COMPARATIVE PSYCHOLOGY BY ANIMAL

NO.7 - RED DEER

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ISBN: 978-1-904542-14-8

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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

No.3 Frogs

Topics

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

No.4 Robins

Topics

1. Territoriality
2. Communication
3. Mating strategy
4. Other behaviours

No.5 Sticklebacks

Topics

1. Foraging Behaviour
2. Courtship Behaviour
3. Parental Care
4. Fighting Behaviour
5. Ethology

No.6 Albatross

Topics

1. Mating Behaviour
2. Migration

No.7 Red Deer

Topics

1. Social Behaviour
2. Mating 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 → 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 RED DEER

The deer family (Cervidae) contains 31 species and 47 sub-species (Heck 1972). It is characterised by the presence of antlers in males, except for musk deer and Chinese water deer, and reindeer where the females also have antlers.

The focus here is red deer (Cervus elaphus), which has 23 sub-species - eg: Central European red deer (Cervus elaphus hippelaphus) and Rocky Mountain elk (Cervus elaphus nelsoni) (Heck 1972). The red deer of Scotland, and particularly on the island of Rhum, have been studied extensively (Clutton-Brock and Albon 1989).

Deer in Europe tend to show a common annual pattern of rutting (mating behaviour) and birth of offspring (Hutton 1995) (table 4).

TYPE OF DEER	LATIN NAME	PERIOD OF RUT	YOUNG BORN
Red deer	Cervus elaphus	Sept-Nov	May-July
Fallow deer	Cervus dama	Sept-Nov	June/July
Sika deer	Cervus nippon	Sept-early Dec	May-July
Roe deer	Capreolus capreolus	July-Aug	May-June
Reindeer	Rangifer tarandus	Sept-Oct	April-June
Elk	Alces alces	Aug-Oct	April-June

Table 4 - Annual pattern of six types of deer.

The development of the male antlers also shows an annual cycle, as shown by the roe deer (Haltenorth 1972) (table 5).

JAN-MARCH
Pituitary gland and thyroid gland stimulates testes to secrete hormones to develop antlers

APRIL-AUGUST
Testes also secretes increased testosterone, which inhibits growth. The antlers calcify and become polished (known as "cleaning")

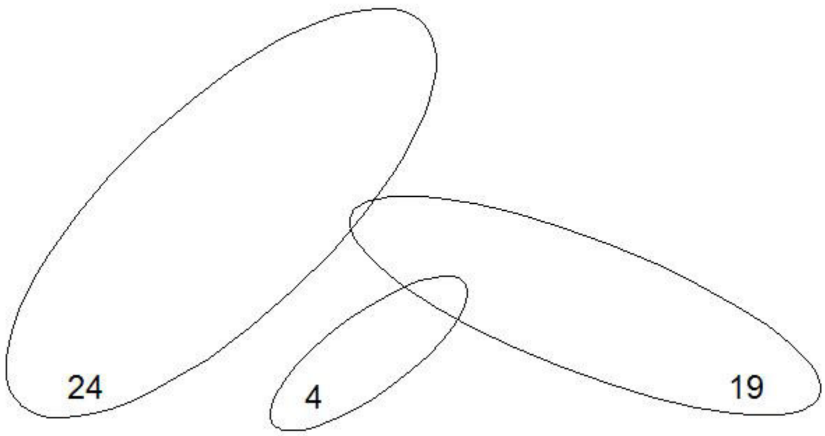
SEPT-DEC
Reduction in testosterone and antlers drop off

Table 5 - Annual cycle of antler development in roe deer.

SOCIAL BEHAVIOUR

Hinds (female deer) live in groups ranging from two to fifty plus. These groups are temporary, except for the family.

Individual animals have well defined home ranges (1) varying in size from 1 to 5km (Clutton-Brock and Albon 1989). The daughters adopt home ranges overlapping those of their mother (figure 2).



(Numbers = identity of matriline)

(After Clutton-Brock et al 1982)

Figure 2 - Example of matrilineal hind group's range on Rhum, Scotland.

The family parties consist of grandmother, daughters and grand-daughters. These are called matrilines (based on female line of inheritance). The females are more concerned with staying in their range.

Stags (male deer) tend to wander more, though they do have ranges as well. However, the attachment to a particular range is less than for hinds. The stag leaves the mother's group at 3-4 years old, and wanders until finding a home range (Clutton-Brock et al 1982).

Why are the sexes segregated most of the year, except for the period of the rut? One suggestion is that the males distance themselves from defenceless females as an anti-predator strategy (Geist and Bromley 1978 quoted in Putman 1988).

Table 6 shows the distances between ranges and places of birth at 4 years old of 110 hinds and 113 stages in the West Grampians of Scotland (Red Deer Commission 1983-1985).

It is common in non-migratory mammals for males to disperse from areas of birth and females to remain close by (Greenwood 1980).

DISTANCE FROM PLACE OF BIRTH	MALE	FEMALE
less than 3km	20	50
3-8km	35	40
8-16km	25	8
greater than 16km	20	2

(After Clutton-Brock and Albon 1989)

Table 6 - Approximate percentages of stags and hinds and distance between home range and place of birth.

MATING BEHAVIOUR

The number of offspring and the reproductive strategy of the species can be viewed as "r-strategy" or "K-strategy" (MacArthur and Wilson 1967) (table 7). Red deer are an example of the latter.

	"r-strategy"	"K-strategy"	Red deer
OFFSPRING	many	few	1 per year
PARENTAL INVESTMENT	low for each one	high	high for mother
INFANT MORTALITY	high	low	20% *
LIFESPAN	short	long	
SPEED OF DEVELOPMENT	rapid	slow	hinds continue growing until 5-6 years old
REPRODUCTIVE AGE	early	delayed	
BODY SIZE	small	large	stags = 40-65kg carcass weight
POPULATION SIZE	variable	stable	
COMPETITION	lax	keen	
OVERALL	high productivity	high efficiency	

(* Guinness et al 1978)
(After Daly and Wilson 1983)

Table 7 - Comparison of "r-strategy" and "K-strategy" for reproduction.

The reproductive interests of each sex is different (Trivers 1985): for hinds, it is the period of pregnancy and the rearing of the individual offspring, while the stag, who may only give the sperm, must fight for that right. This leaves a low-investing male and a high-investing female, and their behaviour will be different (Cartwright 1996) (table 8). The situation of different levels of investment is known as anisogamy.

	MALE	FEMALE
COMPETITION	high male-male	low female-female
REPRODUCTIVE SUCCESS	variable: dominant males high; subordinate males low	guaranteed mate each year

Table 8 - Behaviour of low-investing males and high-investing females.

SEXUAL SELECTION

Darwin (1871) noted that males compete for females by strength or ornaments (characteristics that signal "good genes" - eg: peacock's tail). This leads to the evolution of sexually dimorphic characteristics; ie: the male and female of the species can appear quite different.

Females can then choose to mate with the best males. This is an important advantage for the females, particularly if there is no male involvement in caring for the offspring. She must get something important from the male in copulation (Halliday 1978). Mating with the best male guarantees "good" quality sons and thus more grandchildren (Fisher 1930). The female's genes are passed more successfully into future generations this way. But how does a particular female preference become established in the first place (Halliday 1978)? Also female selection must be based on a relative criterion rather than an absolute one (ie: the best males of those available) (Trivers 1972).

Zahavi (1975) suggested that male ornaments should be understood as part of the "handicap principle". Males who survive with handicaps show their strength to females. For example, male antlers are a handicap. They give no advantage against predators and only appear at the time of the rut, though they are used in fighting other males (McFarland 1999). Antlers are expensive in to produce energy terms, requiring phosphorus and calcium salts.

But there is no guarantee that future generations will inherit such quality of ornaments because genes recombine during mating (Davis and O'Donald 1976). Thus males who survive with non-inherited handicaps (eg: broken leg) are a better sign of gene quality (Maynard Smith 1976).

Trivers (1976) has proposed the "resource accrual theory". It is important for females to be able to discriminate real advantages which will benefit future female offspring, and only to mate with males with genes twice as good as hers. For example, antler size is a sign of the ability to acquire and process calcium in the synthesis of bone. This could benefit female offspring in terms of stronger bones (Halliday 1978).

But if females are always mating with males twice as good as themselves, there will be a limited number of males available as female genes will improve over generations. Eventually, there will not be males good enough available (Halliday 1978).

Whatever the exact explanation for sexual selection, it is important for males to signal their strength and quality of genes to females.

PREPARATION FOR MATING

Stags and hinds are quite different in size and appearance. This can be seen as due to selection pressures on each sex as different - hinds are adapted to produce offspring, while stags have maximum ability to acquire mates in autumn which includes fighting ability (Clutton-Brock et al 1982).

Males have the costs of elaborate weaponry (antlers), larger body size, and higher activity levels, which obviously require more food. Thus males are more affected by severe weather and food shortages than females (Clutton-Brock and Albon 1989).

Observations in Scotland suggest that stags choose areas of food abundance (irrelevant of quality of vegetation) in order to increase body size rapidly. While females prefer higher quality vegetation (less coarse and easier to digest) to aid milk production (Clutton-Brock and Albon 1989). Lactation removes protein from the body, and the hinds must replace this (2). The changes in male body weight throughout the year are large (table 9).

	AUTUMN PEAK	SPRING LOW
AVERAGE CARCASS WEIGHT (Kg)	65	45
AVERAGE KIDNEY FAT (g)	1300	100
AVERAGE RUMP FAT (g)	750	close to 0

(After Mitchell et al 1976)

Table 9 - Changes in male body weight throughout the year.

The seasonal variation in appetite seems to be triggered by changes in day length, in Spring particularly, and thus hormonal controls. Kay (1978) compared the annual food intake of stags with castrated ones (which would reduce the production of testosterone). The latter group showed a more consistent amount of intake throughout the year.

The reproductive cycle shows a clear annual pattern. In July, the stags' testes grow (tripling in weight; Lincoln 1971), which increases the amount of testosterone in the blood. The stags gain weight, and the antlers develop as horns (along with neck muscle development and the appearance of the mane) ready for September.

The males move to the traditional "rutting grounds" close to the females (Lincoln et al 1970). Mature stags return to the area where they first held successfully a harem (Clutton-Brock et al 1982).

POLYGYNY

There are a number of mating systems that mammals use depending upon the dispersion of males and females, and the need for parental care (Clutton-Brock 1989) (table 10).

Male red practice polygy with a harem. The hinds are herded together and defended. Hinds in the same harem tend to develop synchronous oestrus, possibly using olfactory cues.

The herding of females leads to fighting between stags. The ability to defend the hinds is known as resource holding power (RHP) (Parker 1974). Success in fights, and thus RHP, depends on body size and weight (3). Larger stags can father over a dozen calves per year, and smaller males may not breed at all (Clutton-Brock and Albon 1989). Peak breeding occurs in October.

Fights can last up to 20 minutes, and 20% of them lead to some form of injury (Clutton-Brock et al 1979).

Larger antler size, however, does not seen to relate to successful fighting and breeding as much as overall body size (Clutton-Brock 1982) (4).

The struggle to maintain the harem leads to a loss of 20% of body weight and 80% of body fat by stags over 4-6 weeks of the rut (Clutton-Brock and Albon 1989). Furthermore, the stags rarely feed during this time, mainly because guarding the harem is a 24 hour job.

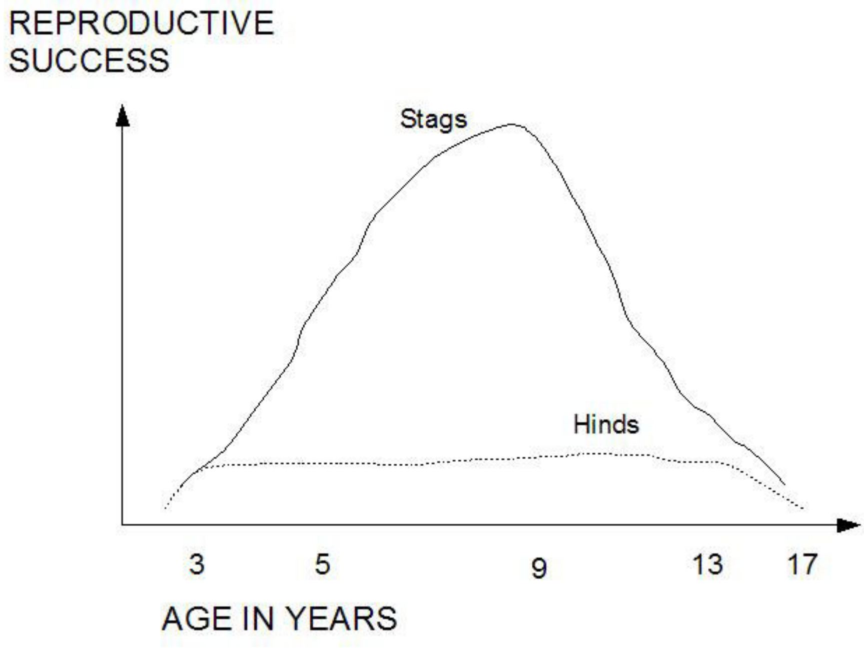
Such demands mean that males struggle to breed after 10 years old. Hinds can produce calves up to 12 years old (Clutton-Brock and Albon 1989). The peak age of reproductive success for stags is 9 years old, while for hinds, the period is longer (figure 3). Also adult stag mortality can be as high as 20% per year compared to 15% for hinds (Albon and Clutton-Brock 1988).

FEMALE DISPERSION	MALE DISPERSION	MATING SYSTEM
A. MALE ASSISTANCE REQUIRED FOR REARING OF YOUNG		
solitary	1 male defends 1 female territory	obligate monogamy
solitary	several males defend 1 female's territory	polyandry
B. MALE ASSISTANCE NOT REQUIRED FOR REARING OF YOUNG		
solitary with defendable range	1 male defends 1 or more female territories	monogamy/polygyny
larger social group	several males defend females' range	multi-male polygyny
small groups in undefendable range	**1 male defends females for mating only**	**harem polygyny**
large unstable groups	males defend small territory for mating only	lek polygyny
widely distributed	solitary males search for females	scramble competition polygyny

(Bold = red deer behaviour)

(After Davies 1991)

Table 10 - Different types of mating systems in mammals.



(After Clutton-Brock and Albon 1989)

Figure 3 - Reproductive success of stags and hinds at different ages.

Males also roar up to three times per minute while holding harems (Clutton-Brock and Albon 1989), leading to nearly 3000 roars per day (Morell 2003).

Roaring rate is seen to reflect fighting ability, which are signs of the quality of the genes. Good quality genes will produce strong animals who can fight and roar longer. This is a signal to other males to stay away, but also to females.

"Female choosiness" (though this is limited; McFarland 1999) will be based upon the best genes (ie: those stags who can keep the harem).

Stags conflict with other mature males, yearlings (young males), and even evict male calves (as young as a few months old) from their harem.

Observations on Rhum island show that hinds mate with a single stag each year, but do not necessarily produce a calf each year (Clutton-Brock et al 1982).

SEX RATIO OF OFFSPRING

Most calves are born in June after a 33 week gestation period. It has been observed that larger, dominant hinds produce proportionately more male calves than smaller, subordinate hinds (Clutton-Brock et al 1986).

Observations over twenty years on Rhum show a clear pattern between "maternal rank" and the production of male offspring.

Maternal rank is defined as "the ratio of animals which the subject threatened or displaced to animals which threatened or displaced it weighted by the identity of the animals displaced" (Clutton-Brock and Godfray 1991) (table 11).

MATERNAL RANK		APPROXIMATE PERCENTAGE OF OFFSPRING BORN MALE
low	0.1	20
	0.3	30
	0.5	45
	0.8	65
high	1.0	75

(After Clutton-Brock et al 1986)

Table 11 - Correlation between "maternal rank" and percentage of male offspring born.

But there is a cost to producing male offspring. Hinds who produced male calves in one year, calved later the following year and were twice as likely to be barren in the next year than those hinds who had female offspring (Clutton-Brock et al 1981).

The sex of the offspring in polygynous mammals is influenced by maternal conditions. Mothers in good conditions produce sons and those in poor conditions produce daughters. This is known as the Trivers-Willard hypothesis (Trivers and Willard 1973).

The maternal conditions will be linked to the resources available to survive and raise the offspring. Where resources are plentiful, then the maximum genes can be passed into future generations by male offspring based on grandchildren (figure 4). Daughters will always find a mate even if this limits the number of grandchildren. The production of daughters is a better strategy where resources are limited.

GOOD MATERNAL CONDITIONS

MOTHER
↓
MANY OFFSPRING
↓
SONS BETTER STRATEGY
↓ ↓ ↓
FEMALE FEMALE FEMALE
↓ ↓ ↓
MANY GRANDCHILDREN FOR MOTHER
= MORE GENES INTO FUTURE

BUT SONS = RISK OF MANY MATINGS VS MAY NOT MATE

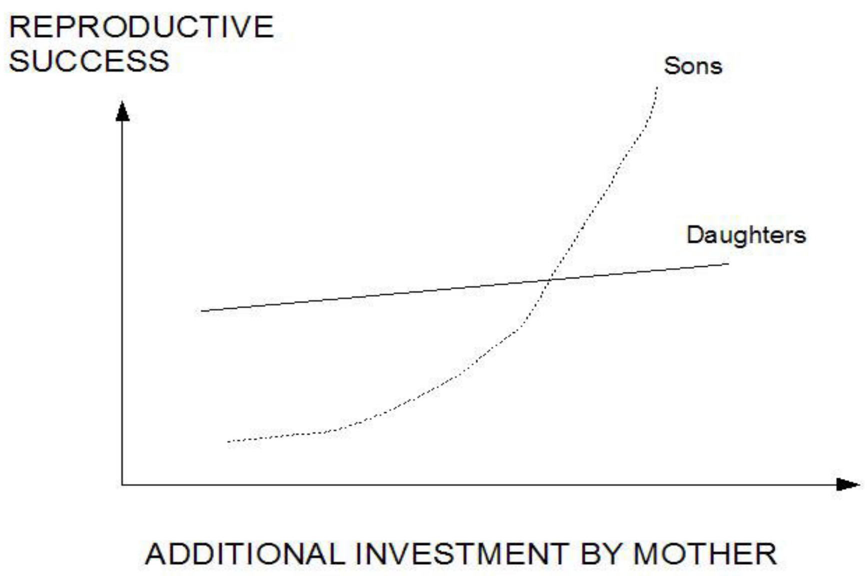
POOR MATERNAL CONDITIONS

MOTHER
↓
ONE OFFSPRING
↓
DAUGHTERS - ALWAYS FIND MATE
↓
GRANDCHILD GUARANTEED

DAUGHTERS GUARANTEED MATE, BUT LIMITED GRANDCHILDREN

Figure 4 - Different strategies for offspring in different maternal conditions.

The dominance of the female will also influence the success of the offspring. High-ranking hinds produce more sons because of the greater lifetime reproductive success for those sons, and low-ranking hinds produce more daughters (Cockburn 1999). Thus the preference for male offspring when the mother invests more is shown in figure 5.

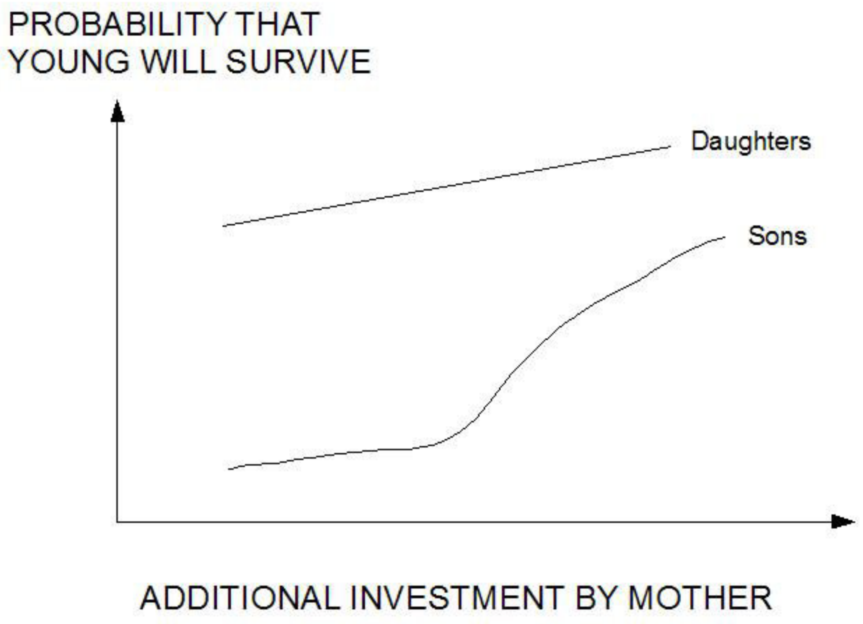


(After Cockburn 1999)

Figure 5 - Trade-off for sons or daughters as offspring.

Work by Kruuk et al (1999 quoted in Cockburn 1999) on Rhum island has noted that with increasing population density, high-ranking females produce more daughters. Increasing population density is an example of poor maternal conditions, and thus the production of daughters is a better evolutionary strategy.

However, Cockburn (1999) argues that male foetuses are more sensitive to resource availability, and more of them may be dying before birth with the increasing population density. The increase in female births is in fact the increased survival of females at birth (figure 6).



(After Cockburn 1999)

Figure 6 - Trade-off between sons and daughters based on survival rate.

It is unclear how the process of "choosing" the sex of the offspring works. For example, the hormones from the mother could influence the production of girls, and testosterone from the fathers for boys. High social ranking males could have more testosterone and thus "determine" the sex of the offspring as male (Cartwright 2000). Maybe high-ranking hinds have more testosterone as well, and this explains the situation in red deer.

MALE-MALE COMPETITION

The competition between males for mates occurs before mating and after. Competition between males can be both direct and indirect.

Direct competition involves males confronting each other and fighting, as with red deer. This leads to the evolution of larger body size in the male compared to the female of the species. This is known as body size dimorphism (Harvey and Bradbury 1991), and is found most commonly in monogamous or harem situations.

However, in situations where many males are living with many females, a more indirect type of male competition evolves. Here it is not body size that matters because the males rarely confront each other. It is the ability to produce a lot of sperm quickly. This is known as sperm competition, and leads to the evolution of larger testes relative to body size (eg: in chimpanzees).

Sperm competition occurs also in the size of the penis and the number of sperm in an ejaculation. The presence of other males in the vicinity as in multi-male/multi-female groups leads to larger number of sperm in each ejaculation. This requires larger testes to carry them (Baker 1996). Table 12 shows the data for primates.

	PAIR-LIVING	POLYGYNY	MULTI-MALE/ MULTI-FEMALE
BODY SIZE DIMORPHISM (adult male divided by adult female weight; the higher the number, the larger the male relative to the female)	1.1	1.7 male competition direct	1.3
RELATIVE TESTES SIZE * (5) (a measure of testes size after body size affects have been removed; the higher the number, the larger the testes relative to body size)	0.7	0.6	1.8 male competition indirect

(* Harcourt et al 1981)

(After Clutton-Brock and Harvey 1984)

Table 12 - A comparison of body size dimorphism, relative testes size and mating system among primates.

1. Pre-copulation competition

The stags are competing throughout the rutting period for access to females. They are competing in asymmetric contests (Maynard Smith and Parker 1976), in that individual animals differ in strength or fighting potential.

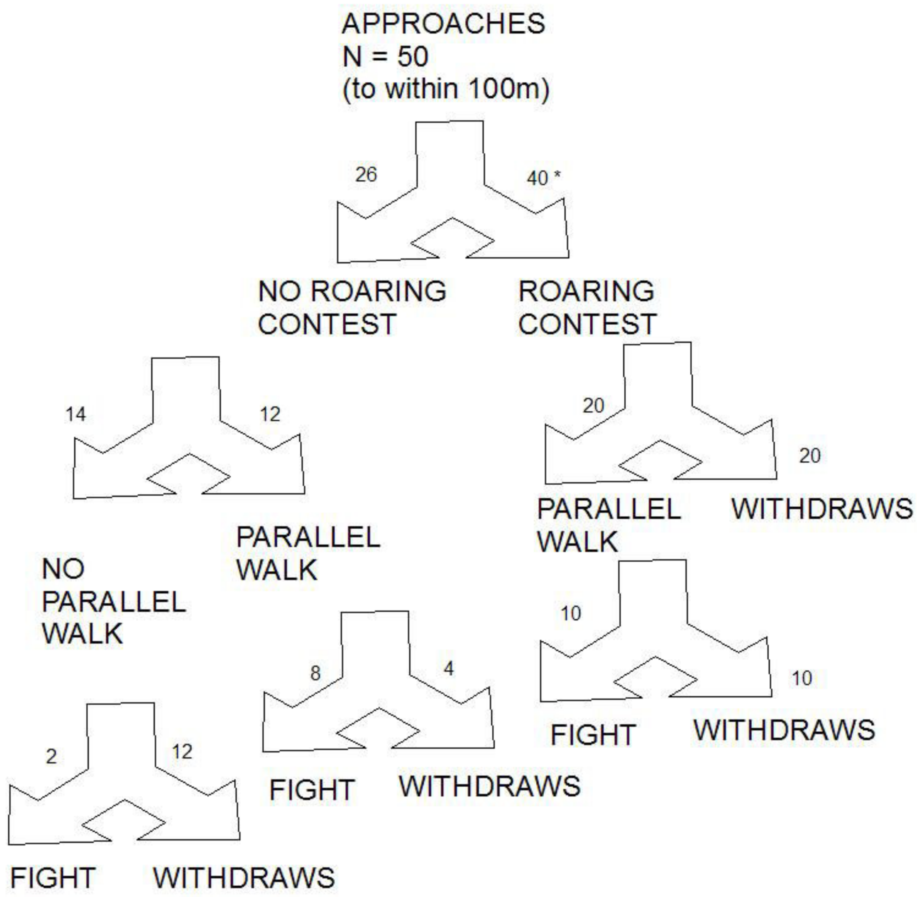
How to signal that ability to other males? The most obvious way is by winning the fight, but this is costly in terms of the risk of injury, and the loss of strength and using up energy.

Also during a fight, the females are left unattended which could allow the opportunity for subordinate males to mate with them. Dawkins and Krebs (1978) call this the "sneaky fucker" strategy.

Because of the risks involved in fighting, "ritualised fighting" or pre-fighting assessments have evolved. These are contests that show which male is stronger without actual fighting.

But weaker animals may be able to bluff in such situations, and signal strength that they do not really have. Thus the "ritualised fighting" must be such that it is a genuine signal of ability.

Figure 7 shows the number of approaches by males that led to fights based on observation of red deer on Rhum (Clutton-Brock and Albon 1979).



(* approximate percentage of total approaches)
(After Manning and Stamp Dawkins 1998)

Figure 7 - The development of fifty approaches by stags on Rhum.

Only a small number of approaches (20%) end in fights. Where the stags did fight, they usually had equal roaring rates (Clutton-Brock and Albon 1979). The stags may take up to 30 minutes to assess each other.

This pre-fight assessment is an "Evolutionary Stable Strategy" (ESS) in game theory (Maynard Smith 1982) (6). It is the best strategy based on costs and benefits of fighting (table 13).

	COST OF FIGHTING eg: injury	NO COST
BENEFITS FROM FIGHTING eg: access to females	pre-fight assessment and "ritualised fighting" evolves	always fight
NO BENEFITS	no fighting	co-existence

Table 13 - Costs and benefits and strategies of fighting.

This trade-off between fighting and not fighting seems a good strategy. However, the benefits are very high; ie: the value of the resource is great. Thus the stags are willing to risk injury in fighting because of the limited availability of female each year. Mating opportunities are so few that this makes the benefits of winning so much greater. This can be seen in that the peak time for fights, injuries and conceptions is mid-October on Rhum (Clutton-Brock et al 1982) (table 14).

SMALL BENEFITS FROM FIGHTING eg: mating often in year	LARGE BENEFITS eg: females only available for few weeks each year
pre-fight assessment very important; little actual fighting	pre-fight assessment important, but males more willing to fight if necessary

Table 14 - Benefits of fighting

Stages in "ritualised fighting"

i) Roaring contest

The first stage of the contest between two males involves the ability to roar. As the contest develops, the stags increase their speed of roaring until one of them cannot keep up. In experiments with tape recordings, stags compete until the tape becomes too fast, and then they withdraw.

This signal of strength cannot be bluffed because of the great energy demands of roaring. Zahavi (1977) argues that animals can signal their dominance by the degree of cost it is willing to incur. Also the maximum and mean roaring rates have been found to correlate with fighting ability (Goodenough et al 1993).

Clutton-Brock (quoted in Dawkins and Krebs 1978) uses the case of two stags on Rhum called "Pincer" and "Fingal". Their speed of roaring increases in parallel until "Pincer" wins. They begin at one roar per four minute observation period (baseline measure) which increases to 30 roars per four minute period. This is the point at which "Fingal" cannot match "Pincer", and his rate drops back to the baseline. The whole observed contest lasted 40 minutes, and involved nearly 200 roars each. This is a vast amount of energy expended, but it is less riskier than actual fighting.

ii) Parallel walking

If a contest cannot be decided by roaring, then the next stage is for the animals to walk side by side allowing them to assess each other's body size.

Both males face in the same direction, and perform a slow walk with antlers held high. Parallel walks often occur between evenly matched males, and those who hold harems (Alvarez 1993).

Body size can be faked by expanding the body, and this is done in some species (McFarland 1999). There needs to be a way to overcome this type of bluffing. Physical contact would find this out.

Recent detailed observations have been made of parallel walking by male fallow deer in a captive population in Dublin (Jennings et al 2003). A sample of contests were video-recorded and analysed by the researchers. This research did not find that parallel walking resolved more contests before the actual fighting began.

However, parallel walking was found to occur often in the middle of a fight (as a means of reassessing the opponent's size), or sometimes after the fight (as a means of withdrawing from further fighting) (table 15).

iii) Fighting

This involves the interlocking of antlers and pushing.

	PARALLEL WALK	NO PARALLEL WALK
RESOLVED FIGHTS (%)	34	59
PARALLEL WALKING PRIOR TO FIGHTING		
RESOLVED (%)	17	35
NOT RESOLVED (%)	28	20
PARALLEL WALKING FOLLOWING FIGHTING		
RESOLVED (%)	12	26
NOT RESOLVED (%)	44	18

(After Jennings et al 2003)

Table 15 - Summary of findings by Jennings et al (2003).

2. Post-copulation competition among males

After the male has mated with a particular female, it is still important to stop other males from mating with her. There are strategies used by the male and his competitors (Wilson 1975) (table 16).

STRATEGIES USED BY

MALE WHO HAS MATED	COMPETITOR MALE
- mating plugs and repellants	- sperm displacement (remove first male's sperm)
- prolonged copulation	- induce abortion and then re-inseminate
- male remains attached to female	- infanticide of first male's offspring and then re-inseminate
- guarding	
- departure of mated pair from rival males	

(Bold = strategy used by red deer)

Table 16 - Post-copulation competition strategies by males.

FEEDING BEHAVIOUR

Detailed observations have been made of red deer in Scotland and their feeding behaviour (Clutton-Brock and Albon 1989). Outside the rutting period, red deer spend 10-12 hours per day feeding, divided into 10 periods. The peak grazing occurs between 16.00-20.00 each day. The major food is grass, but also heather.

The feeding areas vary over the year with the lower sheltered grounds used in winter. Models of optimal foraging argue that animals will stay in an area as long as the net gains are greater than elsewhere. What are the factors in the decision to move between feeding sites?

1. Extreme weather conditions

Red deer lose twice as much body heat in exposed areas because of the low temperature, wind and rain, which increases the energy needs (Grace and Easterbee 1979). Thus during winter, when the vegetation may be less and temperature colder, it is better to use sheltered areas.

2. Predators

For red deer in Scotland, predators are limited because the areas of habitat are controlled. But there is still harassment by biting and sucking flies which occurs at higher altitudes.

3. Competition from other species

Sheep feed on similar grasses, and the density of sheep influences the amount of food available, and the level of parasites (eg: tapeworms, ticks).

4. Population density

The increased size of the population affects the deer directly through lack of food, and indirectly through calf survival and growth. Males tend to move area more in situations of high population density. This may be because they need more food to achieve the large increase in body weight ready for the rut.

FOOTNOTES

1. A range is a specific area that the animal moves around in order to feed. It is different to territory, which is usually a fixed area defended by the animal. Ranges can overlap between animals without conflict occurring.

2. Calves take between 200-600 grams of milk per feed, giving a total as high as 2000g per day (Arman et al 1974).

3. Resource holding power (RHP) has three dimensions: size, weaponry, and information about past experiences (Hayes 1994). Concerning the latter, female deer may resolve a conflict between two stags based on her previous experience with those males (Thouless and Guinness 1986).

4. Antler size is linked to food intake as shown by captivity studies that control food intake (Fennessy and Suttie 1985) (table 17).

AVERAGE WEIGHT OF ANTLERS ON UNRESTRICTED DIET	2.20 kg
AVERAGE WEIGHT ON 80% DIET	1.87 kg

(After Putman 1988)

Table 17 - Antler weight and food intake.

5. Gorilla who live in harems have an average testes size of 10g relative to body size of 250kg. Testes are 0.02% of body weight. Male chimpanzees, who live in multi-male/multi-female groups, have testes' size of 0.03% of body weight - 60g to 50kg body weight (Short 1994).

6. Game theory is a mathematical theory applied to decision-making. An "Evolutionary Stable Strategy" (ESS) is a strategy that if most members of the population adopted cannot be bettered; ie: the best individual strategy depends on the population strategy (Dawkins 1989).

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