needs than in searching for something suitable in the literature. Also, you can probably save yourself a great deal of money.

4.2 HOW TO DESCRIBE BEHAVIOR

> At the heart of the modern approach to the analysis of behavior in animals is the problem of description. *[Marler, 1975:2]*

When developing a catalog of behaviors, you will be describing and applying names to the behaviors you observe. For descriptive studies, your catalog (discussed below) can contain names for behaviors which carry implicit descriptions, as well as *descriptions* which, by themselves, serve as terms for those specific behaviors. As you shape your catalog of behaviors into an ethogram (discussed below) you will probably apply *terms* to the behaviors you have named and described, primarily for ease of data collection. For further ease of data collection, you may replace the terms with code letters and numbers (Chapter 8). For experimental studies, especially, you will further sharpen the descriptions into operational definitions (Chapter 6).

The discussion below applies primarily to the early phases of a study in which you are making reconnaissance observations, taking *ad libitum* field notes, or beginning to compile a catalog of behaviors. Therefore, I have interspersed the words 'term', 'name' and 'description' as synonyms.

4.2.1 Empirical versus functional descriptions

As you first observe the behavior of an animal you will likely be confused by the complexity of what the animal does: but in time some order will appear in the types of behavior engaged in, the contexts in which they appear, and the movements and postures that are involved (Marler, 1975). Familiarity with an animal's behavior and insight into its function are continuing processes that generally lead to revision of both hypotheses and terminology.

Nevertheless, in time, it will be necessary to describe what you have observed in terms which are clear yet unassuming. The problem of description is resolved through experience in observing the animal's behavior and your ability to select terminology that will assist, not hinder, future analysis.

There are two basic types of behavioral description (see Tables 4.7 and 4.8):

- *Empirical description*: description of the behavior in terms of body parts, movements and postures (e.g. baring the teeth).
- *Functional description*: incorporation of reference to the behavior's function, proximally or ultimately (e.g. bared- teeth threat).

Table 4.7. *Examples of empirical and functional descriptions (terms) for observation of a flying mourning dove (see text)*

Type of description	Behavior description
	a. Behavior X
Empirical descriptions	b. Rapid alternate contraction and relaxation of the pectoralis muscle
	c. Wing flapping
Functional descriptions	d. Flying
	e. Escape flight

These types are nearly synonymous with the two types used by Hinde (1970): 1. description by spatio-temporal patterns of muscular contraction, including patterns of limb and body movement; and 2. 'description by consequence', respectively. Wallace (1973) calls Hinde's first type 'description by operation'.

The type of description selected will depend in part on your knowledge of the animal's behavior and type of study you wish to pursue. Descriptions can be thought to lie along a continuum of information conveyed. At some stage, conveying additional information generally entails drawing conclusions from data about function. After careful study the researcher may be able to use a term which more clearly describes the context of a behavior. For example, W. J. Smith (1968) studied the use of the 'kit-ter' call by the eastern kingbird (*Tyrannus tyrannus*) and concluded from observational data that it provides information relative to the caller's indecision about flying versus staying put, flying towards versus flying away, or flying versus landing. Hence, he labeled the call the 'locomotory hesitance vocalization.'

As another example, let us say we are walking through a wheat stubble field, and 50 m ahead of us a mourning dove flies up out of the stubble and lands in a tree 50 m to our right. We can describe the behavior of the dove in flight using, at least, five different levels of description (Table 4.7).

Describing (i.e. naming) the behavior as 'behavior X' provides us with no information unless we have access to a definition of the ethogram code being used. Rapid alternate contraction and relaxation of the pectoralis muscle tells us something about the mechanics of the behavior but does not provide the ethologist with much useful information. Wing flapping creates an image in the mind of the ethologist but we do not know if the dove was standing and flapping its wings (perhaps an intention movement) or actually flying. By describing the behavior as flying we get a clearer picture of the behavior and still are not assuming anything about underlying motivation. By describing it as escape flight we are assuming that the dove was

responding to a stimulus from which it was motivated to escape. We probably do not really know if that was the true function of the flight or if, for example, it had finished feeding and was merely flying to the tree where it could rest with relatively greater safety.

This example illustrates that the same behavior may be used in several contexts. Mounting may occur in sexual or dominant–subordinate contexts in dogs, just as urination may be marking or merely elimination (Bekoff, 1979b). Functional descriptions should be avoided, except when the function is intuitively obvious (see below) or supported by data, since they can be confusing and misleading (Marler, 1975) and lead to changes in terminology as the study progresses (Tinbergen, 1959).

The type of behavior, as well as the type of data being collected, often force the use of both empirical and functional descriptions. Hinde (1970) suggests that since threat and courtship behavior in birds involves both relatively stereotyped motor patterns and an orientation with respect to the environment, both description by operation (empirical) and consequence (functional) are necessary.

Eisenberg (1967) provided a list of behaviors for rodents (Table 4.8) that included both empirical and functional terms for convenience of presentation. It is useful to examine the list and identify those terms that are borderline, as well as those that are clearly empirical or functional.

As Table 4.8 illustrates, the distinction between empirical and functional descriptions is not always clear-cut, so that the problem is generally resolved in terms of the observer's intent. For example, does 'sniffing' imply searching for olfactory stimuli or merely wiggling the nose and vibrissae. This type of confusion over the observer's intent is clarified through the definition of behavior units (discussed in section 6.3.3).

Some descriptive terms are clearly functional, but they are readily accepted since the motivation and goal of the behavior appears obvious. For example, the terms 'nest building' and 'egg retrieval' are accepted in ethological parlance, but they still must be clearly described and/or defined for each species.

Your descriptions should inform others of your observations in an objective way without bias to your own experiences or personal beliefs. *Anthropomorphism*, the attribution of human characteristics to nonhuman animals, is often considered one of the gravest sins that an ethologist can commit (Carthy, 1966); recently, the use of anthropomorphism by ethologists has become a more controversial topic. Anthropomorphism is a form of 'functional description' (described below), but how can we categorize its various forms of usage? Is it a fatal flaw when used in research? Can it, in fact, be useful to ethologists? Anthropomorphism, as I've defined it above, is only one of three forms described by Topoff (1987) and is in the category 'interpretive anthropomorphism' according to Fisher's (1990) scheme (Fisher should be consulted for a philosopher's perspective on anthropomorphism).

Table 4.8. *List of rodent general maintenance behaviors utilizing both empirical and functional terms*

- *Sleeping and resting*
  - Curled
  - Stretched
    - On ventrum
    - On back
  - Sitting
- *Locomotion*
  - On plane surface
    - Diagonal
    - Quadrupedal saltation
    - Bipedal walk
    - Bipedal saltation
    - Jumping
  - Climbing
    - Diagonal coordination
    - Fore and hind limb alteration
  - Swimming
- *Care of the body surface and comfort movements*
  - Washing
    - Mouthing the fur
      - Licking
      - Nibble
    - Wiping with the forepaws
    - Nibbling the toenails
  - Scratching
  - Sneezing
  - Cough
  - Sandbathing
    - Ventrum rub
    - Side rub
    - Rolling over the back
    - Writhing
  - Stretch
  - Yawn
  - Shake
- *Care of the body surface and comfort movements*
  - Defecation
  - Urination
  - Marking
    - Perineal drag
    - Ventral rub
    - Side rub
- *Ingestion*
- Manipulatin with forepaws
- Drinking (lapping)
- Gnawing (with incisors)
- Chewing (with molars)
- Swallowing
- Holding with the forepaws
- *Gathering foodstuffs and caching*
  - Sifting
  - Dragging, carrying
  - Picking up
    - Forepaws
    - Mouth
  - Hauling in
  - Chopping with incisors
  - Digging
  - Placing
  - Pushing with forepaws
  - Pushing with nose
  - Covering
    - Push
    - Pat
- *Digging*
  - Forepaw movements
  - Kick back
  - Turn and push (forepaws and breas
  - Turn and push (nose)
  - Molding

Table 4.8. (*cont.*)

Nest building	*Isolated animal exploring*
Gathering	Elongate, investigatory
Stripping	Upright
Biting	Testing the air
Jerking	Rigid upright
Holding	Freeze (on all fours)
Pushing and patting	Escape leap
Combing	Sniffing the substrate
Molding	Whiskering
Depositing	

Source: From Eisenberg (1967).

Regardless of how strongly one might attempt to avoid anthropomorphism, it is very difficult, if not impossible, to do so (Crocker, 1981). It can be argued that we cannot have knowledge of anything which we have not ourselves experienced either directly or indirectly; therefore, researchers sometimes unconsciously slip into its use (Kennedy, 1992). As Rioch (1967) has remarked, we are both limited and directed by our vocabulary (symbolic behavior) in describing observed behavior.

> I will readily admit that observation has one great drawback; it is hard to convey to others. Experimental conditions can be reproduced, pure observation unfortunately cannot. Therefore it does not have the same objective character. The observer who studies and records behavior patterns of higher animals is up against a great difficulty. He is himself a subject, so like the object he is observing that he cannot be truly objective. The most 'objective' observer cannot escape drawing analogies with his own psychological processes. Language itself forces us to use terms borrowed from our own experience. *[Lorenz, 1935:92]*

Lorenz (1974) has also suggested that in some instances the use of terms like 'falling in love,' 'friendship' or 'jealousy' is not anthropomorphic, but rather refers to functionally determined concepts. In this regard, anthropomorphism might be useful as a metaphor for describing what an animal does (Kennedy, 1992; Ristau, 1986) and what its 'emotional' and motivational states appear to be (e.g. fear), without implying that some level of conscious thought is involved. For example, the phrase 'the ship *plows* the sea' provides us with a visual image analogous to a farmer's plow pushing aside the soil. Wiley (1983:167) notes that 'In thinking about opportunities

for manipulation in animal communication, analogies drawn from human interactions tend to dominate'; commonly used terms include 'deceit', 'selfishness', and 'spite'. Wiley (1983:167) concludes that the use of 'these familiar words make visualization of technical discussions easier', but we should provide technical definitions of the terms in order to 'guard against misleading inferences'

Where and how does the beginner draw the line? The safest approach is to avoid using terms that could be misinterpreted and use only empirical descriptions. You should especially consider avoiding terms which may be inflammatory and offensive, as well as misleading. For example, Estep and Bruce (1981) argue against the use of the term 'rape' by ethologists. An integral part of their argument goes beyond Wiley's (1983) call for technical definitions to the issue of redefining terms, stated as follows:

> Beach (1978, 1979) has warned both of the danger of taking words from common usage and applying specialized meaning to them without definition, and of resorting to Humpty-Dumptyism (taking a word from common usage and redefining it to mean only what you want it to mean). Both of these problems exist in the current application of the term rape to non-human behavior. *(Estep and Bruce, 1981:1272)*

What should we call behavior in nonhuman species that we know as rape in humans? Estep and Bruce (1981) suggest the term 'resisted mating' as a purely descriptive term, or we could use the term 'forced copulation' (e.g. Sorenson, 1994).

In summary, anthropomorphism can be perceived as a gradient:

1 No anthropomorphism.
2 Human terms technically defined.
3 Human terms used as a metaphor.
4 Human terms freely used with all the underlying implications.

You should give considerable thought to choosing at what point along the gradient you will report your observations.

Descriptions are often quantified to delineate more accurately and completely delineate what the animal does when it performs the behavior. Some examples of these quantitative descriptions are illustrated in Chapter 10.

4.2.2 Catalog, repertoire and ethogram

4.2.2a Catalog and repertoire

We begin every ethological study by compiling a catalog of behaviors for the species. The *catalog* is a list of all the behaviors that we have observed, listened to, or have knowledge of. Catalogs can be restricted to only the specific type of behaviors (e.g.

courtship), sex or age group we are interested in studying. The catalog is only a portion of an animal's *repertoire* – all the behaviors that the animal is capable of performing. We call the catalog an *ethogram* when we believe that it closely approximates the complete repertoire. The size of the repertoire will, of course, vary from species to species as well as between individuals, depending on sex, age and experience.

One decision that you must make during reconnaissance observations is when to stop. When do you have sufficient information to ask incisive questions, formulate precise hypotheses, and design a sound research project? At what point do you have a reasonably complete ethogram for the animal(s)?

If we were to observe an individual animal continuously for an extended period of time and record the behaviors that it showed, we could then plot the cumulative number of observed behaviors by the time (Figure 4.4a).

An asymptote is reached after many hours of observation (arrow, Figure 4.4a), beyond which few additional behaviors are seen for each unit of time spent observing. This asymptote may take tens, hundreds or thousands of hours to reach, depending on the species studied. Nolan (1978), for example, spent 5524 hours observing the behavior of prairie warblers (*Dendroica discolor*), yet he saw only nine copulations. If only one type of behavior (e.g. agonistic) is under study, then the time to the asymptote will generally be shortened. Fagen and Goldman (1977:268) concluded that 'familiarity with an animal's behavior will tend to require years of experience if the animal is a mammal or bird with a complex repertory. But if the animal's behavior is simple and relatively stereotyped such familiarity may be gained in a few months'. The objective of descriptive studies of a species (and to a certain degree of developing an ethogram) is to determine the true frequency of rare or unusual behaviors: short-term studies record too many unusual behaviors. The result is that we often overestimate the importance of some unusual behaviors since we lack the perspective provided by long-term studies (Weatherhead, 1986).

Hailman and Sustare (1973) described an interesting laboratory exercise in 'the analytical power of biological observations'. The objective was to deduce the 'behavioral organization' of a talking, stuffed toy elephant – Horton. The first step consisted of listening to Horton's total vocal repertoire by pulling the string and listing the vocalizations emitted. These data were transferred to a cumulative graph (Figure 4.5) and examined for an asymptote to determine if the entire repertoire had been recorded after 100 successive vocalizations.

Another way to look at the behavioral repertoire of an animal is through the time devoted to particular behaviors (i.e. time budget) or by frequency of occurrence (Hutt and Hutt, 1970). Since the frequency of occurrence varies for the behaviors in an animal's repertoire, a plot of cumulative percentages of total time spent in the various behaviors against their rank order by frequency of occurrence will show

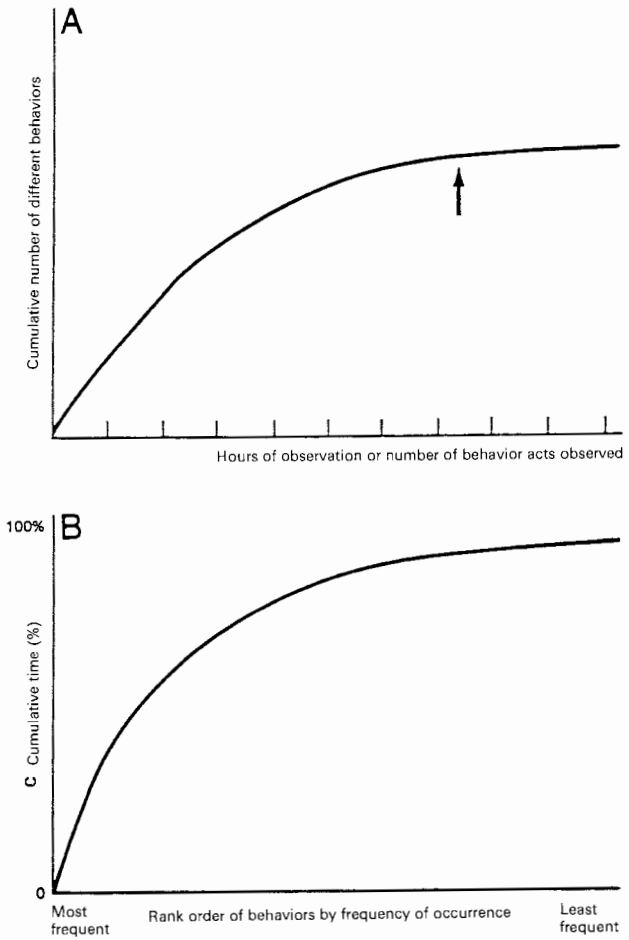


Fig. 4.4 A hypothetical example of cumulative number of different behaviors plotted against hours of observation. The arrow denotes the approximate asymptote. b. Conceptual representation of an animal's repertoire plotted as a cumulative percentage of the time spent in the various behaviors (adapted from Hutt and Hutt, 1970).

a curve which reaches an asymptote at the less frequently occurring behaviors (Figure 4.4b).

Fagen and Goldman (1977) researched methods of analyzing behavioral catalogs and concluded that most distributions (types of behavioral act/number of acts observed) could be described by a logarithmic regression slope of approximately 0.3 (e.g. Figure 4.6).

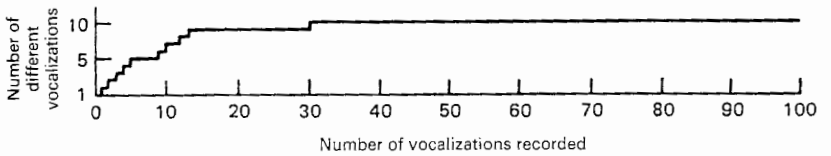


Fig. 4.5 The cumulative number of different vocalizations as a function of the total number of vocalizations recorded (from Hailman and Sustare, 1973).

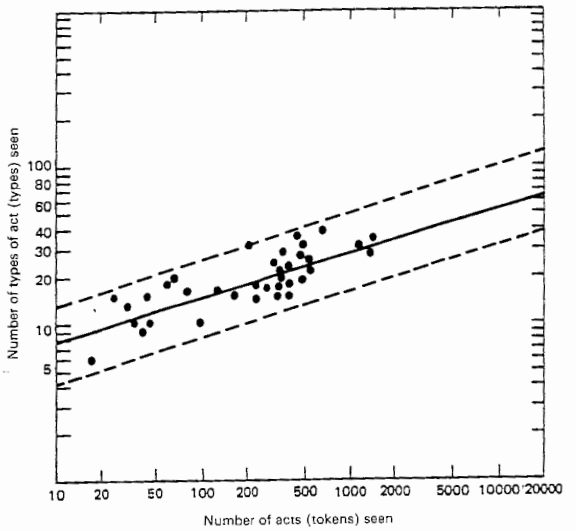


Fig. 4.6 Plot of cat behavior data with fitted regression line $Y=4.01X^{0.29}$ (solid line) and 95% confidence bounds for regression line (dashed lines) (from Fagen and Goldman, 1977).

Since the regression line has no finite asymptote, it does not allow the observer to predict repertoire size. However, this procedure did encourage Fagen and Goldman (1977:263) to recommend the following rule: 'A ten fold increase in the total number of acts will, on the average, double the number of behaviour types in the catalog'.

We can estimate our *sample coverage* ($\hat{\theta}$) by calculating the probability that the next behavioral act will be a new type (Fagen and Goldman, 1977). If $\hat{\theta}$ approaches 1, the probability of observing a new behavioral act is low.

$$\hat{\theta}=1-\frac{N_1}{I}$$

N_1 is the number of behavior types seen only once, and I equals the total number of acts seen. When N_1 is small relative to I then $\hat{\theta}$ will approach 1; the closer that $\hat{\theta}$

approaches 1, the more complete the sample coverage. For example, S. Altmann (1965) observed 5507 acts in rhesus monkeys and saw 32 behavioral types only once.

$$\hat{\theta}=1-\frac{32}{5507}=0.9942$$

This indicates that Altmann's sample coverage was essentially complete. Fagen and Goldman (1977) caution that this method emphasizes the significance of rare behavioral acts. They provide a more complex procedure for estimating the repertory fraction which properly weighs the frequency of occurrence of different behavioral types.

Of primary importance to any ethological study and particularly to a consideration of catalogs and repertoires is a determination of a behavioral unit. The size of the catalog will vary according to the way in which behavioral units have been defined. The more inclusive (i.e. lumping several different behavioral acts, such as threat and submission, into a single behavioral unit – agonistic behavior), yet mutually exclusive (e.g., agonistic versus ingestive; see below), the smaller the catalog will be. The selection and definition of behavior units will vary according to the objectives and logistics of the individual study (Chapter 6).

4.2.2b ***Ethogram***

An ethogram is a set of comprehensive descriptions of the characteristic behavior patterns of a species (Brown, 1975). It is the result of refining your catalog of behaviors after many hours of observation (in some cases audio recording) and description, and it should be the starting point for any ethological research, especially species-oriented research. Schleidt *et al.* (1984) provide a brief history of the use of ethograms by ethologists.

When concept-oriented research is conducted, researchers may compile an ethogram of only those behaviors within, or closely related to, the category in which they are interested. For example, Fraser and Nelson (1984) compiled an ethogram of the courtship behaviors of male and female Madagascan hissing cockroaches (*Gromphadorhina portentosa*) (Table 4.9).

Limiting our knowledge, as well as our research, to only one type of behavior in a species does pose potential hazards. For example, Tinbergen (1953) argued that the more we restrict our view of the animal's total behavior patterns, the greater the probability of misinterpreting results.

> The need for a broad, observational approach cannot be stressed too much. The natural tendency of many people, particularly of young beginners, is to concentrate on an isolated problem and to try to penetrate into it. This laudable inclination must be kept in check or else it leads to an accumulation of partial, disconnected results, to a

Table 4.9. *Courtship behaviors performed by male and female Madagascan hissing cockroaches*

Behavioral unit	Description
Approach	One animal (either male or female) moves forward and makes contact with the other animal
Antennate	Two behaviors can be distinguished: mutual antennation by both male and female where contact is antennae–antennae; and solo male or female antennation of the other animal's dorsal surface. The latter form of antennation can take the form of 'tapping' or 'horizontal rubbing' movements. These movements are very different from the rapid vertical 'fencing' movements of aggressive behavior (Nelson and Fraser 1980)
Hiss	This audible sound results from the forceful expulsion of air through a specialized abdominal spiracle. Male courtship hissing can be separated by its acoustic characteristics and behavioral context into type-1 and type-2 hissing. Type-1 hisses are isolated, soft hisses, whereas type-2 hisses are shorter and occur in trains (for a more detailed description of the acoustics of sound production, see Nelson and Fraser, 1980)
Mount and palpate	One animal puts one or more legs on the other and taps the other animal's body surface, usually the dorsum, with the labial or the mandibular palps
Posture	Male stands high off the substrate with the abdomen curved upward and extended. This is sometimes accompanied by extrusion of the phallomeres and/or type-1 hissing. During posturing a distinct odour is noticeable to the (human) observer
Cross-over	Female crawls over the posterior tip of the male's abdomen, dragging her abdomen over his
Copulation attempt	Male attempts to copulate by rapidly thrusting the tip of the abdomen towards the female's abdomen. Usually the male starts thrusting towards the lateral ventral surface of the female abdomen, moving to an opposed position for copulation
Stand	Female stands with legs braced laterally, body close to the ground, the abdomen flexed downward at the tip. This normally accompanies copulation attempts by the male
Move away	One or both animals walk or run away from each other

Note:
From Fraser and Nelson (1984)
Source: Copyrighted by Bailliere Tindall.

> collection of sociological oddities. A broad, descriptive reconnaissance of the whole system of phenomena is necessary in order to see each individual problem in its perspective; it is the only safeguard for a balanced approach in which analytical and synthetical thinking can cooperate. This, of course, is true not only of sociology, it is true of each science, but in ethology and sociology it is perhaps forgotten more often than in other sciences. *[Tinbergen, 1953:130]*

Descriptions of the behaviors in the ethogram should be clear and concise, yet complete. A useful adjunct to a written description is a photograph or line drawing. Figure 4.7 shows how Enquist *et al.* (1985) used line drawings to supplement the written descriptions in their ethogram of behaviors performed by fulmars (*Fulmarus glacialis*) when competing for fish.

Schleidt *et al.* (1984) pointed out the large variation in description, format and completeness of published ethograms. They designed a 'standard ethogram' which they hoped would serve as a prototype for future ethograms of birds and, perhaps, other taxa. The ethogram, which consists of the 60 most commonly observed visual behavior patterns, was tested and refined in a study of the bluebreasted quail (*Coturnix chinensis*).

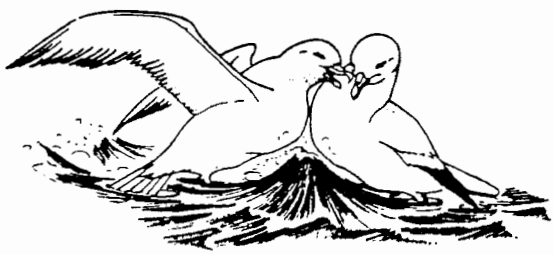
The discussion above dealt with ethograms for descriptive studies or experimental studies of normal behaviors in a natural environment. An ethogram of behaviors to be measured is also compiled when conducting a manipulation experiment (e.g. Godwin, 1994); in this case, the behaviors are operationally defined, instead of being described (Chapter 6), and they are normally mutually exclusive.

4.2.2c ***Mutually exclusive behaviors***

Mutually exclusive behaviors are those that cannot occur simultaneously, either because the animal cannot perform them simultaneously or we have defined them so as to eliminate two behaviors being recorded simultaneously. The behaviors described in your ethogram *must* be mutually exclusive if you are determining time budgets (i.e. the amount and percentage of time devoted to each behavior). Time budget studies also require that your ethogram be *exhaustive* (i.e. the animal must always be engaged in one of the behaviors in your catalog). Also, the behaviors measured in an experimental study are almost always defined so that they are mutually exclusive, so that the animal is recorded as responding with only one of several possible behaviors (see Chapter 6).

The behaviors in your ethogram *should* be mutually exclusive if you are unable to record accurately more than one behavior at once, either because of your lack of experience or because you are using a data logger (or software) that will not allow for the recording of simultaneous behaviors (Chapter 9).

Bill-pointing. The bird points with the bill against the opponent. This behaviour varies in intensity from a turn of the head to an unsuccessful attempt to peck the opponent. The mouth is often open and a sharp sound is utterred. The owner also directs this behavior to flying birds. Bill-pointing is always combined with Wing-raising.



Breast-to-breast. The two birds meet, orientating the body somewhat upright with their breasts touching. Breast-to-breast is nearly always preceded with rushing behavior performed by one, or both, birds.

Fig. 4.7 Line drawings and descriptions of two behavior patterns performed by fulmars when competing for food (from Enquist *et al.*, 1985). Copyright by Bailliere Tindall.

Using only mutually exclusive behaviors may provide a high enough level of resolution to answer some research questions, but it is unrealistic to believe that it will accurately reflect the animal's true behavior. Probably all animals are capable of, and do perform, simultaneous behaviors.

4.3 INFORMATION RESOURCES

The usually accepted dogma states that before embarking on your research you should learn as much as you can about your subject animal, especially about its behavior; however, this might not always be true (see section 4.3.1). You should collect information, in addition to your initial reconnaissance observations, from all the sources at your disposal, including available literature, data from other