COMPARATIVE PSYCHOLOGY BY ANIMAL

NO.6 - ALBATROSS

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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.

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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 ALBATROSS

The order is Procellariiformes, and the family is Diomedeidae (table 4), of which there are 13 species (table 5)(14; Gill 1995) in 2 genera (Diomedea and Phoebetria) (Snow and Perrins 1998). Smaller members of Diomedea are known as "mollymawks" (Cramp and Simmons 1977). Of the 13 species, 2 are classed as threatened by extinction (Rands 1991).

The albatross is mainly found in the southern hemisphere, and the north Pacific. Their food is usually fish and squid secured while floating on the surface, or shallow diving.

- Body short and broad
- Head relatively large
- Neck short
- Wings long and narrow, fold in three when closed
- Bill heavy, hook at tip

Table 4 - Main characteristics of Diomedeidae.

TYPE OF ALBATROSS	LATIN NAME
1. Black-browed	Diomedea melanophris
2. Grey-headed	D. chrysostoma
3. Yellow-nosed	D. chlororhynchos
4. Shy	D. cauta
5. Black-footed	D. nigripos
6. Wandering	D. exulans
7. Royal	D. epomophora

Table 5 - Examples of different species of the albatross.

The albatross spends much time in the air, often gliding because of the large wing span. It flaps the wings only occasionally. It tends to be silent when solitary, and active nocturnally. There are reports of many albatross following ships, and taking discarded food.

It seeks remote islands for breeding sites on steep slopes at the top of cliffs. Eggs are laid in September-October, the birds disperse in March-April, and return to the colonies in August-September for those with an annual cycle, like the Shy albatross. Other albatross may follow a biennial cycle (every two years).

MATING BEHAVIOUR

DELAYED BREEDING

From an evolutionary viewpoint, it makes sense to have as many offspring as possible over an animal's lifetime. Yet there are some animals, including albatrosses, that have delayed breeding. This means that breeding does not take place as soon as the animal is physically able.

The albatross first breeds at between 7-13yrs old. There are a number of reasons for delayed breeding (Gill 1995):

i) The life expectancy of the animal.

Animals that live longer have greater opportunities for breeding over the lifetime, so can afford to wait. The Wandering Albatross produces one chick every two years for up to 50 years (Gill 1995).

ii) The interval between generations (mean generation time).

Successful breeding is not just about having many offspring, but about them surviving into adulthood. Spacing out the offspring allows more time to be spent on their upbringing, and thus increases their survival.

iii) Costs of early reproduction can be severe.

Animals that breed young may be more likely to die from lack of food or poor predator avoidance, and thus so will the offspring die. Older animals may be better at collecting food for the incubation/pregnancy period, and finding nests that avoid predators.

The albatross lays one egg usually with an incubation period of 80-90 days (Gill 1995). This is a long time to remain stationary on the nest. Being stationary means vulnerability to predators, and the need for food to be provided by a mate.

Ainley and DeMaster (1980) studied the risk of breeding among Adelie Penguins, who show delayed breeding patterns. In one year, 39% of breeding animals died compared to only 22% of non-breeders. While 75% of 3-year-old females died at first breeding compared to only 10% of 11-year-olds at first breeding. There are survival advantages to delayed breeding.

iv) Divorce more common among younger individuals of monogamous species (eg: short-tailed Shearwater; Wooller and Bradley 1996).

Table 6 compares delayed breeding to immediate breeding, and table 7 compares the albatross to other seabirds.

	ALBATROSS	DUCK
Type of breeding	delayed	immediate
Survival before breeding (per year)(%)	30	15
First reproduction (age in years)	7-13	1
Fecundity (young per year)	0.2	3
Adult mortality (per year) (%)	5	50

(After Gill 1995)

Table 6 - Comparison of delayed and immediate breeders.

	ALBATROSS	OTHER SEABIRDS*
First breeding (age in years)	7-13	none less than 2
Adult survival rate (per year) (%)	92-97	75+
Clutch size	1	6 families: 1 3 families: 1-2 1 family: 1-3 3 families: 2-3
Chick-rearing period (days)	116-150 (Great albatross 280)	15-20 to 140-170

(* 13 families)

(After Croxall and Rothery 1991)

Table 7 - Comparison of albatross and other seabirds.

MATING STRATEGY - MONOGAMY

There are a number of mating strategies (table 8) and parental care decisions (table 9). There are advantages and disadvantages to monogamy (table 10).

MALE STRATEGIES	
1. monogamy	
2. polygyny	
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 STRATEGIES	
1. monogamy	
2. polyandry	
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)

Table 8 - Different types of mating strategies.

	FEMALE STAYS AFTER BIRTH	FEMALE LEAVES AFTER BIRTH
MALE STAYS AFTER BIRTH	**equal investment by both partners; monogamy**	male greater investment than female; sex-role reversal
MALE LEAVES AFTER BIRTH	multiple partners for male; female greater investment than male	multiple partners for male; many eggs must survive

(Bold = albatross)

Table 9 - Different parental care decisions and mating strategies.

ADVANTAGES	DISADVANTAGES
1. Know quality of partner from past offspring	1. Fear of extra-pair copulations (EPC); males can have EPC while away getting food, and female is vulnerable at nest to EPC while male away
2. Help with rearing offspring	2. Lack of variety of genes

Table 10 - Advantages and disadvantages of monogamy.

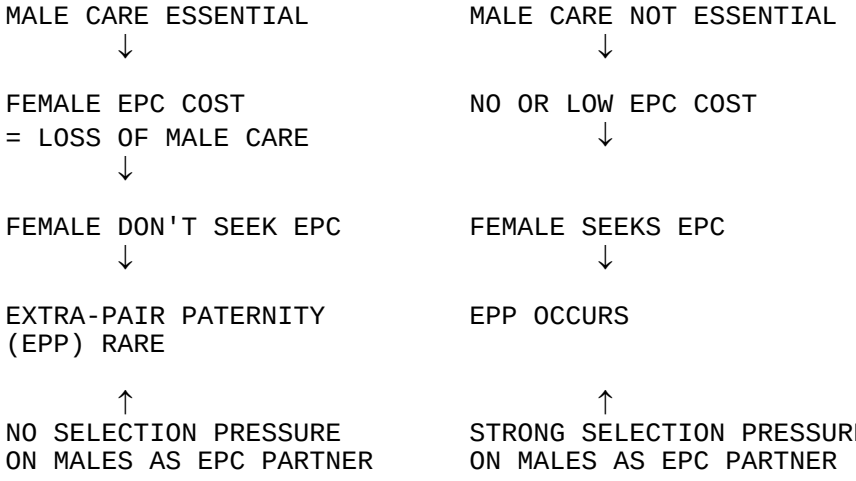
The albatross is monogamous because of the need for dual egg tending. With the length of incubation (up to 90 days), and chick-rearing (up to 150 days in total), both parents are required. Initially the female is gathering food to build her strength, and the male stays at the breeding colony to protect the site. This behaviour is the opposite after the egg is laid.

Because of the "shift work" of the two birds, there is little time for copulation. The birds will copulate when they can, and the females will carry the sperm (for up to 8 weeks) until she is ready for fertilisation (Birkhead 2000).

There are three main reasons for monogamy:

i) Dual parental care is essential.

Where male care is essential, this will influence females from seeking extra-pair copulations (EPC) (figure 2).



(After Birkhead and Moller 1996)

Figure 2 - Females seeking extra-pair copulations.

ii) Resources do not allow polygyny (one male with several females) or polyandry (one female with several males).

Gowaty (1996) notes the "constrained female hypothesis", where females in "poor" environments are not promiscious.

iii) Female-female aggression limits polygyny and male-male aggression limits polyandry.

Table 11 shows the three reasons that influence mating strategies.

	WHY MALE STAYS	WHY FEMALE STAYS	WHY ONE MALE	WHY ONE FEMALE	WHY MALE EXCLUSIVE	WHY FEMALE EXCLUSIVE
1.		X				
2.	X					
3.						X
4.					X	
5.	X	X	X	X	X	X
6.	X		X		X	
7.		X		X		X

1 = maternal care needed
2 = paternal care needed
3 = geographical distribution of breeding females; eg: sparse
4 = geographical distribution of breeding males
5 = resource distribution; eg: limited
6 = male-male aggression
7 = female-female aggression

(After Gowaty 1996)

Table 11 - Factors influencing mating strategies.

The choosing of monogamy as the mating strategy has been shown with Waved Albatross (Harris 1973) and Laysan Albatross (Rice and Kenyon 1962) (table 12).

Detailed studies of Waved Albatross on Bird Island, South Georgia have found that they breed biennially (every two years) or occasionally every 3-4 years. But those birds who fail to breed may return the following year (Croxall et al 1990).

	WAVED ALBATROSS	LAYSAN ALBATROSS
Broods	single	single
Pair-bond	monogamy, but partnership habitually broken after breeding season	
Residency	migration - more than 110km	
Breeding site fidelity	return to "exact" breeding site each time	
Divorce rate (per year)(%)	0.0	2.1

(after Ens et al 1996)

Table 12 - Breeding behaviour of Waved and Laysan Albatross.

MIGRATION

Albatross, like many birds, are moving around most of the time, but migration refers to "regular movements between areas uninhabited at different times of the year" (Cocker 1993).

There are a number of general patterns and variations in migration (Cocker 1993):

i) Differences in migratory/non-migratory behaviour within the species based on the habitat eg: more northerly birds more likely to migrate;

ii) Differences between male and female of the species in migratory behaviour;

iii) Migration only based on the severity of the weather;

iv) Regular migration - this is the situation for the albatross.

There are three key questions related to migratory behaviour.

1. What are the advantages to migration for the birds?

Table 13 shows the general advantages and disadvantages of migration.

ADVANTAGES	DISADVANTAGES
- find specialist site for breeding that does not need all year food supply	- energy needed to travel long journey; eg: 800 miles for albatross
- move to good food supply when not breeding	- problems of navigating
- being stationary means risk of predation	- problems of remembering where breeding site
- escape bad weather	- leaving home territory empty and other residents may move in

Table 13 - Advantages and disadvantages of migration.

2. How do the birds know when to migrate?

Migration is about moving to the right place at the right time. Birds seem to have circannual (annual) biological clocks which trigger the migratory restlessness (Zugunruhe) and put on weight beforehand (Elphick 1995). The biological clock, probably linked to the pineal gland in the brain and connected to the visual system, responds to changes in light and darkness with the seasons.

But there is also an endogenous biological clock which works irrelevant of changes in the environment. Gwinner (1986) kept wild birds in special cages for over three years. The environment was controlled so that there was always 12 hours of daylight and 12 hours of darkness. Thus the removal of external cues to migration. But the birds showed the migratory restlessness at the appropriate time of the year still.

However, the Wandering albatross breeds biennial, and so migrates to the breeding site every other year; even less frequently in some cases. How does the biological clock work in this situation?

3. What the mechanisms by which the birds use to navigate?

Table 14 shows the different cues that animals use to navigate.

1. Sun compass - movement of sun; angle of sun*; polarised light (pattern of light based on sun's position and reflection on water)

2. Magnetic compass - sensitivity to magnetic North

3. Star compass or position of moon

4. Other visual cues - patterns of waves*; cloud patterns*

5. Smell

6. Sound

7. Electric

(* cues believed to be used by the albatross)

Table 14 - Different cues used by animals to navigate.

The albatross tends to be at sea except when on duty at the nest during the breeding season. The distance of migration is often difficult to ascertain because of the limited information available.

Studies of ringed populations of birds found in different places is one way to study the migration distances. For example, Black-browed albatrosses from the Falkland Islands (south Atlantic) have been discovered in South America mainly, but ringed birds from South Georgia (south Atlantic) mainly found in southern Africa (quoted in Cramp and Simmons 1977). One suggest is that the young birds have separate winter ranges to older breeding birds, as the young sent from breeding sites for 3-5 years.

While migration for the Wandering albatross is seen as circumpolar (not crossing the equator); eg: South Georgia to Australia.

There are cases from displacement experiments of albatrosses migrating very long distances. Displacement experiments involve taking birds to a point of release that is different to their normal migration point, and to see if they return to the original home. The birds are ringed so records can be kept. For example, Laysan albatrosses returned 5200km in 10-12 days from the west coast of the USA to Midway Island (Pacific), or from the Philippines to Midway Island (6500km taking one month) (Alerstam 1993).

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PICTURES FROM WIKIMEDIA

(Source: Mark Jobling; in public domain)

Wandering Albatross

(Source: US Fish and Wildlife Service; in public domain)

Laysan Albatross