COMPARATIVE PSYCHOLOGY BY ANIMAL

NO.4 - ROBINS

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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:

- 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 ROBINS

Of all the species of birds, 60% (ie: 5276 living species) are classed as Passeriformes (Raven and Johnson 2002). These have specific characteristics (table 4). Within this grouping are a number of families: robins (Erithacus rubecula) are part of the Thrush family (Turdinae) (Fitter and Richardson 1968). It is not related to the American robin.

- songbirds
- well developed vocal organs
- perching feet
- dependent young

Table 4 - Main characteristics of Passerines.

There are a number of "races" of robins, but eight in the west Palearctic area (Europe, North Africa, and the Middle East) (Harper 1988a) (table 5).

LATIN NAME	MAIN AREA OF HABITAT
1. rubecula	continental Europe
2. melophilus	Great Britain and Ireland
3. tataricus	north west Asia
4. superbus	Gran Canaria and Tenerife
5. witherbyi	Algeria and Tunisia
6. valens	west Russia
7. caucasicus	central Russia
8. hyrcanus	Iran

Table 5 - Eight "races" of robin in west Palearctic area.

Robins are about 14cm high (Walters 1995). The red breast only appears in adults, while juveniles are brown.

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TERRITORIALITY

Generally the robin is a solitary bird, and is strongly territorial [2] (except during severe winters; Lack 1965). Territoriality has both advantages and disadvantages (table 6).

ADVANTAGES	DISADVANTAGES
- attractive to mate	- energy involved in establishing and defending territory
- area for breeding and raising young	
- local knowledge of predators and resources	- higher risk of predation if territory within predator's territory
- dispersion of nests reduces predation	- difficult to move if resources exhausted

Table 6 - Advantages and disadvantages of territoriality.

Both sexes have their own individual territories outside of the breeding season. There are two phases to the territorial behaviour in the year. The individual territory for most of the year, and the joining together of two birds to breed.

a) Individual territory

The average size in English studies varies between 0.27-0.73 hectares (approximately 450-2000m²) per bird (Harper 1988b). There is no evidence of sex differences in the size of the territory, nor it being related to food density.

Sedentary (non-migratory) birds defend the same territory for their whole life, while migrants return to the same sites each year.

b) The breeding territory

Two birds will join together during the breeding season, usually by the female moving to a male's territory (78% of cases observed). In 10% of observations, the male goes to the female's wintering territory, and 9% of times adjacent territories are

[2] Migrant robins have been found to be territorial even during a stop-over in migration. Nelson (1907) observed territorial behaviour on a boat at sea where a group of robins had rested.

fused together.

Occasionally, the birds will pair together and then move to a new site: only 3% of 92 pairs studied in Cambridge did this (Harper 1985c quoted in Harper 1988b). The average size of the breeding territory is 0.55-1.44 hectares (approximately 900-2500m^2) (Harper 1988b).

Unpaired males can be evicted from their territories at this time.

Aggression

Because robins are strongly territorial, there is a high level of antagonistic encounters. Most occur when territories are being established or when there are boundary changes (at the beginning of the breeding season). Usually the display of the red breast is enough.

The back of male European robins is camouflaged, but the puffed-up red chest is a warning signal to other males. Lack (1943) has found the red breast is a "sign stimulus" [3] for territorial aggression against intruders.

Robins will attack just red feathers, such is the strength of the stimulus. The resident bird flies at the intruder with a high-pitched call. If the intruder does not leave, the resident then perches on a branch and displays its red breast. Occasionally this "show of strength" does not work, and a fight ensues.

But 13% of 1067 encounters observed end in fights (Harper 1988b). These fights can be fatal: in a Cambridge study, 10% of 98 males and 3% of 86 females died in this way (Harper 1988b).

Once the territories have been established, the residents are able to distinguish the calls of their neighbours from strangers occupying territories further away. In this situation, the direct neighbour is not seen as a threat. This is known as the "dear enemy phenomenon" (Wilson 1975). Recognition of the neighbour avoids wasteful conflicts, and makes clear the boundary edges of the territory.

There are a number of possible explanations for the "dear enemy phenomenon":

i) habituation to the neighbour's song - each time it is heard, it produces less of a territorial aggression response until there is no response at all to the song;

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[3] "Sign stimulus" is a trigger for instinctive behaviour (Hinde 1982). For example, the red of the breast triggers the territorial aggression response. The trigger must have certain specific characteristics. Lack (1943) found no territorial aggression response to models of robins without the red breast.

ii) mere exposure effect - similar to above;

iii) dialect convergence - the similarity in the neighbours' songs reduces the territorial aggression response.

Residents Always Win

Research has found that residents in a territory tend to defeat the challengers in most cases. Maynard Smith and Parker (1976) suggest possible explanations:

i) value asymmetries - greater investment and local knowledge about predators and resources gives the resident advantages to win the contest;

ii) resource-holding power (RHP) variations - those in residence have superior abilities (eg: size) that allows them to defeat intruders;

iii) "owners always win" convention - the individual in possession of the territory fights harder than the intruder.

This is an example of a "bourgeois strategy" - ie: a strategy that cannot be bettered in a population. This idea is the part of the application of game theory to animal behaviour (Maynard Smith 1982).

Tobias (1997) tested the first explanation with a series of "removal-replacement experiments" with 75 robins. This involves removing the residents from their territories for a period of time, and then returning them, to see if they can win the territory back from the "new residents". Tobias removed 37 males and 13 females from their winter territories, and 19 males and six females from the spring territories. The length of the removal varied from 1-14 days.

Two observations came from the research:

a) for winter territories, the longer the resident was away the less likely they were to win back the territory. Less than five days away, all won back their territory, but if away for more than 10 days, no returnees won;

b) with the spring territories, there was an immediate loss no matter how short the period away. This is because territory is crucial for males at this time of the year. Males without territory have little chance of breeding.

COMMUNICATION

Robins communicate by sound (auditory communication) (table 7), and the use of the red-breast as visual communication. The red is used as a warning when birds stray into the territory of the resident.

ADVANTAGES	DISADVANTAGES
- ability to pass obstacles eg: trees, undergrowth	- eavesdropping: abused by predators and competitors
- flexibility of message	- expensive in energy terms
- complex and variable messages possible	- low durability: does not last long
- can be used in darkness	
- does not need visual recognition or attention of recipient	

Table 7 - Advantages and disadvantages of auditory communication.

The sound communication takes place within the range of 2-9 kHz, and shows a difference in complexity between the "races" of robins.

The song begins with very high notes, checks, and goes bounding off again - "tic-ic-ic" ("sounding like an old grandfather clock being wound up") (Bruun et al 1992). The song will be different in autumn and winter compared to spring. The autumn and winter songs are usually quieter. The sequence of notes sung by the males is important for recognition of the same species (Bremond 1968 quoted in Wilson 1975).

One study of three males and one female recorded them using over one hundred different songs, and the birds shared only three of them (Hoelzel 1986 quoted in Harper 1988c).

Singing is the means by which males attract females, and the quality of the song is a sign of the quality of the genes. It is also a means of male-male competition. Most song-bouts occur from a perch rather than in flight (Harper 1988b).

Circadian Rhythms and Singing

There is a circadian rhythm to the singing - mainly at dawn, but also at dusk.

This rhythm is affected by the temperature of the

environment, and thus the body temperature of the bird. Thomas (1999a) has shown a positive correlation between the amount of time spent singing and the environmental temperature. At lower temperatures, the bird needs to forage more, which leaves less time for singing. Singing at dusk is also linked to reserves of energy to survive the night. Based on the current temperature, the bird will sing in relation to the current and expected future energy expenditure.

The reliability of the food supply also influences singing at dawn and dusk. This is linked to whether the food supply is constant or variable. The bird uses the size of its fat reserves as an indicator of energy stores and then predicts the needs of the day (Houston and McNamara 1987).

Thomas (1999b) set up an experiment to vary the food supply, and then record the amount of singing at dawn and dusk. There was either a constant food supply, or it was varied to be plentiful one day and then scarce the next. The song rate was measured as the number of songs per hour. The results appear in table 8.

	DAWN	DUSK
FOOD SUPPLY VARIABLE	180	180
FOOD SUPPLY CONSTANT	250	140

(After Thomas 1999b)

Table 8 - Approximate number of songs per hour.

Generally when the food supply is variable, there is less singing at dawn then dusk, and more singing at dawn when the food supply is constant. In other words, birds sing more at dawn when the fat reserves are high (Thomas and Cuthill 2002). This is a signal to females of a well-fed bird (with good territorial resources).

Surviving the night is important for the bird. It must build up fat reserves during the day to do this, but not too much because of increased predation risk if too fat. There is an optimal level of fat resources. Thomas (2000) found that the body mass of a group of robins studied was always the same at dusk, irrelevant of the food made available in the experiment during the day.

Singing and Aggression

Singing acts as a form of contest between males.

Usually the birds will alternate their songs, but in certain situations, they will overlap. Overlapping of the other bird's song is an indicator of a high level of arousal or willingness to escalate the contest by a male, particularly when the opponent is close to the singer. Dabelstein et al (1997) used a playback experiment to assess the amount of twitterings (continuous, low amplitude pattern of singing) in male robins. Twitterings are the sign of arousal.

The experiment involved three conditions of playback:

a) alternating interactive playback - playing a recording of a male song in response to the song heard;
b) overlapping interactive playback - playing a recording that overlaps with the singing male;
c) non-interactive loop playback (control condition) - playing a recording constantly, and irrelevant of any birds singing.

The number of twitterings per playback were noted (table 9). Overlapping of the other male's song is an aggressive tactic by males.

	AVERAGE NUMBER OF MALE TWITTERINGS
NON-INTERACTIVE LOOP PLAYBACK	0
ALTERNATING INTERACTIVE PLAYBACK	3
OVERLAPPING INTERACTIVE PLAYBACK	9

(After Dabelstein et al 1997)

Table 9 - Number of male twitterings based on playback in experiment by Dabelstein et al 1997.

Is Robin Communication A language?

Harper (1988c) lists the different types of calls recorded by robins (table 10).

There are a wide variety of calls that have been recorded, but are they the same as those used in a language? There are a number of criteria that have to be satisfied before communication can be called a language (table 11). Generally it is not the same as the use of language by humans.

TYPE OF CALL	FREQUENCY (kHZ)	WHEN CALL GIVEN
tic-call	3-6	short, sharp "tic" sound; to warn of territory or alarm, particularly mammal predators
contact-alarm call	7	thin "tswee" sound; mild alarm when bird wanders off territory, encounters novel object, territory being established, non-antagonistic meetings
alarm-call	7	high-pitched, sharp sound; in presence of predators, particularly avian
antagonistic calls	7.5	one for dominant bird, one for subordinate
contact-call	7	given when two birds meet
feeding-call	6-7	begging call given by females when mate is courtship feeding; also heard when searching for mate, or by subordinate robin
copulation-call		similar to contact-call, given by female at mounting
foraging-call	8	
flight-call	6-7	given by nocturnal migrants
churring-call	3-6	made by adults tending nest
brooding-call		given by female during incubation and brooding; similar to contact-call and churring-call
sigh-call		made during fight or when cornered by predator
hiss-call	7	heard during fights
distress-call	5-7	made when seized by predator
juvenile calls		calls from chicks in eggs, and young nestlings before produce recognisable adult versions
miscellaneous		bill-snapping sound made during fights

Table 10 - Different types of calls made by robins.

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

(After Thorpe 1972, 1974)

Table 11 - Characteristics of human verbal language compared to calls of robins.

MATING STRATEGY

Robins breed between March and July. The mean clutch size is five eggs (Roselaar 1988). It is important to have as many eggs as possible that can be fed and will survive. But too many can lead to the death of more through lack of food, for example. Thus there is an optimum clutch size. Incubation of eggs is usually about 14 days. Fledging lasts a similar length of time before the young leave the nest. Thus, for 28 days, the young are highly vulnerable to predators.

Lack (1948b quoted in Roselaar 1988) did a detailed study of breeding success in England and Wales (table 12).

1426 eggs laid - 71%: hatched - 77%: fledged - breeding success = 55%	282 nests - 54%: hatched full clutch - 18%: lost one egg - 6%: lost two or more eggs - 22%: all failed	407 nests hatched - 73%: all young fledged - 4%: lost one bird - 3%: lost two or more birds - 20%: none fledged

Table 12 - Percentage of success in hatching and fledging in robins.

In early spring, the birds begin to pair. Robins are so strongly territorial that the pair are often aggressive towards each other (giving threat displays) (Lindsay-Blee 1939 quoted in Harper 1988b). Harper (1988b) reports the case of a mate blinded in one eye by their partner. After nest-building the level of aggression drops.

Pairing involves a song-and-following ceremony, where the male chases the female usually. This is not always successful. Harper (1988b) noted that 18% of 939 copulations were preceded by a display by either bird.

Courtship-Feeding

When the pair has been established, there will be courtship-feeding, where the male finds food for the female during nest-building and incubation. 65% of 1489 copulations followed courtship-feeding (Harper 1988b). The feeding can involve 30-50 feeds per day from two days before the first egg is laid until hatching. This may peak at feeding every five minutes during incubation (East 1981).

There is a positive correlation between the rate of

courtship-feeding during egg-laying and the clutch size (Harper 1988b). In other words, the more effort the male puts into feeding the female will be rewarded with more eggs, and thus more chance of survival for his offspring (50% of his genes are in each bird).

Females have a strategy to encourage courtship-feeding as well. Females beg for food with a "seep" call similar to the fledglings' begging call. It is a loud call (which can be heard up to 70 metres away), and increases in frequency in the fertile period. There is a negative correlation between the call and courtship-feeding. In other words, the more the female is fed, the less she makes the call. Thus the pair male can reduce this call by courtship-feeding and so protect his paternity.

Tobias and Seddon (2002) noted that competitor males can eavesdrop, and respond to the increasing frequency of this call. Furthermore, the female may move to the edge of the territory, and thus is vulnerable to the competitor males. When the female is being fed, she remains static in the centre of the pair male's territory.

In their experiments, Tobias and Seddon recorded an average of six "seep" calls per 30 seconds when the male was courtship-feeding. The male was removed for 90 minutes, and the rate of call increased to nine per 30 seconds. The female is almost saying: "feed me or I will call another male to do it".

Monogamy and Parental Care

There are a number of parental care decisions and thus mating strategies (table 13).

	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 = robin's strategy)

Table 13 - Different parental care decisions and mating strategies.

Robins are monogamous for a breeding season. Though there are cases of re-pairing the next season (Lack 1965: 70% of those observed). However, this is due to "site-fidelity" rather than pair choice (Harper 1988b). In other words, the birds remain in or return to the same territory each year and thus find the same partner this way.

Harper (1988b) noted in a Cambridge study that only 6% of 71 males were bigamous, while 20% of males failed to pair.

Usually the male remains with the female to care for the young: both parents feeding the nestlings. Lack (1965) noted that only 12% of males deserted the nest in a Devon study, and this was usually due to loss of territory. Deserted females generally have less success in fledglings that survive: half compared to when the male does not desert in pied flycatchers and great reed warblers (Clamp and Russell 1998). The vulnerability of the young makes desertion a risky strategy.

If a new male moves in, they do not help with raising the young, and they may even attack them (Harper 1988b).

Where animals are monogamous, there is usually a complex system of courtship - a series of tests for males to show to the females their commitment to her and the care of the young as well as the quality of their genes (table 14).

1. Ensures pairing with the right species
2. Permits survival in aggressive species - ie: to approach without being attacked
3. Display of fitness
4. Improves species - ie: only fittest survive

Table 14 - Functions of courtship.

In a monogamous situation, there will be an emphasis on the male to guarantee the paternity of their offspring. Tobias and Seddon (2000) compared the different techniques of "paternity guarding" that males can use. Model male robins were placed in the bird's territory at different distances from the female. It appears that mate attendance (ie: time spent with the female), and number of copulations do not increase with the presence of competitors.

The male uses the territory size, their song, and patrolling the territory as "paternity guards". Models were detected in the territory in half the time compared to outside the breeding season. When males were removed, on their return to the territory, they increased their

rate of patrolling the territory.

Occasionally there will be extra-pair helpers at the nest (Harper 1988b). These may be genetic relatives: ie young born in the last breeding season. More fledglings survive per nest with such a helper (found in Tasmanian native hen, kookaburra, and Harris' hawk; Trivers 1985). This makes sense for genetic relatives because of inclusive fitness. But what about when the helpers are not genetically related?

OTHER BEHAVIOUR

PREDATOR-PREY RELATIONS

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

(Bold = strategies used by robins)

(After Alcock 1993)

Table 15 - Strategies used by predators and prey.

Robins are prey to both mammals and other birds. There are various strategies that robins can use against the predators (table 15).

1. To protect the nest

a) Hide the position of the nest from predators

i) When the male returns with food for the female during incubation, he will call her off the nest.

ii) Sometimes the males are driven away from the nest area until hatching.

iii) When the bird's return to the nest area, they wait a period of time nearby before going to the actual nest (up to three minutes; Harper 1988b).

iv) Females are also aware of being watched, and been known to make false nests (Harper 1988b).

v) If the nest is discovered, males can attack other birds if they are the predators.

b) Response of young

At an alarm-call, the nestlings from five days old will go silent and cower in the nest. At ten days old, they leave the nest to hide at the sound of the distress-call. Getting the younger birds to sit still is less of a risk than them wandering around at that age.

2. Individual birds

a) The use of alarm-calls to warn others.

b) Fear screams

Hogstedt (1983) noted that when caught by predators, many prey scream loudly. European robins show this behaviour. Why might the animals make these screams?

i) To startle the predator and thereby escape - but the screams are persistent and not sudden, thereby little startling effect.

ii) To warn others of danger - other animals appear to show no response to the cries.

iii) To enlist parental aid - but adult robins scream as much as juveniles.

iv) To attract other predators, and start competition, which allows them to escape. Hogsedt found that playing recordings of "death screams" of birds attracted different predators.

FORAGING BEHAVIOUR

Robins tend to eat insects, and fruit and seeds. Lack (1948a quoted in Brooks 1988) analysed the stomach contents of thirteen robins: 74% was meat (including

adult beetles and larvae), and the remainder was fruit and seeds. These tend to be eaten more in the winter: up to 42% of stomach contents in a Spanish study (Herrara 1977 quoted in Brooks 1988).

For the capture of prey, there are a number of possible strategies: fly down from a perch to capture insects on the ground (perch hunting), or hopping on the ground looking for prey (ground foraging). Rarely is the insect caught in mid-air (fly-catching).

The time of the year and the temperature influences which strategy used. As the temperature drops, there is more ground foraging because this requires less energy (table 16).

The temperature also influences the amount of time spent foraging and number of attempts to capture prey (table 17).

When the ground is frozen, the robins will feed where the surface has been broken by other animals (eg: pheasants, moles).

TEMPERATURE(C)	GROUND FORAGING	PERCH HUNTING
0-5	63	30
6-10	43	40

(After East 1980 quoted in Brooks 1988)

Table 16 - Number of times two different foraging techniques used in winter based on temperature in Sussex study.

TEMPERATURE (C)	LENGTH OF GROUND FORAGING BOUTS	TIME BETWEEN CAPTURE ATTEMPTS
0-5	21	29
6-10	14	50

(After East 1980 quoted in Brooks 1988)

Table 17 - Median time in seconds spent in foraging in winter based on temperature in Sussex study.

MIGRATORY BEHAVIOUR

Robins are partially migratory. This means that some "races" and some birds within those "races" migrate, while others are sedentary. The robins of Britain and

Ireland that do migrate go South South-West to Iberia (Spain/Portugal). This occurs from September-October through to March-April (Roselaar 1988). Most migration occurs at night (Elphick 1995).

There are sex differences in migration. Males are more sedentary than females generally. Table 18 lists the estimates of the number of robins who were sedentary in four different studies.

STUDY	MALE	FEMALE
Enniskillen (1926)	75	36
Devon (1965)	70	33
Cambridge (1984)	77	30
Oxford (1988)	69	3

(After Harper 1988a)

Table 18 - Percentage of robins who are sedentary by sex in four different studies.

Whether the birds migrate or not depends on the local conditions, like unpredictable winters. There are three stages to the evolution of migratory behaviour in a species (Gill 1995):

i) partial migration - some of the species migrates while others do not;

ii) division - species separated into two clear groupings: migratory and non-migratory;

iii) natural selection leads to the elimination of one group.

Migration has a number of advantages and disadvantages (table 19).

ADVANTAGES	DISADVANTAGES
- find food easier	- energy needed to travel long distance
- escape cold weather	- problems of navigation
	- leaving home territory empty and other residents may move in

Table 19 - Advantages and disadvantages of migration.

As a species, robins are probably between stages 1 and 2 above. Birds build up their body mass in late summer to coincide with the "zugunruhe" behaviour (migratory restlessness) (Biebach 1983).

Experiments with robins in steel cages with magnets attached have found that they are influenced by magnetic cues (Merkel and Wiltschko 1965 quoted in Gill 1995). Magnetic cues are used by many birds to help in navigation during migration.

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