consorting males are in close proximity (Packer and Pusey 1982).

Maynard Smith (1976) views this behaviour as a "bourgeois strategy". In stable social groups (ie: where animals have met before) contests are settled by observable asymmetries (eg: size of mane) rather than combat. The costs of injury during a fight are greater than the payoff for winning. The best strategy here is respect of ownership.

Lions have teeth and claws which could easily mean death in a fight, plus the fact that most of the males are usually matched in age and size. There are few differences between males in resource-holding power, and thus respect of ownership of females.

Table 8 shows the factors affecting respect of ownership as compared to chimpanzees where there are many fights (Packer and Pusey 1985).

FACTOR	LIONS	CHIMPS	LION STUDIES ON WHICH CONCLUSIONS BASED
MALES			
1. respect of temporary ownership	high	low	Packer and Pusey 1982
2. chances of injury in one-to-one fight	high	low	Packer and Pusey 1982; Schaller 1972
3. percentage of oestrous periods leading to conception	high 20-28%	low less 20%	Schaller 1972; Packer and Pusey 1983
4. percentage of pregnancies leading to young surviving to breeding age	14-44%	approx 40%	Bertram 1975
5. average litter size	2.5	1	Hanby and Bygott 1979
6. value of oestrous female (ie: 3 x 4 x 5)	0.07-0.32	0.05-0.08	Schaller 1972
7. differences in age/size of males in same group	low	high	Packer and Pusey 1982
FEMALES			
1. respect of temporary feeding site	high	low	Schaller 1972; Bertram 1978a
2. chances of injury in one-to-one fight	high	low	Packer and Pusey 1985
3. value of specific feeding sites	moderate	low	Schaller 1972
4. differences in age/size of females in same group	moderate	high	Packer and Pusey 1985

(After Packer and Pusey 1985)

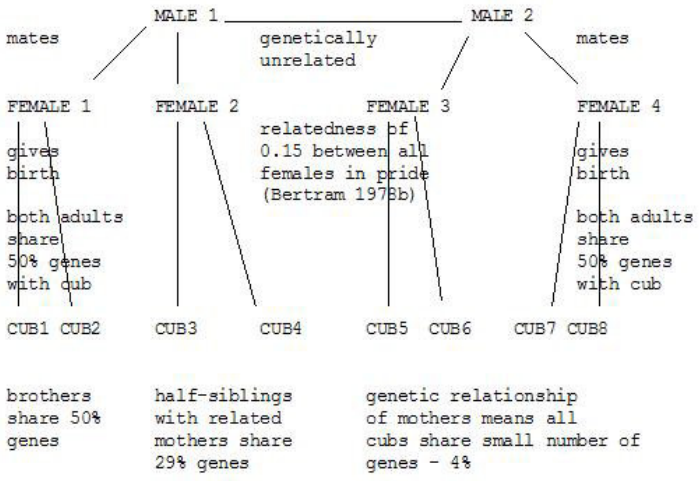
Table 8 - Factors affecting respect of ownership of females by other males among lions and chimpanzees.

Altruistic Behaviour

Males give cubs preference to food, females suckle any cub in the pride, and there is a lack of competition between males for females as described above. All these behaviours appear to go against the logic of evolution. But when looking closer there is evolutionary logic to this apparent altruistic behaviour. The key is the genetic relationship of members of the same pride.

Bertram (1978b) calculated the average coefficient of genetic relationship between members of the pride to be 0.15 (15%) for females and 0.22 (22%) for males. Thus males can be tolerant of cubs because of "inclusive fitness".

For example, in figure 3, adult females will be related to all the cubs, but males only to those fathered. Because females remain in the pride, future generations will still be genetically related to the adult females, but in smaller amounts.



(After Kat 2000)

Figure 3 - Model of genetic relationships in pride.

Altruistic behaviour will also take into account the costs and benefits of the behaviour. Hamilton (1964) explains the evolution of altruism based on kinship or benefits greater than costs of the behaviour. He produced mathematical models (figure 4):

Altruism occurs where: $K > 1/r$

$K = b/c$

KEY: c = cost of behaviour in terms of evolution
b = benefits of behaviour
K = ratio of costs to benefits
r = degree of kinship - eg: parent/offspring = 0.5

(After Clamp and Russell 1998)

Figure 4 - Mathematical model for apparent altruistic behaviour.

MATING STRATEGIES

MALE	
1. monogamy: one partner for breeding season	
a. mate-assistance monogamy	male assists female in child-rearing
b. mate-guarding monogamy	female dispersal
2. polygyny: one male with multiple females	
a. female defense polygyny	**male defends cluster of females**
b. resource defense polygyny	male defends resources and females come
c. Lek polygyny	male defends territory and females come to mate only
d. scramble competition polygyny	males find scattered females
FEMALE	
1. monogamy	
a. female-enforced monogamy	male keeps other females away and assists in child-rearing
2. polyandry: one female with multiple males	
a. fertility-insurance polyandry	greater fertilisation of eggs
b. better sperm polyandry	genetically diverse sperm
c. more material benefits polyandry	more resources from males
d. more paternal care polyandry	more males help in child-rearing

(After Alcock 1993)

Bold = mating strategy used by lions

Table 9 - Types of mating strategy.

The young males tend to leave the pride and wander looking for females, who maintain a territory dominated usually by one male. If the dominant males are all related, then the lionesses may copulate with all of them. This makes paternity of the cubs unclear, and may

reduce the chances of infanticide (Sparks 1999). The territory allows the female to know about food sources and safety for their young.

This fits the theory of sexual selection - females have more investment in each offspring, while males can mate many times. Pusey and Parker (1987) noted that the majority of female lions on the Serengeti Plains in Africa remained in the natal pride (birth pride), all their lives, while none of the males did.

A dominant male, or usually males, will tend to control the pride, at least temporarily for two or three years. But the position of this male is regularly challenged by nomadic males. Thus the strength of the male has to be obvious to discourage attackers.

One sign is the mane. Researchers attempted to identify the importance of the mane using "dummy male lions". One experiment gave the choice of a "dummy male" with large or sparse mane. The latter model was approached most by male lions suggesting seen as least threatening. The second experiment gave a choice of the same length of mane, but either dark or light coloured. The latter again was attacked more often.

The mane is expensive in evolutionary terms because it limits the loss of heat in high temperatures. More so with large, dark manes which are seen as a sign of strength by other males. Only the strongest animals can survive such demands on their body (Caputo 2002).

INFANTICIDE

Incoming males to the pride will kill the cubs less than nine months old already in the pride. Pusey and Parker (1992) believed that up to a quarter of all cubs die this way. The reason is known as sperm competition (table 10).

The infanticide causes the females to become reproductively susceptible immediately, whereas normally lionesses give birth every two years.

The benefits to the male are obvious from this behaviour, particularly as the male will stay for around two years.

There is no seasonal breeding pattern in lions, and the lionesses will come on heat for 4-8 days. If she does not breed, then she comes on heat 1-3 months later (Grzimek 1975).

The gestation period is 102-113 days which produces a litter size of between 1-6 cubs (Whitfield 1998). Weaning occurs around 6-7 months old.

	SEXUAL COMPETITION (1)	CANNIBALISM (2)	SOCIAL PATHOLOGY (3)
- male kills other males' infants	Y	M	M
- eats them	N	Y	N
- abnormal conditions only	N	M	Y
- takeover without male conflict	Y	N	N

KEY: N = not common; M = special conditions only; Y = evidence.
(1) to remove offspring of competitors; (2) eg: for food; (3) due to abnormal conditions

(After Alcock 1993)

Table 10 - Reasons for infanticide.

Intra-Pride Relations

The driving out of the young males at sexual maturity could be an evolutionary mechanism to stop mating with close genetic relatives ("homozygosity"; Wilson 1975). There are greater risks of genetic problems when mating with genetically similar relatives.

Even without infanticide, 60% of the young die before maturity. Leyhausen et al (199) observed two groups of eighteen lionesses on the Serengeti Plains, and hypothesized that they could have 79 cubs. The high death rate is a means of keeping a balance because if all cubs became adults, there would be food shortages. Also, from an evolutionary point of view, the "best" animals should survive.

Cubs die from being left in the nest and overcome by heat or predators (eg: leopards), or the female may eat for herself and not provide food for the young.

The relationship between the newly-arrived males and the females is not easy. When the pride is taken-over, the female will mate continuously for four months without becoming pregnant.

Why is this? There are a number of possible reasons:

i) To test the sexual stamina of the male, and thus his strength to hold the pride. Observation of one couple recorded 157 copulations in 2.5 days with only an average rest of 21 minutes inbetween (Sparks 1999).

ii) To stop the male deserting immediately.

iii) To bond the new male to the pride.

iv) To allow time for the strongest male to dominate.

Kat (2000) suggests that there may be a physiological reason. The stress of the pride take-over, and thus the hormones released in the body, means the female is unable to ovulate.

Observation at the Okavango lion project suggests that the females have little bond to the males. Kat (2000) reports the case of attempted deception by "Vouvray" (lioness). She had found a carcass killed by a leopard, and tried to call her cubs from the pride to eat. But two adult males followed, so "Vouvray" took the cubs to the water-hole away from the carcass. The males followed. She then tried to sneak off with her cubs to the food, but it failed and the males found the food.

COMMUNICATION

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

- Lions use auditory and chemical communication mainly.

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

Table 11 - Three main types of communication used by non-human animals and their advantages and disadvantages.

The prime means of communication is auditory/vocal. Males communicate usually by the roar. This is an example of the "proclamation song" (McFarland 1981), which can be heard up to four miles away. It fulfils a number of functions:

i) To indicate to others the existence of a resident in a particular territory (ie: the dominant male).

ii) To indicate to others the existence of an individual in transit (ie: wandering male) who may challenge the dominant male.

iii) To indicate the limits of a territory - ie: as a "spacing device for neighbours" (Wilson 1975).

iv) To call females.

v) The volume of the roar can give a clue to the strength of the animal - ie: whether to challenge or not, or as a vocal display during confrontation to avoid actual fight.

vi) Helps individuals to find the pride during separation.

vii) Bond-reinforcing during contact.

The familiarity of the roar is important, as are the scent trails left to mark territory boundaries. Urination on bushes, trees and ground to leave scent, and defecation and rubbing against bushes are used.

Within the pride, communication consists of grunts, meows, growls, and moans. There is mutual grooming by the females and larger cubs, but rarely with the adult males. Play among cubs and wrestling by adult females establishes social bonds.

While the adult male invites the cub to play by lowering his forequarters, and latter clubbing the cub lightly on the head. This play invitation is an example of "meta-communication", as is status signalling.

Meta-communication is the communication about meaning of other acts of communication (Wilson 1975) - ie: using a signal in an opposite way to the normal use. The lowering of the forequarters by an adult male is a sign of subordination, which the adult male would never normally do to a cub. But, by doing so, the adult male is using this normal sign of subordination to initiate play.

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