Behavioural Ecology

Sources:

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Dawkins, R. (1989) The Selfish Gene.

Subjects

1. Natural selection, ecology and behaviour
2. Testing hypotheses in behavioural ecology
3. Economic decisions on the individual level
4. Predators versus prey: Evolutionary arms races
5. Competing for resources
6. Living in Groups
7. Sexual selection and sexual conflicts
8. Parental Care and Family Conflicts
9. Mating systems
10. Cooperation
11. Communication and Signals
12. Human social behaviour in ecological environments

1. Natural selection, ecology and behaviour

Watching a bird searching in the grass for food (Starling)

Several questions:

How the bird feeds?

Why has it chosen this particular place to forage?

Why is it alone rather than in a flock?

Does it collect every item of food it encounters or is it selective for prey type or size?

What influences its decision to stop collecting and fly back to feed its chicks?

Another set of questions emerges when we follow the starling back to its nest.

Why has it chosen this site?

Why this number of chicks in the nest?

How do the two adults decide on how much food each should bring?

Are these two adults the mother and father of all the chicks?

Why are the chicks begging so noisily and jostling to be fed?

What determines how much effort the adults put into reproduction versus their own maintenance, about the factors influencing the timing of their seasonal activities, their choice of mate, the dispersal of their offspring and so on.

Behavioural ecology provides a framework for answering these kinds of questions.

Tinbergen's four 'why' questions

Niko Tinbergen (1963), one of the founders of scientific studies of animal behaviour in the wild, emphasized that there are four different ways of answering 'why' questions about behaviour.

For example, if we asked why male starlings sing in the spring, we could answer as follows:

(1) In terms of **causation**. Starlings sing because the increasing length of day triggers changes in their hormones, or because of the way air flows through the vocal apparatus and sets up membrane vibrations. These are answers about the mechanisms that cause starlings to sing, including sensory and nervous systems, hormonal mechanisms and skeletal–muscular control.

(2) In terms of **development** or **ontogeny**. For example, starlings sing because they have learned the songs from their parents and neighbours, and have a genetic disposition to learn the song of their own species. This answer is concerned with genetic and developmental mechanisms.

Tinbergen's four 'why' questions

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(3) In terms of **adaptive advantage** or **function**. Starlings sing to attract mates for breeding and so singing increases the reproductive success of males.

(4) In terms of **evolutionary history** or **phylogeny**. This answer would be about how song had evolved in starlings from their avian ancestors. The most primitive living birds make very simple sounds, so it is reasonable to assume that the complex songs of starlings and other song birds have evolved from simpler ancestral calls.

Tinbergen's four 'why' questions

Causal and developmental factors are referred to as **proximate** because they explain how a given individual comes to behave in a particular way during its lifetime.

Factors influencing adaptive advantage and evolution are called **ultimate** because they explain why and how the individual has evolved the behaviour. To make the distinction clearer, an example is discussed in detail.

Reproductive behaviour in lions

In the Serengeti National Park, Tanzania, lions (Panthera leo) live in prides consisting of between three and twelve adult females, from one to six adult males and several cubs.

Reproductive behaviour in lions

Within a pride all the females are related; they are sisters, mothers and daughters, cousins and so on. All were born and reared in the pride and all stay there to breed. Females reproduce from the age of four to eighteen years and so enjoy a long reproductive life.

Reproductive behaviour in lions

For the males, life is very different. When they are three years old, young related males (sometimes brothers) leave their natal pride. After a couple of years as nomads they attempt to take over another pride from old and weak males.

After a successful takeover they stay in the pride for two to three years before they, in turn, are driven out by new males. A male's reproductive life is therefore short.

Reproductive behaviour in lions

Lions may breed throughout the year but, although different prides may breed at different times, within a pride all the females tend to come into oestrus at about the same time. The mechanism, or **causal** explanation, is likely to be the influence of pheromones on oestrus cycles. - **proximate**

But why are lionesses designed to respond in this way?

One adaptive advantage of oestrus synchrony is that different litters in the pride are born at the same time and cubs born synchronously survive better. This is because there is communal suckling and, with all the females lactating together, a cub may suckle from another female if its mother is out hunting.

In addition, with synchronous births there is a greater chance that a young male will have a similar-aged companion when it reaches the age at which it leaves the pride. With a companion a male is more likely to achieve a successful take-over of another pride. - **ultimate**

Reproductive behaviour in lions

When a new male, or group of males, takes over a pride they sometimes kill the cubs already present.

The **causal** explanation is not known but it may be the unfamiliar odour of the cubs that induces the male to attack them.

But, whatever the mechanism, why are male lions designed to respond in this way?

Reproductive behaviour in lions

The benefit of infanticide for the male that takes over the pride is that killing the cubs fathered by a previous male brings the female into reproductive condition again much more quickly.

This hastens the day that he can father his own offspring. If the cubs were left intact then the female would not come into oestrus again for 25 months.

By killing the cubs the male makes her ready for mating after only nine months.

Remember that a male's reproductive life in the pride is short, so any individual that practises infanticide when he takes over a pride will father more of his own offspring and, therefore, the tendency to commit infanticide will spread by natural selection.

The take-over of a pride by a new coalition of adult males also contributes to the reproductive synchrony of the females; because all the dependent offspring are either killed or evicted during the take-over, the females will all tend to come into oestrus again at about the same time.

The females play an active role in soliciting copulations from several males and this appears to elicit competition between different male coalitions for the control of the pride, with the result that larger coalitions eventually become resident.

High sexual activity in females at around the time of take-overs may therefore incite male–male competition and so result in the best protectors taking over the pride

Observation	Causal explanations	Functional explanations
1 Females are synchronous in oestrus	Chemical cues? Take-overs by males	Better cub survival Young males survive better and have greater reproductive success when they leave pride if in a group
2 Young die when new males take over pride	Abortion Take-over males kill or evict young	Females come into oestrus more quickly Male removes older cubs which would compete with his young

Table 1.1 Summary of causal and functional explanations for two aspects of reproductive behaviour in lions (Bertram, 1975; Packer and Pusey, 1983a, 1983b).

Natural selection

The aim of behavioural ecology is to try and understand how an animal's behaviour is adapted to the environment in which it lives.

When we discuss adaptations we are referring to changes brought about during evolution by the process of natural selection.

Darwin theory of natural selection can be summarized as follows:

(1) Individuals within a species differ in their morphology, physiology and behaviour (**variation***).*

(2) Some of this variation is **heritable***;* on average offspring tend to resemble their parents more than other individuals in the population.

(3) Organisms have a huge capacity for increase in numbers; they produce far more offspring than give rise to breeding individuals. This capacity is not realized because the number of individuals within a population tends to remain more or less constant over time. Therefore, there must be **competition** between individuals for scarce resources, such as food, mates and places to live.

(4) As a result of this competition, some variants will leave more offspring than others.

These will be those that are best at competing for the scarce resources. Their offspring

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(4) As a result of this competition, some variants will leave more offspring than others. These will be those that are best at competing for the scarce resources. Their offspring will inherit the characteristics of their successful parents and so, through **natural selection** over the generations, organisms will come to be **adapted** to their environment. The individuals that are selected, naturally, will be those best able to find food and mates, avoid predators and so on.

(5) If the environment changes, then new variants may do best and so natural selection can lead to **evolutionary change**.

Darwin's theory in modern genetic terms as follows:

(1) All organisms have genes which code for proteins. These proteins regulate the development of the nervous system, muscles and structure of the individual, and so influence its behaviour.

(2) Within a population many genes are present in two or more forms, or alleles, which code for slightly different forms of the same protein or determine when, where and how much of the protein is expressed. These will cause differences in development and function, and so there will be variation within a population.

(3) Any allele that results in more surviving copies of itself than its alternative will eventually replace the alternative form in the population. Natural selection is the differential survival of alternative alleles through their effects on replication success.

The individual can be regarded as a temporary vehicle or survival machine by which genes survive and replicate (Dawkins, The Selfish Gene). Because selection of genes is mediated through phenotypes, the most successful genes will usually be those that are most effective in enhancing an individual's survival and reproductive success.

Genes and behaviour

Behavioural differences may have a genetic basis

Natural selection can only work on genetic differences, so for behaviour to evolve:

(a) there must be, or must have been in the past, behavioural alternatives in the population;

(b) the differences must be, or must have been, heritable; in other words a proportion of the variation must be genetic in origin;

(c) some behavioural alternatives must confer greater reproductive success than others.

Genes work in concert and many genes together will influence an individual's mating preference, foraging, migration and so on.

Behavioural development is an outcome of a complex interaction between genes and environment.

Genes and behaviour

Drosophila courtship song

Single gene differences can also cause differences in Drosophila courtship song. Males produce a courtship song by vibrating their wings and the temporal pattern of the song varies between species. Breeding experiments and molecular genetic analysis reveal that these differences in song structure are caused by differences in the period gene.

Transfer of a small piece of the period gene from D. simulans to D. melanogaster causes melanogaster males to produce the simulans song rather than melanogaster song

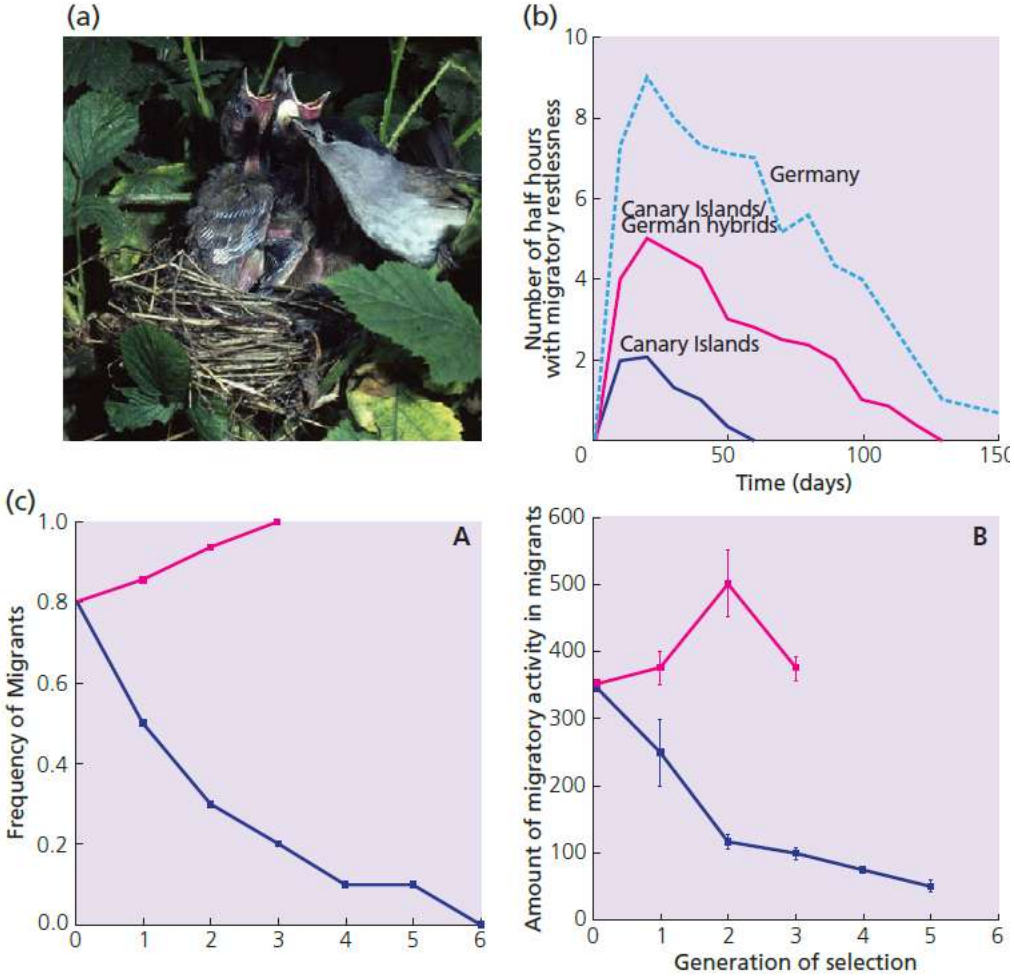
Genes and behaviour

Blackcaps: migratory behaviour

Most species of warblers are summer visitors to Europe. If individuals are kept in a cage, they show a period of restlessness' in the autumn at the time they would migrate south to the Mediterranean or beyond to Africa.

Populations in southern Germany are highly migratory while those in the Canary Islands are sedentary.

When birds from these two populations were cross-bred in aviaries, their offspring showed intermediate migratory restlessness, suggesting genetic control



In the Rhone Valley of southern France, three-quarters showed migratory restlessness while one quarter did not. By selectively breeding from either migratory or non-migratory parents, lines of blackcaps were produced that were either 100% migratory (in three generations) or 100% resident (in six generations)

Genes and behaviour

Blackcaps: migratory behaviour

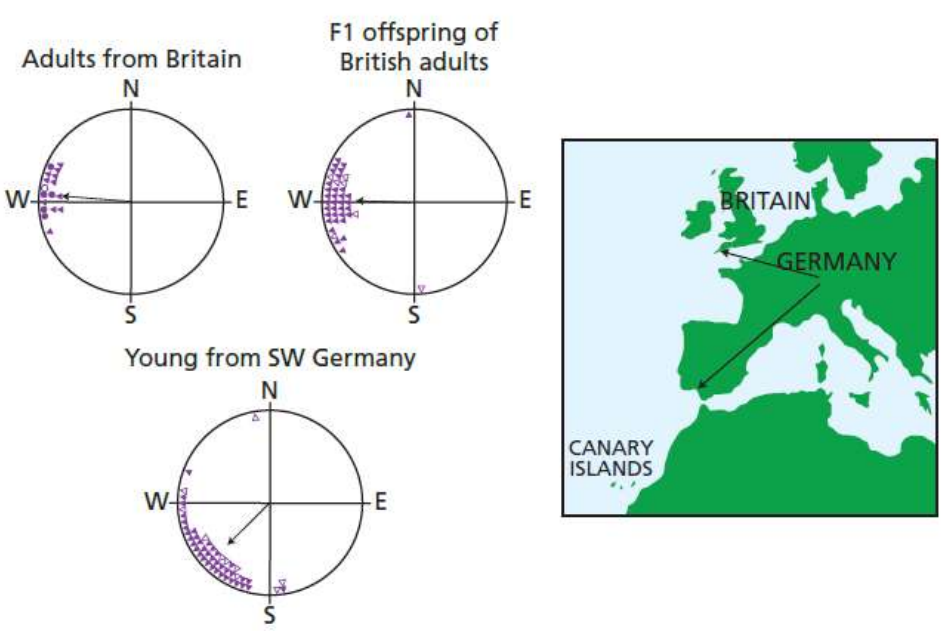
Central European populations of blackcaps traditionally winter to the southwest of their breeding grounds in the western Mediterranean.

During the past 40 years, however, the number of blackcaps wintering in Britain and Ireland has steadily increased.

Ringing recoveries indicated that they were breeders from central Europe with an entirely new migration habit.

Blackcaps wintering in Britain were caught and kept in aviaries. When their migration behaviour was tested in cages, they exhibited a westerly autumn migration direction, shifted 70° from the traditional south-westerly route.

Furthermore, their offspring inherited this new autumnal orientation.



The new migration direction is probably being favoured because of milder winters and more winter food in Britain, both from garden feeders and winter fruit bushes planted in recent decades.

This new population of migrants enjoys a shorter distance to winter quarters and an earlier arrival back in the central European breeding grounds in spring.

Selfish individuals or group advantage?

Not so long ago, however, many people thought that animals behaved for the good of the group, or of the species. It was common to read (and sometimes still is) explanations like, ‘lions rarely fight to the death because, if they did so, this would endanger survival of the species’ or, ‘salmon migrate thousands of miles from the open ocean into a small stream where they spawn and die, killing themselves with exhaustion to ensure survival of the species’.

Because ‘group thinking’ is so easy to adopt, it is worth going into a little detail to examine why it is the wrong way to think about the evolution of behaviour.

The most famous proponent of the idea that animals behave for the good of the group was V.C. Wynne-Edwards. He suggested that if a population over-exploited its food resources it would go extinct, and so adaptations have evolved to ensure that each group or species controls its rate of consumption. He proposed that individuals restrict their birth rate to prevent over-population, by producing fewer young, not breeding every year, delaying the onset of breeding and so on. This is an attractive idea because it is what humans ought to do to control their own populations. However, there are two reasons for thinking that it is unlikely to work for animal populations.

Selfish individuals or group advantage?

Imagine a species of bird in which a female lays two eggs and there is no over-exploitation of the food resources. Suppose the tendency to lay two eggs is inherited.

Now consider a mutant that lays three eggs. Since the population is not over-exploiting its food supplies, there will be plenty of food for the young and because the three-egg genotype produces 50% more offspring it will rapidly increase at the expense of the two-egg genotype.

Will the three-egg type be replaced by birds that lay four eggs? The answer is yes, as long as individuals laying more eggs produce more surviving young. Eventually a point will be reached where the brood is so large that the parents cannot look after it as efficiently as a smaller one.

The clutch size we would expect to see in nature will be the one that results in the most surviving young because natural selection will favour individuals that do the best.

A system of voluntary birth control for the good of the group will not evolve because it is unstable; there is nothing to stop individuals behaving in their own selfish interests.

Selfish individuals or group advantage?

‘Group selection’ can work, but it would require that groups are selected during evolution, with some groups dying out faster than others. Individuals will nearly always die at a faster rate than groups, so individual selection will be more powerful.

In addition, for group selection to work populations must be isolated, such that individuals cannot successfully migrate between them. Otherwise there would be nothing to stop the migration of selfish individuals into a population of individuals all practising reproductive restraint. Once selfish individuals arrive, their genotype would soon spread.

Empirical studies: optimal clutch size

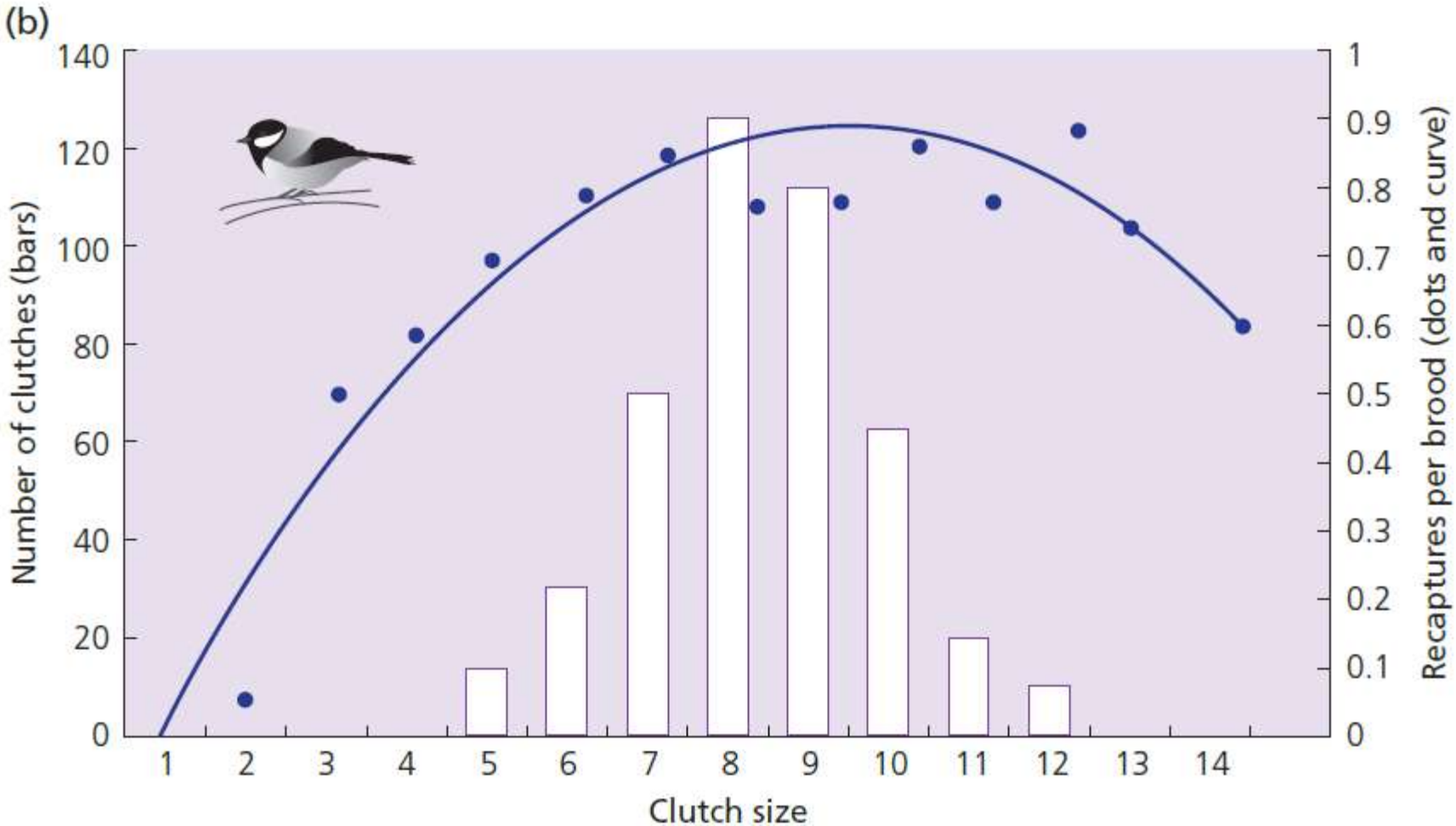
There is good field evidence that individuals do not restrict their birth rate for the good of the group but rather maximize their individual reproductive success.

Clutch size in great tits

The great tits nest in boxes and lay a single clutch of eggs in the spring. (Wytham Woods, near Oxford, UK, started in 1947)

Empirical studies: optimal clutch size

Most pairs lay 8–9 eggs. The limit is not set by an incubation constraint because when more eggs are added the pair can still incubate them successfully.



Empirical studies: optimal clutch size

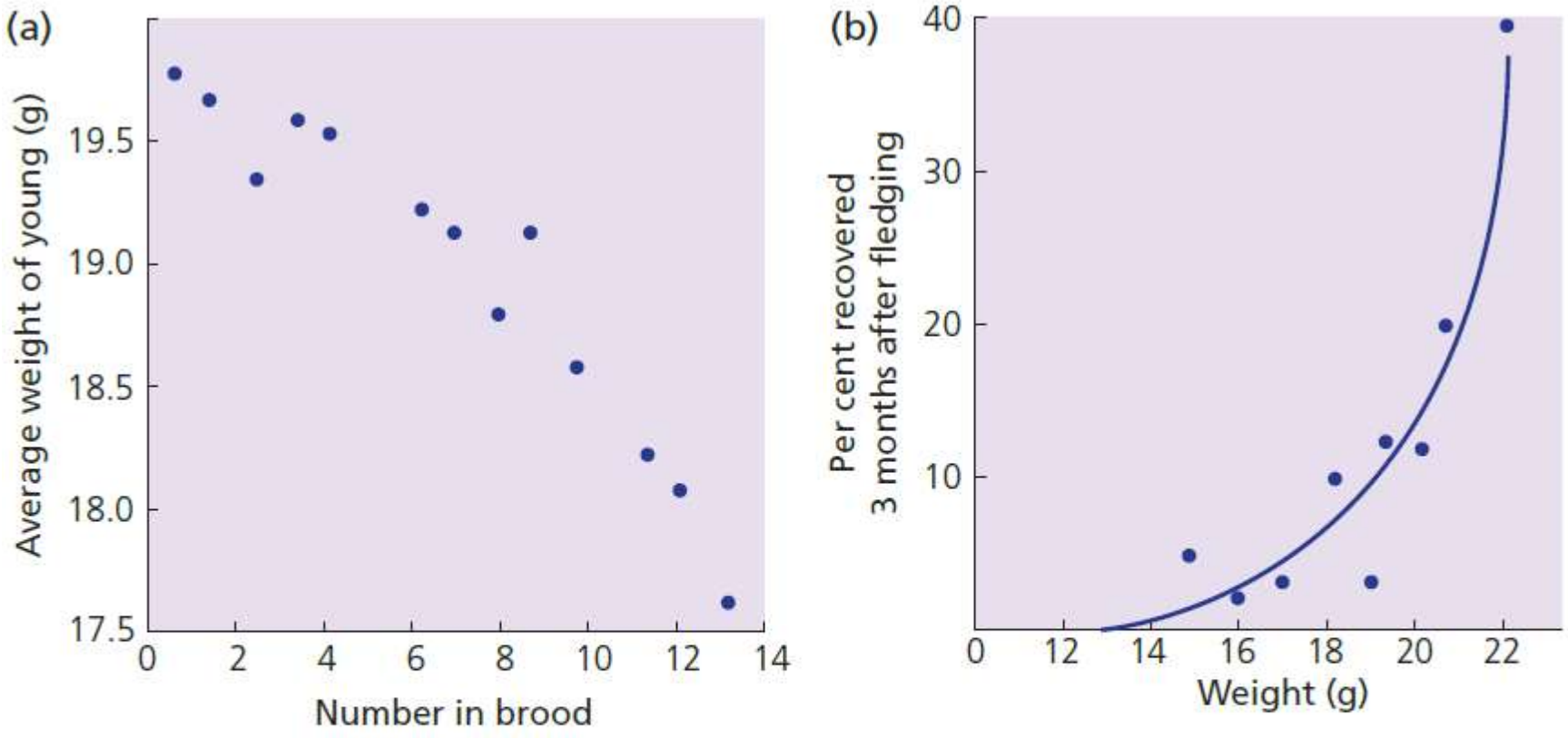


Fig. 1.6 Experimental manipulation of brood sizes in great tits. (a) In larger broods of great tits the young weigh less at fledging because the parents cannot feed them so efficiently. (b) The weight of a nestling at fledging determines its chances of survival; heavier chicks survive better. From Perrins (1965).

Empirical studies: optimal clutch size

By creating broods of different sizes experimentally and allocating them at random to different nests, it was demonstrated that there is an optimum to maximize the number of surviving young per brood from a selfish individual's point of view.

The most commonly observed clutch size is close to the predicted optimum but slightly lower.

Why is this?

One hypothesis is that the optimum is the one which maximizes the number of surviving young per brood whereas, at least in stable populations, we would expect natural selection to design animals to maximize their lifetime reproductive output. If increased brood sizes are costly to adult survival, and hence chances of further reproduction, then the clutch size which maximizes lifetime breeding success will be slightly less than that which maximizes success per breeding attempt.

Empirical studies: optimal clutch size

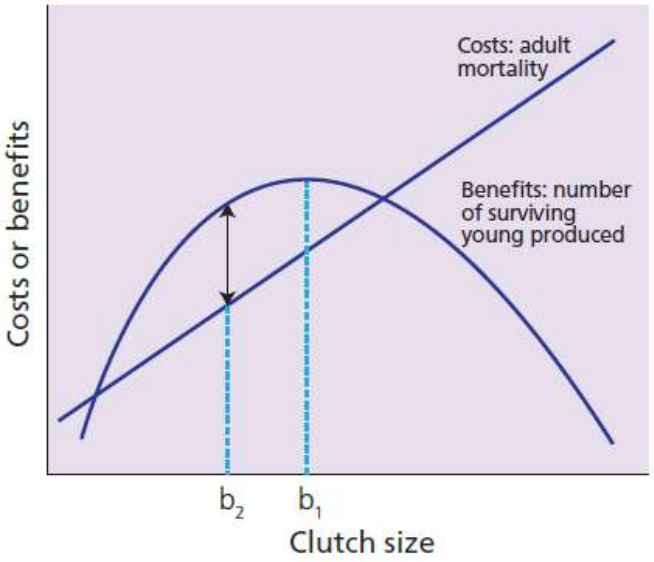
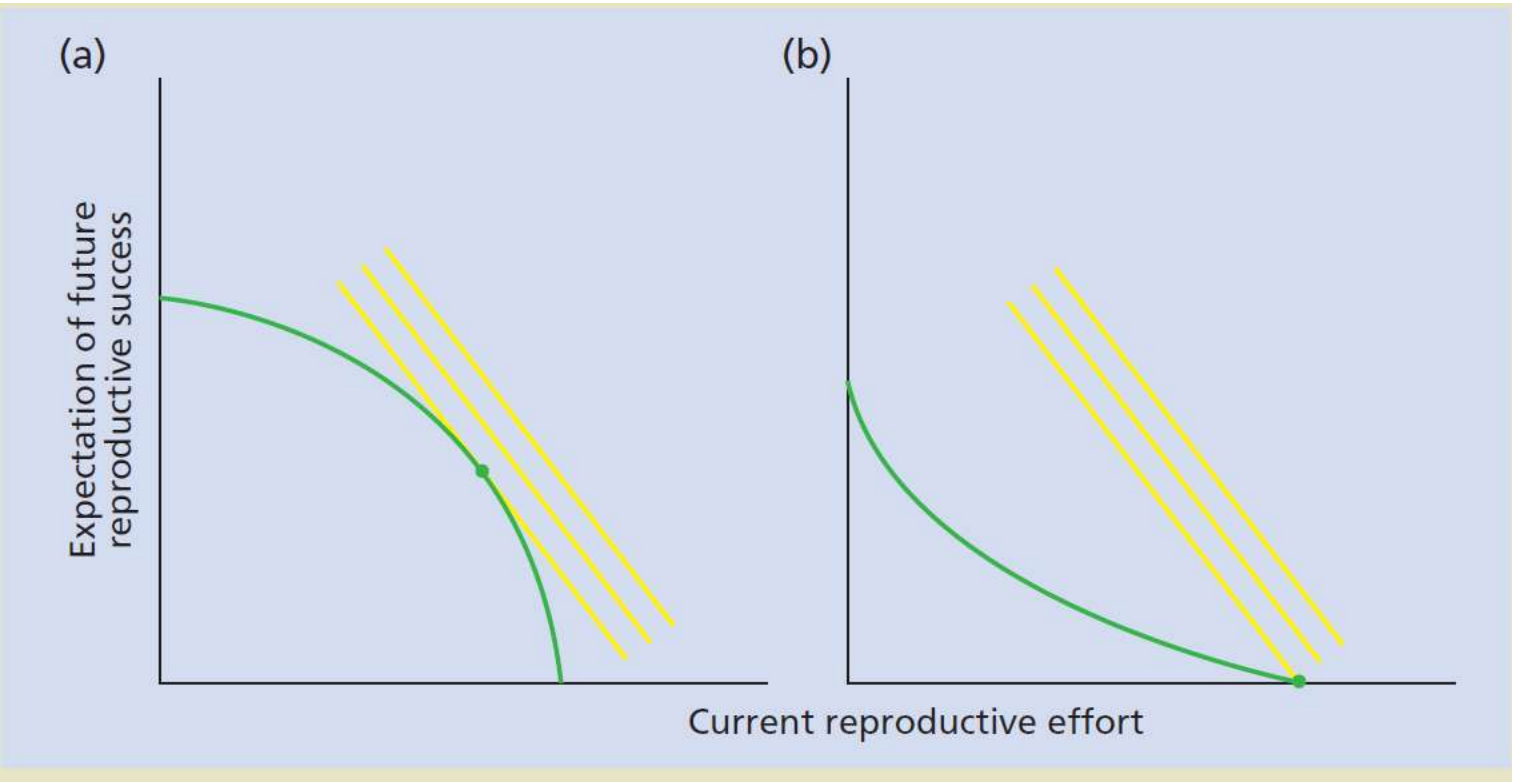


Fig. 1.7 The influence of adult mortality on the optimal clutch size. The number of young produced versus clutch size follows a curve, as in Fig. 1.5, with b_1 being the clutch size which maximizes the number of young produced per brood. Increased clutch size, however, has the cost of increased adult mortality, shown here for simplicity as a straight line. The clutch size which maximizes lifetime reproductive success is b_2, where the distance between the benefit and cost curves is a maximum. This is less than the clutch size b_1, which maximizes reproductive success per brood. From Charnov and Krebs (1974).

The optimal trade-off between survival and reproductive effort

When the trade-off curve is convex (a), fitness is maximized by allocating part of the resources to current reproduction and part to survival (i.e. iteroparity, or repeated breeding).

When the curve is concave (b), it is best to allocate all resources to current reproduction, even at the expense of own survival (semelparity, or ‘big bang’ suicidal reproduction).



families of straight lines (yellow) represent fitness isoclines, that is equal lifetime production of offspring

Empirical studies: optimal clutch size Difference among individuals

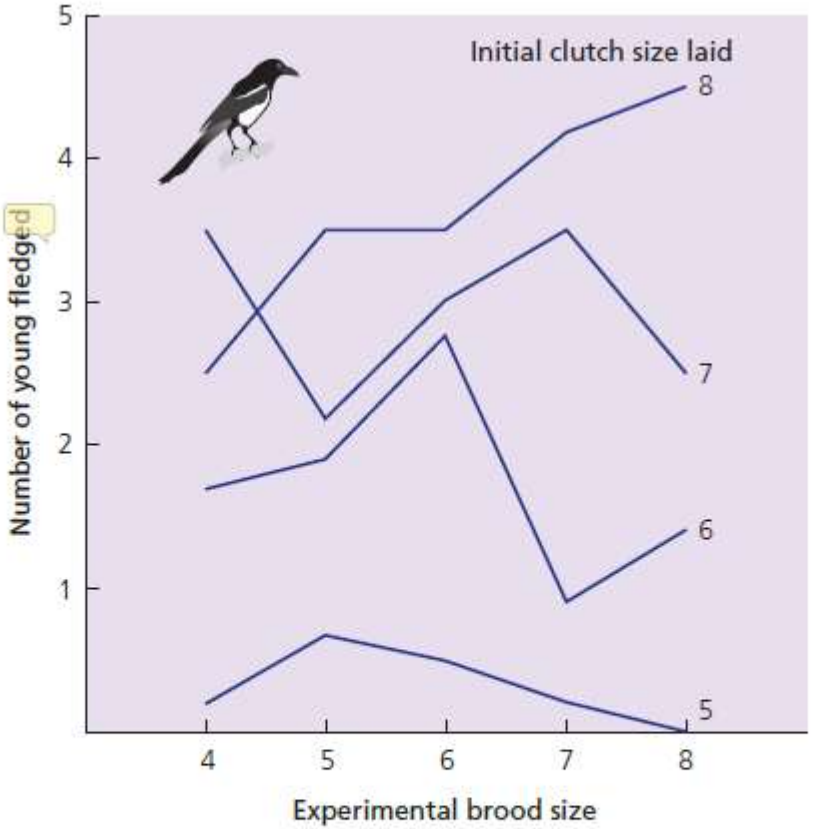


Fig. 1.9 Experiments on clutch size in magpies. Pairs that had initially laid 5, 6, 7 or 8 eggs were given experimentally reduced or enlarged broods. Pairs that had naturally laid large clutches did better with large broods and those naturally laying small clutches did better with small broods. From Högstedt (1980). Reprinted with permission from AAAS.

Phenotypic plasticity

The ability of a single genotype to alter its phenotype in response to environmental conditions is termed phenotypic plasticity

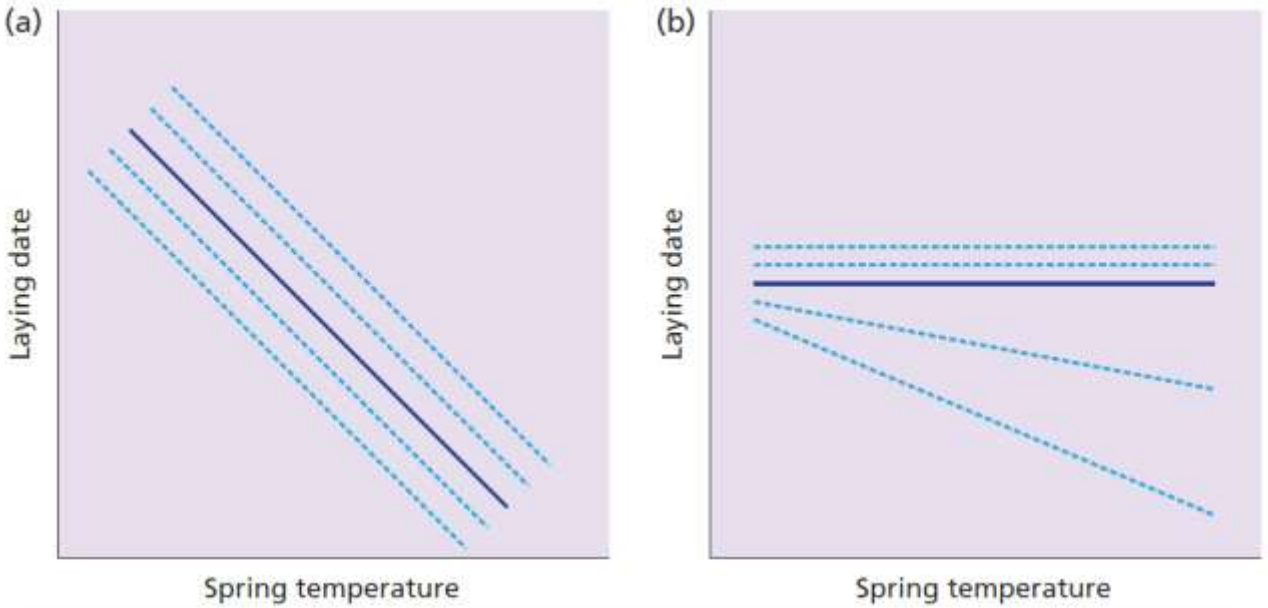


Fig. 1.10 Phenotypic plasticity in laying dates in response to spring temperatures. Dashed lines represent examples of reaction norms for different individual females, who may differ in their average laying date (elevation) or in their plasticity in response to spring temperatures (slope). In Wytham Woods, UK, the great tits respond as in (a), with no significant variation between females in plasticity and a strong average population response to temperature (solid line). In the Hoge Veluwe, The Netherlands, the great tits respond as in (b), with no significant average population response (solid line) but significant variation in individual female plasticity. After Charmantier *et al.* (2008). Reprinted with permission from AAAS.

Phenotypic plasticity

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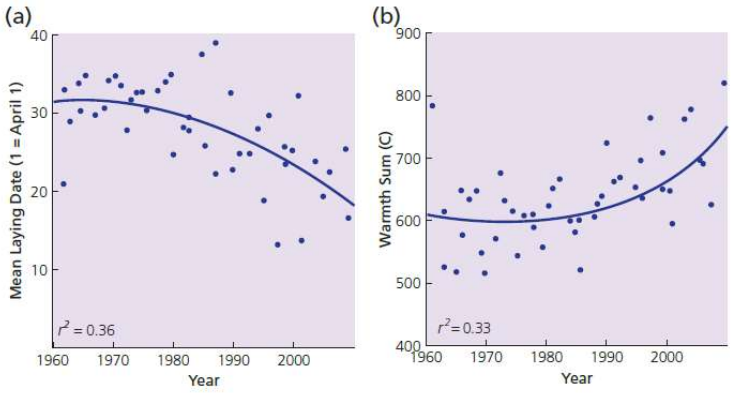
Dates of laying eggs and spring temperature

- How they managed? (proximate)



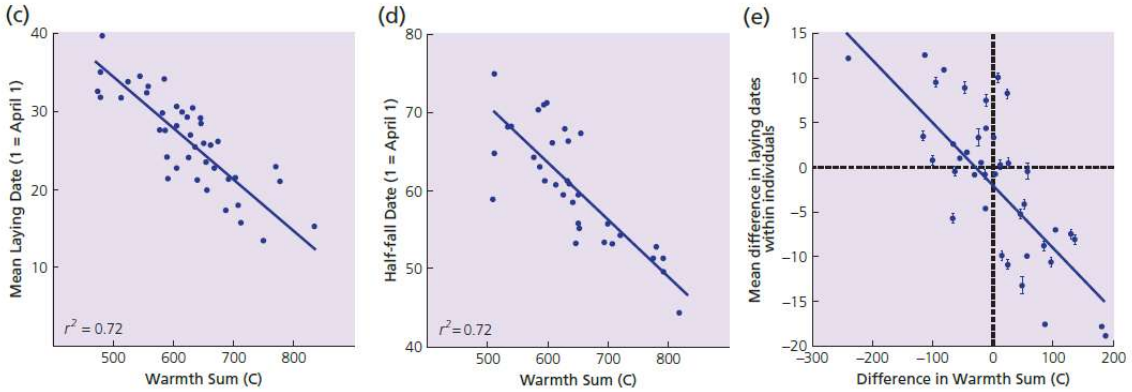
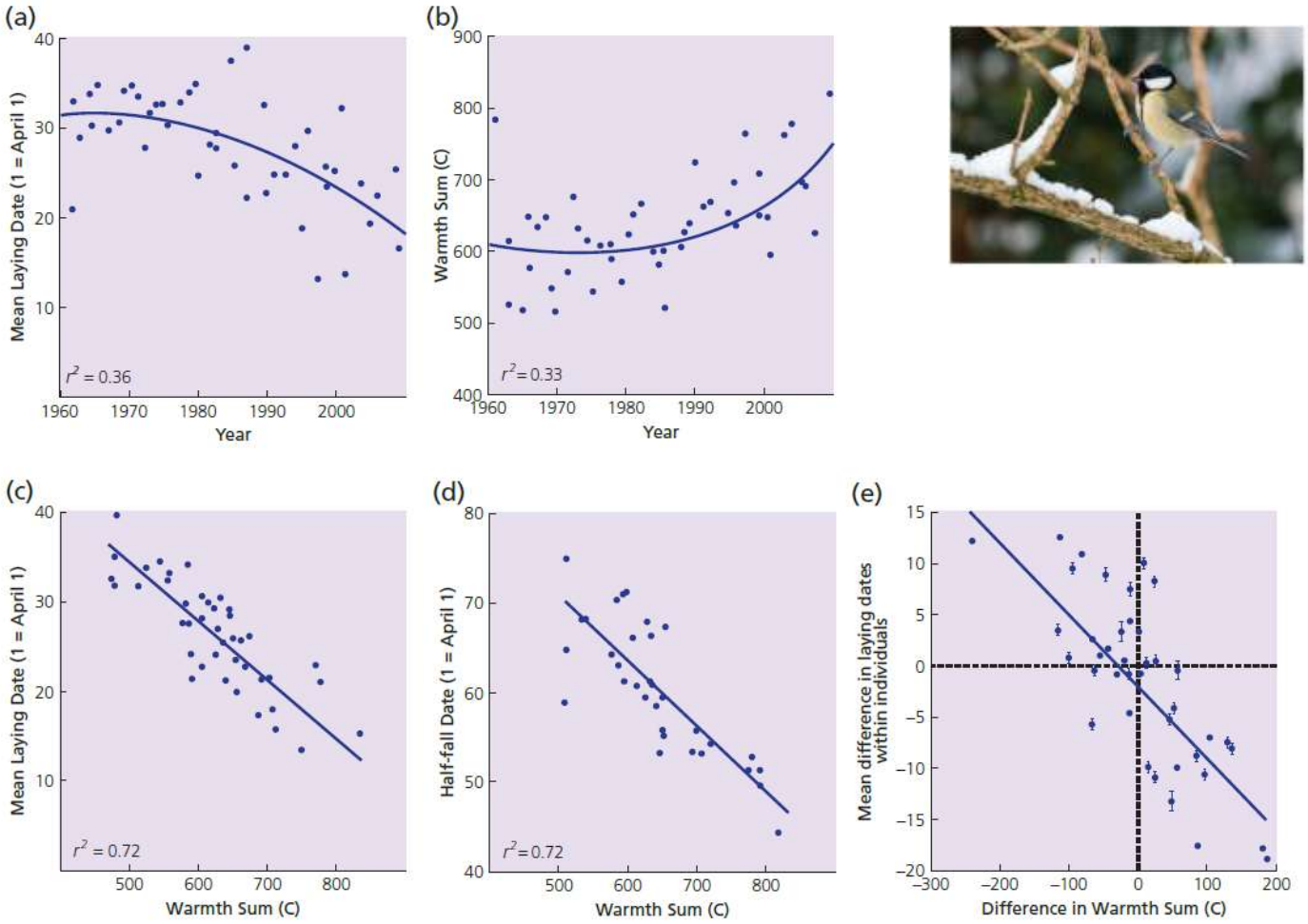


Fig. 1.11 (a) In Wytham Woods, UK, the mean laying date of great tits has become earlier, especially since the mid 1970s. (b) Spring temperatures have also increased, as measured by 'Warmth Sum', which is the sum of daily maximum temperatures between 1 March and 25 April (the pre-laying period). The rates of change in mean egg laying date with temperature (c) and caterpillar emergence with temperature (d) are similar. (e) Phenotypic plasticity in response of individual female great tits, measured as their difference in laying date in successive years plotted against the difference in spring warmth in the same pair of years. Figures a-e from Charmantier *et al* (2008). Reprinted with permission from AAAS. (f) Female great tit. Photo © Thor Veen. (g) Winter moth caterpillar on oak. Photo © Jane Carpenter.

Genetic change or phenotypic plasticity?



In UK, phenotypic plasticity explain the change, flourishing population

In Netherland (NL), no change in the tits' egg laying date. Female lifetime reproductive success has declined over the study period. The last three decades there has been little change in early spring temperatures (NL)

Importance of both proximate and both ultimate mechanisms

Fig. 1.11 (a) In Wytham Woods, UK, the mean laying date of great tits has become earlier, especially since the mid 1970s. (b) Spring temperatures have also increased, as measured by 'Warmth Sum', which is the sum of daily maximum temperatures between 1 March and 25 April (the pre-laying period). The rates of change in mean egg laying date with temperature (c) and caterpillar emergence with temperature (d) are similar. (e) Phenotypic plasticity in response of individual female great tits, measured as their difference in laying date in successive years plotted against the difference in spring warmth in the same pair of years. Figures a-e from Charmantier *et al* (2008). Reprinted with permission from AAAS. (f) Female great tit. Photo © Thor Veen. (g) Winter moth caterpillar on oak. Photo © Jane Carpenter.

Behaviour, ecology and evolution

During evolution natural selection will favour individuals who adopt life history strategies that maximize their gene contribution to future generations

Individual's success at survival and reproduction depends critically on its behaviour, selection will tend to design individuals to be efficient at foraging, avoiding predators, finding mates, parental care and so on

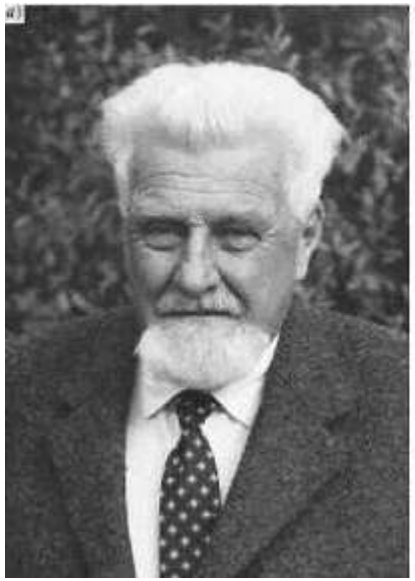
Resources are limited, so there will always be trade-offs involved, both within and between these various activities

Individuals are likely to have to compete with others for scarce resources

Ecological conditions influence how individuals behave

Founders of Behavioural Sciences

- Nobel prise 1973 in Physiology or Medicine for their studies of animal behavior and for being “the most eminent founders of a new science, called ‘the comparative study of behaviour’ or ‘ethology’ ”



Konrad Lorenz

1903-1989

Studies of animal behaviour by means of comparative zoological methods

Niko Tinbergen

1907-1988

Revitalizing the science of ethology

Karl von Frisch

1886-1982

Studies of communication among bees

2. Testing hypotheses in behavioural ecology

Testing Hypotheses in Behavioural Ecology

Scientific approach to the function of behaviour involves four stages: observations, hypotheses, predictions and tests

Three methods of hypothesis testing:

- Comparison between individuals within a species
- Experiments
- Comparison among species

Breeding behaviour of gulls in relation to predation risk

Breeding behaviour of gulls in relation to predation risk - **comparison among species**

Most species of gulls nest on the ground, where their eggs and chicks are vulnerable to predation by mammals and by birds

The camouflage of the nest by refraining from defecation nearby and, soon after hatching, they remove the empty eggshells, which have white interiors likely to attract predators

How might we test our hypothesis that these traits have evolved in response to predation?

- A comparison with the breeding traits of a ground-nesting gull and cliff-nesting gull (kittiwake). Kittiwake nests are safer from mammalian
- predators, who cannot so easily climb down steep cliffs, and they are also safer from avian predators

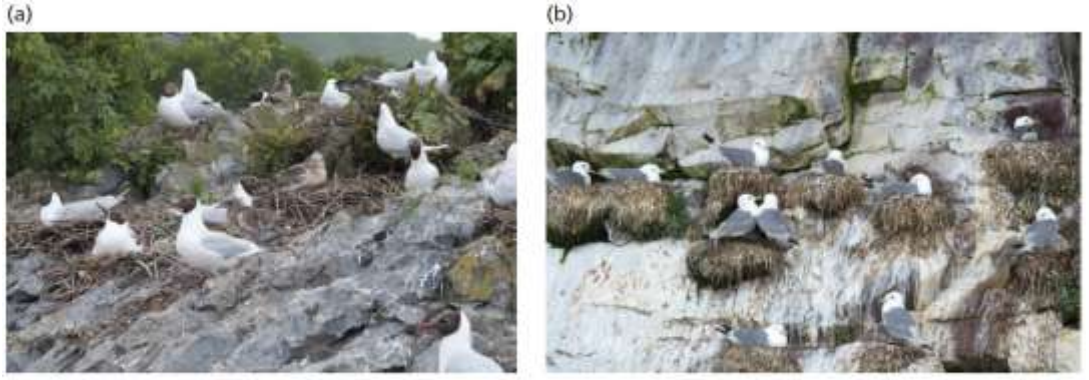


Fig. 2.1 (a) The black-headed gull nests on the ground. Photo © osf.co.uk. All rights reserved. (b) The kittiwake nests on tiny ledges on steep cliffs. Photo © iStockphoto.com/Liz Leyden.

Breeding behaviour of gulls in relation to predation risk

The different traits of black-headed gulls and kittiwakes, provide strong support for our hypothesis that these various suites of behaviour have evolved as adaptations in response to predation differences between the two sites

Traits	Black-headed gull	Kittiwake
Nest site	On ground	On ledge on steep cliffs
Predation risk to nest	High	Low
Adult response to predators	Take flight early; alarm calls, attack predator	Remain on nest until predator close; rarely alarm, weak attack
Nest construction	Loosely built, shallow cup	Elaborate, deep cup
Nest concealment	Adults do not defecate near nest	Adults defecate near nest
	Adults remove eggshells	Adults do not remove eggshells
Chick behaviour	Cryptic colouration (brown with black markings) and behaviour (crouch or hides in vegetation)	Not cryptic (white and grey) and ignores disturbance.
	Weaker claws	Strong claws and muscles for clinging
	Leaves nest after a few days	Remains in nest until can fly (about six weeks)
	Runs off when attacked	Does not run off
	Vigorous wing flapping and jumping during development	Less vigorous movements
Chick recognition by parents	Within a few days	Not until about five weeks, just before young fledge
Chick feeding	Parents give food calls to attract hidden young	No parent food calls
	Adults often regurgitate food onto ground	Adults pass food directly to young's bill

Table 2.1 Comparison of breeding traits of two gulls: the ground-nesting black-headed gull *Larus ridibundus* and the cliff-nesting kittiwake *Rissa tridactyla* (Cullen, 1957).

Social organization of weaver birds

90 species of weaver birds (Ploceinae) studied, small sparrow-like birds which live throughout Africa and Asia (Crook 1964).

Some are solitary, some go around in large flocks. Some build cryptic nests in large defended territories while others cluster their nests together in colonies.

Some are monogamous, with a male and a female forming a permanent pair bond; others are polygamous, the males mating with several females and contributing little to care of the offspring.

How can we explain the evolution of this great diversity in behaviour?

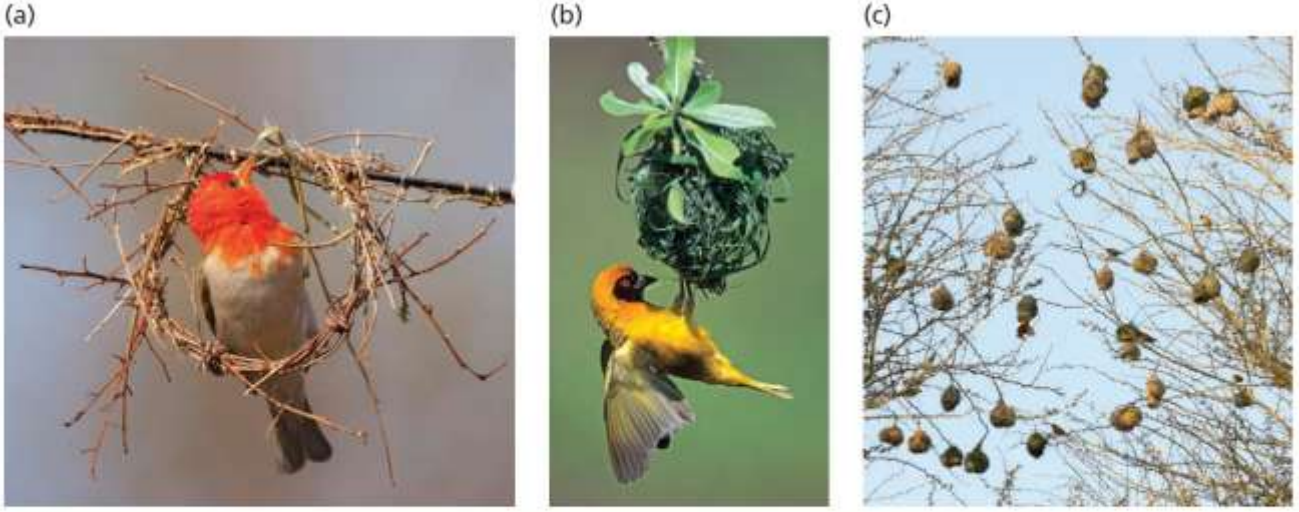


Fig. 2.2 Differences in social organization in weaver birds. (a) Red-headed weaver *Anaplectes melanotis*; a woodland insectivore which often breeds in monogamous pairs on dispersed territories. (b) Southern masked weaver *Ploceus vellatus*; a savannah seed-eater which nests in colonies and is polygynous. (c) Village weaver *Ploceus cucullatus*, another colonial, polygynous savannah species. All photos © Warwick Tarboton.

Social organization of weaver birds

		Number of species in each category				
		Pair bond		Sociality		
Habitat	Main food	Monogamous	Polygynous	Solitary	Grouped territories	Colonial
Forest	Insects	17	0	17	0	1
Savannah	Insects	5	1	4	0	2
Forest	Insects + seeds	3	0	2	0	1
Savannah	Insects + seeds	1	7	1	0	7
Grassland	Insects + seeds	1	1	1	0	1
Savannah	Seeds	2	11	0	1	16
Grassland	Seeds	0	15	0	13	3

Table 2.2 Social organization of weaver bird species (Ploceinae) in relation to habitat and diet (Crook, 1964; Lack, 1968).

Predation and food dispersion are key selective forces

Comparative approach to primate ecology and behaviour

Primates vary in their social organization

There are solitary insectivores, like tarsiers, which live in forests and are nocturnal.

There are diurnal forest monkeys, like colobus monkeys, which go around in small groups, feeding on leaves or fruit.

Other monkeys, like baboons, are terrestrial and live in large troupes of 50 or several hundred individuals.

Among the apes, the orang-utan is solitary, the gibbon lives in pairs and small family units, while the chimpanzee may live in bands of 50.

Fig. 2.4 Differences in social organization in primates. (a) A solitary insectivorous tarsier. Photo © iStockphoto.com/ Holger Mette. (b) A small group of black and white colobus monkeys, which eat leaves in the forest. Photo © iStockphoto.com/ Henk Bentlage. (c) A large group of gelada baboons, which feed on the ground on grass leaves and roots. Photo © iStockphoto.com/ Guenter Guni.

Comparative approach to primate ecology and behaviour

Home range size - Variation with weight and diet

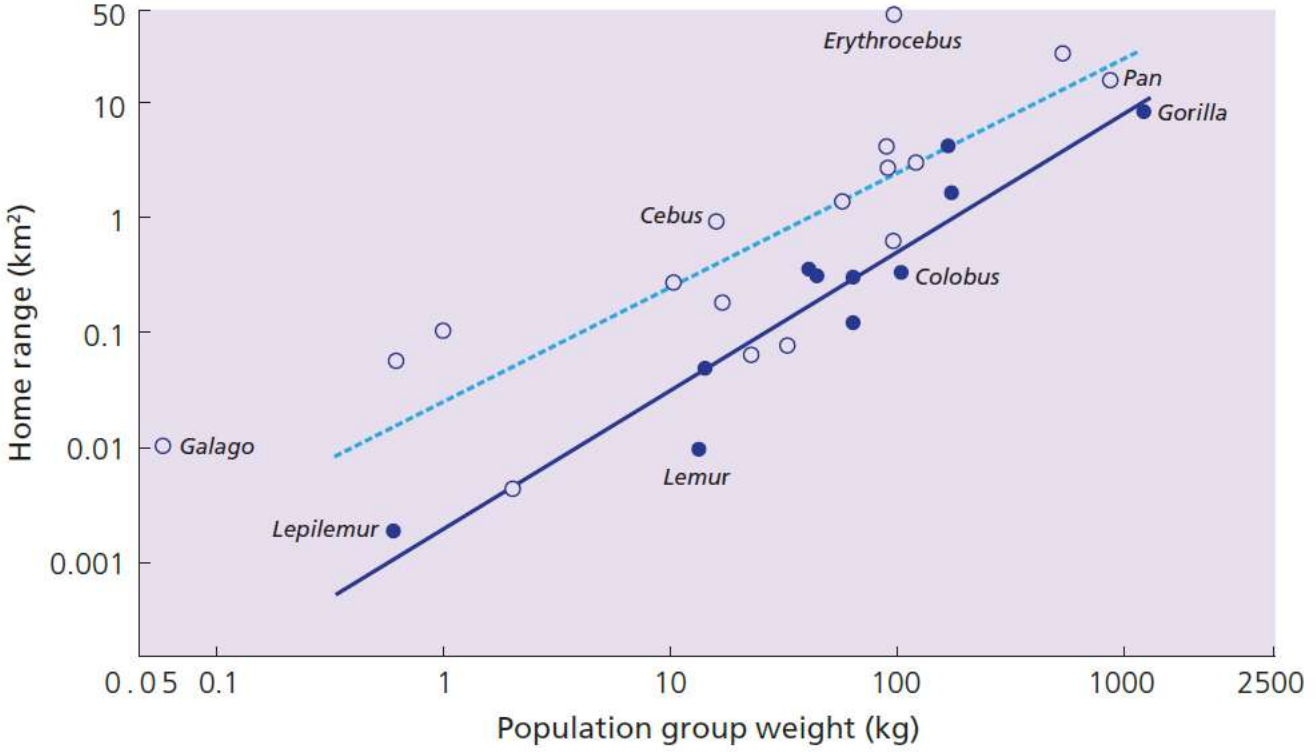


Fig. 2.5 Home range size plotted against the weight of the group that inhabits the home range for different genera of primates. The solid circles are folivores, through which there is a solid regression line. The open circles are specialist feeders (insectivores or frugivores) and the regression line through these points is dashed. Some of the genera are indicated by name. From Clutton-Brock and Harvey (1977).

Comparative approach to primate ecology and behaviour

Sexual dimorphism evolves from sexual competition

- Sexual dimorphism in body weight
  - sexual competition hypothesis; the more females per male in the breeding group, the larger the male is in relation to the female

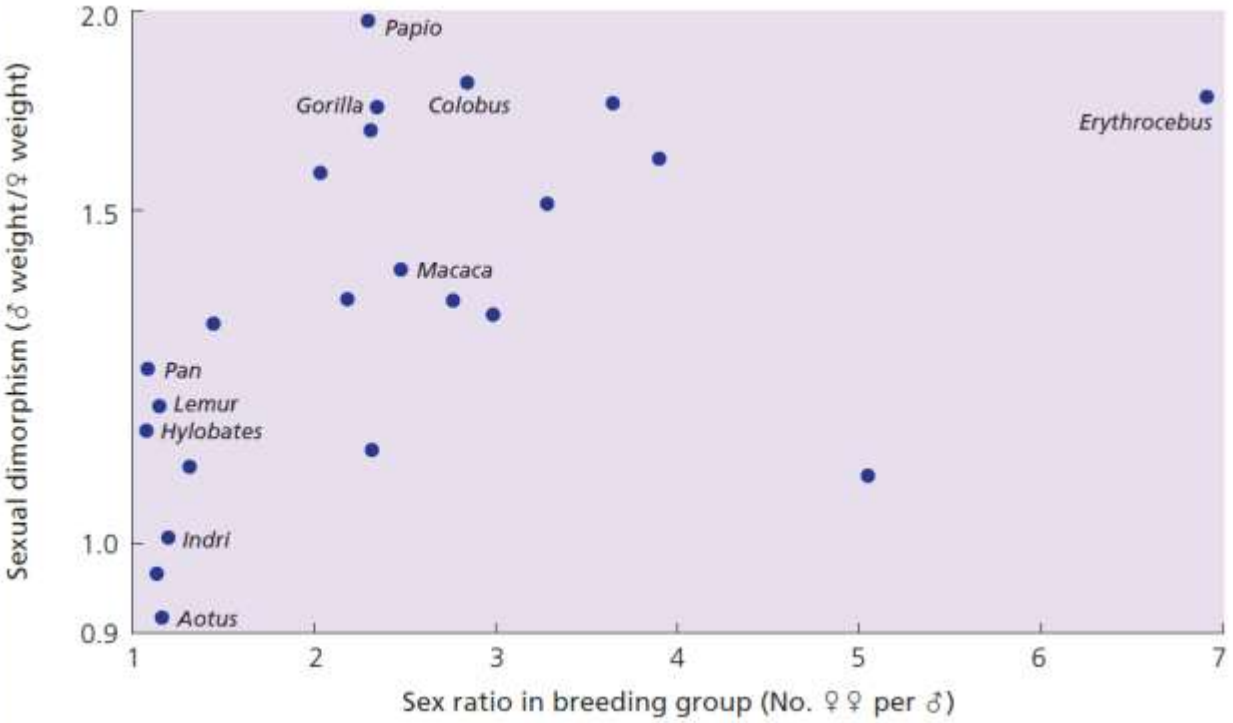


Fig. 2.6 The degree of sexual dimorphism increases with the number of females per male in the breeding group. Each point is a different genus, some of which are indicated by name. From Clutton-Brock and Harvey (1977).

- Sexual dimorphism in tooth size
  - in monogamous species male tooth size is as expected for a female of equivalent body weight. However, it is larger than expected in harem-forming species.
  - predation pressure may have been responsible for the evolution of larger teeth in terrestrial species

Comparative approach to primate ecology and behaviour

Testis size and breeding system

Larger testes in multimale groups

- The heaviest primates, the gorilla (Gorilla gorilla) and orang-utan (Pongo pygmaeus) have breeding systems that involve one male monopolizing mating with several females, and have testes that weigh 30 and 35 g, respectively (average weight of both testes).
- The smaller chimpanzee (Pan troglodytes), by contrast, has a breeding system where several males copulate with each oestrus female and this species has testes weighing 120 g.

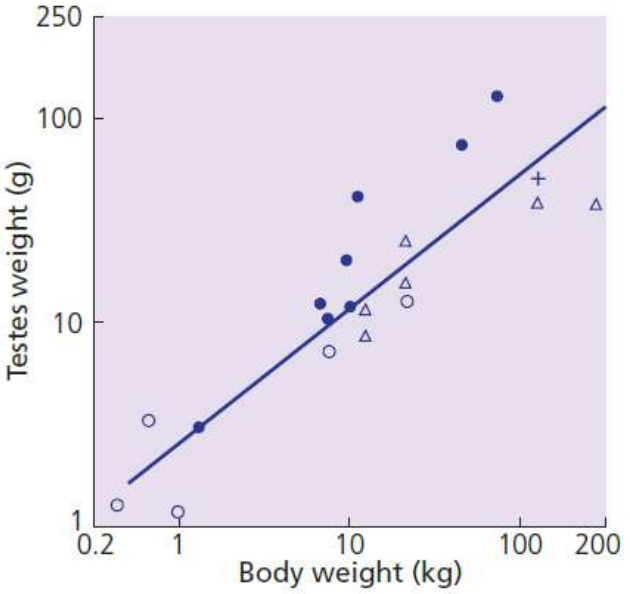


Fig. 2.7 Log combined testes weight (g) versus body weight (kg) for different primate genera. Solid circles are multimale breeding systems. Open circles are monogamous. Open triangles are single-male systems (one male with several females). The cross is our own species, *Homo*, for comparison. From Harcourt *et al.* (1981). Reprinted with permission from the Nature Publishing Group.

Using phylogenies in comparative analysis

- Statistical testing of hypotheses requires that data points are independent
- Species may be similar through common descent – need to estimate ancestral states

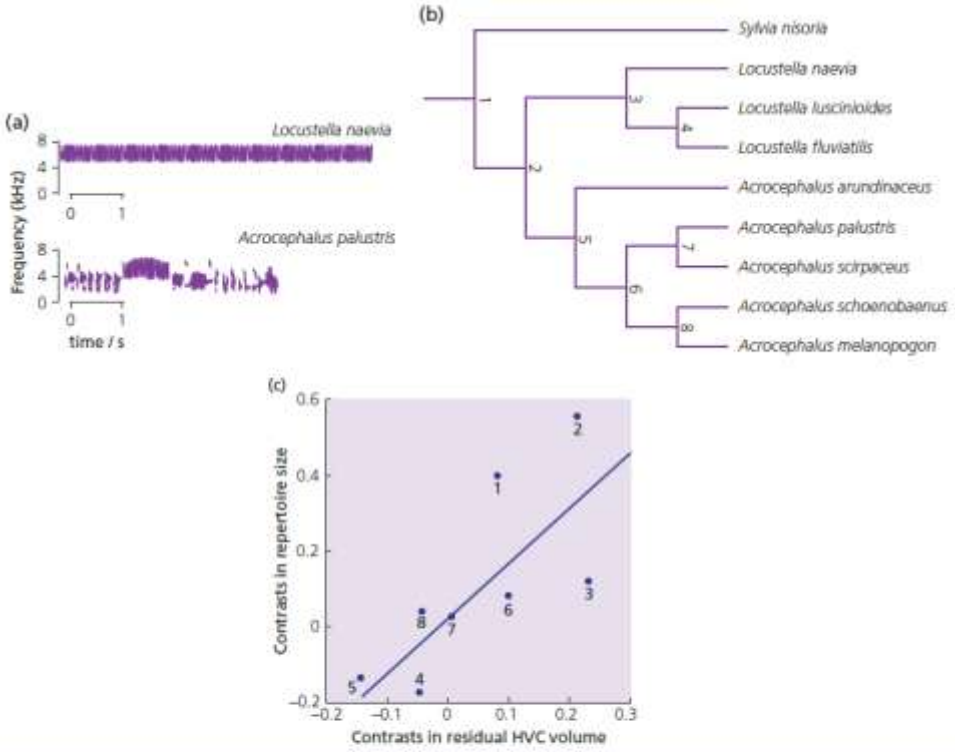


Fig. 2.9 Song complexity and brain anatomy in European warblers (family Sylviidae) from the genus *Acrocephalus* and *Locustella*. (a) Some species, like the grasshopper warbler *L. naevia*, have very simple songs (in this species, one syllable is repeated). Others, like the marsh warbler *A. palustris*, have a complex song with up to a hundred different syllable types in their repertoire. (b) Phylogeny of the *Acrocephalus* and *Locustella* warblers. The numbers refer to the eight independent contrasts used in the analysis. (c) Correlation between contrasts in syllable repertoire size and contrasts in volume of the higher vocal centre (HVC) of the brain (corrected for body size). The eight independent contrasts are labelled. From Szekely *et al.* (1996).

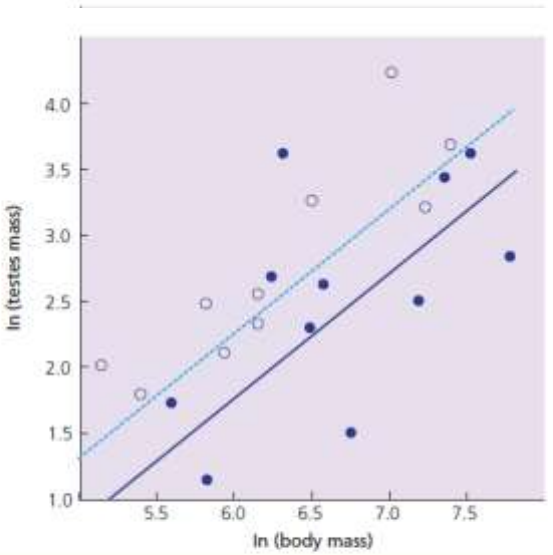


Fig. 2.10 Relationship between testis mass and body mass in bushcricket species (Tettigoniidae) with low (filled circles) and high (open circles) degrees of polyandry. Phylogenetic information was incorporated into the statistical analysis by weighting current species values by the distance separating them in the phylogeny. The lines, fitted from a phylogenetic model, are for low (solid line) and high (dashed line) degrees of polyandry. From Vahed *et al.* (2010).

Using phylogenies in comparative analysis
Sexual swellings in female primates

Female sexual swellings occur in multimale groups

The graded signal hypothesis

- may gain from copulating with the dominant male
  - the best genetic sire, best able to protect her and offspring
  - enables the female to bias paternity chances to the dominant male while at the same time enhancing opportunities of mating with subordinate males, too, at times when she is still potentially fertile

Fig. 2.11 Sexual swellings in female chimpanzees (Bossou, Guinea, West Africa). (a) Female on the left with male retreating on the right. Photo © Kathelijne Koops. (b) A 42-year old female carrying her five-year old daughter on her back, being inspected by an adult male. She became pregnant soon after this photo was taken. Photo © Susana Carvalho.

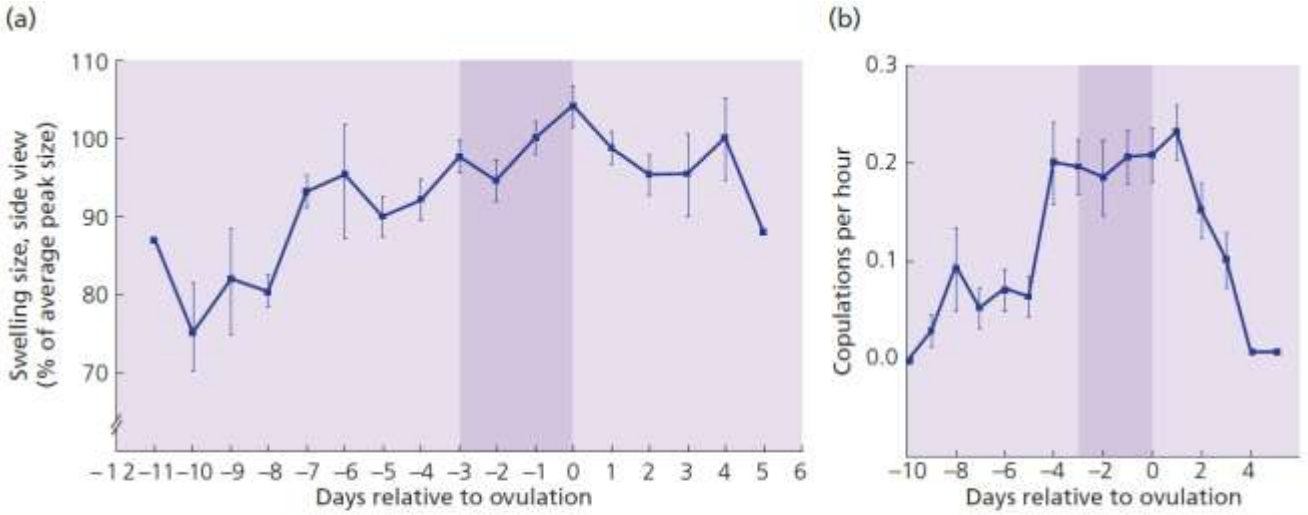


Fig. 2.14 Sexual swellings in a group of wild chimpanzees studied in an evergreen forest in the Tai National Park, Côte d'Ivorie. (a) Swelling size in 12 females (mean ± SE) aligned to the day of ovulation (day 0). Swellings measured from photographs and ovulation determined by enzyme immunoassays from urine samples. The shaded area indicates the fertile phase, when fertilization is most likely. (b) Alpha male copulation rate (mean ± 1SD) during the phase of maximum swellings. Data from 10 females, aligned to the day of ovulation (day 0). Fertile period shaded. From Deschner *et al*. (2004). With permission from Elsevier.

Using phylogenies in comparative analysis
Sexual swellings in female primates

Female sexual swellings occur in multimale groups

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  - enables the female to bias paternity chances to the dominant male while at the same time enhancing opportunities of mating with subordinate males, too, at times when she is still potentially fertile

Swellings have evolved **three times** independently in the old world monkeys and apes, and in all three cases this transition is associated with the evolution of multimale groups from a single-male ancestral state.

Across 70 species, none of 29 species living in single-male groups has sexual swellings compared to 29 out of 41 species (71%) living in multimale groups

Fig. 2.11 Sexual swellings in female chimpanzees (Bossou, Guinea, West Africa). (a) Female on the left with male retreating on the right. Photo © Kathelijne Koops. (b) A 42-year old female carrying her five-year old daughter on her back, being inspected by an adult male. She became pregnant soon after this photo was taken. Photo © Susana Carvalho.

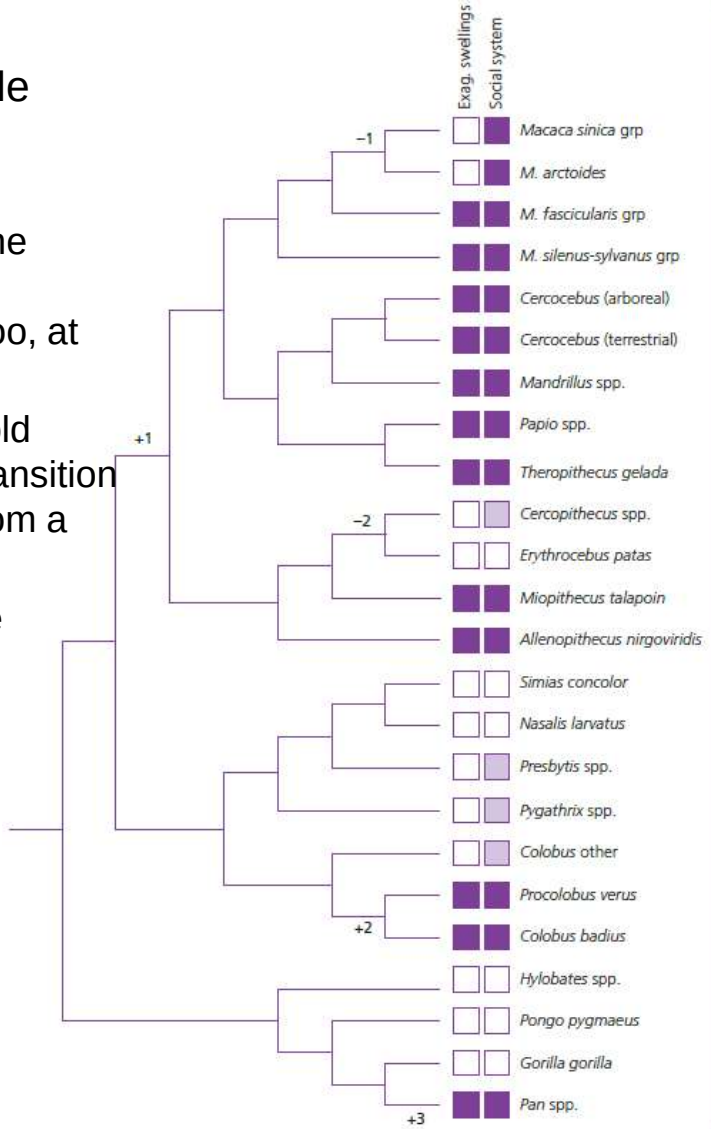


Fig. 2.12 Phylogeny of old world monkeys (Purvis, 1995), with some clades collapsed to facilitate presentation of data. The terminal branches are extant species and their traits are indicated. In the left hand column is presence (purple box) or absence (white box) of sexual swellings. In the right hand column is multimale (purple box) or single-male (white box) mating system. The pale shaded boxes indicate taxa with both single-male and multimale mating systems. The ancestral state is most likely that of no swellings. There have been three gains of sexual swellings in this tree (indicated by +1, +2, +3) and two losses (−1, −2). From Nunn (1999). With permission from Elsevier.

Experimental studies of adaptation

Costs and benefits of eggshell removal in gulls

Tinbergen (1963) observed that in a colony of black-headed gulls nesting on sand dunes in northwestern England, incubating parents always pick up the broken eggshell after a chick has hatched and carry it away from the nest.

Test the hypothesis that the conspicuous white broken shell reduces the camouflage of the nest.

He painted hens' eggs to resemble cryptic gull eggs and laid them out at regular intervals in the gull colony.

Next to some he placed a broken shell.

Further specific behaviour:

The parent does not remove the eggshell immediately; it stays with the newly hatched chick for an hour or more and then goes off with the shell. WHY?

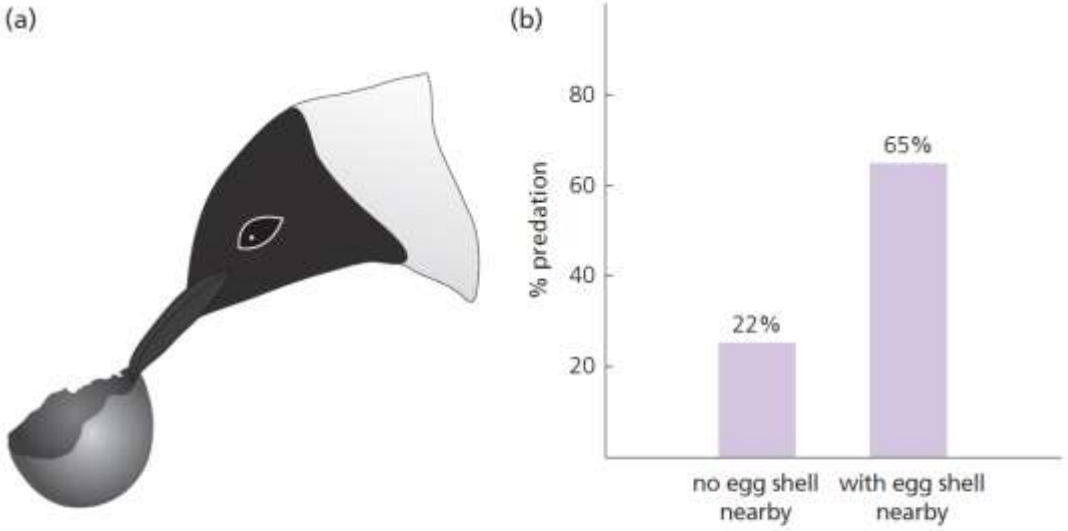


Fig. 2.15 (a) Black-headed gull removing an eggshell. (b) Results of an experiment in which single hen's eggs, painted to resemble black-headed gull eggs, were placed in the dunes, near a nesting colony. Those with an empty eggshell next to them (5 cm away) were more likely to be taken by predators (n = 60 in each treatment). From Tinbergen *et al.* (1963).

Black-headed gull:

<u>White egg shell: risk of predation</u>

<u>Wait with transporting white egg shell: neighbours not eat the nestlings</u>

Neighbours are the same threat as predators

What the oystercatcher do?

Solitary breeders: predators are more threat than

→ take the white egg shell immediately

<u>Optimalisation</u>:

Net benefit = benefit- cost

3. Economic Decisions and the Individual

Economic Decisions and the Individual

Quantitative models of costs and benefits

An optimality model seeks to predict which particular trade-off between costs and benefits will give the maximum net benefit to the individual.

Crows and whelks

- Crows preferred the very largest whelks
- Crows minimize ascending flight to break the whelk
- drop was made from a height somewhat greater than 5.2 m, as optimality model expected

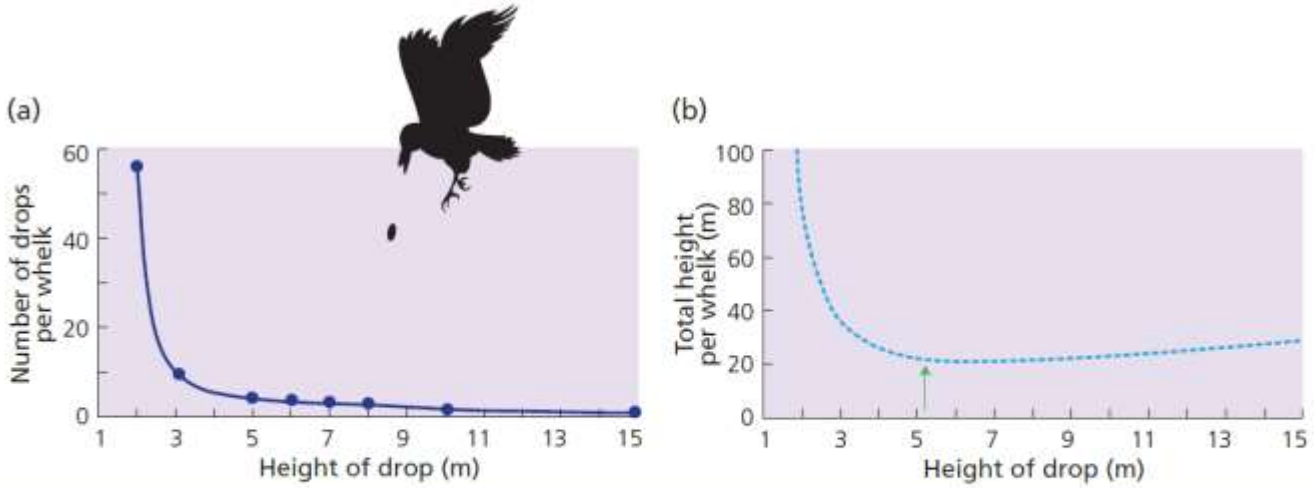


Fig. 2.16 Dropping of whelks by crows. (a) When whelks are dropped, experimentally, from different heights it is found that fewer drops are needed to break the shell when it is dropped from a greater height. (b) Calculation of the total ascending flight needed to break a shell (number of drops × height of each drop). This is minimized at the height most commonly used by the crows (arrow). From Zach (1979).

Economic Decisions and the Individual

The economics of carrying a load

Starlings feed their young mainly on leatherjackets (Tipula fly larvae) and other soil invertebrates

Parents in the breeding season makes up to 400 round trips from its nest to feeding sites every day, ferrying loads of food to its nestlings

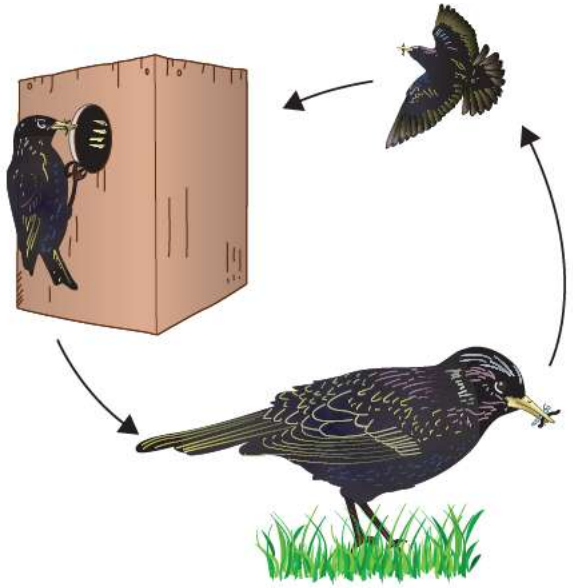


Fig. 3.1 Starlings fly from their nest to a feeding site, search for a beak-full of leatherjackets by probing in the grass, then take them home to the nestlings. The question examined in the first part of this chapter is how many items the parent should bring on each trip in order to maximize the rate of delivery of food to the nestlings.

Economic Decisions and the Individual

Optimal load size in starlings: diminishing returns

The model predicts smaller loads with shorter travel times

The field test:

- load size increase with distance from the feeder to the nest
- close quantitative correspondence between the observed load sizes and those predicted by the model of maximizing delivery rate

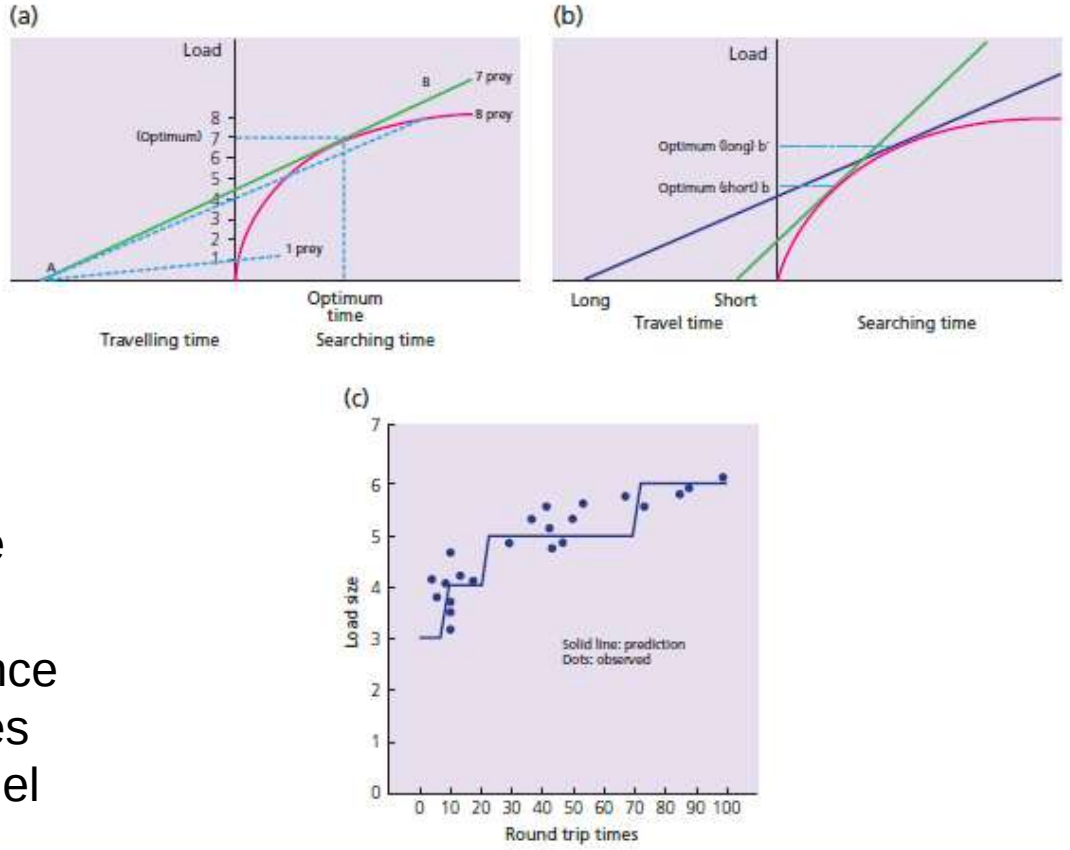


Fig. 3.2 (a) The starling's problem of load size. The horizontal axis shows 'time' and the vertical axis shows 'load'. The curve represents the cumulative number of leatherjackets found as a function of time spent searching. The line AB represents the starling's maximum rate of delivery of food to the nestlings. This rate is achieved by taking a load of seven leatherjackets on each trip. Two other lines, corresponding to loads bigger (eight) and smaller (one) than seven, are shown to make the point that these loads result in lower rates of delivery (shallower slopes). Note that although the cumulative load is shown here as a smooth curve, in reality it is a stepped line since each food item is a discrete package. (b) When the round trip travel time is increased from short to long the load size that maximizes delivery rate increases from b to b'. (c) When starlings were trained to collect mealworms from a feeder, they brought bigger loads from greater distances. Each dot is the mean of a large number of observations of loads brought from a particular distance. The predicted line goes up in steps because the bird is predicted to change its load size in steps of one worm (of course the mean loads do not have to be integers). The prediction shown here is one based on the model of Fig. 3.2b, but it also includes the refinement of taking into account the energetic costs to the parent of foraging and to the chicks of begging. From Kacelnik (1984).

Economic Decisions and the Individual

Reproductive decisions can be analysed with the same model

How male dung flies search for mates

Males compete with one another for the chance to mate with females arriving at cowpats to lay their eggs

The longer the male mates the more eggs he fertilizes

Cost of long copulation: the male misses the chance to go and search for a new female

Often one male will succeed in kicking another male off a female during copulation and take her over

When two males mate with the same female the second one is the individual whose sperm fertilizes most of the eggs

Travel time among females can be used to predict how long the male spends copulating with a female

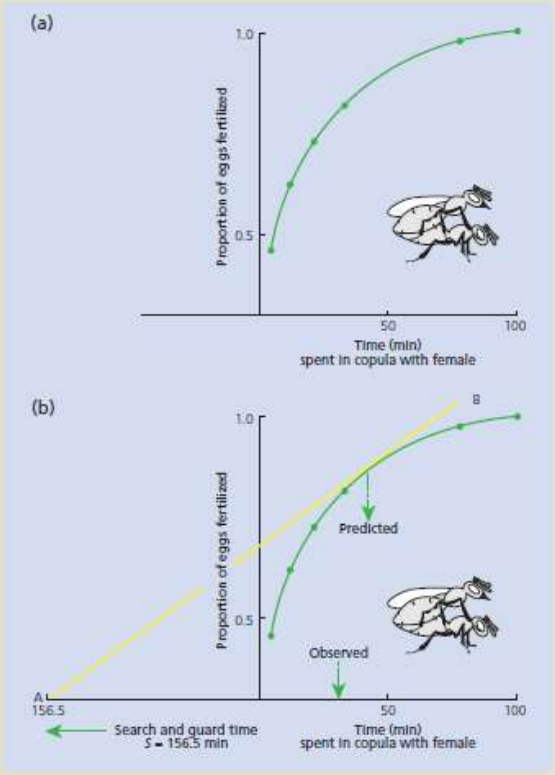


Fig. B3.1.1 (a) The proportion of eggs fertilized by a male dung fly (*Scatophaga stercoraria*) as a function of copulation time: results from sperm competition experiments. (b) The predicted optimal copulation time (that which maximizes the proportion of eggs fertilized per minute), given the shape of the fertilization curve and the fact that it takes 156 min to search for and guard a female, is 41 min. The optimal time is found by drawing the line AB. The observed average copulation time, 36 min, is close to the predicted value (Parker, 1970a; Parker & Stuart, 1976) (photo of a pair of dung flies © Leigh Simmons).

Economic Decisions and the Individual

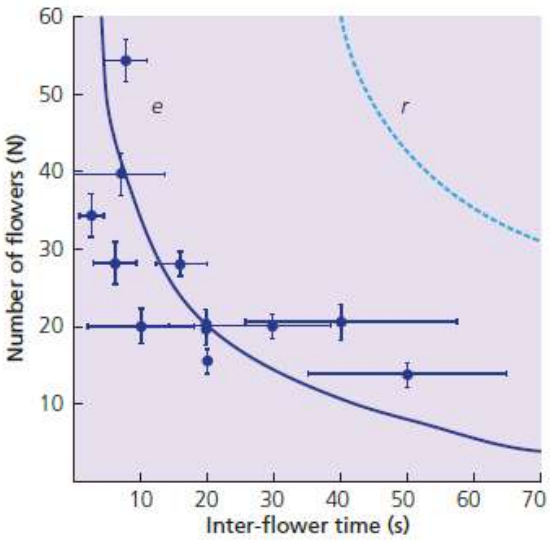
In bees, diminishing returns arise from the cost of carrying nectar

How much nectar should a bee carry home?

Bees maximise efficiency, not rate of energy gain

Life expectancy of bees depends on work load

Adding weight to the bee's back causes it to fly home with a smaller load



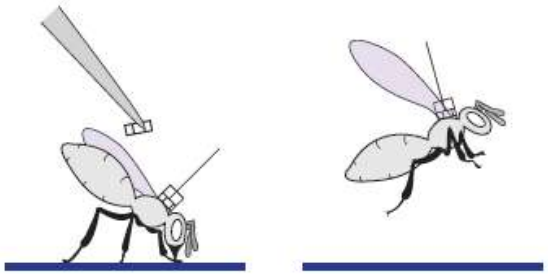


Fig. 3.3 (a) The relationship between load size (expressed as number of flowers visited) carried home by worker bees and flight time between flowers in a patch. Each dot is the mean of an individual bee and the two lines are predictions based on maximizing efficiency (*e*) and maximizing rate (*r*). From Schmid-Hempel *et al*. (1985). (b) By placing tiny weights on the bee's back while it is foraging Schmid-Hempel was able to study the bee's rule of thumb for departure from a patch to go home to the hive with a load of nectar. The weights, in the form of brass nuts, are placed on a fine rod that is permanently glued to the bee's back. They can be added or removed to simulate loading and unloading. From Schmid-Hempel (1986). With permission from Elsevier.

The economics of prey choice

Optimal prey choice depends on energy values, handling time…

Why should they sometimes eat smaller and larger mussels?

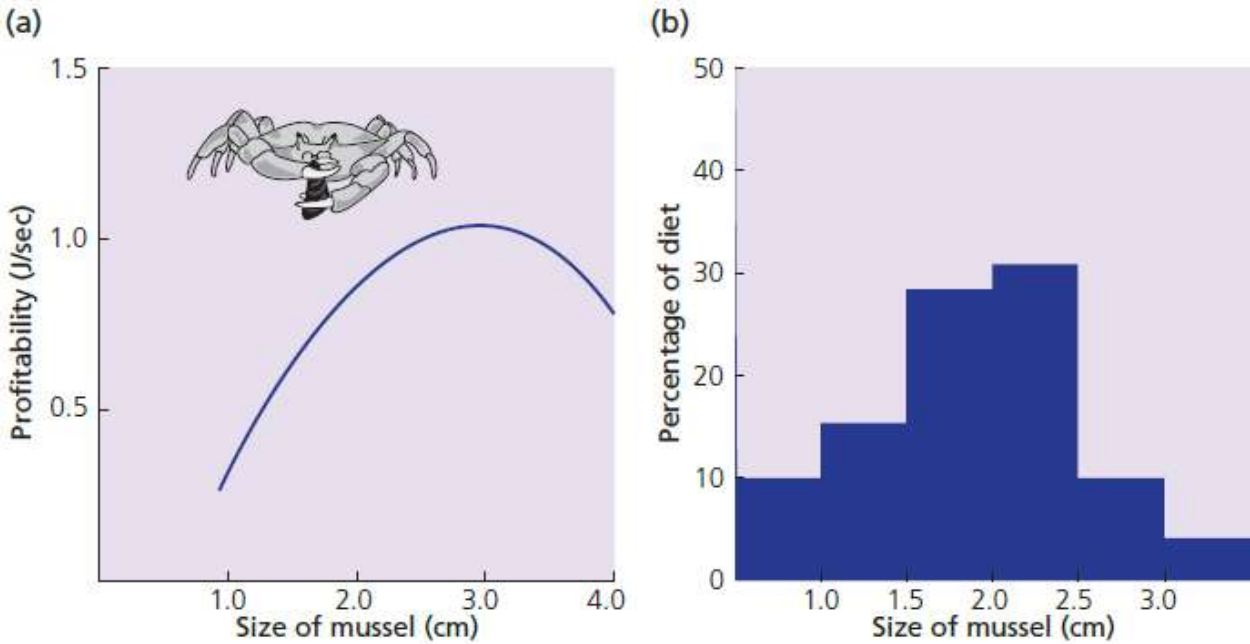


Fig. 3.4 Shore crabs (*Carcinus maenas*) prefer to eat the size of mussel which gives the highest rate of energy return. (a) The curve shows the energy yield per second of handling time used by the crab in breaking open the shell and eating the flesh; (b) the histogram shows the sizes eaten by crabs when offered a choice of equal numbers of each size in an aquarium. From Elner and Hughes (1978).

The economics of prey choice

Optimal prey choice depends on energy values, handling time…

… and search time

A test of the optimal diet model

When big worms were abundant the birds, as predicted, were selective even if small worms were extremely common

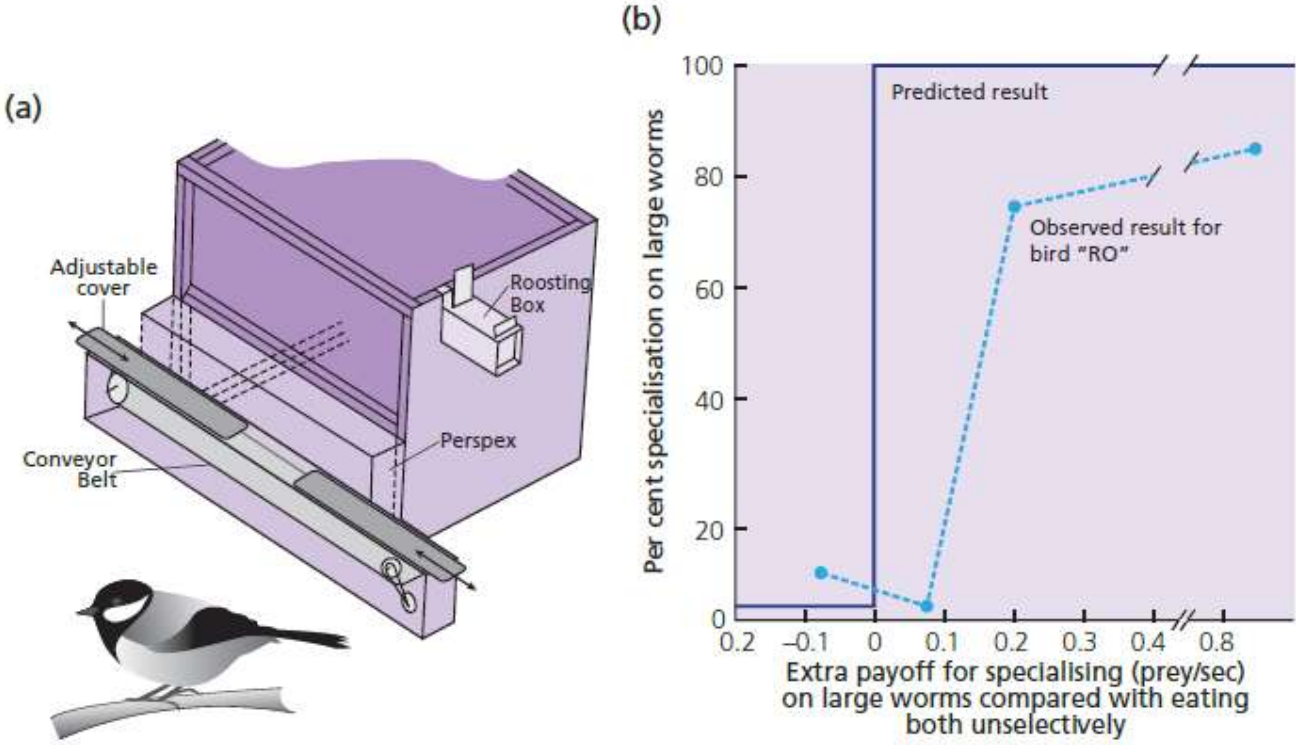


Fig. 3.5 (a) The apparatus used to test a model of choice between big and small worms in great tits (*Parus major*). The bird sits in a cage by a long conveyor belt on which the worms pass by. The worms are visible for half a second as they pass a gap in the cover over the top of the belt and the bird makes its choice in this brief period. If it picks up a worm it misses the opportunity to choose ones that go by while it is eating. (b) An example of the results obtained. As the rate of encounter with large worms increases the birds become more selective. The x-axis of the graph is the extra benefit obtained from selective predation. As shown in Box 3.2, the benefit becomes positive at a critical value of S_1, the search time for large worms. The bird becomes more selective about the predicted point, but in contrast with the model's prediction this change is not a step function. From Krebs *et al*. (1977). With permission from Elsevier.

Sampling and information

The animal need to learn their environment as it goes along

Downy woodpeckers trained in the field to hunt for seeds hidden in holes drilled in hanging logs

Each log had 24 holes and in each experiment some logs were quite empty and others had seeds hidden in some or all of the holes

They had to use information gathered at the start of foraging on each log to decide whether or not it was likely to be empty and therefore should be abandoned

When the logs contained 0 or 24 seeds the task was easy: looking in a single hole in theory gave sufficient information to decide and the woodpeckers, in fact, took an average of 1.7 looks in an empty log before moving on.

The task was more complicated when the two kinds of log contained 0 and 6 or 0 and 12 seeds

The calculated values were 6 and 3 while the observed means were 6.3 and 3.5; thus, the woodpeckers use information gleaned while foraging in a way that comes close to maximizing their overall rate of intake

The risk of starvation

Risk-averse versus risk-prone behaviour

Yellow-eyed juncos (Junco phaeonotus) (small birds) in an aviary a sequence of choices between two feeding options: one variable and one with a fixed pay-off.

- variable option in one treatment was either 0 or 6 seeds with a probability of 0.5 each
- fixed option was always three seeds

Experiment at two temperatures: 1 and 19°C

At the low temperature the rewards from the fixed option were inadequate to meet daily energy needs

At 19°C they were sufficient.

As predicted by the theoretical argument, the birds switched from risk-averse behaviour at 19°C to risk-prone behaviour at 1°C

Environmental variability, body reserves and food storing

Small birds in winter often experience large daily fluctuations in body mass: the 20-g great tit, for example, typically loses 10–15% of its body mass overnight in winter

Should we expect small birds to carry as much fat as possible at all times, as an insurance against starvation?

Birds usually carry less than the maximum reserves

In winter, birds are usually heaviest on the coldest/harshest days - on other days they are carrying fewer reserves than the maximum

Optimal fat reserves: trade-off between starvation and predation

When sparrowhawks (Accipiter nisus) re-colonized the wood in the 1980s (after a decline due to pesticides, Oxford, UK), the winter mass of great tits trapped in the wood declined by about 0.5 g

Environmental variability, body reserves and food storing

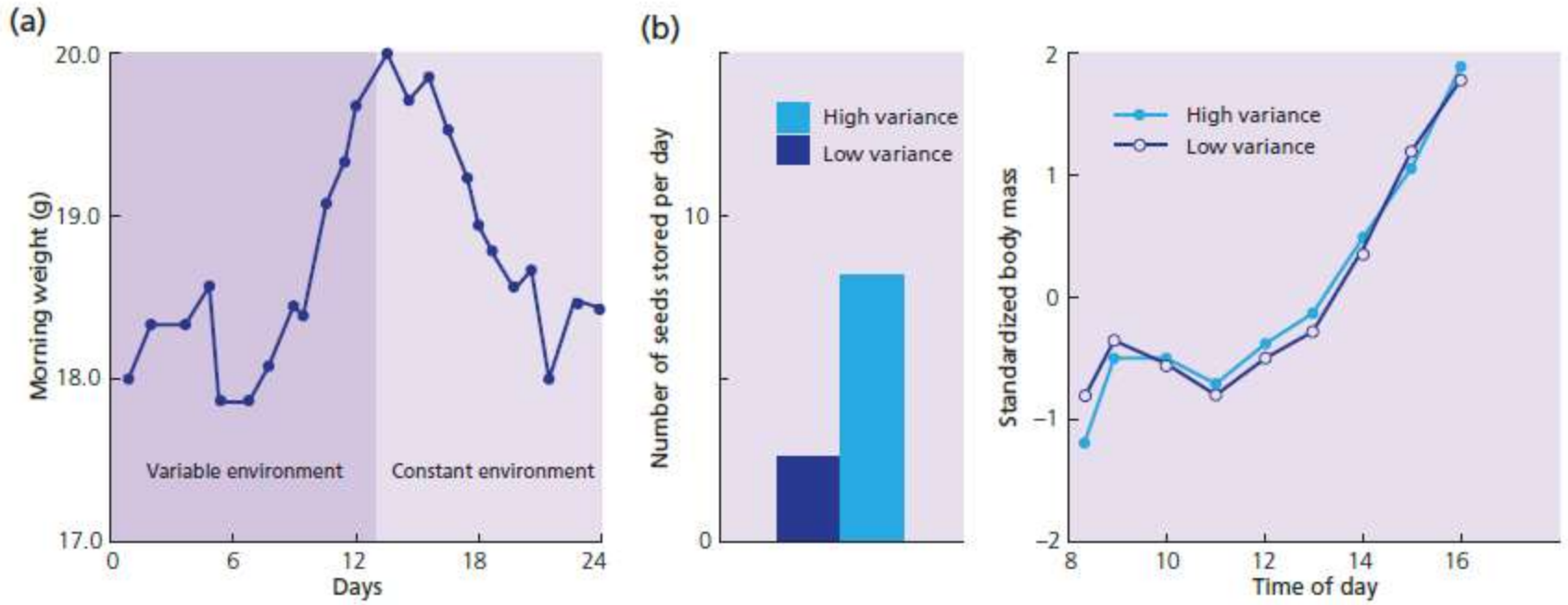


Fig. 3.6 (a) Body reserves and environmental variability. The graph shows the body mass of a captive great tit (one of eight in the experiment) which was transferred from a constant to a variable environment for 12 days before returning to the constant environment. Variability in this experiment was produced by randomly altering the length of the night-time period of no foraging. From Bednekoff & Krebs (1995). (b) Food storing and variability. In this experiment, captive marsh tits (one example is shown) stored more food (left), but did not put on more body reserves (right), in a more variable environment. These results suggest that food storing, like fat storage, is a method of coping with environmental variability: whilst great tits, which do not store food, cope with environmental variability by putting on extra fat reserves, marsh tits store extra food in the environment. The right-hand graph also shows the daily weight trajectory of a marsh tit. In the afternoon, the bird transfers food from its hoards to its body, so reserves rise steeply towards the end of the day. From Hurly (1992).

Feeding and danger: a trade-off

Balancing foraging and safety

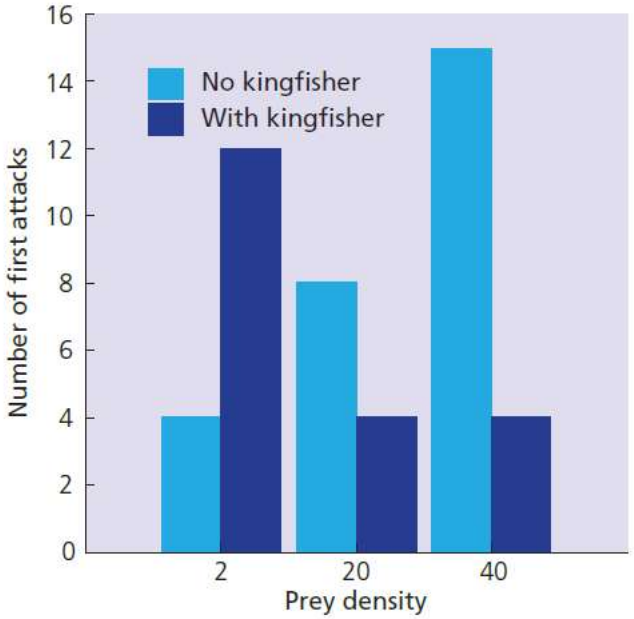


Fig. 3.11 Hungry sticklebacks normally prefer to attack high density areas of prey but after a model kingfisher was flown over the tank they preferred to attack low density areas. From Milinski and Heller (1978). Reprinted with permission from the Nature Publishing Group.

Feeding and danger: a trade-off

Balancing foraging and safety

Squirrel eating chocolate chip cookies in the park

If you put out small fragments of cookie the squirrel will often make repeated sorties to the table and take each morsel back to the tree to eat it

Not a very efficient way to eat food: if maximizing net rate of energy intake or efficiency was the only important factor for a squirrel it would simply sit on the table and eat pieces of cookie until it was full

When the feeding table was close to the trees the squirrels were more likely to take each item to cover.

Big pieces of cookie were more likely to be taken to cover than small ones; they take a long time to eat and are, therefore, more dangerous to handle out in the open and when handling time is long the relative cost of travelling back and forth is reduced.

Feeding and danger: a trade-off

Balancing foraging and safety

Bluegill sunfish: age changes in habitat choice

The fish could obtain a higher rate of food intake by foraging on benthic invertebrates such as chironomid larvae than they could by foraging either on the plankton or near the emergent vegetation at the edge of the pond

The fish spend most of their time (more than 75%) foraging on the benthos.

However, when predators in the form of largemouth bass (Micropterus salmoides) were added to the pond, a significant change in habitat use by the sunfish was seen.

The bass could eat only the smallest sunfish (the others were too big) and these fish now spent more than half their foraging time in the reeds feeding on plankton where they were relatively safe even though as a result their food intake was reduced by about one-third and their seasonal growth rate by 27%.

The bigger sunfish continued to forage with equanimity on the benthos

Table 3.1
A summary of some of the decisions, currencies and constraints discussed

Animal	Decision	Currency	Some constraints	Test
Starling	Load size	Maximize net rate of gain	Travel time, loading curve, energetic costs	Load versus distance
Bee	Crop load	Maximize efficiency	Travel time, sucking time, energetic costs	Load versus flight time
Dung fly	Copulation time	Maximize fertilization rate	Travel time, guarding time, fertilization curve	Predict copula duration
Great tit	Size of worms	Maximize net rate of gain	Handling time, search time	Choice of large or small prey
Downy woodpecker	Patch time	Maximize net rate of gain	Travel time, recognition time	Number of holes inspected
Yellow-eyed junco	Where to feed	Minimize risk of starvation	Handling time, daily energy budget	Choice of variable or certain reward
Great tit/ marsh tit	Body reserves/ hoard size	Maximize survival	Energetic cost of carrying reserves	Body reserves/ hoard size in predictable and unpredictable environments
Squirrel	Where to eat	Maximize survival	Travel time, handling time	Vary size of food and distance
Stickleback	Where to feed	Minimize danger and starvation	Vigilance and foraging incompatible	Vary hunger and danger
Bluegill sunfish	Habitat choice	Maximize survival	Growth depends on food intake, danger related to size	Habitats used at different ages

Optimality models and behaviour: an overview

- Optimality models often make testable, quantitative predictions
- Advantage is that the assumptions underlying the currency and constraint hypotheses are made explicit
- Optimality models emphasize the generality of simple decisions facing animals

What should we do when a model fails to predict observed behaviour?

- The currency of the model was incorrect
- The currency is correct but that the constraints have not been identified correctly
- Animals may simply not be that well tuned by the process of natural selection or they may be lagging behind when some aspect of the environment changes

The important point is that discrepancies between observed and predicted behaviour can be used to inspire further studies of currencies, constraints and the animal's environment, and so build up a better understanding of the animal's decision making