Behavioural Ecology

Sources:

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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

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

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

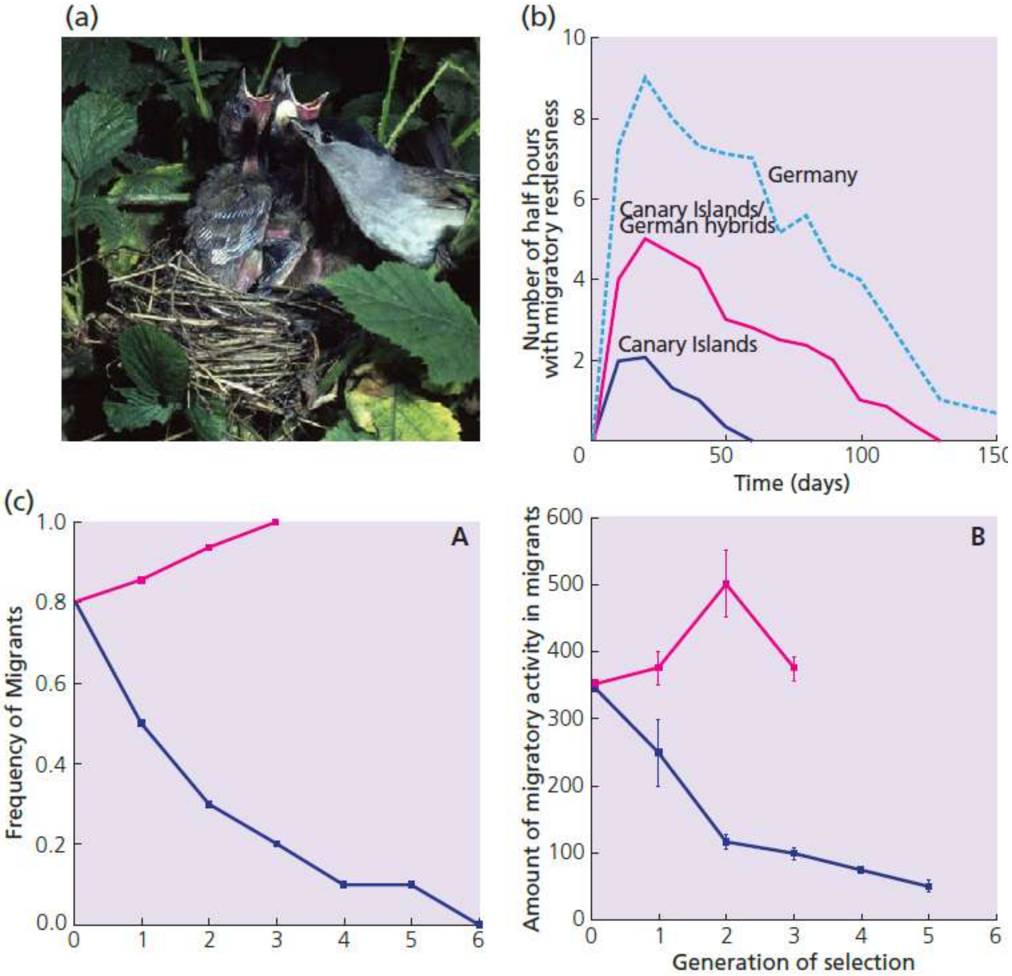
Genes and behaviour

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

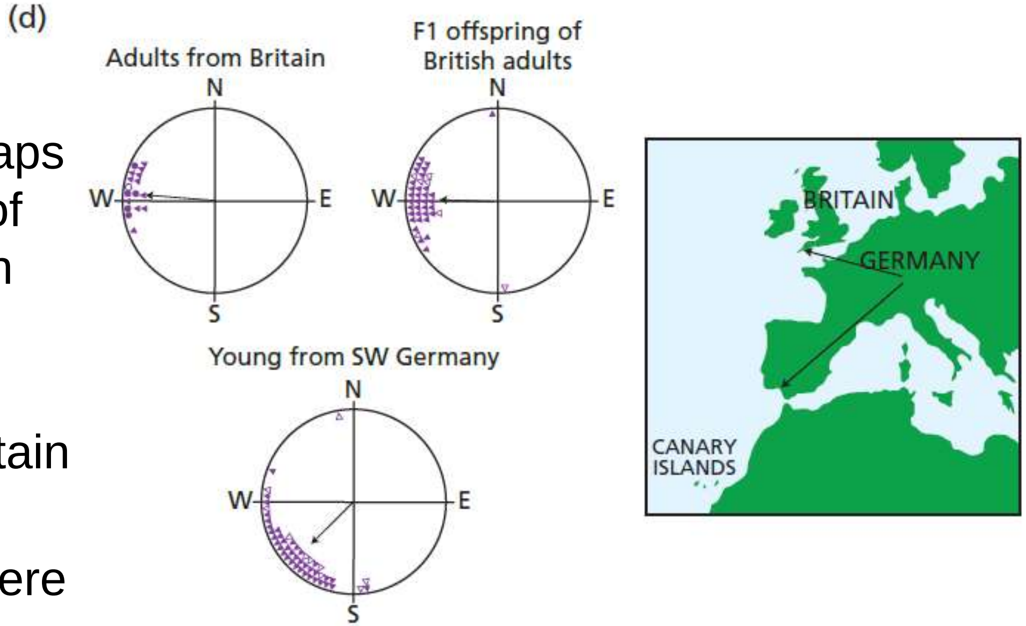
Central European populations of blackcaps traditionally winter to the southwest of their breeding grounds in the western Mediterranean.

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

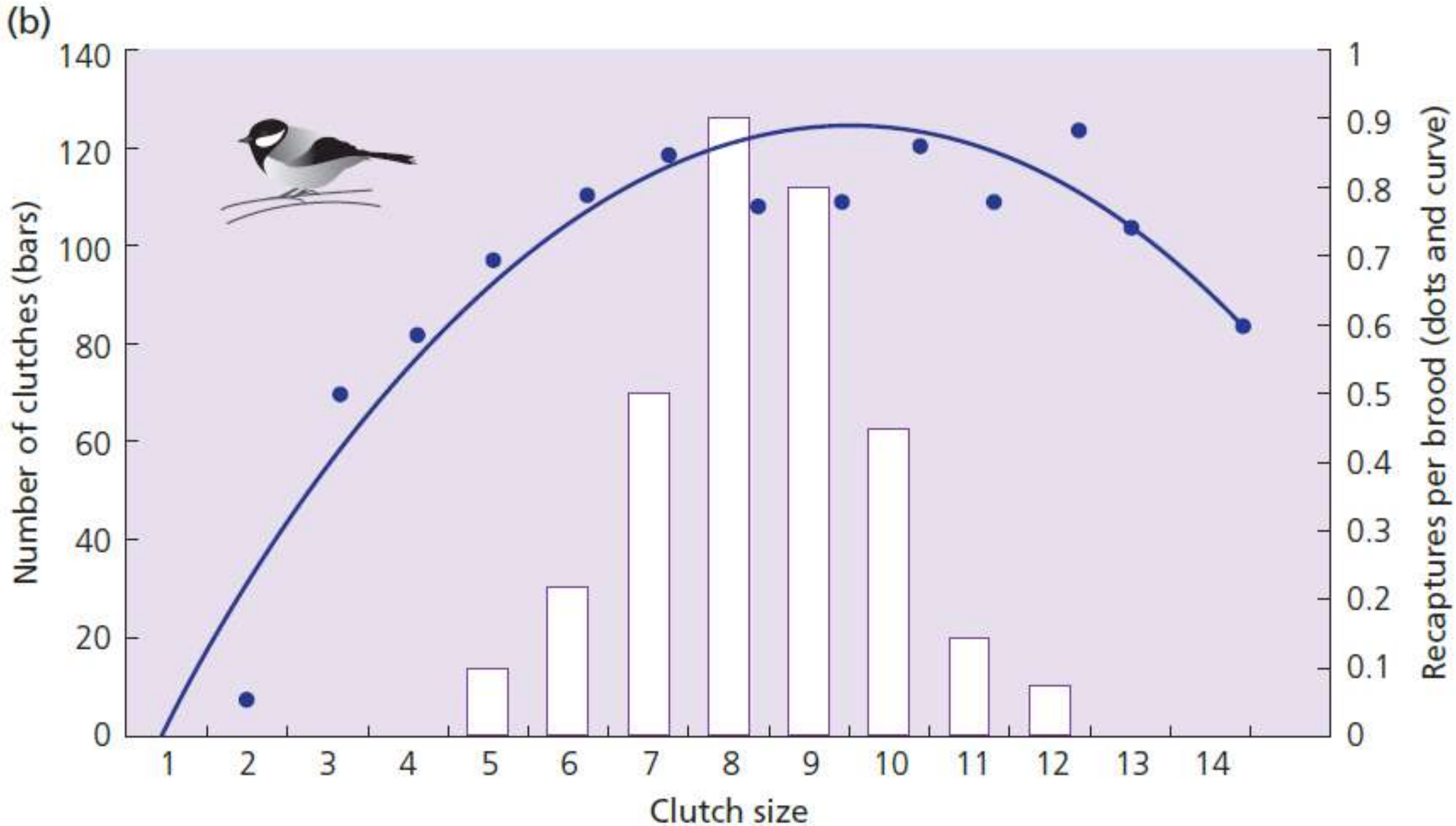
There is good field evidence that individuals do not restrict their birth rate for the good of the group but rather maximize their individual reproductive success.

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

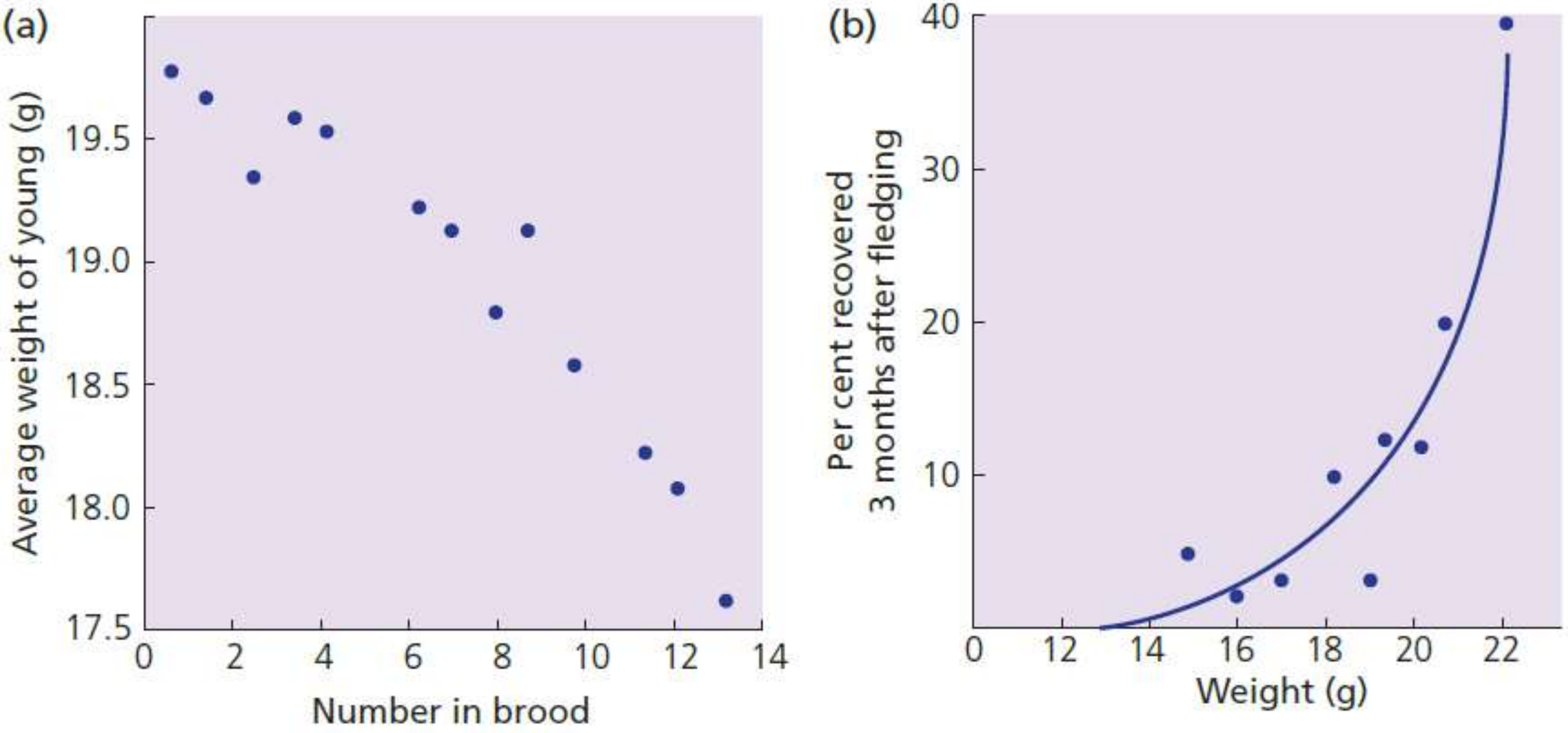


Fig. 1.6 Experimental manipulation of brood sizes in great tits. (a) In larger broods of great tits the young weigh less at fledging because the parents cannot feed them so efficiently. (b) The weight of a nestling at fledging determines its chances of survival; heavier chicks survive better. From Perrins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

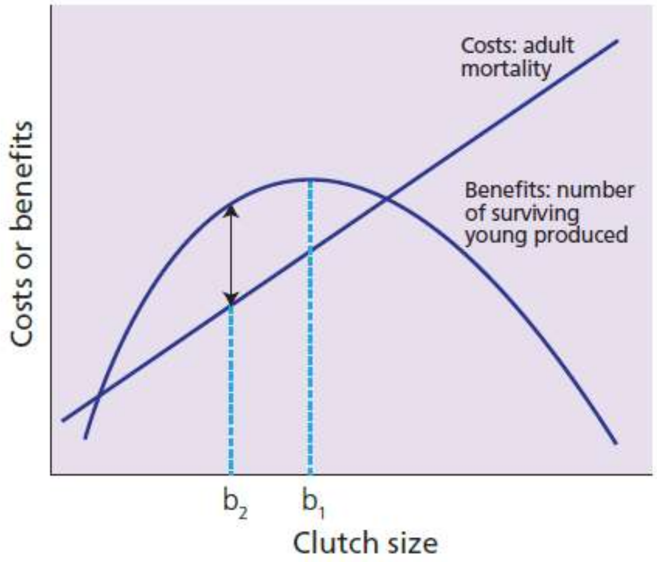
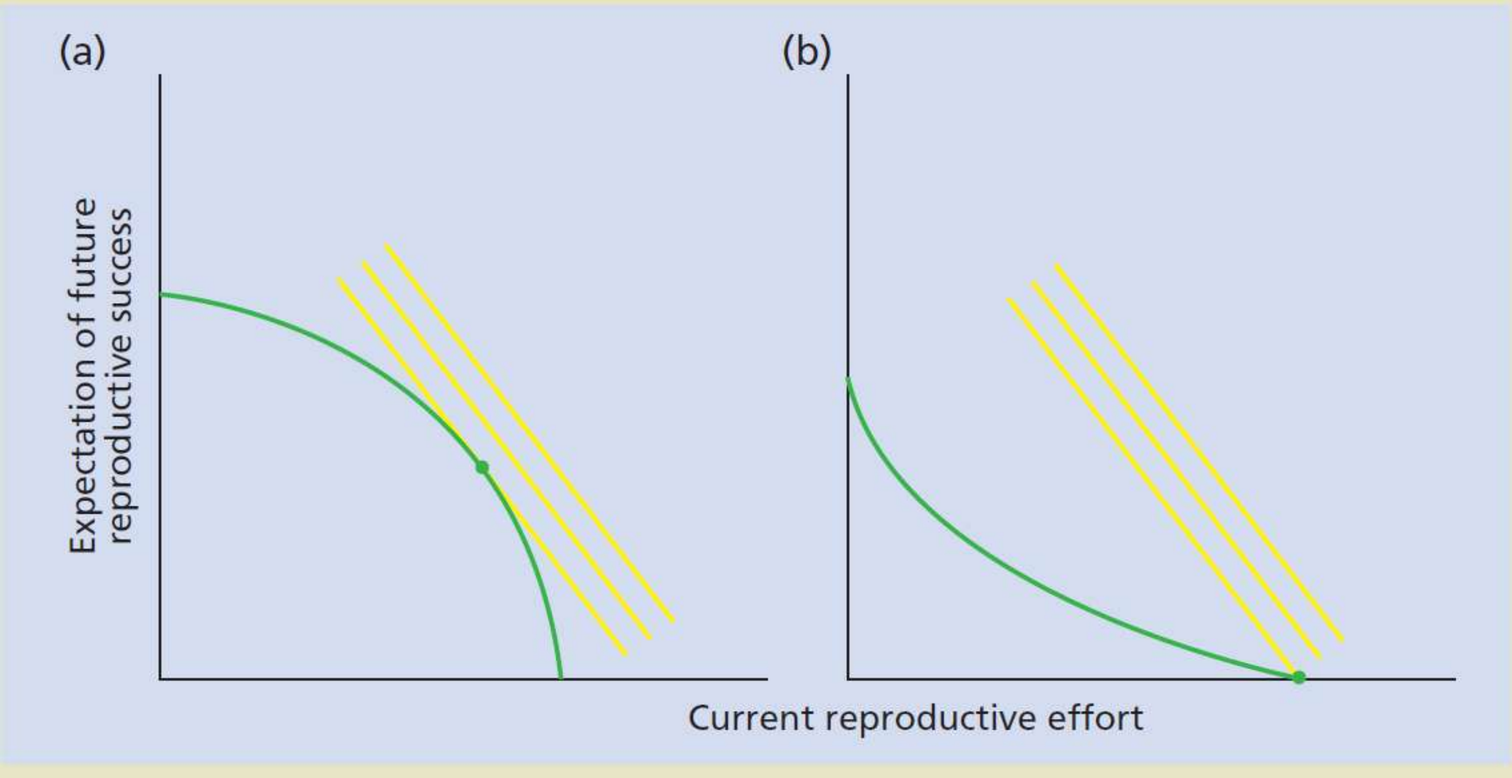


Fig. 1.7 The influence of adult mortality on the optimal clutch size. The number of young produced versus clutch size follows a curve, as in Fig. 1.5, with b_1 being the clutch size which maximizes the number of young produced per brood. Increased clutch size, however, has the cost of increased adult 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

Phenotypic plasticity

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

Dates of laying eggs and spring temperature

- How they managed? (proximate)

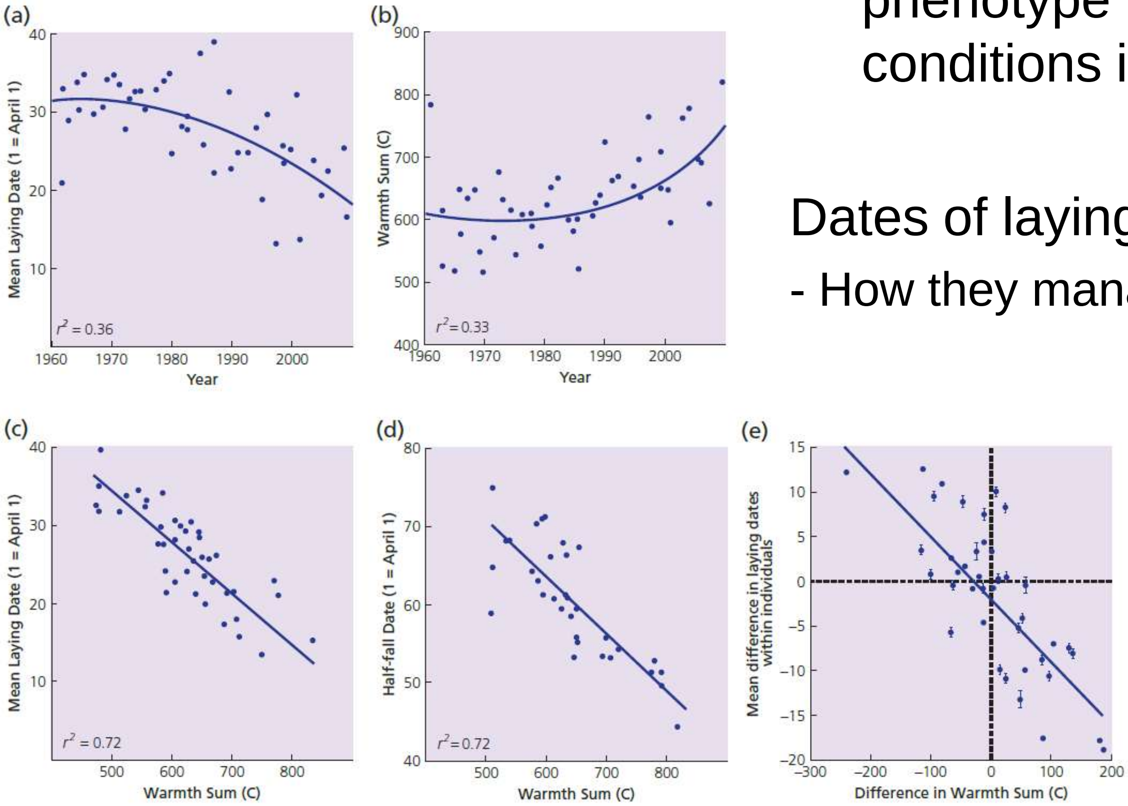
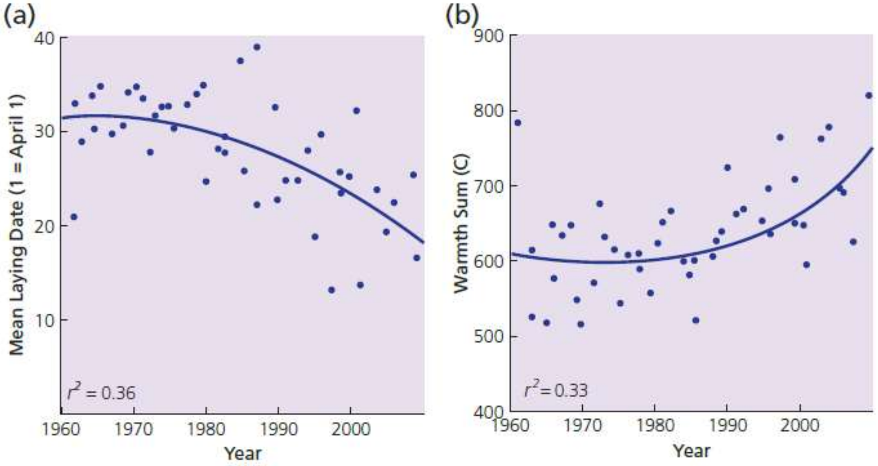
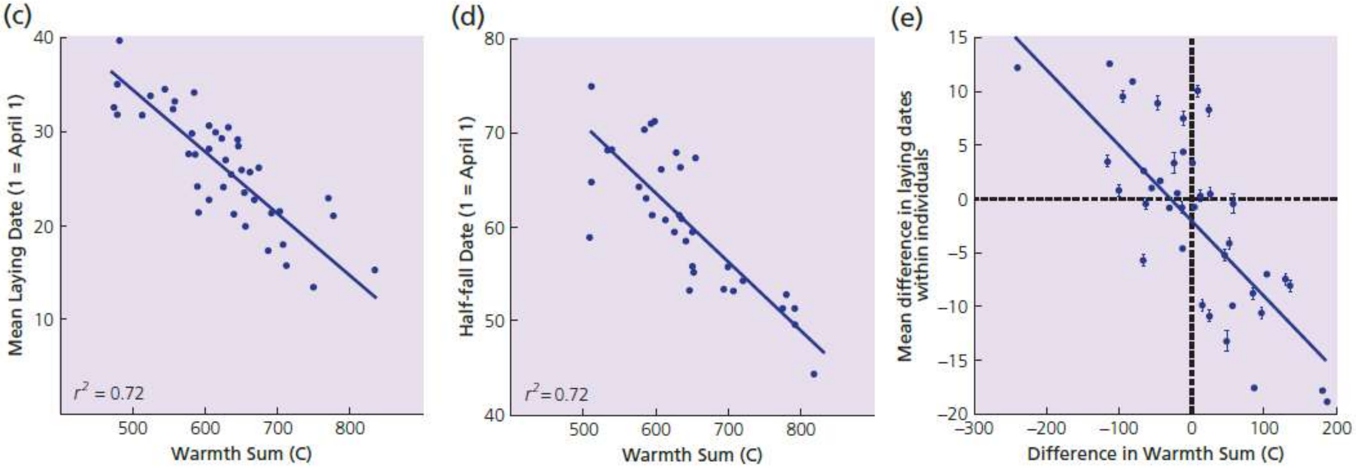


Fig. 1.11 (a) In Wytham Woods, UK, the mean laying date of great tits has become earlier, especially since the mid 1970s. (b) Spring temperatures have also increased, as measured by 'Warmth Sum', which is the sum of daily maximum temperatures between 1 March and 25 April (the pre-laying period). The 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?





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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

Phenotypic plasticity

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

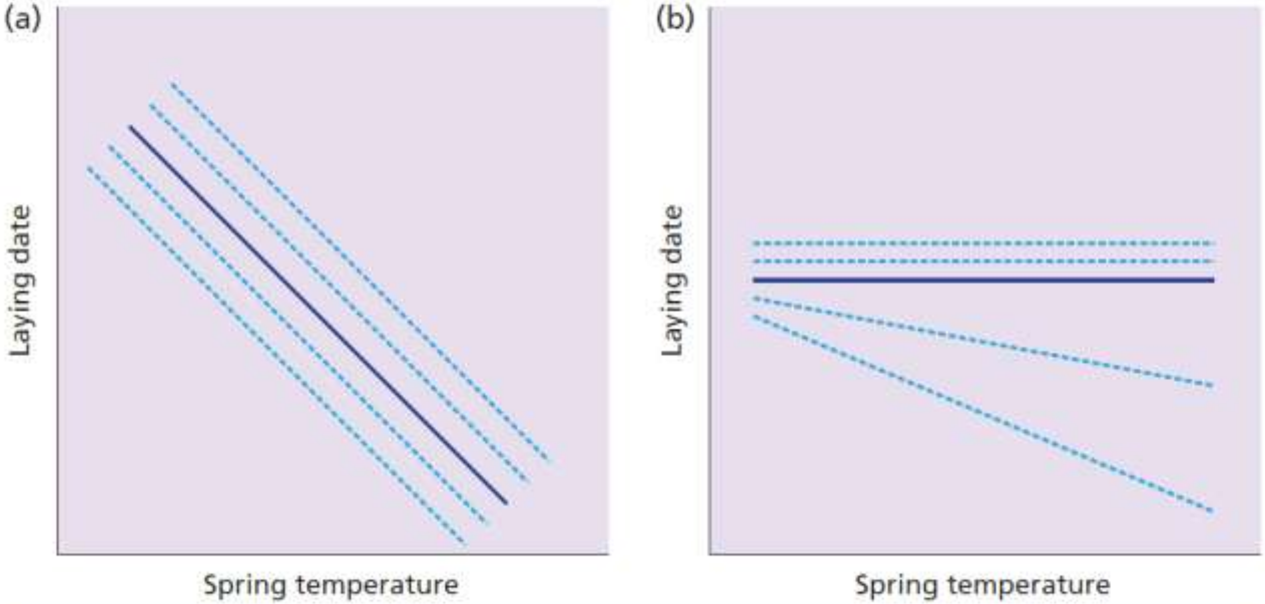


Fig. 1.10 Phenotypic plasticity in laying dates in response to spring temperatures. Dashed lines represent examples of reaction norms for different individual females, who may differ in their average laying date (elevation) or in their plasticity in response to spring temperatures (slope). In Wytham 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.

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

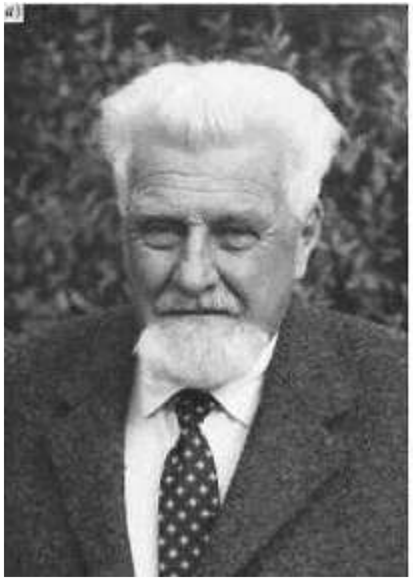
Resources are limited, so there will always be trade-offs involved, both within and between these various activities

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

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

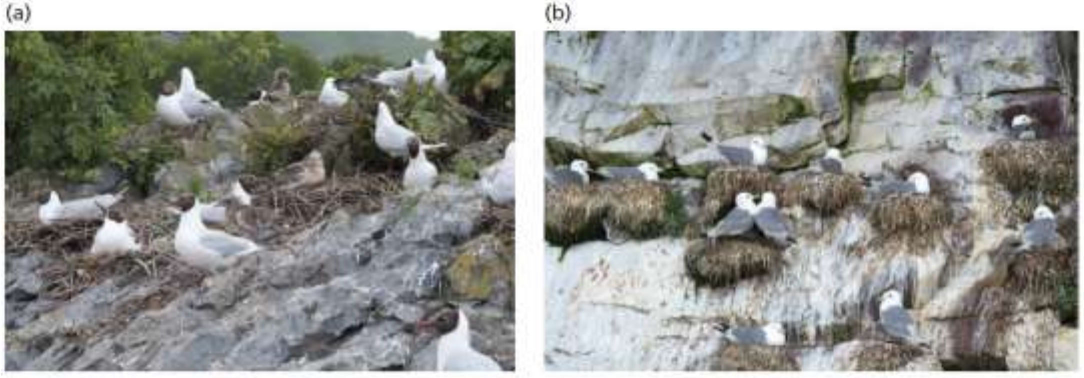
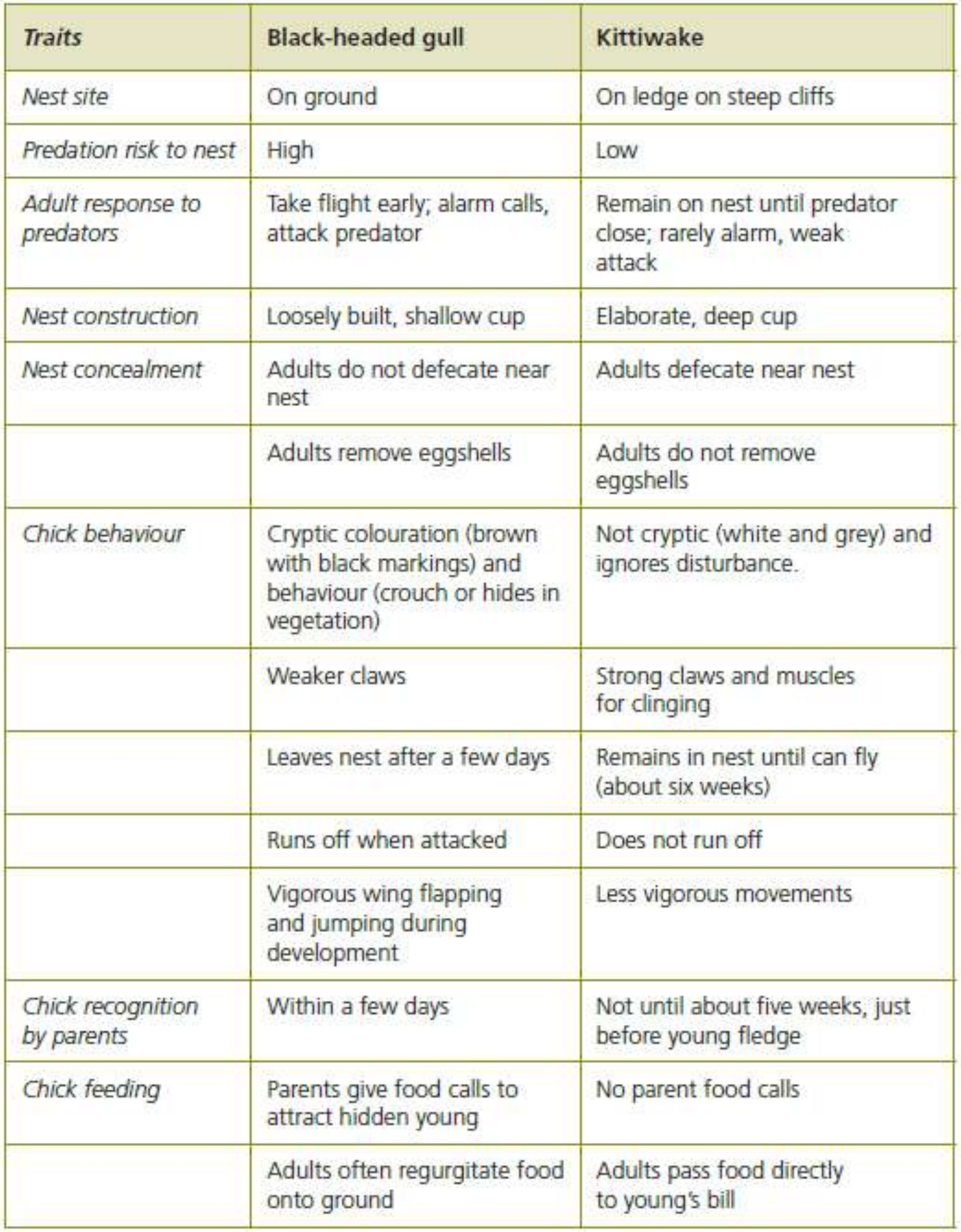


Fig. 2.1 (a) The black-headed gull nests on the ground. Photo © osf.co.uk. All rights reserved. (b) The kittiwake nests on tiny ledges on steep cliffs. Photo © iStockphoto.com/Liz Leyden.

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?

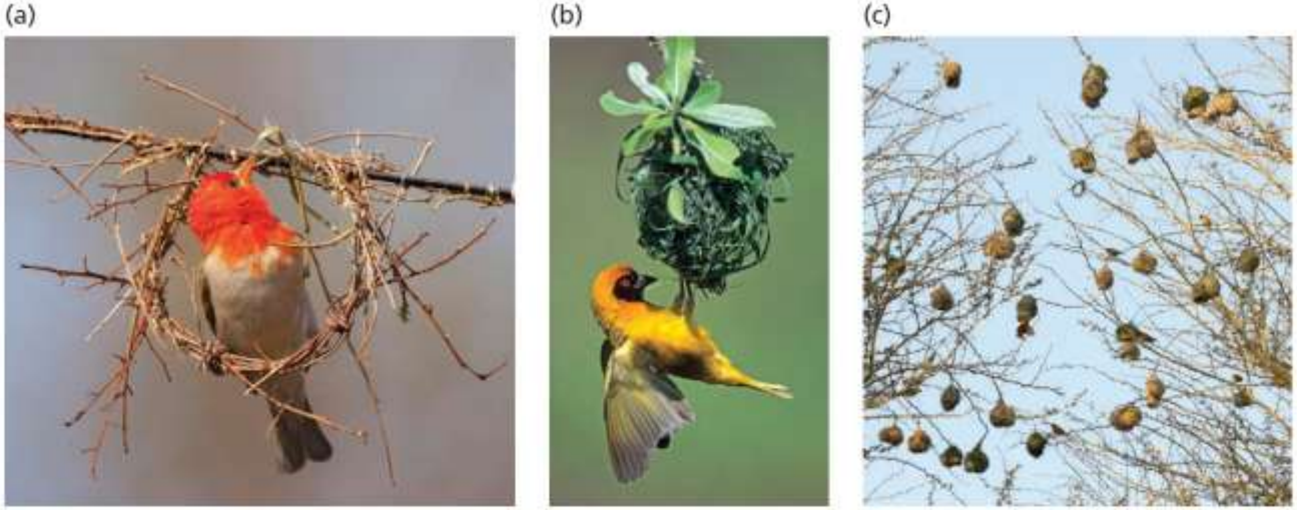
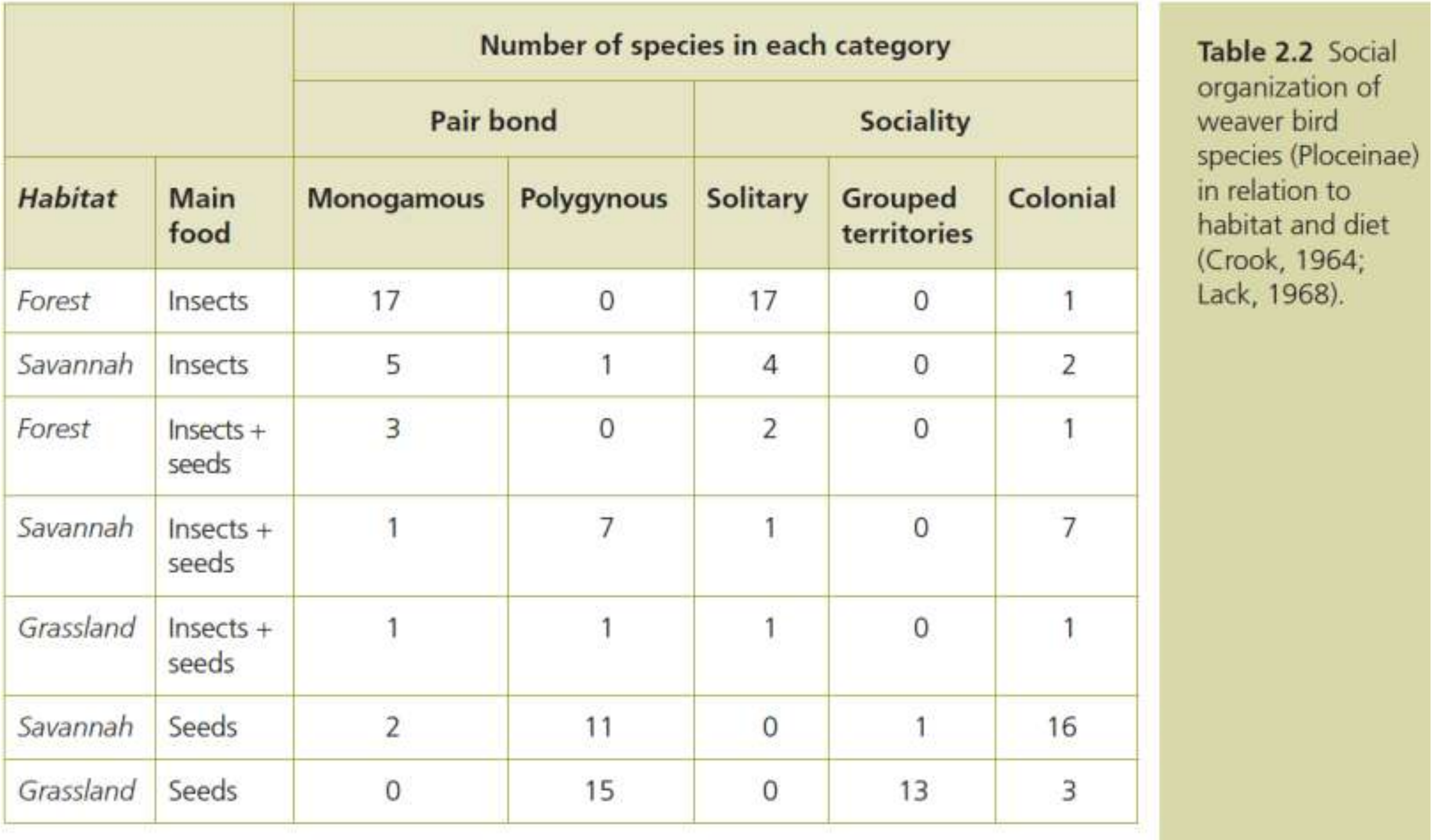


Fig. 2.2 Differences in social organization in weaver birds. (a) Red-headed weaver *Anaplectes melanotis*; a woodland insectivore which often breeds in monogamous pairs on dispersed territories. (b) Southern masked weaver *Ploceus vellatus*; a savannah seed-eater which nests in colonies and is polygynous. (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.

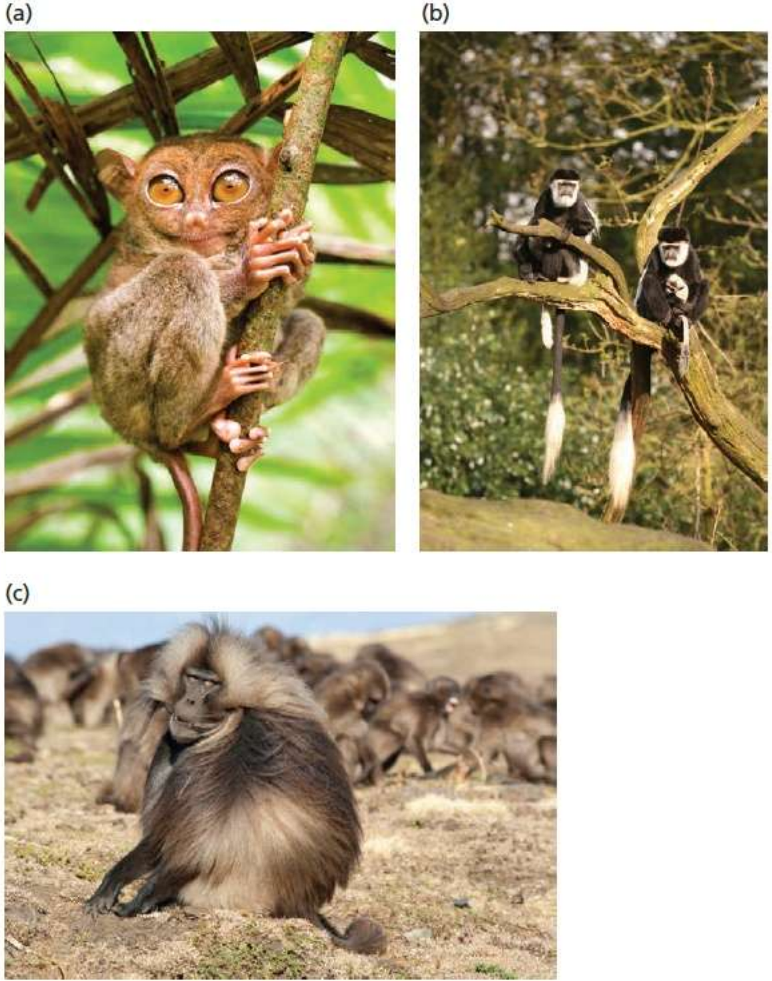


Fig. 2.4 Differences in social organization in primates. (a) A solitary insectivorous tarsier. Photo © iStockphoto.com/ Holger Mette. (b) A small group of black and white colobus monkeys, which eat leaves in the forest. Photo © iStockphoto.com/ Henk Bentlage. (c) A large group of gelada baboons, which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

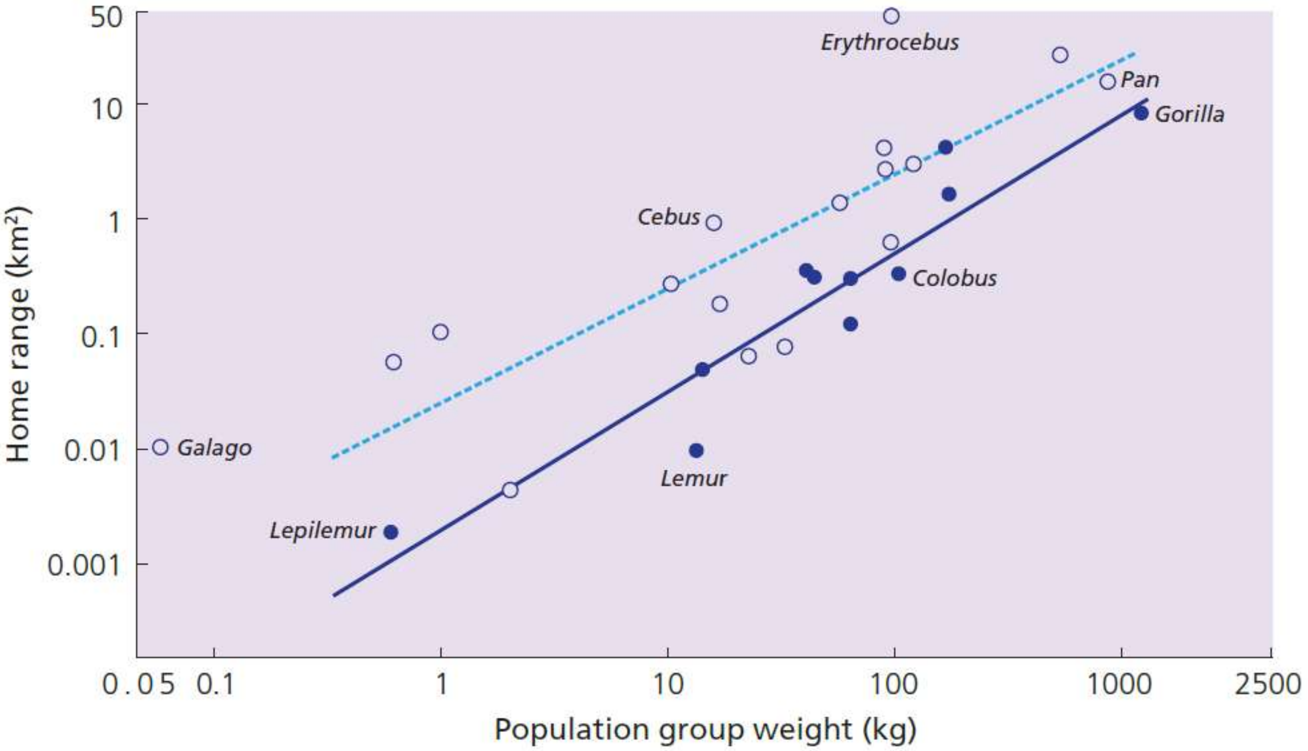


Fig. 2.5 Home range size plotted against the weight of the group that inhabits the home range for different genera of primates. The solid circles are folivores, through which there is a solid regression line. The open circles are specialist feeders (insectivores or frugivores) and the regression line 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

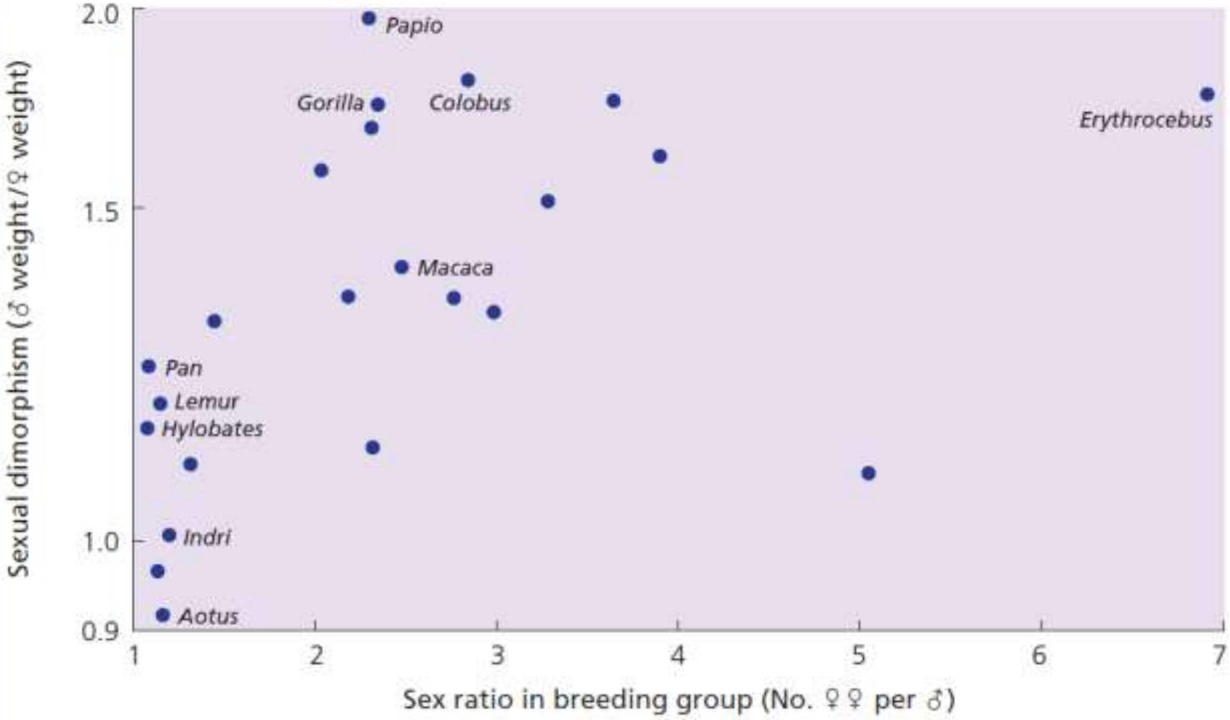


Fig. 2.6 The degree of sexual dimorphism increases with the number of females per male in the breeding group. Each point is a different genus, some of which are indicated by name. From Clutton-Brock and Harvey (1977).

- 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.

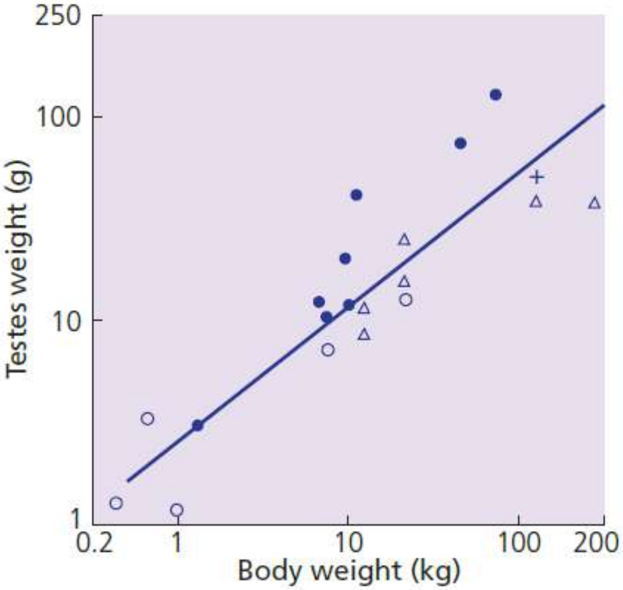


Fig. 2.7 Log combined testes weight (g) versus body weight (kg) for different primate genera. Solid circles are multimale breeding systems. Open circles are monogamous. Open triangles are single-male systems (one male with several females). The cross is our own species, *Homo*, for comparison. From Harcourt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

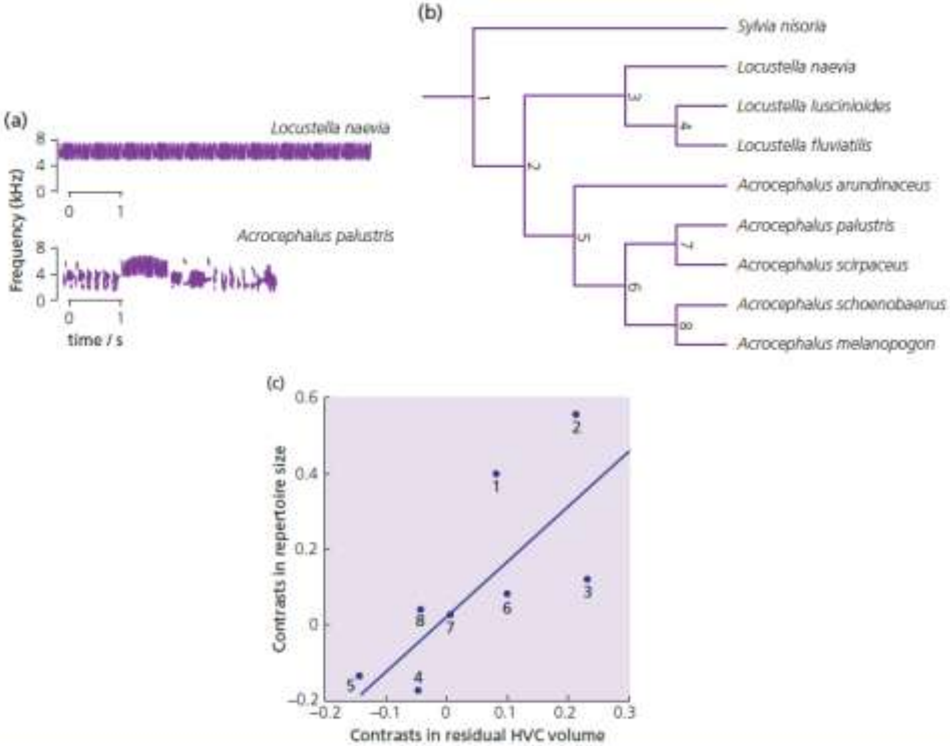


Fig. 2.9 Song complexity and brain anatomy in European warblers (family Sylviidae) from the genus *Acrocephalus* and *Locustella*. (a) Some species, like the grasshopper warbler *L. naevia*, have very simple songs (in this species, one syllable is repeated). Others, like the marsh warbler *A. palustris*, 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).

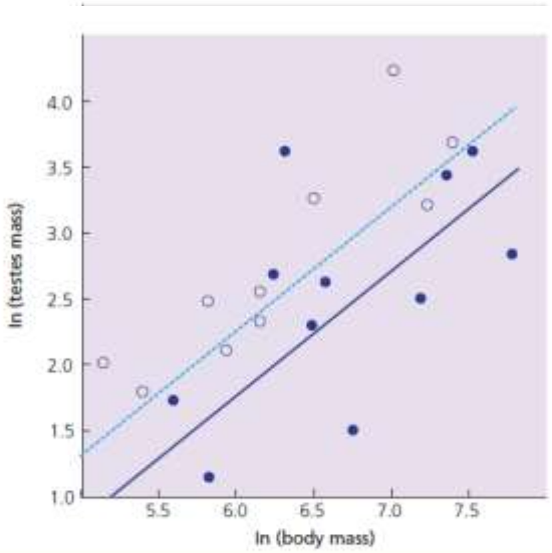


Fig. 2.10 Relationship between testis mass and body mass in bushcricket species (Tettigoniidae) with low (filled circles) and high (open circles) degrees of polyandry. Phylogenetic information was incorporated into the statistical analysis by weighting current species values by the distance separating 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.

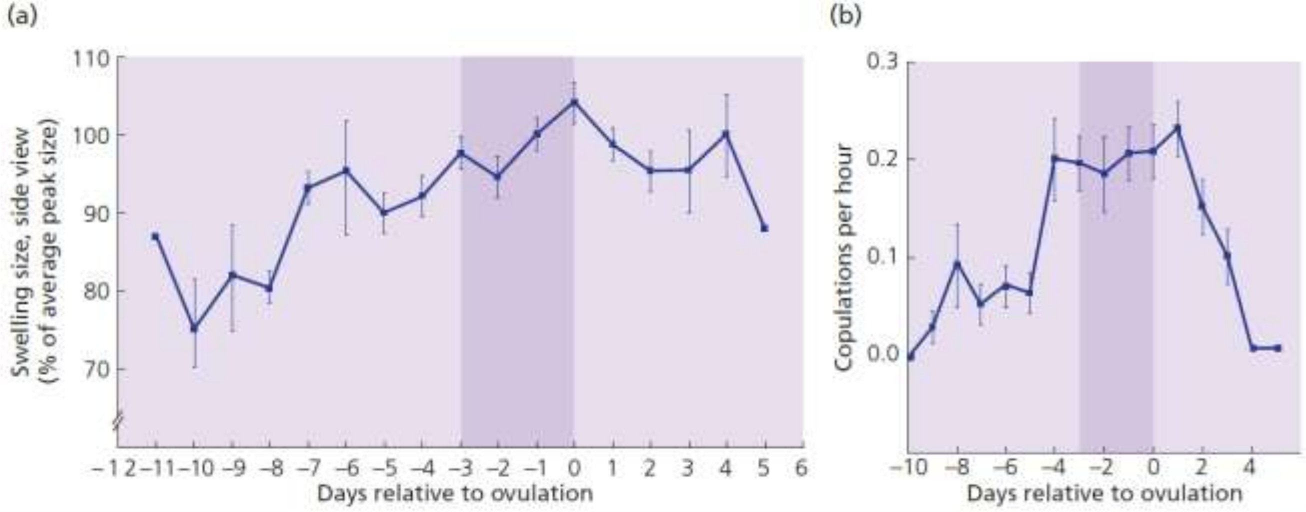


Fig. 2.14 Sexual swellings in a group of wild chimpanzees studied in an evergreen forest in the Tai National Park, Côte d'Ivorie. (a) Swelling size in 12 females (mean ± SE) aligned to the day of ovulation (day 0). Swellings measured from photographs and ovulation determined by enzyme immunoassays from 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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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.

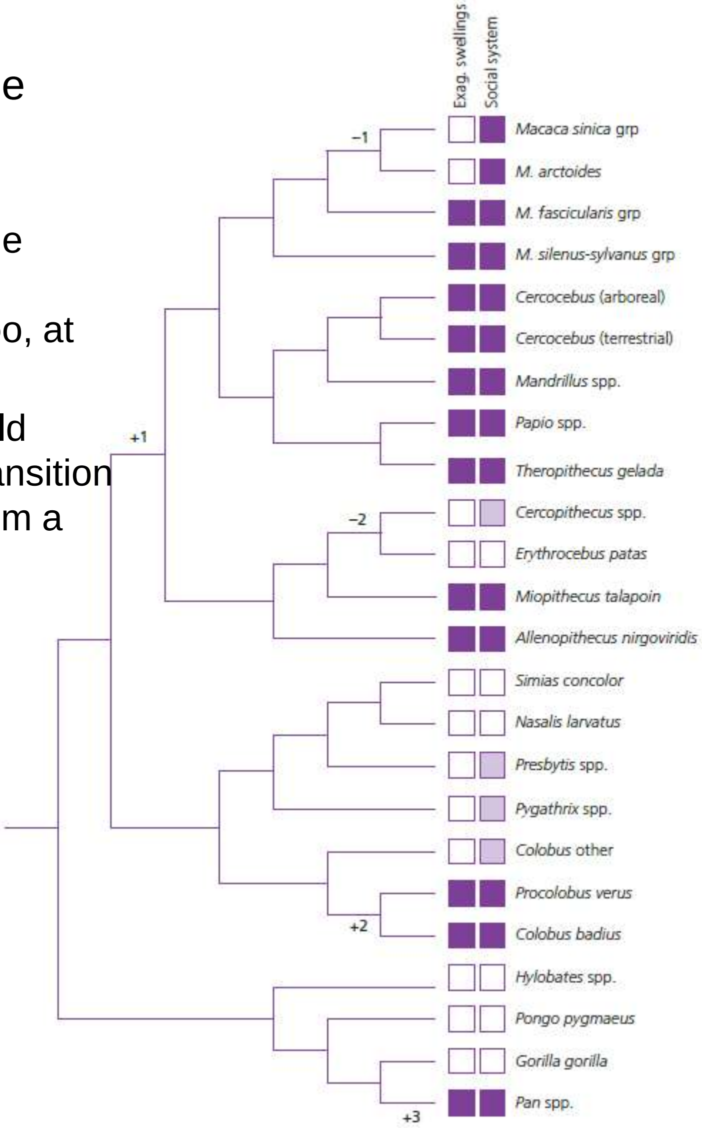

Fig. 2.12 Phylogeny of old world monkeys (Purvis, 1995), with some clades collapsed to facilitate presentation of data. The terminal branches are extant species and their traits are indicated. In the left hand column is presence (purple box) or absence (white box) of sexual swellings. In the right hand 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?

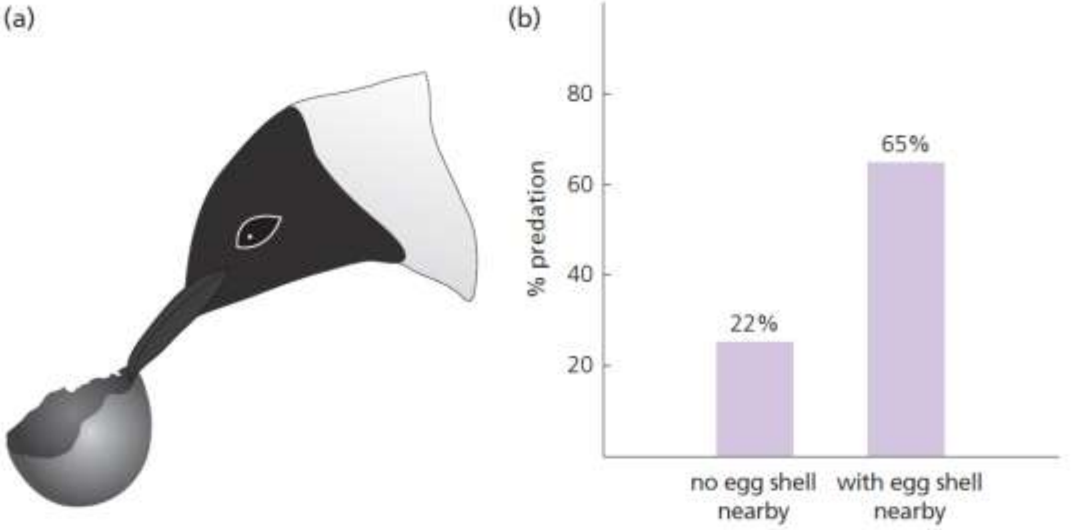

Fig. 2.15 (a) Black-headed gull removing an eggshell. (b) Results of an experiment in which single hen's eggs, painted to resemble black-headed gull eggs, were placed in the dunes, near a nesting colony. Those with an empty eggshell next to them (5 cm away) were more likely to be taken by predators (n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

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

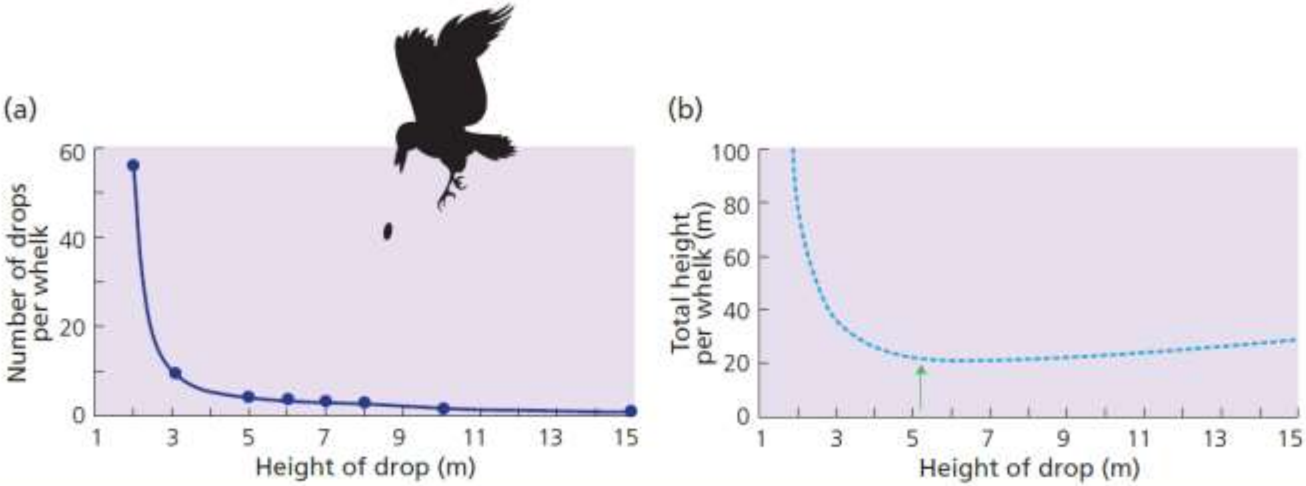

Fig. 2.16 Dropping of whelks by crows. (a) When whelks are dropped, experimentally, from different heights it is found that fewer drops are needed to break the shell when it is dropped from a greater height. (b) Calculation of the total ascending flight needed to break a shell (number of drops × height 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

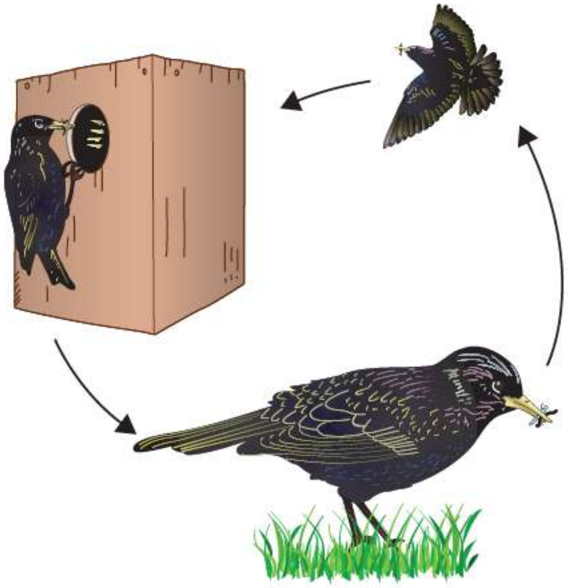

Fig. 3.1 Starlings fly from their nest to a feeding site, search for a beak-full of leatherjackets by probing in the grass, then take them home to the nestlings. The question examined in the first part of this chapter is how many items the parent should bring on each trip in order to maximize the rate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

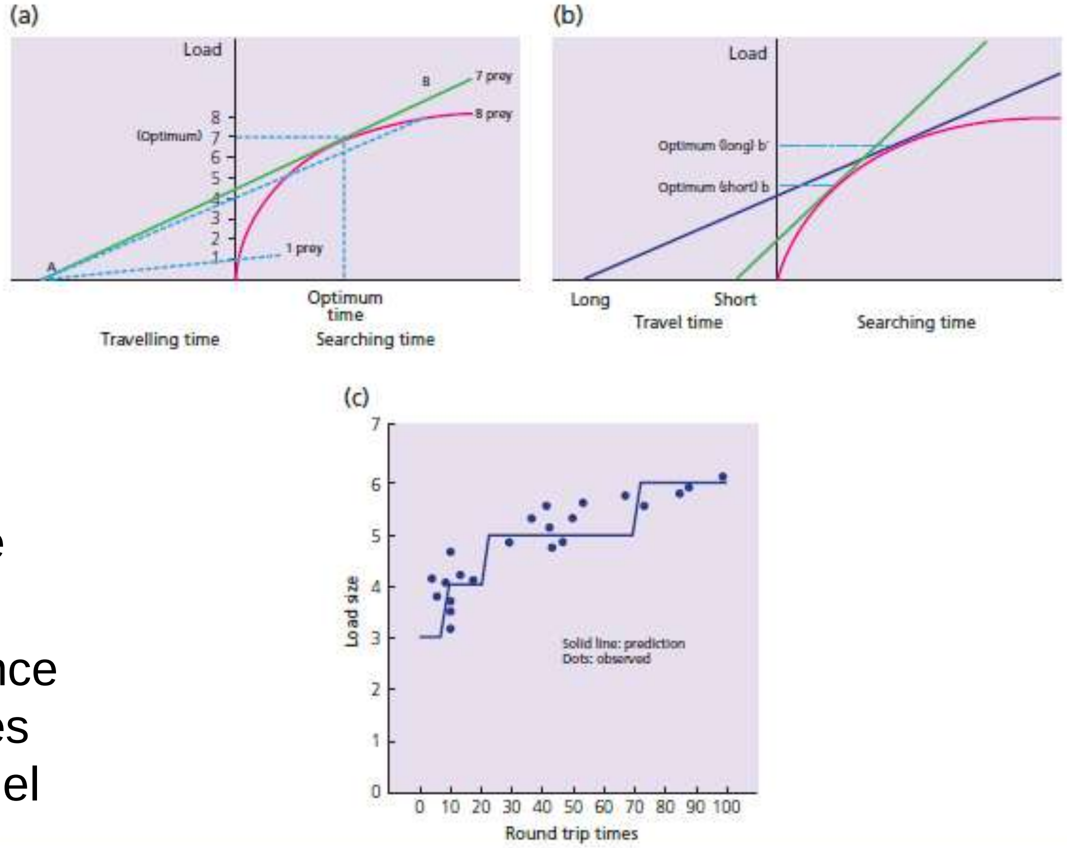

Fig. 3.2 (a) The starling's problem of load size. The horizontal axis shows 'time' and the vertical axis shows 'load'. The curve represents the cumulative number of leatherjackets found as a function of time spent searching. The line AB represents the starling's maximum rate of delivery of food to the 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

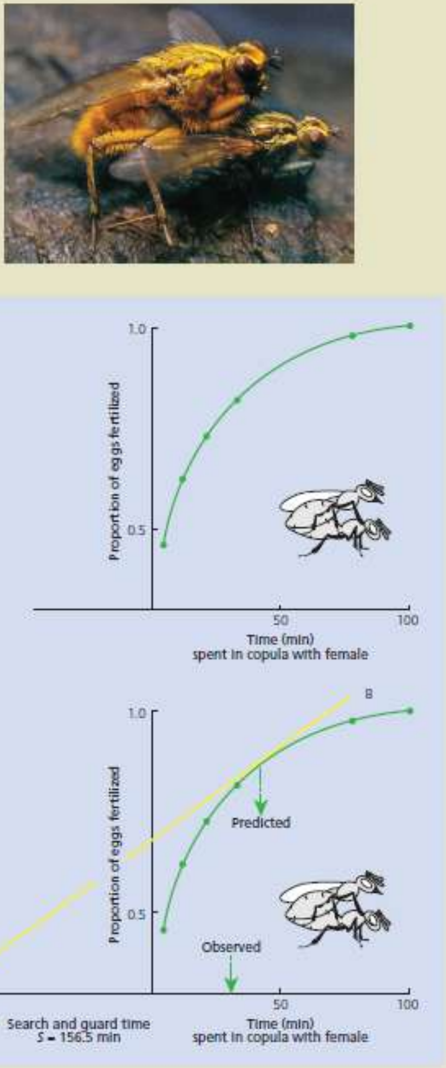

Fig. B3.1.1 (a) The proportion of eggs fertilized by a male dung fly (*Scatophaga stercoraria*) as a function of copulation time: results from sperm competition experiments. (b) The predicted optimal copulation time (that which maximizes the proportion of eggs fertilized per minute), given the shape 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

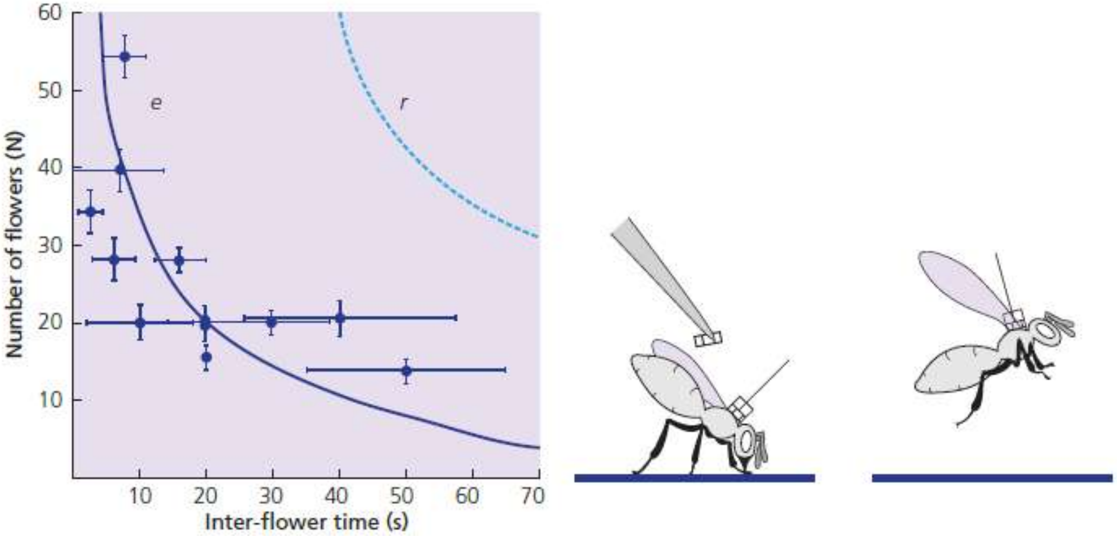

Fig. 3.3 (a) The relationship between load size (expressed as number of flowers visited) carried home by worker bees and flight time between flowers in a patch. Each dot is the mean of an individual bee and the two lines are predictions based on maximizing efficiency (*e*) and maximizing rate (*r*). 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?

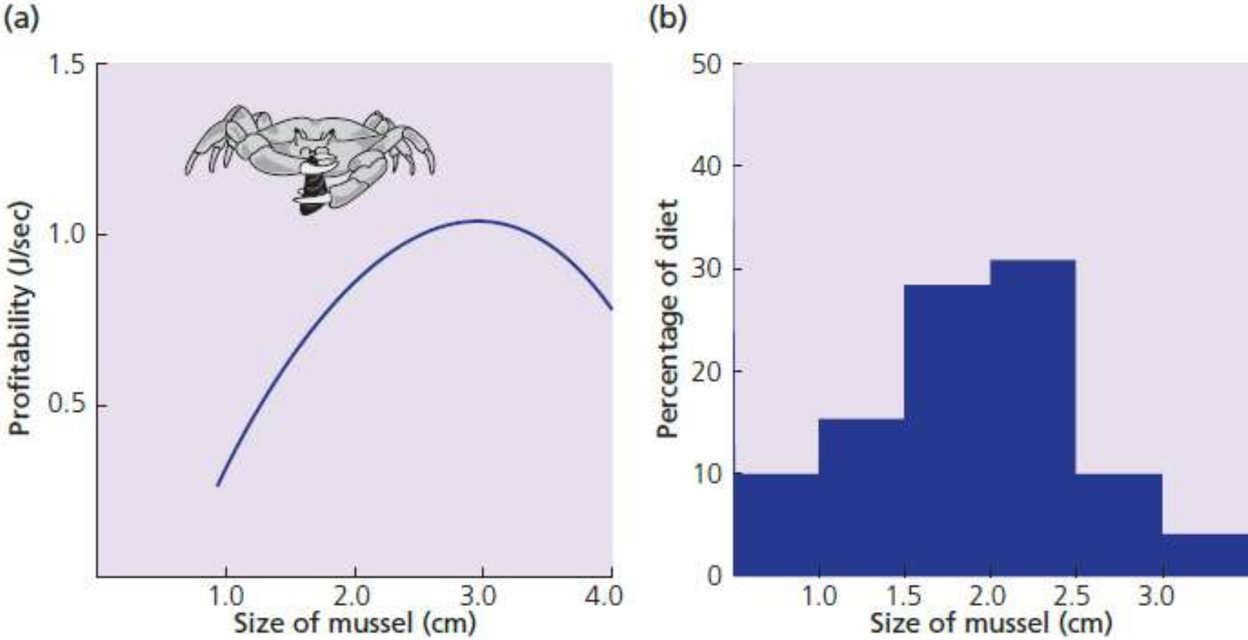

Fig. 3.4 Shore crabs (*Carcinus maenas*) prefer to eat the size of mussel which gives the highest rate of energy return. (a) The curve shows the energy yield per second of handling time used by the crab in breaking open the shell and eating the flesh; (b) the histogram shows the sizes eaten by crabs 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

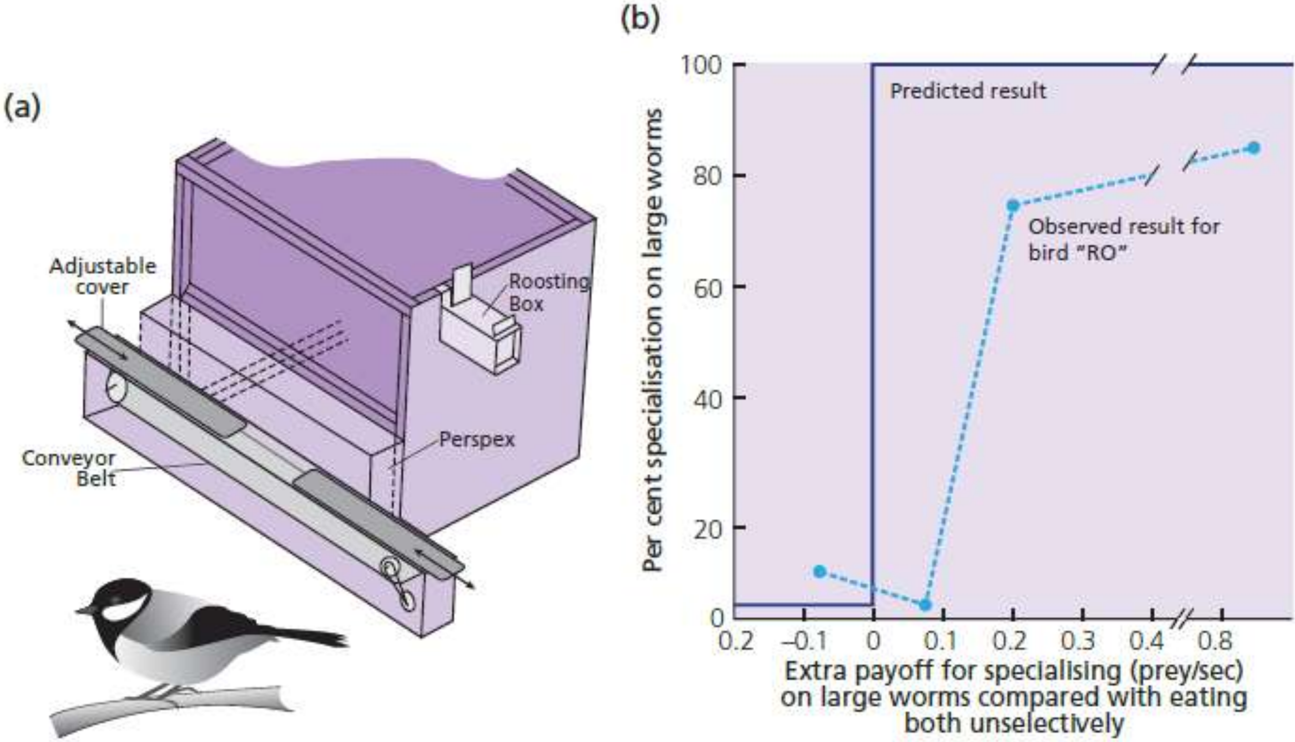

Fig. 3.5 (a) The apparatus used to test a model of choice between big and small worms in great tits (*Parus major*). The bird sits in a cage by a long conveyor belt on which the worms pass by. The worms are visible for half a second as they pass a gap in the cover over the top of the belt and the bird 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

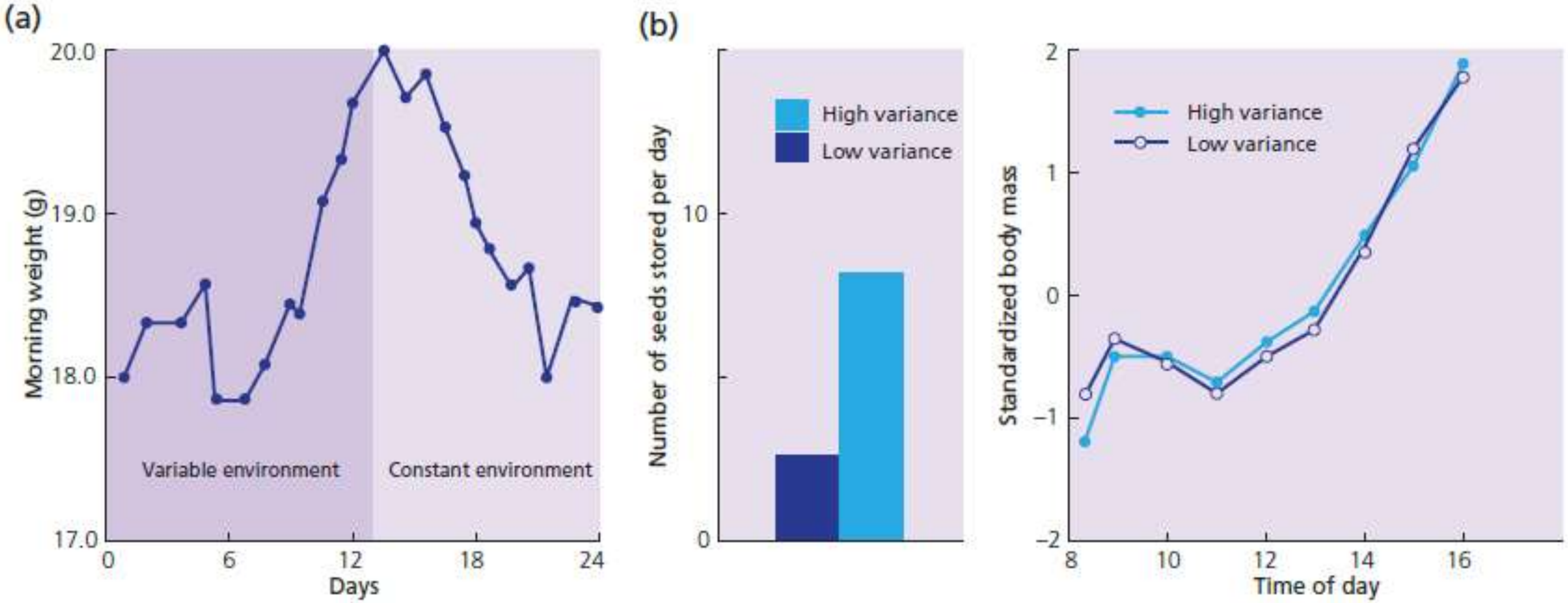

Fig. 3.6 (a) Body reserves and environmental variability. The graph shows the body mass of a captive great tit (one of eight in the experiment) which was transferred from a constant to a variable environment for 12 days before returning to the constant environment. Variability in this experiment was 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).
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Feeding and danger: a trade-off

Balancing foraging and safety

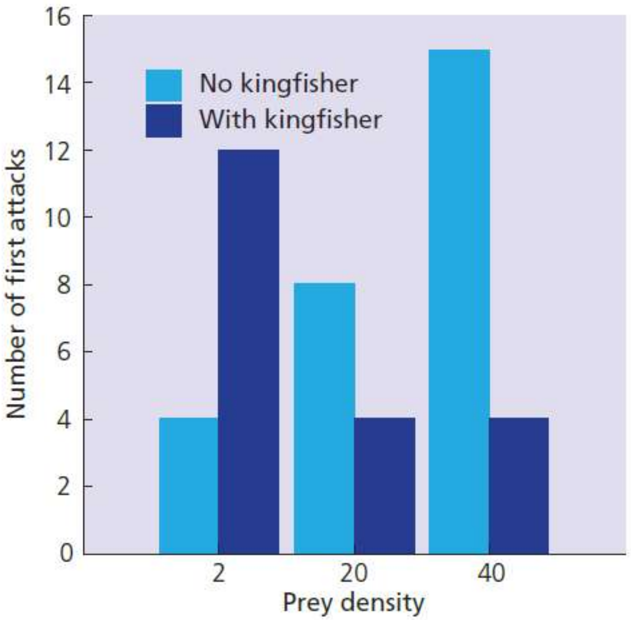


Fig. 3.11 Hungry sticklebacks normally prefer to attack high density areas of prey but after a model kingfisher was flown over the tank they preferred to attack low density areas. From Milinski and Heller (1978). Reprinted with permission from the Nature Publishing Group.

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

Predators versus Prey: Evolutionary Arms Races

Predators versus Prey: Evolutionary Arms Races

If both predators and prey improve over evolutionary time then, whereas their tactics may change, the relative success of each party may not do so.

Antagonistic interaction leading to reciprocal evolutionary change is termed ‘co-evolution’, and any escalation of adaptations and counter-adaptations has been likened to an arms race

This kind of never-ending arms race called ‘Red Queen’ evolution

PREDATORS
selection for improvements
in foraging

PREY
selection for improvements
in defences

Fig. 4.1 Selection for efficient foraging by predators selects for better prey defences, which in turn selects for predator improvements, further prey improvements and so on.

Water fleas versus bacteria

- Water fleas, Daphnia magna, and their bacterial parasite, Pasteuria ramosa (Decaestecker et al., 2007)
- Both the host and the parasite produce resting stages that accumulate in lake sediments, providing a living ‘fossil record’ of past generations.
- Host and parasite populations from different generations (over a 39-year period) were restored by reactivating dormant host eggs and parasite spores.
- Daphnia were then exposed to parasites from the same sediment layer (contemporary parasites) and from sediment layers with past and future parasite populations.
- Infectivity was higher with contemporary parasites than with parasites from previous growing seasons; therefore, the Daphnia evolved to beat past parasite genotypes while the parasites, in turn, rapidly evolved to adapt to the changing host genotypes.
- Infectivity was also lower with parasites from future growing seasons; therefore, parasite adaptations were specific to their current host populations.

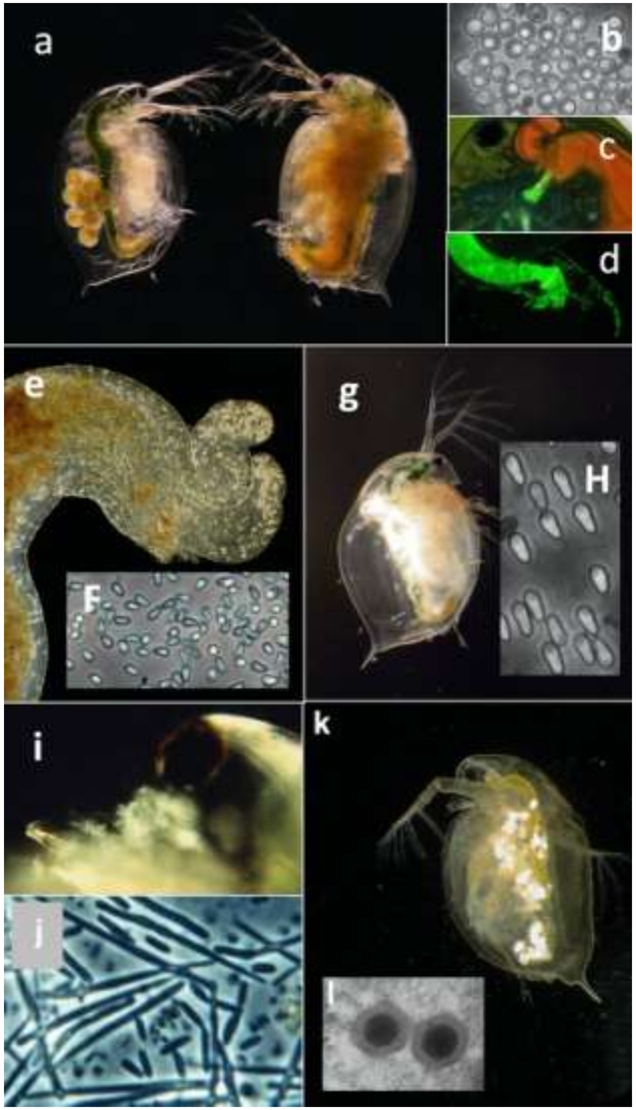


Table 4.1 Examples of predator adaptations and counter-adaptations by prey.

Predator activity	Predator adaptations	Counter-adaptations by prey
Searching for prey	Improved visual acuity	Crypsis (background matching, disruptive patterns, countershading)
	Search image	Polymorphism
	Search limited area where prey abundant	Space out
Recognition of prey	Learning	Masquerade (resemble inedible object) Warning signals of toxicity (aposematism, Müllerian mimicry) Deceive predators by mimicking defended prey (Batesian mimicry)
Catching prey	Secretive approach, motor skills (speed, agility)	Signal to predator that it's been detected Escape flight Startle response: eyespots
	Weapons of offence	Deflect attack Weapons of defence
Handling prey	Subduing skills	Active defence, spines, tough integuments
	Detoxification ability	Toxins

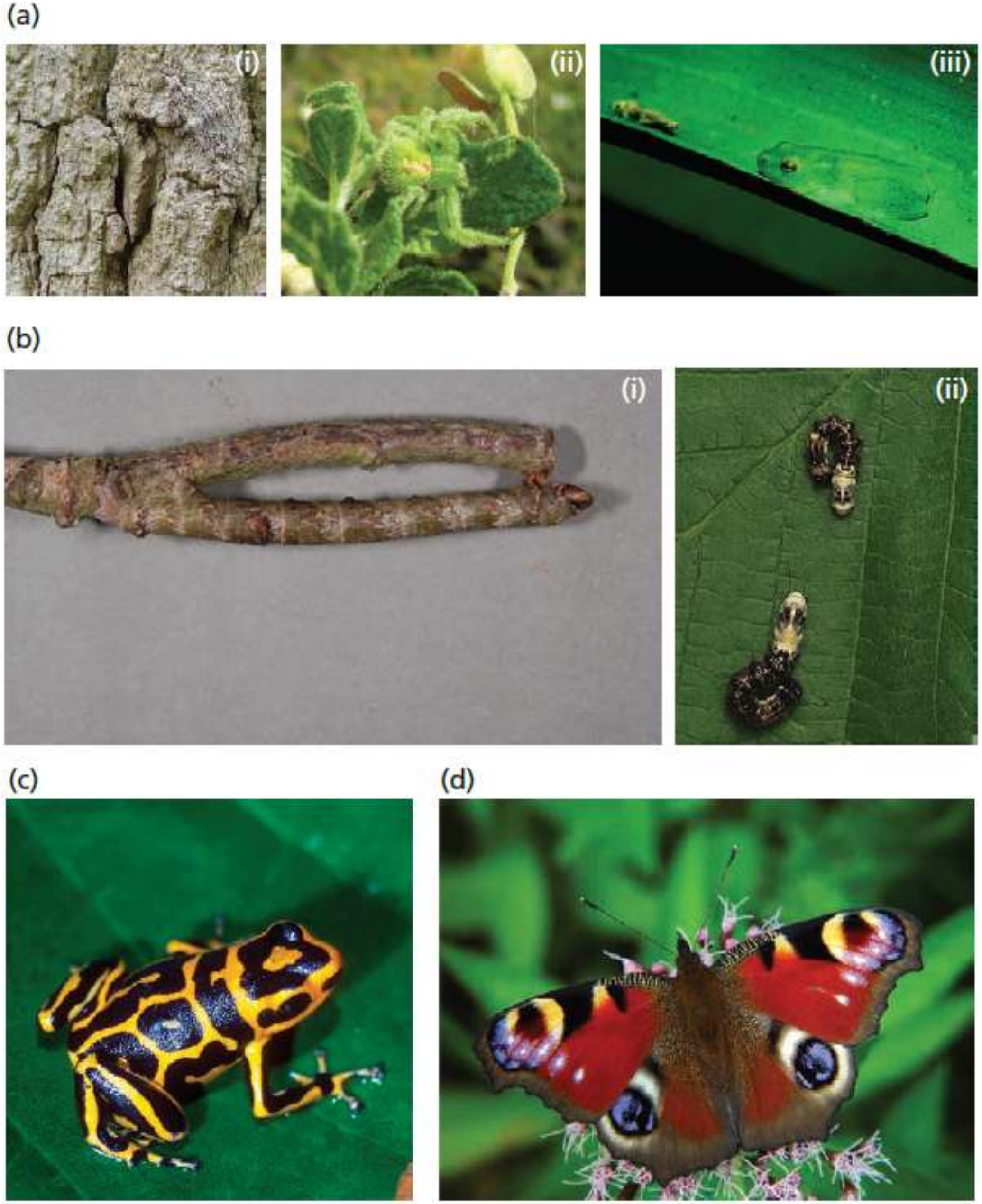


Fig. 4.2 Prey defences include: (a) Camouflage: examples from (i) a moth, (ii) a spider. Photos © Martin Stevens, and (iii) a leaf frog. Photo © Oliver Krüger. (b) Masquerade: (i) this moth caterpillar, *Biston betularia,* mimics a twig. Photo © Nicola Edmunds. (ii) This first instar alder moth, *Acronicta alni*, mimics a bird dropping. Photo © Eira Ihalainen. (c) Bright colouration signals toxicity, as in this poison frog, *Ranitomeya fantastica*. Photo © Kyle Summers. (d) Eyespots: as in this Peacock butterfly. Photo © iStockphoto.com/ Willem Dijkstra.

Predators versus cryptic prey

Underwing moths (Catocala spp), there are up to 40 species living in a particular locality and they are hunted extensively by birds, including blue jays and flycatchers.

‘cryptic’ forewings and ‘startling’ hindwings?

Fig. 4.3 Underwing moths, *Catocala* spp., have cryptic forewings and conspicuously coloured hind wings. This is *C. sponsa*. Photo © Martin Stevens.

Hypotheses, that the forewings decrease detection and the hindwings may have a ‘startle’ effect on a predator that has found the moth, causing the bird to stop momentarily and thus giving the moth time to escape.

Hypothesis about crypsis

Test the importance of crypsis by giving a slideshow to blue jays in an aviary

It was found that the jay made many more mistakes if the moth was presented on a cryptic background than if presented on a conspicuous background.

This provides direct support for the hypothesis about crypsis.

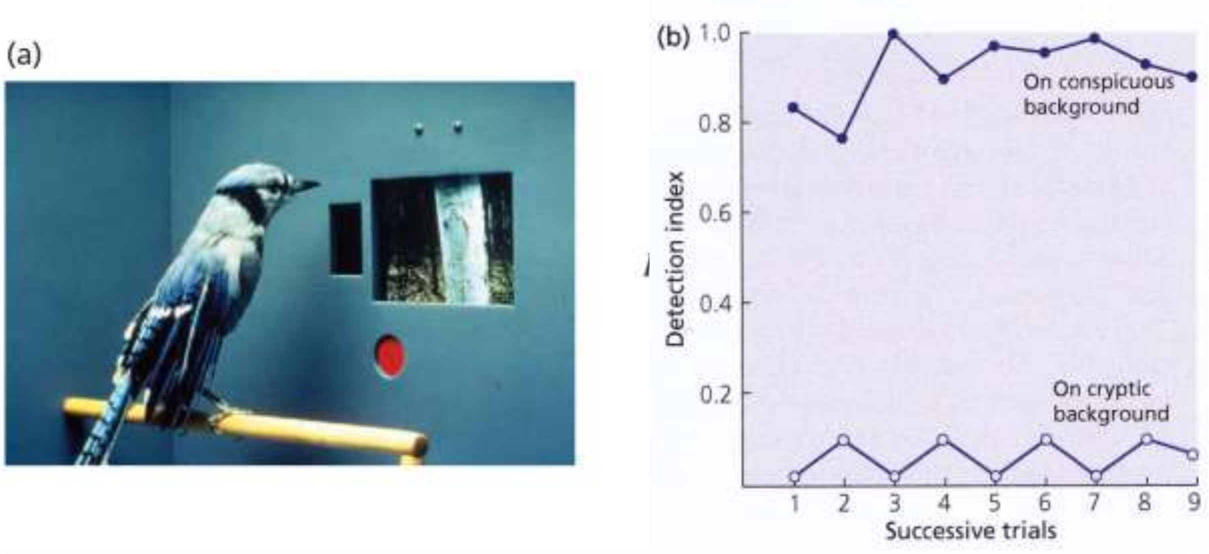


Fig. 4.4 (a) A blue jay in the testing apparatus. The slides are back projected on a screen in front of the bird. The advance key (see text) is to the left. A mealworm is delivered through the circular red hole if the jay makes a correct response. Photo by Alan Kamil. (b) The jays were more likely to detect *Catocala* moths on a conspicuous background. A jay pecking indiscriminately at all slides gets a low score on the detection index. From Pietrewicz and Kamil (1981).

Fig. 4.3 Underwing moths, *Catocala* spp., have cryptic forewings and conspicuously coloured hind wings. This is *C. sponsa*. Photo © Martin Stevens.

Polymorphic cryptic colouration

In many species of underwing moths the forewings are polymorphic, that is there are different colour forms coexisting within the same population.

One hypothesis for this is that when a predator discovers a moth it may form a 'search image' for that particular colour pattern and concentrate on looking for another which looks the same.

Polymorphic prey prevents search image use by predators

Polymorphisms could be maintained if predators focused on common prey types, so that individuals of rarer forms of prey were more likely to be overlooked.

This is known as 'apostatic selection'

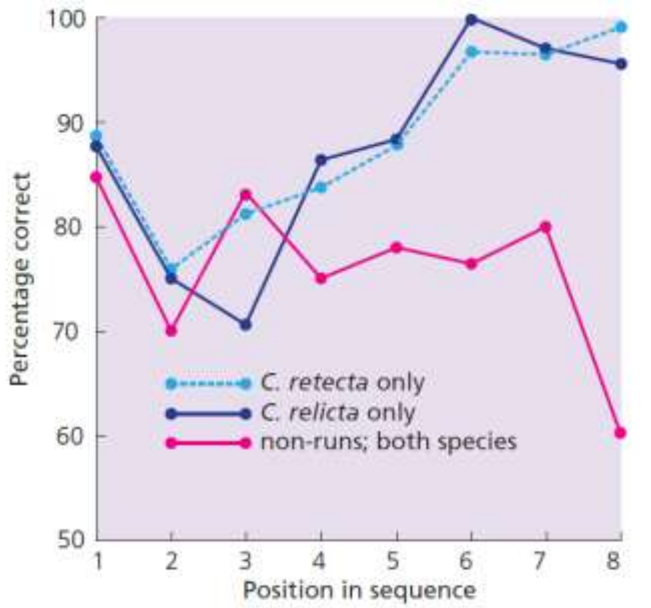


Fig. 4.5 The mean percentage of correct responses by jays when moths are presented in sequences of the same species (runs of either *Catocala retecta* or *Catocala relicta*) or in a sequence containing both species in random order. The jays improved their performance when runs of the same species were presented but not when the two species were presented in a mixed sequence. From Pietrewicz and Kamil (1979). Reprinted with permission from AAAS.

Evolution of prey polymorphisms

Experiment: founding population of equal numbers of three morphs of moth, one of which was more cryptic.

At the end of each day, detected moths were considered as killed and were removed from the population.

The population was then regenerated back to the initial size, maintaining the relative abundance of surviving morphs.

Over thirty days ('generations') the abundance of the most cryptic morph increased but it then stabilized at about 75% of the population, with the other two morphs decreasing to about 12.5% each (Fig. 4.7).

Therefore, a stable polymorphism was produced because of the way the predators focused on the most detectable morph, which depended on both its abundance and crypsis.

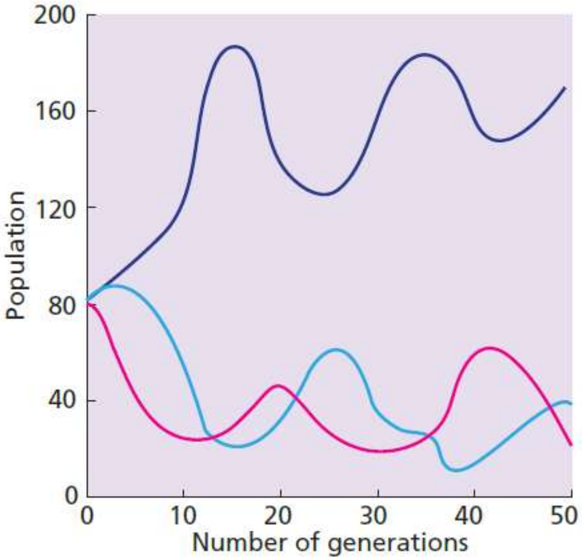


Fig. 4.7 In this experiment, blue jays hunted for digital images of moths on a computer screen (with rewards as in Fig. 4.4). The founding population had equal numbers (80 each) of three morphs, one (dark blue line) being more cryptic. The moth population 'evolved' over 50 generations (see text) to a stable distribution of the three morphs, with the more cryptic form becoming the most abundant. From Bond and Kamil (1998). Reprinted with permission from the Nature Publishing Group.

Experimental evidence for the startle effect

Test : the responses of blue jays to models which had variously patterned ‘hindwings’ concealed behind cardboard ‘forewings’

Jays which had been trained on models with grey hindwings showed a startle response when they were exposed to the brightly patterned hindwings typical of Catocala, whereas subjects trained on brightly patterned models did not startle to a novel grey hindwing.

These results provide good evidence for the startle hypothesis, and the habituation effect suggests an adaptive advantage for the great diversity in hindwing patterns of different sympatric species of Catocala.

Fig. 4.3 Underwing moths, *Catocala* spp., have cryptic forewings and conspicuously coloured hind wings. This is *C. sponsa*. Photo © Martin Stevens.

Enhancing camouflage

Disruptive colouration

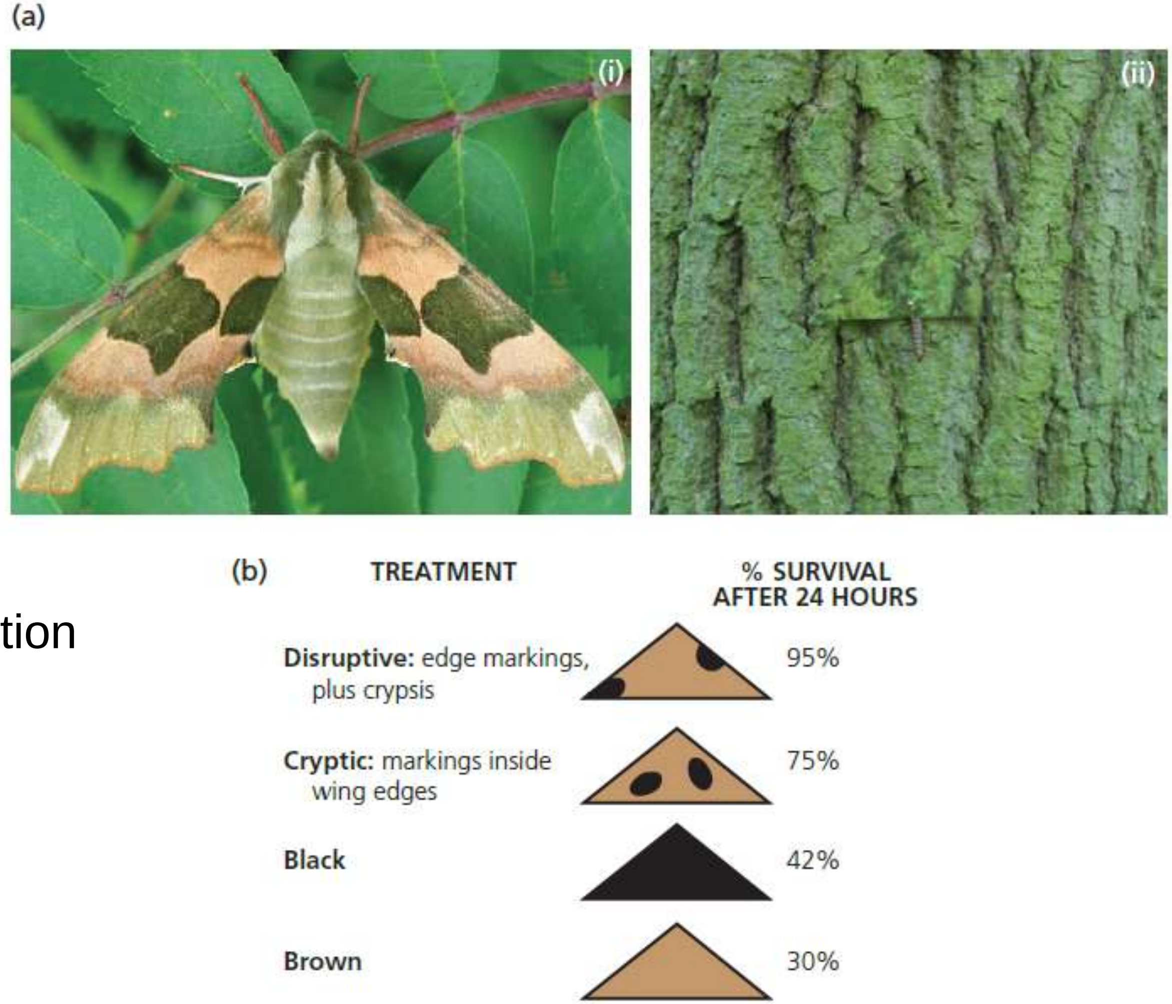


Fig. 4.9
(a) (i) Disruptive patterns on the wing margins of this lime hawk moth conceal the body outline. (ii) An artificial moth with cardboard wings and a mealworm body, pinned to a tree trunk to test the effects of disruptive patterns Photos © Martin Stevens. (b) Results of a field experiment with artificial moths (see text). Disruptive patterns increase survival beyond a cryptic pattern, which in turn survives better than plain black or brown wings. From Cuthill *et al*. (2005). Reprinted with permission from the Nature Publishing Group.

Enhancing camouflage

Countershading

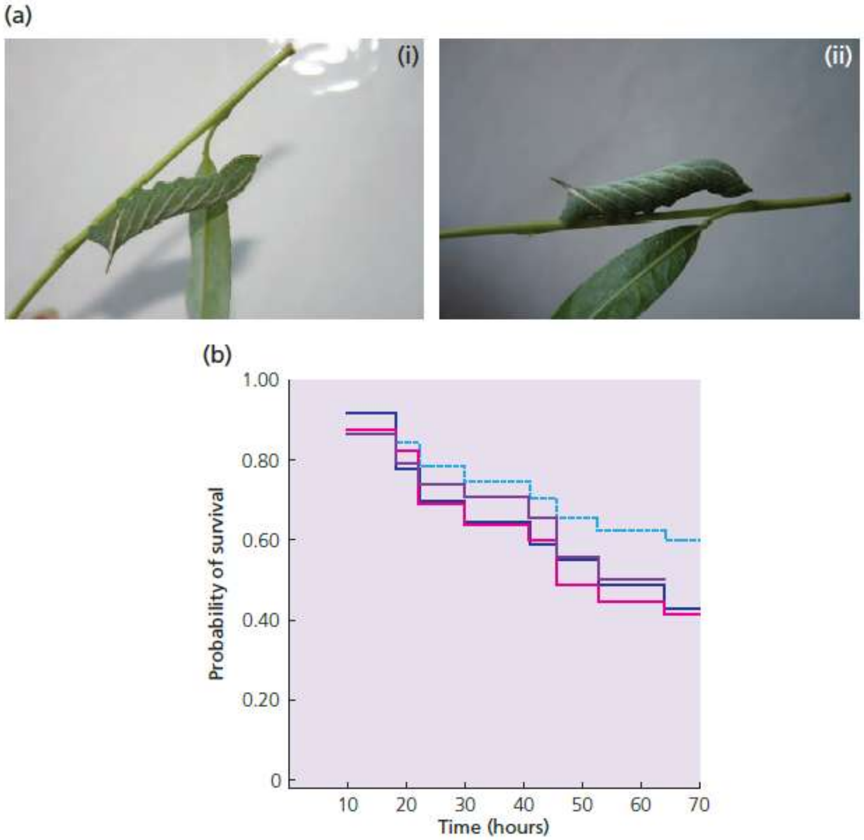


Fig. 4.10 Countershading. (a) (i) This eyed hawkmoth caterpillar, *Smerinthus ocellata*, feeds with its ventral surface uppermost. It has a darker ventral surface which, when lit from above combines with the shadow on the dorsal surface (below) to give it a uniform reflectance, which helps to conceal its body shape. (ii) When turned, so it is now illuminated dorsally, the lighter dorsal surface is highlighted and the darker ventral surface is now in shadow, creating a more pronounced gradient and rendering the caterpillar more conspicuous. Photos © Hannah Rowland. (b) An experiment with pastry 'caterpillars' pinned to the upper surface of branches in a wood. The countershaded caterpillars (dashed light blue line) survived better than plain dark (red line), plain light (purple line) or reverse-shaded prey (darker ventral surface; dark blue line). From Rowland *et al*. (2008).

Masquerade

Warning colouration: aposematism

Why bright colours?

Some prey are brightly coloured rather than cryptic.

Fruit often becomes more brightly coloured when ripe, which increases the chance that it is eaten and so the seeds are dispersed. This is an example of a prey which is selected to be eaten by predators.

On the other hand, many prey are also brightly coloured, yet they are presumably selected to avoid predation.

Prey often have red, yellow or orange markings, often combined with black, which makes them especially conspicuous against the green vegetation

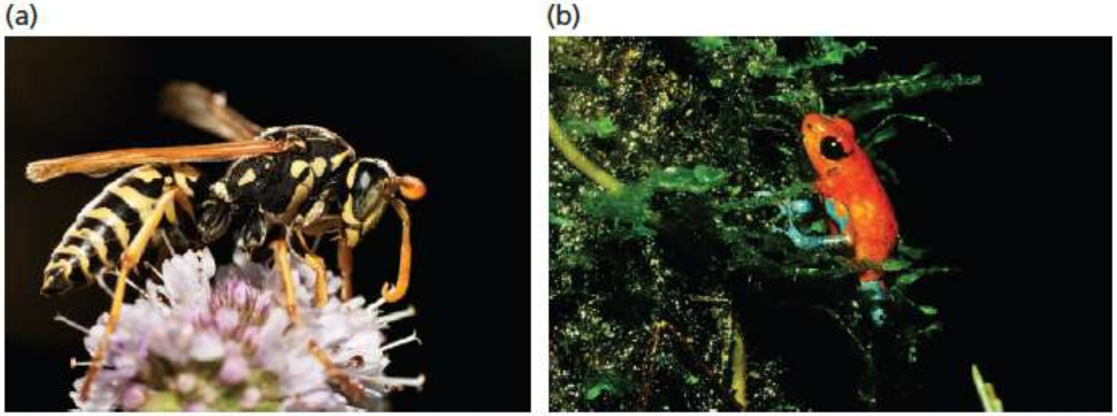


Fig. 4.11 Brightly coloured prey often have repellent defences. (a) A stinging wasp. Photo © iStockphoto.com/ElementalImaging (b) A red poison dart frog. Photo © Oliver Krüger.

Brightly coloured prey are often toxic or have other defences

Poisson frogs (Dendrobatidae) of tropical central and south America are a monophyletic group with some 210 species

Some are cryptic and palatable and they tend to have a generalized diet.

Others are brightly coloured (yellow, blue, red or lime green, often combined with black) and they are highly toxic, deriving at least some of their skin alkaloids from their specialized diet of ants, termites and mites

Such warning colouration is known as **aposematism**

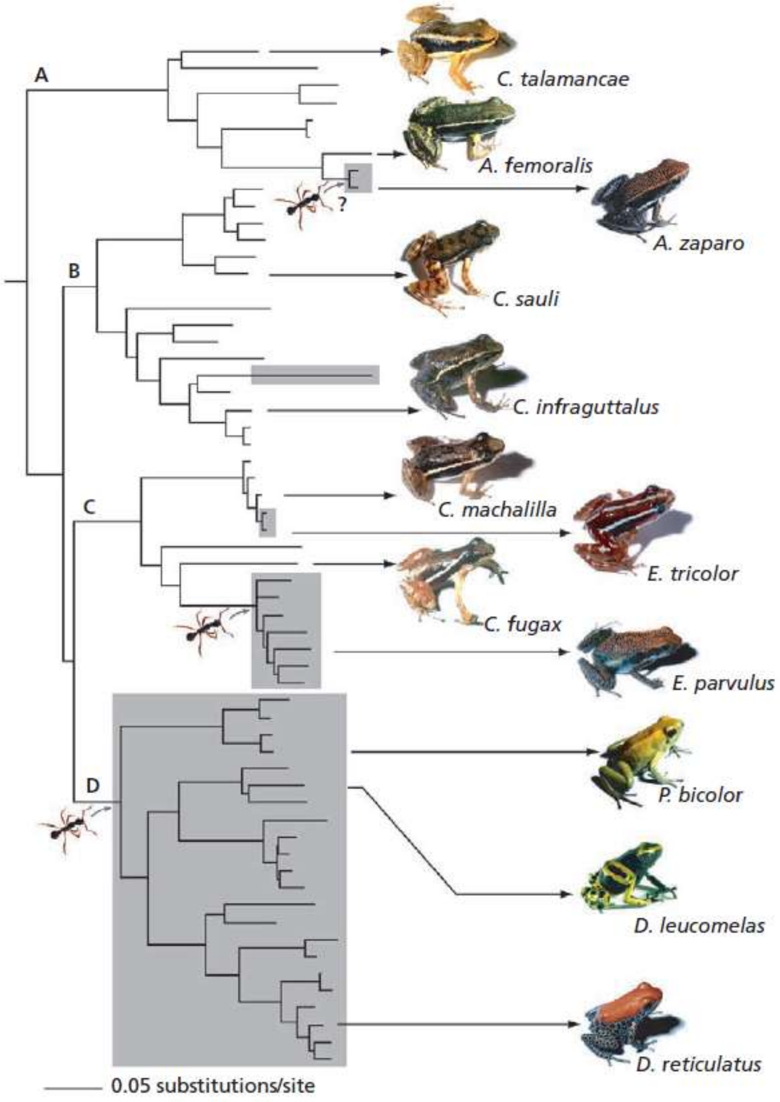


Fig. 4.12 Phylogeny of poison frogs (Dendrobatidae) based on molecular genetic analysis. The ant icons indicate two origins of a specialized diet, and a possible third origin is indicated by a question mark. The column of photos on the left shows representative cryptic and non-toxic species. The column on the right shows conspicuous and toxic species (the toxicity of *A. zaparo* is unknown). Figure from Santos *et al.* (2003); by courtesy of David Cannatella and Juan Carlos Santos.

Conspicuous colours help predators to learn to avoid unpalatable prey

Domestic chicks with different coloured breadcrumbs.

The chicks showed equal preference for blue or green crumbs.

In the experiment, all the crumbs were made distasteful by dipping them in quinine sulfate and mustard powder.

Whatever the background colour, the chicks took more of the conspicuous prey early on in the experiment.

However, overall the cryptic prey suffered the greatest predation. This suggests that it does indeed pay a distasteful prey to be conspicuous.

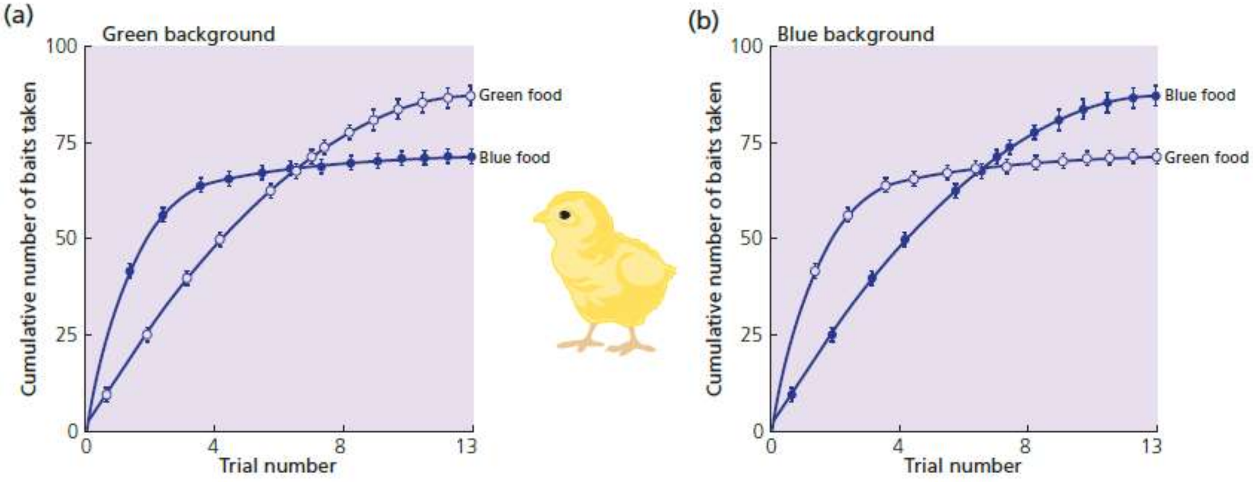


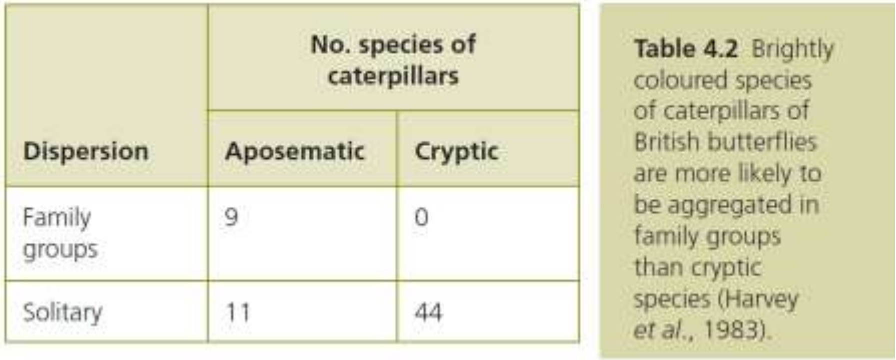
Fig. 4.13 Cumulative number of conspicuous and cryptic distasteful prey taken in successive trials by chicks. In (a) the green food is cryptic, in (b) the blue food is cryptic. In both experiments, by the end of the trial the distasteful prey has been eaten less when it is conspicuous. From Gittleman and Harvey (1980). Reprinted with permission from the Nature Publishing Group.

The evolution of warning colouration

Conspicuousness and distastefulness: which evolved first?

Distasteful, brightly coloured insects were often clumped in family groups

Traits can be favoured because they benefit relatives, who share copies of the same genes, is termed kin selection



	No. species of caterpillars	
Dispersion	**Aposematic**	**Cryptic**
Family groups	9	0
Solitary	11	44

Table 4.2 Brightly coloured species of caterpillars of British butterflies are more likely to be aggregated in family groups than cryptic species (Harvey *et al.*, 1983).

Many predators are reluctant to attack a novel prey item ('neophobia') which would also promote the survival chances of a mutant, more conspicuous prey type

Grouping is not always critical for the evolution of bright colours

Trade-off between the costs of conspicuousness in increasing the probability of attack by naïve predators, and the benefits from increased protection against experienced predators through more memorable and detectable signalling

Mimicry

The association between bright colours and repellent defences has led to the evolution of various forms of mimicry

Müllerian mimicry: repellent species look alike

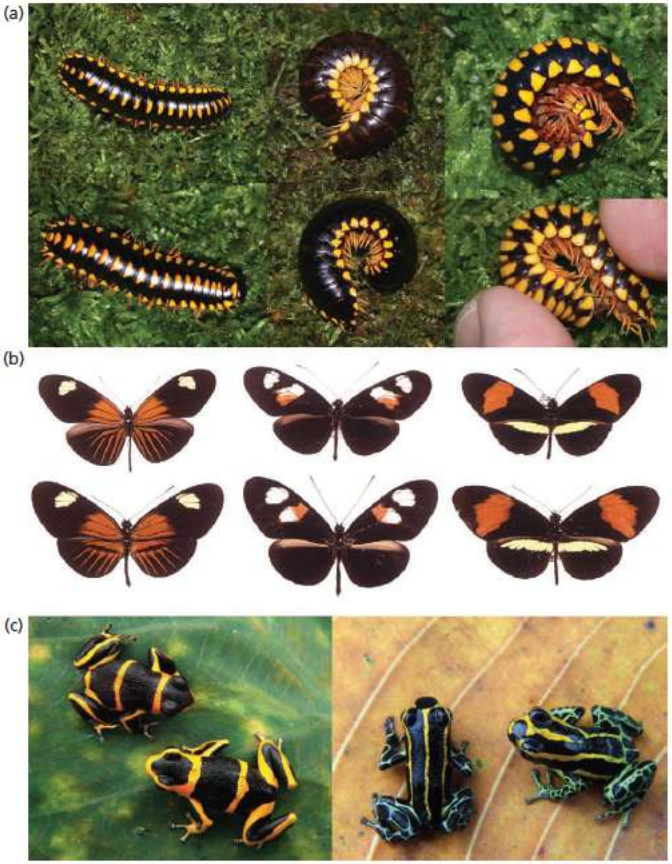


Fig. 4.14 Müllerian mimicry. In each case, populations of distantly related species converge on the same brightly coloured warning pattern within a single locality but the patterns vary across their range. (a) North American millipedes of the *Apheloria* clade (top row) and their mimics in the *Brachoria* clade (below) in three geographical regions. Photo © Paul Marek. (b) *Heliconius erato* (top row) and its mimic *Heliconius melpomene* (bottom row) in three geographical regions of the neotropics. Photo © Bernard D'Abrera and James Mallet. (c) Peruvian *Ranitomeya* (*Dendrobates*) frogs from two regions. *Ranitomeya imitator* (left in both panels) and its mimics *R. summersi* (left panel) and *R. ventrimaculata* (right panel). Photo © Jason Brown. From Merrill and Jiggins (2009).

Mimicry

The association between bright colours and repellent defences has led to the evolution of various forms of mimicry

Batesian mimicry: cheating by palatable species

Fig. 4.15 Batesian mimicry. (a) The highly venemous Sonoran coral snake, *Micruroides euryxanthus*, is the model for (b) its non-venemous Batesian mimic, the Sonoran mountain kingsnake, *Lampropeltis pyromelana*. These photographs were taken within 3 km of each other in Arizona. Photos © David W. Pfennig (c) An English pub sign fooled by a Batesian mimic; this is a hoverfly (*Syrphidae*)! Photo by Francis Gilbert.

Trade-offs in prey defences

Costs of aposematism

Allocation costs: Increased investment in defence means fewer resources for growth and reproduction.

Opportunity costs: Improved crypsis on an oak tree may limit habitat choice because of increased conspicuousness on other backgrounds, and may restrict other activities, for example signalling to rivals or mates.

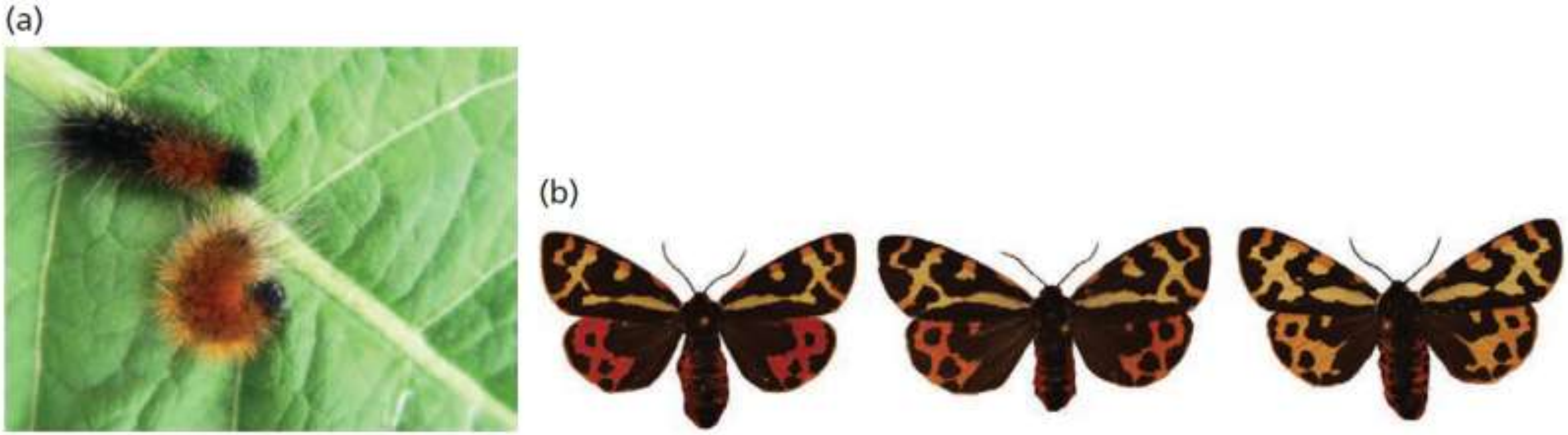


Fig. 4.16 Variation in aposematic colouration among individual wood tiger moths, *Parasemia plantaginis*. (a) The caterpillars vary in the size of the orange patch. (b) The hindwings of female moths vary from bright red to pale orange. Photos © Eira Ihalainen.

Trade-offs in prey defences

Wood tiger moth, Parasemia plantaginis, the colouration of both caterpillars and adult moths varies locally and geographically; the orange patch on the caterpillars may cover from 20 to 90% of the body, while the female moth’s hindwing varies from pale orange to bright red

More orange caterpillars and redder adult moths are more likely to be rejected by predatory birds

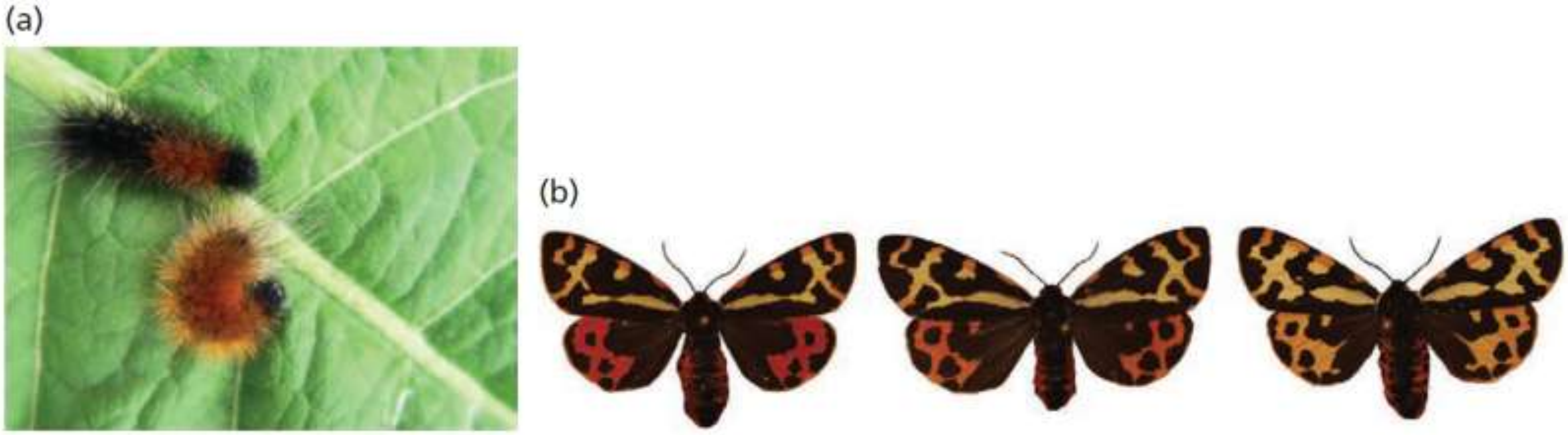


Fig. 4.16 Variation in aposematic colouration among individual wood tiger moths, *Parasemia plantaginis*. (a) The caterpillars vary in the size of the orange patch. (b) The hindwings of female moths vary from bright red to pale orange. Photos © Eira Ihalainen.

Trade-offs in prey defences

Costly to wear: The size of the caterpillar’s orange patch is heritable, so laboratory selection lines were used to produce caterpillars with large and small orange patches.

At low temperatures, caterpillars with smaller orange patches (hence more black) grew faster because they could absorb heat more effectively and, hence, forage for longer each day.

Caterpillars reared at low temperatures developed smaller and darker orange patches, suggesting that the costs of thermoregulation have selected for phenotypic plasticity in aposematic colouration.

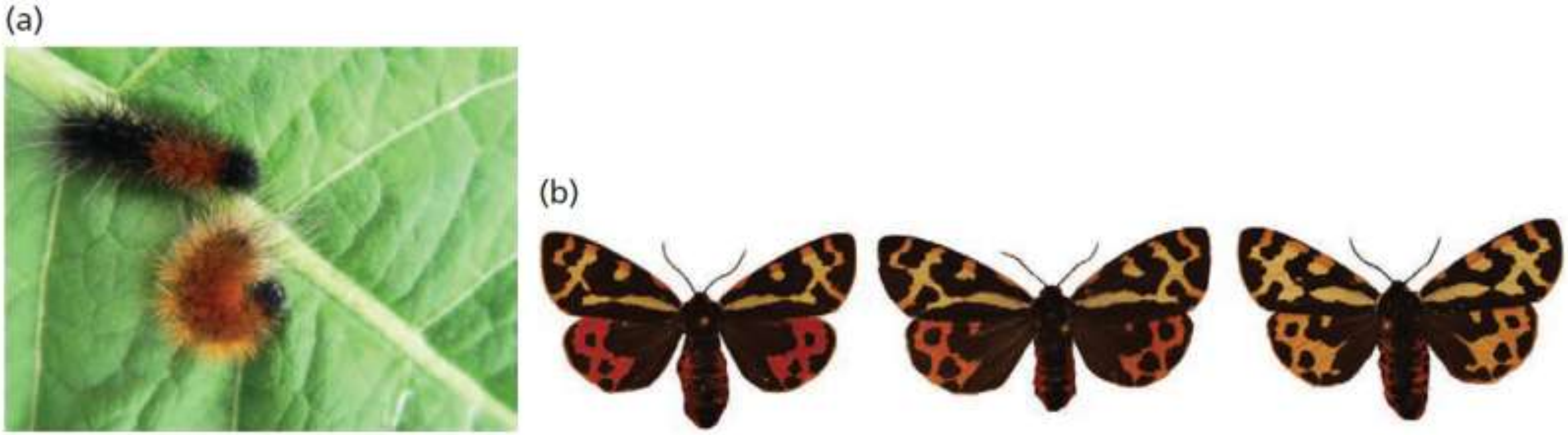


Fig. 4.16 Variation in aposematic colouration among individual wood tiger moths, *Parasemia plantaginis*. (a) The caterpillars vary in the size of the orange patch. (b) The hindwings of female moths vary from bright red to pale orange. Photos © Eira Ihalainen.

Trade-offs in prey defences

Costly to make: In another experiment, caterpillars were reared on plants with either a low or a high concentration of glycosides. Both groups of caterpillars and subsequent adult moths had equal levels of toxins in their bodies, so excess toxins were disposed of effectively.

However, detoxification was costly because moths reared on the high concentrations produced fewer offspring. Furthermore, although the diet did not affect caterpillar colouration, female moths reared on high toxin concentrations developed less bright hindwings.

This suggests that resources devoted to getting rid of toxins left fewer resources for pigment production

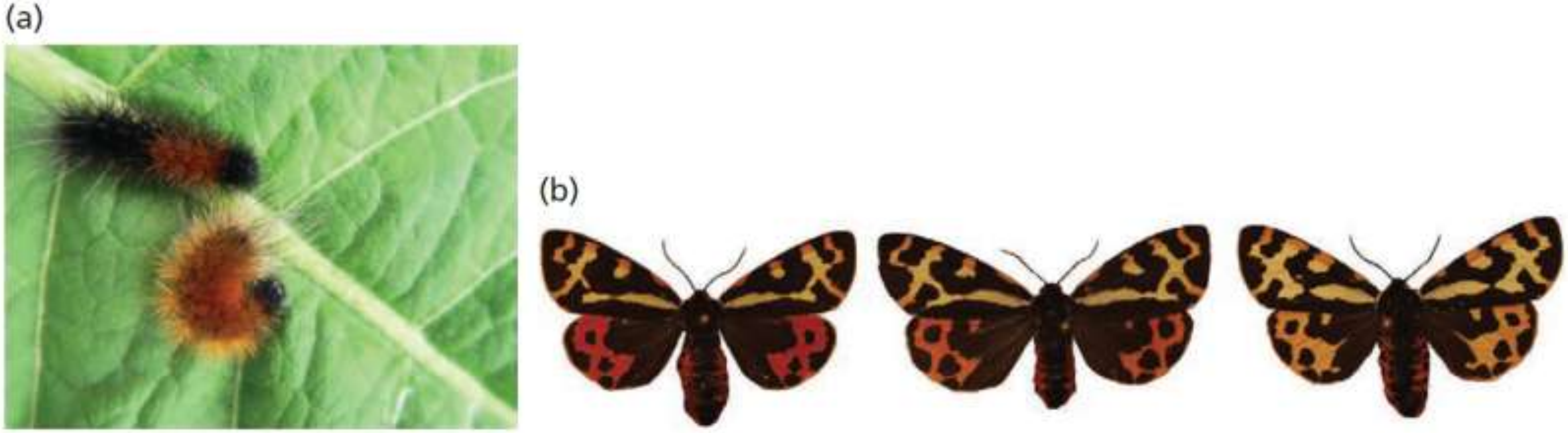


Fig. 4.16 Variation in aposematic colouration among individual wood tiger moths, *Parasemia plantaginis*. (a) The caterpillars vary in the size of the orange patch. (b) The hindwings of female moths vary from bright red to pale orange. Photos © Eira Ihalainen.

Conspicuousness versus crypsis

As a defence against predators it may pay to be cryptic, but this may conflict with the advantage of being conspicuous for other activities such as territory defence or mate attraction.

The coloration of guppies (Poecilia reticulata)

Laboratory experiments showed that brighter colours brought a mating advantage. Females were particularly attracted to the orange spots

In controlled laboratory populations studied over many generations, males kept with predators evolved to be duller, while those kept isolated from predators evolved to be brighter, with both larger and more spots

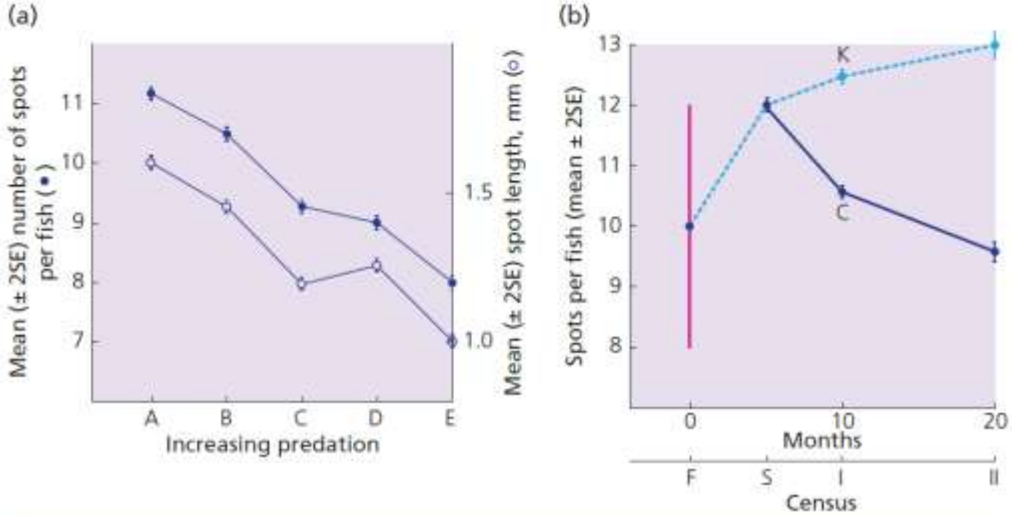


Fig. 4.17 Influence of predation on colour pattern of male guppies. (a) Both number of colour spots per fish and spot size are smaller in streams with greater predation. The main predators are other fish and prawns. Data from five streams in Venezuela with increasing levels of predation from A to E. From Endler (1983). (b) A selection experiment in the laboratory. F, foundation population of guppies kept with no predators. S, start of the experiment; predators added to population C but not to population K. Note the rapid change in population C after predation began. I and II are the dates of two censuses. From Endler (1980).

Cuckoos versus hosts

Some species of birds, fish and insects are brood parasites; they lay their eggs in the nests of other species (hosts) and so get their young raised for free.

Fig. 4.19 (a) A female common cuckoo parasitizing a reed warbler nest. Firstly she removes a host egg. Then, holding it in her bill, she sits briefly in the nest and lays her own egg in its place. Photo by Ian Wyllie.
(b) A cuckoo egg (right) in a reed warbler nest. (c) A newly-hatched cuckoo chick ejecting host eggs one by one. Photo © Paul Van Gaalen / ardea.com (d) The reed warbler hosts continue to feed the young cuckoo even as it grows to seven times their own weight. Photo © osf.co.uk. All rights reserved.

Fig. 4.18 The common cuckoo, *Cuculus canorus*, has several genetically different host-races each of which lays a distinctive egg (central column) which matches, to varying extents, the eggs of its particular host species (left-hand column). In the examples here, the host species and their corresponding cuckoo host races are, from top to bottom: robin, pied wagtail, dunnock, reed warbler, meadow pipit and great reed warbler. The right-hand column is of variously coloured model eggs used to test host discrimination. From Brooke and Davies (1988).

Hosts have evolved in response to cuckoos

Compared to species with no history of brood parasitism, species exploited by cuckoos have less variation in the appearance of eggs within a clutch and more variation between clutches of different females.

This makes life harder for the cuckoo, since it is easier for a host to spot a foreign egg if all its own eggs look exactly the same, and distinctive markings for individual host females makes it harder for the cuckoo to evolve a convincing forgery of that species' eggs.

Fig. 4.21 Tawny-flanked prinia eggs (outer circle) and cuckoo finch eggs (inner circle). The diversity of egg 'signatures' in the host leads to a signature-forgery arms race between host and cuckoo and remarkable diversity in egg colours and markings within a species. From Spottiswoode and Stevens (2012). Photo by Claire Spottiswoode.

The egg arms race: a coevolutionary sequence

(i) At the start, before small birds are parasitized, they show little, if any, rejection of foreign eggs (small birds with no history of cuckoo parasitism, because they are unsuitable as hosts, do not reject).

(ii) In response to parasitism, hosts evolve egg rejection (hosts do reject) and more distinctive individual egg signatures (hosts have more egg variation).

(iii) In response to host rejection, cuckoos evolve egg mimicry (egg mimicry in the different host races reflects the degree of host discrimination).

(iv) If cuckoo egg mimicry is sufficiently good, and if parasitism levels are not too high, then it may be best for hosts to accept most cuckoo eggs to avoid the costs of mistakenly rejecting their own eggs from unparasitized clutches.

Competing for Resources

Competing for Resources

When many individuals exploit the same limited resources, they become competitors

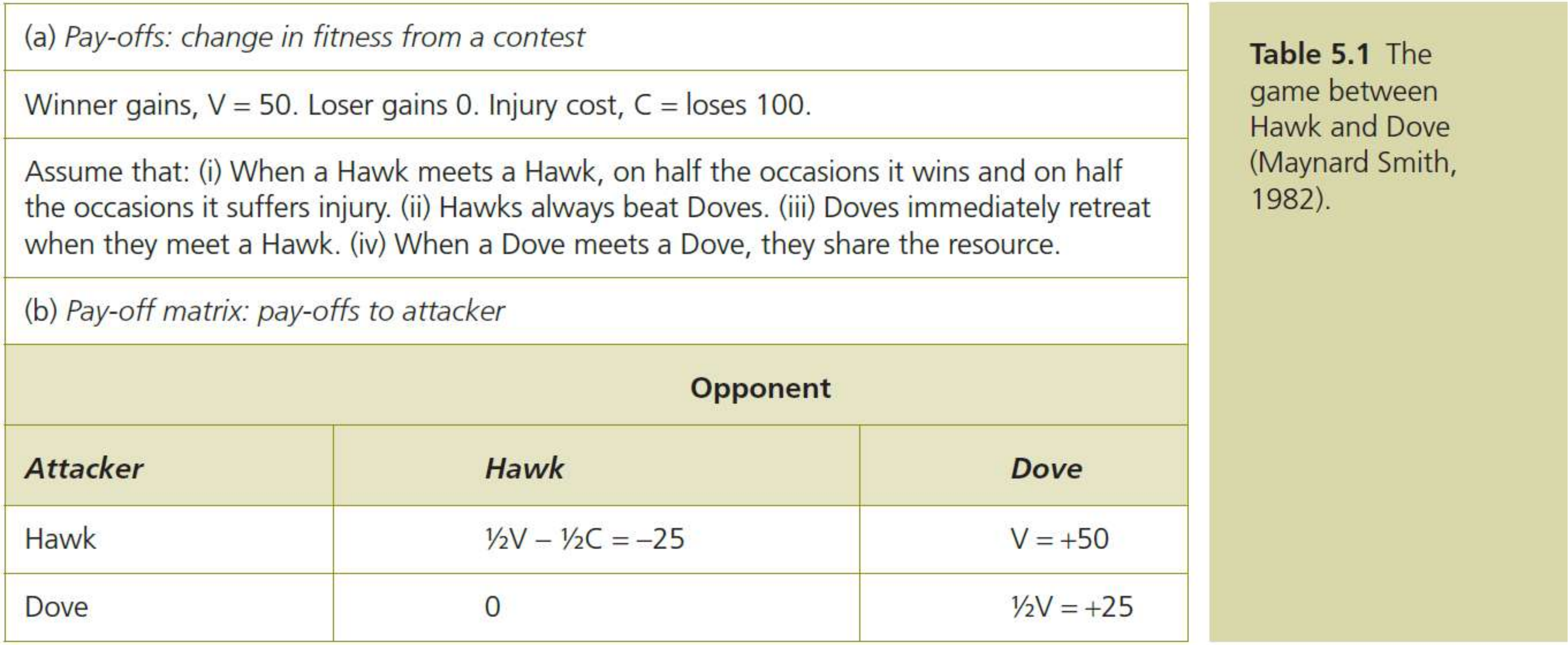
The best way for one individual to behave often depends on what its competitors are doing

The pay-offs for various strategies are frequency dependent

Evolutionarily Stable Strategy (ESS), a strategy that, if all members of a population adopt it, cannot be bettered by an alternative strategy

The Hawk–Dove game

Assume contestants meet randomly to compete for a resource



(a) *Pay-offs: change in fitness from a contest*

Winner gains, $V = 50$. Loser gains 0. Injury cost, $C =$ loses 100.

Assume that: (i) When a Hawk meets a Hawk, on half the occasions it wins and on half the occasions it suffers injury. (ii) Hawks always beat Doves. (iii) Doves immediately retreat when they meet a Hawk. (iv) When a Dove meets a Dove, they share the resource.

(b) *Pay-off matrix: pay-offs to attacker*

	Opponent	
Attacker	***Hawk***	***Dove***
Hawk	$\frac{1}{2}V - \frac{1}{2}C = -25$	$V = +50$
Dove	0	$\frac{1}{2}V = +25$

Table 5.1 The game between Hawk and Dove (Maynard Smith, 1982).

How would evolution proceed in this game, if all individuals in the population are Doves ?

A mixture of Hawk and Dove is evolutionarily stable

h: be the proportion of Hawks in the population, the proportion of Doves must be $(1 - h)$.

The average pay-off for a Hawk is the pay-off for each type of contest multiplied by the probability of meeting each type of contestant:

H average = $-25h + 50 (1 - h)$

Dove the average pay-off will be:

D average = $0h + 25 (1 - h)$

At the stable equilibrium, H average must equal D average. In this case $h = 0.5$

The ESS could come about in two ways:

(1) There is an evolutionarily stable polymorphic state, with individuals all playing pure strategies, half of them Hawk and half of them Dove.

(2) Individuals all adopt a mixed strategy, playing Hawk randomly with probability ½ and Dove with probability ½.

The Hawk–Dove game

At the ESS, the average pay-off per contest is +12.5.

If only everyone had agreed to be Doves, the pay-off would be +25!

The optimal strategy to maximize everyone’s fitness is often higher than the pay-offs at the ESS!

Nevertheless, we expect evolution to lead to stable strategies because, in the words of Richard Dawkins, ‘they are immune to treachery/cheat from within’.

At the stable equilibrium there is often variation in the population; either between or within individuals. Variation is, therefore, not always noise about a population norm.

The difference between V (winner gain) and C (injury cost) influence the ratio of Hawk (aggresive) strategy

If V > C, higher ration of Hawk is an ESS

If V < C, higher ration of Dove is an ESS

Competition by exploitation: the ideal free distribution

The ideal free model

It assumes that animals are free to go where they will do best (there is no exclusion of weaker competitors by stronger ones) and that the animals are ideal in having complete information about the availability of resources.

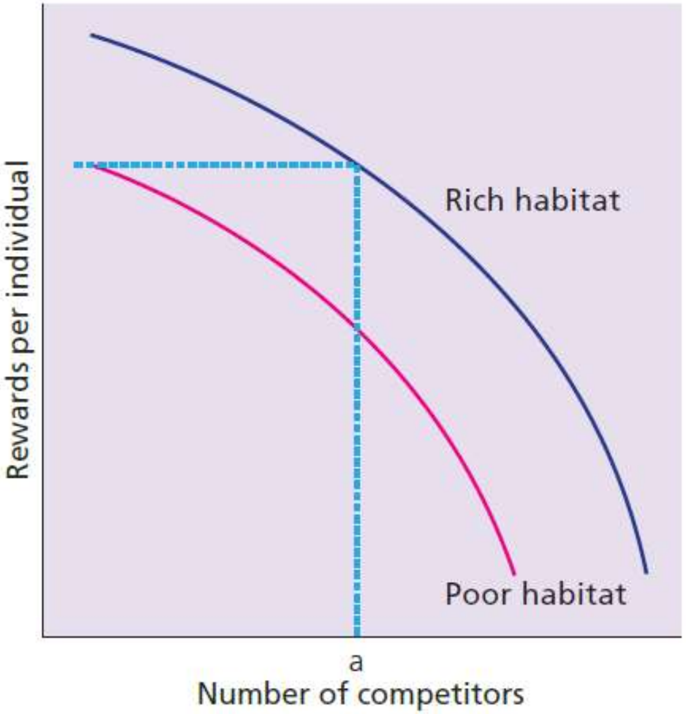


Fig. 5.1 The ideal free distribution. There is no limit to the number of competitors that can exploit the resource. Every individual is free to choose where to go. The first arrivals will go to the rich habitat. Because of resource depletion, the more competitors the lower the rewards per individual so at point *a* the poor habitat will be equally attractive. Thereafter, the two habitats should both be filled so that the rewards per individual are the same in each. After Fretwell (1972).

Competing for food: sticklebacks and ducks

Fish and ducks settle in a stable distribution between feeding patches

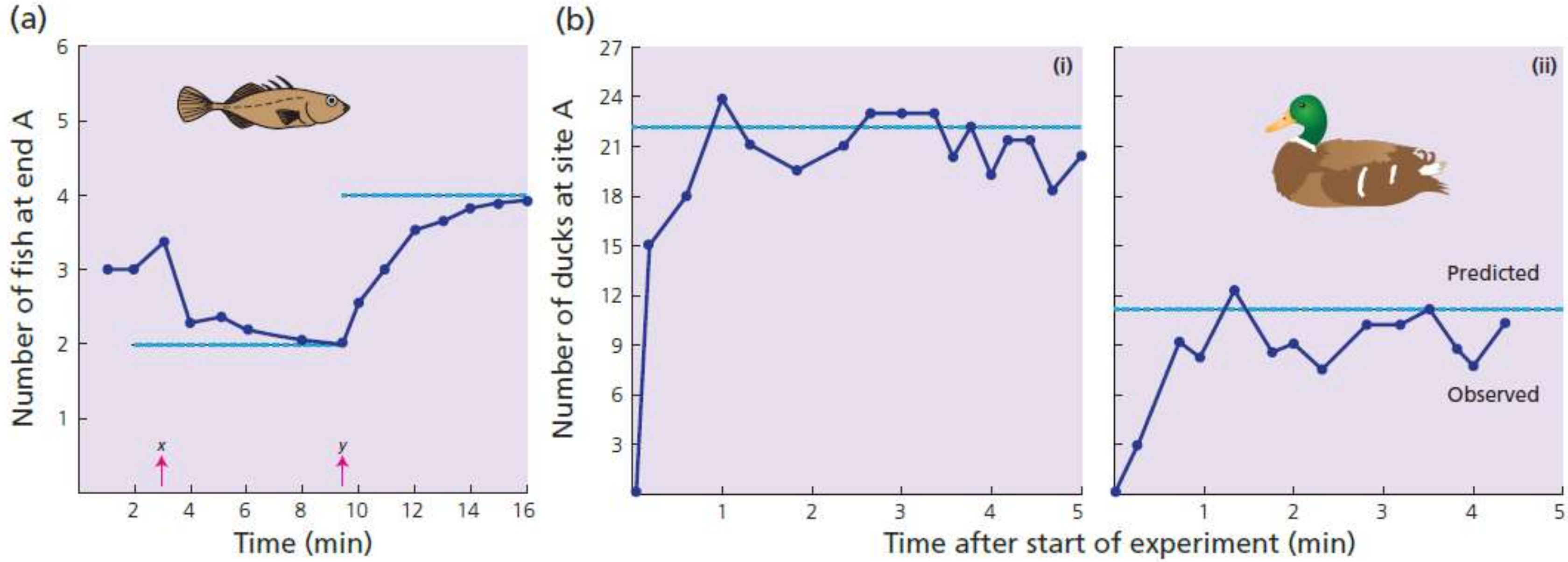


Fig. 5.2 (a) Milinski's (1979) feeding experiment with six sticklebacks. At time *x*, end B of the tank had twice the amount of food as end A. At time *y* the profitabilities were reversed. The pale blue lines indicate the number of fish predicted at end A according to ideal free theory, and the points and dark blue line are the observed numbers (mean of several experiments). (b) Harper's (1982) feeding experiment with a flock of 33 mallard ducks. In (i) food was thrown into the pond at twice the rate at site A compared to site B. In (ii) the profitabilities were reversed. Pale blue lines indicate the predicted numbers at site A according to ideal free theory. The points and dark blue line are the observed numbers (means of many experiments).

Competing for mates: dung flies

A competitive game for male dung flies: how long to wait for a female at a cowpat?

The best decision for one individual depends on what other competitors are doing

-If most males wait for short times then a male who stayed a little longer would have high mating success because he could claim all the late arriving females.

-If, on the other hand, most males were staying a long time then it would pay our male to move quickly to a new pat to claim the early arriving females there.

Competing for mates: dung flies

Males vary their stay time depending on their direct assessment of female arrival rate, or indirect assessment based on pat age and competitor numbers.

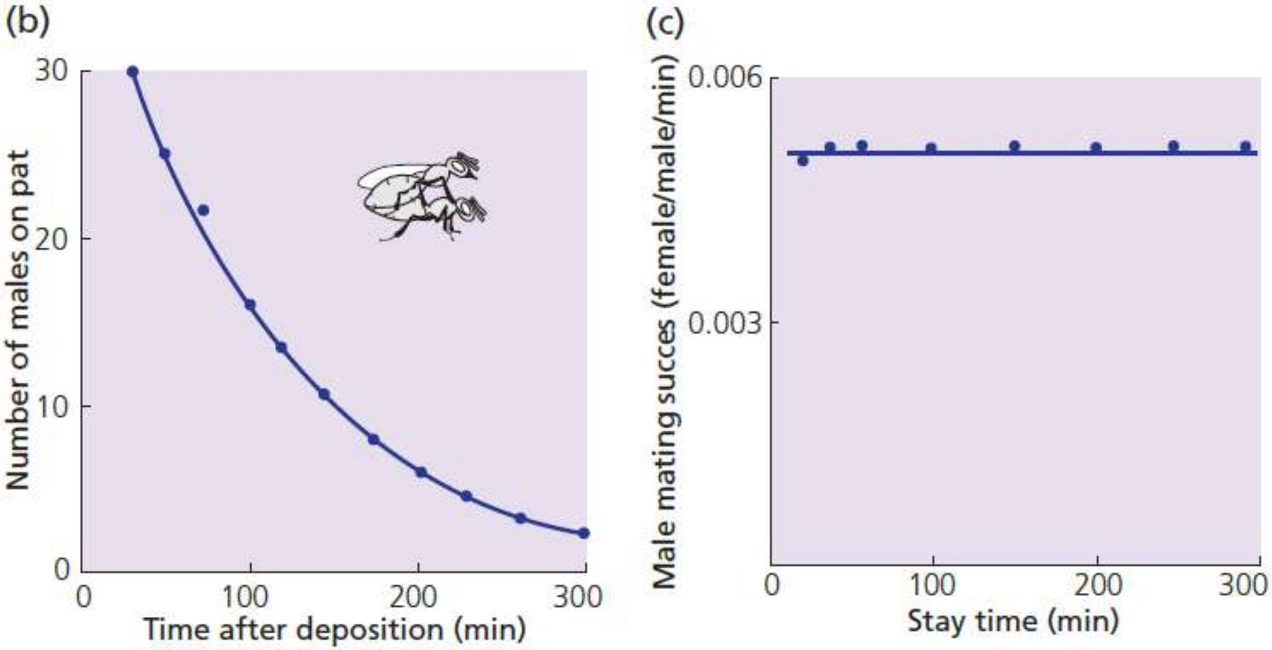


Fig. 5.3 (a) Male dung flies on a cowpat, waiting to mate with females that come to lay their eggs in the dung. In this photo, there are six searching males. Two pairs are being attacked by another male while the male is guarding his egg-laying female (centre and left), and there is a struggle for possession of a single female (top margin of the pat in the centre). Photo © G. A. Parker. (b) The number of males declines exponentially with time after pat deposition. (c) Given this distribution of stay times, the result is that mating success of males adopting different stay times is about equal, as predicted by the ideal free model. From Parker (1970).

Competition by resource defence: the despotic distribution

The first competitors to settle in the rich habitat defend resources by establishing territories (pieces of ground containing the resource), so later arrivals are forced to occupy the poor habitat even though they do less well there than the individuals in the rich area.

The strongest individuals are despots, grabbing the best quality resources and forcing others into low quality areas or excluding them from the resource altogether.

e.g. great tit

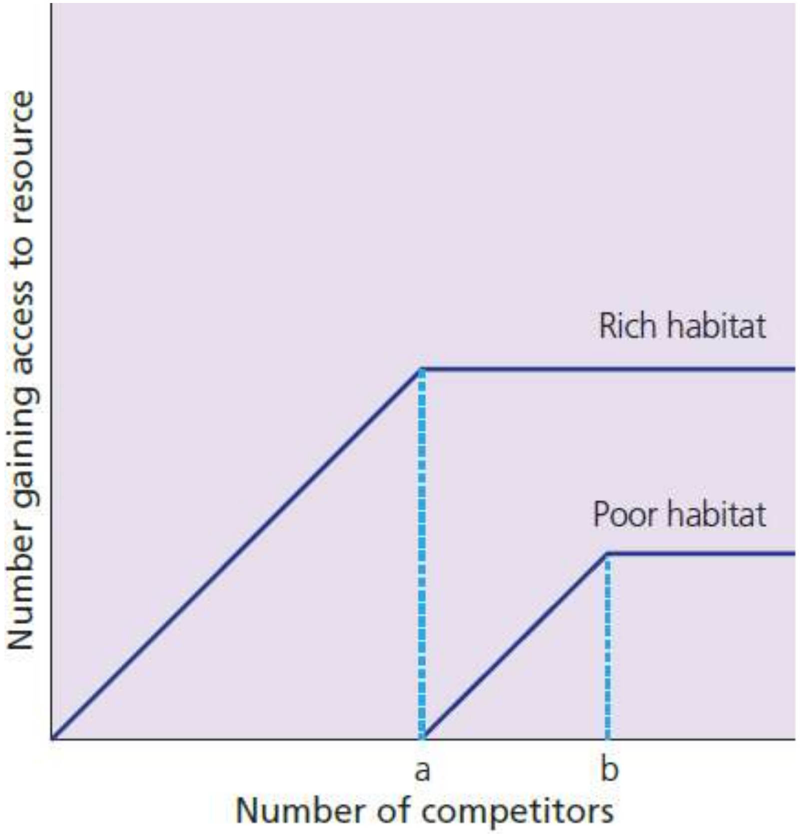


Fig. 5.4 Resource defence. Competitors occupy the rich habitat first of all. At point a this becomes full and newcomers are now forced to occupy the poor habitat. When this is also full (point b), further competitors are excluded from the resource altogether and become 'floaters'. After Brown (1969).

The economics of resource defence

Economic defendability

Defence of a resource has costs (energy expenditure, risk of injury and so on) as well as the benefits of priority of access to the resource

If resources are at low density, the gains from excluding others may not be sufficient to pay for the cost of territorial defence. Instead, the animal might abandon its territory and move elsewhere.

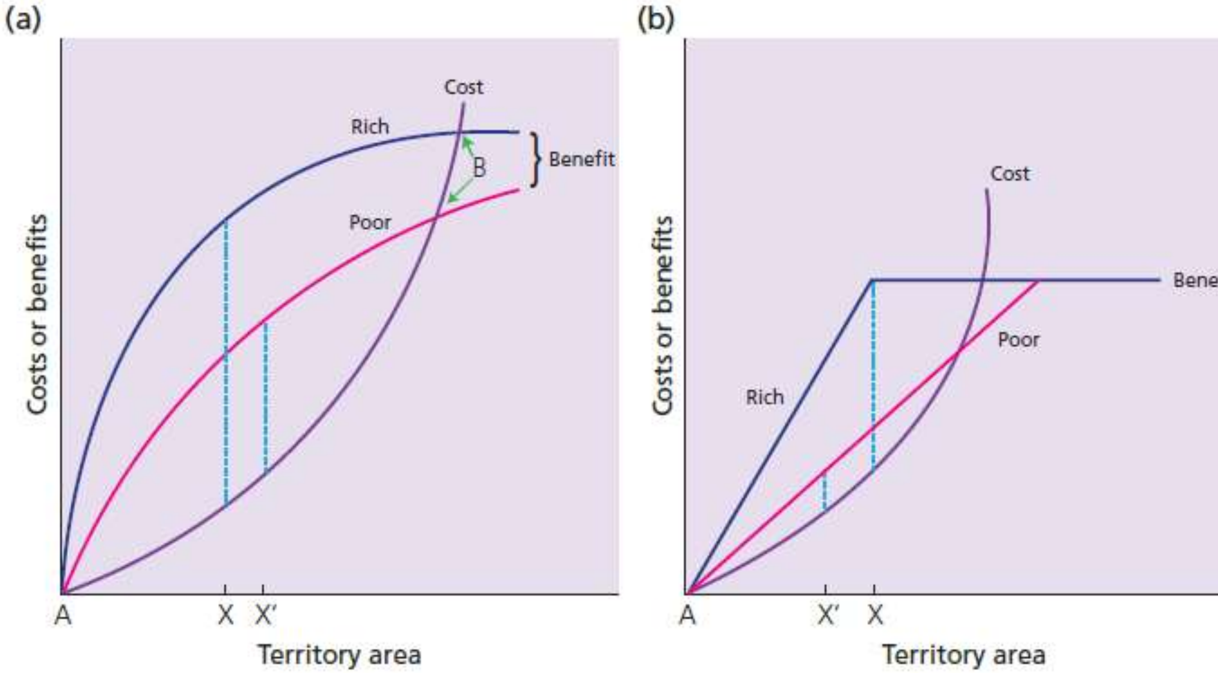
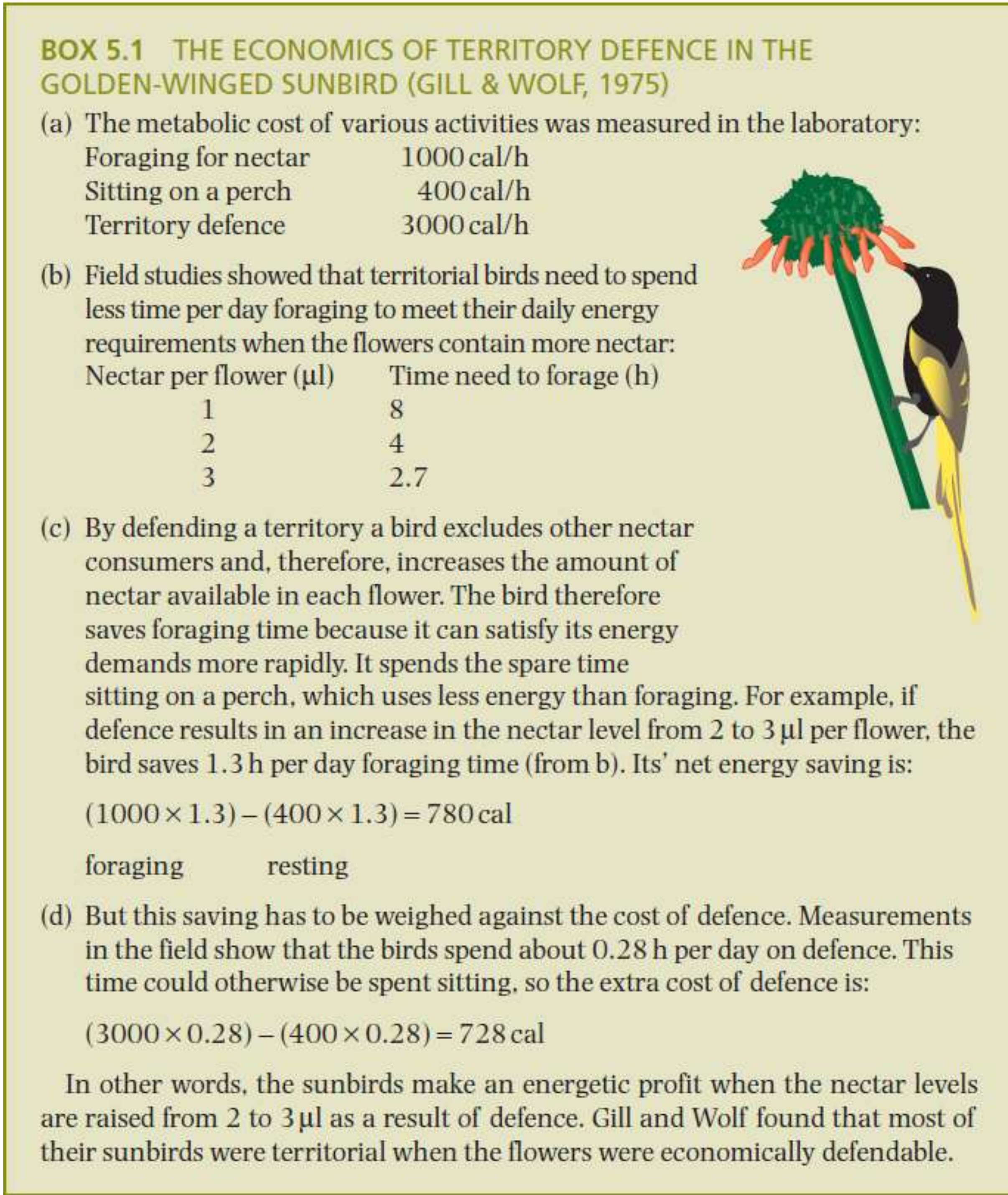


Fig. 5.7 (a) The idea of economic defendability. As the amount of resource defended (or territory size) increases, so do the costs of defence. The benefits (e.g. amount of food available) are assumed to increase at first but level off as the resource becomes superabundant in relation to the animal's capacity to process the resource. Two benefit curves are shown, one for a rich environment and one for a poor environment: the benefit curve rises more steeply in the former because the density of resources is higher. The resource is economically defendable between A and B. Within this range the optimal territory size depends on the currency: for maximizing net gain (B–C) the optimal size is smaller for the rich environment (X) than for the poor one (X′) (note that this is where the slopes of the cost and benefit curves are equal). (b) The same model, but with slightly different shaped curves. In this case the optimal territory size to maximize net gain is predicted to *increase* in a rich environment (X now greater than X′). Therefore, the shapes of the cost and benefit curves are crucial for the predictions that are made! After Schoener (1983).

Sunbirds, one advantage of territorial defence was that it raised the amount of nectar per flower (by exclusion of nectar thieves) and, hence, saved foraging time.

But if nectar levels are already high, the extra increment resulting from territorial defence saves hardly any foraging time.

Gill and Wolf calculate that an increase from 4 to 6 μl per flower would save the birds less than 0.5 h of foraging time while an increase from 1 to 2 μl saves four hours.



BOX 5.1 THE ECONOMICS OF TERRITORY DEFENCE IN THE GOLDEN-WINGED SUNBIRD (GILL & WOLF, 1975)

(a) The metabolic cost of various activities was measured in the laboratory:

Foraging for nectar	1000 cal/h
Sitting on a perch	400 cal/h
Territory defence	3000 cal/h

(b) Field studies showed that territorial birds need to spend less time per day foraging to meet their daily energy requirements when the flowers contain more nectar:

Nectar per flower (μl)	Time need to forage (h)
1	8
2	4
3	2.7

(c) By defending a territory a bird excludes other nectar consumers and, therefore, increases the amount of nectar available in each flower. The bird therefore saves foraging time because it can satisfy its energy demands more rapidly. It spends the spare time sitting on a perch, which uses less energy than foraging. For example, if defence results in an increase in the nectar level from 2 to 3 μl per flower, the bird saves 1.3 h per day foraging time (from b). Its' net energy saving is:

$(1000 \times 1.3) - (400 \times 1.3) = 780$ cal

foraging resting

(d) But this saving has to be weighed against the cost of defence. Measurements in the field show that the birds spend about 0.28 h per day on defence. This time could otherwise be spent sitting, so the extra cost of defence is:

$(3000 \times 0.28) - (400 \times 0.28) = 728$ cal

In other words, the sunbirds make an energetic profit when the nectar levels are raised from 2 to 3 μl as a result of defence. Gill and Wolf found that most of their sunbirds were territorial when the flowers were economically defendable.

Shared resource defence

Sometimes the economics of resource competition may favour shared defence

The wagtail study illustrates:

- it is an example of how apparently different kinds of costs and benefits (defence and feeding) can sometimes be reduced to a single currency – feeding rate
- it shows that one advantage of group living is shared resource defence.

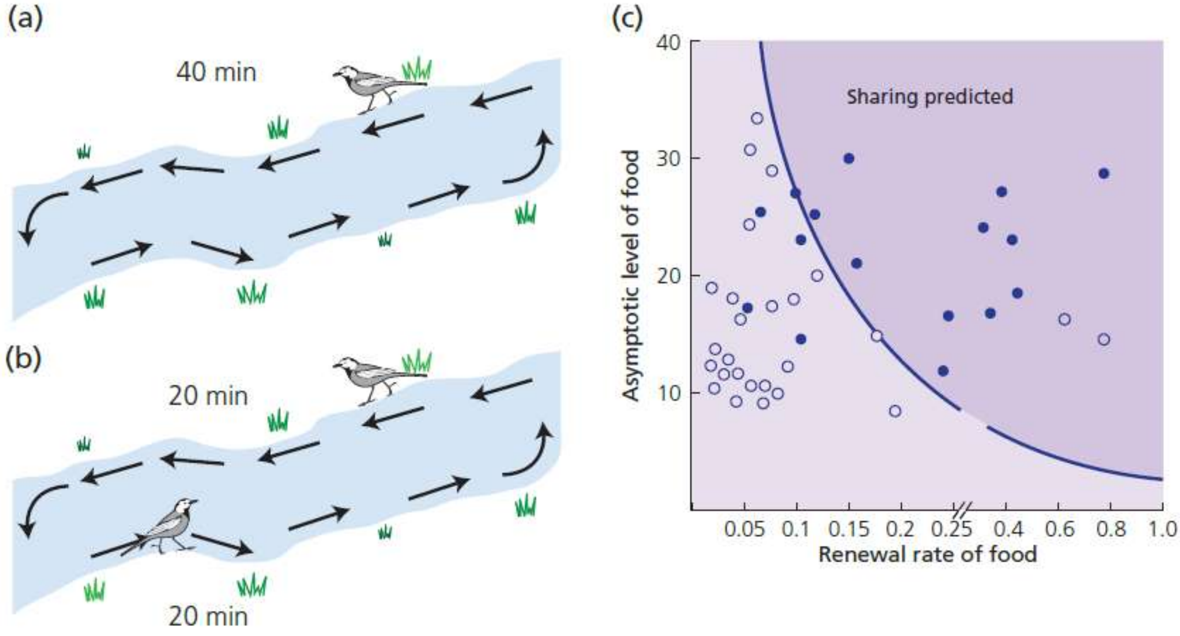


Fig. 5.8 (a) A pied wagtail territory owner exploits its riverside territory systematically, feeding along one bank and then back down the other bank (a circuit of about 40 min) to allow time for prey renewal between successive visits to the same stretch. (b) Sharing the territory with a satellite brings benefits in terms of help with defence, but costs in reducing prey renewal times by half when each bird walks half a circuit behind the other. (c) An owner was predicted to share its territory when the rate of renewal of food and the asymptotic abundance of food were above the curve. These combinations represent instances where the owner gains a net benefit in feeding rate because costs of sharing are outweighed by the benefits. The observed outcomes are shown as dots, each one representing a single day: solid dots – satellite accepted, open dots – satellite chased off. From Davies and Houston (1981).

Producers and scroungers

Competition for scarce resources often leads to variable competitive behaviour within a population.

Example: there are two foraging alternatives:

- producers make food available by digging or otherwise exposing prey, while
- scroungers steal the food found by the producers.

How could a mixture of producers and scroungers be maintained?

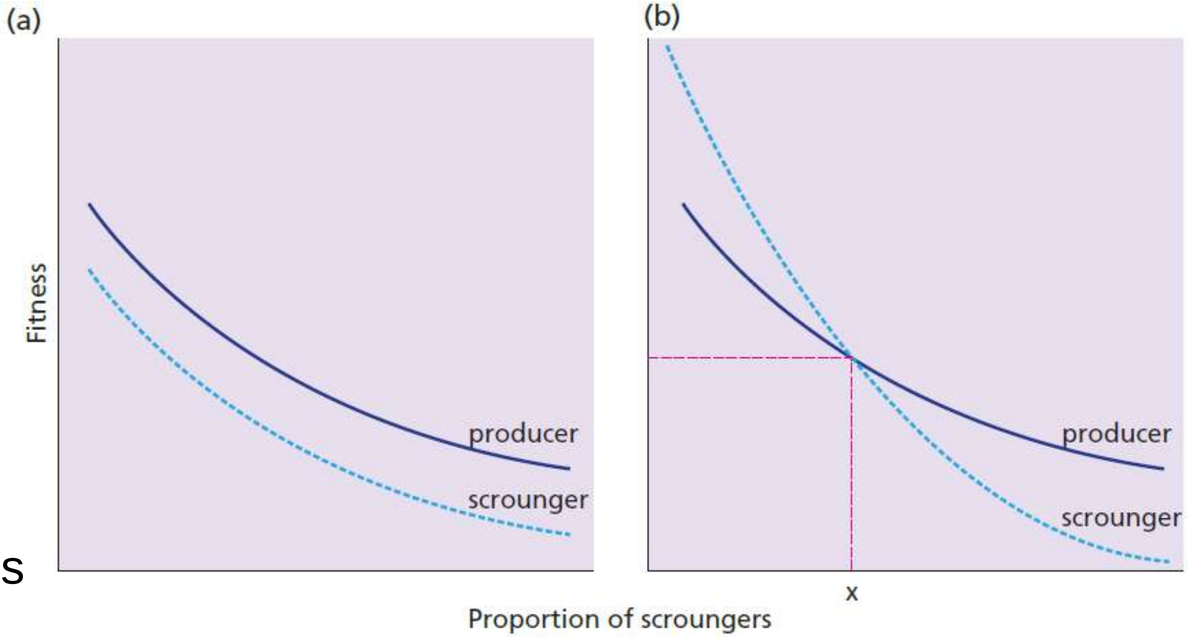


Fig. 5.9 Two models for how a mixture of producers and scroungers may be maintained in a population. (a) As the proportion of scroungers increases, both producers and scroungers have declining fitness, but producers always do best. Scroungers are poorer quality competitors. (b) There may be no difference in competitive ability. Each behaviour does best when rare. The stable equilibrium frequency of the two is at x, where producers and scroungers have equal fitness. Model (b) after Barnard and Sibly (1981). With permission from Elsevier.

Producers and scroungers

On the ‘producer’ side individuals had access to a string next to each perch. By pulling on the string, a producer released seeds into a dish on the scrounger side opposite.

The producer could feed on the seeds by stretching its neck through a small hole in the division between the compartments.

Individuals on the scrounger side had no string, so they searched for patches made available by the producers.

Two treatments were tested:

- scroungers could gain easy access to the seeds (dish uncovered) and
- only partial access (dish covered).

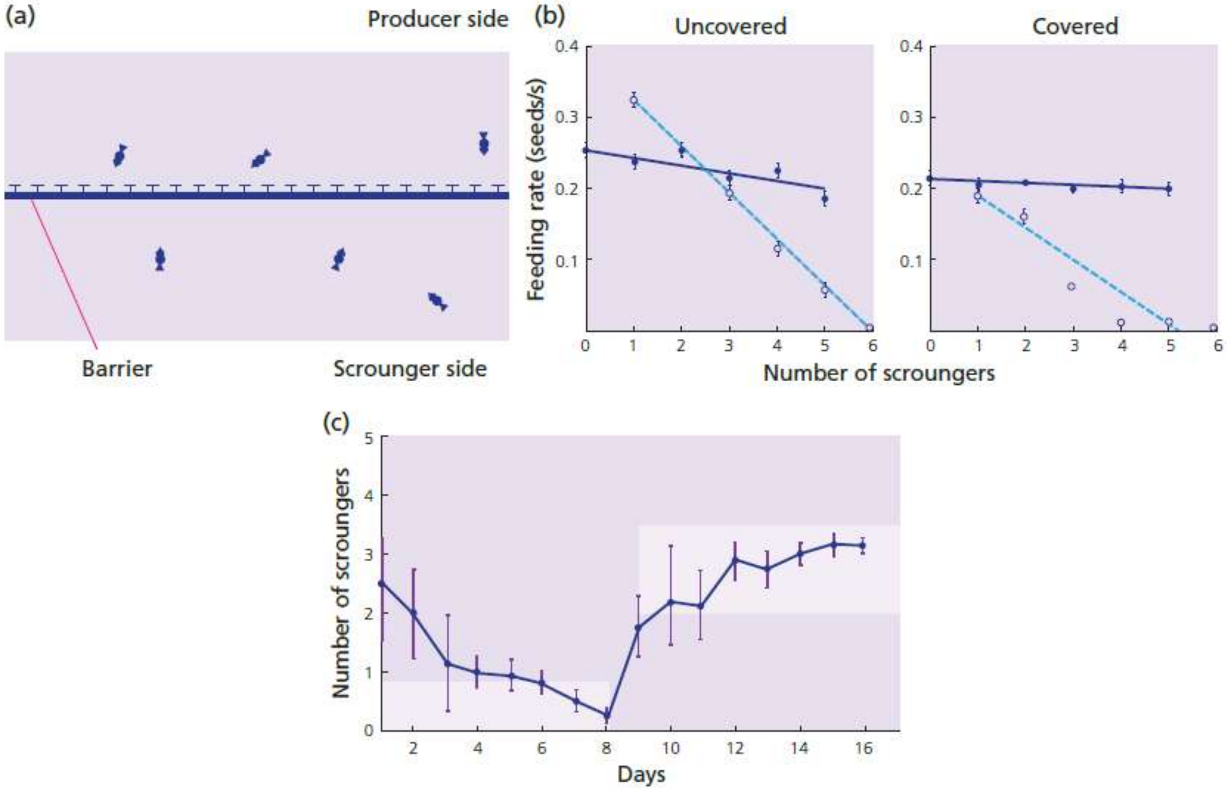


Fig. 5.10 Mottley and Giraldeau’s (2000) experiment with spice finches to test the model in Fig. 5.9b. (a) Experimental aviary. On the producer side, birds can sit on little perches (the T shapes) and pull a string to release food into a dish. On the scrounger side, birds have to wait for producers to make food available (see text for details). (b) Results from one flock, showing how foraging rate of producers (p – solid dots) and scroungers (s – open circles) varies with the number of birds in the scrounger compartment. There are six birds in total in the flock. In the graph on the left, the feeding dishes were uncovered and scrounger = producer feeding rate when 2–3 birds of the flock are scroungers. In the right-hand graph, the dishes were covered, which reduced scrounger (but not producer) food access; here equal success occurs when 0–1 birds are scroungers. (c) When all six birds have free access to either side, the numbers converge on the predicted stable equilibrium (shaded areas) over successive days of the experiment. On days 1–8, dishes were covered and on days 9–16 they were uncovered.

Alternative mating strategies and tactics

Individuals within a population often vary in the way they compete for mates

Strategy:

- ‘always fight’

-‘always sneak’

Strategies might also be conditional strategies, where individuals vary their competitive behaviour depending on their body size (‘fight if larger than size x, sneak if smaller than x’), or depending on the environment (‘fight above threshold cue y, sneak below threshold cue y’).

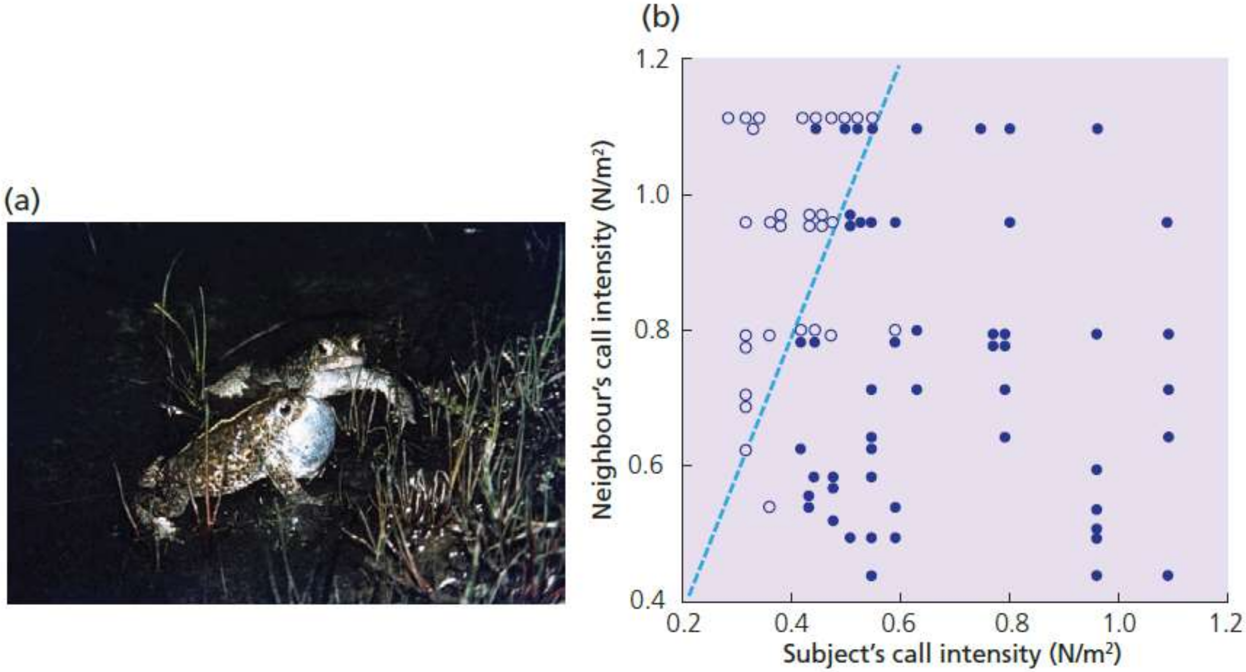


Fig. 5.11 (a) A calling male natterjack toad with a silent satellite male next to him, waiting to intercept any females that are attracted. Photo © Nick Davies. (b) How a male natterjack toad decides whether to be a caller or a satellite. The subject’s call intensity is plotted against the call intensity of his nearest neighbour. Males were predicted to become satellites when their neighbours produced calls twice as loud as their own calls (the area to the left of the dashed line). The open circles refer to males who were satellites and the closed circles males who called. From Arak (1988). With permission from Elsevier.

Morphological switches with body size: dung beetles

Male dung beetles in the genus Onthophagus come in two morphs:

-large males (‘majors’) have long horns on their heads while

-small males (‘minors’) are hornless

The development of horns is facultative and depends on the amount of dung available to a growing larva. A hormonal switch during larval development leads to horn growth only above a critical threshold body size

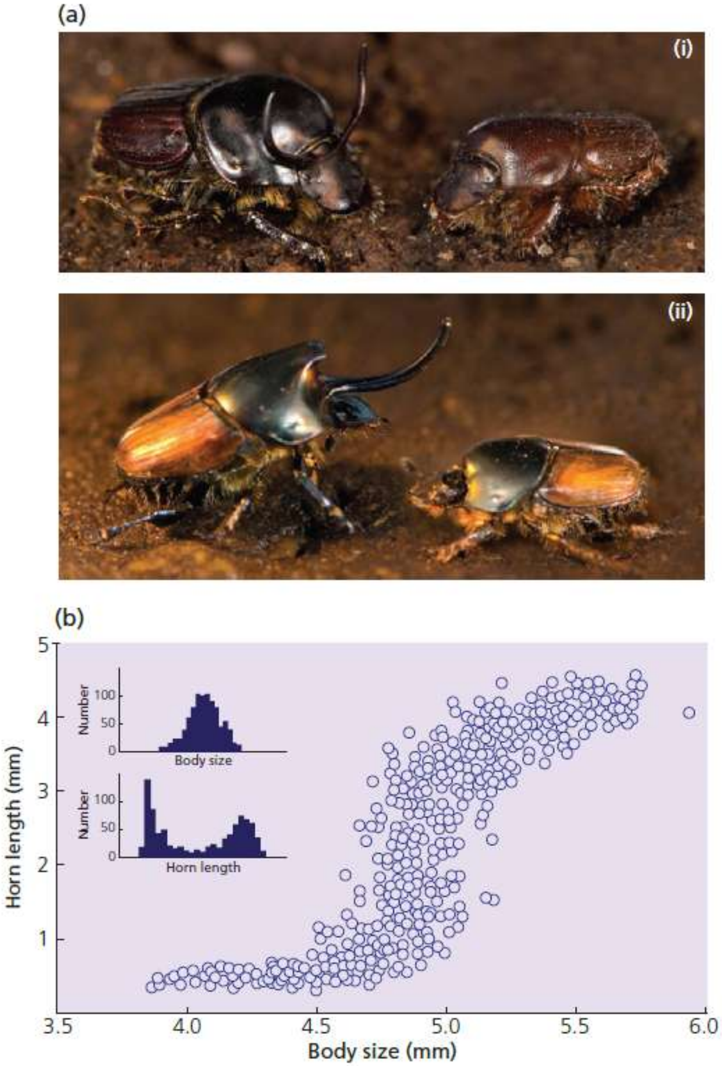


Fig. 5.13 (a) Horned (left) and hornless (right) males of the dung beetles: (i) *Onthophagus taurus* and (ii) *O. nigriventris*. Photos © Douglas Emlen. (b) Scaling relationship between horn length and body size (thorax width) for 810 *taurus* males collected from pastures in Durham County, North Carolina. Inserts illustrate the frequency distribution of body sizes and horn length. From Moczek and Emlen (2000). With permission from Elsevier.

Males of the two morphs compete for females in different ways.

Major males fight to defend a female's tunnel and then guard the entrance.

Minor males attempt to sneak matings through side tunnels and they scuttle off to safety if attacked by a major male

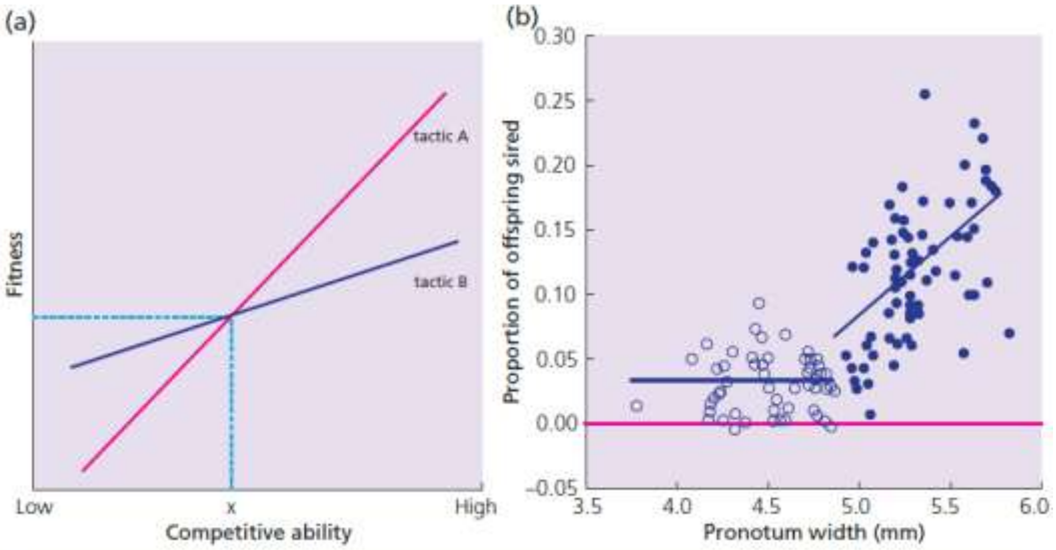


Fig. 5.15 (a) Gross's (1996) model for the threshold morphological switch between alternative tactics within a conditional strategy. The fitness of each alternative tactic A and B varies with an individual's competitive ability. On average tactic B has the lower pay-off. However, below threshold x, B does best while above the threshold A does best. With permission from Elsevier. (b) The reproductive success of horned (solid symbols) and hornless (open symbols) male dung beetles *Onthophagus taurus*. Horned males begin to do better at a body size of about 5 mm pronotum width, which corresponds to the threshold for horn development in the population under study. Hunt and Simmons (2001).

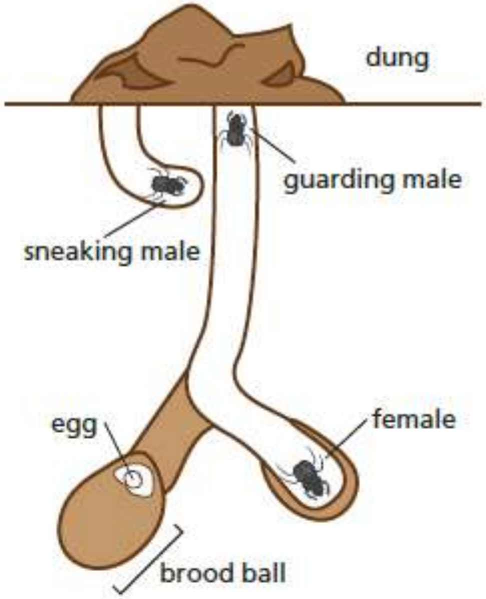


Fig. 5.14 Alternative mating tactics in *Onthophagus* dung beetles. Large, horned males guard burrow entrances and fight to defend females. Small, hornless males sneak matings through side tunnels. From Emlen (1997).

Ruffs: fighters, satellites and female mimics

The ruff is a shorebird with a remarkable difference between males and females

Males: they have dark ruffs and tufts and they fight to defend small territories to which females are attracted for mating.

However 16% of males have white ruffs and tufts and their behaviour is very different; they do not fight but instead act as satellites on the edge of territories and attempt to steal copulations while the fighters are busy defending their territories

A third male morph looks just like a female (1% or less of males) with enormous testes (2.5 times the volume of those of fighter males) and are likely to behave as sneakers

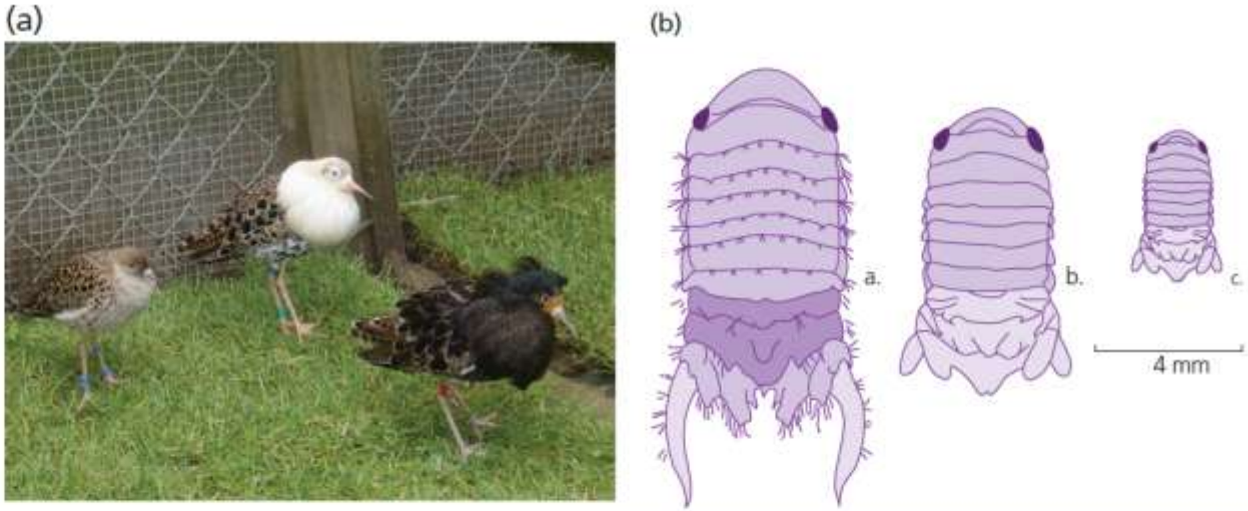


Fig. 5.18 Alternative genetic mating strategies. (a) In the ruff there are three male strategies: territorial males (right) have dark ruffs, satellite males (centre) have white ruffs and female mimics (left) have no ruffs. Photo © Susan McRae. (b) In the marine isopod *Paracerceis sculpta* there are three male morphs which differ in size and behaviour; from left to right: alpha, beta and gamma males. From Shuster (1989).

Side-blotched lizards: cycles of orange, blue and yellow

Frequency dependent pay-offs but here there is no stable equilibrium - frequencies of the strategies cycle over time.

-Orange-throated males are aggressive and defend large territories within which live several females

-Yellow-throated males look like receptive females (which also have yellow throats). They do not defend territories. Instead, they attempt to sneak matings

-Blue-throated males are less aggressive than orange-throated males. They defend small territories in which they guard a single female

During the years 1990–1999, the frequencies of the three morphs changed along a 250 m sandstone outcrop

Each strategy had a strength, which enabled it to outcompete neighbours of one morph, but also a weakness which left it vulnerable to neighbours of another morph

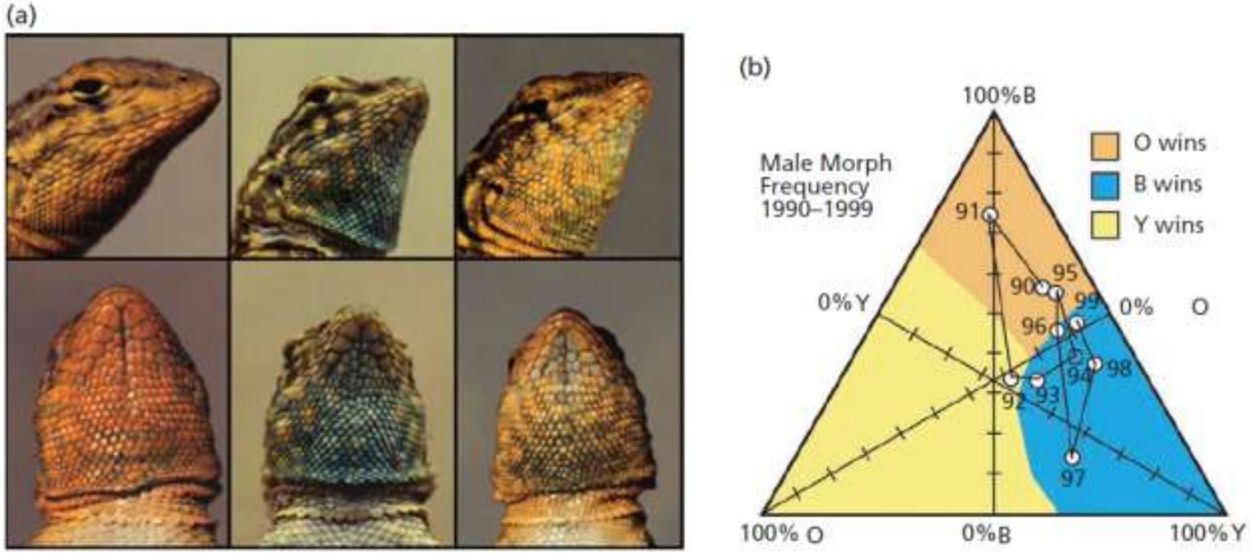


Fig. 5.19 (a) The three male colour morphs of the side-blotched lizard: orange, blue and yellow. Each has a different mating strategy (see text). Photo © Barry Sinervo. (b) Observed frequencies of each male strategy (O, Y, B) in a Californian population from 1990 to 1999. The triangle plots the frequencies as follows: 0–100% blue from base to apex, 0–100% orange from right side to left vertex, and 0–100% yellow from left side to right vertex. Shaded areas indicate the zones where each morph has highest fitness. From Alonzo and Sinervo (2001).

Animal personalities

Animals often differ in their behaviour, with individual differences in tactics or strategies arising as an evolutionary outcome of competition for resources

Differences often involve suites of correlated traits:

In birds, rodents and fish, individuals that are relatively aggressive to conspecifics are also often bolder in their approach to predators and quicker to explore novel environments

Personalities in great tits are heritable:

- Exploratory behaviour repeatable (individuals were consistent when re-tested) and heritable (offspring scores correlated with those of their parents)
- Great tits were bred in aviaries and two selection lines were created:
  - one breeding from juveniles who had the highest exploration scores and
  - one from those with the lowest scores.
- Over four generations, there were strong responses to selection in both lines showing that there is a genetic basis to exploratory behaviour
- More exploratory individuals were more aggressive towards conspecifics, bolder in their approach of novel objects, more likely to scrounge food from others and showed lower physiological signs of stress when handled

Animal personalities

In great tits, different personality types do better under different ecological conditions

-In years with high winter food supplies (beech nuts), relaxed competition for food led to better survival for slow exploring females (no benefit to fast explorers from seeking out novel feeding sites).

However, the resulting high survival of the tits led to more intense male competition for breeding sites, in which fast exploring males did best.

-By contrast, in years with low winter food supplies, fast exploring females survived better (they found novel food sources more quickly) but, curiously, among the males it was the slow explorers who did best.

In the case of number of species bolder individuals tend to have higher reproductive success but lower survival than shyer conspecifics

ESS thinking

Evolution is the outcome of competitive games

When individuals compete for scarce resources, such as food or mates, their best options will be influenced by what their competitors are doing

Could a mutant strategy do better?

What is the stable outcome of competition?

Optimal versus Stable

In theory, personality variation may be maintained by frequency dependent selection as an ESS. Or, different personalities may do best under different social and ecological conditions.

Living in Groups

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Living in Groups

Why individuals often form groups like these, despite the potential costs of increased competition for resources and infection by pathogens?

Fig. 6.1 Living in groups: (a) In winter, tens of thousands of starlings gather in spectacular amoeba-like flocks at dusk, prior to their night-time roost. Photo © osf.co.uk. All rights reserved (b) When a predator approaches, many fish form tight shoals. Why do individuals form groups? How are group movements coordinated? Photo © iStockphoto.com/stevedeneef.

Potential benefits of grouping

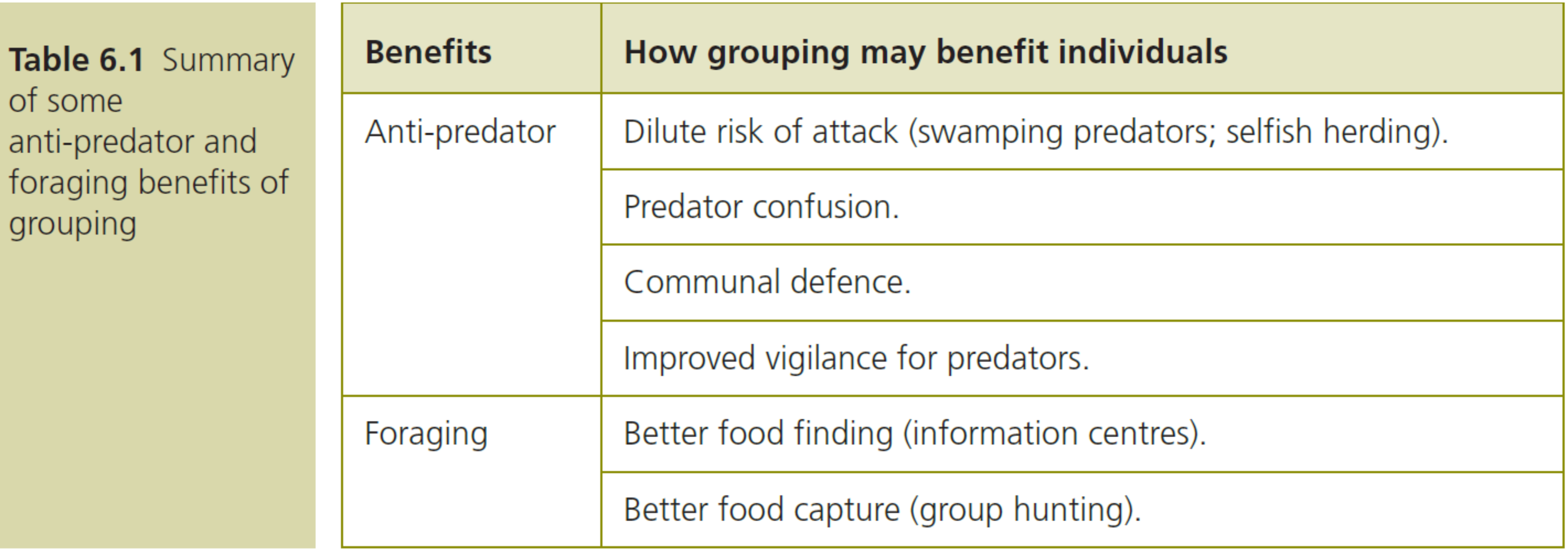


Table 6.1 Summary of some anti-predator and foraging benefits of grouping

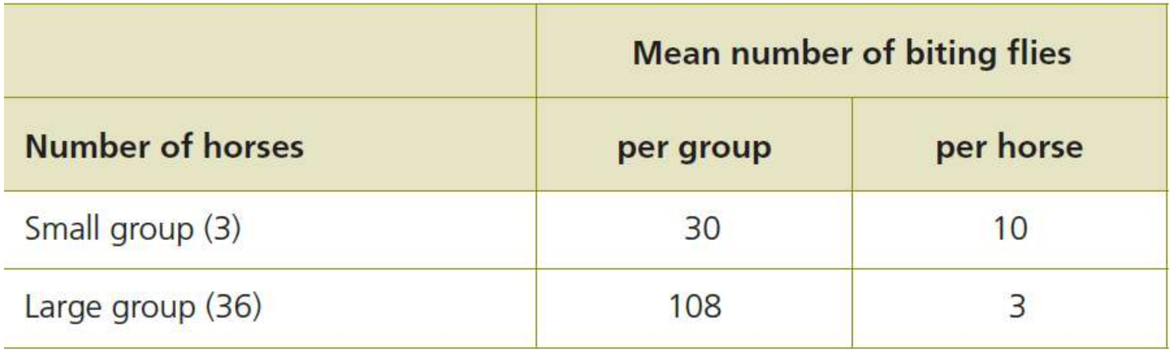
Benefits	How grouping may benefit individuals
Anti-predator	Dilute risk of attack (swamping predators; selfish herding).
	Predator confusion.
	Communal defence.
	Improved vigilance for predators.
Foraging	Better food finding (information centres).
	Better food capture (group hunting).

Diluting the risk of attack

Grouping can dilute an individual prey's risk of being attacked

In the Camargue marshes of the South of France, wild horses are attacked by blood sucking flies (Tabanidae), which not only remove blood but also transmit bacterial and viral diseases. During the weeks when these flies are most active, the horses aggregate into larger groups.

Table 6.2 Dilution advantage from grouping. Wild horses in the Camargue, southern France, were kept in a group of three or in a group of 36. Although the larger group attracted more biting tabanid flies, individual horses suffered fewer attacks in the larger group (Duncan & Vigne, 1979).



	Mean number of biting flies	
Number of horses	**per group**	**per horse**
Small group (3)	30	10
Large group (36)	108	3

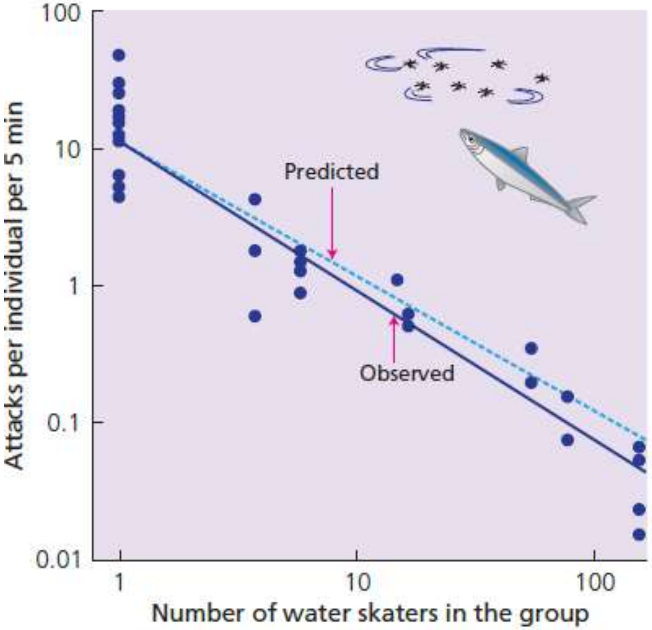


Fig. 6.2 An example of the dilution effect. The prey are insects called water skaters (*Halobates robustus*) that sit on the water surface; their predators are small fish (*Sardinops sagax*). The fish snap the insects from below, so there is little possibility that vigilance increases with group size. The attack rate by the fish was similar for groups of different sizes, so the attack rate per individual varies only because of dilution. The 'predicted' line is what would be expected if the decline in attack rate with group size is entirely caused by dilution; this line is very close to the observed. From Foster and Treherne (1981). Reprinted with permission from the Nature Publishing Group.

Synchrony in time: predator swamping

Dilution may also be achieved by synchrony in time, which swamps the capacity of predators to capture prey.

Tisza mayfly

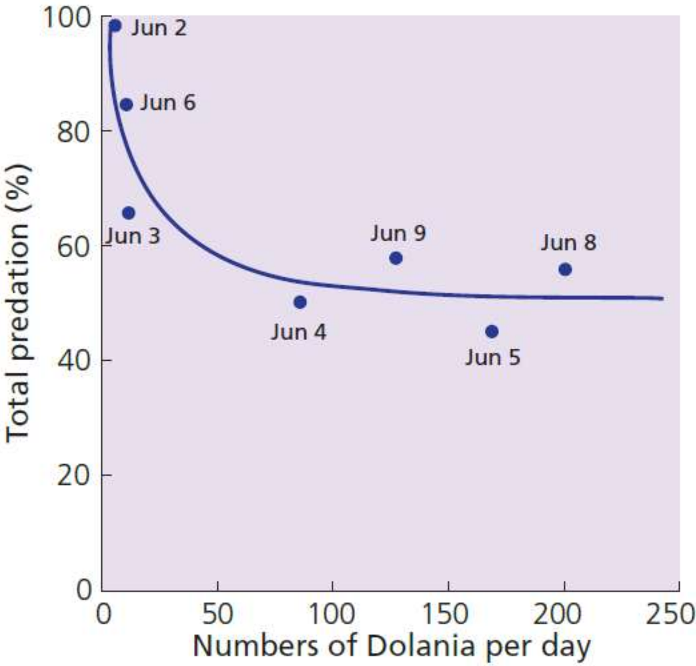


Fig. 6.3 Synchronous emergence swamps predators. The percentage of adult female mayflies *Dolania americana* preyed upon by aquatic and aerial predators combined, during seven days in June. Individual mayfly are safest on days where more females emerge. From Sweeney and Vannote (1982).

Selfish herds

- Individuals in the middle of a group may enjoy greater security than those at the edge

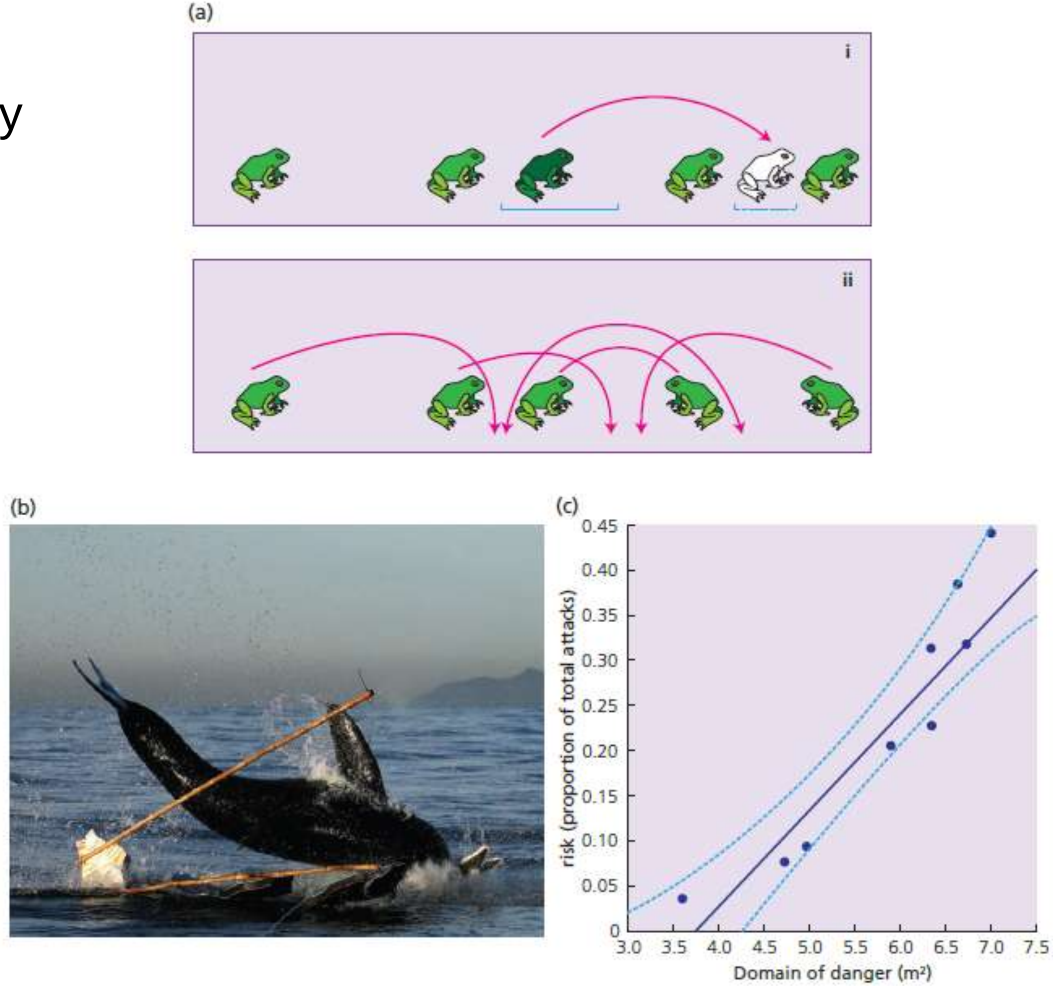


Fig. 6.4 (a) W.D. Hamilton's (1971) model of the selfish herd. Each frog has a 'domain of danger' in which it is likely to be selected for attack if a predator appears: this is shown for one individual in (i) as the solid bar, and is the zone stretching half way to the neighbour on either side. Any predator approaching this zone will select this frog as the nearest potential victim. The frog can reduce its zone of danger by jumping to settle in between two closer neighbours (arrowed movement, new domain of danger shown by dashed line). If all frogs follow this principle, the result will be increased aggregation (ii). (b) A test of Hamilton's model. An experiment with groups of decoy styrofoam seals, attached to a raft using reed poles, and then presented to great white sharks (see text). A shark attacking the decoys. Photo © Claudio Velasquez Rojas/Homebrew Films. (c) An individual seal decoy's risk of shark attack increased with its domain of danger, as assumed in Hamilton's model. De Vos and O'Riain (2010).

Predator confusion

Individuals in groups may also be safer from attack because the predator has difficulty in focusing on one target as different individuals in the group continually move across its line of sight

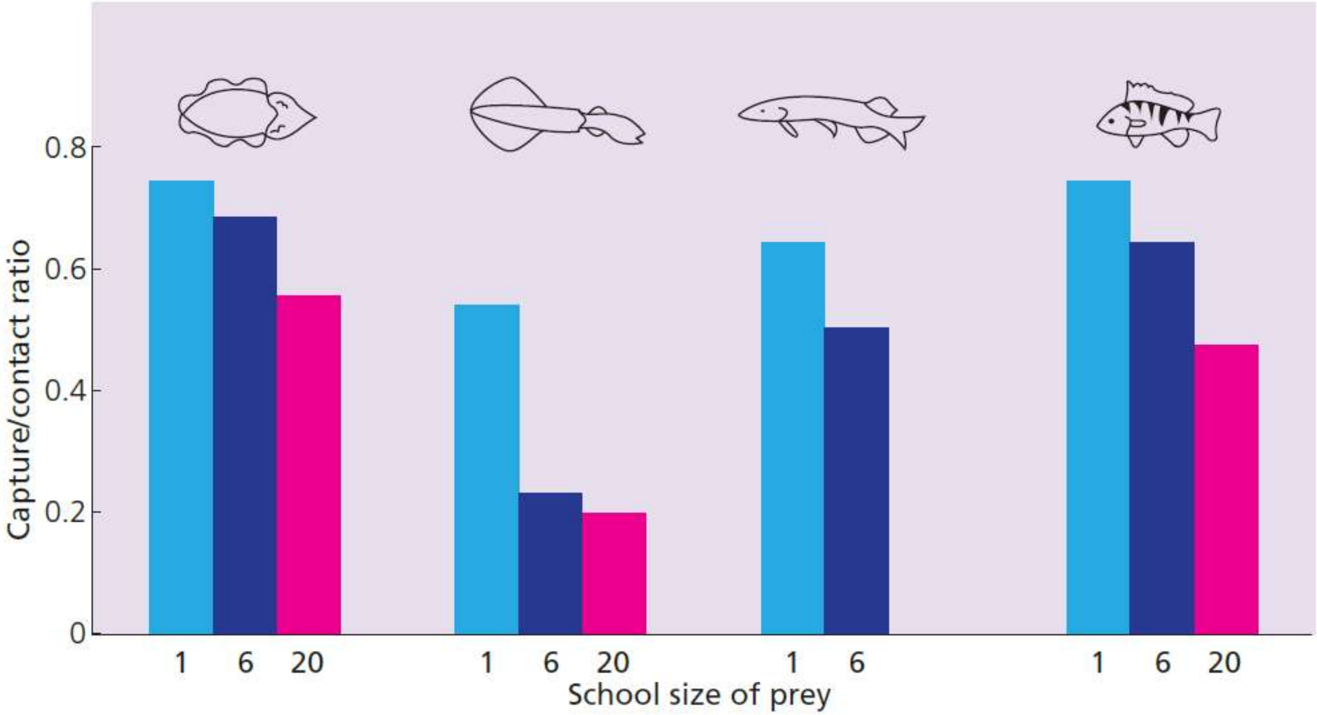


Fig. 6.5 The confusion effect of grouping by prey. The capture success per attack of, from left to right: squid, cuttlefish, pike and perch, when attacking small prey fish in singles, groups of six, or groups of twenty. In all cases, capture success declines with increasing prey group size. From Neill and Cullen (1974).

Communal defence

Prey are often not just passive victims but may actively defend themselves by attacking or mobbing a predator and grouping may enhance prey defence

Communal mobbing of predators

Fig. 6.6 Group defence. In dense colonies of guillemots, like this one, breeding success is higher than in sparse colonies because of more effective defence against nest predators such as gulls. From Birkhead (1977). Photo © T. R. Birkhead.

Improved vigilance for predators

Groups detect predators sooner For many predators success depends on surprise; if the target is alerted too soon during an attack it has a good chance of escape

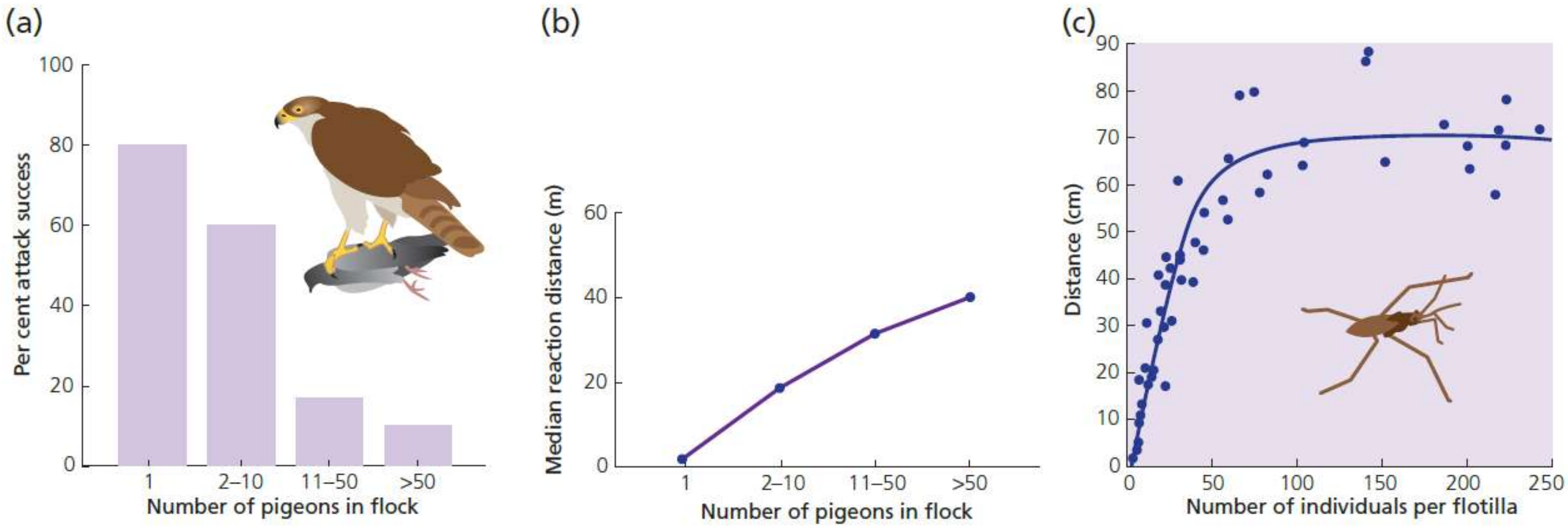
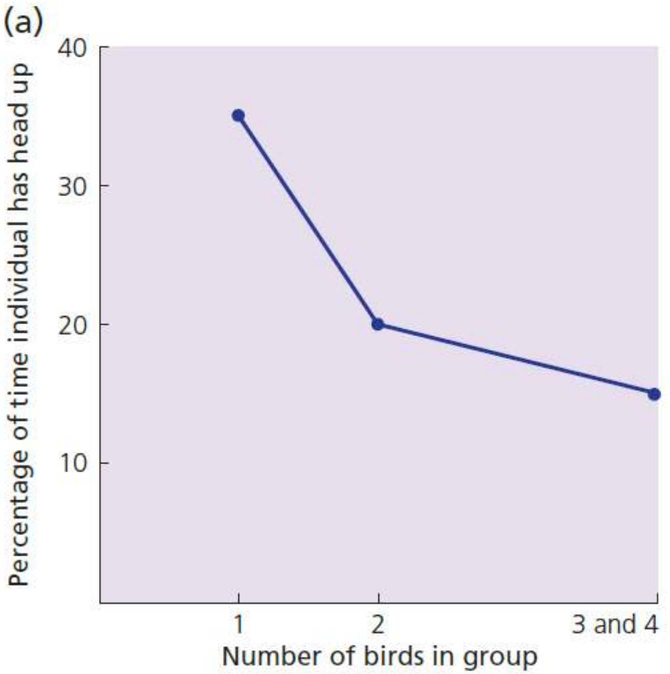


Fig. 6.7 (a) Goshawks are less successful when they attack larger flocks of wood pigeons. (b) This is largely because bigger flocks take flight at greater distances from the hawk. The experiments involved releasing a trained hawk from a standard distance. From Kenward (1978). (c) Water skaters, *Halobates robustus*, in larger groups also respond sooner to an approaching model predator, by agitated movements on the water surface when the predator is further away. From Treherne and Foster (1980).

Improved vigilance for predators

As group size increased, individual ostriches reduced the proportion of time they had their head up, scanning the environment. Nevertheless, the overall vigilance of the group (at least one individual scanning) increased with group size



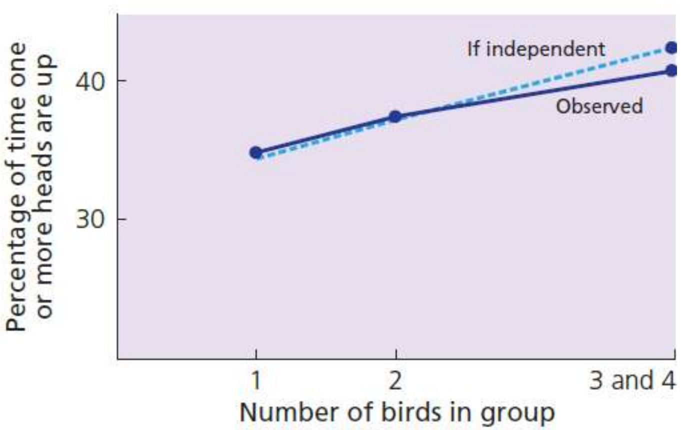


Fig. 6.8 Vigilance in groups. (a) An ostrich spends a smaller proportion of its time scanning (head up) when it is in a larger group. (b) The overall vigilance of the group (at least one bird scanning) increases with group size (solid line) and follows the relationship expected if each individual looks up independently of others in the group (broken line). From Bertram (1980). With permission from Elsevier.

Improved vigilance for predators – option for Cheating?

In theory, in scanning groups it may pay individuals to cheat

The temptation to cheat will be reduced if individuals who spot the predator gain an extra advantage over their non-vigilant companions

the cheetah targeted the least vigilant gazelle in 14 out of 16 cases

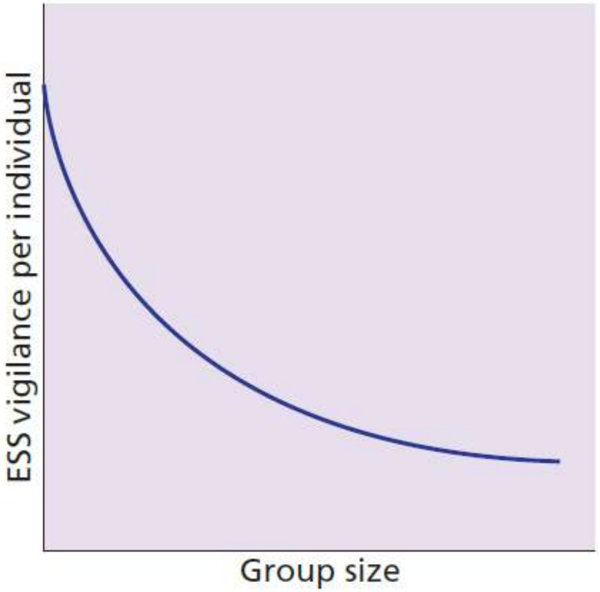


Fig. 6.9 The evolutionarily stable vigilance (ESS) for individuals in groups of different sizes (see text for explanation). From McNamara and Houston (1992). With permission from Elsevier.

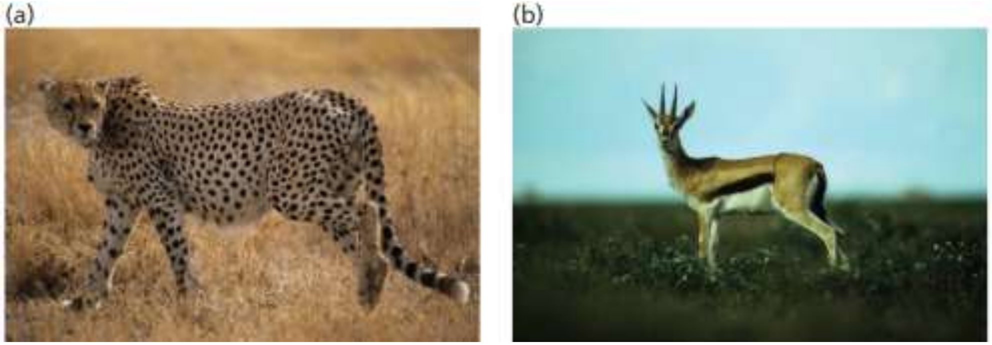


Fig. 6.10 A cheetah (a) is less likely to attack the more vigilant Thomson's gazelles (b) in a group. Photos © Oliver Krüger.

Small birds at feeders have shown that individuals who are more vigilant at the initiation of an alarm flight depart more quickly to safety than nonvigilant individuals

Improved vigilance for predators – Sentinels

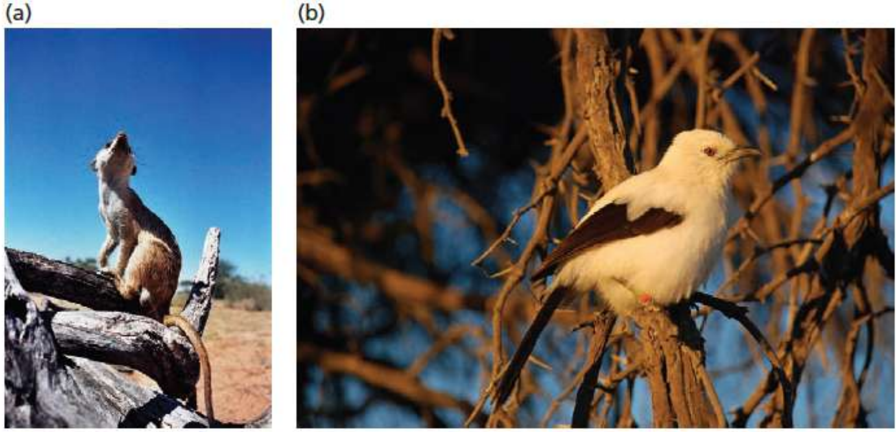
watching for predators from prominent look-out perches while the rest of the group forages on the ground below

Sentinel behaviour could be best for selfish individuals

Sentinels give quiet vocalizations while on guard

Individuals are more likely to become sentinels when they are satiated, either after a natural feeding bout or after experimental provisioning with extra food

Fig. 6.11 Sentinels in: (a) meerkats and (b) pied babblers. These individuals watch for predators from look-out perches while the rest of the group forages. Is the sentinel altruistic or selfish? Photos © Tom Flower.



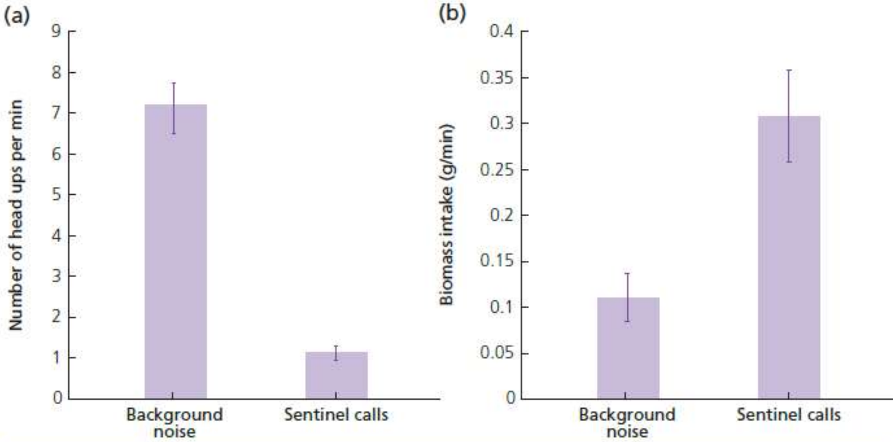


Fig. 6.12 The watchman's song. Sentinels give quiet vocalizations while on guard. Playback of sentinel calls to foraging pied babblers leads to lower vigilance (a), and improved foraging success (b) by the foragers in the group, compared to control playback of background noise. From Hollen, Bell and Radford (2008). With permission from Elsevier.

How grouping can improve foraging

Better food finding

Communal roosts and nesting colonies of birds may act as ‘information centres’, in which individuals find out about the location of good feeding sites by following others.

Two studies of ravens, Corvus corax, provide strong evidence that communal roosts act as information, successful foragers actively share information about the location of good feeding sites

Large winter roost of up to 1500 ravens (mainly unpaired juveniles)

- At distances of 2–30 km from the roost, they put out sheep and hare carcasses embedded with small, colour-coded plastic beads
- The ravens ingested these beads at the carcass and then regurgitated them in pellets back at the roost
- Beads from each carcass tended to appear at specific sites within the roost, showing that birds which fed together also slept together

Better prey capture

Predators may sometimes improve their ability to capture prey by hunting in a group

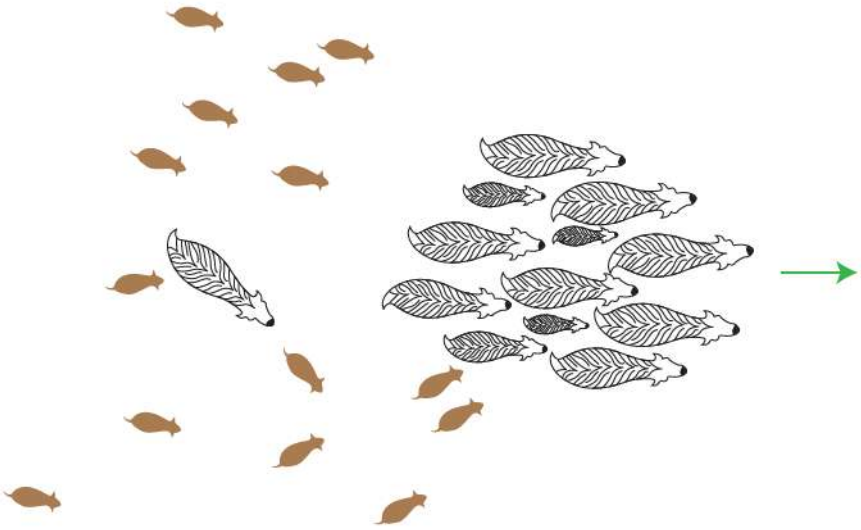


Fig. 6.14 A pack of fourteen spotted hyenas hunting a group of zebras. The zebra mares and foals run in a tight formation, followed by the stallion, who repeatedly charges at the hyenas. From Kruuk (1972).

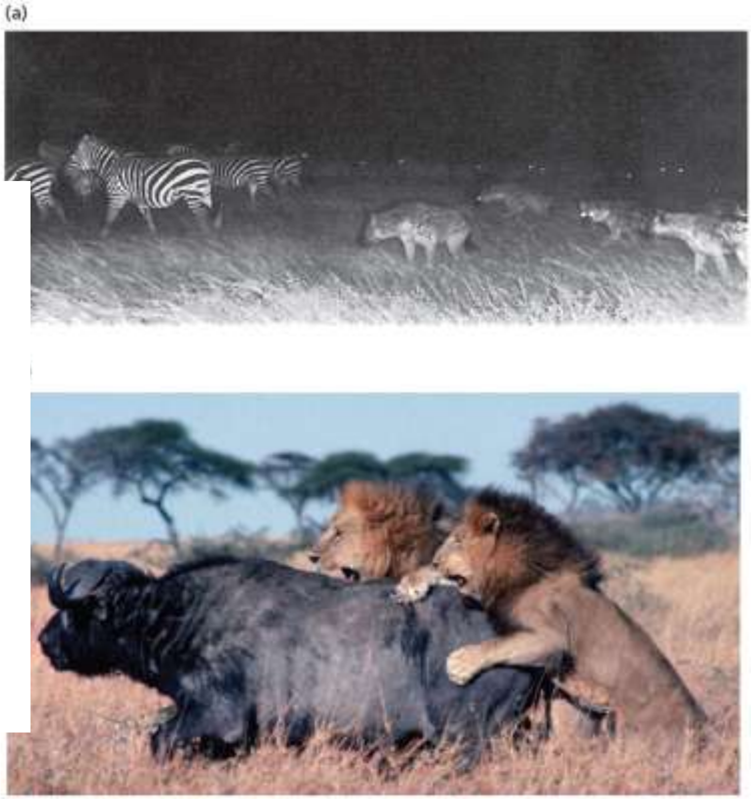


Fig. 6.13 Group hunting. When they hunt in a group, (a) spotted hyenas and (b) lions can successfully attack prey which are larger than themselves. Photo (a) © Hans Kruuk and (b) © Craig Packer.

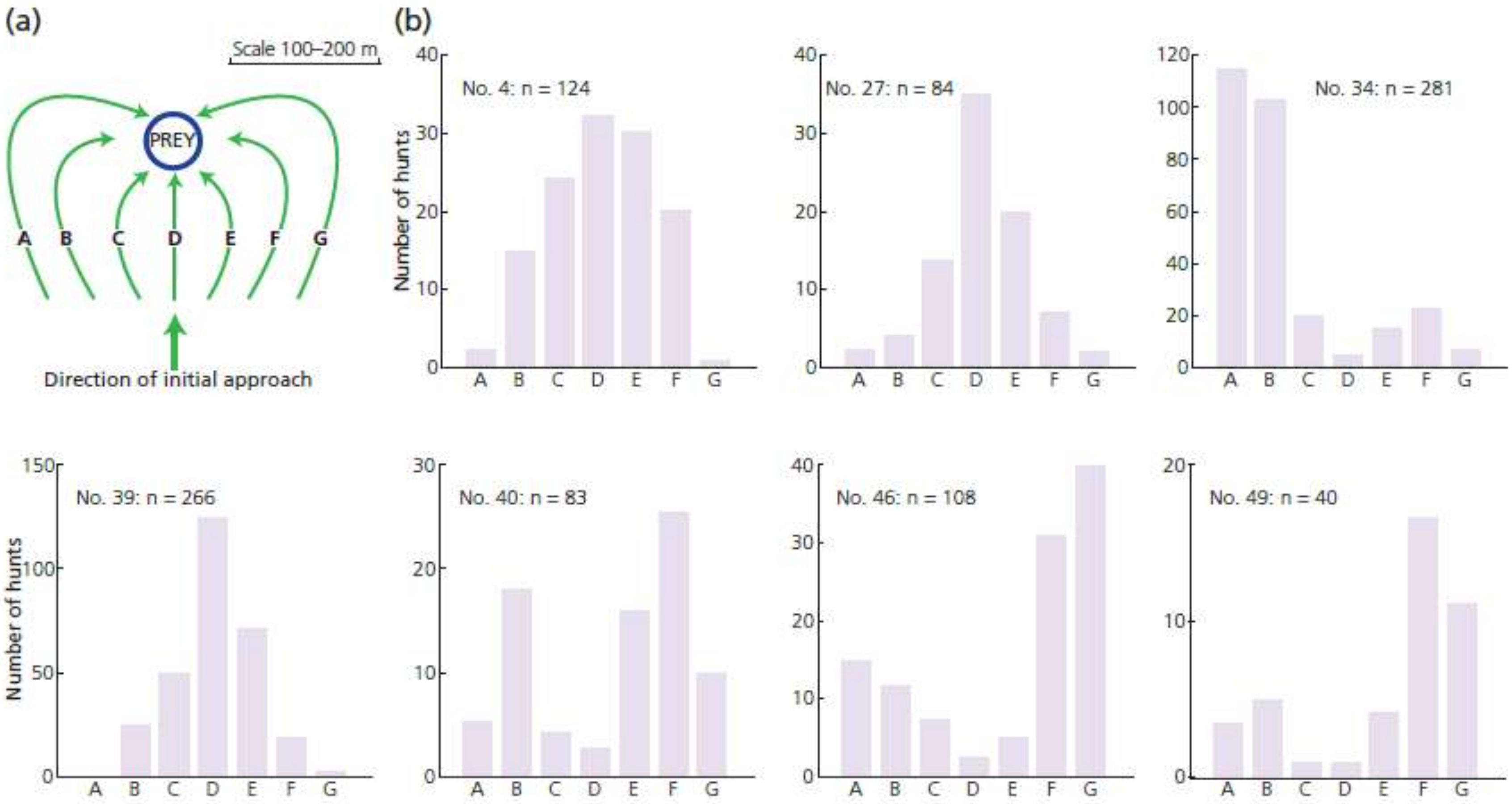


Fig. 6.15 Cooperative hunting in lions may involve individual specializations. (a) Seven stalking roles taken by lionesses towards a prey: A–B positions are 'left wings', C–E are 'centres' and F–G are 'right wings'. (b) Stalking roles of seven lionesses of the Okondeka pride in Etosha National Park, Namibia. The number of hunts is shown above each set of histograms. Individuals clearly differed in their positions: for example, number 34 preferred the 'left wing', numbers 4, 27 and 39 were 'centres', while numbers 46 and 49 preferred the 'right wing'. From Stander (1992).

Evolution of group living

Larger groups may bring benefits to individuals, by improving protection from predators or foraging success. However, larger groups may also bring increasing costs, from resource competition or disease

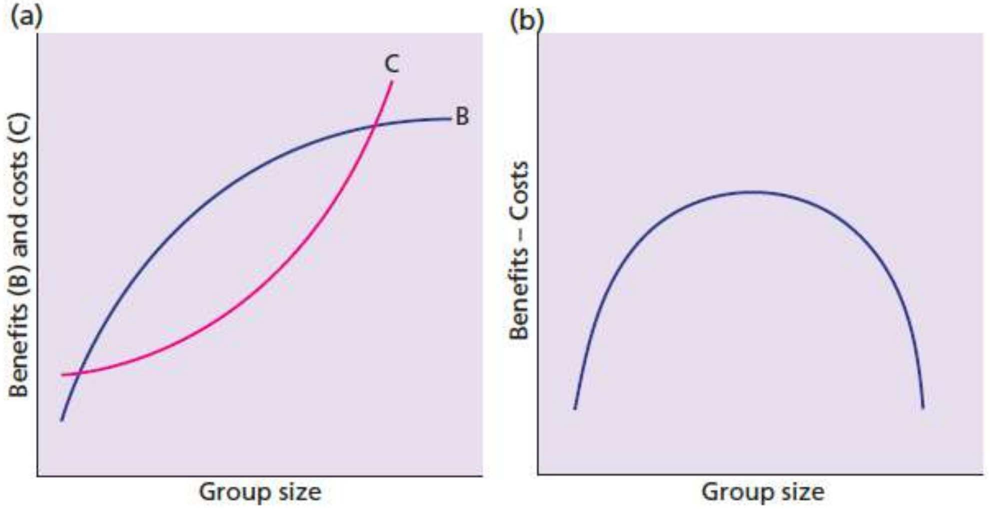


Fig. 6.17 The idea of optimal group size. (a) As group size increases both benefits and costs increase. However, in theory the increase in benefits will be a decelerating function (with each added individual having less effect than the last), while the increase in costs will accelerate (each added individual having more effect than the last). Therefore, costs will eventually exceed the benefits at large group sizes. (b) In theory, there will be an optimal group size (benefits – costs a maximum) at an intermediate group size. After Krause and Ruxton (2002).

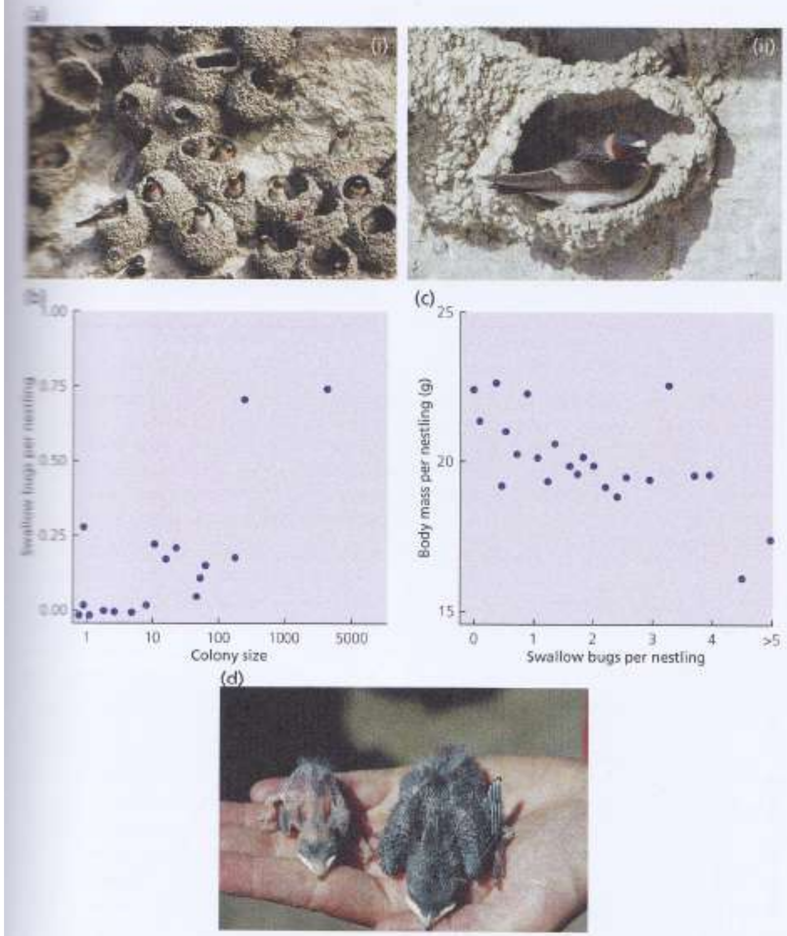


Fig. 6.16 An example of the benefits and costs of group living. (a) (i) A cliff swallow breeding colony. (ii) A bird at its nest entrance. Individuals gain benefit from the colony, which is an information centre enhancing food finding (ephemeral insect swarms; Brown 1988). (b) However, there are also costs; the number of blood-sucking hemipterans (swallow bugs, *Oeciacus vicarius*) on nestlings increases with colony size and (c) nestling body mass declines with increasing numbers of these ectoparasites. (d) Two nestlings, both 10 days old. The one on the right is from a fumigated nest, where the bugs were removed. The one on the left is from a naturally infested nest in the same colony. Photos (a) and (d) © Charles R. Brown. Figures (b) and (c) from Brown and Brown (1986). With permission of the Ecological Society of America.

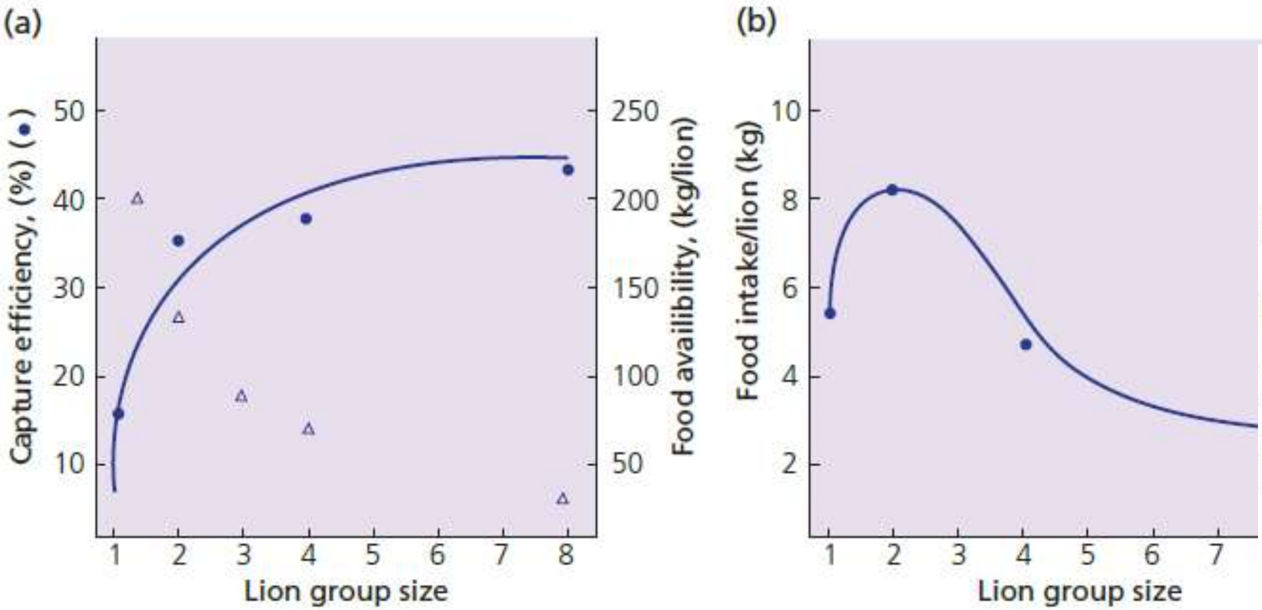


Fig. 6.18 Caraco and Wolf's calculation of optimal hunting group size for lions when hunting wildebeest in the Serengeti. (a) With increasing lion group size, capture success increases (solid circles) but if a kill is made, then food per lion decreases (open triangles). (b) This results in an optimal group size of two lions, to maximize food per lion per chase. Observed group sizes, however, are larger, on average three to four lions per hunt. From Caraco and Wolf (1975).

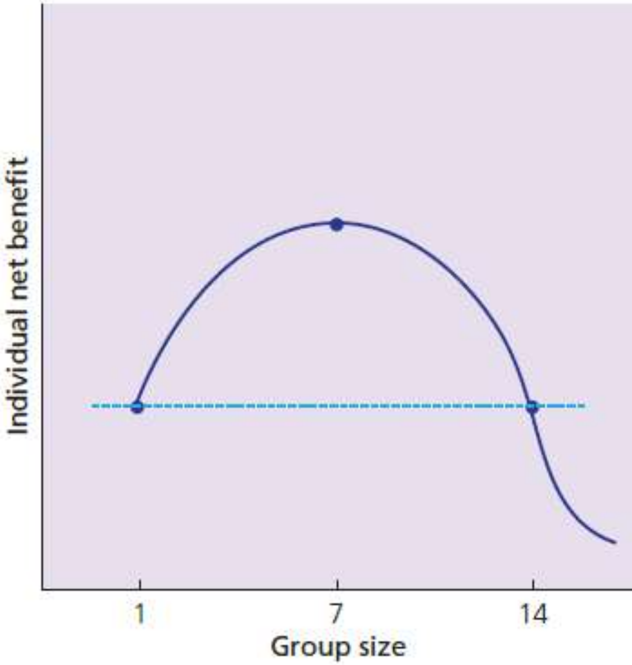


Fig. 6.19 Optimal group sizes may not be stable. In this example individual fitness is maximal at a group size of seven, but a new arrival would do better to join this group than to be solitary because individual fitness in a group of eight is higher than in a group of one. Further individuals should continue to join until the group size is 14. Only after this would the next newcomer do better alone. After Sibly (1983). With permission from Elsevier.

Individual differences in a group

Skew Theory

In most groups there will be individual differences in the net benefit from group living

Skew models consider the effects of group size on individual reproductive success, which will be the outcome of all the potential costs and benefits of group living, including foraging and protection from predators

Individual differences in benefits: who is in control of skew?

Subordinates may restrain their growth to avoid eviction by dominants

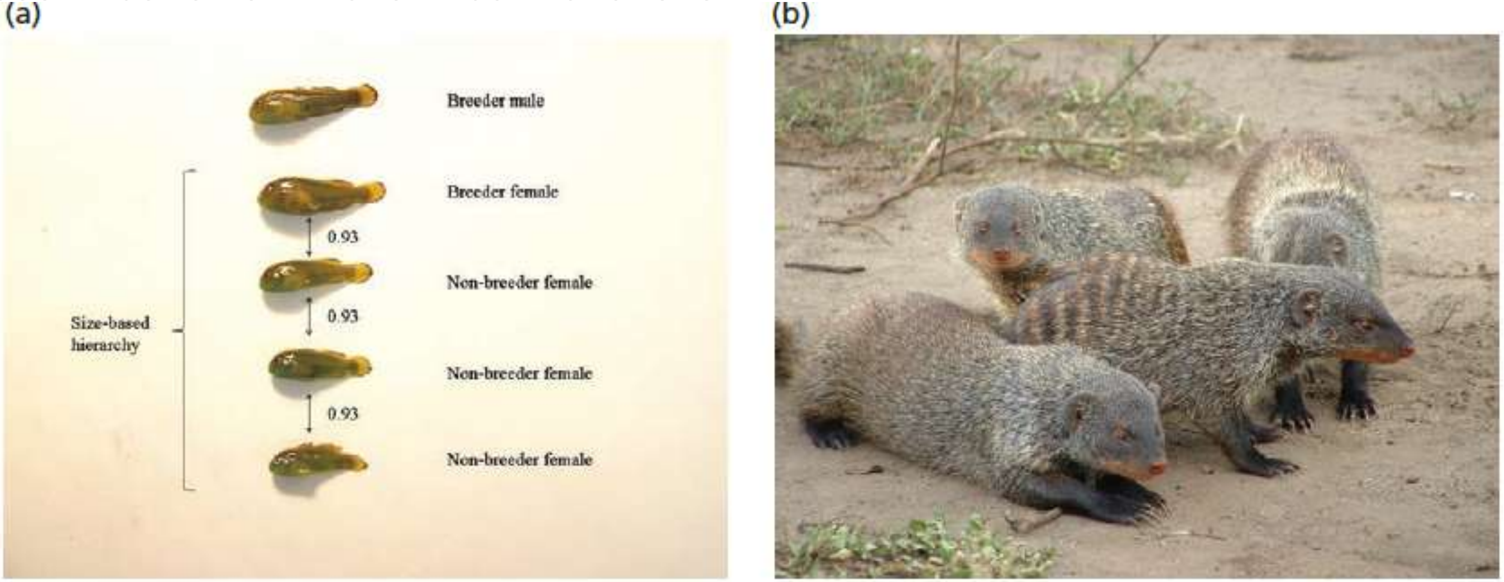


Fig. 6.20 Reproductive skew. (a) Size hierarchy in a group of the coral-dwelling goby, *Paragobiodon xanthosomus*. These individuals were anaesthetised to enable this photo to show the size ratios within the group. Subordinates restrain their growth to avoid being evicted by the dominants. Photo © Marian Wong. (b) A banded mongoose group. Dominant females evict pregnant subordinates when the group size exceeds the optimum from the dominant's point of view. Photo © Hazel Nichols.

Sexual Selection, Sperm Competition and Sexual Conflict

Sexual Selection, Sperm Competition and Sexual Conflict

Why, for example, is it only male kudu that have enormous horns, and only male birds of paradise that have such remarkable, ornamented plumage?

Darwin argued that these structures could not be essential for survival, otherwise surely the females would have them too. Instead, he proposed that these traits had evolved simply because they were of advantage in competition for mates, a process he called ‘Sexual Selection’.

Fig. 7.1 Darwin’s theory of sexual selection was proposed to explain the evolution of traits, usually found in males, concerned with competition for mates, either by force or by charm. (a) Horns of the male kudu *Tragelaphus strepsiceros*. Photo © Oliver Krüger. (b) Ornaments of the male Raggiana bird of paradise *Paradisaea raggiana*, left, on display to a female, right. Photo © Tim Laman/naturepl.com

Males and females - differences in gamete size

Why it is usually the males who compete for females, rather than vice versa.

Isogamous – two gametes are of the same size
Anisogamous - two gametes of unequal size

Small gametes parasitize the investment of large gametes

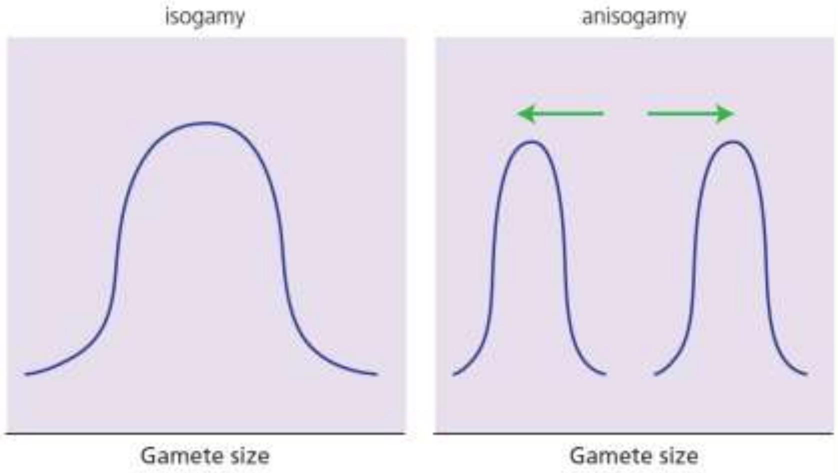
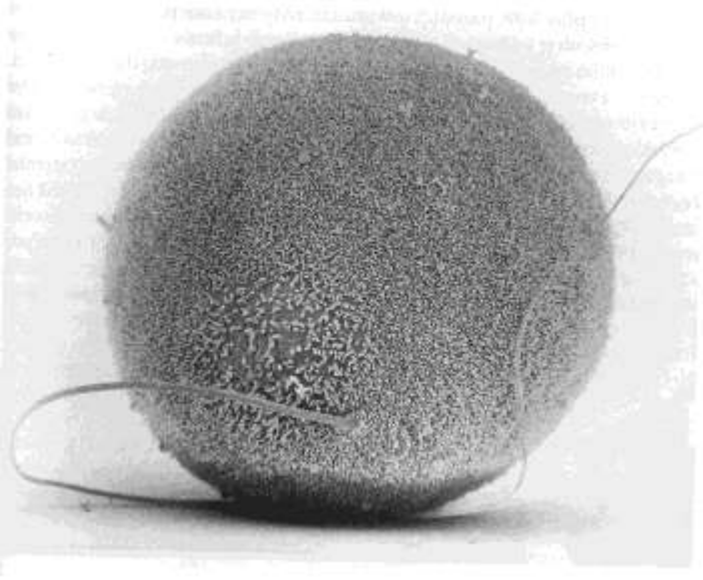


Fig. 7.2 Parker *et al.* (1972) proposed that anisogamy evolved from isogamy by disruptive selection for two gamete sizes: large gametes with food reserves (eggs) and small gametes (sperm) which parasitize the investment of the large gametes.



Sperm competition maintains anisogamy

Differences in parental care

Females produce relatively few large gametes and males produce many small ones. In addition, females often invest more than males in other forms of care.

The sex with the least parental investment has a greater potential rate of reproduction.

In general, a male can potentially fertilize eggs at a much faster rate than a female can produce them.

While a female can usually best increase her reproductive success by increasing the rate of converting resources into eggs and offspring, a male can best increase his success by finding and fertilizing many different females.

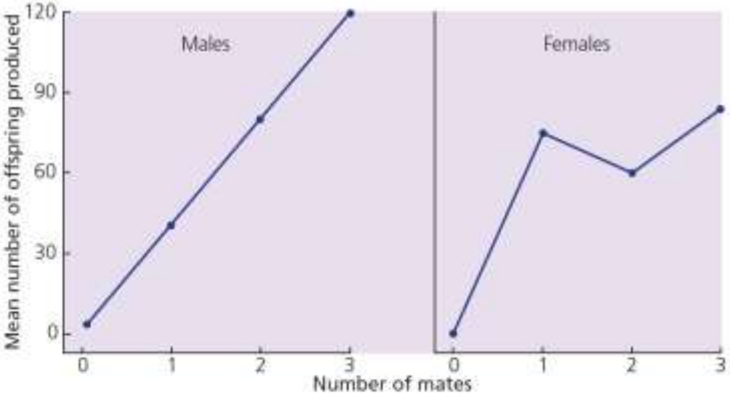
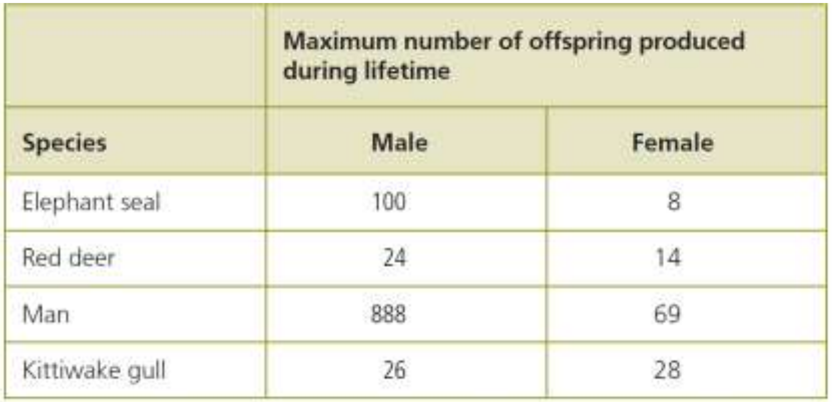


Fig 7.3 A.J. Bateman (1948) put equal numbers of male and female fruit flies (*Drosophila melanogaster*) in bottles and scored the number of matings and offspring produced by each individual, using genetic markers to assign parentage. For males reproductive success goes up with number of matings, for females it does not, beyond the first mating.



	Maximum number of offspring produced during lifetime	
Species	**Male**	**Female**
Elephant seal	100	8
Red deer	24	14
Man	888	69
Kittiwake gull	26	28

The data for man came from the Guinness Book of Records: the male was Moulay Ismail the Bloodthirsty, Emperor of Morocco, the woman had her children in 27 pregnancies. The data for elephant seals are from Le Boeuf and Reiter (1988), for red deer from Clutton-Brock *et al.* (1982). In the monogamous kittiwake, where male and female invest similarly in each offspring, the difference in maximum reproductive output is negligible (Clutton-Brock, 1983).

Table 7.1 In polygamous or promiscuous species some males have a much higher potential reproductive rate than females

Why do females invest more in offspring care than do males?

Males to be less likely to care in species where paternity is shared between multiple males.

As females provide more care prior to mating, there will be competition among males for female investment -> this will lead to greater variance in male success -> sexual selection on males intensifies, so there is positive feedback, making it even less likely that males will care.

Evidence for sexual selection - Traits that improve a male’s success in combat – Intrasexual competition

In California by Burney Le Boeuf and Joanne Reiter (1988), each year as few as five out of 180 competing males were responsible for 48–92% of the matings with 470 females.

Adult males were from three to seven and a half times as heavy as adult females.

Whereas a female’s reproductive success depended on her ability to nurture offspring, a male’s depended on his mating success resulting from fights and defence of harems.

Fig. 7.4 (a) Male southern elephant seal. (b) Two males fighting for harems of females. (c) The male is huge compared to the female. These are two subadults. Photos © Oliver Krüger.

Female choice – Intersexual selection

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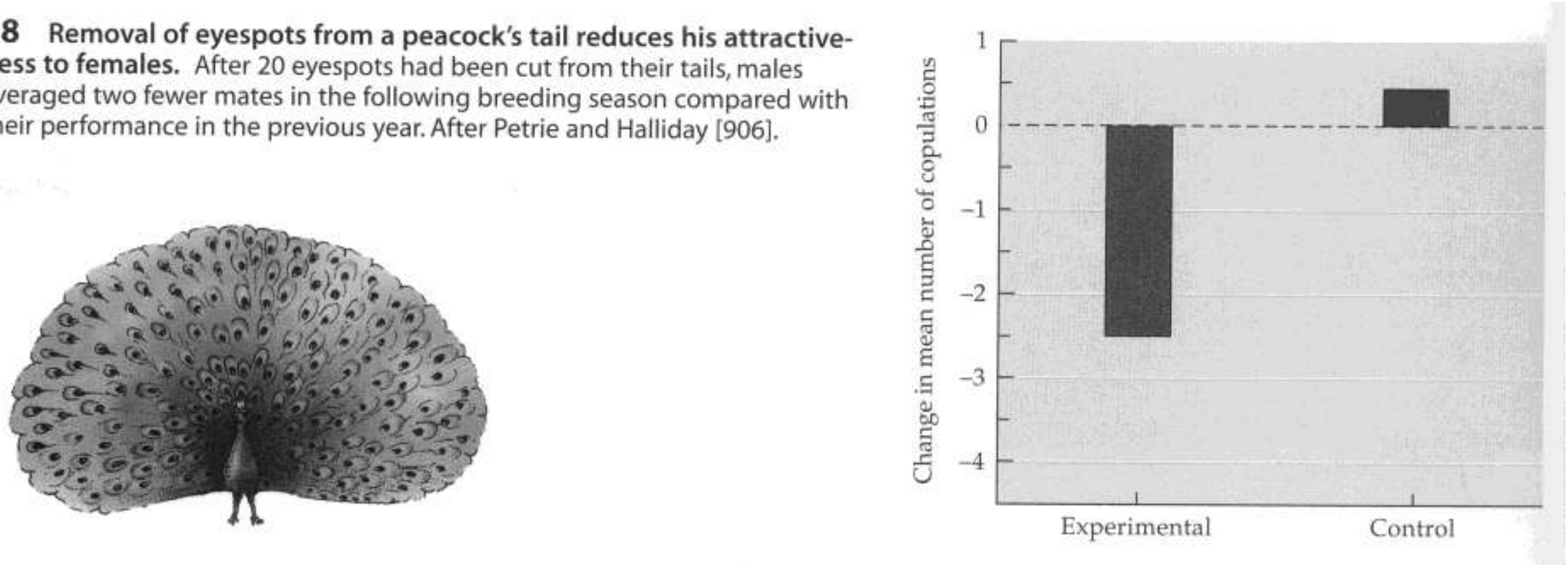
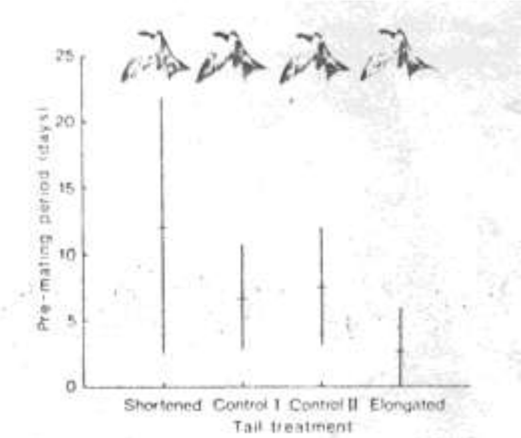


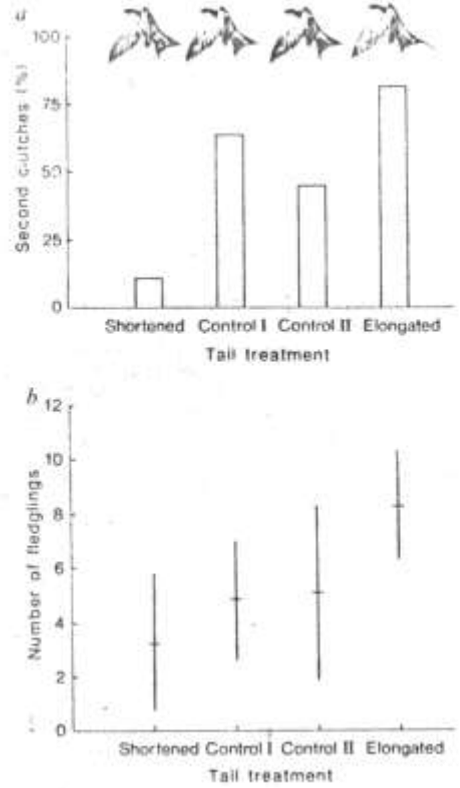
38 Removal of eyespots from a peacock's tail reduces his attractiveness to females. After 20 eyespots had been cut from their tails, males averaged two fewer mates in the following breeding season compared with their performance in the previous year. After Petrie and Halliday [906].

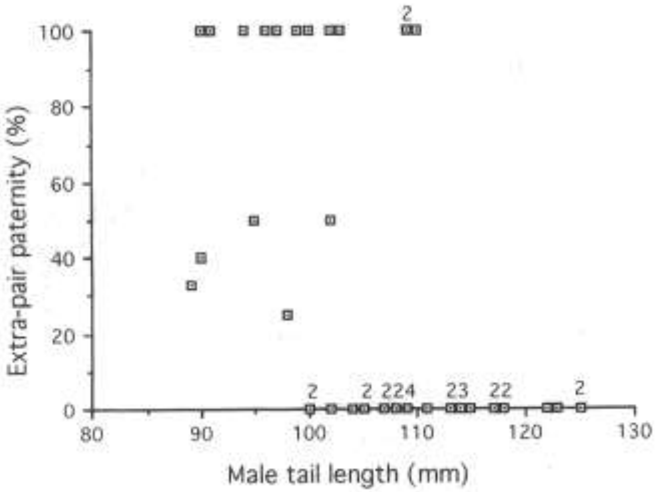
Female choice – Intersexual selection

Barn Swallow

Males with experimentally elongated tails paired up more quickly, with more offsprings and were also preferred by females seeking extra-pair matings compared to males with shortened tails (Møller, 1988).







Why not all males has long tails?

However, males were handicapped with elongated tails in their foraging; they caught smaller prey and grew poorer quality feathers and shorter tails with more fault bars in it (higher chance for feather damage -> lower survival) comparing to males in control and shortened groups at the next moult.

As a result, they were slower to attract a mate the following year and suffered reduced reproductive success

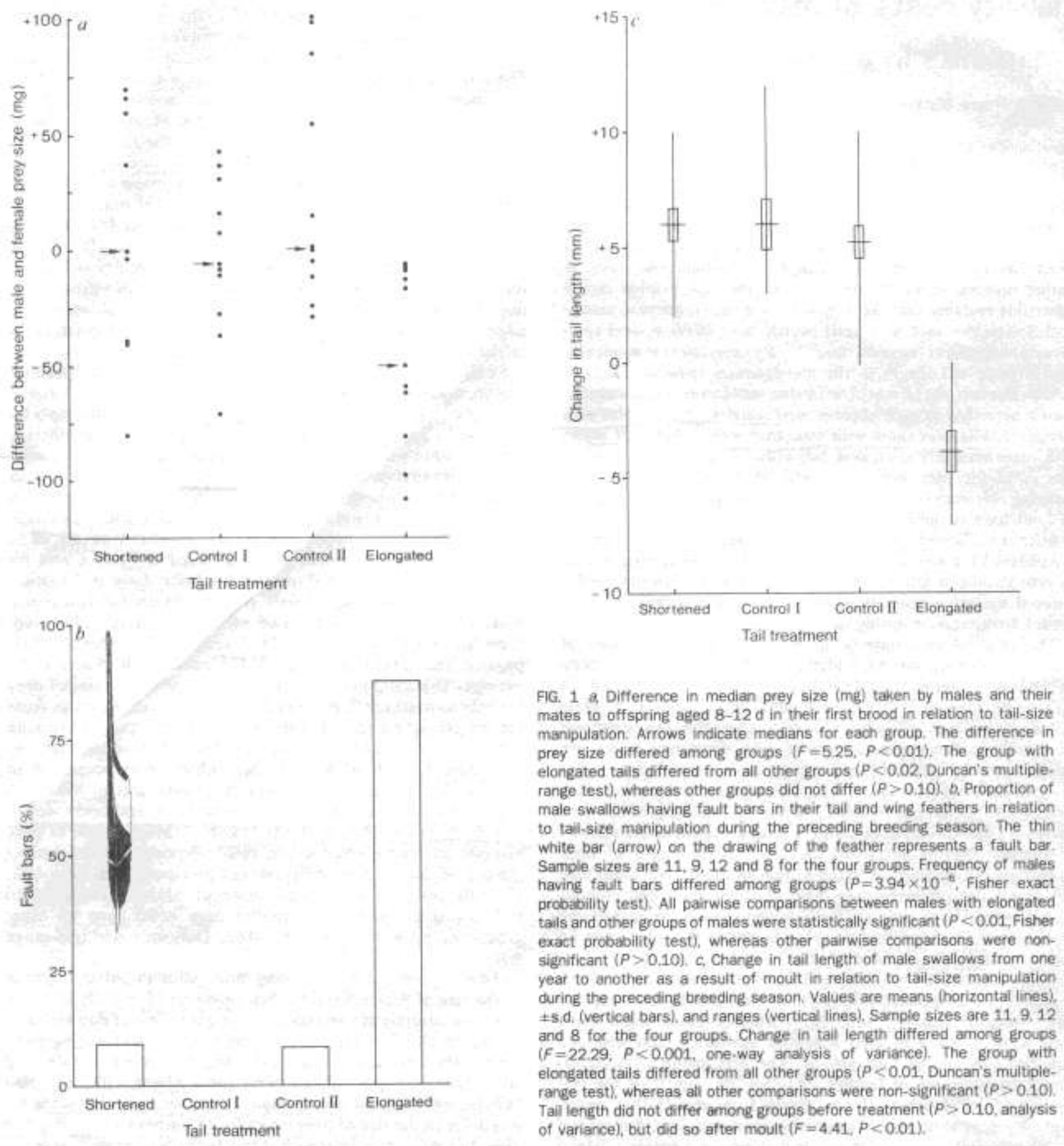


FIG. 1 *a*, Difference in median prey size (mg) taken by males and their mates to offspring aged 8–12 d in their first brood in relation to tail-size manipulation. Arrows indicate medians for each group. The difference in prey size differed among groups ($F=5.25$, $P<0.01$). The group with elongated tails differed from all other groups ($P<0.02$, Duncan's multiple-range test), whereas other groups did not differ ($P>0.10$). *b*, Proportion of male swallows having fault bars in their tail and wing feathers in relation to tail-size manipulation during the preceding breeding season. The thin white bar (arrow) on the drawing of the feather represents a fault bar. Sample sizes are 11, 9, 12 and 8 for the four groups. Frequency of males having fault bars differed among groups ($P=3.94\times10^{-6}$, Fisher exact probability test). All pairwise comparisons between males with elongated tails and other groups of males were statistically significant ($P<0.01$, Fisher exact probability test), whereas other pairwise comparisons were non-significant ($P>0.10$). *c*, Change in tail length of male swallows from one year to another as a result of moult in relation to tail-size manipulation during the preceding breeding season. Values are means (horizontal lines), ±s.d. (vertical bars), and ranges (vertical lines). Sample sizes are 11, 9, 12 and 8 for the four groups. Change in tail length differed among groups ($F=22.29$, $P<0.001$, one-way analysis of variance). The group with elongated tails differed from all other groups ($P<0.01$, Duncan's multiple-range test), whereas all other comparisons were non-significant ($P>0.10$). Tail length did not differ among groups before treatment ($P>0.10$, analysis of variance), but did so after moult ($F=4.41$, $P<0.01$).

Female choice – Intersexual selection

European sedge warbler - Female choice for more complex songs (acustic peacock’s tail)

The song consists of a long stream of trills, whistles and buzzes and is sung by the male after arriving back on its breeding territory from the winter quarters in Africa.

As soon as the male has paired, it stops singing.

Males with the most elaborate songs were the first to acquire mates

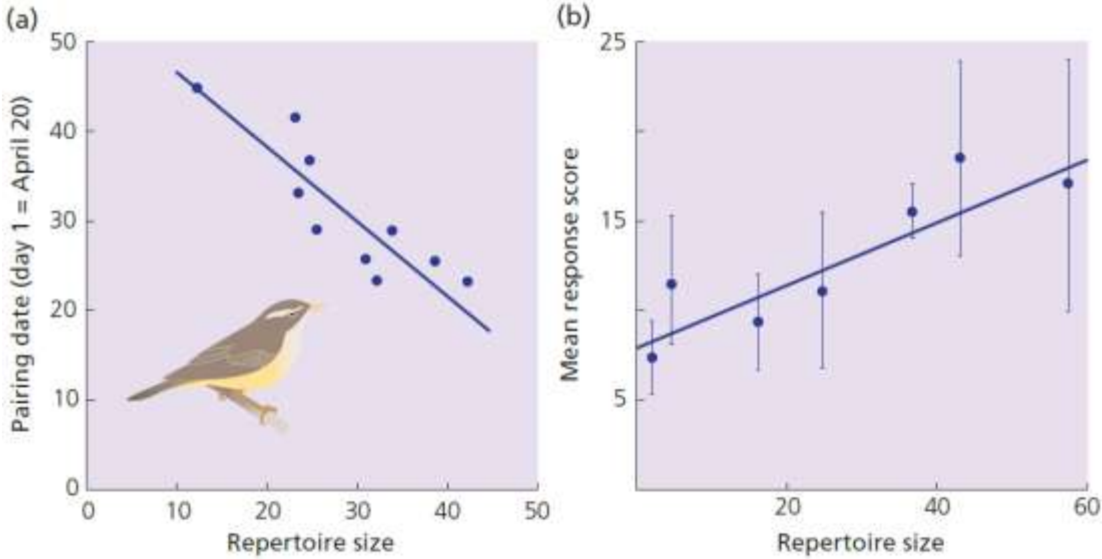
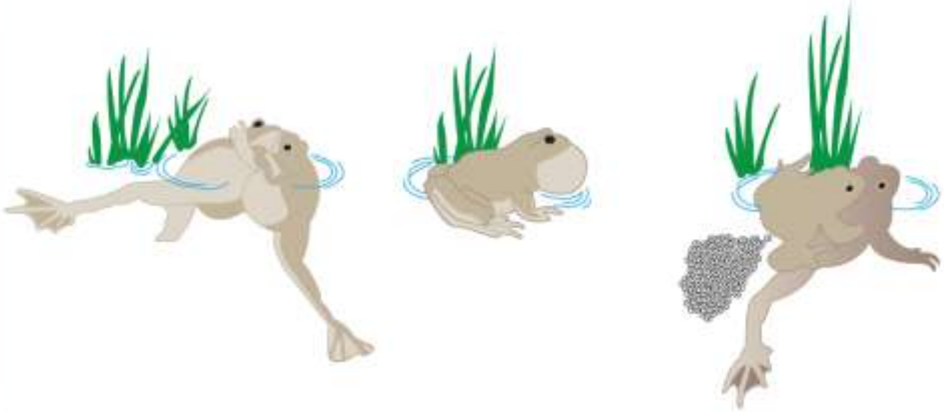


Fig. 7.6 (a) Male sedge warblers with the largest song repertoires are the first to acquire females in the spring. The size of song repertoire is estimated from sample tape recordings of each male. The results were collected in such a way as to control for the possibilities that older males, or males in better territories, both mate first and have larger repertoires. From Catchpole (1980). (b) The mean ± s.e. response score of five females to repertoires of different sizes. The response score measures sexual behaviour. From Catchpole *et al.* (1984). Reprinted with permission from the Nature Publishing Group.

Why are females choosy?

Good resources

Fig. 7.7 Male bullfrogs compete for good egg-laying territories by wrestling (left). The winners then advertise for females by calling (middle) and females lay their eggs in the male's territory. From Howard (1978a,b).



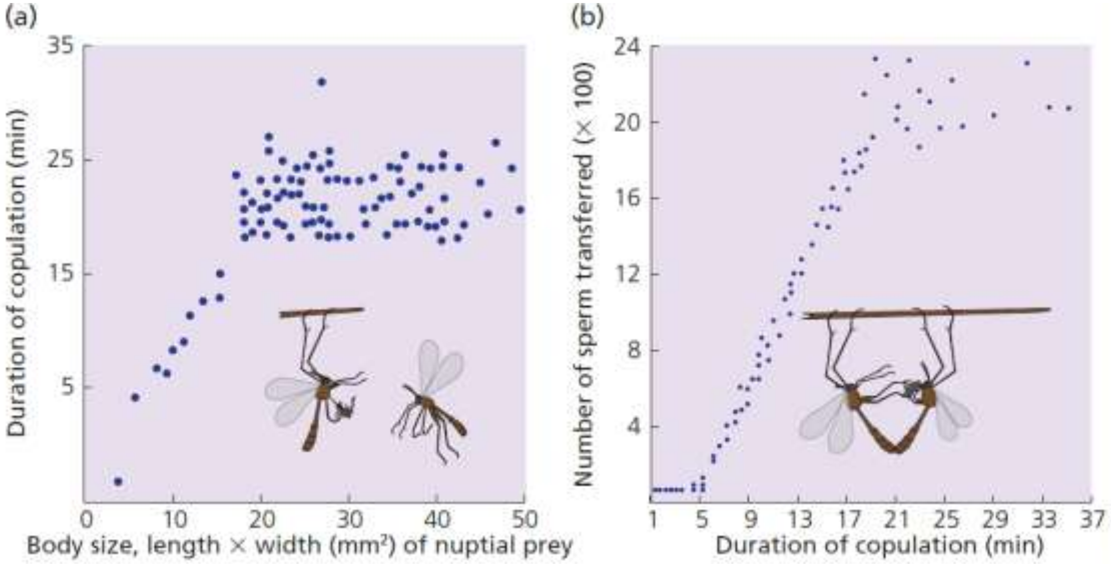


Fig. 7.8 Female choice for good resources. (a) Female hanging flies (*Hylobittacus apicalis*) mate with males for longer if the male brings a larger prey item for her to eat during copulation. (b) The male benefits from long copulation because he fertilizes more eggs. From Thornhill (1976).

Why are females choosy?

Good genes

Bowerbirds - The males play no part in parental care; all their reproductive effort is put into display. The males then decorate their bowers with colourful fruits, flowers, feathers, bones, stones, shells and insect skeletons.

Males with the best decorated bowers gain the most matings.

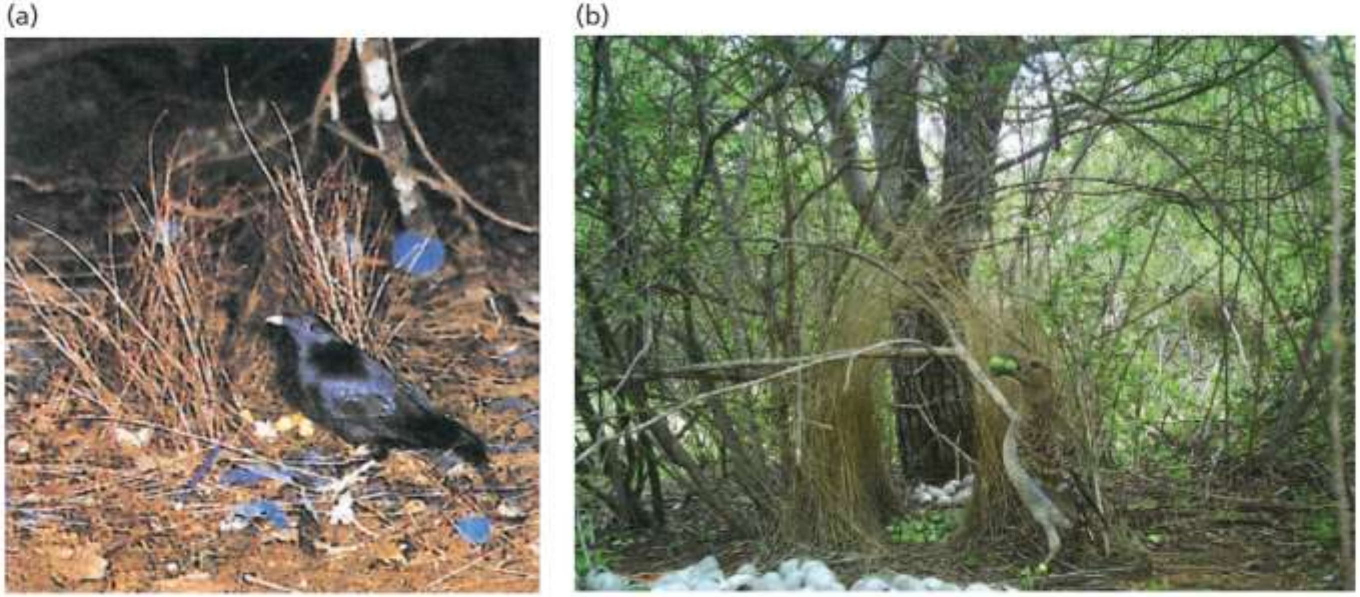


Fig. 7.9 The bowers of: (a) Satin bowerbird. Photo by Michael & Patricia Fogden/Minden Pictures/FLPA. (b) Spotted bowerbird. Satin bowerbirds prefer blue objects. This bower has feathers and human debris including pens, pieces of plastic and toothbrushes. Spotted bowerbirds prefer green objects, especially *Solanum* berries. Photo © Joah Madden.

Genetic benefits from female choice: two hypotheses

Fisher’s ‘runaway’ hypothesis: females gain attractive sons - Elaborate male displays may be sexually selected simply because it makes males attractive to females

Good genes for sons and daughters

Amotz Zahavi’s handicap hypothesis - females prefer males with elaborate ornaments and display precisely because they are handicaps and, therefore, act as a reliable signal of a male’s genetic quality. Selection for increased genetic quality of offspring

How is genetic variation for quality maintained over the generations?

- Mutations
- Many genes are involved in influencing male condition
- Females may choose different male traits in different years
- Host–parasite arms races: female choice for disease resistance

The Fisher process

Covariance of male trait and female preference in stalk-eyed flies

Small flies have their eyes held out on stalks which are particularly long in the males where the eye span can exceed their body length.

Wilkinson and Reillo then conducted artificial selection experiments:

in one line they selected for males with the longest eye spans and in the other for males with the shortest.

After 13 generations they found that female choice had changed too, as a correlated response:

- in the long eye span male line females preferred long eye span males
- while in the short eye span line they preferred males with short eye spans

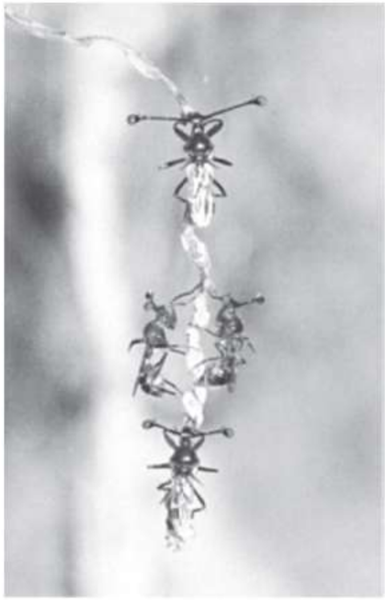


Fig. 7.10 A male (top) and a group of three female stalk-eyed flies roosting on a root hair. Note the much greater eye span of the male. From Wilkinson and Reillo (1994).

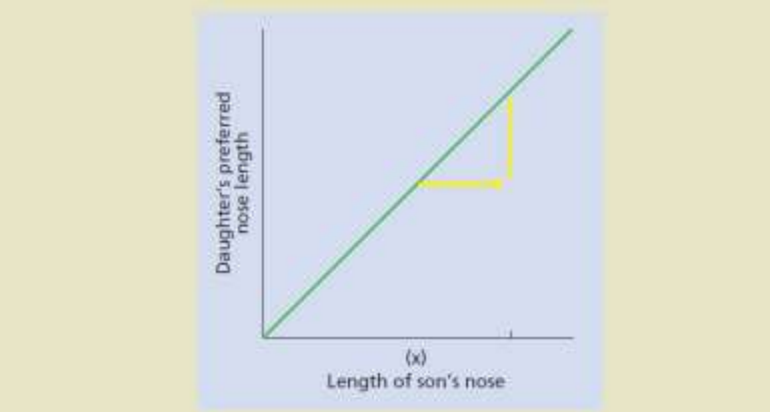


Fig. B7.3.1 Genes for long nose and long preference go together in the offspring. The slope of the line represents the degree of association or covariance.

‘Good genes’ hypothesis

Peacocks

Experiment in which females were paired at random with males of different natural tail ornamentation.

The eggs were all collected and raised by chickens under standard conditions, and the peafowl chicks were then given food ad libitum in aviaries.

Both the sons and the daughters of males with the more ornamented tails grew better.

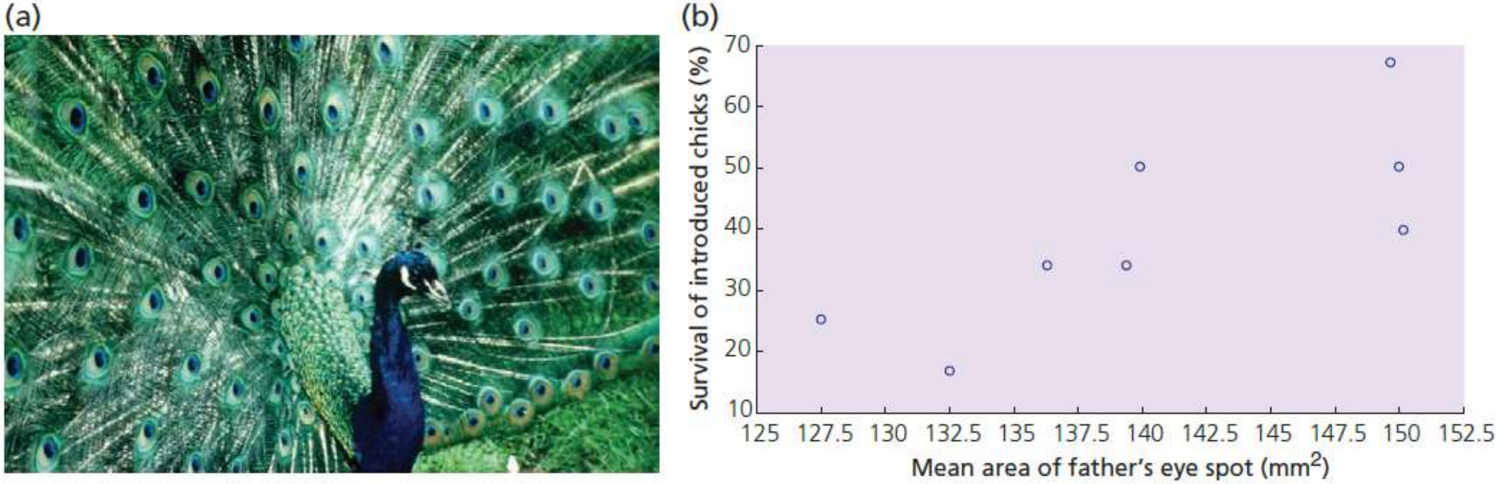


Fig. 7.11 (a) Male peacock displaying. Photo © Marion Petrie. (b) Males with larger eyespots on their tails sired offspring that survived better. From Petrie (1994).

Sexual selection in females and male choice

When males make a large contribution to parental investment, males may be choosy about whom they mate with; this can lead to sexual selection in females, who evolve traits to increase their access to males.

In monogamous birds both sexes often invest heavily in parental care and it pays both to choose high quality partners.

Female advertisement takes on an extreme form in some primates which live in multimale groups, where a female has access to several males.

In baboons, individual differences in the size of the swellings are correlated with female quality (ability to rear offspring. Females may compete for matings with the dominant male (who is best able to protect them or their offspring), or they may compete to mate with several males in the group to give each a sufficient paternity chance that they will desist from infanticide

Fig. 7.13 Sexual ornaments in females. (a) In great crested grebes, both sexes have head-feather ornaments, likely to have evolved through mutual mate choice. Photo © osf.co.uk. All rights reserved. (b) Sexual swellings in a female Chacma baboon, *Papio ursinus*, from the Cape Peninsula, South Africa. Photo © Esme Beamish.

Sex role reversal

In some cases, female competition for males becomes so strong that there is reversal of the usual sex roles.

In the pipefish, Syngnathus typhle, it is the male who becomes pregnant; he has a brood pouch in which a clutch of fertilized eggs are kept safe and provided with nutrients and oxygen. During his pregnancy, which lasts several weeks, a female could produce several clutches of eggs. Therefore, males become a limiting resource for female reproductive success and females compete for males, with males preferring larger, more ornamental females who produce larger clutches.

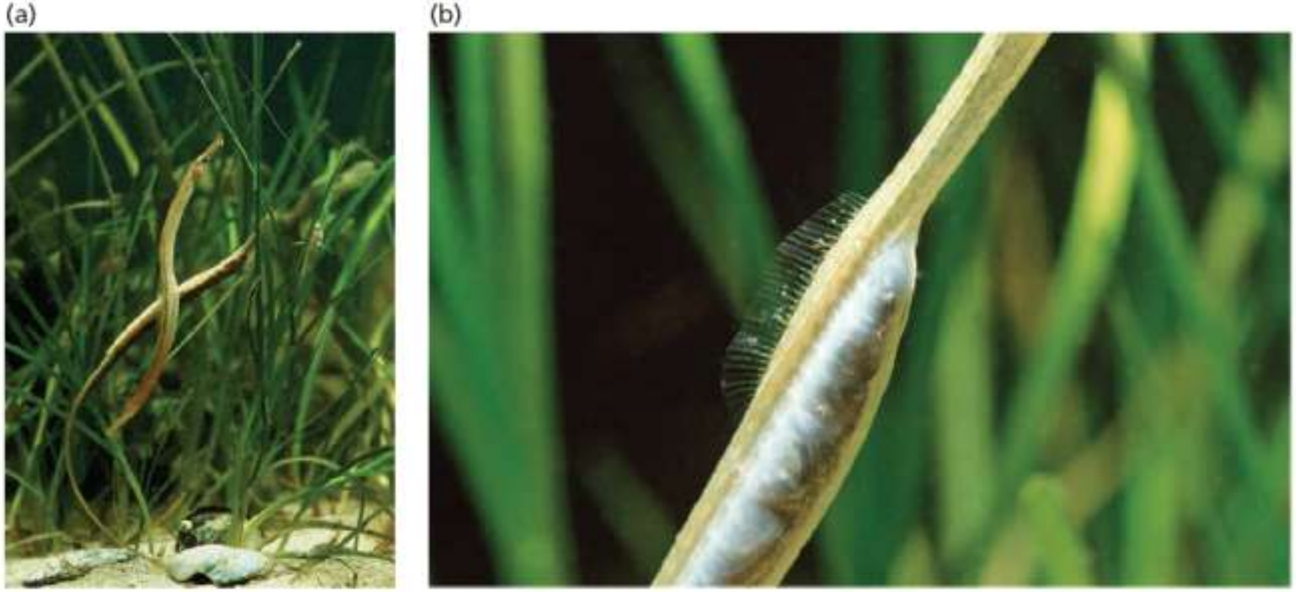


Fig. 7.14 Sex role reversal. (a) A pair of pipefish *Syngnathus typhle*. The male is in front, the female is upside down below him. (b) A pregnant male pipefish with a brood pouch full of developing young. Photos © Anders Berglund.

Sex role reversal

Seasonal variation in food availability leads to changes in sex roles in Kawanaphila katydids in Australia.

When food is scarce, the male’s large protein-rich spermatophore is costly to produce and also very valuable to females. Females compete for males and males are choosy, preferring larger females who lay more eggs.

However, when pollen-rich grass trees come into flower, males can produce spermatophores more rapidly. Access to receptive females now limits male success, and males compete for females, with females rejecting some males.

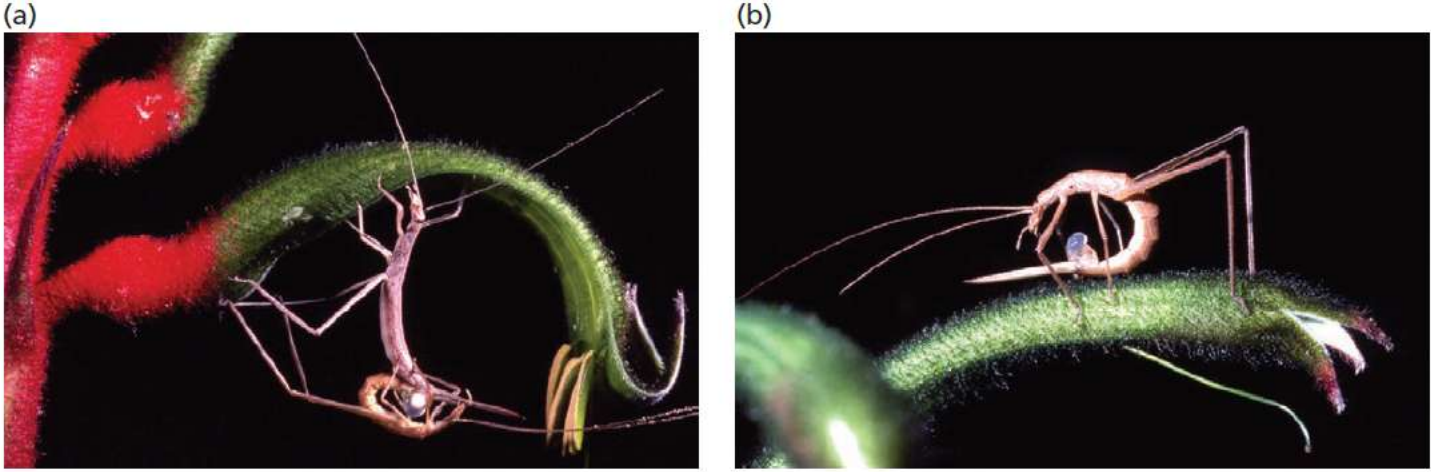


Fig. 7.15 The katydid (bush cricket) *Kawanaphila nartee* from Australia on kangaroo paw flowers. The male produces a large protein-rich spermatophore. (a) A pair together at the end of copulation, with the male (curled up behind the female) depositing his spermatophore. (b) The female bending over to eat the spermatophore. She will use this food to help her form eggs. Photos © Darryl Gwynne.

Sex differences in competition

Eclectus parrot

The bright red and blue females compete for scarce nest hollows. Females are hidden inside these nest hollows during incubation and nestling care, so they do not need to be cryptic. They display below the canopy, where their bright colours contrast with the dark limbs and trunks of the trees.

The bright green males compete for access to females with the best nest sites and their colouration reflects a compromise between camouflage from predators and the advantage of conspicuousness (scarlet underwing coverts) for displays.

Both sexes are likely to have to compete with members of their own sex.

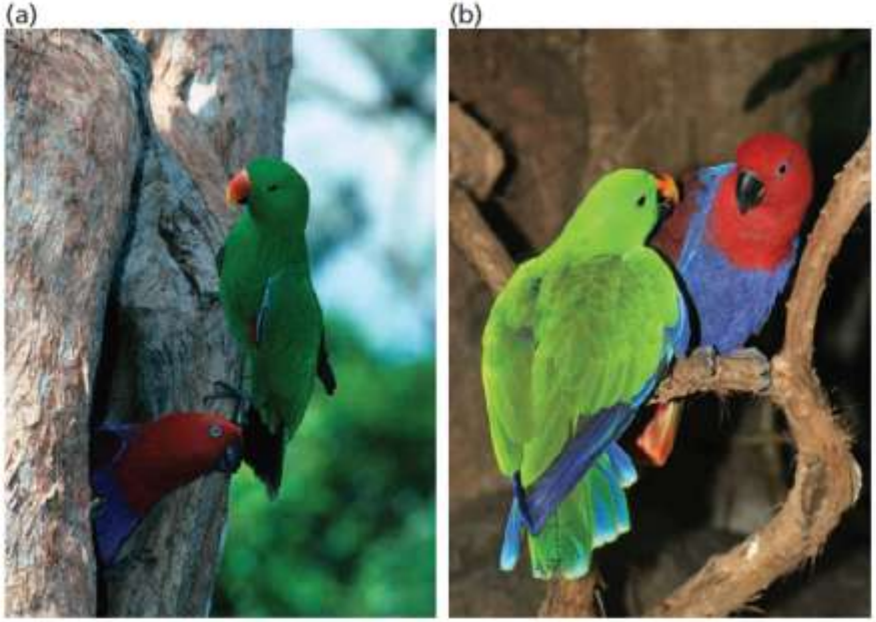
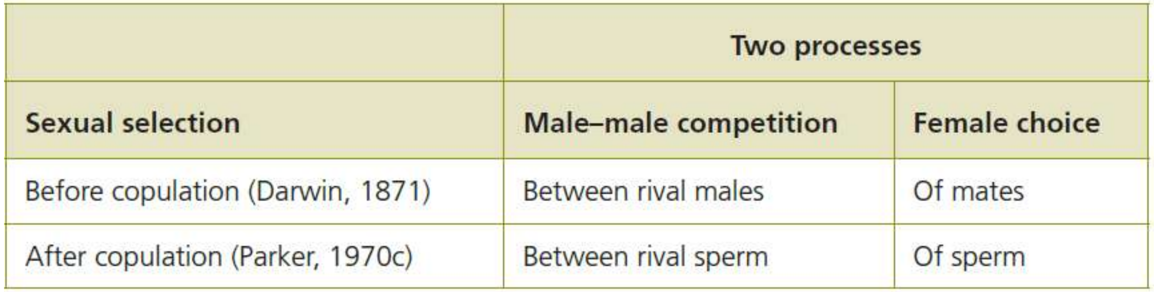


Fig. 7.16 Sexual dimorphism in the eclectus parrot. The male is bright green, with red underwing coverts. The female is bright red and blue. Photos © (a) Lochman Transparencies, (b) © Michael Cermak.

Sperm competition

Sexual selection continues after mating



	Two processes	
Sexual selection	**Male–male competition**	**Female choice**
Before copulation (Darwin, 1871)	Between rival males	Of mates
After copulation (Parker, 1970c)	Between rival sperm	Of sperm

Table 7.2 Sexual selection operates both before and after mating

Why do females copulate with more than one male?

- Material (or direct) benefits from multiple mating - increases the number of young that a female can produce
- Genetic (or indirect) benefits - the female increases the genetic quality of her offspring by mating with more than one male

Typically, 10–40% ofcthe offspring are sired by males who are not the female’s social mate in monogamous birds.

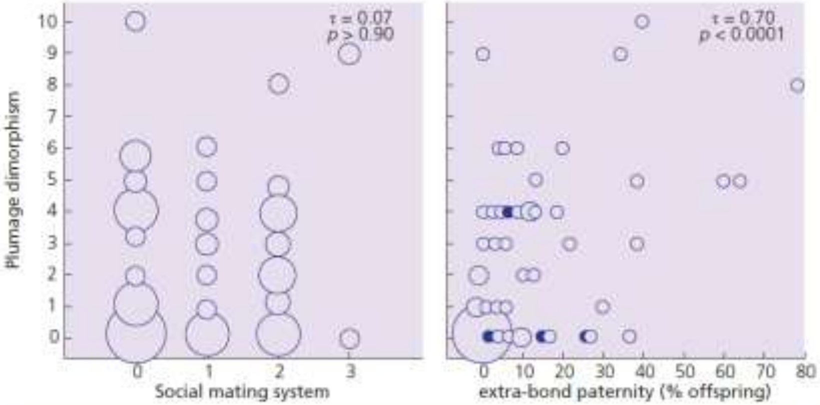


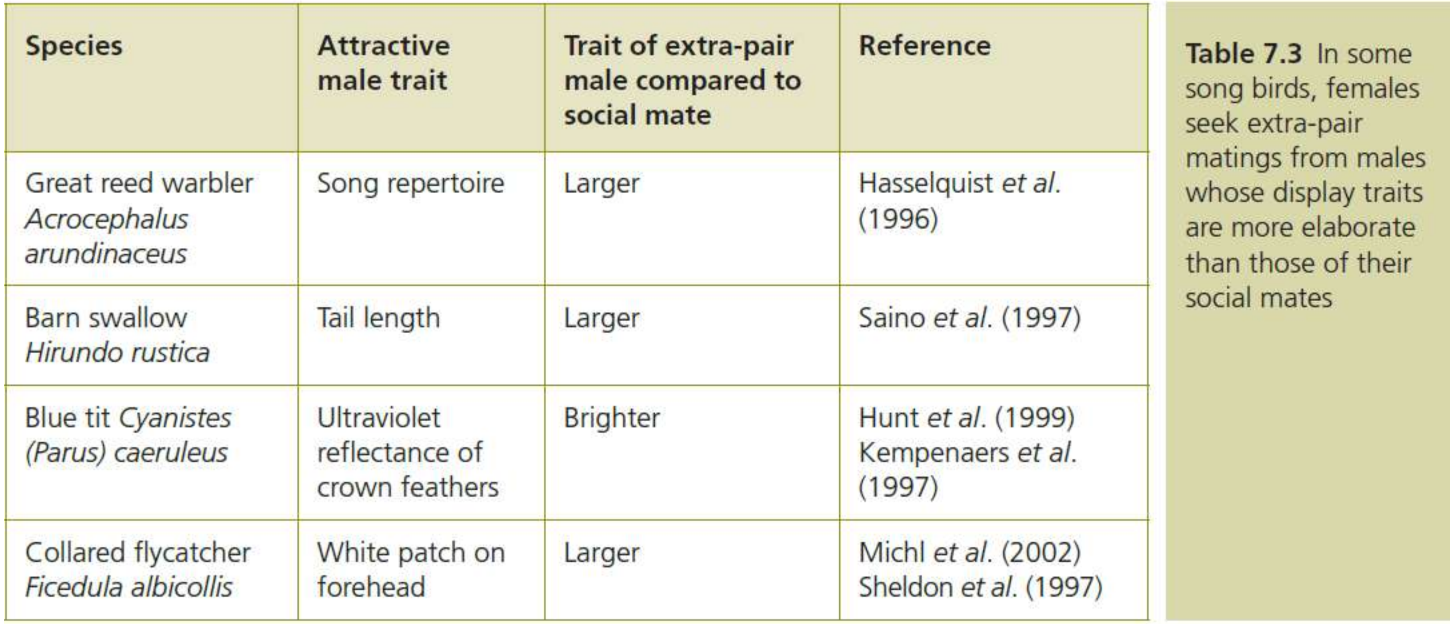
Fig. 7.17 A comparative study of bird plumage dimorphism by Owens and Hartley (1998) showed that sexual dimorphism did not correlate with social mating system (number of mates: 0 – social monogamy, 1 to 3 – increasing levels of male polygyny), but increased significantly with extra-bond paternity (percentage offspring sired by extra-bond males). Plumage dimorphism is scored on a scale from zero (no difference between males and females) to ten (males much brighter than females). Circle sizes reflect sample size.

Females paired to attractive males (as measured by these traits) tend to be more faithful; those paired to males with poorer developed traits are the ones who most actively seek extra-pair matings.

Extra-pair males do not provide care, only sperm.

The comparison of extra-pair sired young with that of their within-pair sired half-siblings (raised in the same nest), the extra-pair sired young survived better, suggesting that females did indeed gain a genetic benefit from extra-pair matings.

Multiple mating improves a female’s reproductive success



Species	**Attractive male trait**	**Trait of extra-pair male compared to social mate**	**Reference**
Great reed warbler *Acrocephalus arundinaceus*	Song repertoire	Larger	Hasselquist *et al.* (1996)
Barn swallow *Hirundo rustica*	Tail length	Larger	Saino *et al.* (1997)
Blue tit *Cyanistes (Parus) caeruleus*	Ultraviolet reflectance of crown feathers	Brighter	Hunt *et al.* (1999) Kempenaers *et al.* (1997)
Collared flycatcher *Ficedula albicollis*	White patch on forehead	Larger	Michl *et al.* (2002) Sheldon *et al.* (1997)

Table 7.3 In some song birds, females seek extra-pair matings from males whose display traits are more elaborate than those of their social mates

Constraints on mate choice and extra-pair matings

Why do females not choose to mate with an ideal male in the first place?

- In cases where competition for the best males is intense, females may be forced to settle for less than the best social mate and then rely on extrapair matings to increase the genetic quality of their offspring.

What limits extra-pair mating?

- Cuckolded males may reduce parental care - trade-off benefits from extra-pair fertilizations with loss of help in raising the chicks

A hypothesis is that different sires are best for sons and daughters - Sexually antagonistic genes, which have a beneficial effect in one sex but a harmful effect in the other sex

- In red deer on the isle of Rum, Scotland, males with high lifetime reproductive success fathered, on average, daughters with low fitness

The female might temper her extrapair matings because her social mate is a better sire for offspring of one sex while an extra-pair male is a better sire for the other sex.

Sexual conflict

Sexual conflict over mating

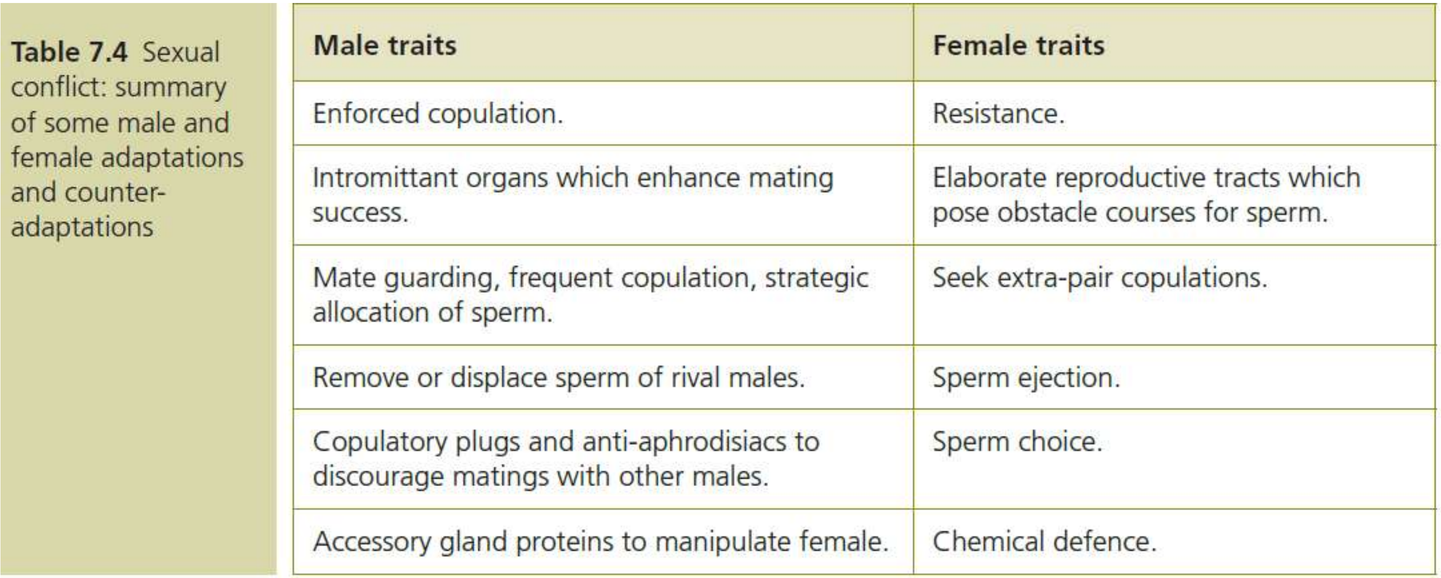


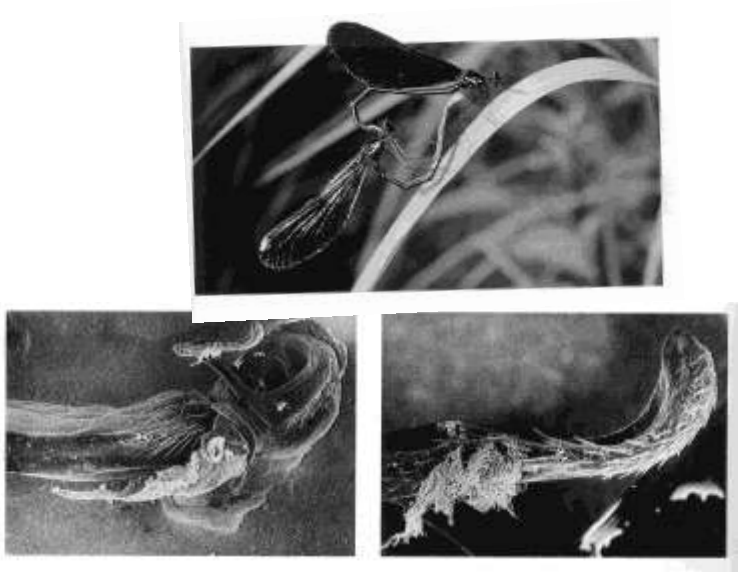
Table 7.4 Sexual conflict: summary of some male and female adaptations and counter-adaptations

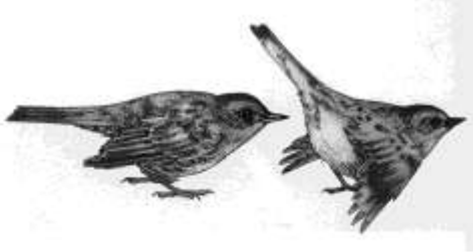
Male traits	**Female traits**
Enforced copulation.	Resistance.
Intromittant organs which enhance mating success.	Elaborate reproductive tracts which pose obstacle courses for sperm.
Mate guarding, frequent copulation, strategic allocation of sperm.	Seek extra-pair copulations.
Remove or displace sperm of rival males.	Sperm ejection.
Copulatory plugs and anti-aphrodisiacs to discourage matings with other males.	Sperm choice.
Accessory gland proteins to manipulate female.	Chemical defence.

Sexual conflict after mating

Male adaptations

- Sperm removal. Male damselflies and dragonflies may remove sperm deposited by rival males before inserting their own.
- Sperm displacement. A male’s insemination flushes out inseminations of previous males.
- Copulatory plugs. In some invertebrates (especially insects) the male cements up the female’s genital opening after copulation to prevent other males from fertilizing her.
- Anti-aphrodisiacs. The female Heliconius erato butterflies have a peculiar odour after they have mated
- Sterile sperm. In some invertebrates, males produce two types of sperm: ‘eusperm’, which have the potential to fertilize the female’s ova, and ‘parasperm’ which are sterile (and may or may not contain a nucleus).
- Accessory gland proteins (Acps). In many insects the male’s ejaculate contains not only sperm but also a cocktail of proteins that influence female behaviour and physiology
- Strategic allocation of sperm. Testis size relative to body size increases with the degree of female promiscuity





Sexual conflict after mating

Female adaptations - Cryptic female choice

Feral fowl - Females prefer to copulate with dominant males. However, subordinate males can sometimes force matings despite female resistance. In these cases, the female retaliates immediately after mating by cloacal contractions which eject the subordinate male's sperm.

Field crickets - Female preferentially stored sperm from the unrelated males inside her spermathecae, and it was this biased storage that enabled females in the sibling and non-sibling treatment to avoid the costs of inbreeding

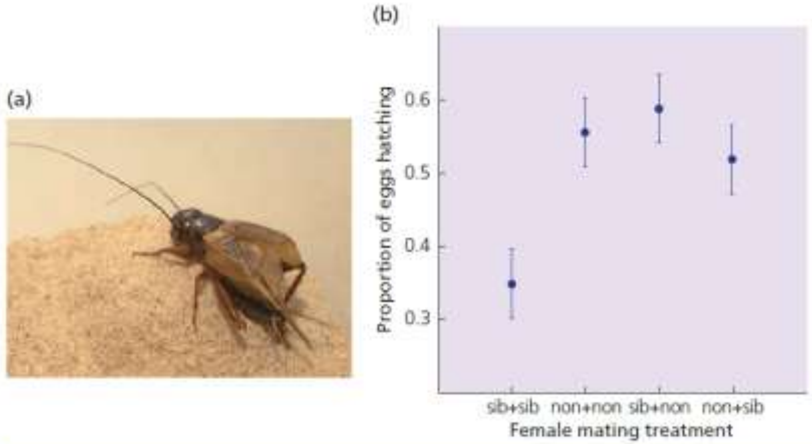


Fig. 7.22 (a) Field cricket, *Gryllus bimaculatus*. Photo © Tom Tregenza. (b) Results of a double mating experiment. Females mated to two of the female's own siblings suffer reduced hatching success due to inbreeding depression. Females mated to a sibling plus a non-sibling (in either order) do just as well as those mated to two non-siblings, suggesting the female can bias fertilization success in favour of the unrelated male. From Tregenza and Wedell (2002).

Sexual conflict: who wins?

Theoretical models suggest that the outcome is often a never-ending evolutionary chase leading to rapid evolutionary change by both parties.

Experiment Drosophiles (Holland & Rice, 1999), they had two selection lines, each run for 47 generations in the laboratory, during which they selected for the most successful males and females.

- In one line, there was intense sexual selection: each vial had three males and one female. In this environment there was strong selection for males who were successful at sperm competition and for females able to cope with male–male competition.
- In the second line, sexual selection was eliminated altogether by the neat trick of enforced random monogamy. In these vials, one male and one female spent their whole lives together. Here, in the absence of male–male competition, a male was guaranteed paternity of all his female’s ova

The monogamous line males did indeed evolve to be less harmful to females. They had a decreased courtship and mating rate. As a result, female survival and fecundity was greater than in the sexual selection line.

The females from the monogamous line were mated to males from the intense sexual selection line. These females had significantly lower survival and reproductive success than sexually selected females mated to sexually selected males. Therefore, in the monogamous line not only did males evolve to be less harmful to females, but females, in turn, evolved to be less resistant.

Coevolution of male and female genital morphology in waterfowl

The morphological consequences of post-mating conflicts are dramatically illustrated by coevolution of male and female genital morphology in waterfowl.

Male waterfowl have a phallus whose length varies between species from 1.5 to 40 cm and is positively correlated with the frequency of forced extra-pair matings.

However, female reproductive traits have coevolved with male morphology; in species where males have the longest and most elaborate phallus (with spines and grooves), females havethe most elaborate vaginal morphology, including dead end sacs and coils, which are likely to reduce the chances of male intromission without female cooperation

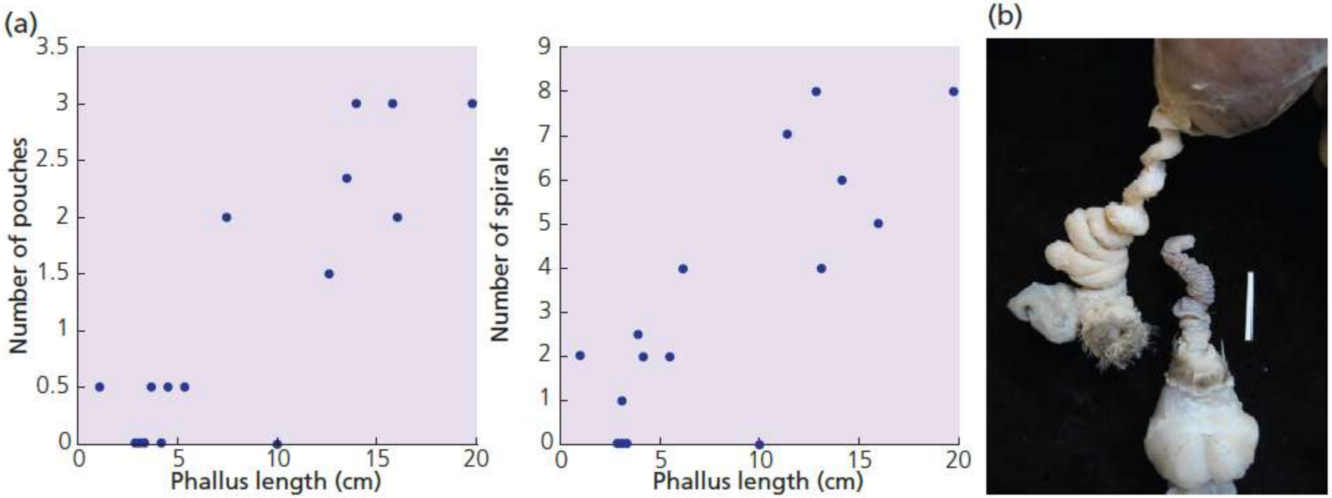


Fig. 7.23 Coevolution of male and female genitalia in waterfowl. (a) In species where the male has a longer phallus, the female has a more elaborate vagina, with more spirals (right) and 'dead end pouches' (left). The vaginal spirals are in the opposite direction to male phallus spirals, suggesting antagonistic rather than mutualistic 'lock and key' coevolution. (b) Mallard duck, *Anas platyrhynchos*, a species with high levels of forced copulations in which the male has a long phallus (bottom right) and the female has a long and elaborate vagina (top left). The white bar is 2 cm. From Brennan *et al*. (2007).

Chase-away sexual selection

Holland and Rice (1998) to propose a new model of sexual selection.

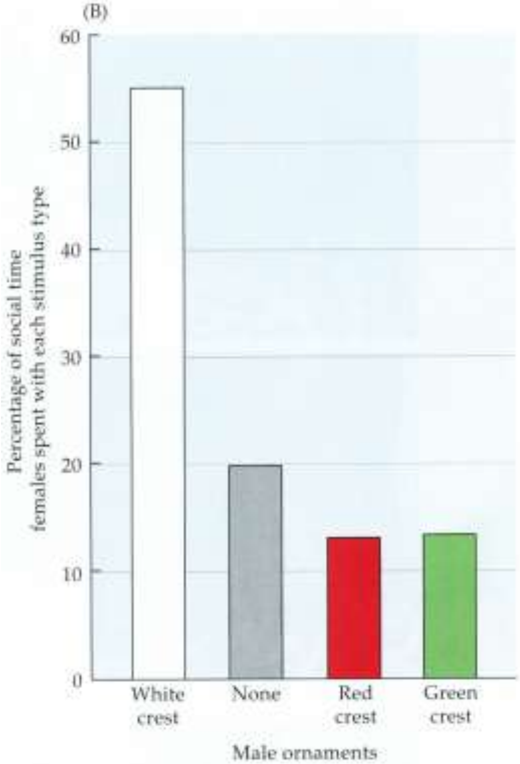
A process in which males are selected to induce females to mate, either by force or by charm, and females are then selected to resist, leading to ‘chase-away’ coevolution of male traits to stimulate females and female traits to improve resistance.

The ‘good genes’ and ‘Fisher’s runaway’ models, where females evolve preferences for male traits because of genetic benefits. <-> The ‘chase-away’ model is the precise opposite; females evolve resistance to male ploys because acquiescence is costly.

Male ploys

e.g. sensory exploitation

Finding pre-existing sensory bias of females



Parental Care and Family Conflicts

Parental Care and Family Conflicts

Sexual conflicts continue further when there is parental care of the eggs or young

-conflicts between male and female parents over how much care each should provide;

-conflicts between siblings over how much care each should demand

-conflicts between parents and offspring over the supply and demand of care

Parental care in invertebrates tends to occur only where fewer young are produced and they can be protected from the physical or biotic environment (predators, parasites)

Parental care includes the preparation of nests and burrows, the provisioning of eggs with yolk food reserves and the feeding and protection of eggs and young before and after birth

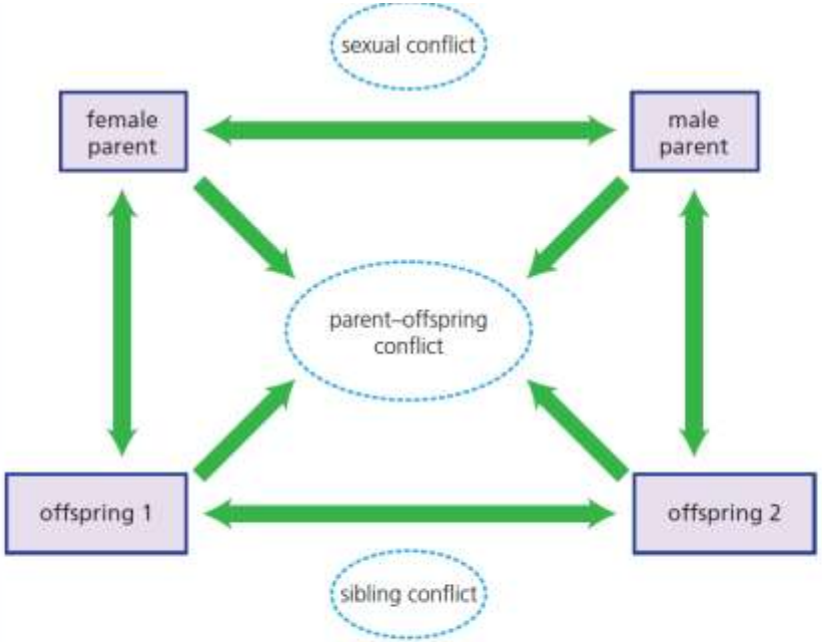


Fig. 8.1
The three types of intra-familial conflict discussed in this chapter. Male and female parents are in conflict over who should invest and how much. Siblings compete over the investment from parents. Offspring have different interests from their parents over supply and demand of investment. From Parker *et al.* (2002).

Evolution of parental care

Variation in parental care across the animal kingdom

Table 8.1 Sex roles in parental care (Kokko & Jennions, 2008)

Taxon	Parental care	References
Invertebrates	Uncommon, but when it occurs mainly female only. Biparental care uncommon. Male-only care rarer.	Zeh & Smith (1985); Tallamy (2000).
Fish	Ratio of genera with male-only: biparental: female-only care is 9:3:1.	Reynolds *et al*. (2002).
Amphibians	Female-only care and male-only care equally common. Low frequency of biparental care.	Beck (1998); Summers *et al*. (2006).
Reptiles	Either female alone or both parents.	Reynolds *et al*. (2002).
Birds	In 90% species, biparental care (including 9% where helpers assist), but females often invest more in care. Females care alone in majority of the remaining species. Male-only care is rarer.	Lack (1968); Cockburn (2006).
Mammals	Females care in all species. In 95% species, the female cares alone. In 5% the male helps too. No cases of male-only care.	Clutton-Brock (1991).

Evolution of parental care

Birds

Biparental care common

Polygyny often occurs in fruit and seed eaters, probably because these food supplies become so seasonally abundant that one parent can feed the young almost as efficiently as two

Why is it the male who deserts?

- The male has the opportunity to desert before the female. With internal fertilization, she is left literally holding the babies inside her.
- The male can often gain more by desertion than the female because his lifetime reproductive success depends more on his number of matings

Mammals

Female only care common

- The offspring often have a prolonged period of gestation inside the female, during which the male can do little direct care
- Once the young are born they are fed on milk and only the female lactates
- The male can desert first, it is not surprising that most mammals have parental care by the female alone, with the male deserting to seek further matings

Monogamy and biparental care occur in a few species where the male contributes to feeding (carnivores) or to carrying the young (e.g. marmosets)

Evolution of parental care

Fish

In the bony fish (teleosts), most families (79%) have no parental care

In those families which do care for the eggs or young, it is usually done by one parent; biparental care occurs in less than 25% of the families which show care

In fish is a simple affair often consisting of just guarding or fanning eggs. These tasks can usually be done effectively by one parent alone

Which parent will provide care?

Female care is commonest with internal fertilization (86% female care) and male care with external fertilization (70% male care). The overall predominance of male parental care in fish is related to the prevalence of external fertilization

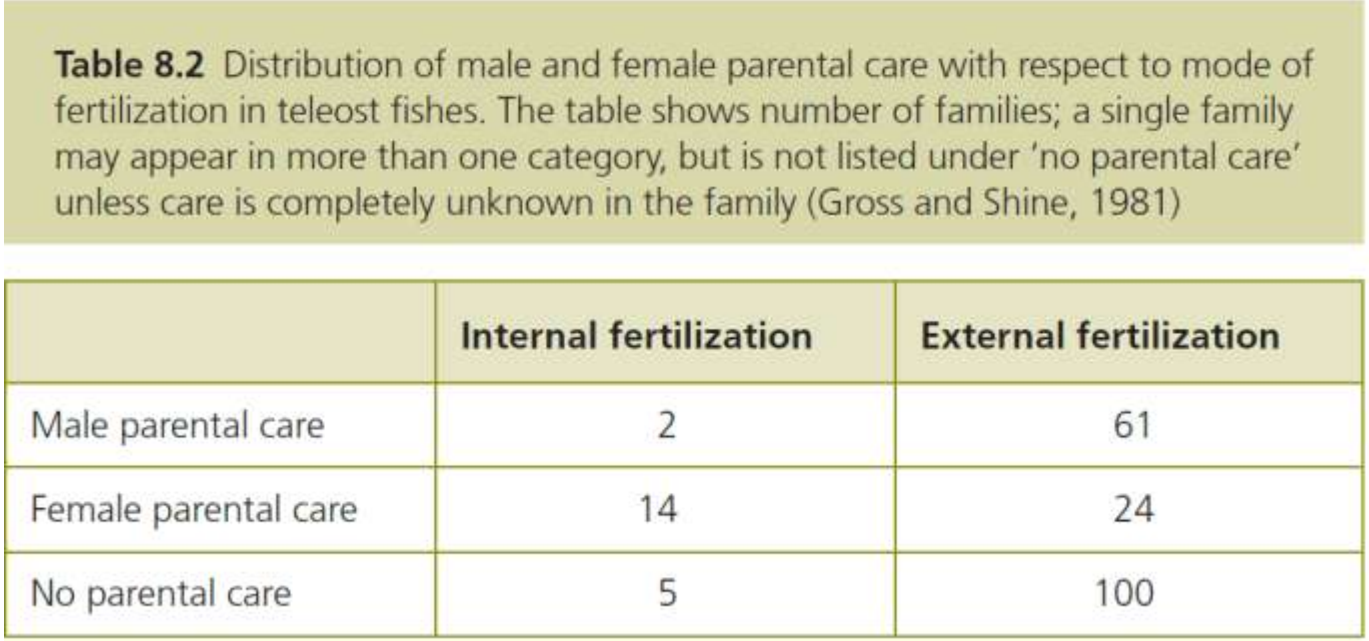


Table 8.2 Distribution of male and female parental care with respect to mode of fertilization in teleost fishes. The table shows number of families; a single family may appear in more than one category, but is not listed under 'no parental care' unless care is completely unknown in the family (Gross and Shine, 1981)

	Internal fertilization	External fertilization
Male parental care	2	61
Female parental care	14	24
No parental care	5	100

Three hypotheses proposed to explain why mode of fertilization influences which sex cares

Paternity certainty

With internal fertilization a male should be less prepared to provide parental care than the female because he is less certain that the offspring are his

BUT

In some external fertilizers, for example sunfish Lepomis, cuckoldry takes place during oviposition

Order of gamete release

Internal fertilization gives the male the chance to desert first and thus leave the female to care. With external fertilization the roles may be reversed

BUT

The most common pattern of gamete release in external fertilizers is simultaneous release by male and female. In these cases both sexes have an equal chance to desert, but 36 out of 46 species which have simultaneous gamete release and monoparental care have care provided by the male

In some families of fish, the male builds a foam nest and releases sperm before the female lays eggs. In these cases, the ‘opportunity for desertion’ hypothesis predicts that males can desert first, but nevertheless parental care is provided by the male

Three hypotheses proposed to explain why mode of fertilization influences which sex cares

Association

Association with the embryos preadapts a sex for parental care

- With internal fertilization the female is most closely associated with the embryo and this may set the stage for the evolution of embryo retention and live birth, followed by care of the young fry
- With external fertilization, on the other hand, the eggs are often laid in a male’s territory and it is the male who is most closely associated with the embryos. Defence of the territory in order to attract further females becomes, incidentally, defence of the eggs and young, and therefore provides a preadaptation for more elaborate parental care by males

Male care involves fewer opportunity costs (lost matings) than in other cases, because a male that guards eggs can still attract more mates. In fact, females sometimes prefer males that already have eggs in their nest

Parental investment: a parent's optimum

Trivers (1972) introduced the concept of parental investment, which he defined as

'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring.'

Parental investment will include any investment, such as guarding or feeding, that benefits the eggs and young. Lifetime parental investment will be the sum of all the resources a parent can gather in its lifetime and use for offspring care.

Investment trade-offs within broods and between broods

Trade-offs within broods

In theory, there will be an optimal brood size to maximize productivity per brood

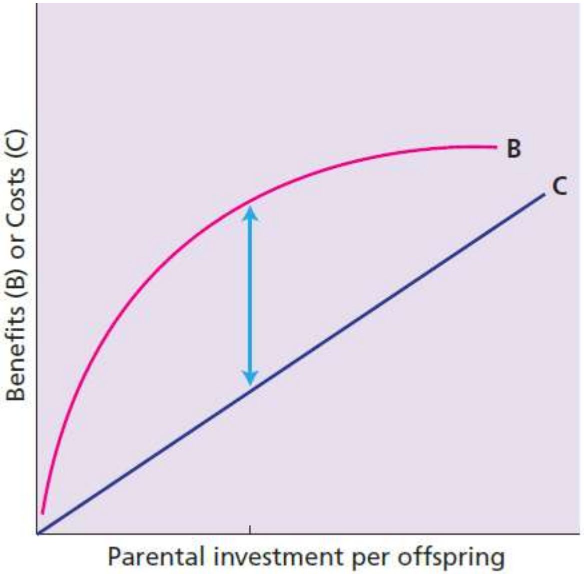


Fig. 8.2 The optimal parental investment per offspring from a parent's point of view is where the Benefits minus Costs are at a maximum. Increasing investment brings diminishing benefits as the offspring's needs become saturated, but costs continue to increase because every unit of continued investment deprives other offspring (current and future) of a parent's limited lifetime resources for care.

Parental investment: a parent's optimum

Trade-offs between broods

current versus future broods

In side-blotched lizards (Uta stansburiana), gravid females not only have the extra mass of their eggs to carry, but their distended abdomens hinder their leg movements. When some females had half their eggs removed surgically, they had improved locomotary performance (measured on a treadmill) and were more likely to survive to produce another clutch, probably because of reduced predation

Increased investment reduces an adult's future fecundity, rather than survival

When male and female burying beetles (Nicrophorus vespilloides) were induced to care for a large brood of larvae in their first breeding attempt, they subsequently produced fewer larvae from future broods than those that cared for a small brood the first time they bred

When collared flycatchers (Ficedula albicollis) were induced to increase their feeding rates to their current brood (by increasing brood size), both males and females survived as well as control birds but they had reduced fecundity the following year

Varying care in relation to costs and benefits

Bird species in temperate North America tend to have large clutch sizes (typically four to six eggs) and low adult survival to the next breeding season (around 50% or less).

By contrast, species in tropical South America tend to have small clutches (typically two to three eggs) and high adult survival (around 75% or more).

The selective forces leading to these different life histories are likely to be complex, including a greater flush of food during northern temperate breeding seasons (which permits larger clutches) but harsher climatic conditions in the non-breeding seasons (which reduces adult survival).

Parent birds modulate risk-taking in relation to value of current versus future broods

South American species should respond more strongly than their North American counterparts to a predator of adult birds (a hawk) because South American parents have greater expectations of future reproduction.

Conversely, North American parents should respond more strongly to a nest predator (a jay) because their current brood is more valuable than is a brood for a South American parent

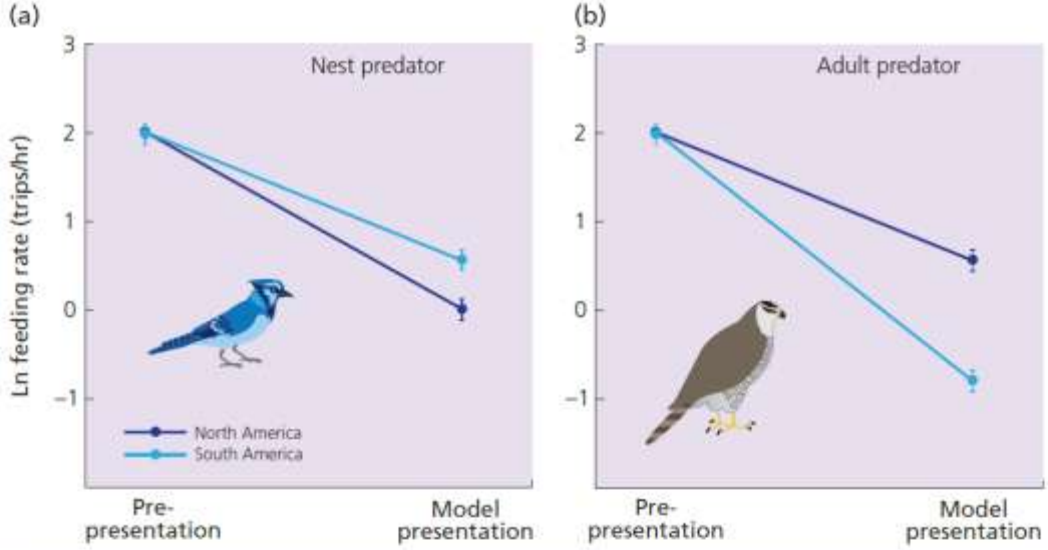


Fig. 8.3 Responses of North American and South American songbird parents to presentations of: (a) a nest predator (experimental playback of calls of a jay) and (b) a predator of adults (presentation of taxidermic mount of a hawk). Responses measured as reduction in feeding visits to a brood of nestlings. South American parents value their own lives (future broods) more (stronger response to adult predator) while North American parents value their current brood more (stronger response to nest predator). From Ghalambor and Martin (2001). Reprinted with permission from AAAS.

Response to current brood demands varies with parents' future breeding prospects

A nectar-feeding passerine bird from New Zealand, the hihi (Notiomystis cincta)

On territories where broods were fed experimentally with extra carotenoids in a sugar solution, their mouths became redder and this enhanced begging display led to increased provisioning by the parents, probably because redder mouths signalled healthier offspring, worth more investment.

However, on other territories, where the adults were also provided with carotenoid-rich sugar feeders, this increased the chance that they had a second brood that season. The pairs that had second broods did not respond to the enhanced begging signals of their current brood.

Therefore, parents strategically varied their sensitivity to their current brood's demands in relation to their future prospects of breeding that season.

Response to current brood demands varies with parents' future breeding prospects

Galilee St Peter's fish, Sarotherodon galilaeus, is a mouth brooding cichlid found in rivers and lakes throughout Africa and Asia minor.

Mating is monogamous; pairs dig a shallow depression in the substrate together, then the female lays batches of 20–40 eggs into the depression and the male glides over them, fertilizing each batch in turn until the clutch is complete. Then either the female, or the male, or both parents pick up the eggs in their mouths, where they protect the eggs and young fry for about two weeks

When the sex ratio was female-biased, males increased their likelihood of desertion.

Conversely, when the sex ratio was male-biased, female desertion increased

Therefore, both males and females deserted their offspring more frequently when the costs of care were higher (in terms of lost mating opportunities)

Smaller males were more likely to desert

Uniparental care (either by male or female) was more likely when clutch size was small

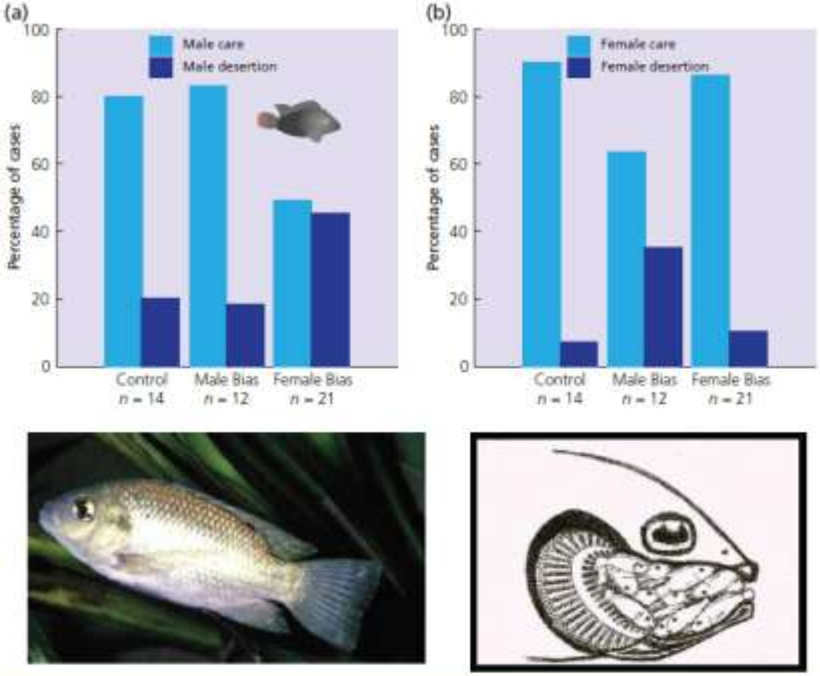


Fig. 8.4 St Peter's fish: a mouth brooder. Photo and drawing © Sigal Balshine. Experiments to test how opportunities for further matings influence: (a) male care and (b) female care in St Peter's fish. Three conditions are tested: Control (2 male, 2 females); Male bias (3 males, 1 female); female bias (1 male, 3 females). Available females increases male desertion (a), while available males increases female desertion (b). From Balshine-Earn and Earn (1998).

Varying investment in response to mate attractiveness

In theory, a parent should invest more when paired with a mate of better phenotypic or genetic quality, to take advantage of the enhanced potential benefits of the current breeding attempt

Females may invest more when paired to an attractive male

Zebra finches (Taeniopygia guttata) males have bright red beaks and they can be made more attractive to females experimentally, by giving them red leg bands. When paired to these attractive males, females increased their effort in chick-feeding, and raised more young, compared to when given less attractive males with blue or green leg bands

Female mallard ducks lay larger (better provisioned) eggs when paired with more attractive males

Female peacocks lay more eggs after copulating with males with more elaborate tails

Sexual conflict

Conflict over who should care, and conflict over how much care to provide

Sexual conflict will also occur during biparental care

If either parent is removed temporarily, then the other parent often increases its work rate

This shows that each parent has the capacity to work harder.

How then do cooperating parents come to an agreement over how hard each should work?

At the ESS, each parent will invest a fixed level of effort that maximizes its own fitness, given the effort invested by its mate

If one parent reduces its effort, the other will increase its effort but not sufficiently to compensate for the loss. Such incomplete compensation leads to stable biparental care.

If conditions led to a partner fully compensating, or even over-compensating for a reduction in effort by the other partner, then biparental care would be unstable and the ESS is for uniparental care

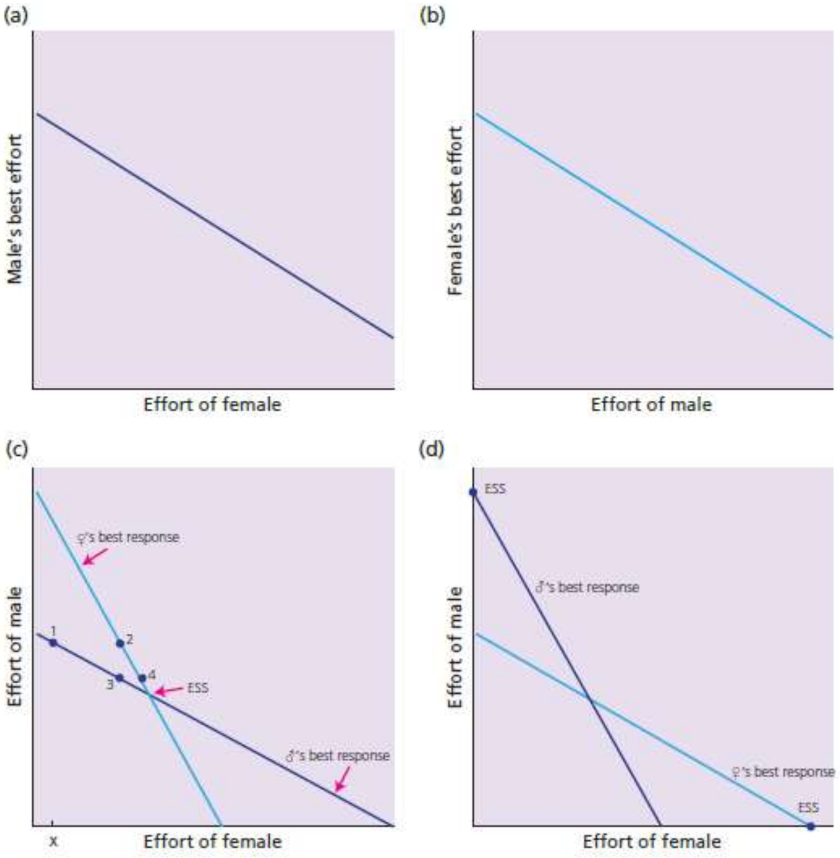


Fig. 8.5 Male-female conflict over how much care to provide (Houston & Davies 1985). (a) A male's best response to the female's parental effort; (b) a female's best response to the male's parental effort. These shallow slopes involve incomplete compensation, so if the partner reduces its effort, the other increases but not sufficiently to compensate for the loss. (c) Plotting both responses together shows that these lead to stable biparental care. Imagine, for example, that the female plays effort *x*. The male's best response is one. The female then replies with two, the male with three, the female with four, and so on, reactions proceeding by smaller and smaller amounts until the intersection which is the ESS. (d) If reactions have slopes steeper than one (over-compensation) the intersection is unstable; responses proceed by larger and larger amounts until one parent ends up doing all the work. The reader is invited to start with any female effort and then follow the male's best response, the female's best reply, and so on. The ESS is for uniparental care by either male or female. Which parent it is depends on the starting point of the game.

In theory, incomplete compensation stabilizes biparental care

In cases of biparental care, parents should respond to reduced partner effort with incomplete compensation. A partner who cheats, by reducing its effort, will suffer reduced fitness because its young will get less well fed

Great tits „forced” into increasing parental effort by augmenting the begging calls of their brood with playback of extra calls through a little loudspeaker placed next to the nest

When one parent only (either male or female) was exposed to the playback, it increased its provisioning rate (the expected response to an apparently more hungry brood). However, the other parent also increased its provisioning, even though it did not experience increased chick begging (the playback had no effect on the chicks themselves).

The unmanipulated adult must, therefore, have responded directly to its partner, increasing its own effort in response to the partner’s increase.

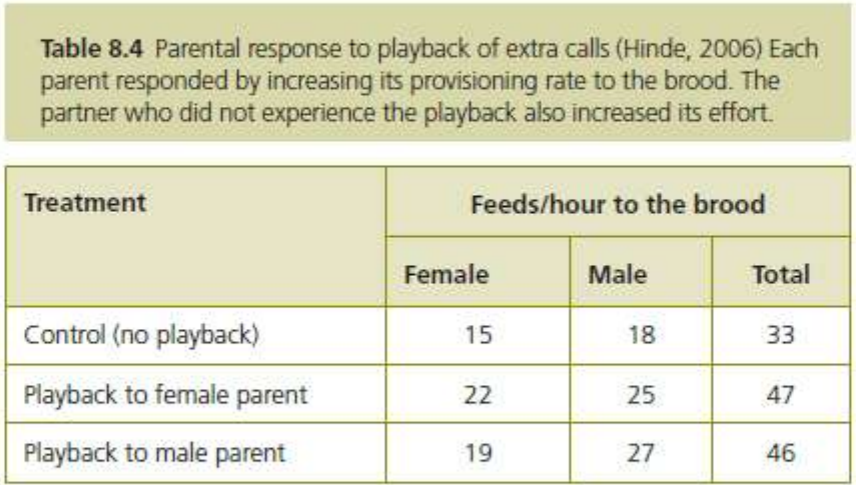


Table 8.4 Parental response to playback of extra calls (Hinde, 2006) Each parent responded by increasing its provisioning rate to the brood. The partner who did not experience the playback also increased its effort.

Treatment	Feeds/hour to the brood		
	Female	Male	Total
Control (no playback)	15	18	33
Playback to female parent	22	25	47
Playback to male parent	19	27	46

Fig. 8.6 Camilla Hinde's (2006) experiment with great tits. (a) A great tit brood. A speaker is hidden inside the nest, so begging calls of the brood can be augmented by playback. Photo © Simon Evans. (b) Male parent great tit. Photo © Joe Tobias.

Sibling rivalry and parent–offspring conflict: theory

Intrabood conflict: each offspring should demand more than its fair share from the parent’s point of view

Interbrood conflict: current broods should demand more, at the expense of future broods

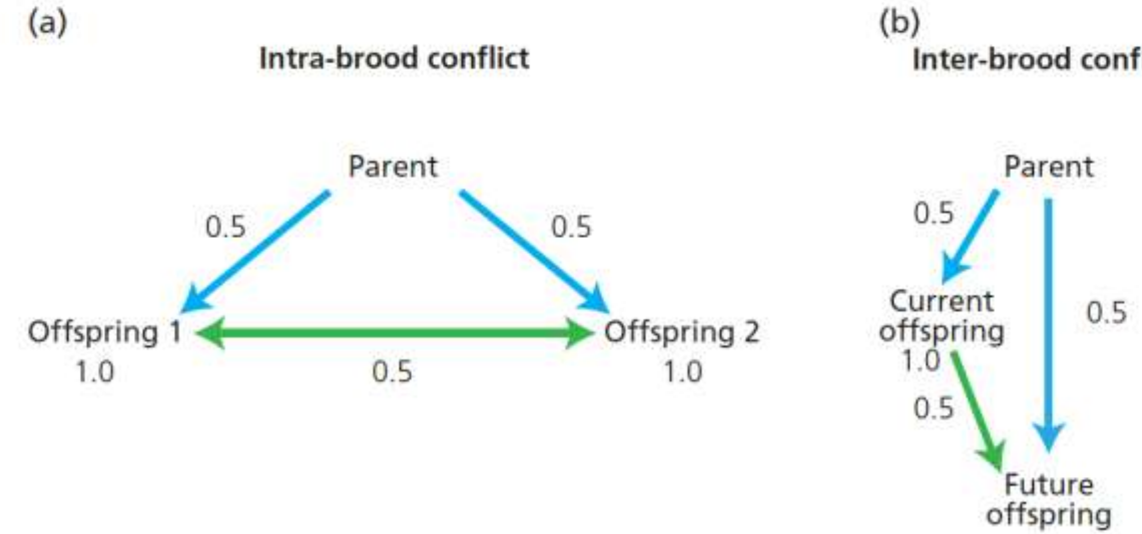


Fig. 8.7 (a) *Intrabrood conflict*. A parent with two offspring in a brood; the parent is equally related to both offspring (r = 0.5) but each offspring is more related to itself (r = 1) than to its sibling (r = 0.5, if full sibling). (b) *Interbrood conflict*. A parent with one offspring per brood. Again it is assumed that the offspring in the next brood is a full-sibling (same father and mother). The current offspring values itself (r = 1) more than its future full sibling (r = 0.5), whereas the parent is equally related to both offspring (r = 0.5).

Parent–offspring conflict graphically

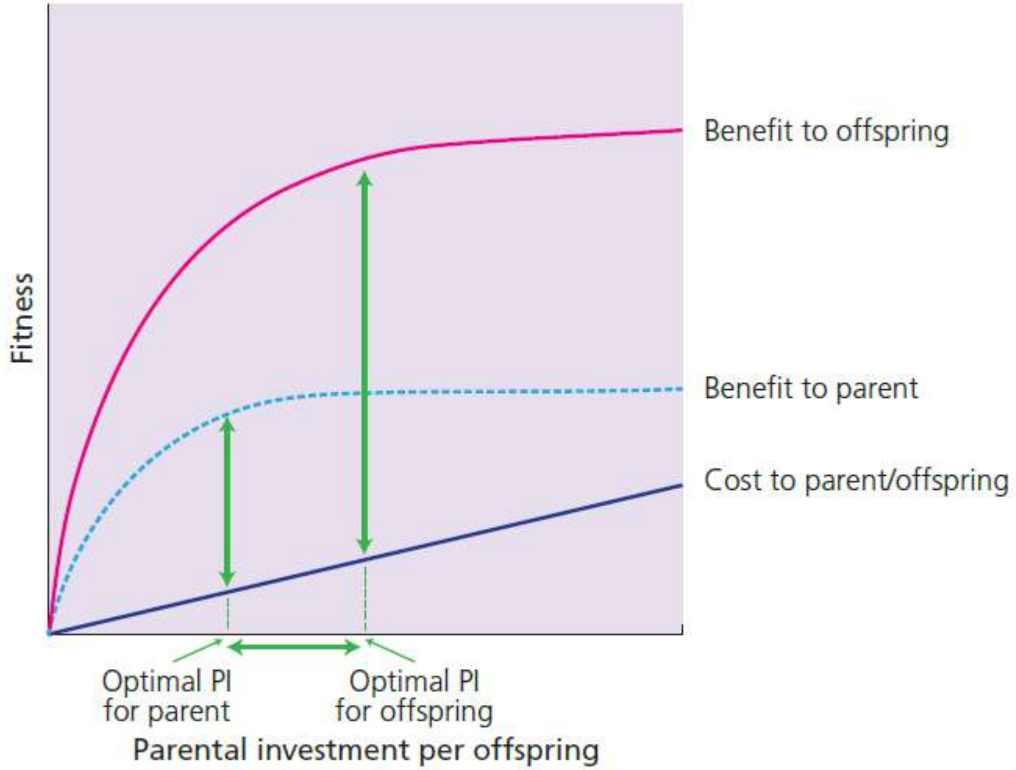


Fig. 8.8 Trivers's (1974) theory of parent–offspring conflict. The benefits and costs from the parent's point of view are the same as for Fig. 8.2. However, an offspring will value its own life (r = 1) twice as much as it is valued by its parent (r = 0.5), so the benefit curve for the offspring is twice that for the parent. If siblings are full siblings (r = 0.5) then the cost curve for the offspring is the same as that for the parent (see text). The optimal parental investment from an offspring's point of view is greater than the parental optimum. From Lazarus and Inglis (1986). With Permission from Elsevier.

Sibling rivalry: evidence

There is abundant evidence that siblings compete for parental resources.

This often arises because food availability in the environment is unpredictable. It then pays mothers to produce an optimistic brood size, in the hope that conditions will be good. If food turns out to be scarce, sibling competition leads to brood reduction.

The Galapagos fur seal female have one pup at a time. When fish are abundant, a mother produces plenty of milk and can wean her pup when it is 18 months of age, but in poor conditions pups grow more slowly and suckling can continue for two to three years.

As a result of this variation, up to 23% of pups per year are born while the older sibling is still being nursed.

The two pups then compete for the mother’s milk and, in most cases, the younger pup dies within a month, either from starvation or from direct attacks by the older sibling, who may grab it and toss it in the air.

Mothers sometimes intervene, leading to a fatal tug of war as the older sibling pulls one end of the newborn pup while the mother attempts to retrieve it

Facultative siblicide

Sibling rivalry: evidence

The blue-footed booby is a tropical seabird which lays two eggs. Incubation begins after the first egg is laid, so the first chick has about four days' growth before its younger sibling hatches.

This size advantage means the older chick can reach up higher to intercept the regurgitated fish from its parent's bill, and only after it is satiated does the younger chick get fed.

If food is abundant, then both chicks can take their turn.

However, when food is scarce the younger chick rarely gets fed and it starves to death within the first two to three weeks.

The key predictor of the younger chick's survival chances is the weight of its elder sibling. When the elder sibling is 20–25% below its expected weight, it attacks the younger sibling by pecking it. The younger sibling then cowers, becomes reluctant to beg and starves to death

In some birds of prey, pelicans and boobies the mother lays two eggs, yet the older sibling always kills the younger sibling (Obligate siblicide)

Sibling relatedness influences rivalry

As relatedness to other offspring declines, they become less valuable (genetically), so the costs of depriving them of parental resources will decline

Nestlings begged more vigorously (as measured by the loudness of their begging calls) in species with higher levels of extra-pair paternity in the brood (where fellow nestlings were more likely to be half-siblings, and hence of lower relatedness

Increased offspring selfishness when brood mates are of lower relatedness

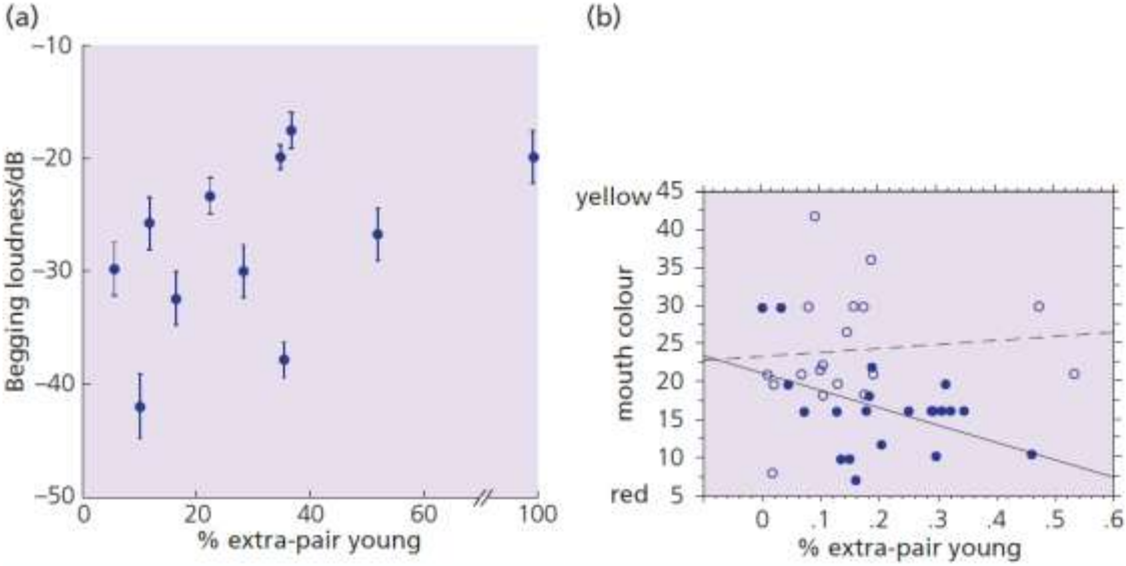


Fig. 8.9 Sibling conflict within broods of nestling birds increases as relatedness declines. (a) Nestlings beg more loudly in species where there is higher extra-pair parentage (i.e. lower average relatedness between siblings). This significant relationship still holds when controlling statistically for phylogeny, brood size and body mass. The species with 100% extra-pair parentage is the brown-headed cowbird, a brood parasite unrelated to the host young (Briskie *et al.* 1994). (b) Nestlings also have redder mouths in species with higher extra-pair parentage, but only in species nesting in open nests (solid symbols; solid line), not in those nesting in dark nests (open symbols: dashed line) (Kilner, 1999).

Chick ornaments charm parents

American coot, in which newly-hatched chicks have long, bright orange tips to their black body feathers

When broods were manipulated so that half of the chicks had their orange plumes intact and half were trimmed, then parents showed a clear preference for feeding the ornamented chicks and the black chicks grew less well

Parental preference is relative, a key element in the evolution of exaggerated traits

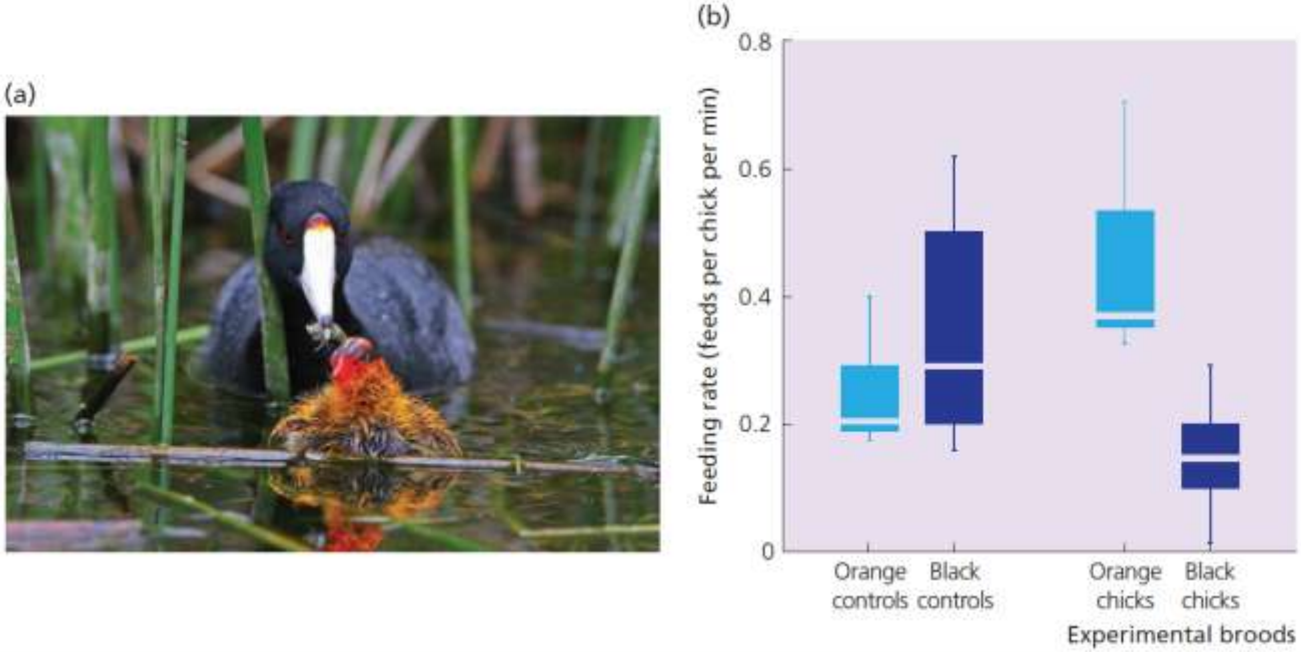


Fig. 8.10 (a) American coot chicks have orange-tipped ornamental plumes. Photo © Bruce Lyon. (b) Parental provisioning to broods where all the chicks have had their orange plumes trimmed (black controls) is no different than to normal broods (orange controls). However, in experimental broods where half the chicks have been trimmed, the black chicks are fed less than their orange sibs. (Lyon *et al.* 1994).

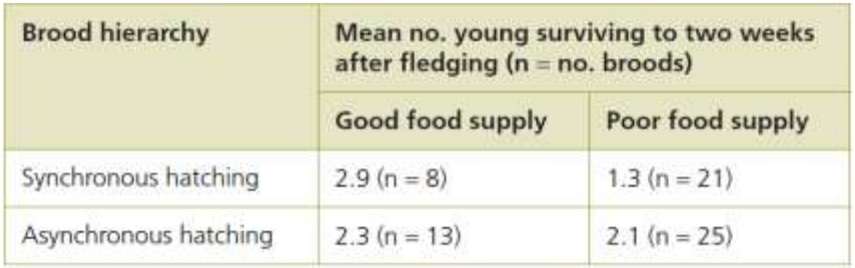
Parent–offspring conflict: evidence

Behavioural squabbles

David Lack suggested that parents profited by beginning incubation before their clutch was complete, because the resulting asynchronous hatching produced a brood hierarchy which led to efficient brood reduction if food was scarce.

By contrast, Lack supposed that synchronous hatching would produce chicks of similar size; with no clear dominance hierarchy among the brood a parent would waste resources on producing many weedy offspring, all with poor survival prospects, rather than a few, healthy survivors.

Table 8.5 Robert Magrath's (1989) experiment with blackbirds, to test the influence of a brood hierarchy on the parent's reproductive success. All broods were of four chicks (Synchronous, same size; Asynchronous, different size). Photo of a female blackbird feeding a worm to her chicks © W.B.Carr.



Brood hierarchy	Mean no. young surviving to two weeks after fledging (n = no. broods)	
	Good food supply	Poor food supply
Synchronous hatching	2.9 (n = 8)	1.3 (n = 21)
Asynchronous hatching	2.3 (n = 13)	2.1 (n = 25)

Parent–offspring conflict: evidence

Conflicts during pregnancy

Genomic imprinting may evolve from parent–offspring conflict

In many species a female mates with several different males during her lifetime. A maternally derived gene in a current offspring is thus more likely to have copies in future offspring (because the mother remains the same) than a paternally-derived gene (because different offspring can have different fathers).

Therefore, paternal genes in offspring are predicted to demand more maternal resources than are maternal genes in the same offspring.

Two antagonistic genes in mice support this idea.

- Insulin-like growth factor 2 (lgf2) is paternally-imprinted (expressed only when inherited from the father). It encodes IGF-II, an insulin-like polypeptide that plays a role in extracting resources from the mother during pregnancy. When expression of this paternal allele is experimentally inactivated, offspring are 60% their normal weight at birth, whereas inactivation of the maternal allele has no effect on birth weight.
- Counteracting the effects of Igf2 is a maternally-imprinted gene, the insulin-like growth factor 2 receptor (lgf2r). This encodes a receptor that degrades the product of lgf2, thus reducing the resource transfer from mother to offspring. When expression of the maternal allele is inactivated, offspring are 20% larger than normal at birth, whereas inactivation of the paternal allele has no effect on birth weight

Parent–offspring conflict: evidence

Conflict resolution

Nestling begging displays provide a good example of how the conflict might lead to a stable resolution

An offspring should increase its demand with need - however, if it pays offspring to demand more than the parental optimum, parents should require an honest, unfakable demonstration of need, otherwise they will be tricked into providing too much investment

An evolutionarily stable resolution to this conflict can be achieved if begging nestlings suffer a fitness cost from soliciting care

A parent might demand an honest signal from offspring in investment choice

In an experiment, pairs of canaries siblings were hand-fed with the same amount of food, but one member of the pair had to beg for just ten seconds before it was fed, while the other had to beg for 60 s (both times were within the natural range for begging bouts).

The sibling that begged for longer had lower mass gain (which reduces survival to independence), demonstrating that increased begging is costly to chick fitness and thus restrains chick selfishness

Parent–offspring conflict: evidence

Experiment: Swapped newly-hatched great tit young between nests, so that parents raised a mixed brood of foster-young, half of which came from one foreign nest and half from another foreign nest

When the chicks were ten days old, each had its begging measured in the laboratory at two levels of hunger; after 60 min and 150 min of food deprivation. This gave a measure of a nestling's begging intensity, or demand for food, in response to increased hunger.

Parental responses to chick begging signals were recorded in the field by measuring their increase in provisioning in response to playbacks of high versus low intensity begging calls.

The results showed that a nestling's demand varied with the nest of origin. In other words, nestlings from the same original brood, but reared in different foster nests, tended to have similar demands -> a nestling's demand was related to its genetic mother's generosity; nestlings with more generous mothers demanded more, while those with less generous mothers demanded less

Cross-fostering experiments with burying beetles *Nicrophorus vespilloides have* shown the same positive correlation between offspring demand and parental provisioning

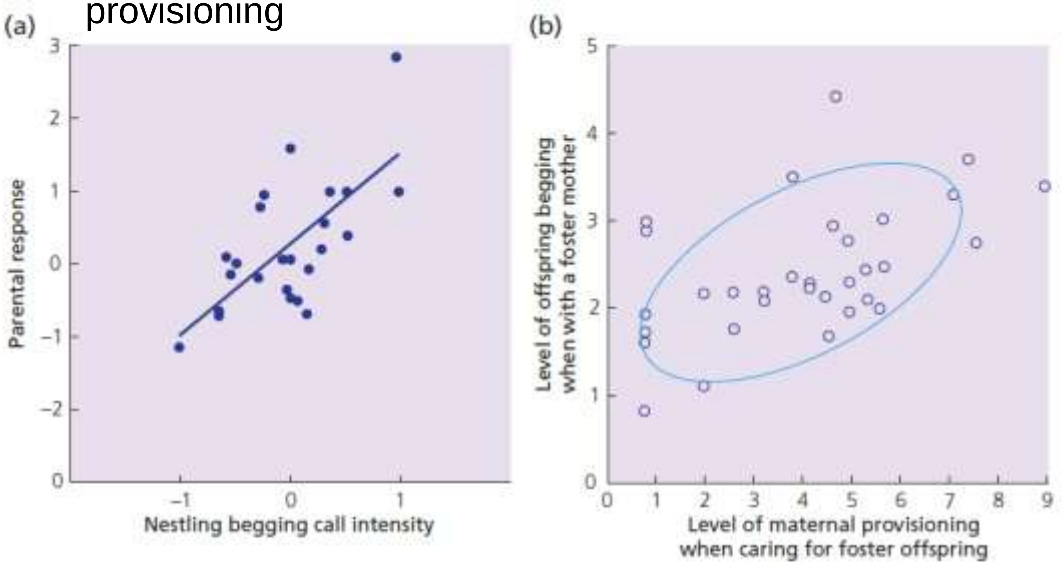


Fig. 8.11 Cross-fostering experiments reveal that within families parental supply is coadapted to offspring demand. (a) Great tits: each point refers to a different brood. Offspring begging intensity (measured in a foster-parent's nest) is correlated with its genetic mother's generosity (measured as increased provisioning response to begging playbacks). From Kölliker *et al.* (2000). (b) Burying beetles: each point again refers to a different brood. More generous mothers (response to foster offspring) have offspring which beg more strongly (response measured when raised by a foster mother). From Lock *et al.* (2004).

Parent–offspring conflict: evidence

Maternal effects can also influence offspring begging behaviour.

In canaries, an experimental increase in yolk testosterone leads to more vigorous nestling begging at hatching, suggesting that mothers could vary their nestlings' demand through varying maternal hormones in the egg

An increase in food quality led to increased maternal androgens and increased provisioning effort by the mother, and also to an increase in nestling androgens and nestling begging intensity

Foster young did best when their begging level matched those that the parents expected from their own brood,

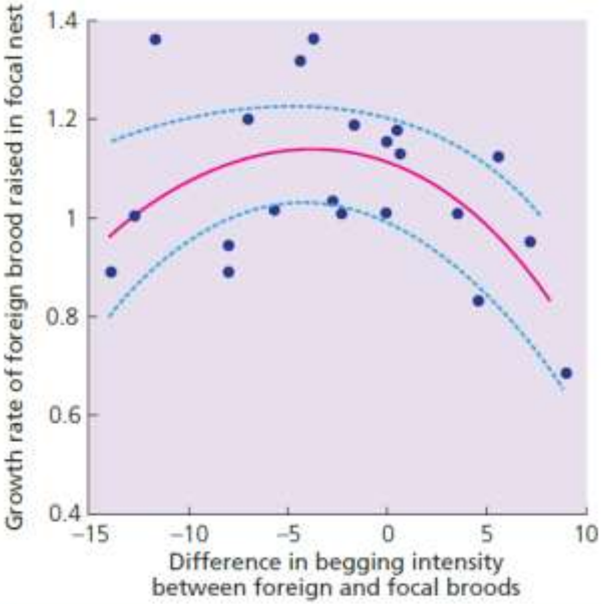


Fig. 8.12 Cross-fostering experiments with canaries. The growth rate of a foreign brood is greatest when its begging levels match those that the parents expected from their own (focal) brood. From Hinde *et al.* 2010. Reprinted with permission from AAAS.

Brood parasites

Some species of birds, fish and insects are brood parasites; they lay their eggs in the nests of other (host) species and trick the hosts into providing all the parental care. In theory, parasitic offspring should behave exceptionally selfishly because they are unrelated to the host parents and host offspring

In contrast to many cuckoos and honeyguides, the young cowbird tolerates the company of the host young. Why?

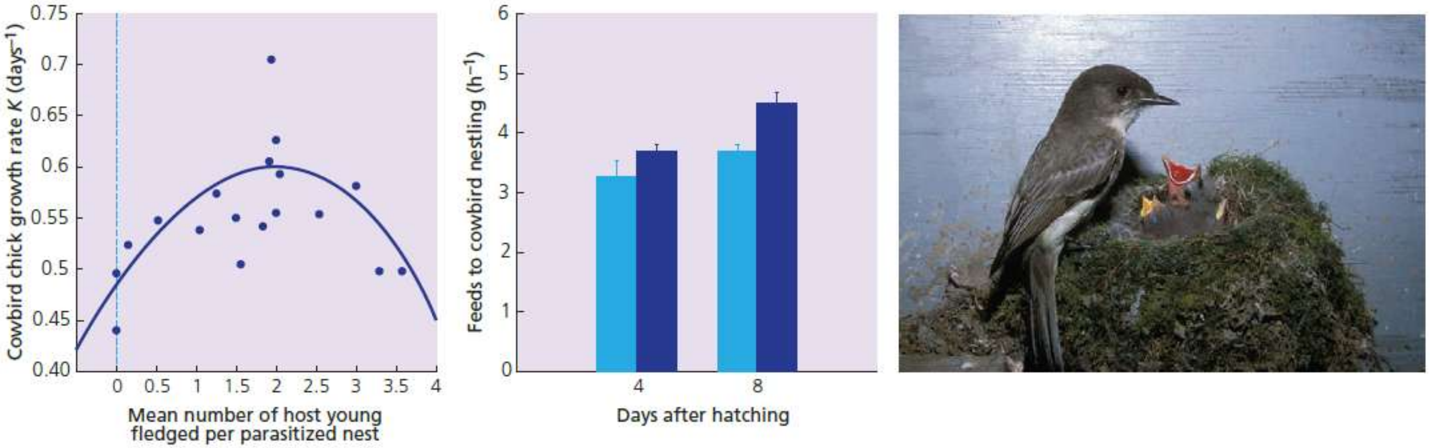


Fig. 8.13 (a) A brown-headed cowbird chick grows best when it shares the nest with two host young. Each point refers to a different host species. The curve is the fitted polynomial regression. (b) An experiment in which a cowbird chick is raised by eastern phoebe host parents, either on its own (light blue bars) or together with two host young (dark blue bars). The cowbird grows best when it is with host young. From Kilner *et al.* (2004). Reprinted with permission from AAAS. The photograph shows an eastern phoebe with two of its own chicks (yellow gapes) and a brown-headed cowbird chick. Photo © Marie Read.

Brood parasites

Common cuckoo, by ejecting all the host young from the nest, it benefits by removing the competition, but then faces the cost of having to do all the work in soliciting food

The common cuckoo's trick is a remarkable rapid begging call, which sounds like many hungry host young

The cuckoo has to boost the vocal component by producing extraordinarily rapid calls

In Japan, Horsfield's hawk-cuckoo (Cuculus fugax) has an equivalent trick, but it manipulates the visual component of the begging display.

When it begs for food it exposes yellow wing patches which are the same colour as its yellow gape

These false gapes spur the hosts into collecting more food; hosts sometimes try to place food into a patch instead of the gape, and experimental darkening of the patches with dyes reduces provisioning

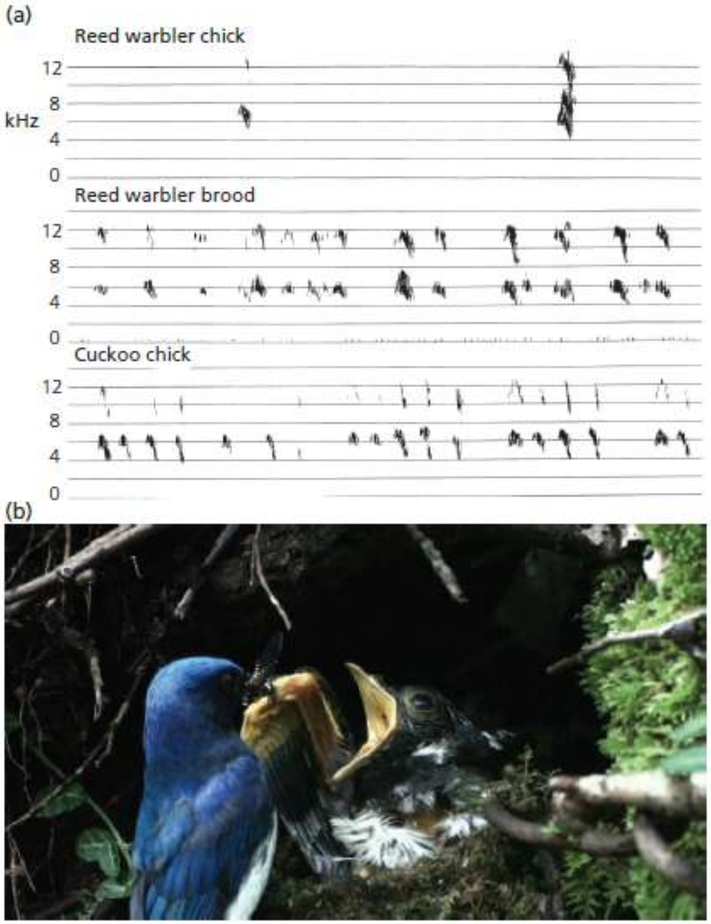


Fig. 8.14 Vocal and visual trickery by cuckoo chicks. (a) A common cuckoo chick's vocal trickery in a reed warbler nest. The sonograms, each 2.5 s long, show the begging calls of six day-old chicks recorded in the laboratory one hour after they had been fed to satiation. The cuckoo's begging calls are much more rapid than a single reed warbler chick and at a week of age are more like those of a whole brood of hungry host chicks. From Davies *et al.* (1998). (b) A Horsfield's hawk-cuckoo exposing a false gape – a yellow wing patch – next to its own yellow gape. The host is a blue and white flycatcher *Cyanoptila cyanomelana*. Photo courtesy of Keita Tanaka.

Mating systems

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Mating systems

Mating systems as outcomes of the behaviour of individuals competing to maximize their reproductive success.

Different mating systems might emerge depending on two factors:

(i) male and female dispersion in space and time (which will influence how easy it is for either sex to gain access to mates);

(ii) (ii) patterns of desertion by either sex (which will depend on the costs and benefits of parental care).

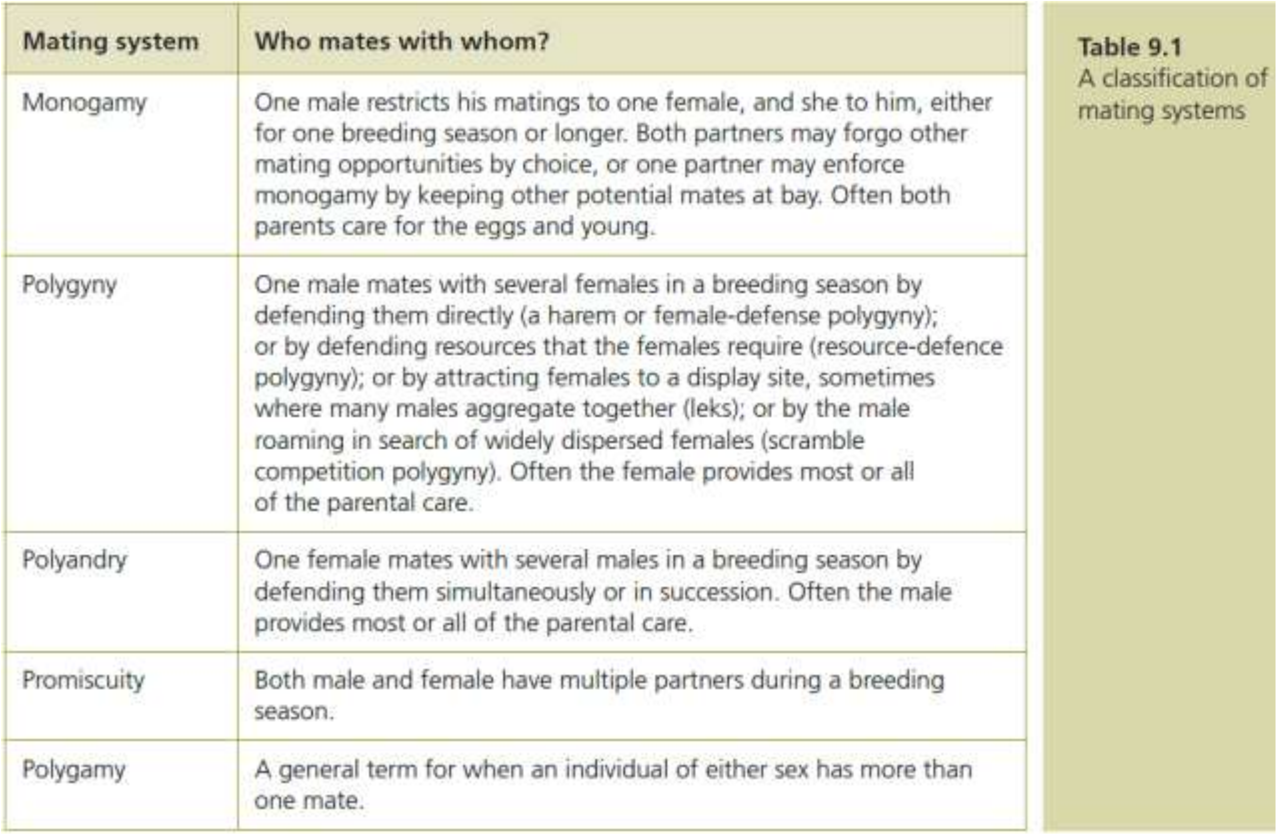

Table 9.1
A classification of mating systems

Mating system	Who mates with whom?
Monogamy	One male restricts his matings to one female, and she to him, either for one breeding season or longer. Both partners may forgo other mating opportunities by choice, or one partner may enforce monogamy by keeping other potential mates at bay. Often both parents care for the eggs and young.
Polygyny	One male mates with several females in a breeding season by defending them directly (a harem or female-defense polygyny); or by defending resources that the females require (resource-defence polygyny); or by attracting females to a display site, sometimes where many males aggregate together (leks); or by the male roaming in search of widely dispersed females (scramble competition polygyny). Often the female provides most or all of the parental care.
Polyandry	One female mates with several males in a breeding season by defending them simultaneously or in succession. Often the male provides most or all of the parental care.
Promiscuity	Both male and female have multiple partners during a breeding season.
Polygamy	A general term for when an individual of either sex has more than one mate.

Mating systems with no male parental care

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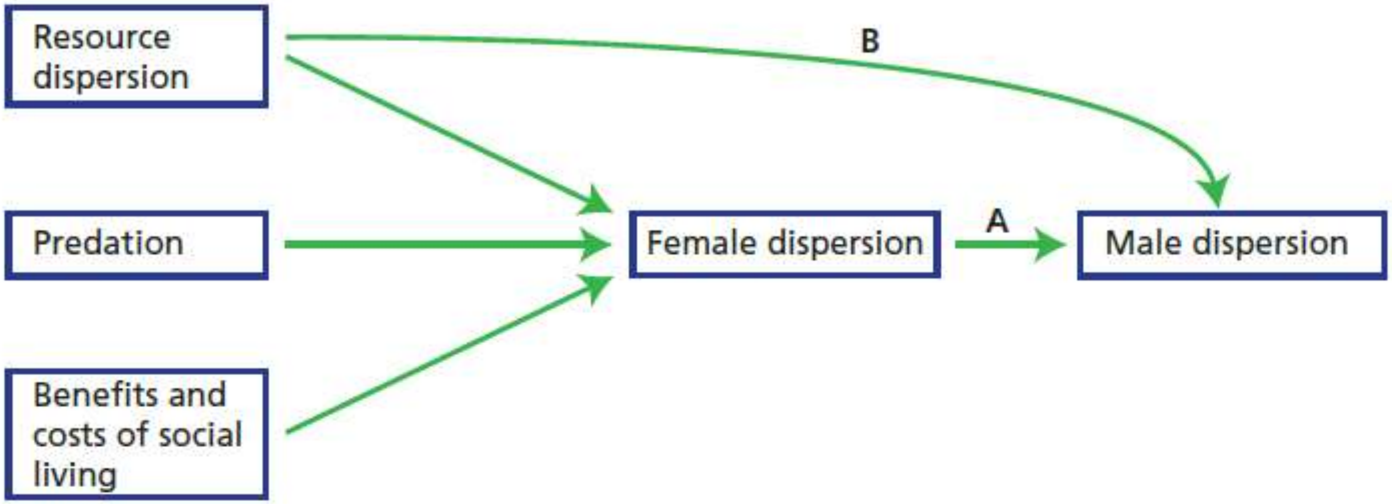


Fig. 9.1 The two-step process influencing mating systems in cases where males do not provide parental care. Because female reproductive success tends to be limited by resources, whereas male reproductive success tends to be limited by access to females, female dispersion is expected to depend primarily on resource dispersion (modified by predation and benefits and costs of social living), while male dispersion is expected to depend primarily on female dispersion. Males may compete for females directly (A) or indirectly (B), by anticipating how resources influence female dispersion and competing for resource-rich sites.

The economics of female defence or resource defence by males will depend on their distribution both in space and in time.

The key factor for determining the temporal distribution of mates is the ‘operational sex ratio’, which is the ratio of receptive females to sexually active males at any one time.

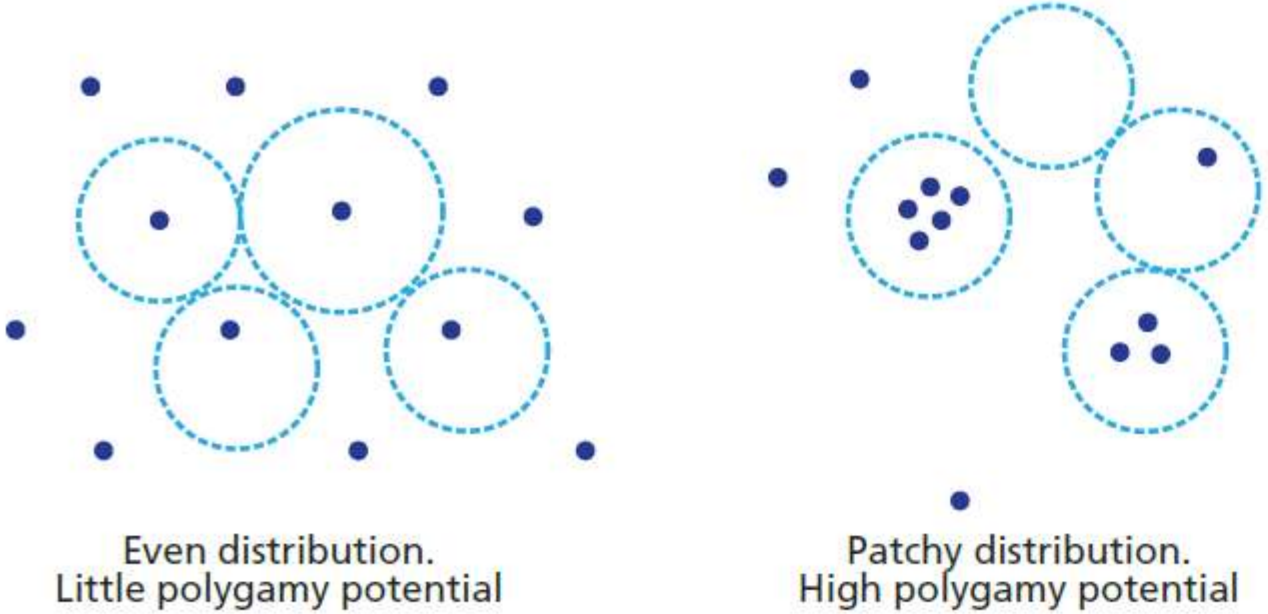


Fig. 9.2 The influence of the spatial distribution of resources (food, nest sites) or mates on the ability of individuals to monopolize more than others. Dots are resources or mates and circles are defended areas. With a patchy distribution of resources or mates there is greater potential for some individuals to ‘grab more than their fair share’.

Comparative evidence: mammalian mating systems

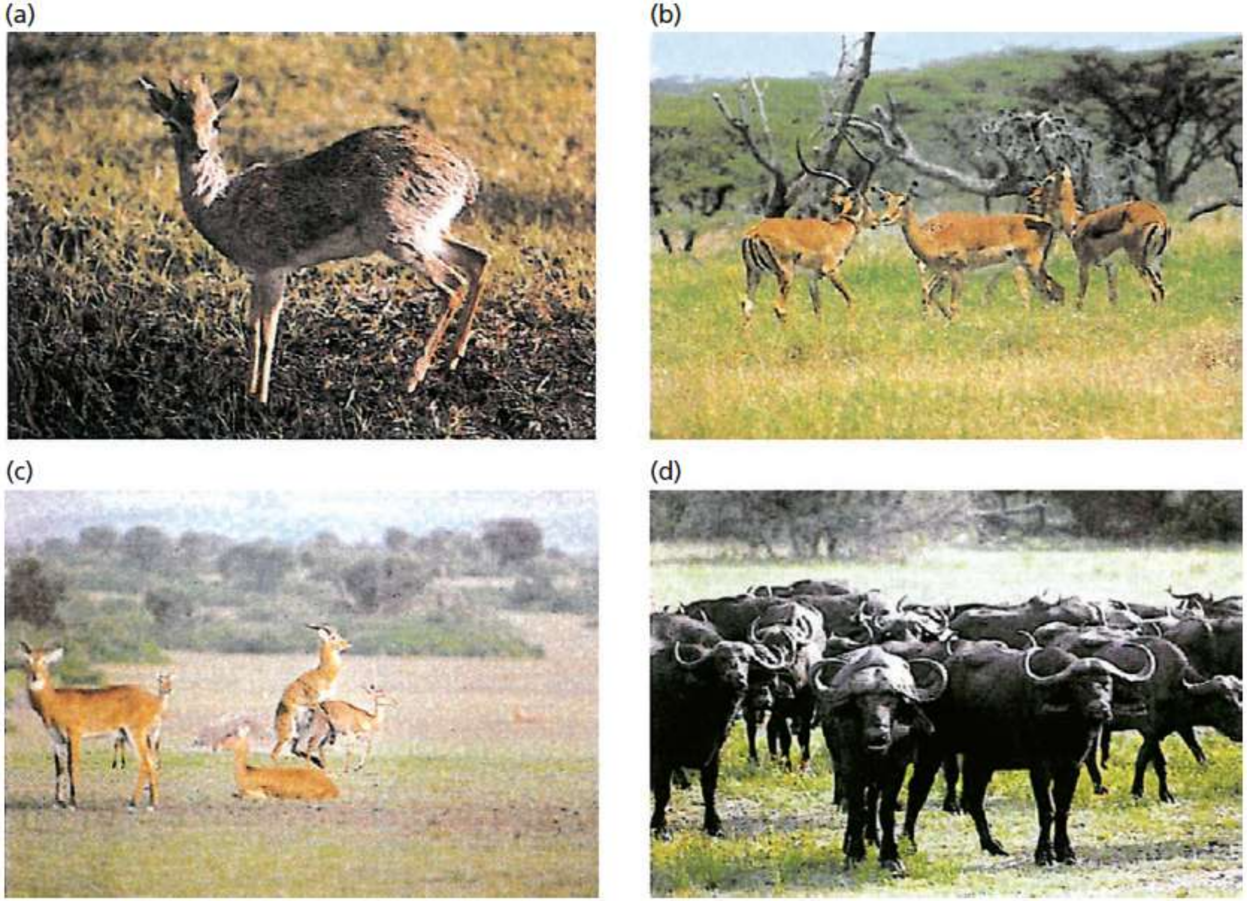


Fig. 9.3 Diversity of mammalian mating systems, illustrated by ungulates. (a) The dik-dik *Madoqua kirki* is monogamous: a male defends one female, probably because female ranges are too large for a male to defend more than one mate. Courtesy Oxford Scientific Films. Photo by Zig Leszczynski. (b) Male impala *Aepyceros melampus* defend herds of females temporarily during oestrus. Here a male is preventing a group of three females from leaving his territory. Courtesy Peter Jarman, photo by Martha Jarman. (c) Male Uganda kob *Kobus kob thomasi* defend tiny territories (15–30 m diameter) on leks and display to attract females. The male in the centre of the photo is mating with a female who has visited his territory. Photo by James Deutsch. (d) In the buffalo *Syncerus caffer*, several males associate with a large group of females and compete for matings in the multimale group. Courtesy Oxford Scientific Films. Photo by G.I. Barnard.

Comparative evidence: mammalian mating systems

Females solitary: range defensible by male

In over 60% of mammalian species females are solitary and a male defends a territory which overlaps one or more female ranges.

-If female ranges are small relative to the area which a male can defend then the male can be polygynous.

-If female ranges are larger, then the male may only be able to defend one female, hence monogamy

Females solitary: range not defensible by male

Where females wander more widely, then males may rove over wide ranges, associating with females temporarily while they are in oestrus. This occurs in moose, (Alces alces) and orang-utans, (Pongo pygmaeus); in the latter species the females move over large ranges following the fruiting seasons of different species of plants

Females social: range defensible by male

Where females occur in small groups in a small range, then a single male may be able to defend them as a permanent harem within his territory. Where females occur in larger groups several males (often relatives) may defend the territory together (e.g. red colobus, chimpanzees, lions).

Females social: range not defensible by male

Sometimes groups of females wander over ranges which are uneconomic for one or more males to defend. The ways in which males compete for females then depend on how predictable female group movements are in time and space.

Seasonal or permanent harems

Leks and choruses

Males aggregate into groups and each male defends a tiny mating territory containing no resources at all – often the territory is no more than a bare patch of ground just a few metres across.

The males put a great deal of effort into defending their territories and advertise themselves to females with elaborate visual, acoustic or olfactory displays. In these mating systems, known as leks, females often visit several males before copulating and appear to be very selective in their choice of mate.

Mating success is strongly skewed, with the majority of matings performed by a small proportion of males on the lek

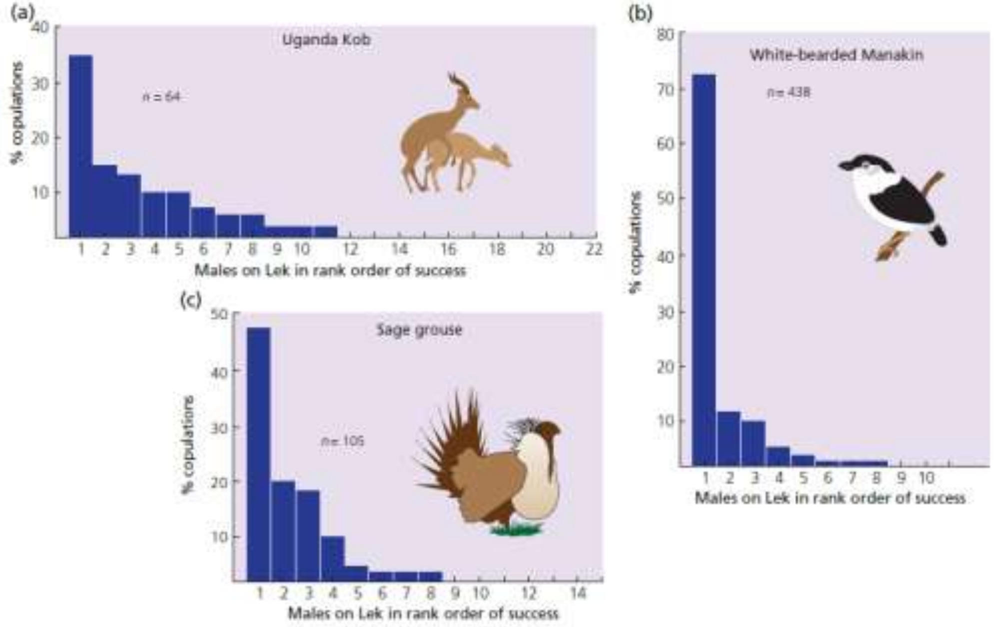


Fig. 9.4 On leks, most of the copulations are performed by just a few of the males. (a) Uganda kob *Adenota kob thomasi*. From Floody and Arnold (1975). (b) White-bearded manakin *Manacus manacus trinitatis*. From Lill (1974). (c) Sage grouse *Centrocercus urophasianus*. From Wiley (1973).

Why do the males aggregate into leks?

-Males aggregate on ‘hotspots’

Areas where female encounter rate is particularly high (hotspots)

-Males aggregate to reduce predation

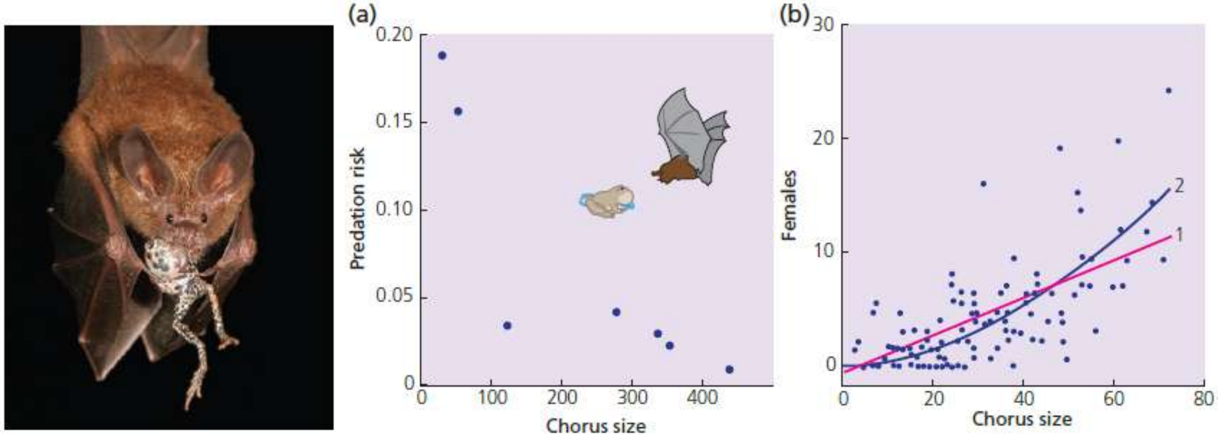


Fig. 9.5 Male frogs, *Physalaemus pustulosus*, aggregate into choruses. In larger choruses individuals are safer from predatory bats (a). The number of females attracted also increases with chorus size (b). The curve (2) gives a better fit to the observed points than a straight line (1), which suggests that the number of females per male increases with chorus size. From Ryan *et al*. (1981). Photo © Alexander T. Baugh.

-Males aggregate to increase female attraction

-Males aggregate around attractive ‘hotshot’ males

-Females prefer male aggregations because these facilitate mate choice

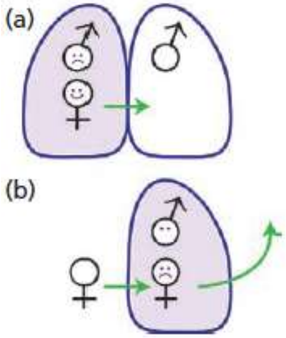
Mating systems with male parental care

Monogamy (is the predominant mating system in birds (90% of species)

Obligate monogamy

Fidelity: annual reproductive success increases with the duration of the pair bond

Divorce: The decline in success in later years most likely reflects reproductive senescence



Initiators and victims of divorce in oystercatchers

Fig. 9.7 Two causes of divorce: (a) desertion; (b) usurpation. This cartoon refers to a territorial species, such as the oystercatcher, where the male remains on his territory and the female moves to another territory. The territory where the divorce occurs is shaded. From Ens *et al*. (1996).

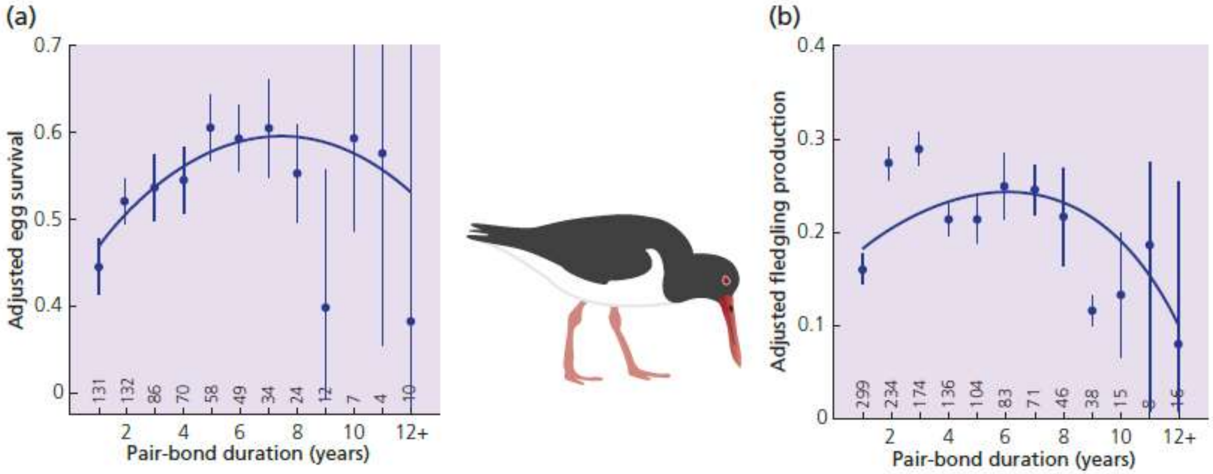


Fig. 9.6 Effect of pair-bond duration in oystercatchers on: (a) egg survival and (b) annual fledgling production. These 'adjusted' measures control statistically for other effects, such as male and female age, individual identity and territory quality. Sample sizes are shown above the x axes. From van de Pol *et al*. (2006).

Mating systems with male parental care

Constrained to be monogamous

Experiments suggest that the predominance of monogamy in many birds arises not because each sex has the greatest success with monogamy but because of the limited opportunities for polygyny.

The two most obvious constraints are:

(i) strong competition among males may make it difficult for a male to gain a second female

(ii) females are likely to suffer in polygyny through the loss of male help and, as predicted, females are often aggressive to other females, which may decrease the chance that their partners are able to gain a second mate

Social monogamy in birds does not mean genetic monogamy: extra-pair matings are often common

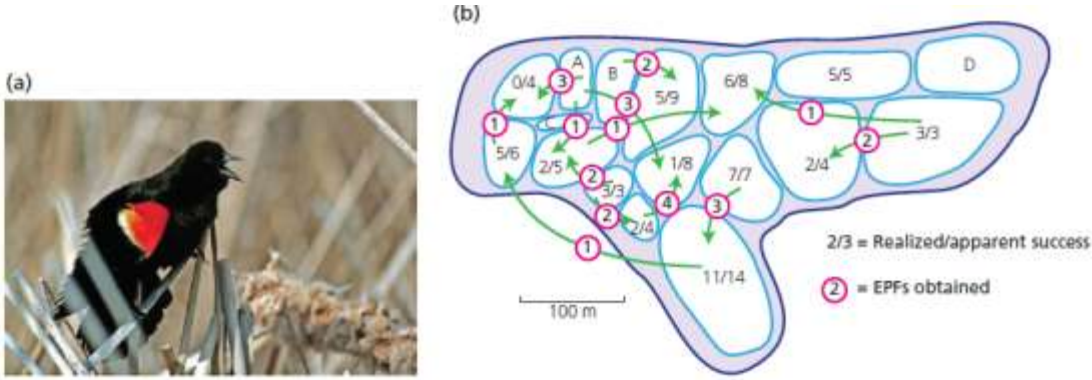


Fig. 9.8 (a) A male red-winged blackbird displaying his red epaulets. Photo © Bruce Lyon. (b) Reproductive success of male red-winged blackbirds on a marsh in Ontario, Canada, assessed by DNA markers. The fractions in each male territory show the number of chicks sired by the resident male over the total chicks raised. Arrows refer to extra-pair fertilizations (EPF's): the origin of the arrow shows the identity of the cuckolding male; the arrowhead indicates the territory in which he fertilized chicks; the number in the circle indicates the number of extra-pair chicks he sired. The map shows that most, but not all, cuckolders were near neighbours. From Gibbs *et al.* (1990). Reprinted with permission from AAAS.

Polygyny

Polygyny (one male with several females) in birds usually arises through males monopolizing females indirectly, by controlling scarce resources such as food or nest sites

- In some species, females may experience no polygyny costs
- In other species, females may be forced to accept polygyny costs

Females may choose polygyny because the costs are outweighed by the benefits

Females benefit by choosing polygyny on a good territory rather than monogamy on a poor territory

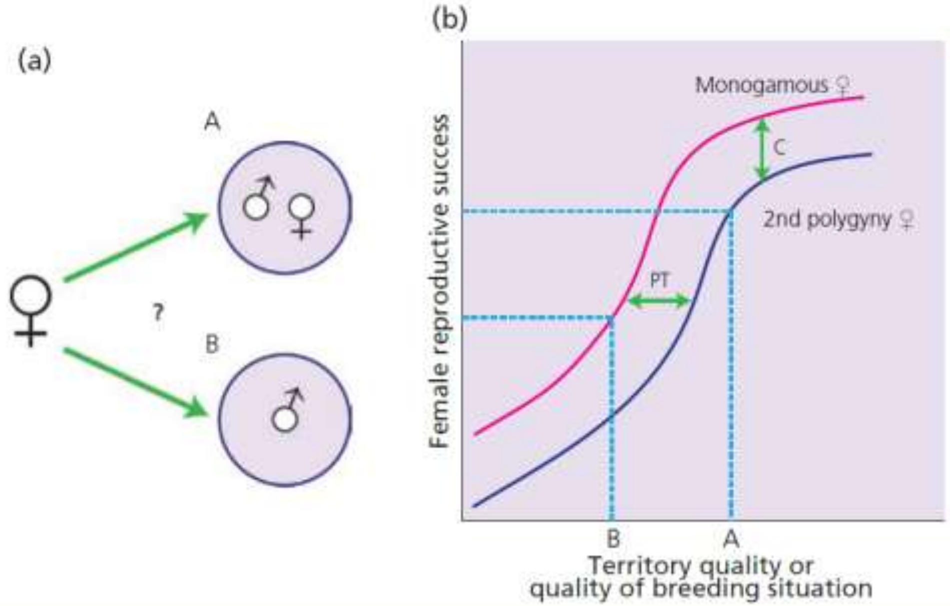


Fig. 9.9 The polygyny threshold model. (a) A female has the choice of settling with an unmated male on a poor quality territory B, or with an already-mated male on a good quality territory A. (b) Female reproductive success increases with territory quality. There is a cost C of sharing with another female, so the curve for the second female in polygyny lies below that for a monogamous female. Provided the difference in territory quality exceeds PT (the polygyny threshold), a female does better by choosing to settle with an already-mated male on territory A rather than with an unmated male on territory B. Modified from Orians (1969).

Sexual conflict and polygamy

The assumption that polygyny arises from ideal free female settlement may often be unrealistic

- If the first female suffers from the arrival of a second female then it will pay the first female to try to prevent her from settling

Males of pied flycatcher defend nest sites, holes in trees or nest boxes, and sing to attract a female. Once a male has attracted one female and she has laid her eggs, he then goes to another nest hole and tries to attract a second female.

Males do not simply advertise from the next nearest nest site but go, on average, 200 m away and even up to 3.5 km from their first site! About 10–15% of the males succeed in gaining a second female.

Compared to monogamous females the first female suffers little, if at all, from polygyny because she usually gains the male’s full-time help, but the second female, who is left to raise her brood on her own, suffers reduced success, raising on average only 60% of the number of young she would have gained in monogamy

Fig. 9.11 Once a male pied flycatcher has attracted one female, he flies off to another nest site some distance away and tries to attract another. Secondary females suffer because they get little or no help from the male in chick rearing. However, females probably are unable to assess whether the male they pair with has another female because of the large distance between a male’s two nest sites.

Why, do females ever settle polygynously?

- The ‘sexy son’ hypothesis
- Deception

  it is too late in the season for it to be profitable to start another clutch, so she has to make the best of a bad job and rear her offspring alone
- Unmated males hard to find

Experiment of erecting nest boxes in careful sequence, arranged for neighbouring boxes, less than 100 m apart, to be occupied by an unmated male and a mated male

Result supports the deception hypothesis, females did not discriminate between mated and unmated males even when they had a simultaneous choice between them, and even though it would have paid them to make a choice.

Promiscuity

Dunnock, including simple pairs (monogamy), a male with two females (polygyny) and a female with two (unrelated) males (polyandry)

Various factors behind:

- differences in individual competitive ability
- the adult sex ratio influences mating systems
- territory characteristics

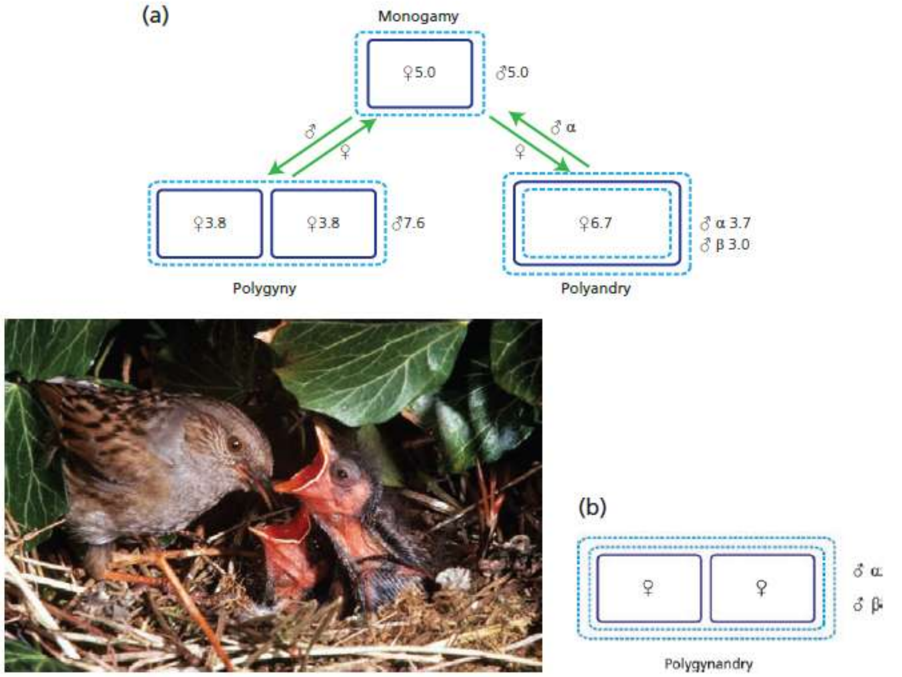


Fig. 9.12 Male dunnock feeding a brood of chicks. Photo © W. B. Carr. (a) Sexual conflict in dunnocks. Female territories (solid lines) are exclusive and may be defended by one or two unrelated males (dashed lines). The numbers refer to the number of young raised per season by males and females in the different mating combinations (maternity and paternity measured by DNA fingerprinting; Burke *et al*. (1989)). Arrows indicate the directions in which dominant (alpha) male and female behaviour encourage changes in the mating system. A male does best with polygyny; the cost of polygyny to females is shared male care. A female does best with polyandry; the cost of polyandry to males is shared paternity. (b) Polygynandry as a stalemate to the conflict: the alpha male is unable to drive the beta male off to claim polygyny, and neither female can evict the other to claim polyandry. From Davies (1989, 1992).

Polyandry

There may be conditions when the increased production of offspring from cooperation by a team of males does offset the costs to an individual male of paternity sharing

Two situations in which the benefits of cooperation among males are likely to outweigh the cost of sharing paternity are:

- a scarcity of food (so more than two individuals are needed to raise offspring effectively)
- intense competition for territories or females (so a team of males is more effective in gaining reproductive opportunities)
  - In lions, male teams often consist of relatives (brothers, half brothers), so there is kin selection for cooperation

Female desertion and sex role reversal

Spotted sandpipers (Actitis macularia) and jacanas a female competes to defend a large territory in which she may have several males simultaneously incubating her clutches or caring for her chicks

Reproductive success is no longer limited by her ability to form reserves for the eggs but rather by the number of males she can find to incubate them

Fig. 9.13 Sex role reversal in birds. This male African jacana performs all the parental duties. Females are larger than males and compete for males by defending large territories. Photo © Tony Heald/naturepl.com.

Sex Allocation

Sex allocation is the allocation of resources to male versus female reproduction in sexual species

The sex of an individual can be determined by sex chromosomes, the environment, or even change during its lifespan

In species with genetic (chromosomal) sex determination, such as birds or mammals, sex is determined by whether individuals have two of the same kind of sex chromosome (homogametic) or two distinct sex chromosomes (heterogametic)

Fig. B10.1.1 Temperature dependent sex determination in reptiles. In many reptiles sex is determined by the temperature during development. For example, in (a) the box turtle (*Terrapene ornate*) and (b) the green turtle (*Chelonia mydas*), males are produced at cool incubation temperatures and females at warm incubation temperatures. In other species, such as (c) the Australian freshwater crocodile (*Crocodylus johnstoni*), the opposite pattern occurs, with males produced at relatively high temperatures. Finally, one sex may be preferentially produced at extreme temperatures (both hot and cold), such as (d) the frill-necked dragon (*Chlamydosaurus kingii*), where both sexes are produced at intermediate temperatures, but only females at extreme temperatures. Photo (a) © Fred Janzen; (b) © Annette Broderick; (c) and (d) © Ruchira Somaweera.

Sex Allocation

All else being equal, a 1:1 sex ratio will be favoured by natural selection

If the sex ratio is perturbed from 1:1, it will evolve back to this point

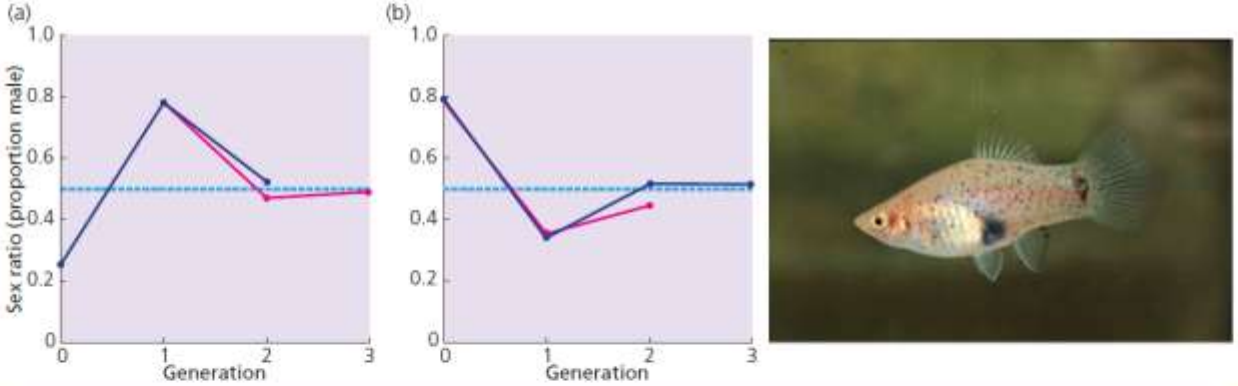
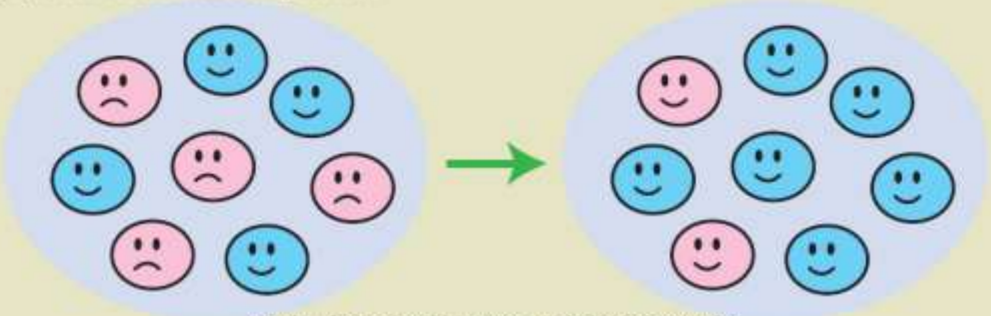


Fig. 10.1 Sex ratio evolution in the southern platyfish. When the sex ratio is perturbed away from equal numbers of males and females, it quickly evolves back to this point. The perturbation is towards a female (a) or a male (b) biased sex ratio. Different lines are different replicates. From Basalo (1994). Reprinted with permission from the University of Chicago Press.

Sex allocation when relatives interact

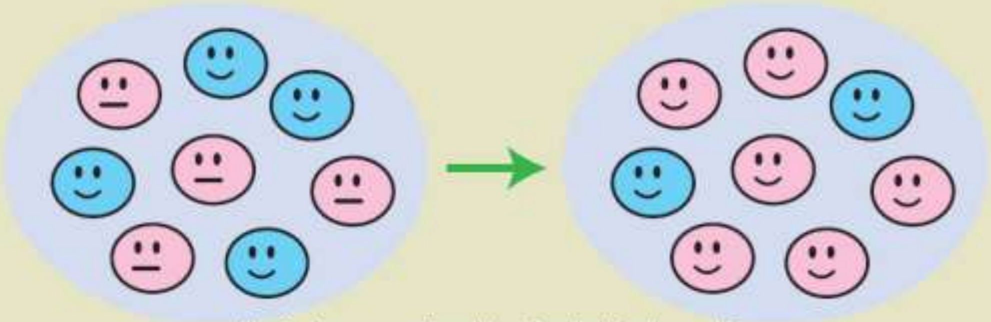
Local resource competition

(a) Local resource competition



Moving from an unbiased to a male-biased sex ratio reduces LRC between females

(b) Local resource enhancement



Moving from an unbiased to a female-biased sex ratio increases the amount of cooperation between females

Fig. B10.2.1 Selection for biased sex ratios when relatives interact. (a) If sisters compete for resources, then a male-biased sex ratio is favoured to reduce competition between sisters. (b) If sisters cooperate with each other, then a female-biased sex ratio is favoured to facilitate cooperation. Males are blue, females are pink. From West (2009).

Sex allocation when relatives interact

Local resource competition

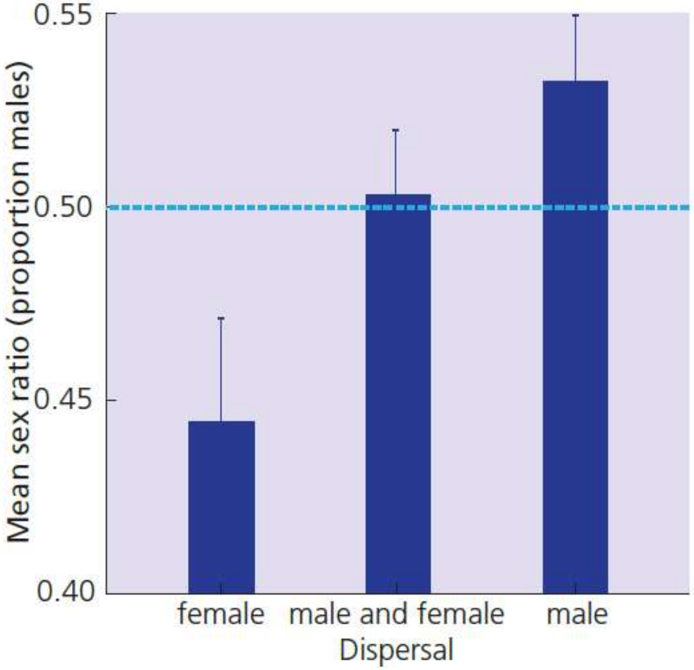


Fig. 10.2 The sex ratio at birth in primate species where either females, males and females or males are the dispersing sex. The sex ratio is biased towards the dispersing sex. From Silk and Brown (2008). The photo shows chimpanzee by Joan Silk.

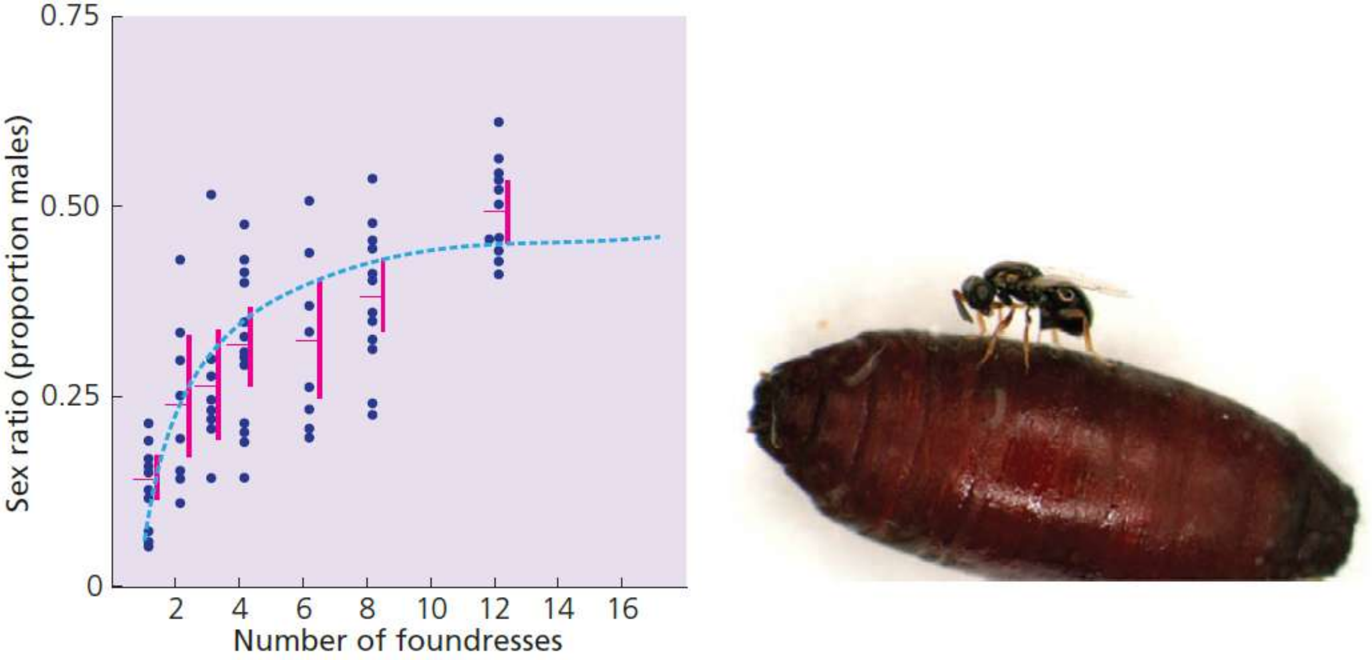
Sex allocation when relatives interact

Local mate competition

If brothers compete for mates, the sex ratio should be female biased

Parsitoid wasps adjust the sex of their offspring, depending upon how many females are laying eggs in that patch

Fig. 10.4 Sex ratio adjustment in the parasitoid wasp *Nasonia vitripennis*. A less female-biased sex ratio is produced when larger numbers of females lay eggs in a patch. From Werren (1983). Photo by Michael Clark.



Sex allocation when relatives interact

Local resource enhancement

Relatives may not only compete, they may cooperate. In many cooperative breeding vertebrates, offspring of one sex are more likely to remain in the group and help parents rear further offspring – e.g. females are more likely to help in the Seychelles warbler, whereas males are more likely to help in African wild dogs

Many researchers argued that, in such species, the population sex ratios should be biased towards the helping sex

The benefit of producing the helping sex can be reduced or removed on low quality territories

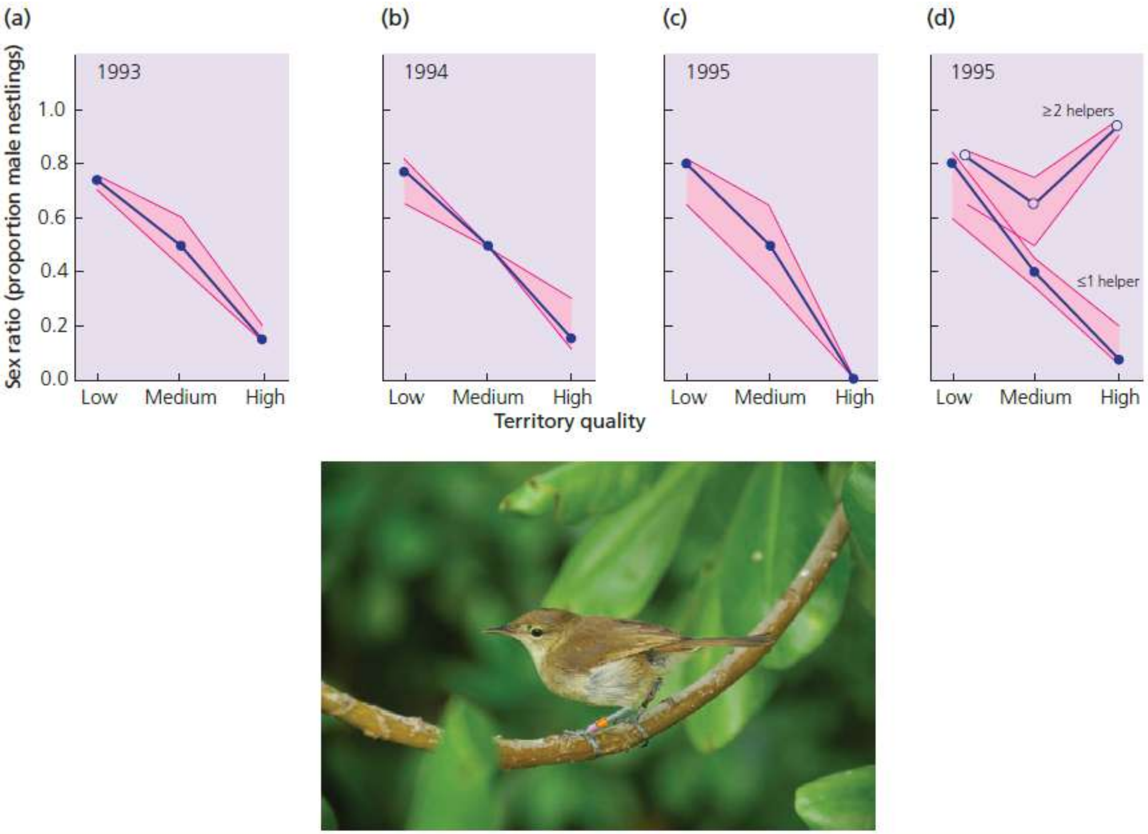


Fig. 10.6 Sex ratio adjustment in the Seychelles warbler. The offspring sex ratios (proportion male) produced on different quality territories in (a) 1993, (b) 1994 and (c) 1995. Mothers produced daughters on high-quality territories and sons on low-quality territories. (d) The data from 1995 are also shown distinguishing between nests that had either one (solid circles) or more than one (open circles) helper already at the nest. When mothers already had more than one helper, they produce sons, irrespective of territory quality. From Komdeur *et al.* (1997). Reprinted with permission from the Nature Publishing Group. Photo © Martijn Hammers.

Sex allocation in variable environments

Maternal condition

Females in better condition can be selected to preferentially produce sons

- Red deer adjust their offspring sex ratios in response to maternal condition, with mothers in better condition being more likely to produce sons

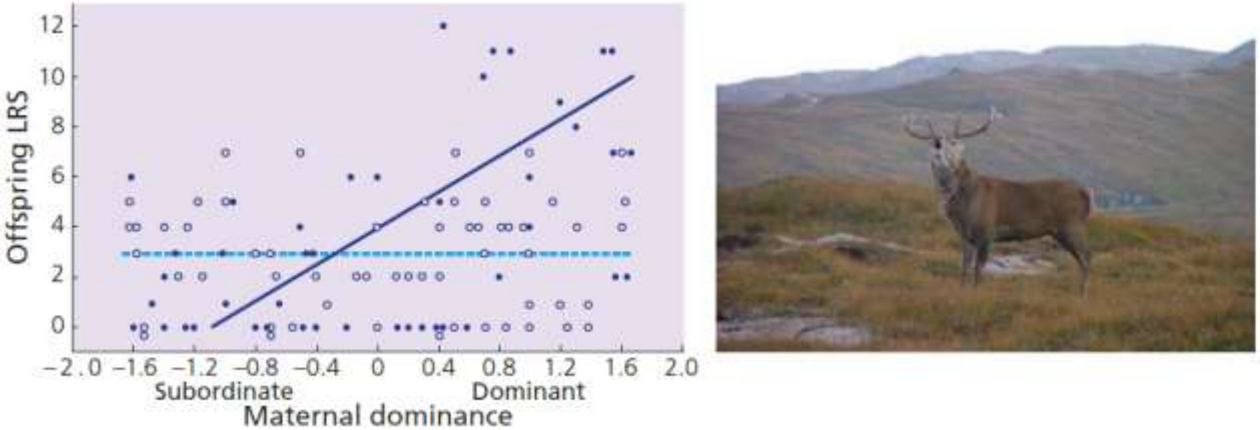


Fig. 10.9 In red deer, the lifetime reproductive success (LRS) of sons (filled circles and solid line) increases more rapidly with their mother's social rank than daughters (open circles and dashed line). From Clutton-Brock *et al*. (1984). Photo © Alison Morris.

Sex allocation in variable environments

Mate attractiveness

Females who mated with attractive males can be selected to preferentially produce sons

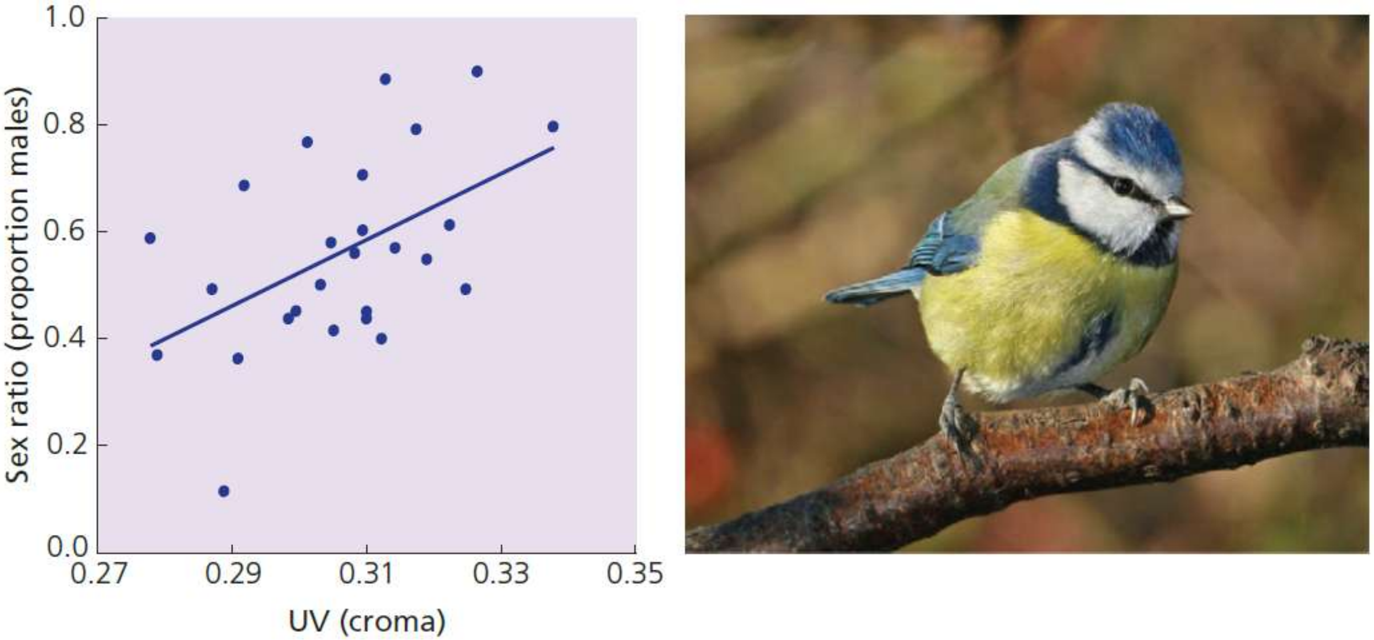


Fig. 10.10 Female blue tits which mate males with a brighter UV patch (crown) produced a higher proportion of male offspring. From Griffith *et al.* (2003). Photo © Joseph Tobias.

Sex change

Sex change, where individuals mature as one sex, and later change to the other, occurs in a variety of fish, invertebrates and plants

In many coral reef fish, female first (protogynous) sex change occurs. If the largest males on a reef are removed, the next largest individuals (females) will change sex and become brightly coloured males

Sex change can also be favoured in the other direction, from male to female (protandry). An example of a fish that changes from male to female is the anemonefish, or clownfish (Amphiprion akallopisos), which lives on coral reefs

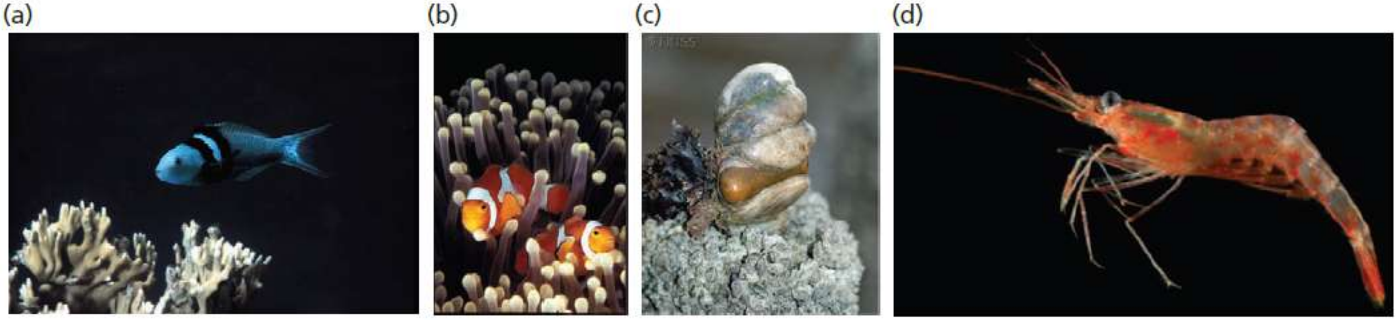


Fig. 10.12 Sex changers. Sex change may be from female to male, as in (a) the bluehead wrasse (terminal male); or male to female, as in (b) the Clownfish *Amphiprion percula*; (c) the common slipper limpet (*Crepidula fornicata*; photograph of a mating stack, where the largest individuals at the bottom are female and the smaller individuals at the top are male; and (d) the Pandalid shrimp. Photo (a) © Kenneth Clifton; (b) © Peter Buston; (c) © Rachel Collin; (d) © David Shale/naturepl.com