E-CONTENT PREPARED BY

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NAAC Accredited "A" Grade College

(Recognized under Section 2(f) and 12(B) of UGC Act 1956)

E-Content prepared for students of

M.Sc.(Semester-I) in Conservation Biology

Name of Course: Principles of Ecology

Topic of the E-Content: Behavioural Ecology

Behavioral Ecology

Definition: Behavioral ecology is the study of behavioral interactions between individuals within populations and communities, usually in an evolutionary context. It looks at how competition and cooperation between and within species affects evolutionary fitness.

Approaches to behavioral studies

I. Vitalistic approach: Behavioral activities are explained in terms of what animals are seen to do in relation to changes in the environment. It involves total rejection of any study of the animal outside its natural environment. The technique is non-scientific since all the observations relate to past events which cannot be tested experimentally.

II. Mechanistic approach: It is an experimental approach and involves the study of particular aspects of behavior under controlled conditions in a laboratory. It was pioneered by Pavlov and used extensively in psychological study. It may be criticized on the basis of the artificiality of the experimental conditions and the way in which results are interpreted.

III. Ethological approach: Ethology is the scientific study of animal behavior. It explains responses observed in the field in terms of stimuli eliciting the behavior. This was pioneered by Lorenz, von Frisch and Tinbergen.

Thoughts of Ethology:

1. European School: Mainly inspired by Darwin's theory of evolution and proposed the concept

   AB = CDEF,

   Where AB = Animal Behaviour
   C= Causation
   D = Development
   E = Evolution
   F = Function

2. American School: Combined the above mentioned concept into two basic questions that can be addressed to many behavioral patterns based on hypothesis. Each hypothesis for a

particular behavior is tested through experiments and starts usually with WHY and HOW. WHY answers the C and D factor whereas HOW answers E and F.

1. The evolutionary history: - How did various forms of behavior evolved? i.e. (Innate/instinctive/genetic or learned?) - How does the behavior compare with similar behavior in related species?
2. Development: - Why does behavior change with age? - What are the early experiences necessary for the behavior to express?
3. Causation: What are the stimuli that elicit the response?
4. Function: How does the behavior impact on the animal’s chances of survival and reproduction?

Types of animal behavior:

a) Innate: Innate behavior involves a collection of responses that are predetermined by the inheritance of specific nerve or cytoplasmic pathways in multi-cellular or single-celled organisms. As a result of these ‘built-in’ pathways a given stimulus will produce invariably, the same response. These behavior patterns have developed and been refined over many generations (selected) and their primary adaptive significance lies in their survival value to the species. Innate behavior patterns include orientations (taxes and kinesis), simple reflexes and instincts. Instincts are extremely complex and include biological rhythms, territorial behavior, courtship, mating, aggression, altruism, social hierarchies and social organization.
b) Learned: Learning can be defined as an adaptive change in individual behavior as a result of experience. The degree of permanence of newly acquired learned behavior patterns depends on memory storing information gained from the experience. Learning alters the range of behaviors shown by an individual, and allows it to adapt to and control its environment.

Possible questions:

1. Define animal behavior.
2. What do you mean by ethology?

3. What are the basic approaches to study animal behavior? Explain the term AB = CDEF.
4. Differentiate instinctive and acquired behavior.
5. Explain with an example the proximate and ultimate factors related to behavior study. (will be done in next class)

Stereotyped behavior

A repetitive behavior shown by every individual of the species in a specific pattern called fixed action pattern.

A fixed action pattern (FAP) is a specific, sequence of behaviors which is hard wired, that occurs in response to an external stimulus, called a sign stimulus. The behavior is “fixed” because it is essentially unchangeable and fixed of a species and also repetitive in nature.

This term was coined by Konrad Lorenz, who is the founder of the concept. FAPs are produced as the innate releasing mechanism which is triggered as a neural network by the external stimulus. The FAP is triggered by a sign stimulus, or, if it is a signal from one individual to another, it is called a releaser. Lorenz identified six characteristics of fixed action patterns (Dewsberry, 1989).

1. **Stereotyped**: Fixed action patterns occur in rigid, predictable, and highly-structured sequences
2. **Complex**: Fixed action patterns are not a simple reflex. They are a complex pattern of behavior
3. **Species-characteristic**: Fixed action patterns occur in all members of a species of a certain sex and/or a given age when they have attained a specific level of arousal
4. **Released**: Fixed action patterns occur in response to a certain sign stimulus or releaser
5. **Triggered**: Once released, a fixed action pattern continues to completion, even when there are changes in the surrounding environment
6. **Independent of experience**: A fixed action pattern is not learned. This is known as a fixed action pattern is complete upon the very first release

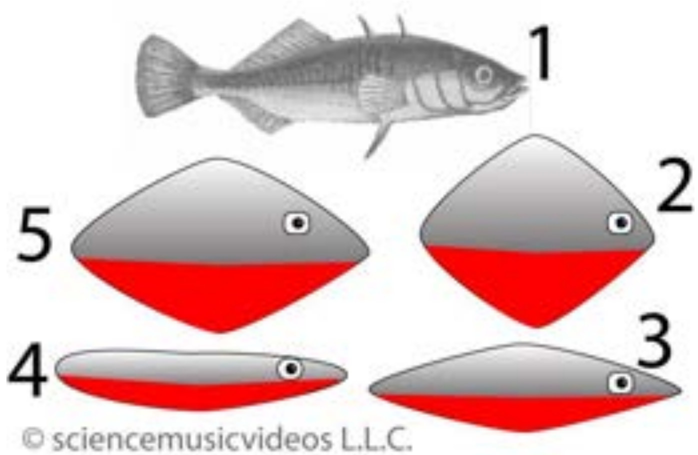
Konrad and Tinbergen (1970) studied that fixed action pattern occurs in ground-nesting water birds, like Greylag geese. If a female Greylag goose's egg rolls out of her nest, she will instinctively use her bill to push the egg back into the nest in a series of very stereotyped, predictable, movements. The sight of an egg outside the nest is the stimulus that triggers the retrieval behavior. Goose mothers that retrieve their lost eggs are likely to have more surviving offspring, on average, than those that don't. However, this fixed action pattern can also occur under instances which are not required for the survival, or where it does not benefit the goose. Such instances are:

- If the egg that rolls out of the nest is picked up and taken away, the goose will keep moving her head as though pushing an imaginary egg.
- If the eggs are replaced by any object such as a volley ball or a golf ball near the nest, same egg rolling behavior is observed in the birds

Anothers classic example of a FAP was described in three-spined stickleback fish by Nikolaas Tinbergen (1952). During the breeding season, the male fish develop a red throat and belly and build a nest. The major stimulus for such development is the change in the day length during onset of spring which elicits hormonal response. Male sticklebacks attract females to the nest with a courtship dance which is a peculiar ZIG-ZAG pattern and encourage her to lay eggs, which the male then fertilizes. After the female lays eggs it is driven away from the nest to prevent sharing of resource. He protects the fertilized eggs and, later, the newborn young. During these phases of courtship, breeding, and parental care, the male aggressively attacks any other males who come near his nesting territory. It also sends threat signal by keeping a HEAD-DOWN posture during the mating process. This increases the likelihood of his genes being successfully passed on to future generations.

Tinbergen (1952) discovered that male sticklebacks would also attack models of fish of any shape but only if the undersides are painted red like the red belly of a breeding male. Even realistic models (exact shape of the female) were used without a red belly or a different colour, males do not attack or no zig-zag dance is initiated. It was concluded that the red belly is the sign stimulus that triggers the attack behavior or the dance in Stickleback fish.

FAPs are innate, i.e it is inbuilt from birth, and therefore does not need to learn it. FAPs are also usually completed once initially triggered. These behaviors may be critical to increasing an animal’s fitness, for instance, by allowing them to instinctively recognize and attack prey, or—as in sticklebacks—increase the production of offspring that can survive to maturity.



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2. Lorenz, K., Tinbergen, N. (1970). Taxis and instinct in egg-rolling response of the greylag goose. *Studies in Animal and Human Behavior*, 1, 328–342.
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COMMUNICATION :

Communication means the social interactions in which animals convey information to members of their own species, and to other species as well, through an incredible discovery of sounds, colors, flashing lights, smells, and postures. There may be lots of definitions of communication which are as follow :-

- " Any sharing of information" .... Smith (1984).
- Wilson (1975) defined biological communication as an "action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell) in a fashion adaptive to either one or both of the participants."
- According to Slater (1983), " transmission of a signal from one animal to another, such that the sender benefits on average, from the response of the recipient."

Who benefits from communication - the sender, the receiver or both ? Animal behaviorists have disagreed on this issue. One classification scheme considers the value of any information communicated to both sender and receiver (Wiley 1983) (following table).

i. Both sender and receiver benefit = true communication
ii. Sender benefits, receiver is unaffected or harmed = manipulation or deceit
iii. Sender is unaffected or is harmed, receiver benefits = eavesdropping or exploitation
iv. Neither sender nor receiver benefits, both may be harmed = ignoring or spite

Terms used to describe interactions, depending on the value of the information to sender and receiver

	Receiver value of Information	
Sender value of Information	**POSITIVE**	**ZERO(or NEGATIVE)**
POSITIVE	True communication	Manipulation
ZERO(or NEGATIVE)	Eavesdropping (exploiting)	Ignoring (spite)

- The most important is the **Signal**, it is the physical form in which a message is coded for transmission through environment. Signals may be of different types :

1. **Discrete & Graded signals** : some signals are discrete (distal or all or none) but others are graded (analog). For example, **Discrete signals** : equids, such as zebras, communicate hostile behavior by flattening their ears and communicate friendly by raising their ears. **Graded signal** : the intensity of either emotion is indicated by the degree to which the mouth opens. The mouth opening pattern is the same for both hostile and friendly behavior. Graded signals thus vary in intensity in proportion to the strength of the stimulus.

2. **Composite signals** : two or more signals combine to form a composite signal with a new meaning. In the zebra example, the meaning of open mouth depends on whether the ears are forward (friendly) or backward (hostile).
3. **Syntax** : animals can convey additional information with a limited number of displays by changing the syntax or sequence of display. For example the two signals A and B would have different meanings depending on whether A or B came first. A → B, or B → A.
4. **Context** : the same signal can have different meanings depending on the context; that is, depending on what other stimuli are impinging on the receiver. For example, the lion's roar can function as a spacing device for neighboring prides, as an aggressive display in fights between males, or as a means of maintaining contact among pride members.
5. **Metacommunication** : increasing the information content of displays by metacommunication, or communication about communication, is theoretically possible : one display changes the meaning of those that flows. A good example is that found in the play behavior : animals use aggressive, sexual, and other displays in play, but they precede such behavior by an act that communicates the message, "what follows is play, join in" (Bekoff 1977). Canids such as dogs and wolves play with the play bow. Monkeys communicate play behavior through a relaxed, open mouthed face.

CHANNELS OF COMMUNICATION :

The sensory channel is the physical form used to transmit the signal from sender to the receiver. From an evolutionary perspective, there are costs and benefits associated with different channels, depending on the environment and the information being transmitted. The following table summarizes costs and benefits for four major channels.

General properties of the four major sensory channels of communication

	SENSORY CHANNELS			
Signal properties	**Olfactory**	**Auditory**	**Visual**	**Tactile**
Range	Long	Long	Medium	Short
Transmission rate	Slow	Fast	Fast	Fast
Travel around objects ?	Yes	Yes	No	No
Night use ?	Yes	Yes	Little	Yes
Fade-out time	Slow	Fast	Fast	Fast
Locate sender	Difficult	Varies	Easy	Easy
Cost to send signal	low	high	medium	low

FUNCTIONS OF COMMUNICATION :

The ultimate function of any communication is increased fitness. Although many criteria can be used to classify proximate functions of communication, these classifications tend to be artificial and arbitrary and are made mainly for researchers' convenience to help keep things organized. The following functions of communication are modified from Wilson (1975), Smith (1984), and Bradbury & Vehrencamp (1998). These are as follows :-

1. **Group spacing & Coordination** : group living animals use a variety of signals that seems to keep members in tough. Marler (1968) suggested that primates use the following types of spacing signals :
   a. Distance-increasing signals, such as branch shaking, which may result in another group's moving away;
   b. Distance-maintaining signals, such as the dawn chorus of howling monkeys (*Alouatta* spp.), which regulate the use of overlapping home ranges;
   c. Distance-reducing signals, such as the contact or lost calls of *Cebus* monkeys;
   d. Proximity-maintaining signals, such as those that occur during social grooming within groups.

2. **Recognition** : these are of following types -
   a. **Species recognition** before mating is assumed to be crucial to avoid infertile mating between members of closely related species. For example, there are striking differences in the courtship songs of three species of picture-winged Hawaiian *Drosophila*. The sound producing mechanisms differ radically from those of mainland populations because they use their abdomen as well as wings (Hoy et al. 1988). In this instance, the songs may have evolved by means of sexual selection, where females choose males based on certain attributes of the song. Here in this example, the courtship songs of *D. fasciculisetae*, *D. crytoloma*, and *D. silvestris* are so different that this might secondarily come to serve as a species-isolating mechanisms, reducing or eliminating matings among closely related species.
   b. **Deme recognition** : local dialects in bird songs have been demonstrated for a number of geographically separated populations of white-crowned sparrows. Females from one population in Colorado perform copulation-solicitation displays when they here songs of males from their own populations but rarely do so when hear songs of another population (Baker 1983). These mating preference may lead to the mating with members of locally adapted demes.
   c. **Class recognition** :in occurs mainly in the social insect groups in which casts are treated differentially. In many species, the nest queen receives preferential treatment (food and care) from workers because of pheromones she produced. Males are discriminated against as a group; they receive less food from the workers and, in times of food scarcity, are even driven from the colony (Wilson 1971).

d. **Individual** recognition : Indigo-buntings (*Passerina cyanea*) produce a complex song that is quite variable. Most of the phrases are paired (sweet-sweet, chew-chew, and so forth).

e. **Neighbor** recognition : to test whether white-throated sparrow males recognize neighbors individually or as a class, Fall & Brook (1975) studied the effect of playback location on the resident males, moving the speaker in and around his territory. When they placed the speaker at the boundary between his territory and his neighbor's, his response to a stranger's song was stronger than his response to his neighbor's, as expected. But when they placed the speaker on the opposite boundary, he respond vigorously to the neighbor's song as if it were a stranger's.

f. **Kin recognition** : communication may be involved in the differential responses of many organisms to their close relatives. For example, tadpoles of American toad (*Bufo americanus*) prefer to associate with siblings over nonsiblings, even after being reared in isolation (Waldman 1982). How can kin identify each other over if they never interacted ? One possibility is Phenotype Matching, where the individual "refer to" the kin whose phenotypes are learned by association – the referent. The referent is then compared with the stranger (Holmes and Sherman 1983).

3. Reproduction : many of the most striking displays occur during courtship. For example, the different mating calls of two populations of cricket frogs (*Acris crepitans*) just 65 km apart in the central Texas (Ryan & Wilczynski 1988).

4. **Agonism & Social status** : in social groups, when members of a species are in close proximity, it is sometimes beneficial for an individual to compete and fight with others profession of a resource, be it food, space, or access to another individual. Social species have evolved displays that communicate information about an individual's mood ;the 'S'-shape posture of tail of Rhesus monkey, this display indicates that it is dominant and in an aggressive mood.

5. **Alarm** : animals use vocalizations and chemicals to alert group members to danger.
   - **Vocalization** : Animals of same species live in a group and endangered by the same predators, are mutually benifitted by minimizing the difference in alarm vocalization. E.g., Vervet monkeys (*Chlorocebus aethiops*) communicate semantically by using different signals to warn about different dangers in their environment. Group members climb trees when they hear alarm calls given in response to arrival of leopards (called **leopard** call), they look up when they hear eagle alarms (called **eagle** call), and they look down when they hear snake alarms(called **snake** call) (Struhsaker 1967). Young vervets

give alarm calls in response to different animals, and their ability to classify predators and give appropriate alarm calls improves with age (Cheney & Seyfarth 1990; Seyfarth et al. 1980).

- **Chemicals** :- both vertebrates and invertebrates produce certain chemicals used as the alarm signals -
    i. Sea urchin leave the area quickly that contains crushed members of its own species.
    ii. Rat & mice secrete certain chemicals with urine when they are given to electric shock or other stress. This chemicals serve as an alarming signal causing other rats to avoid the place.

6. **Finding food** : an important selective advantage of group living is increased efficiently in finding food. One possible advantage of such behavior is that roosts serve as information centers (Ward & Zahabi 1973). The African wild dog (*Lycaon pictus*) is a canid distantly related to domestic dogs and wolves. Just prior to hunting prey that often consists of large ungulates, members of the pack engage in an intense greeting ceremony, or "rally", consisting of a frenzy of nosing, lip licking, tail wagging, and circling (Creel & Creel 1995). Such behavior seem important in coordinating activities. Their calling displcy is also called "war cry".

7. **Giving and soliciting care** : a wide variety of signals is used between parents and offspring and among other relatives in the begging and offering of food. As Tinbergen (1951) demonstrated, red spot on the herring gull's lower bill stimulates and directs a pecking response by the hatchlings, and the hatchling's resultant pecking of the parent's beak stimulates the parent to regurgitate the food.

8. **Soliciting play** : play consists of behavioral patterns that may have many different functions in the adult : sex, aggression, exploration, and so forth. The play bow in canids is communication about play and informs others that the motor patterns that follow are not the real thing. The function of play itself is a subject of debate.

9. **Synchronization of hatching** : Precocial birds, such as pheasants and ducks, lay large clutches of eggs. Synchronous hatching is very important because to feed or to get into the water to escape predation by terrestrial vertebrates, the mother leaves the area with all her young following. Species that nest in tree holes leave the area permanently the day the chicks hatch. Late-hatching chicks are vulnerable to predation. A few days before hatching, the chicks begin to vocalize. This communication contributes to hatching synchrony, since similarly aged eggs incubate separately hatch over a period of several days (Vince1969).

→ COMPLEX COMUNICATION :

i. Bee dance is an example of complex communication, basically this is for locating food, i.e., "communication for foraging". The main survival strategy of all the animals is for foraging and reproduction. The ants follow a pheromonal triad to reach the destination for food but this is not effective in case of bees - as in air the pheromone will be dispersed. Bee is a flying insect, and many flying insects orient themselves according to position of the sun. The dance of honeybee , first described by Karl von Frisch, and for long questioned because it seemed so extraordinary . is certainly one of the most remarkable forms of communication to have been discovered. Karl von Frisch worked more than 25 years continuously.

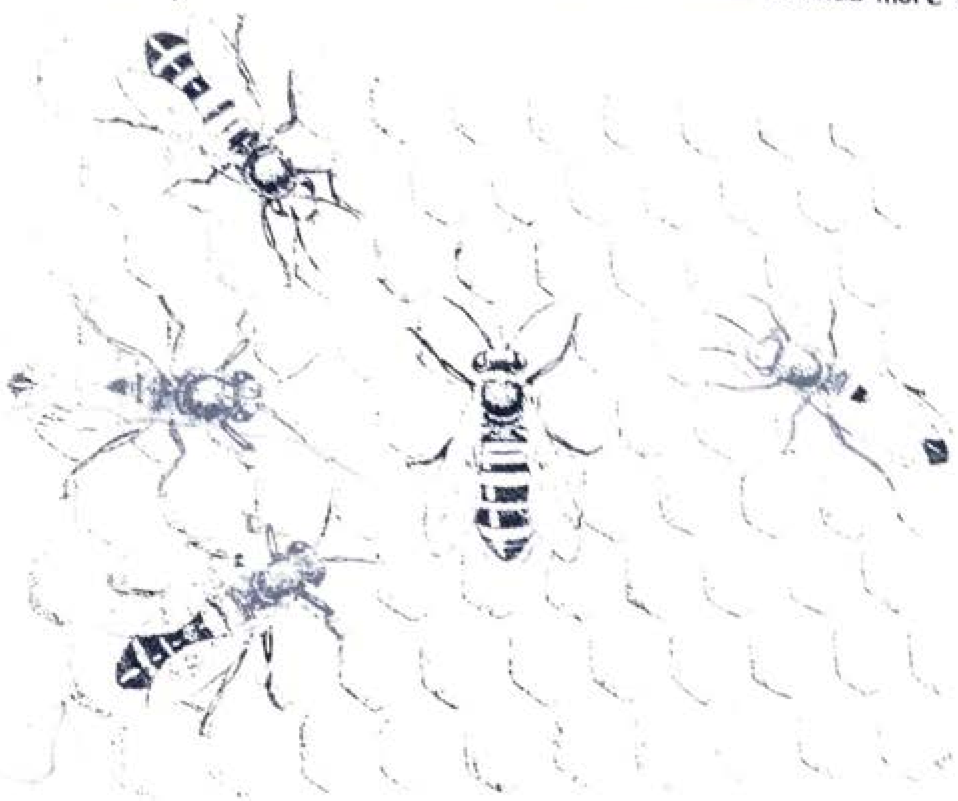


Figure 8.13. [illegible]

- **Food location in honey bees :-** Hours or days may go by before a foraging honey bee (*Apis mellifera*) discovers a sugar solution placed outdoors, but after that new bees arrive within minutes.
- **Hypothesis about the mechanism :-**
  - Aristotle : He thought that the other bees simply followed the foragers to the food.
  - Von Frisch (1967) :-

i. The recruitment take place even when the forager is not allowed to return from the hive to the food source.

ii. Bees obtain information about the food location through odor communicated in the hive by the forager's dance. Hive members maintain antennal contact with the dancer's body and takes the samples of the regurgitated food.

iii. Later, he got more specific information about the 'food locating mechanism of honey bee' and went on to develop his famous - "Dance-language hypothesis".

✦ THE POSSIBLE MECHANISM (After Von Frisch, Davies etc.)

After returning to hive, foragers give necessary information to the other members of colony about -

1. THE NATURE OF FOOD,
2. DISTANCE OF FOOD SOURCE FROM HIVE (ROUND & WAGGLE DANCE),
3. THE DIRECTION OF THE FOOD (TOWARDS OR AWAY FROM SUN),
4. RICHNESS OF THE FOOD SOURCE.

1. NATURE OF FOOD :-

A. Flower with a specific scent :-

i. Honey bees possess 600 antennal pores that detect the specific scent of flower.

ii. Honey bees also possess scent glands. When bees visit a particular flower, the scent glands are activated and recognize the specific scent of the flower.

iii. When foragers return to the hive, these scent glands provide the necessary information about food source to the other members of colony - so that they can easily trace out the source.

B. Flower without a specific scent :-

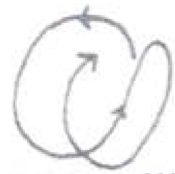
i. When bees visit a particular flower without specific scent, the pollen grains of the flower get attached to their lower portions of the bodies.

ii. When foragers return to hive, these pollen grains serve as a signal to other members of colony to trace out the food source.

2. DISTANCE OF FOOD FROM HIVE :-

A. Distance of food source - short (50 - 100 meter from hive) :

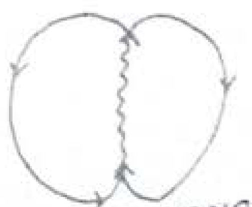
After returning to hive, foragers perform - **"round dance"** - here a series of circles formed with the reversal of direction at every second or so.



ROUND DANCE

B. Distance of food source - long

i. After returning to the hive, bees perform "waggle dance" - this dance follows a figure of eight with a straight line in the middle. The foragers waggle its body and emits sound bursts during the straight run.



WAGGLE DANCE

ii. In waggle dance, duration of each cycle, duration of sound burst are all correlated with the distance of the food source.

iii. *Apis mellifera* completes one turn in waggle dance at 1.5 seconds - when the food is 100 meter away; while it takes 7.5 seconds to complete one turn - when the food is 6000 meter away from the hive.

3. **DIRECTION OF THE FOOD SOURCE :-**

A. **In a sunny day :-**

i. Let us consider an imaginary triangle whose apex is the sun. there are two straight lines formed between the hive & sun and the hive & food source. The angle (θ in the figure) between these two straight lines serves as a signal for honey bee to detect the direction of the food source.

ii. Now depending upon the angle thus formed, the bees start their dance. But during their movement towards food source, the sun automatically changes its position - so the angle thus formed is also altered. But these do not cause any problem to the bees - as are capable to measure the angle through which the sun moves and thus accordingly can alter the pathway of dance.

The honey bee can orient its dance pattern according to change in ~~action~~ angle of sun. This particular phenomenon is called menotaxis or telotaxis.

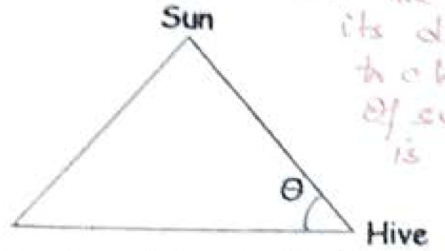


Fig :- Honey bee - how to locate the direction of food.

B. **In a cloudy day :-**

Honey bees can measure the polarized light of the sun and thus detect the direction of food source.

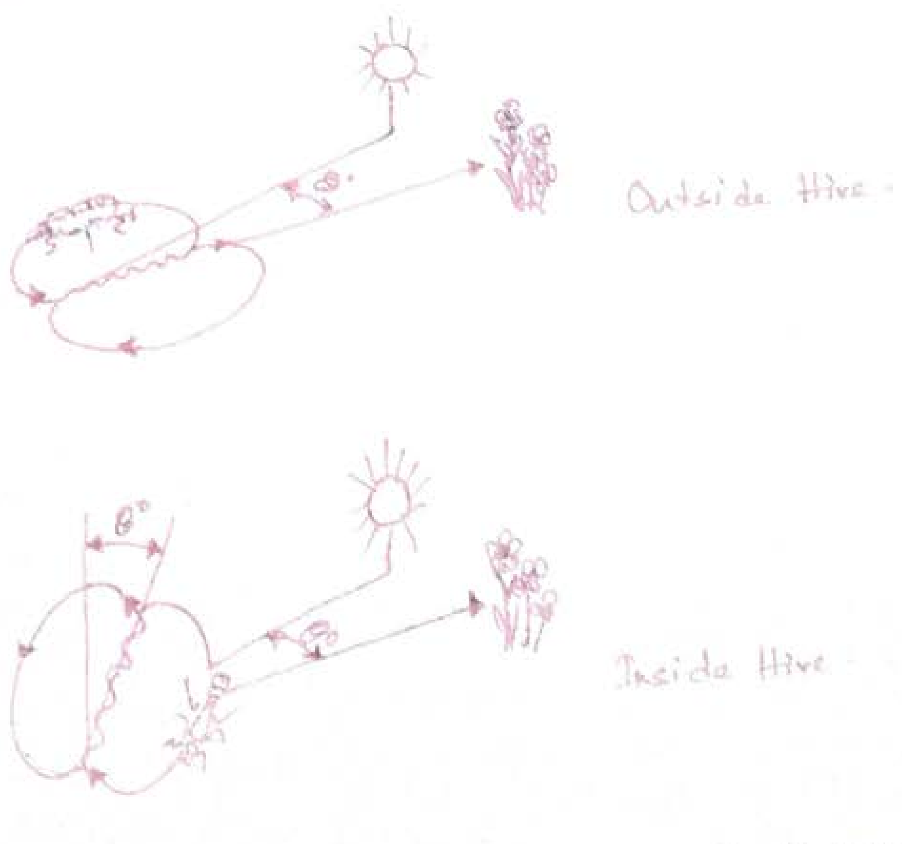


Fig : Waggle dance of a foraging honey bee after discovering a food source.

i. If bee dances outside the hive, it waggles or vibrates its body as it passes through the straight run, which points directly to the source.
ii. If it dances on an enclosed vertical comb, it orients itself by gravity and substitutes a point directly overhead for the sun.
The angle θ between sun & the food source is the same as that between a point directly overhead and the food source.

4. RICHNESS OF FOOD SOURCE :-
   A. **Food source - extremely rich** :- after returning to the hive, foragers dance vigorously for a long period.
   B. **Food source poor** :- after returning to hive, foragers dance slowly for a short duration.

✦ PHEROMONES IN COMMUNICATION :

- **DEFINITION** : Pheromone is a volatile chemical substance that is used for the purpose of communication between two individuals of the same species.

- **SOME BASIC PROPERTIES** :
  i. It is recognized as the oldest form of communication.
  ii. Mostly pheromones are excreted through the urine of feces. N.B. however, both in vertebrates & invertebrates, a number of pheromones are found to be secreted by various skin glands, digestive glands etc.
  iii. Transmission of pheromones require medium like air, water.
  iv. Pheromone is mostly secreted by males and is received by the members of same species near or at distance through olfaction and evoke a behavioral response.

- **ADVANTAGES OF PHEROMONE** :Advantages of pheromone are of many folds, viz.,
  i. Pheromones can travel around the solid objects like rocks etc., that may hinder visual signals.
  ii. Its efficiency is quite high i.e., Bombykol is a pheromone produced by female silk moth & received by male. A signal molecule of bombykol may induce nerve impulse on antennal cells of male in several miles away.
  iii. Pheromones can transmit signals in day as well as in night.
  iv. Sometimes the spread of pheromone depends upon the speed of the carrier. It may be fast or may be delayed.
  v. The fade out time of pheromone is quite long. So it can last for hours or days in normal circumstances. But if there is a rain, it may be washed away.
  vi. If we take the cost-benefit question, pheromone secretion is highly economic. For example, secretion of 1 microgram can elicit thousands of male reactions.

- **TYPES OF PHEROMONES** : Author - Bronson (1971). Basis - two general classes of pheromones are recognized on the basis of "their effects on mice"

1. **Priming Pheromones** :-
   i. These produce a generalized response.
   ii. These chemicals yield responses with the help of hormonal priming
   iii. Eg:- (a) Estrus inducer : substances excreted in male mouse urine, trigger estrogen & progesterone production in young females leading to estrus (b) Estrus inhibitor, (c) Adrenocortical activator

Priming pheromone → Generalized response → Estrus inducer, Estrus inhibitor, Adrenocortical inhibitor

2. **Signaling Pheromones** : -
   i. Signaling pheromones produce an immediate motor response
   ii. These chemicals yield a marked behavioral response without any help of hormonal priming.
   iii. E.g., (a) FEAR SUBSTANCES, (b) MALE SEX ATTRACTANT, (c) FEMALE SEX ATTRACTANT, (d) AGGRESSION INDUCER, (e) AGGRESSION INHIBITOR

N.B., 1. **LORDOSIS** :- a typical mating behavior of female rodent switched on by signaling pheromones excreted in male urine. In this behavior, female arches its back in a typical way, thus preparing itself for accepting the male.

2. **FLEHMEN** :- A typical mating behavior found among the male members of cow, tiger etc. most possibly switched on by the signaling pheromones secreted in female's urine.

Male when touches the anogenital region & sniffs the urine of female, a) it retracts it's upper lip (cow), or b) it ejects the tongue (tiger).

By this, male recognizes whether the female is reproductively prime or not during breeding season.

- **PURPOSE OF PHEROMONE COMMUNICATION** :

1. **MATE IDENTIFICATION & ATTRACTION** :-

A. **Importance of mate identification during reproduction** :-

i. The main purpose of life is to propagate - for this, the offsprings must not be sterile.

ii. Fertile offsprings are produced by conspecific reproduction only - therefore identification of mates must be conspecific during breeding season.

C. **Mechanism** :-

Pheromones are species specific chemicals.

So pheromones of one species can not be received by another species. This specificity ensures coordination of behaviors resulting into successful breeding & production of fertile offsprings.

⊙ Examples :-

a) **INSECTS :- SILK MOTH**

Female silk moth produces a sex-attractant pheromone called bombykol. Bombykol triggers nerve impulse in specialized receptor cells on males antennae. This induces male to fly upwind, equalizing the pheromone concentration on both the antennae until it reaches the female.

N.B. : SYNTHETIC BOMBYKOL : it is commercially synthesized bombykol. It is used as baits on the traps to lure the male sexes of insect pests like gypsy moth - and latter killed. Thus bombykol is used as a control measure for the insect pests.

b) **FISHES :-**

i. An experiment :- during breeding season, female fishes are first released into aquarium water, then removed and then males are released - latter start shivering. Now females again released in water & this is followed by nudging (physical contact between sexually attracted male & stimulated females).

Remark :-

- The females must release some substances (pheromones) received by the males.
- Blatt et al. found that fishes released two types of pheromones viz.,
  a) Sulfated steroid (preovulatory pheromone) - 17, 20 - P(17α , 20 β- dihydroxy - 4 - Pregnen - 3 - one).
  b) PG-metabolite(preovulatory & postovulatory quinonoid steroid), e.g., 15 - K - PGF [F - Prostaglandin (PGF 2α)].

Electro-olfactogram (EOG) i.e., lesion of olfactory tract revealed that there are two types of receptors for such pheromones typeI & typeII.

ii. THREE SPINED STICKLEBACK FISH :-

Female fish secretes preovulatory pheromone that induces a special behavior "chasing" in males in a zig-zag dance pattern following a definite orientation. Chasing is then followed by "nudging" - in which male pushed with its head at the gonopore of the female & stimulate the latter to spawn.

iii. IN BIRDS :- birds have no pheromones. Here conspecific mate identification occurs by species specific - a) spectacular display, b) courtship, & c) song pattern etc.

2. **CLASS RECOGNITION :-**

i. Three castes of honey bee exist in a bee colony - queen, worker & drone. Among them, queen is always cared by workers while drones are not - therefore workers can recognize the two classes (queen & drone) separately, but how ?

ii. Actually in a honey bee colony, only queen secretes a special pheromone - by which workers can recognize her & giving her special care.

3. **SPACING :-**

In mammals (Tiger, Wolves, Hyena) - pheromones produced by GI tract & anal glands, serve as a mean of spacing i.e., used to mark boundary of their territories.

⊙ **Examples :-**

1) Tiger :-

i. Tiger presses its anogenital glands, so anus is everted and a jet of urine is ejected.

ii. Here urine serves as pheromone to mark the territory of a male, into which female members enter, but other males do not enter.

iii. "Amount of urine ejected"- also indicates the health status of a male, as it (urine amount) can be sniffed by female to detect whether the male is reproductively primed or not ?

2) HYENA :-

Hyena clans mark the boundaries of their territories by establishing "LATRINE AREAS". E.g., PAWING & PASTING OF MUNGI HYENA CLAN.

Fig :- Activities of the Mungi hyena clan along its boundary.

a) PAWING :-

i. The members of the same clan defecate simultaneously in an area (previously used by others), then paw the ground.

ii. The feces mixed with urine, then dried, turned white & become quite conspicuous.

iii. Members of the other clan (scratching rock clan), by observing the feces, avoid trace passing into the territory of Mungi clan.

b) **PASTING** :-Hyena paste the anal gland secretion on grasses as follows,

i. Both sexes have two anal glands that open into rectum just inside the anal opening.

ii. When pasting, hyena straddles long stalks of grasses; as the stem pass underneath, the animal everts its rectum and deposits a strong smelling whitish substances on the grass stem.

N.B. : Pasting is also seen in deer & antelope. In pasting, tarsal & metatarsal gland secretions also involve and these secretions become more effective in presence of urine i.e., actually urine contains fat soluble pheromones. So sebum of tarsal & metatarsal glands when come in contact with urine gets dissolved & activate the gland pheromones.

4. **ALARM** : Upon tolerance, fishes, rats, mice etc. produce pheromones as an alarm to other members.

◉ Example :- Rat & mice secrete specific pheromones with urine when they are given electric shock or other stress. This chemicals serve as alarming signals - causing other members to avoid the places.

Because foraging is so clearly related to an animal's fitness, animals are likely to be under natural selection to be effective foragers. A tool for behavioral ecology called optimality modeling has been frequently used in the study of foraging behavior. A optimality model has three parts (Stephens and Krebs 1986) :

1. A set of <u>Decisions</u>, or strategies, that are available to the animals. For example, a foraging bird may choose to eat a particular piece of food, or search for another one instead; a spider may stay where it is, or move its web to a new place. By the words 'decision' and 'strategy' we do not imply that animals are consciously aware, or that they undergo a decision-making process such as we do. All that is meant is that an individual animal performs one action out of a variety of alternatives available to it.

2. The **<u>Currency</u>**, or the criterion used to compare the value of different decisions. In order to decide among the decisions available to the animal, we must be able to compare them with a common measure. For example, many foraging models use the rate of energy intake as the currency. The best strategy would be the one that maximizes this rate. In other models, animals maximize the time they spend for foraging. Later, we'll discuss how the choice of currency may influence the outcome of a model.

3. The <u>Constraints</u>, or limits on the animal. Constraints can be internal, or intrinsic to the animal (such as particular nutritional needs, or the ability to see only certain colors) or external (such as temperature or light levels that effect an animal's ability to forage effectively). An animal can optimize its behavior only within the range of its capabilities and needs, and constraints define the range.

Optimality model, in addition can be used to describe other aspects of behavior, such as mate acquisition and habitat selection; the basic ideas are the same.

- <u>Foraging strategies</u> :

Foraging behavior can be boiled down to several basic problems :

i. What items an animal should include in its diet ?
ii. What 'patch' should an animal look for ?
iii. How long an animal should stay in one patch ?
iv. Which patch it should visit next ?

These are some of the decisions an animal must make. Behavioral ecologists usually assume that the currency (what is being maximized) is the net rate of energy intake, which is intake per unit time. Energy costs are incurred in obtaining food - mainly those of the search, pursuit, handling and eating. These costs must be subtracted from the benefit - the energy in the food. A rate is obtained by dividing the net energy gain by the time it takes to do all of the above :

$$\text{Net rate of Energy intake} = \frac{\text{Energy from food} - \text{search energy} - \text{pursuit energy} - \text{handling energy} - \text{eating energy}}{\text{Search time} + \text{pursuit time} + \text{handling time} + \text{eating time}}$$

➢ Foraging models :

There are usually two types of models, viz., the diet selection models, or prey model that deals with the types of prey a forager should eat; and the patch model which deals with how long a forager should stay in a food-containing patch.

➢ Choice of Food items : The Prey Model

Most species of animals are surrounded by all manner of things that they might consider eating. The barn owl (*Tyto alba*) is a nocturnal predator of small mammals. In South-Western New Jersey, these owls roost in three cavities or silos and forage in fields over a radius of several kilometers. Colvin (1984) found that more than 90 % of the available small mammals are white footed mice (*Peromyscus leucopus*), and house mouse (*Mus domesticus*), and less than 5 % are meadow voles (*Microtus pennsylvanicus*). However, 70 % of the owls' diets were meadow voles (following figure). Clearly, owls are not simply taking prey species in proportion to their abundance in the habitat. How do we model a problem such as this ?

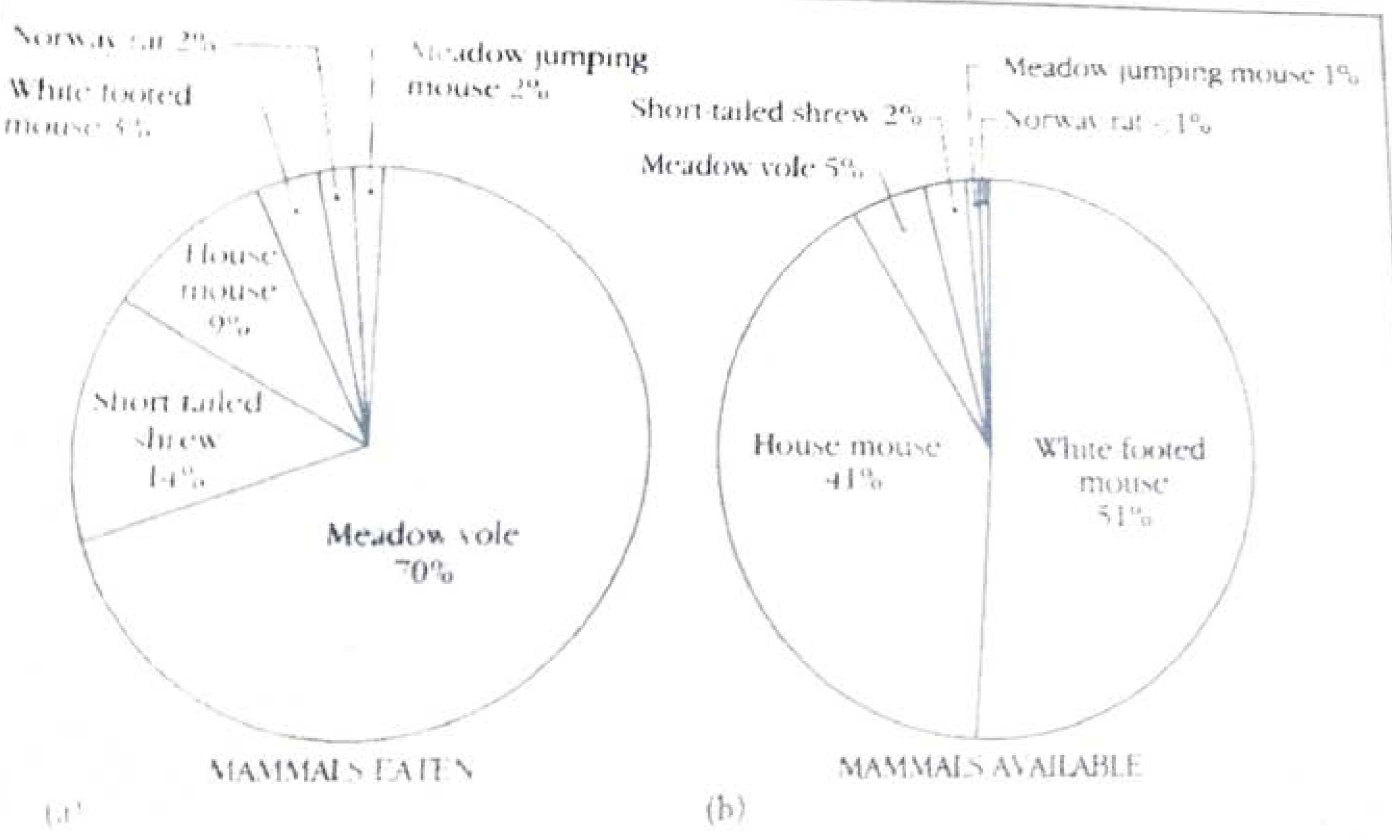


FIGURE 15.1 The percentage of small mammals eaten by barn owls (a), compared to the percentage available based on trapping (b).
In this study from southwestern New Jersey, barn owls are meadow vole specialists.

- Constructing the model :-

The scenario is that a forager is searching for food, and it finds one prey at a time. Lets consider the three parts of this model. The decision variable is whether the forager should eat the prey it finds, or whether it should continue for another type of prey. The currency is the rate of energy (caloric) intake we assume that the animal benefits by maximizing this rate, and we will measure the relative value of the available decisions in this currency. Finally there are various constraints that we can include. Prey, once found, need to be processed in some way : nuts may need to be cracked open, live prey need to be subdued. This takes a certain amount of time called the **Handling time**. Different types of preys may have different handling times. We will also assume that foragers cannot handle prey and search for it at the same time.

ii. First, lets simplify the matter by considering only two different types of available prey, types 1 and 2 (there may be any, as in case of barn owl). Each of these might provide a different amount of energy for the animal, which we define as E_i, where the subscript I represents different prey types. So the number of calories in an item of prey type 1 would be represented as E_1, and that in type2 as E_2. similarly each prey type have its own handling time hi which is h_1 and h_2 for type1 and type2 prey respectively.

iii. Because we are interested in maximizing the rate of energy intake, we need to figure out what this rate would be for each prey item. We need a new term : **Profitability**, or the ratio of energy gained to the handing time of each type of prey.

Profitability of prey 1 = E_1 / h_1 ....(eq. 1).

To simplify matters further, let's define prey type 1 as the more profitable prey type, so that

$$E_1 / h_1 > E_2 / h_2 \quad \text{.. (eq. 2).}$$

v. Finally each prey type can have its own search time, which we will represent as S_i. Search time (S_1 & S_2 for type 1 & 2 respectively) is the amount of time it takes for an animal to locate an item of a particular type. As the density of a prey item increases in the environment, search time for that prey item does down.

There is one more very important assumption : the foragers know the values of the variables we have defined. They know, for example, the probability of finding a prey of a particular type, much as a good gambler knows the odds of drawing a particular set of cards.

Imagine a searching animal has found a prey item. Now we can use the variables we defined to ask the question : should the animal eat the prey item or continue searching to find a new one ? if the prey item is type 1, the more profitable prey, the choice is obvious : the animal should eat it, because it will never find any thing better. So we have the first prediction of the model : always eat the most profitable prey.

The question becomes more challenging if the animal finds prey of type2. should the animal eat the less profitable prey or continue searching until the better prey is found ? we must compare the rate of energetic intake for these two choice :

Gain from eating prey type 2, once it is found : E_2 / h_2 .... (eq. 3).

Gain for searching for and eating prey type1 : $E_1 / S_1 + h_1$ .... (eq.4).

viii. The denominator of equation 4 contain both the search time and the handling time, because the animal must first find prey1, and then consume it. Note that both these are rates of energy intake (calories per second). This means that we can now compare the decisions available to the animal in the currency of model by comparing these values. So a forager should eat the prey type 2 when,

$E_2 / h_2 > E_1 / S_1 + h_1$ .... (eq. 5)

ix. Now we have predictions to test. First the model says that the decision to eat prey type2 should be partially based on the search time for prey type1. If prey type1 is very abundant, S1 will be low, and the value on the right side of the inequality will be large. A second prediction is that search time for prey type 2 should not be important in the forager's decision to eat it. Third prediction states that a forager switch back and forth between eating both kinds of prey to eating only the higher-quality of prey, depending on whether or not this inequality is met. This called the "zero-one" rule : an animal should eat the less profitable prey either none of the time (i.e., with a probability of zero) or all the times (i.e., with a probability of one).

x. So here time is the ultimate factor that drives the predator to take the decision to prey upon the least abundant prey type1 rather than type2, as type1 is more profitable. But it is also true that in absence of type1, the predator will not starve, rather it will shift towards type2. but sometimes it is found in case of some lion prides, that they die due to starvation in absence of their primary prey; but it is only due to their improper decision. Here in this particular model, only two constraints are considered such as handling time and searching time. There may be so many also. And constraints play the vital role in determining the decision. Such decision may vary from place to place, predator to predator, prey to prey. Eg : - group foraging and solitary foraging strategies are altogether different.

➢ <u>Now how long to stay in a patch or patch model</u> :

Whether or not to eat a particular food item is not the only problem faced by foraging animals. Many types of foods are distributed randomly in the environment, but instead occurs in patches; imagine scattered trees that are bearing fruits, or tide pools holding tasty snails. Foragers seeking these foods must decide how long to stay in a particular patch, or when to leave and find a new patch. Several factors should play into the decision. The average richness in the patches is important. We can look at these factors together with a graphical model called the marginal value theorem (Charnov 1976). In this model we again assume that the forager maximizes the rate of energy intake; this is the currency. The decision variable is to stay in the patch, or leave to seek a new patch. Constraints include : searching for patches and foraging within them are mutually exclusive, patches are found one at a time, and the forager knows the parameters in the model and does not have to learn them.In addition we assume that cumulative rate of food intake within each patch can be characterized by a gain curve (15.3a).

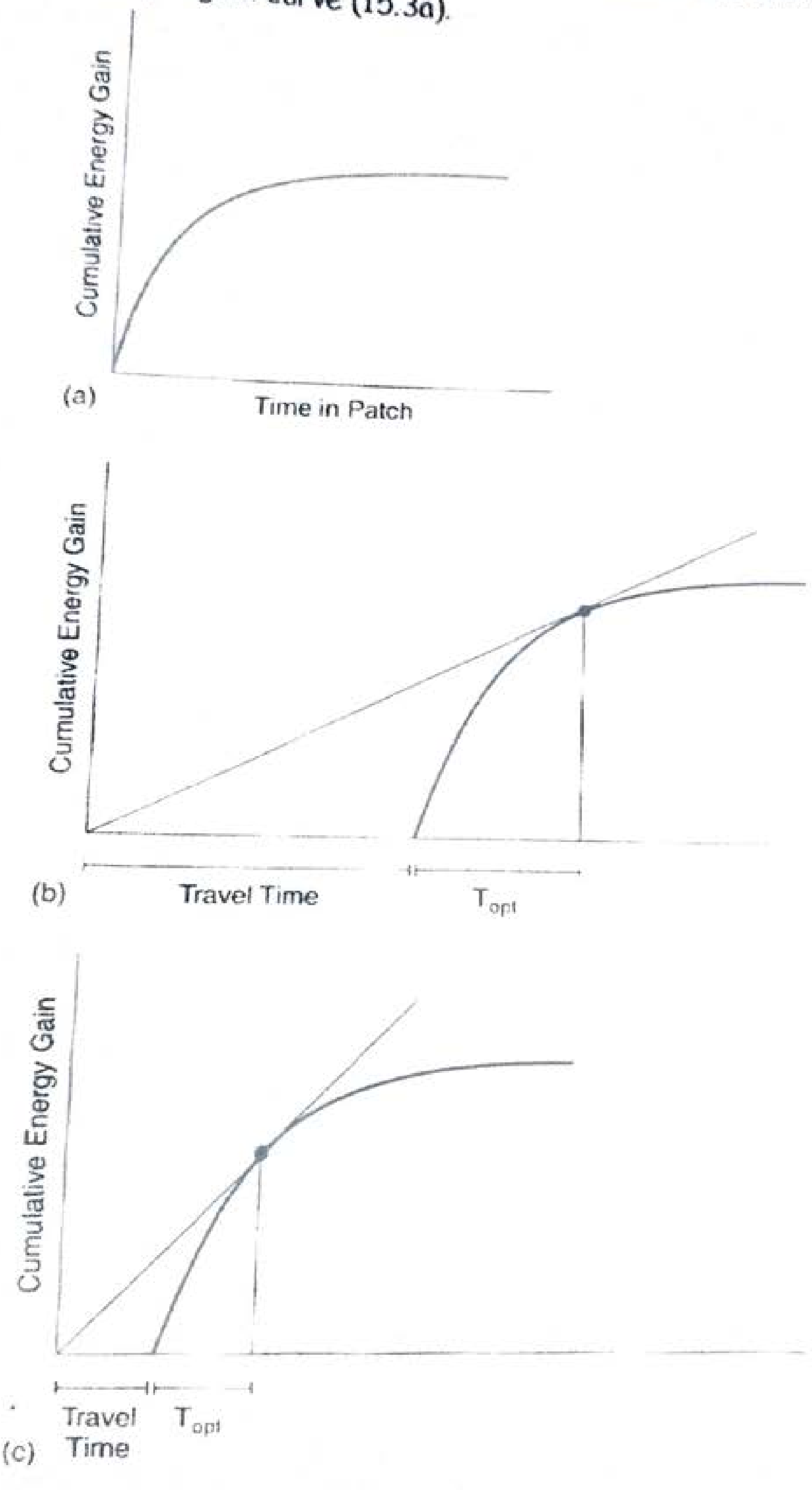


FIGURE 15.3 Predicting when to leave a patch: The marginal value theorem.
(a) A forager's cumulative energy gain in a patch is illustrated by the gain curve. The gain curve rises rapidly as the forager first enters a patch, but then levels out as food resources are depleted. (b) Now travel time between patches is added. The animal does not gain energy while it is traveling. The optimal time to stay in a patch (T_{opt}) is determined by drawing a tangent from the origin to the gain curve. (c) Here, travel time is shortened compared to (b), and the optimal time in a patch is also shorter.

- When the forager first enter a patch, it has gained no energy. As it forages within the patch its net energy gain increases as it finds food. However, as the food within the patch depleted, the gain curve flattens out : it becomes harder and harder to find each food item. It is important to remember that the plot describes the net, or cumulative energy gain. In this model all the patches have the same gain curve.
- We can add to this curve the average time to travel to a new patch (fig 15.3b). food is found only in patches, so before a forager finds a new patch, its net energy gain is zero. Now we have all the information needed to calculate when a forager should leave a patch. If it is maximizing its net energy gain, it should leave when its expected net gain from traveling to and foraging in a new patch (Charnov 1976). In other words, it should stay until it can do better elsewhere, travel costs included. This can be determined by drawing a line tangent to the gain curve, to the point on the x-axis that represent the travel time. The slope of this line is in the units of currency (energy gain per unit time). Of all the lines that could be drawn between the origin and the gain curve, the tangent is the one with the highest possible slope, or the greatest energy gain per unit time.
- Now we can modify some of the variables and see how the prediction changes. For example, we can make the travel time patches exceptionally short (fig 15.3c). the optimal time spent in the patch is now shortened. As a result the steadiness in the energy gain become faster.

An example of Optimality model on gathering food : Crows & Whelks

i. On the west coasts of Canada, as in many coastal areas, crows feed on shellfish. They hunt for whelks at low tide, and having found one they carry it to a nearby rock, hover and drop it from the air to smash the shell on the rock and expose the meat inside.

ii. Reto Zach (1979) observed the behavior of north-western crows in detail and he noted that they take only the largest whelks and on average dropt the shell from a height of about 5 m.

iii. Zach carried out experiments in which he dropped whelks of different sizes from various heights. This together with the data on the energetic costs of flying and searching, gave him the information to carry out calculations of the costs and benefits associated with foraging.

iv. The benefits obtained by the crow and cost paid could both be measured in calories, and Zach's calculations revealed that only the largest whelks (which contains the most calories and break open most readily) give enough energy for the crow to make a net profit while foraging.

v. As predicted from the calculations, the crows ignored all but the very largest whelks even when different sizes were laid out in a dish on the beach.

Crows minimize the upward flight distance needed to break a whelk.

vi. Usually the crows has to drop each whelk twice or more in order to break it open. Since ascending flight is very costly, Zach thought that the crow might have chosen the dropping height which would minimize the total expenditure of energy in upward flight.

vii. If each drop is made from close to the ground, a very large number of drops is required to break open the shell, while at greater and greater heights, the shells become more and more likely to break open on the first drop (fig 2.8a).

viii. The experiment of dropping shells from different heights allowed Zach to calculate the total vertical flight needed to break an average shell from different dropping heights (fig 2.8b). the crow fly to an average height of 5.2 m and at this height the total vertical flight per whelk is close to its minimum.

ix. However the crow would have to under take almost the same total upward flight even if each drop was made from a height some what greater than the 5.2 m (this indicated by a very shallow U-shaped curve of fig 2.8b) because slightly fewer drops would be needed.

x. Zach suggested that there may be an additional penalty for dropping from too great a height : the whelk may bounce away and be lost from view or may break into so many fragments that the pieces are too small to retrieve.

xi. This story of crows and whelks shows how calculations of costs and benefits can be used to produce a quantitative prediction. The crow seems to be programmed to choose a dropping height that comes close to minimizing the total vertical flight per whelk. Other currencies, such as maximizing net rate of energy gain, predict much greater drop heights (Plowright et al. 1989).

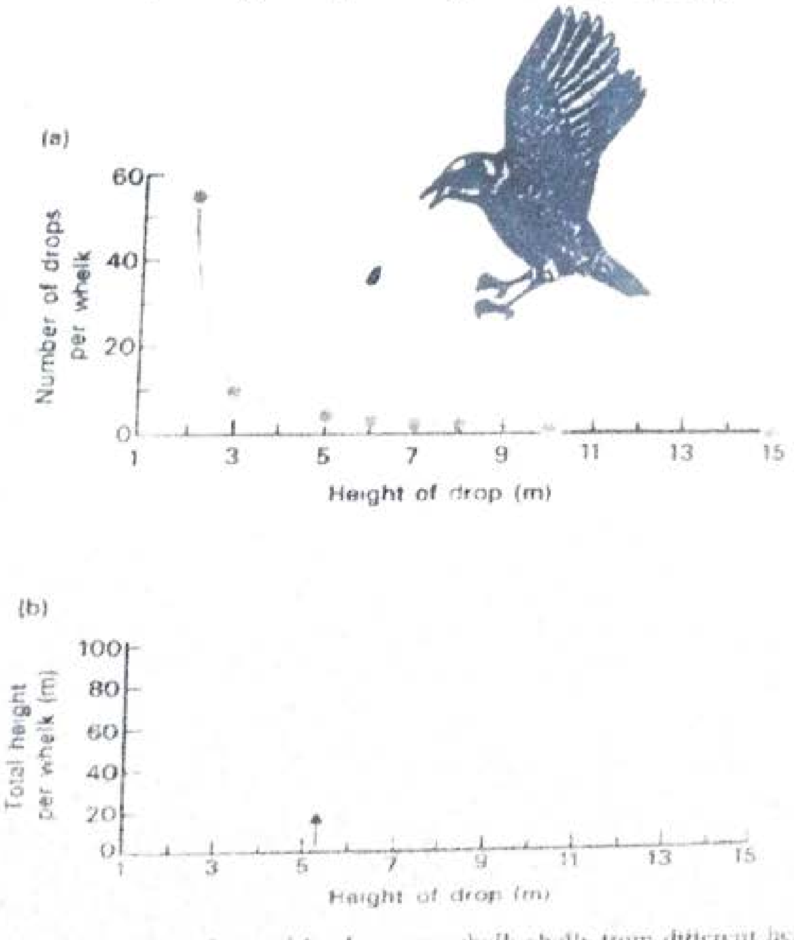


Fig. 2.8 Results obtained by dropping whelk shells from different heights (a) Fewer drops are needed to break the shell if it is dropped from a greater

The economics of prey choice :

i. Here we consider the prey-catching behavior of shore crab (*Carcinus maenas*). When shore crabs are given a choice of different sized mussels they prefer the size which gives them the highest rate of energy return (fig 3.5).

ii. Very large mussels take so long for the crab to crack opening its chelae that they are less profitable in terms of energy yields per unit breaking time (E / h) than the preferred, intermediate sized, shells.

iii. Very small mussels are easy to crack open, but contains so little flesh that they are hardly worth the trouble.

iv. However, the story cannot be as simplé as this, because the crabs eat ranges of sizes centered around the most profitable once. Why should they sometimes eat smaller and larger mussels ?

v. One possible hypothesis to explain why several sizes are eaten is that the time taken to search for the most profitable sizes influence the choice. If it takes a long time to find a profitable mussel, the crab might be able to obtain a higher overall rate of energy intake by eating some of the less profitable sizes.

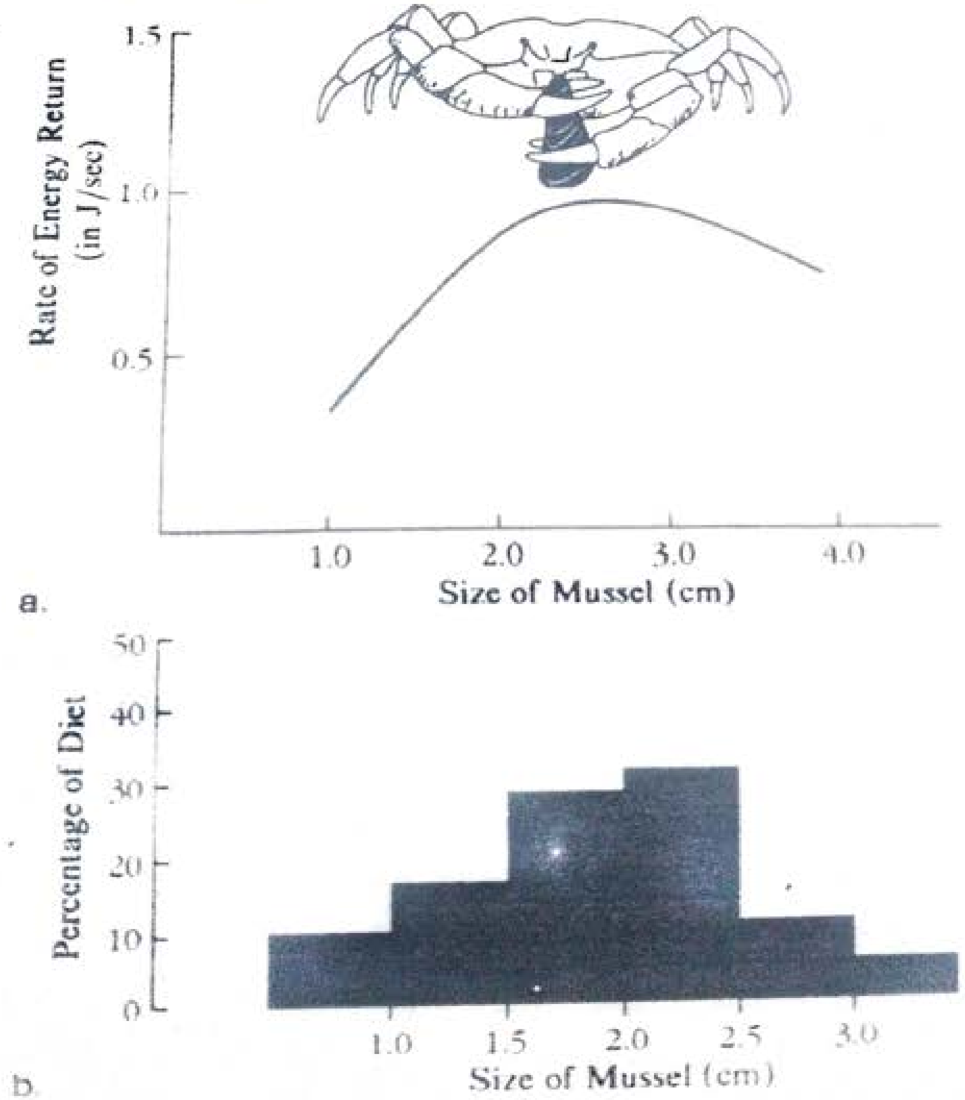


FIGURE 2.7 Shore crabs select mussels for food.
(a)Shore crabs select those sizes of mussels that provide the best