THE FEEDING BEHAVIOUR OF THE OYSTERCATCHER

(*Haematopus ostralegus*)

by

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PREFACE

Oystercatchers on the shore, opening mussels by the score.
Oh, how happy they would be were there no Ethology!

This thesis is about the skilled feeding techniques of the Oystercatcher. I have not set out to analyse any particular 'problem' in the Oystercatcher's behaviour but I have attempted instead to present a general picture of the organisation of a highly complex behavioural system. My analysis is by no means complete, and much of my data is spread very thin.

I describe first the parental feeding system (Part I), and the way in which the behaviour of the young controls the amount of food brought by the parent. During parental feeding the young acquire the skilled feeding techniques from their parents. In Parts II and III, I describe how the skilled techniques of the adults are adapted to deal with a wide variety of hard shelled molluscs and crustaceans, and in Part IV I describe the way in which the young acquire the particular technique of their parents. I am here especially interested in the flexibility of the developmental system. The young have the potential to develop a number of different skills, and yet, through interactions with the parents, only one skill is developed.

Many people have given me help and advice while preparing this thesis, and I have not the space to thank them all individually. However, I should particularly like to thank:

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ABSTRACT

In this study of the functional aspects of a complex behavioural system I have looked at three different aspects of the feeding behaviour of the Oystercatcher. I started by analysing the skilled feeding techniques of the adults, but I soon became interested in the development of these techniques in the young, and in the parental feeding system which is surprisingly different from that of other waders. It forms the 'buffer' between the adults and the young and allows the young to acquire the specialised feeding techniques and skills of their parents.

Part I

I discuss the parental feeding system first because the analysis has focused on a slightly different aspect of the feeding behaviour, namely the way in which the amount of food brought to the young by the parents is precisely controlled by the behaviour of the young. The parental feeding system has two basic characteristics: (a) the parents bring food items to the young and present them, and the young take the food from the parent's bill; and (b) the young accompany their parents out onto the feeding grounds and are fed by them in long 'feeding trains'.

The seasonal development of parental feeding starts with the auditory and tactile interactions between the incubating parent and the hatching eggs. Both parents and young-in-egg become more responsive to each other as hatching proceeds, and both show a marked selective responsiveness. These pre-hatch interactions lead to the transition from incubation to brooding behaviour in the parent, and finally result in the onset of parental feeding. There is the additional possibility that the young learn to respond to the call of their parents while still in the egg.

I then discuss the factors which control the amount of food brought by the parents to the young. In the active phases of the daily feeding cycle, each parent brings food items to the young at random moments in time. Once the food has been presented, the subsequent behaviour of the parent depends upon the speed with which the young seizes and devours the food. If the young takes the food within a certain time (the Waiting-Time-Threshold) the parent will immediately search for and present more food, and it will continue to do this for as long as the young takes the food within the threshold time. In this way the long 'feeding trains' are initiated and maintained. However, the young can also initiate a feeding train by approaching a parent who is feeding. The feeding train is broken off by the parent as soon as the young fails to react within the threshold time. This self-regulating social system is based on complex and highly specialised interactions between the parents and the young.

As the young grow older the organisation of parental feeding changes drastically. The parents initiate fewer feeding trains, they carry less food to the young and, instead of removing the flesh from prey and then presenting it to the young, they begin to leave the prey for the young to open up and clean out. The young however play a more and more important role in the initiation and maintenance of the feeding trains. This switch of control to the young eventually leads to the breakdown of parental feeding, for, as the young learn to feed themselves, they stop eliciting parental feeding. The consequence of this system is that in areas where the young merely have to acquire the simple skills of probing for worms, parental feeding stops at about 6-7 weeks. However, in areas where the young are learning the more difficult skills for dealing with molluscs and crustacea, parental feeding continues for 12-20 weeks,

and in extreme cases for as long as 43 weeks.

Part II and III

I here describe the techniques employed by adult Oystercatchers in dealing with Mytilus, Cardium, Scrobicularia, Tapes, Littorina, Patella and Carcinus. Each of these techniques consists of a sequence of discrete motor patterns of which each has a different form and a different function. To take the feeding techniques on Mytilus as an example: either the Stab (a quick downwards lunge of the bill through the gaping valves) or Hammering (a series of hard blows aimed at the shell) serve to gain initial entry into the valve; Levering (side-to-side movements of the bill) and Prising (forcibly opening the mandibles) serve to force the valves wide apart; and Chiseling (rapid to-and-fro movements of the bill) serves to cut the flesh loose from the valves. Each motor pattern is precisely oriented for maximum effect: the Stab is aimed between the posterior valve margins so that it severs the strong posterior adductor muscle when the bill enters (thus disabling the mussel); the Hammering attack (for which the mussel is first oriented so that the flat ventral surface is uppermost) is aimed at this area which I have shown to be by far the weakest part of the shell; and the Chiseling movements are aimed at the largest attachments between the flesh and the shell, the smaller ones being broken when the main mass of the flesh is shaken free.

I found that these motor patterns are applied to all the prey species mentioned, and that they have always the same general function. However, in each case the oritentation of the motor patterns are specifically adjusted to the anatomy of the particular prey. For example, the Hammering attack is direct at the ventral valve margins of Mytilus; at the posterior, ventral or anterior valve margins

of Cardium (all these valve margins are equally friable); at the lateral walls of Patella (which are most easily dislodged by a blow from this direction); and at the mouth of Carcinus (which kills the crab as well as making a hole in it).

I then analyse the organisation and control of the sequence and duration of the motor pattern. Firstly, each motor pattern is elicited by a different external stimulus. Second, the duration of the motor patterns is likewise under continuous external control; for example, the duration of Levering in Cardium depends solely upon the size of the prey, i.e. in functional terms, to the amount of Levering that is needed to force the valves apart. Thirdly, the sequence in which themotor patterns occur are seen to be simple chain responses in which the performance of one motor pattern brings about the external stimuli necessary to elicit the next. It is this total dependence on external control which imparts a remarkable flexibility, and thus efficiency and economy of effort to the techniques, for each motor pattern is performed only if and when necessary, and only for as long as is necessary.

The skill, efficiency and versatility of the adult techniques are due to two basic factors: firstly, a basic repertoire of motor patterns each adapted to a very generalised function; and secondly, their dependence on external stimuli, which allows (a) the precise adjustment of the orientation of each motor pattern to the anatomy of any one prey, and (b) flexibility in the initiation, duration and sequential organisation of the motor patterns.

Very surprisingly, there is good evidence that individual Oystercatchers specialise not only on one particular prey but even on one particular technique of catching it. For example, the breeding population at

Ravenglass (in Cumberland) is made up of individuals who eat crabs. Furthermore, in each breeding pair both partners have the same specialisation. There are a number of both causal and functional reasons for this specialisation, most of which are bound up with the development of the techniques in the young Oystercatchers.

Part IV

The starting point for my study of the development of the feeding skills were the observations that the young of mussel-Stabbing parents, mussel-Hammering parents and crab-eating parents all develop the same feeding skills and techniques as their parents. I therefore cross-fostered the eggs of individually known pairs with different specialisations. In every case the young developed the specialisations of their foster parents. This meant that the young had the potential to develop a number of different techniques but that some environmental factor was channelling the developmental system, so that only one technique developed. This led to a stdy of (a) the basis of the flexibility of the developmental system, and (b) the ways in which the channelling was brought about so that only one technique was developed, and I have tried to analyse these from both a functional and a causal viewpoint.

I first discuss the Independent Feeding Activities (IFA) of young Oystercatchers. These are shown from a few hours after hatching, and they are easily recognised as incipient forms of the adult feeding behaviour. A full repertoire of discrete motor patterns, all similar to themmotor patterns of the adults, is present in all Oystercatcher young, irrespective of the specialisations of their parents and irrespective (within the range observed) of the environment in which they are growing up. The IFA are directed initially at a wide range of objects (both edible and inedible alike),

and the stimuli that elicit them are very similar to those that elicit the same motor patterns in the adults.

During IVA the young gain experience with the prey species (in this study with mussels or crabs - depending on the specialisations of the parents). The opportunities to experience are the following: (a) the young remove scraps of flesh from the shells discarded by the parents, (b) the young open up and empty out partially prepared prey which the parents leave for them, (c) when the young accompany their parents onto the feeding grounds they constantly see prey being caught and opened in their immediate presence, and (d) there are numerous undisturbed prey on the feeding grounds which the young attempt to catch and open up for themselves.

The actual learning processes that take place are shown at/ to be of least three different types:

1. the first interactions with the prey are seen when the small young (2-3 weeks of age) Chisel scraps of flesh from the discarded prey remains; subsequently, the young spend more and more time in investigating the prey remains. Experiments with hand-raised young (which were given experience of mussel shells containing flesh) showed that neither finding food in mussels by itself, nor Chiseling in mussels without a food reward, nor even performing any other motor pattern than Chiseling - with our without a food reward - leads to conditioning to the mussel. The conditioning only occurs when the young have to Chisel and receive food as a result of Chiseling. This pre-requisite for conditioning has two important functional aspects: firstly, it ensures that the young will become conditioned only to potential prey rather than to any other object lying about, and secondly, the young will become conditioned to whatever prey the parent is feeding to it.

We see here the first example of both the flexibility and the channelling of the developmental system.

2. This experience with the discarded shells also leads to the initial development of Chiseling, and practice with the partly opened prey left by the parents leads to the further development of efficient Chiseling, as well as to the functional organisation of Levering, Prising and Chiseling, i.e. to the correct orientation and sequence of these motor patterns. Much of this change in behavioural organisation can be accounted for by trial-and-error learning, but I also suggest that other factors may lend directionality to such learning processes by biasing what is learned.

3. The development of the hunting techniques (i.e. locating and Stabbing or Hammering mussels, and locating and opening crabs) seem to develop as a direct result of parental example. At 4-5 weeks of age (before the young have started to successfully catch and open prey for themselves) there are already marked differences in the hunting behaviour of the young of mussel-Stabbing parents, mussel-Hammering parents and crab-eating parents. Both the 'Stabbing' and 'Hammering' young show elements of both techniques, but the most frequent behaviours shown in each case are those of their parents' techniques. The 'crab' young at this age completely ignore the mussels and only hunt for and attempt to open crabs. Once the young start to successfully catch and open prey (at 6-7 weeks of age) they employ only the relevant hunting behaviour.

I then discuss the developmental system from the viewpoint of a learning machine with pre-set programmed instructions. The Oystercatcher's 'programming' shows specific adaptations to (a) develop a skilled feeding technique yet (b) retain flexibility so that a number of different feeding skills may potentially be developed. The instructions are therefore of a very general nature when

compared with the instructions of developmental systems where the environment is more 'predictable'.

I also discuss the coadaptation between the parental feeding system and the requirements of the developmental system. Firstly, the parent is instrumental in channelling the developmental system of the young; secondly, there are changes in the organisation of parental feeding as the young grow older which result in the parent leaving the partially opened prey which the young require for practice; and thirdly, I discuss the evolution of parental feeding as a necessary coadaptation to the evolution of a highly specialised feeding behaviour which the young have to acquire at an early age.

Finally, I consider some broader ecological aspects of the development of the feeding skills. The first important point is that the young take at least three years to become fully efficient at eating mussels, and I argue that other feeding techniques will probably take as long to become fully efficient. There are a number of ecological consequences to this protracted development. Firstly, Oystercatchers do not breed until they are three, and usually four years of age, and I suggest that this is an evolutionary adaptation to the prolonged development. Secondly, during the prolonged development it would be disadvantageous to attempt to acquire a new technique, for the feeding behaviour would become even more inefficient. By the time that the one technique has become fully efficient, the bird may have to be so fixated on one particular prey and one particular technique that it will not respond to the relevant stimuli from other prey. This may be the basis of the persistent specialisations shown by adult Oystercatchers. However, some individuals (about 20%) do possess more than one skilled technique, and perhaps they can switch through essentially the same processes that young Oystercatchers employ when

learning from their parents. It may, therefore, be of advantage even for adults to retain a certain degree of flexibility.

PART 1

PART I

THE ORGANISATION, CONTROL AND DEVELOPMENT OF PARENTAL FEEDING IN THE OYSTERCATCHER (Haematopus ostralegus)

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INTRODUCTION

The young of the Oystercatcher (Haematopus ostralegus) is nidifugous like the young of other waders, but is unique in that it is not self-supporting until it is fledged - or even later (Dewar 1915, 1920, Dirksen 1932, Buxton 1939, Tinbergen and Norton-Griffiths 1964, von Frisch 1959a, Lind 1965). Instead, it depends on its parents to supply it with food until such time as it is fully self-sufficient. The Oystercatcher therefore has a well-developed parental feeding system which is rare among waders, although the Snipe (Gallinago gallinago) is thought to have parental feeding (von Frisch 1959b). The Stone Curlew (Burhinus oedicnemus) and the Pratincole (Glareola pratincola), more distant relatives of the Oystercatcher, are also thought to have parental feeding (von Frisch, 1959, 1961).

There are two basic characteristics of the Oystercatcher's parental feeding:-

1. The parents bring food items to the young and present them to the young, and the young then take the food from the parent's bill tip or from the ground immediately beneath the bill tip.
2. The young accompany their parents out onto the feeding grounds where they closely follow their parents and are continuously fed by them in long 'feeding trains'.

The greater part of this paper is concerned with the analysis of the factors which control the behaviour of the parents. The data were collected during 1965 and 1966 by observing Oystercatcher families at the Esk River estuary at Ravenglass, Cumberland. Two categories of families were observed:- Free Living, in which the parents were bringing up their young on the mud flats and mussel beds of the estuary, and Fenced In, in which the parents were bringing up their young behind high fences which enclosed the immediate vicinity of the nest (see Appendix 2).

The paper is divided into four chapters. Chapter 1 provides much of the detailed description required for the subsequent analysis. In Chapter 2 the seasonal development of the parental feeding system is traced from the first interactions between the pipping eggs and the incubating parents, and in Chapter 3 the social interactions between the parents and young which form the basic control of parental control are analysed. The evolution of parental feeding in the Oystercatcher is discussed in Chapter 4.

CHAPTER 1 GENERAL DESCRIPTION OF THE PARENTAL FEEDING

1/A The Transport and Presentation of Food

1/A/I Food Transport

Food transport consists of the parent bringing food items into the immediate vicinity of the young. If the young are nearer than about 50 m the parent will run to them, otherwise he will fly. If, as often happens, the young run towards the parent while the parent is transporting food then the parent will stop and wait for the young to come up to it. Similarly, if the young runs towards the parent before the parent starts to carry the food then the parent will wait where it is for the young to come up.

1/A/II Calls Given by the Parent

There are two different calls given by the parent, the 'weep' and the 'chuck'.

The Weep Call: a strong, short call, rising in pitch towards the end of the -eep.

The Chuck Call: a quiet monosyllabic call, often sounding very liquid.

The parent usually calls when it transports food to the young but rarely calls when it is waiting for the young to come to it (Table 1/a).

TABLE 1 Calls Given by the Parents

(a) when flying, running or waiting:

	Call Given	No Call Given
Fly or Run to young	96% (278)	4% (10)
Wait for young	2% (19)	98% (1076)

TABLE 1 Calls Given by the Parents

(b) type of call given:

	Weep Call	Chuck Call
Flies to young	87%	13%
Runs to young	1%	99%
Waits for young	0%	100%

The Weep is given when the parent is flying to the young, just prior to landing, while the Chuck call is given when the parent runs to the young and when it has arrived to within some 10 m of the young (Table 1/b, see also Buxton 1939). In the few cases when the waiting parent called as the young ran up the Chuck call was given, just as the young came right up to the parent. In the cases where the Chuck call was given when the parent flew to the young, it was not given in the air, but only once the parent had landed and was approaching the young on foot. While the parents are away finding food, the young usually secrete themselves in some cover, and the parents on their return call as they approach the place where the young usually hide, even if for some reason the young are not there. Thus the calls are elicited both by the direct stimuli of the young and by the approach to the locality where the young are usually present (see discussion in 1/C/I).

1/A/III The Presentation of Food

The parents have a number of 'presentation motor

patterns' associated with the presentation of food to the young.

Hold: This is the most frequent motor pattern seen. The food is held in the bill tip about two or three centimetres above the ground, the bill being motionless in either a vertical position or at a slight angle from the vertical. The parent does not move when it is in the Hold position. The Hold is exactly equivalent to what Lind (1965) calls the 'feeding posture', but I prefer my term because 'feeding posture' suggests that there is only one motor pattern - which is not the case.

Mandibulate: The food is moved around between the bill tips and may be moved up and down the bill, the bill being in the Hold position.

Lead: The food is held in the bill tip but the bill is moved around in front of the young, the orientation of the bill to the vertical being very variable. The parent often moves as well. Most usually, the bill is moved from just in front of the young's bill around in a semi-circle to the side of the young's head. Mandibulations can also occur.

Point: The food is dropped on the ground and the parent 'points' to it, the bill being in the Hold position immediately above the food.

Leave: The parent drops the food on the ground and goes off to find more, leaving it for the young to pick up.

All these presentation motor patterns can occur in one presentation, and they can occur any number of times in one presentation. The most frequent are the Hold and Mandibulate which occur in 92% and 90% respectively of all presentations (n=2025). Pointing and Leading occurred in 8% and 3% respectively, and Leaving in 21%. There is no fixed sequence in which these motor patterns occur except that Hold almost always comes first (98% of presentations) and Leaving, by definition, always comes last.

The young may take the food from either the Hold, Point or Leave, the most frequent being from the Hold (77%), followed by the Leave (21%) and the Point (2%). The above data were collected from different parents feeding their young on a wide variety of foods and there is no indication that any of these foods are presented in a different way from any of the others, nor is there any evidence that different parents present food in different ways.

1/B <u>The Reaction of the Young to the Parent</u>

The young may react to either the calls of the parent, or to the presentation of food, or to the preparation of food (i.e. when the parent digs up a worm or opens up a mollusc), and it is often very difficult to decide which was the first reaction of the young in any given feeding situation.

1/B/I Reaction of the Young to the Calls

In the 52 observations of the Beep being given, the young instantly responded in 41 cases, usually by running towards the flying-in parent. Young who were asleep or being brooded also responded in this way. If the young do

not react to the call, or even to the landing parent, then the parent will call again as it runs towards the young, in this case giving the Chuck call.

The young are similarly very responsive to the Chuck call (201 instant reactions in 215 observations). In those cases when the young did not react to the Chuck call, they reacted later to the presentation of food.

1/B/II Reaction of the Young to the Preparation of Food

In 55 cases the young reacted from some 20 m away from the parent by running up and waiting by the bill tip. This had the effect of making the parent wait and immediately present the food, no calls being given. In 253 cases the young were already alongside their parents and merely moved closer while the parent prepared the food. In these cases the parents also made no further move towards the young, and no call was given. Thus, the parents will take food to the young and give the Chuck call unless the young react first by running up to the parent, in which case the parent will wait with the food and will not call.

1/B/III Reaction of the Young to the Presentation of Food

The young react to the presentation of food if they have not already reacted to the parents' calls or preparation of the food. In these cases the parent always makes some movement towards the young, either by running up to them, or, if the young are alongside, by making a half turn towards them.

1/B/IV Repeated Presentations of Food

In the majority of cases the young take the food immediately it is presented. However, if the young do not react at once, or if they drop the food or are

otherwise unable to eat it, then the parent will continue to present the food. This is a very important characteristic of the parental feeding system in that the parents wait until the young has eaten the food before going off to find more.

The most common cause of these repeated presentations is 'clumsiness' on the part of the young, especially when they are small, when they either miss the food in the bill tip or keep dropping it once they have pecked it out of the bill.

Sometimes the young are unable to eat an item of food because it is too big to swallow. Broadly speaking, if the food item presented by the parent is too big, the young will avoid it after first making an initial peck at it. The parent will persist in presenting the food and will eventually break the food up into smaller pieces and present these to the young (see also Safriel 1967). Table 2 shows that there is an initial positive reaction by the young to the food item followed by avoidance until the food is broken up.

TABLE 2 Behaviour of the young towards food items which are too big

	Young Approaches Food	Young Avoids Food
First Presentation of food item	24	7
Subsequent presentations of same food items	32	141

The parents often bring mussels (*Mytilus edulis*) and crabs (*Carcinus maenas*) to the young, and these are

brought either complete with shell or carapace (unprepared) or just the flesh is brought (prepared). The parents' subsequent behaviour after arriving with this type of food is very different depending on whether the food is unprepared or prepared. All the unprepared food is immediately broken up into smaller pieces prior to presentation (Table 3) while the prepared food is immediately presented, even though in some cases it had to be further broken up before the young would eat it.

TABLE 3 Behaviour of the parent after transporting prepared (PR) or unprepared (UPR) food items to the young

	Present food immediately	Break up food immediately	Break up food after avoidance by young
PR food	167	2	48
UPR food	3	83	-

It is not the size of the food item brought by the parent which determines whether or not it will be broken up prior to presentation; for marine worms and fish, which are often larger in bulk than small mussels or crabs, are not broken up prior to presentation, while small unprepared mussels and crabs are broken up prior to presentation.

1/C Discussion of Chapter 1

1/C/I The Interpretation of the Calls

The parents Weep when they fly to the young with food and Chuck when they run to the young with food (1/A/II), so these calls might be considered feeding calls. However, these calls are first heard much earlier in the breeding season as long distance (Weep) and close distance (Chuck) social contact calls between the parents. During incubation, for example, the Weep is given as a parent

flies towards the nest and the Chuck is given as it approaches its mate. Nearness of the mate alone is enough to elicit the Chuck, and during nest relief both parents frequently give the Chuck. In addition, the calls are sometimes heard even when the mate is absent when, for example, the incubating bird approaches the nest on foot after a disturbance.

There are striking similarities between the situations eliciting the calls in the feeding situation and in the earlier mate-mate interactions in that the calling parent is flying either to the nest site or to the vicinity of the young, or is approaching on foot. The calls are given even if the parent approaches the young without food, this being very marked after a disturbance. Thus, although it is certain that the young look upon these calls as feeding calls, it seems very unlikely that the underlying motivation of the parent to give the calls is specifically linked to the feeding situation. These calls should therefore not be considered feeding calls, but rather as family-contact calls.

1/C/II The Presentation of Food

We have seen that, by moving towards the parent or by just being alongside the parent, the young can prevent the parent from moving and cause the parent to present food (1/B/II). When the young causes the parent to present food in this manner, it is operationally inhibiting the parent's own feeding behaviour, and inhibiting it at a very precise point in the feeding behaviour, namely just before the food is eaten. The parent does not present food which it has not yet prepared, nor does it stop preparing food in response to the young running up. It continues until the food is in a state in which it can be eaten, and then it presents the food.

The parent will continue to present food even if the young do not react, and the parent will not continue feeding or searching for more food until the food item has been eaten by the young. In some cases the young run off with the food and take it to some cover to eat, and this is enough for the parent to go off and continue searching. If the young do not react at all to the food (i.e. if they are not hungry) then the parent will eventually eat the food itself, but will not continue searching until it has eaten the food (see also Buxton 1939). The only occasions in which searching continues before either the young or the parent has eaten the food is when the parent leaves the food for the young, but in these cases there has already been a very positive reaction on the part of the young (running up) and, by turning away, the food is out of sight of the parent.

Thus, the approach or near presence of the young can inhibit the parents own feeding, and this causes the presentation of the food, the inhibition remaining until the food vanishes.

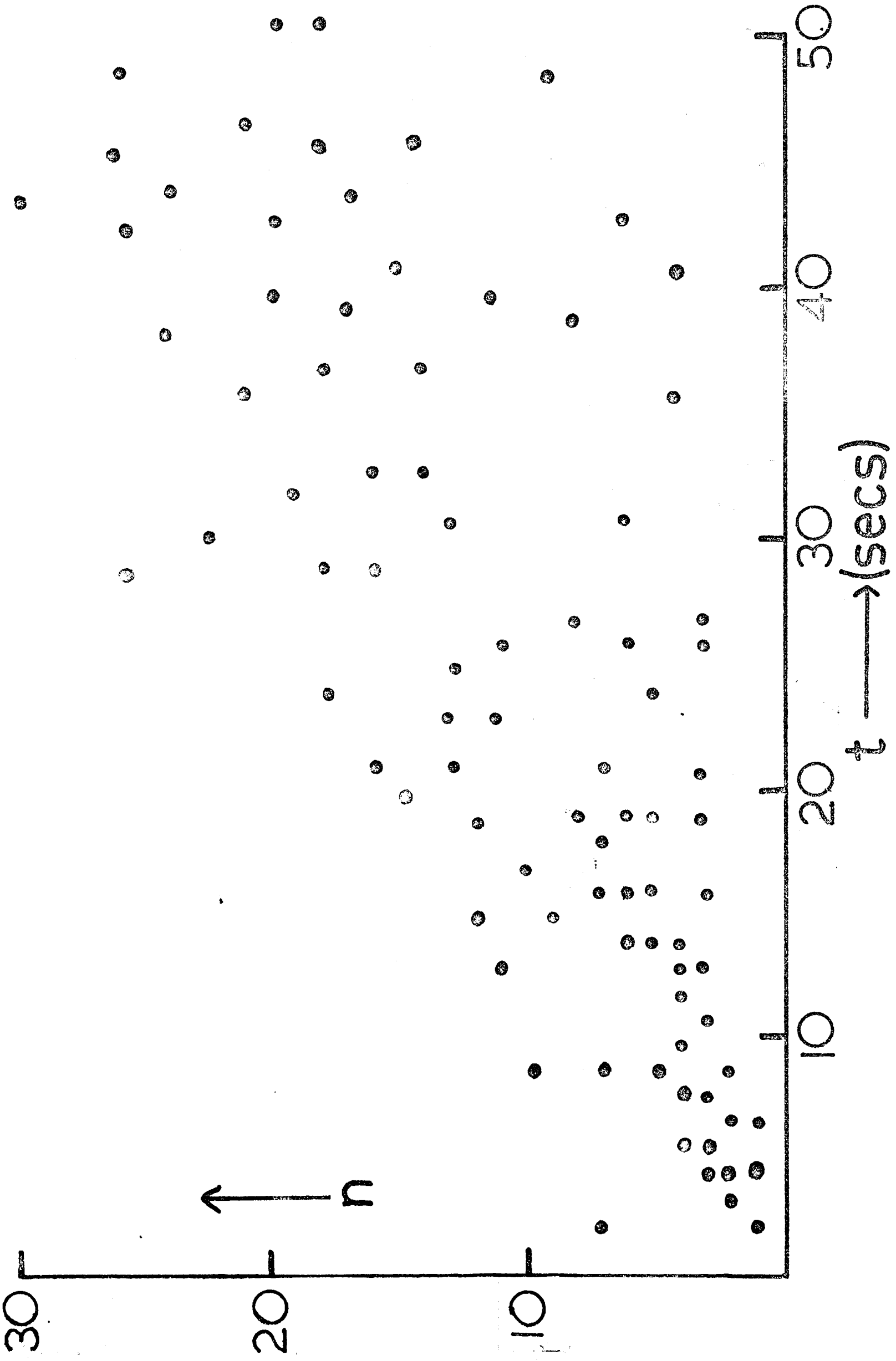
1/C/III The Interpretation of the Presentation Motor Patterns

The presentation motor patterns bear a striking resemblance to the motor patterns seen in the adult's feeding behaviour just prior to ingestion. This pre-ingestion behaviour is carried out with the bill in a vertical or near vertical orientation (for the obvious reason that the food is on the ground and the Oystercatcher has long legs), the food being first gathered into the bill tip with mandibulations and then ingested. The bill is usually motionless when this happens, though it may be moved when, for instance, the food is washed in water prior to ingestion. The similarities between this behaviour and the presentation behaviour is immediately obvious. Both the orientation and lack of movement of the

bill (as in the Hold and the Point) are similar, as is the occurence of mandibulations. The bill movements of the Lead are also similar to those seen when the food is carried prior to washing. I have suggested that the approach or near presence of the young inhibits the parent's feeding behaviour at the precise moment when this non-social pre-ingestion behaviour would be shown. The presentation motor patterns can therefore be interpreted as inhibited forms of this non-social pre-ingestion behaviour of the adults. If the number of presentations motor patterns seen in any one presentation are scored against the time taken over that presentation (i.e. the time elapsing between the first presentation motor pattern and the young taking the food) then it can be seen that there is a very strong positive correlation (Fig.1). This shows that the effect of the young on the parent is merely to 'short circuit' the pre-ingestion behaviour and not to completely inhibit it.

Both the form, frequency and function of the adult's pre-ingestion behaviour become modified in the presentation situation, so the presentation behaviour could be considered as ritualised behaviour in that the whole complex of presentation motor patterns contain stereotyped forms seen under non-social conditions. The most ritualised aspects of the presentation behaviour are that the bill is usually in a vertical or near vertical orientation and that it remains in this orientation for longer periods of time than is seen in the non-social behaviour, and these are the main reasons for Lind's (1965) classification of the presentation behaviour as ritualised. However, there is a very good functional reason why the bill should be in this orientation, and there is little evidence that the duration of the

Fig 1 Correlation between the number of presentation motor patterns (n) and the time (t) taken over the presentation .



presentation behaviour is controlled by anything other than the temporary effect of the young. The concept of ritualisation is that behaviour patterns become phylogenetically altered specifically to enhance their signalling function, and there is little evidence that t is has happened in this case.

This mechanism which controls the presentation behaviour of the parent is a very effective one for not only does it ensure that food items are presented in a state in which the young can eat them (i.e. after preparation) but also that the parent will wait and keep presenting the food until the young eats.

1/C/IV Changes in Parental Feeding as the Young Grow Older

As the young grow older they become more active and independent from their parents. They fledge at about four weeks of age, and begin to forage for food by themselves at three weeks of age. Correlated in time with this change, the parents transport less and less food to the young (Fig.2) and they Leave more food rather than wait for the young to come up (Table 4).

TABLE 4 Food Presentation by the Parent

% of food items presented by:-

Age of young in weeks	HOLD	POINT	LEAVE	(n)
1	94%	6%	0%	320
2	94	3	3	562
3	80	6	15	214
4	81	1	18	84
5	71	0	29	279
6	60	0	40	182
7	50	0	50	160
8	30	0	70	215

The young also show a change in behaviour in that they react more to the preparation of food (Fig.3), i.e. they react to the parent at an earlier stage in the feeding

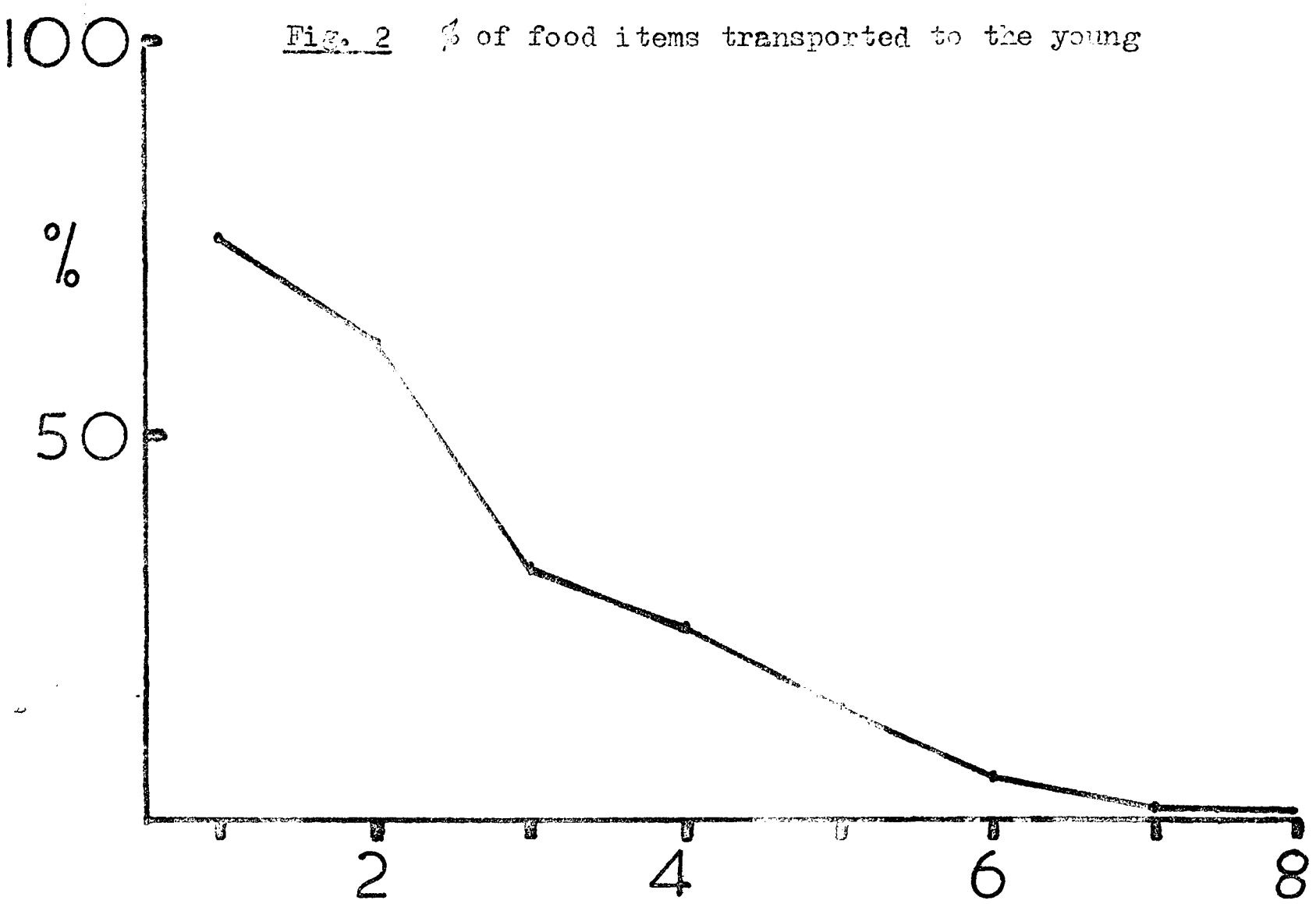


Fig. 2 % of food items transported to the young

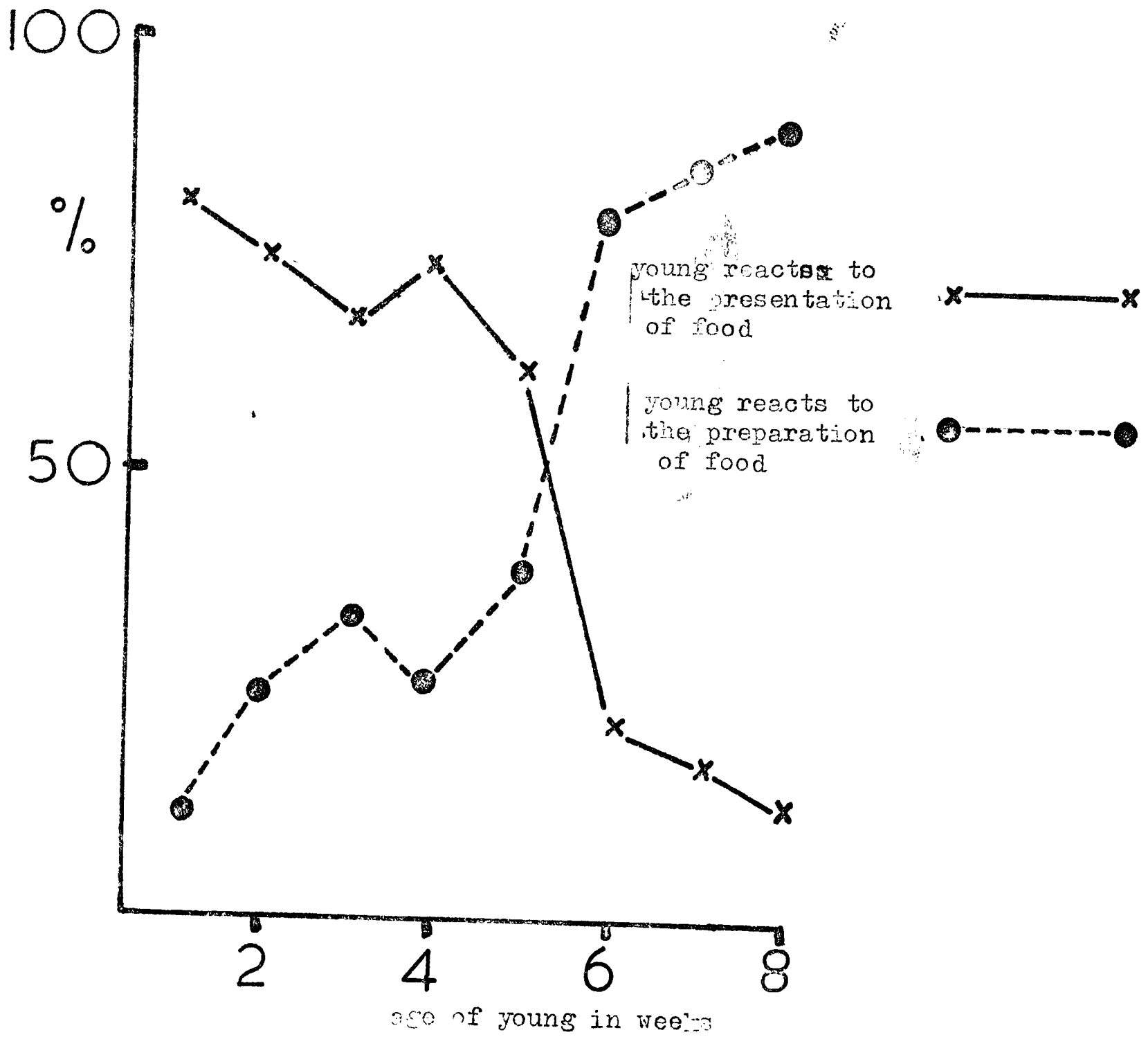


Fig. 3 Initial reaction of the young to the parent

behaviour. The factors underlying these changes in behaviour will be discussed later (Chapter 3), but functionally these changes lead to a much more efficient exploitation of the time available for feeding the young.

CHAPTER 2 THE SEASONAL DEVELOPMENT OF PARENTAL FEEDING

INTRODUCTION

By placing a microphone in the nest of an Oystercatcher which had pipping eggs I observed that there were a great many auditory and tactile interactions between the young in the eggs and the incubating parent. I therefore decided to trace the development of auditory, tactile and visual interactions between the parent and young from two days prior to hatching, and to try and establish what part, if any, these interactions played in the development of parental behaviour, and especially in the development of parental feeding.

In a pilot test I removed the eggs from a nest which had been incubated for two weeks and replaced them with an equal number of pipped eggs. During undisturbed incubation the parent often shuffles on the eggs (see Beer 1961, Lind 1961, Drent 1967 for fuller descriptions of similar behaviour) and sometimes gets up and rearranges the eggs with the bill. In the latter case the parent sometimes gives the Chuck call (see also Webster 1941 for similar behaviour in Haematopus bachmani). At nest relief both parents frequently give the Chuck call when they are near each other, and both the on-coming and off-going parent gives the Weep call as they approach or leave the nest. Once the pipped eggs had been placed in the nest there was, over a four-hour period, a seven-fold increase in the number of bouts of shuffling and rearranging the eggs, and a twenty-fold increase in the number of calls. At nest relief there was a forty-fold increase in the number of calls and, in addition, the parent which had been incubating the pipped eggs for the first time, immediately returned after nest relief with an item of food which it presented near the nest. This illustrated

the dramatic effect of the interactions between parents and young-in-egg on the subsequent behaviour of the parents.

2/A Pre-Hatch and Immediate Post-Hatch Interactions

2/A/I Methods of Observation

Three undisturbed nests were studied in detail from two days prior to hatching to the day on which at least one egg hatched. As far as I know all the parents had bred before. Visual observations were made from a hide some 3 m from the nest and, by burying a microphone under the eggs, auditory interactions could be recorded. The following behaviour was recorded:-

Young-in-egg:

Calls: two calls could be distinguished, isolated peeps and well defined bursts of peeps.

Movements: three types of movement were distinguished, (1) pushing the bill out of the pipping hole, (2) the hatching movements when emerging from the egg, and (3) pushing-up movements under the parent subsequent to hatching. Although the young were usually covered by the incubating parent when these movements occured, each movement made a highly characteristic sound through the microphone and so could be separately identified.

Incubating Parent:

Calls: these consisted entirely of the Chuck call (family contact call).

Movements: these consist of two incubation movements (rearranging the eggs with the bill and shuffling on the eggs) and one brooding movement (half-raising the body and slightly spreading the wings).

Orientation movements:

these consist of waking up, looking down, straw throwing etc. and consist of behaviour shown by the parent in transition between a passive state (i.e. sleeping or quiet incubation) and a more active state (i.e. rearranging the eggs).

The frequency of these different behaviours was recorded, and, where a response took place between the parent and young, the form of the response was recorded. A response was defined by a behaviour of one (i.e. the parent shuffling the eggs) being followed within one second by a behaviour of the other (i.e. a burst of peeps from the young). This, of course, excludes the recording of any possible delayed responses, but this is unavoidable.

The data were not at all easy to analyse for a number of reasons. Firstly, two of the nests had two eggs each, and one had three eggs, which meant that there was much variation in the ages of the eggs in each nest which in turn affected the form of the interactions between the eggs and the parents. Secondly, at times so many interactions were taking place (i.e. at nest relief), that I was unable to record what was going on. Periods of time in which very intense activity occurred have therefore been taken out of the general analysis. Because of these difficulties the data obtained from these three nests have in general been lumped together and averaged.

The recorded behaviour has been divided into spontaneous behaviour (that is behaviour recorded from either the young or parents which was not preceeded within one second by behaviour of the other) and the responses (that is behaviour of the young or parent which occured within one second of behaviour of the other). However, a new difficulty arises here for

some spontaneous behaviour will appear to be a response because it will occur by chance within one second of behaviour of the other. It proved possible to correct for these pseudo-responses by calculating the proportion of each of the behaviours which would be expected by chance to occur within one second of each other and then subtracting these proportions from the observed number of responses. This correction has been made for all the responses referred to in the analysis.

The days on which the nests were studied were denoted by H - 2, (two days before hatching), H - 1 (one day before hatching) and H (the day on which at least one young hatched).

2/A/II Spontaneous Behaviour of the Young (Table 5)

There is a significant increase in the amount of spontaneous activity of theyoung recorded each hour over the whole hatching period (Mann+Whitney: H-2 to H-1, z=2.9, p=0.04; H-1 to H, z=2.2, p= 0.03: two tailed). From H-2 to H-1 the proportion of peeps to bursts remains the same ($\chi^2 = 0.001$, p = 0.9), but from H-1 to H the frequency of bursts does not change although the frequency of peeps significantly increases again. Movements were not recorded on H-2, and only relatively few on H-1, but there was a significant increase in the frequency of movements from H-1 to H.

2/A/III Spontaneous Behaviour of the Parent (Table 5)

There is no significant increase in the amount of spontaneous activity recorded each hour from H-2 to H-1 (Mann-Whitney: z = 1.3, p = 0.18) but there is a highly significant increase from H-1 to H (Mann-Whitney: z = 3.1, p = 0.002). All the various calls and movements change at the same rate, for no significant difference can be found

TABLE 5 SPONTANEOUS BEHAVIOUR AND RESPONSES FROM HATCHING YOUNG AND INCUBATING PARENTS

	H-2	H-1	H
Hatching Young:			
Total spontaneous Behaviour	39	127	256
Spontaneous Peeps	35	109	201
Spontaneous Bursts	4	17	19
Spontaneous Movements	-	1	39
Total Responses	4	11	37
Incubating Parents			
Total Spontaneous Behaviour	17	18	49
Spontaneous Orient. Movements	4	5	5
Spontaneous Calls	3	2	9
Spontaneous Movements	7	9	23
Spontaneous Movements accompanied by calls	3	2	12
Total Responses	6	24	51
% Responsiveness of young	26%	66%	72%
% Responsiveness of parents	16%	19%	20%

(lumped data from 3 nests expressed as average frequency per hour: combined total observation time on H-2 = 17 hours; H-1 = 15 hours; H = 14 hours).

between the proportions of the different behaviour which make up the parent's spontaneous behaviour (H-2 to H-1 by observation, H-2 to H, $\chi^2 = 3.84$, df = 3, p = 0.30). However, the form of the spontaneous movements increases significantly ($\chi^2 = 14.99$, df = 2, p = <0.001).

2/A/IV Responses of the Young to the Parent (Table 5 & Fig.4)

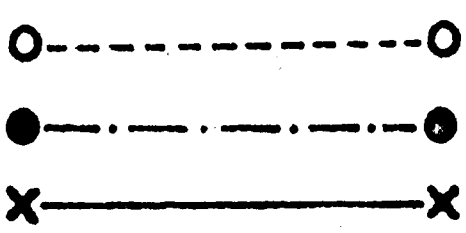
The overall responsiveness of the young to the parents significantly increases from H-2 to H-1 ($\chi^2 = 25.5$, p = <0.001) but then shows no further increase from H-1 to H ($\chi^2 = 2.45$, p = >0.10). The young show little selective responsiveness to the various calls and movements of the parents (Fig.4), with the exception that the orientation movements of the parent are never responded to (which is not surprising). However, the form of the responses given by the young changes in that a greater proportion of them are made up of bursts. 47% of the responses on H-2 consisted of bursts and this increased significantly to 77% on H-1 ($\chi^2 = 9.7$, p = <0.01). There was no further increase by H when 75% of the responses consisted of bursts ($\chi^2 = 1.42$, p = >0.20). There was also no significant difference between the proportion of the bursts given as responses to the various calls and movements of the parent.

I never recorded any movements as responses but this was probably due to the sounds of the movements being masked by background noise.

2/A/V Responses of the Parent to the Young (Table 5 & Fig.5)

The overall responsiveness of the parents to the young does not show any apparent increase as hatching proceeds (from Table 5, H-2 to H-1, $\chi^2 = 0.37$, p = >0.5; H-1 to H, $\chi^2 = 0.31$, p = >0.5; H-2 to H, $\chi^2 = 1.44$, p = >0.2).

Fig. 4


% of movements + calls responded to
% of movements responded to
% of calls responded to

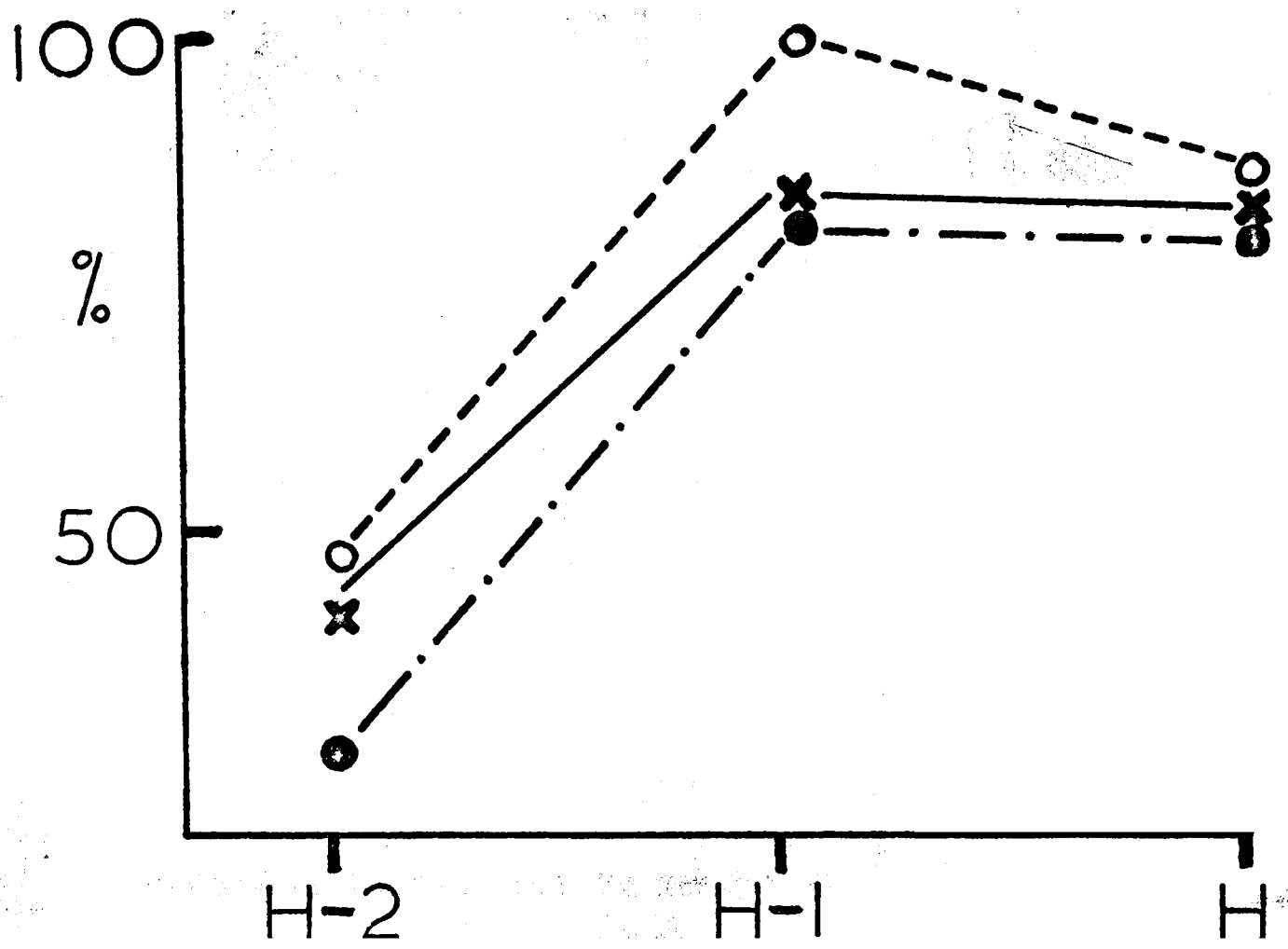
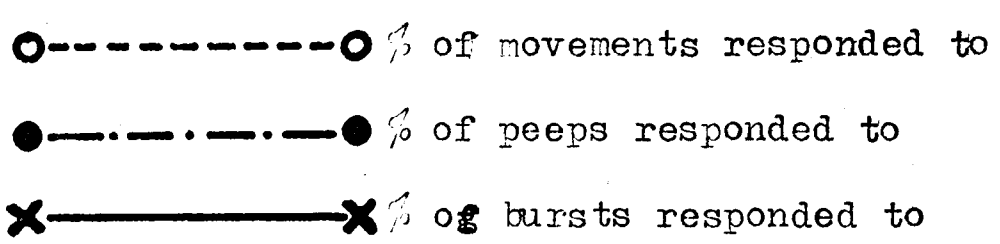

100
%
50
H-2
H-1
H

Fig. 5


% of movements responded to
% of peeps responded to
% og bursts responded to

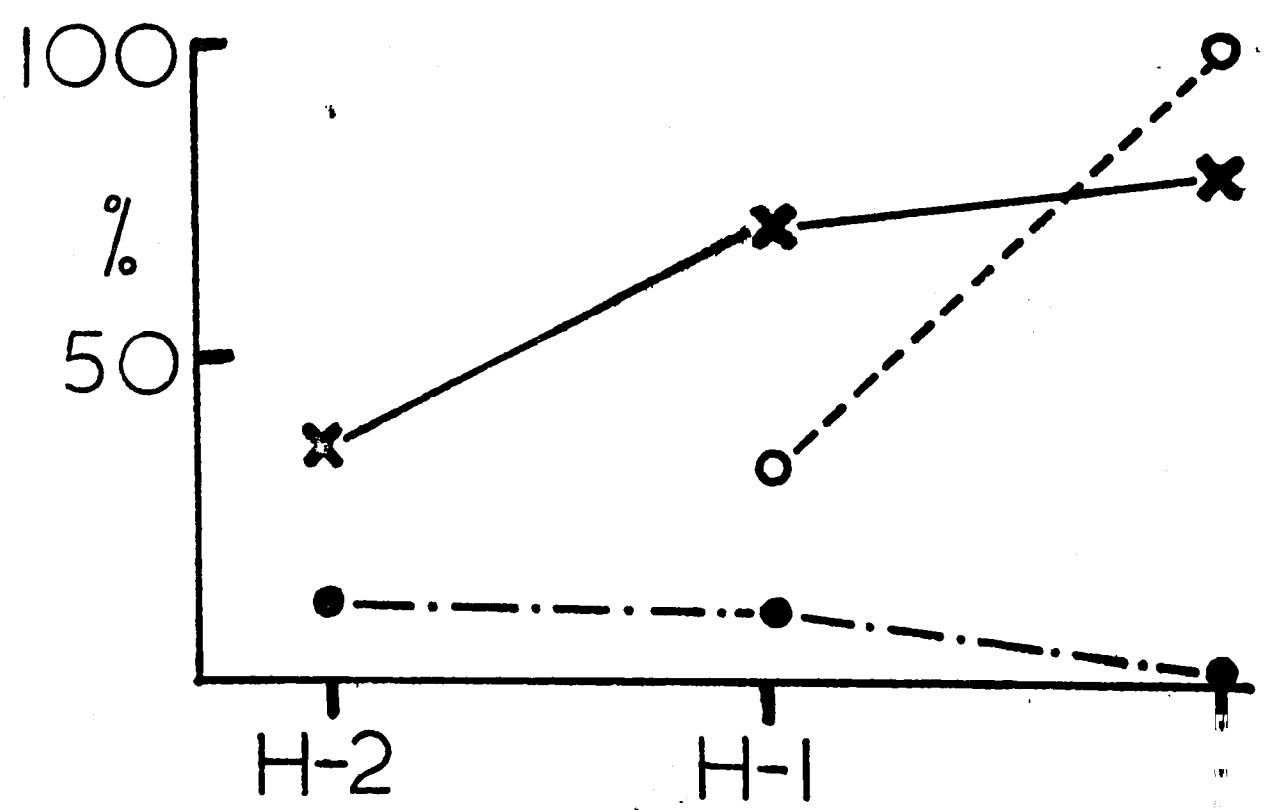

100
%
50
H-2
H-1

Fig. 4 Responsiveness of the Hatching Young to Calls and Movements of the Parents .

no selective responsiveness is shown :

H-2 : chi^2 = 2.38 , df = 2 , p = 0.3

H-1 : chi^2 = 1.67 , df = 2 , p = 0.4

H : chi^2 = 0.93 , df = 2 , p = 0.6

Fig. 5 Selective responsiveness of the Incubating parent to the R[illegible] peeps , bursts and Movements of the hatching young .

however, the parents show a very marked selective responsiveness to the young (Fig. 5). The responsiveness of peeps (whose spontaneous frequency greatly increases) is always low and almost vanishes by H, and this masks the very apparent increase in responsiveness to both the bursts and movements of the young. The responsiveness to bursts increases significantly from H-2 to H-1 ($\chi^2 = 7.7$, $p = <0.01$) but then shows no further increase ($\chi^2 = 1.3$, $p = >0.2$) from H-1 to H. The responsiveness to movements greatly increases from H-1 to H ($\chi^2 = 22.13$, $p = <0.001$). Over the whole hatching period the parent's responsiveness to bursts is always significantly higher than their responsiveness to peeps, and on H the responsiveness to movements is higher than to bursts ($\chi^2 = 30.02$, $p = <0.001$).

The form of the parent's response also changes (Table 6). Peeps are responded to mainly with orientation movements, while both bursts and movements of the young are responded to mainly with movements by H.

The form of the parent's movement response changes in that brooding movements become proportionally more frequent (8% on H-2 and H-1, 54% on H, $\chi^2 = 12.03$, $p = <0.001$).

2/A/VI Factors Underlying the Observed Changes in Behaviour

The spontaneous activity of the young shows a gradual increase over the whole of the hatching period (Table 5) while their responsiveness to the parents only increases from H-2 to H-1 and then shows no further increase. This change in the behaviour of the young can be attributed to a general endogenous change culminating in hatching, although the process is undoubtedly mediated not only by egg-egg interactions (as Vince 1964, 1966a, 1966b has shown) but also by parent-egg interactions.

TABLE 6 FORM OF THE PARENTS RESPONSES TO PEEPS, BURSTS AND MOVEMENTS OF THE YOUNG

Response to Peeps	Orient.Movements	89%	(85)	85%	(180)	100%	(14)
	Calls	7%		4%		-	
	Movements	4%		8%		-	
	Mvnts. + Call	-		3%		-	
Response to Bursts	Orient.Movements	80%	(17)	83%	(165)	48%	(196)
	Calls	10%		2%		8%	
	Movements	10%		13%		41%	
	Mvnts. + Call	-		2%		3%	
Response to Movements	Orient.Movements	-	(0)	50%	(16)	4%	(504)
	Calls	-		-		4%	
	Movements	-		50%		78%	
	Mvnts. + Call	-		-		14%	

(Total observed responses from all three nests: figures in ( ))

(Movements + Call indicates that the parent called as it moved on the eggs)

However, the change in the behaviour of the parent is less simple to understand for different activities of the young affect the parent in different ways. From Table 5 it can be seen that the spontaneous activity of the parent does not change from H-2 to H-1 although the spontaneous activity of the young greatly increases over that period. In addition, the overall responsiveness of the parent does not increase although its selective responsiveness to the young does change. From H-1 to H the spontaneous activity of the parent does increase, and its selective responsiveness changes yet again in that movements of the young are responded to more than bursts or peeps. During this same period the spontaneous activity of the young increases and especially the spontaneous movements of the young greatly increases. This strongly suggests that tactile stimuli from the young (rather than auditory stimuli) cause this increase in the spontaneous activity of the parents. These tactile stimuli could be either the actual movements of the young or the reduced stimulation to the brood patch once a young had hatched (i.e. an apparent reduction in the number of eggs).

Observations similar to these have been made during the hatching of the young of other avian species. Thus, Tschanz (1968) recorded an increase in the spontaneous activity of hatching Guillemots (Uria a. aalge) and a corresponding increase in incubation movements and calls of the parent. Gottlieb (1963a, 1963c) recorded increases in the frequency of incubation movements and calls in various species of ducks and in chickens, as did Goethe (1953) in the Herring Gull (Larus argentatus). Both Tschanz (1968) and Gottlieb (1965) found that the hatching

chicks were responsive to both auditory stimuli (especially to the maternal calls) and tactile stimuli, and Tschanz further showed that both auditory and tactile stimuli from the young could elicit incubation movements and calls from the parent. All these authors stressed the importance of these pre-hatch interactions in the establishment of the social responses between the parents and young after hatching. In the Oystercatcher, the further developments of parental behaviour follows in two stages, and in each stage these pre-hatch interactions play a decisive role. The first stage is the development of brooding behaviour, followed by the development of parental feeding.

2/B <u>The Development of Brooding Behaviour</u>

2/B/1 The Development of the Parent's Behaviour

The Oystercatcher shows the characteristic brooding posture of all waders in which the body is held in a triangular position by raising the shoulders and slightly spreading the wings. The young are brooded while standing under the wings and this seems to be a specific adaptation to enable the young to be brooded on a flat surface.

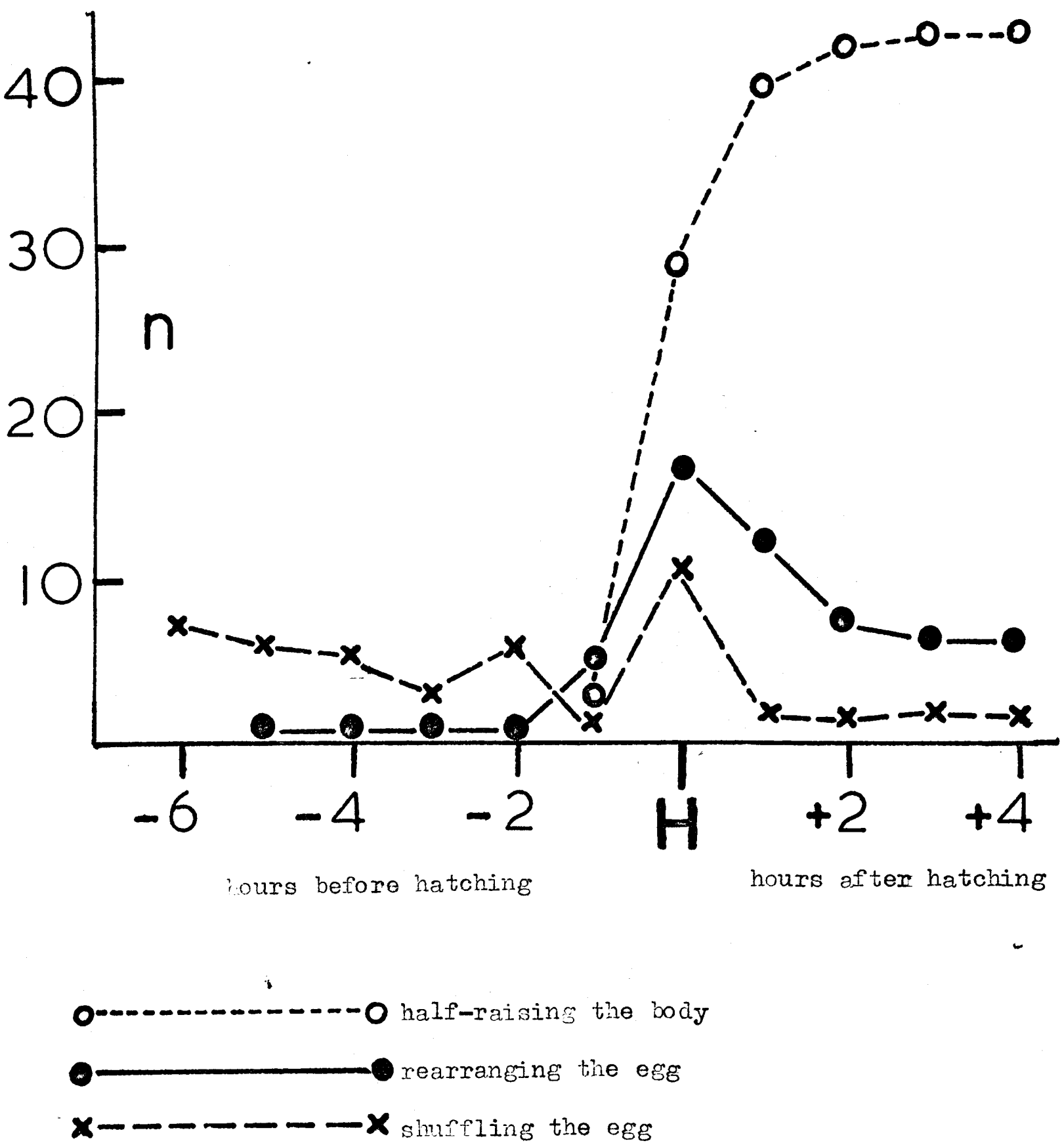
Tactile stimuli are at first very important in eliciting brooding responses from the parent. I have described how the spontaneous movements of the young change as hatching proceeds, pushing the bill out of the pipping hole being superseded by the hatching movements which are in turn superseded by the young pushing-up under the parent once it is hatched. The extrusion of the bill and the hatching movements elicit incubation movements from the parents (i.e. rearranging or shuffling the eggs) while the pushing-up of the young elicits brooding movements (i.e. half-raising the body). This is most clearly shown from data collected from a nest which had

but one egg and which I observed until the young hatched (Fig. 6). It can be seen that the brooding movements are only elicited when the young hatches.

The importance of both auditory and tactile stimuli from the young in the establishment of brooding behaviour has been shown in chickens by Saeki and Tanabe (1955) and Maier (1963), and Maier showed that if the tactile interactions were prevented by anaesthetising the brood patch then brooding behaviour did not develop. In a study on the Herring Gull, Goethe (1953) recorded increases in incubation and brooding responses as hatching proceeded and concluded that the transition in the behaviour of the adult from incubation to brooding was due to tactile and auditory interactions with the hatching young.

When the parent Oystercatcher responds to the pushing-up of the young with brooding movements, it also looks down and Chucks, but it will then often settle on the young and continue to incubate it. The young keeps pushing-up, and eventually the parent will adopt the full brooding posture and will move the young under the wing with the bill, giving the Chuck call as it does so. The parents have a very ambivalent attitude towards the young in the immediate post-hatch period and are as likely to incubate them as they are to brood them. A parent returning to a nest in which there are recently hatched young will roll the young in under the body and attempt to incubate them. It is only then, in response to the frantic pushing-up of the young that the parent will move the young under the wing. The brooding response is thus at first elicited by tactile stimuli from the young, and the complete response of moving the young under the wing is similarly elicited by tactile stimuli. Visual stimuli from the young are not effective in eliciting a brooding response in the immediate post-hatch period, and it is some hours before

Fig. 6 Frequency of Shuffling , Rearranging and Half-Raising of the body in response to movements of the young as the time of hatching approaches (nest with only 1 egg) .



the parent will respond effectively to the visual stimuli from the young. It seems that the parents have to learn to respond appropriately to the visual stimuli (see also Lehrman 1955 for the development of parental behaviour in the Ring Dove).

2/B/II The Development of the Behaviour in the Young

In the immediate post-hatch period the behaviour of the young consists mainly of pushing-up under the parent, but once the young is dry it starts to make brief excursions away from the parent. When the young emerges from under the parent, the parent gives the Chuck call. The young responds to the call by orientating towards it and by giving the contact call (a burst of peeps), and it is very noticable that the first positive movements towards the parents are in response to the Chuck call. When the young wants to be brooded again it pushes against the parent who then adopts the brooding position and moves the young under the wing with the bill, giving the Chuck call as it does so.

Within a few hours of hatching the young are making extended excursions, lasting up to ten minutes, from the parent. The parent still frequently gives the Chuck call and the young still show a marked response to the Chuck call by orienting towards it and by giving the contact call. However, when the young wants to be brooded it now orientates itself towards the bill of the parent. The young approaches the parent and the parent adopts the brooding position, looks down and Chucks, and the young then finds its way in under the wing by following the bill of the parent. It is interesting to note that by this stage of its development the young is making many pecks, mandibulations and levering movements with its bill, yet the only marked positive orientation towards the parent's bill is in the brooding situation.

This marked responsiveness of the young in the post-hatch period to the Chuck call of the parent is of great interest, for this responsiveness first appears well before hatching. The hypothesis which presents itself is that the young learn their parents' call before they hatch and, although I have no direct experimental evidence to show that this does occur, there is much evidence in the literature that learning processes such as this do occur. Gottlieb (1963a) has concluded that in the wood-duck (Aix sponsa), the ducklings learn the maternal call of their parents before hatching, and in another study (Gottlieb 1963b), he showed that the following response of ducklings to models was enhanced if the model emitted auditory stimuli. Grier (1967) reported similar results from experiments on chicken eggs which had been given auditory stimulation during hatching. Gottlieb (1966) also showed that wood-duck chicks could learn their siblings' call notes before hatching and that the learning occured during the auditory egg-egg interactions. Tschanz (1968) has most elegantly demonstrated a similar process in the Guillemot. He observed that in the later stages of hatching the young respond only to the call which it hears most when the young itself is active (this being the luring call of the parent), and that after hatching the young will respond only to the luring call of its own parents. Tschanz then showed experimentally that the young indeed learn the call before they hatch and that the learning phase was restricted to a particular part of the hatching period.

In the Oystercatcher only the one call is given by the parent (the Chuck or family contact call) and it is given most frequently when the young are active (i.e. in response to stimuli from the active young). From these observations,

and from Tschanz's observations and experiments, there is a good possibility that the young Oystercatcher learns its parent's call before it hatches. Such a pre-hatch learning of the call would be functionally very important for it could greatly facilitate the acquisition of visual responses (i.e. approach to the bill for brooding or feeding) which appear later in development.

The possibility also exists that the parent Oystercatcher learns the call of the young during these pre-hatch interactions, for the bursts of peeps given by the young-in-egg develop into the contact call, brooding call and distress call in the post-hatch period. These calls all have the basic form of a burst of peeps but they differ from each other in the intensity and pitch of the peeps. It is interesting that the bursts are given by the pre-hatch young more frequently as a response to the parent than as a spontaneous call, and in the post-hatch interactions the contact, brooding and distress calls are also given most frequently as responses to the parent.

2/C <u>The Development of Parental Feeding</u>

2/C/I The Development of Parental Feeding in the Parent

Parental feeding develops very gradually and its temporal patterning is at first closely related to the times of nest relief in that the oncoming parent brings food to the nest and the off-going parent returns with food soon after nest relief (see also Webster 1941). On the day of hatching the feedings of the young occur near the time of nest relief (Fig.7) while by the second day the pattern is more diffuse. The causation of early parental feeding therefore seems to share factors which control incubation.

The first time a parent brings food to the nest it does

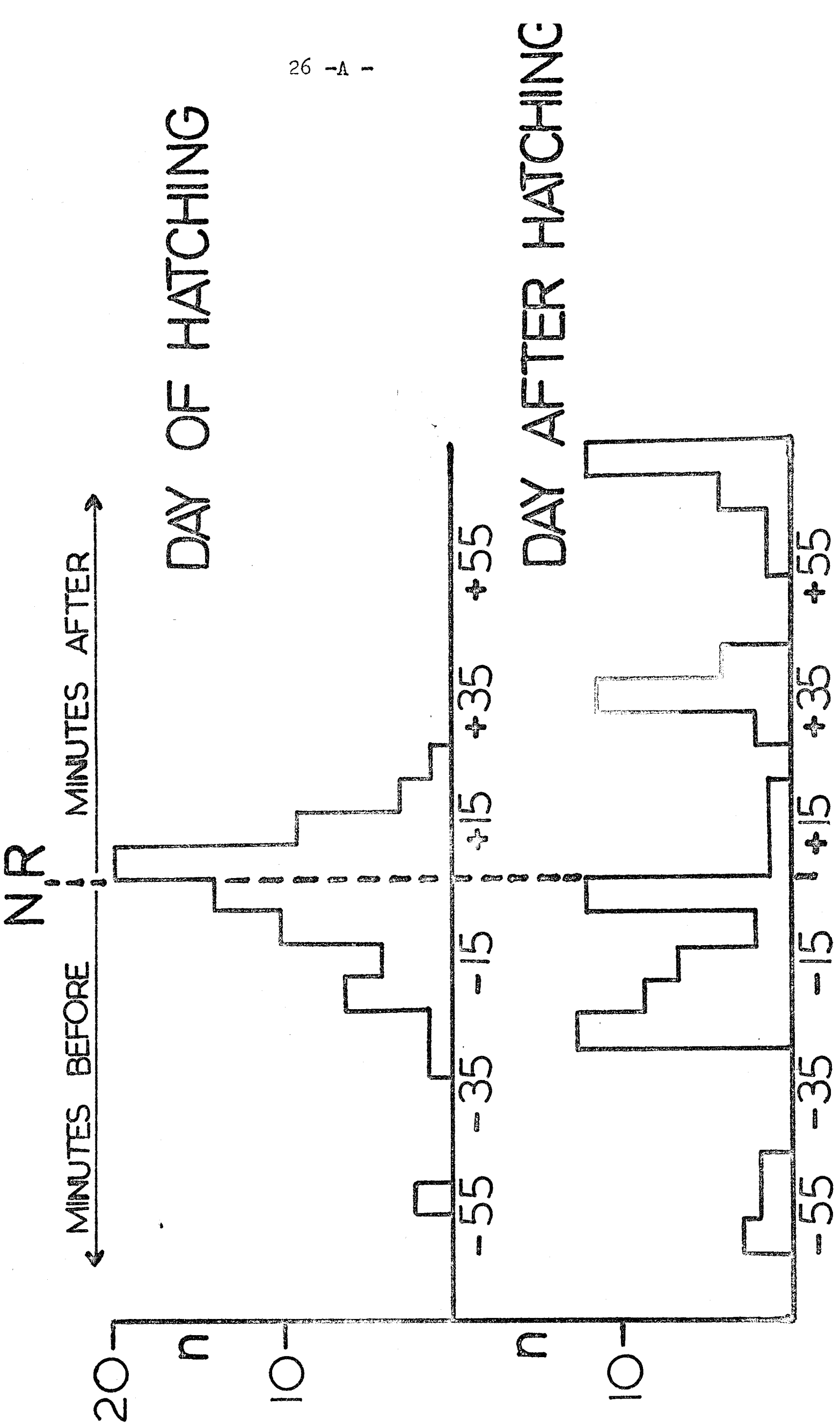


Fig. 7 Distribution of presentation of food to the young with respect to nest relief (NR) in 10 nests on the day of hatching and the day after hatching .

not come very near the nest, it presents the food for only a very short time and it eats the food itself. On subsequent occasions the parent will come nearer to the nest (Fig. 8), and will present the food for a longer period, until eventually the parent brings the food right up to the nest and presents it until the young eat it. With such a gradual development of the parental feeding it is difficult to imagine that it is initiated by specific interactions with the young (i.e. the young pecking at the bill tip) as is suggested for the initiation of parental feeding in Larids (Quine and Cullen 1964 and reference cited, Hailman 1967). Indeed, the six observed cases showed that when food was brought for the first time, the parent Oystercatcher had not had its bill pecked by the young nor had the young shown any begging behaviour. In most of these cases the young would not have been able to eat the food even if the parent had brought the food to the nest. I have already described how, in the pilot test that I carried out, the interactions between pipping eggs and the parent stimulated the parent to bring food to the vicinity of the nest (although this is not seen under normal conditions). In Fig. 9 the distance from the nest to which individual parents first brought food is plotted against the time since the first young hatched, and it can be seen that there is a significant negative correlation. This strongly suggests that the full parental feeding develops as a response to the cumulative effect of the general activity of the young.

2/C/II The Development of Feeding Behaviour in the Young

My observations on this aspect of the development of parental feeding are very poor. The young are rarely successful in feeding from the parent on the first few occasions that the parent brings food right up to the nest. The parent

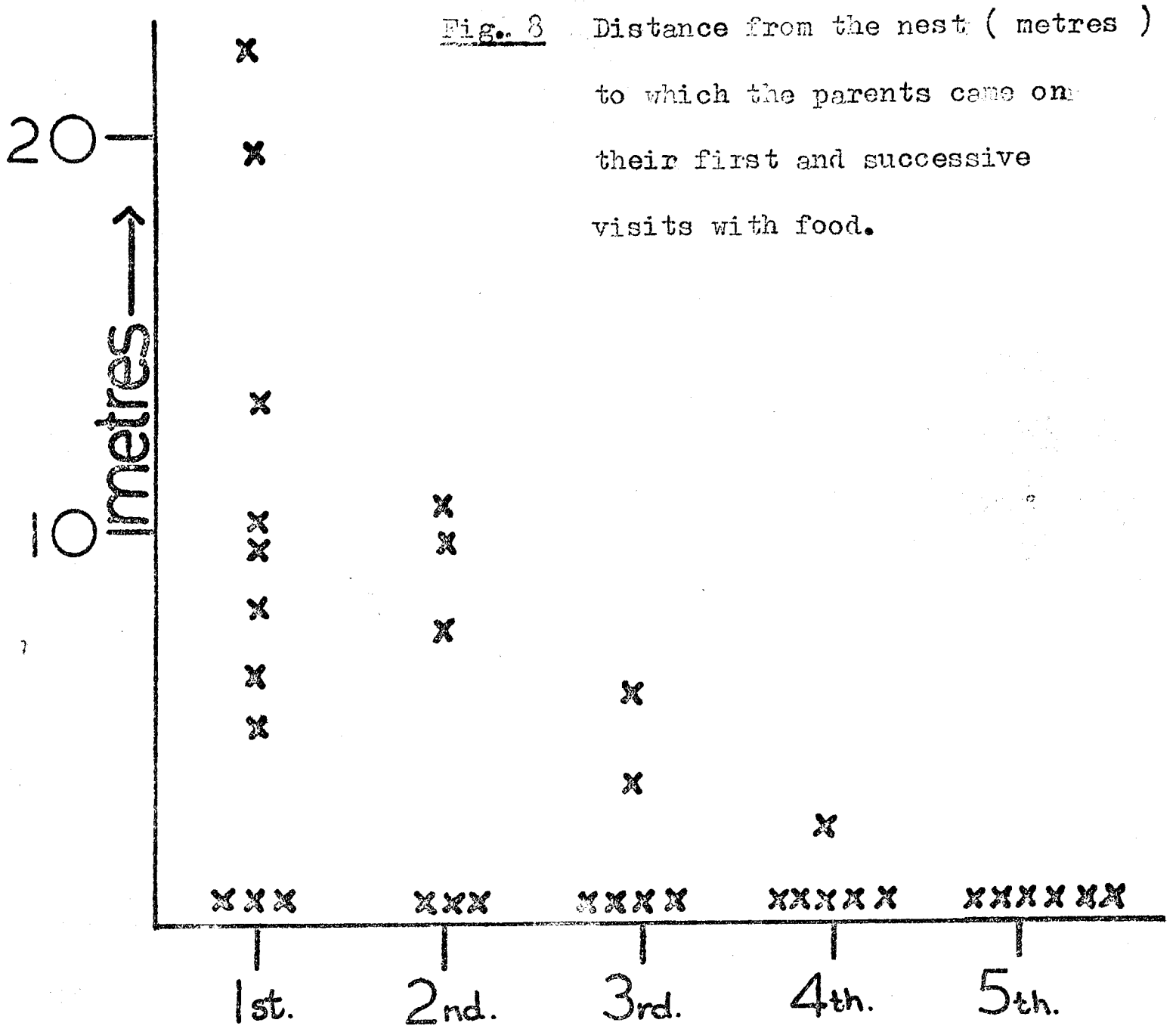
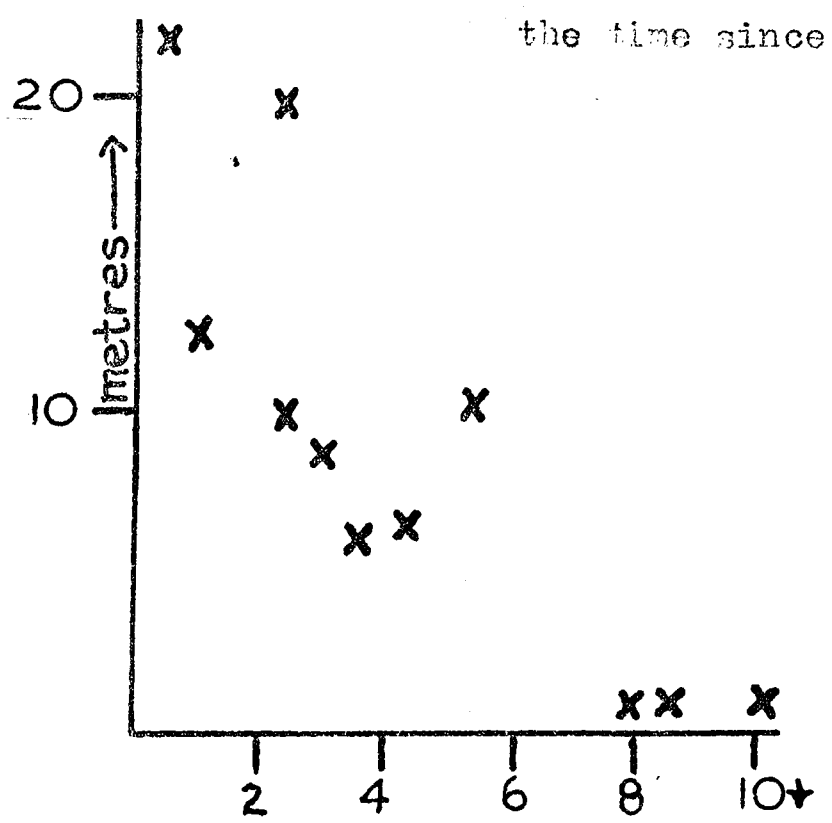


Fig. 8 Distance from the nest (metres) to which the parents came on their first and successive visits with food.

Fig. 9 Distance from the nest to which 11 individual parents came on their first visit with food correlated with the time since the first young hatched.



approaches the nest and presents the food, constantly giving the Chuck call, and the behaviour of the young is little different from their behaviour during a nest relief when no food is presented. They may approach the bill or they may run vaguely between the two parents, both of whom will be giving the Chuck call. Very few pecks, if any, are made either at the bill or at the food in the bill (although by this stage the young are able to peck and grasp objects which are lying around). If the young does peck at the food then the parent usually drops the food (before the peck hits either the bill or the food) and points. The young may then peck again at the bill, or might peck at objects lying under the bill. The parent then picks up the food and presents it, and the whole process is repeated. If the young do not peck at all then the parent will Mandibulate and Lead, and this is often very effective in eliciting a peck from the young. Eventually, the parent eats the food itself.

I have only four times observed young take food from their parent when I knew that this was the first time that the young had managed to take food. The process was exactly the same as described above, except that the young eventually pecked the food and ate it.

However, on the next occasions that food was brought to these four young, there was a dramatic change in their behaviour in that (1) the young moved more quickly and more surely towards the bill of the parent and (2) the young pecked more persistently at the food in the bill tip and at objects lying under the bill tip if the food was dropped. These changes in the behaviour of the young are reflected in the time taken by the young to eat the food (measured from the first reaction of the young towards the parent to when the young managed to eat the food). The times taken over the first and second feeds respectively in the four cases

were 400 sec and 55 sec, 360 sec and 72 sec, 180 sec and 22 sec, and 90 sec and 135 sec. The impression gained from these admittedly very few observations is that the young very rapidly learn to (1) react immediately to the bill of the parent when it is in the Hold position by approaching it and (2) to persist in pecking at, and to restrict their pecking to, objects held in the bill tip or lying immediately below it.

2/C/III Luring the Young from the Nest

Once the young are fully mobile and have been fed a few times the parents start to lure the young away from the nest. Luring usually starts on the first day after hatching and occurs when the parents leave the nest site to forage for food. Many Chucks are given when the parent leaves, and while the parent probes near to the nest. The young follow the parent in response to the Chuck call and in response to the probing bill which is often superficially in the Hold orientation. The young closely follow the bill of the parent and are fed and then brooded away from the nest (which is eventually abandoned). The parent also lures by presenting food 'just out of reach' of the young so that the young has to move away from the nest in order to be fed.

In the fenced-in nests (Appendix 2) the young were unable to leave the nest vicinity, yet the parents made frantic attempts to lure the young through the fence. For hour after hour the parents would present food just outside the fence, call repeatedly, fly in and out, and even try to brood the young through the fence. These luring attempts would often last for two hours or more at a time during the first two days after hatching, but by the third day the luring attempts became infrequent and finally stopped.

It seems unlikely that luring the young from the nest has much anti-predator function, for often the parents will end up

brooding the young on the original nest site a day or so later. Instead it seems to be a specific adaptation to the peculiar parental feeding system which the Oystercatcher shows. Successful rearing of young Oystercatchers depends on the young following their parents out onto the feeding grounds, for the parents are unable to raise young if they have to bring all the food to the young. Luring may thus function to establish a following response in the young as soon as the young are fully mobile.

2/D Discussion of the Development of Parental Feeding

The development of parental feeding can thus be traced back to the interactions between the pipping eggs and the parents. The function of these interactions are twofold: (1) they are the means whereby the young might learn to respond to the call of the parent before hatching and (2) they initiate in the parent both the onset of brooding and parental feeding.

Further development following hatching is more complex. The young first approach the parent in response to the Chuck calls and then seem to learn to approach the bill when it is in the Hold position and to peck specifically at food objects in or under the bill tip. Both these processes may be facilitated by the marked responsiveness of the young to the Chuck call.

The parents have to learn to respond appropriately to the visual stimuli of the young (the similarity between the pre- and post-hatch calls of the young may facilitate this), and the full parental feeding behaviour develops as a response to the cumulative effect of inter-actions with the young. The development of parental feeding does not stop once the young have hatched and have been fed a few times, for there is a continuous process of change and development

mediated by further interactions between the parents and young, which terminates in the final breakdown of parental feeding and the splitting up of the family.

Parental feeding develops in a very different way in Oystercatchers than it does in many Larids. In the Laughing Gull (Larus atricilla) for example, the first regurgitation of food by the parent is in response to the young pecking at the parent's bill (Hailman 1967) while in the Oystercatcher it is the parent who initiates the first feedings of the young. The behaviour of the young of these two species is also very different in that the young Oystercatcher, in the natural situation, does not show such a strong pecking response to the parent's bill as is described for the young of the Laughing Gull (and for the young of other Larids). The young Oystercatcher develops a very marked orientation and approach response towards the bill, but actual pecking at the bill (when there is no food in the bill) is infrequent. The significance of these differences will be discussed later.

CHAPTER 3 THE ORGANISATION AND CONTROL OF PARENTAL FEEDING

3/A Introduction

Parental feeding in the Oystercatcher is organised along the following general lines.

1. All feeding activities (both self-feeding by the parent and feeding of the young) occur in cycles which are basically correlated in time with the state of the tide. The active phases of the cycle occur at the beginning and end of each low tide period, there being a pause of all feeding activities around the time of dead low water.
2. During the active phases of the cycles the parents spontaneously return and present food to the non-feeding young.
3. Depending upon the reaction of the young to the food presented to it, the parent may immediately search for and present more food to the young. A feeding train may thus be initiated.
4. The young can also initiate food presentation from the parent by running up to the feeding parent.
5. As the young grow older there is a fundamental change in the organisation of the parental feeding system in that the young comes to play an increasingly major role in the initiation of food presentation. This eventually cumulates in the breakdown of parental feeding and in the splitting up of the family.

3/B Cycles of Feeding Activities

3/B/I Non-Breeding Birds

Observations made by Davidson (1966) on flocks of non-breeding Oystercatchers in the Burry Inlet in South

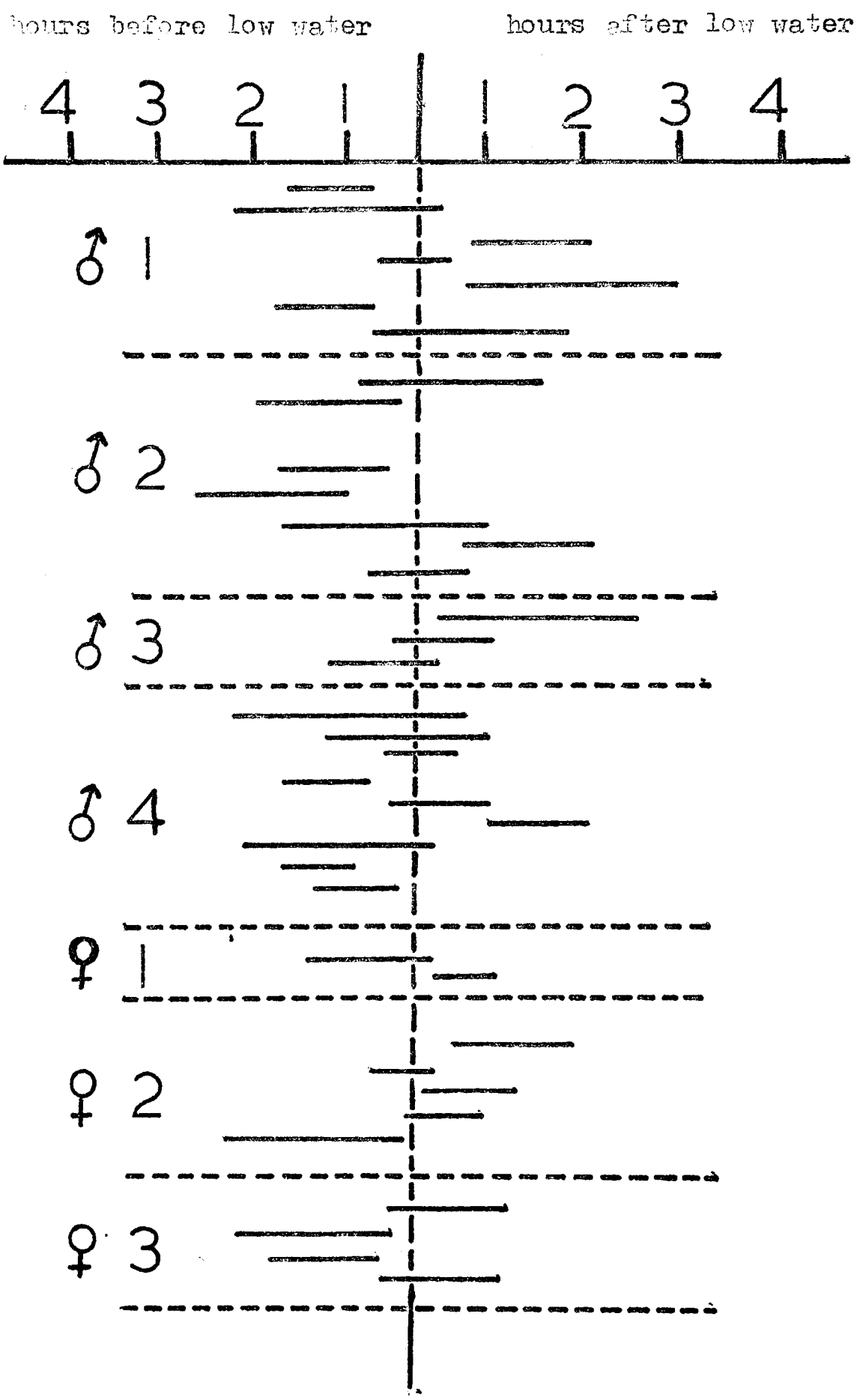
Wales show that the percentage of birds feeding is high at the beginning of the low tide period (i.e. as the tide ebbs) and then drops to a low level during the period of dead low water, only rising again once the tide starts to flow and cover the feeding grounds. Safreil (1967) reports essentially the same cycle of feeding activities in birds feeding on Limpets (Patella vulgata), and I have made similar observations on non-breeding birds feeding both on Mussels (Mytilus edulis), mud flat annelids and terrestrial invertebrates.

This pause from all feeding activities around the period of dead low water cannot be connected with the availability of the food, for Davidson (1967) showed that the feeding rates of the birds were very constant irrespective of when during the low tide period they were feeding. I have made similar observations on the feeding rates of the mussel eating birds, as well as on those feeding on mud flat annelids.

3/B/II Breeding Birds

Breeding Oystercatchers with young show a very similar pattern of total feeding activity. Safreil (1967) showed that both self-feeding and parental feeding fell off and ceased during the period of dead low water and Tinbergen and Norton-Griffiths (1964) reported the same pattern in breeding adults who were feeding their young and themselves on mussels. In Fig. 10 the duration of this pause from all feeding activities in four males and three females is shown. It can be seen that not only is there variation between individuals as to when the pause occurs and in the duration of the pause, but also that there is much variation in each individual over the occurence and duration of the pause on different days.

Fig. 10 Duration of Low Tide pause from all feeding activities in seven breeding Oystercatchers



This again indicates that the pause is not governed by a temporary unavailability of food during the dead low water period.

3/B/III A Common Motivational System

These data show that both the non-breeding and breeding birds have the same basic pattern of feeding activity in that there is a pause from all feeding activities during high water and at some time during low water. Although the high water pause is undoubtedly caused by the food being unavailable, the low water pause cannot be due to this factor. Parental feeding of the young is only observed during the active phases of the feeding cycle.

This suggests that the basic motivation for feeding the young is closely connected with the motivation for self-feeding. This hypothesis in its strongest form states that both self-feeding and parental feeding share common motivational factors, and that parental feeding cannot occur unless there is motivation for self-feeding.

3/C Presentation of Food Initiated by the Parent

3/C/I Fenced-In Families (Appendix 2)

The fenced-in families offered a good opportunity for studying this behaviour of the parents when any effect from direct stimulation of the young was removed, for the parents had to transport all the food into the arena either from the estuary or from nearby dunes and thus interactions between the parents and the young were limited to the brief moments when the parents were within the arena.

The frequency with which each parent of the three families under study brought food to their young was recorded on several days over four to six weeks, a total of 43 individual records being obtained. Each record was analysed to see whether there was any pattern in the intervals between

successive presentations of food to the young during the two active phases of the feeding activity cycle. This was done by calculating the median value of the intervals between successive presentations and then using a one-sample runs test. In every case except one, the short and long intervals were occurring in a random sequence. In addition, in those records which contained enough data, autocorrelation function plots were made between the successive intervals, and this analysis also failed to show any consistant correlations or cycles of correlations from any of the records, except for the one case already referred to (Bendat and Peirsol 1966).

The conclusion is that during the active phases of the feeding activity cycles the parents were initiating presentation of food to their young at random moments in time.

3/C/II Free-Living Families

Some similar data were also collected from free-living families. On three successive days one individual parent of a family which had two three-week old young was observed for seven to eight hours of the low tide period, and records were made of how long it spent feeding the young and how long it was subsequently away feeding itself. On none of the three days was there any correlation between the length of time that the parent spent feeding the young (i.e. the length of time taken over a feeding train), and the length of the subsequent period that the parent was away from the young before returning once more on its own initiative with food.

An analysis of the intervals between feeding trains or isolated presentations of food to the young, similar to the ones described in 3//I, failed to show any non-randomness in the parent's behaviour.

The conclusion is that during the active phase of the

feeding cycle the parent is returning on its own initiative at random moments in time and irrespective of how long it has just spent feeding the young or how long it has been since it last fed the young.

3/D The Initiation, Maintenance and Breaking Off of Feeding Trains

3/D/I Introduction

When the parent presents food to a non-feeding young three things can happen: (1) the young makes no response at all to the parent who will eventually eat the food itself, (2) the young may take and eat the food but only after a great deal of time, and (3) the young may immediately seize and devour the food. In the first two cases the parent will not subsequently present more food to the young and will instead either continue self-feeding or even cease from feeding activity. In the third case the parent will immediately search for and present more food to the young, and a feeding train will be initiated in which the parent presents to the young each item of food as it is found, the young staying very close to the parent. The feeding train will continue in this fashion (often the young is fed 50 times or more in succession) until it can be seen that the young is gradually taking longer and longer to take the food from the parent's bill. Suddenly, instead of presenting an item of food, the parent will eat it itself, and will continue doing so. In other words the feeding train has been broken off by the parent who has reverted to self-feeding. Feeding trains can also be broken off by the parent suddenly ceasing from feeding activity, and a feeding train can also be initiated by the young running up to the parent and thus initiating a presentation (1/C/II).

From observations such as these, it seemed that both the initiation, maintenance and breaking off of a feeding train,

irrespective of who initiated it, was primarily controlled by the speed with which the young took the food from the parent's bill once the parent had presented it. At least that was the most obvious factor to the observer. This hypothesis would mean that the parent had some form of 'Waiting Threshold' against which it could match the time that the young took to seize and eat the food once it had been presented. If the young took and ate the food within the threshold time then the parent would present the next item of food which it found, but if the young took longer than the threshold time then the parent would not present the next item of food, and might even cease from all feeding activities.

The next point to consider is what time measure might be relevant to the parent. Observations in which the young made no reaction at all to the presentation of the food and in which the parent ate the food itself, suggested that the start of the relevant time measure is from when the parent first presents the food. Normally, when the young takes food from the parent, ingestion follows immediately and with very little delay. There are, however, cases in which the young are unable to eat the food either because the food item is too big or because the young is not very hungry (1/B/IV). In these cases the parent will persist in presenting the food again and again until the young eventually eats it, and this sugests that the end of the relevant time measure is when the young actually ingests the food.

The hypothesis which I therefore formed for the control of the feeding trains was that the parent had a Waiting-Time Threshold, and that the waiting-time was measured by the parent as the time elapsing between the initial presentation of the food and the young ingesting the food. If the young took longer than the threshold time, then the parent would not present more food, while if the young took shorter than the waiting time then the parent would present more food. Finally,

if the young made no reaction at all, then the parent would wait until the threshold time was passed and then eat the food itself, and would subsequently not present more food to the young. A model representing this hypothesis is presented in Fig. 11.

3/D/II Methods of Observation and Definition of Terms Used

Two families of free-living Oystercatchers, each with two young, were observed for eight weeks. The parents were feeding their young almost entirely on annelid worms which were caught on a rich mud flat near the two nests. The families were observed from a hide so positioned that it overlooked both families' feeding territories, and long sequences of parental feeding behaviour were observed and tape recorded.

The parental feeding behaviour can be broken down into the following elements:

Feeding Train:	a sequence of feedings of the young by the parent.
Self-Feeding Train:	a sequence of self-feeding by the parent.
YF (Young First):	the first feeding of a young in a feeding train. It is immediately followed by further feedings.
YT (Young Train):	all the subsequent feedings of the young in the feeding train.
YL (Young Last):	the last feeding of the young in a feeding train. It is preceeded by a YT, and it is not followed by another feeding.
Yi (Young Isolated):	an isolated feeding of the young. It is neither preceeded nor followed by another feeding.

Fig. 11 Hypothesis for the control of feeding trains

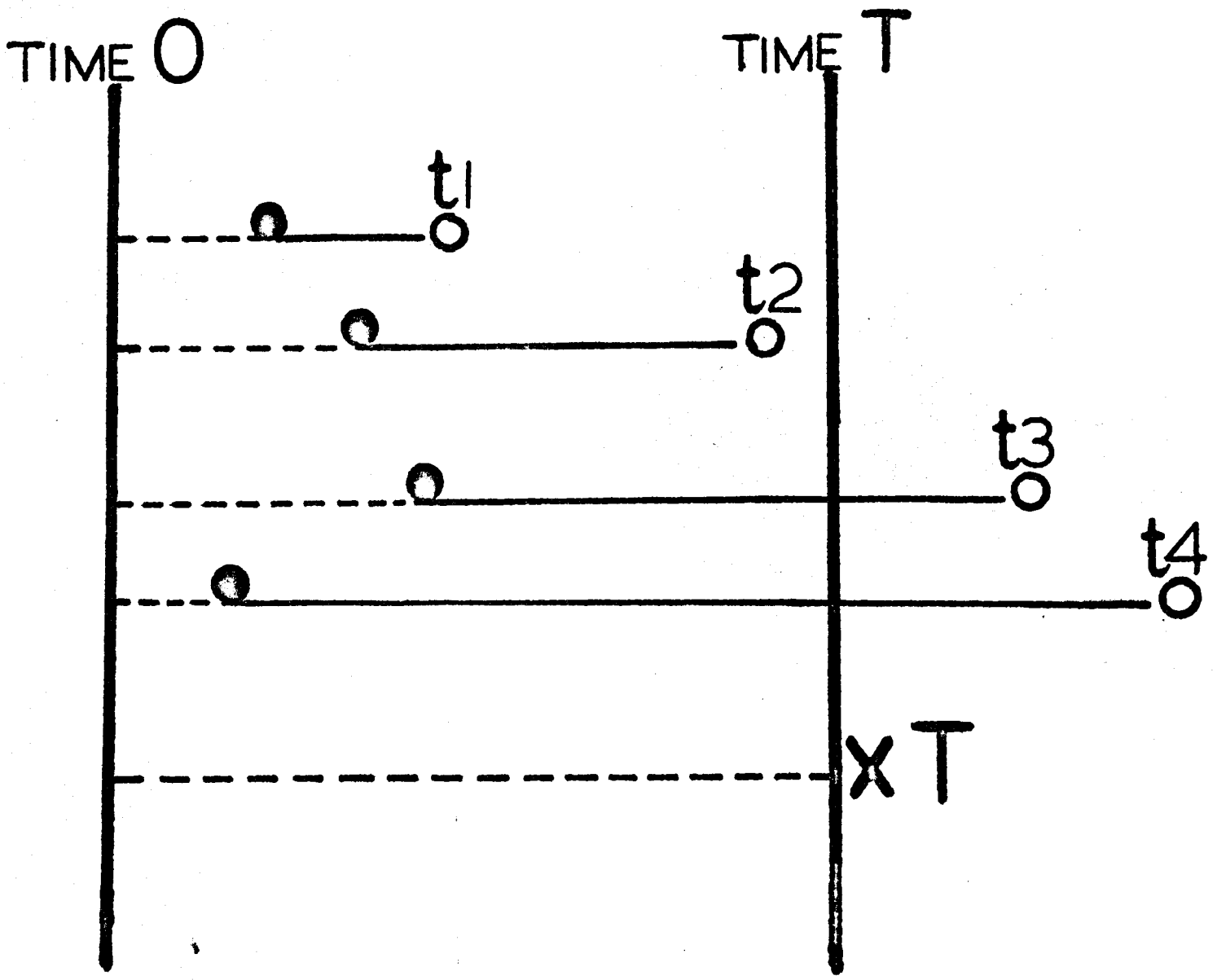
Time O : parent presents the food

Time T : the waiting-time threshold

● young reacts to the presented food

O young eats the presented food

X parent eats the food



t_1 and t_2 : young eats food within the threshold time , parent immediately presents more food .

t_3 and t_4 : young takes longer than the threshold time to eat the food , parent does not present more food .

T : no reaction at all by the young to the presented food . Parent eats the food itself when the threshold time T is reached , and parent does not present more food .

PA (Parent Attempts): the parent attempts to feed the young but the young does not react, the parent eventually eating the food item itself. It is neither preceded nor followed by a feeding of the young.

PF (Parent First): the first self-feeding in a self-feeding train.

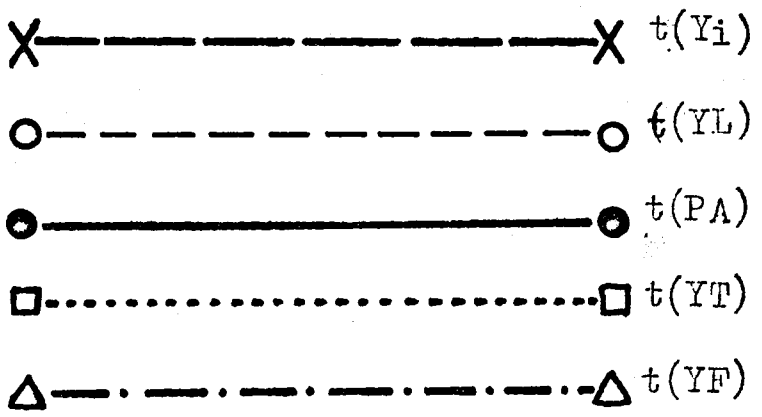
PT (Parent Train): subsequent self-feedings in a self-feeding train.

PL (Parent Last): the last self-feeding in a self-feeding train.

From the tape recorded observations the waiting-time of the parent in each of these feeding situations was measured. The waiting time is defined "the time elapsing between the first presentation of the food and either the young eating the food or the parent eating the food if the young do not react". Thus, t(YF), t(YT), t(YL) and t(Yi) refer to the time elapsing between the first presentation of the food and the young eating the food. Similarly, t(PA) refers to the time elapsing between the first presentation of the food and the parent eating the food. However, t(PF), t(PT) and t(PL) refer to the time elapsing between the food being in a state in which the parent could have presented it (i.e. after preparation) and the parent eating it.

The data obtained from each family were lumped and analysed in weekly blocks according to the age of the young. The median values of the various waiting-times are given in Table 7 and Fig. 12, and the significance levels arising out of the statistical treatment are given in Appendix 1.

Fig. 12 Median Length (sec) of the YF , YT , YL , Yi , and PA .



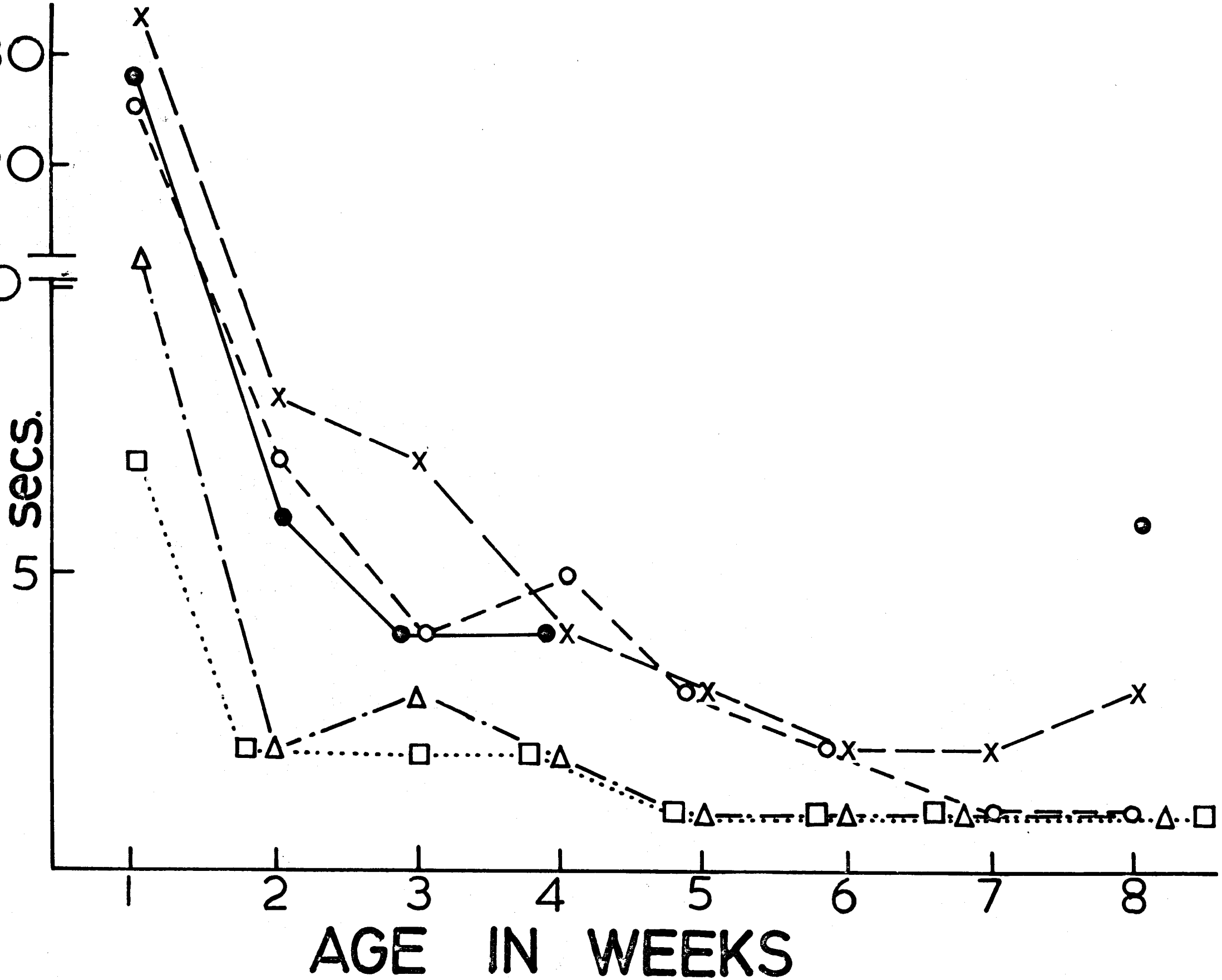

30
20
10
5
secs.
1
2
3
4
5
6
7
8
AGE IN WEEKS

TABLE 7 MEDIAN VALUES (IN SECS) OF THE WAITING TIME OF THE PARENT

Age of young in weeks	t(Yi)	t(YF)	t(YT)	t(YL)	t(PA)	t(PF)	t(PT)	t(PL)
1	39(19)	12(23)	7(104)	26(23)	29(15)	1(16)	1(89)	1(16)
2	8(19)	2(41)	2(360)	7(41)	6(24)	1(35)	1(286)	1(35)
3	7(8)	3(18)	2(260)	4(18)	4 (5)	1(12)	1(163)	1(12)
4	4(15)	2(15)	2(76)	5(15)	4(2)	1(10)	1(100)	1(10)
5	3(5)	1(19)	1(130)	3(15)	-	1(11)	1(240)	1(11)
6	2(8)	1(8)	1(200)	2(8)	-	1(8)	1(209)	1(8)
7	2(13)	1(18)	1(125)	1(18)	-	1(19)	1(76)	1(19)
8	3(10)	1(28)	1(180)	1(28)	6(3)	1(19)	1(78)	1(19)

(Total data from two families: figures in () indicate total number of observations)

3/D/III The Waiting-Time Threshold

According to Fig. 11, the t(PA) must give the actual measurement of the Waiting-Time Threshold. Thus the hypothesis predicts that

$$t(YF) \text{ and } t(YT) < t(PA) < t(YL) \text{ and } t(Yi)$$

and these predictions must be upheld by the data in order for the hypothesis to be tenable. However, the number of observations of PAs are very small, especially after the second week (Table 7). In addition, the PAs fall into two distinct classes, those in which the young made absolutely no reaction at all to the presented food, and those in which the young made some reaction (i.e. approach and one or two pecks). If these two classes of PAs are denoted as PA- (no reaction by young) and PA+ (some vague reaction by young), then it can be seen from Table 8 that

$$t(PA-) < t(PA+)$$

The t(PA-) must therefore be the more accurate measurement of the Waiting-Time Threshold, but unfortunately the number of observations of PA- are very small. It is only with the data from Week 1 and 2 that the t(PA-) can be used to estimate the Waiting-Time Threshold, and, with the data from Weeks 3 - 8, either the t(PA) or the relationships between the t(YF), t(YL) and t(Yi) must be used.

3/D/IV Isolated Feeds (Yi)

The hypothesis predicts that

$$t(PA) < t(Yi)$$

but this prediction is not upheld by the data (Appendix 1/a) for no significant difference can be found between them. However, Table 9 shows that for weeks 1 and 2

$$t(PA-) < t(Yi) = t(PA+)$$

This shows that the t(PA-) is a truer estimate of the

TABLE 8 MEDIAN VALUES (IN SECS) OF t(PA-) and t(PA+)

Age of young in weeks	t(PA-)	t(PA+)	Mann-Whitney z (two tailed probability)
1	19(8)	65(7)	z = 2.32, p = 0.02
2	4(8)	10(16)	z = 2.87, p = 0.004
3	3(3)	6(2)	z = 0.85, p = 0.39

(figures in () indicate total numbers of observations)

TABLE 9 ESTIMATION OF WAITING-TIME THRESHOLD USING t(PA-)

		Week 1	Week 2
t(Yi)	t(PA+)	U = 39	U = 123
		p = 0.1	p = 0.1
	t(PA-)	U = 32	U = 31
		p = 0.04	p = 0.04
t(YF)	t(PA-)	z = 2.17	z = 2.83
		p = 0.03	p = 0.005
	t(PA+)	z = 1.38	z = 1.1
		p = 0.16	p = 0.28
t(YL)	t(PA-)	z = 2.81	z = 2.01
		p = 0.005	p = 0.044

(two tailed probabilities from Mann-Whitney U or z)

Waiting-Time Threshold, and that the predictions are upheld where this estimate can be used.

3/D/V The Initiation (YF) and Maintenance (YT) of a Feeding Train

The hypothesis predicts that

$$t(YF) \text{ and } t(YT) < t(PA)$$

this prediction being upheld by the data (Appendix 1/b, 1/c). As an additional check, Table 9 shows that

$$t(YF) < t(PA-)$$

The t(YT) were not tested against the t(PA-) because of the great difference between the numbers of observations in each case.

3/D/VI Breaking Off a Feeding Train (YL)

The hypothesis predicts that

$$t(PA) < t(YL)$$

but this prediction is not upheld by the data (Appendix 1/d) for no significant difference can be found between them. However, from Table 9, it can be seen that

$$t(PA-) < t(YL) = t(PA+)$$

which is predicted. The hypothesis also predicts that both the t(YF) and the t(YT) should be shorter than both the t(YL) and the t(Yi), and from Appendix 1/e, 1/f, 1/g, 1/h, it can be seen that in general these predictions are upheld although there is a marked tendency for all the predictions to break down as the young grow older. The data (especially from Weeks 1 - 4) therefore support the hypothesis that the waiting-time of the parent when presenting food to the young is of great importance in the general organisation of the feeding trains.

3/D/VII How Rigid is the Waiting-Time Threshold?

Ignoring for the moment the very obvious and pronounced decrease of all the waiting-times as the young grow older, the data were examined to see whether the Waiting-Time Threshold varies over the short time scale. The analysis showed that:

1. There is no correlation between individual t(YF)s and the number of YTs following, except for Week 1 (Appendix 1/i). This one correlation may be an artefact in that very small young are clumsy in taking food and also have a limited capacity for food, but in general this result means that the t(YF) only initiates a feeding train and does not determine how long the feeding train will be.
2. There is no correlation between the number of YTs in a train and the length of the individual t(YL)s (Appendix 1/j). This means that the length of a feeding train has no effect in determining when the parent will break off from feeding the young, i.e. the parent can only be reacting to the waiting-times.
3. No significant difference can be found between the t(YF)s of feeding trains initiated by the parent and the t(YF)s of feeding trains initiated by the young except for Week 1 where the parent-initiated t(YF)s are significantly longer. This one significant difference is again understandable in terms of the limited capacity of very small young for food (Appendix 1/k).
4. No significant difference can be found between the t(YL)s of feeding trains initiated by the parent and the t(YL)s of feeding trains initiated by the young (Appendix 1/l). These results show that the Waiting-Time Threshold is not affected by whether or not the parent is motivated to feed the young on its own

initiative.

5. Analysis of successive t(YT)s in individual feeding trains revealed no sign of a gradual increase in the t(YT) as the train proceeded, except for some of the feeding trains recorded from young of less than one week of age. This shows that the t(YL) must be responsible for the breaking off of a feeding train and that the parent is therefore not responding to the cumulative effect of gradually lengthening t(YT)s.

6. Observations showed that after breaking off a feeding train the parent sometimes stopped feeding altogether but most usually immediately reverted to self-feeding. By comparing the t(PF) and the t(PT) it can be seen that there is no 'lag' prior to the commencement of a self-feeding train (Appendix 1/n), i.e. the parent does not 'wait' to see whether the young may still be hungry but instead immediately eats the food itself. Similarly, by comparing the t(PT) and the t(PL) it can be seen that the parent shows no lag prior to initiating a feeding train (Appendix 1/n). There is in addition no significant difference between the t(PL) which occur before the parent initiates a feeding train or before a young initiates a feeding train from self-feeding parents.

These data will show that not only is the Waiting-Time Threshold fixed over the short time scale but also that it must be a most important factor in the organisation and control of the feeding trains.

3/D/VIII Flexibility in the Control System

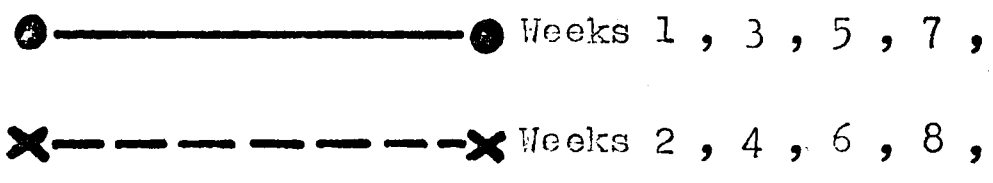
If the waiting-time was the only factor to which the

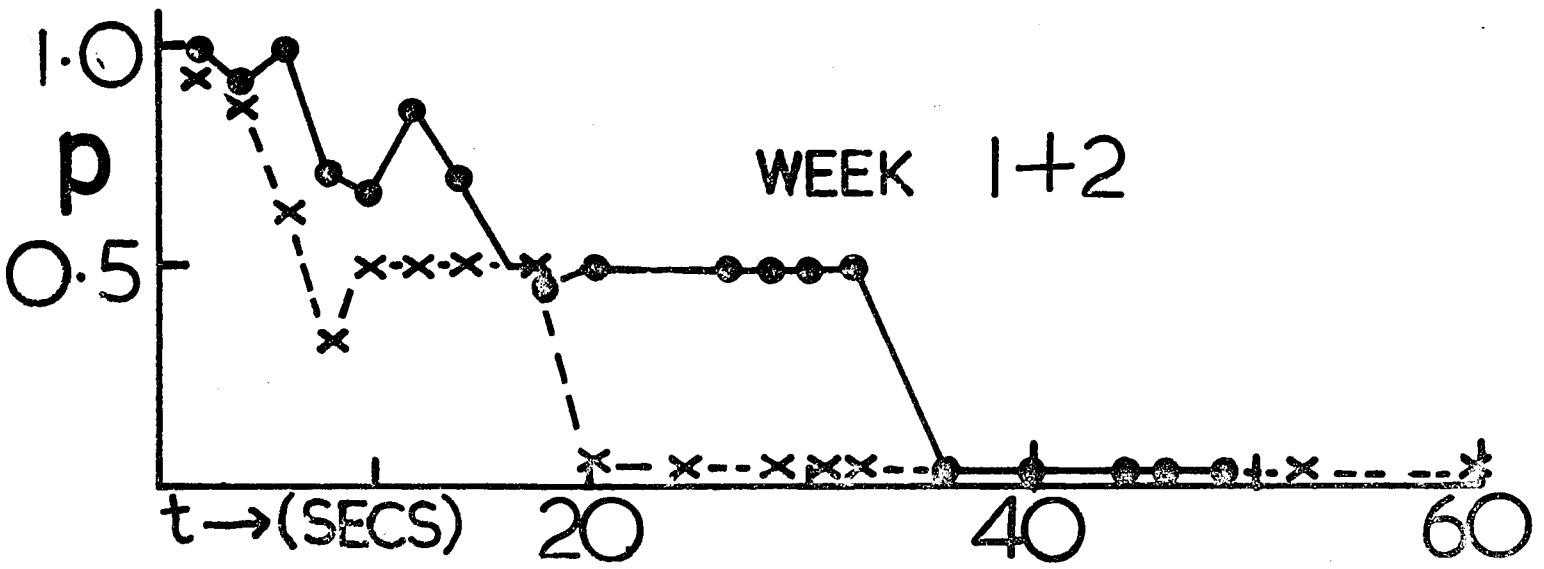
parent was responding, then the observed waiting-times should fall into two distinct classes, (1) those which were followed by further presentation of food and (2) those which were not. To examine this I lumped all the observed waiting-times together (i.e. all the t(YF), t(YT), t(YL) and t(Yi)) and calculated the probability of a waiting-time of any given length being followed by the parent presenting more food (Fig. 13). It is immediately obvious that the waiting-times do not fall into two distinct classes for the probability of waiting-times of gradually increasing length being followed by further presentations of food only gradually drops to zero. The 'saddles' can be ignored as they are probably an artefact due to decreasing numbers of observations of long waiting-times. The analysis presented in 3/D/VII showed that the Waiting-Time Threshold was fixed over the short time period, so Fig.13 must mean that the parents are reacting to other factors in the behaviour of the young as well as to the waiting-time.

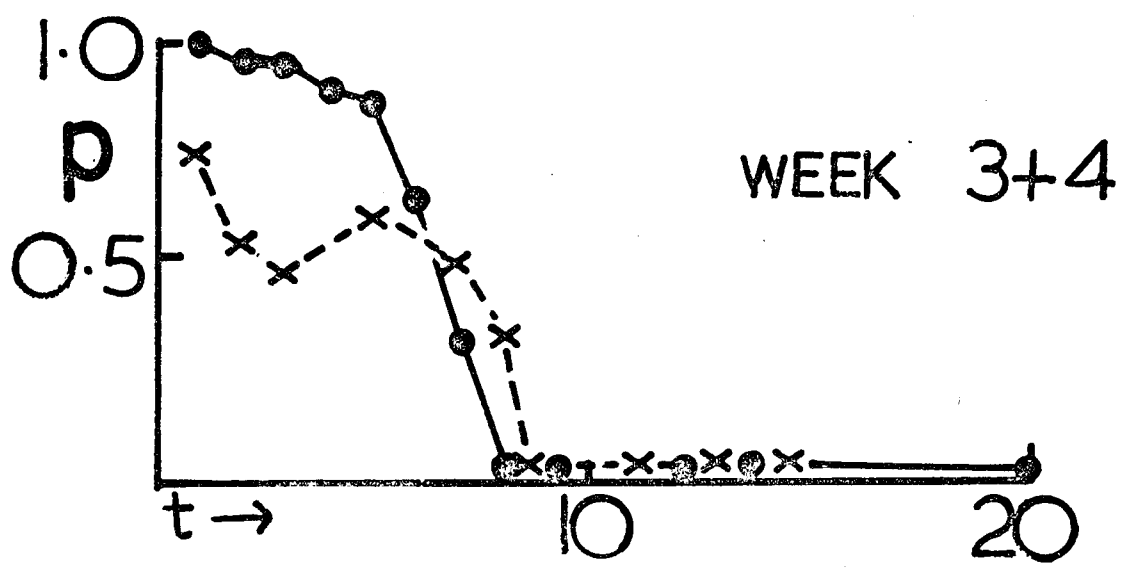
1. I have already described (1/B/IV) how a parent will break up food items which are too big for the young to eat. This process would cause a waiting-time (as I have measured it) far in excess of the threshold level, yet in these cases the parent will continue to present more food. Similarly, a young running from 8 m away from the parent might also cause a waiting-time in excess of the threshold level, but here again the parent will continue to present more food. In both of these cases some aspect of the general behaviour of the young must have counteracted the effect of the prolonged waiting-time.

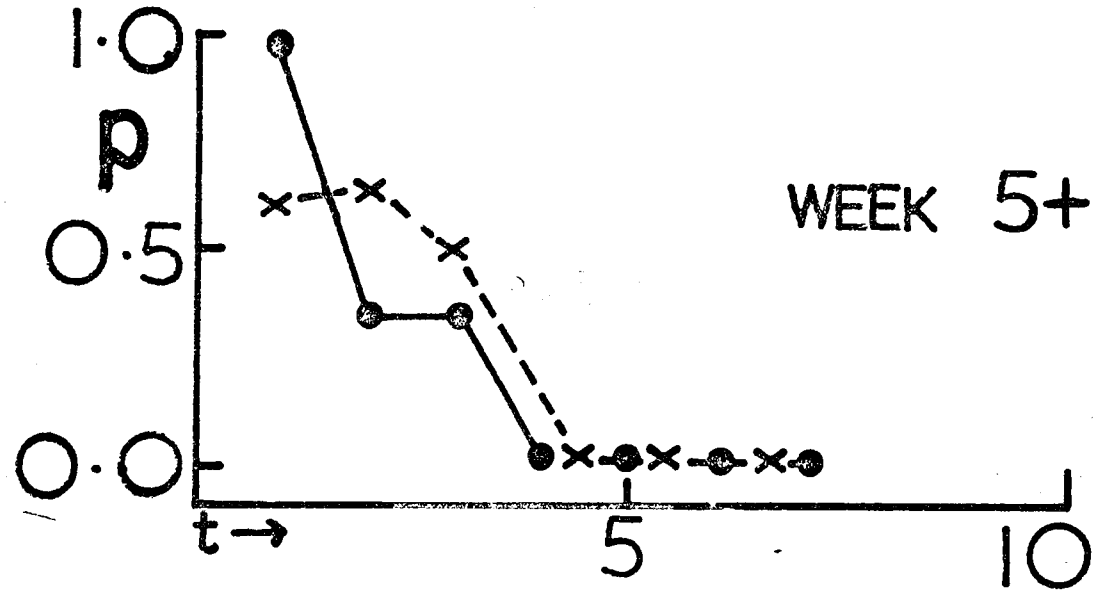
2. Begging of the young may cause the parent to present

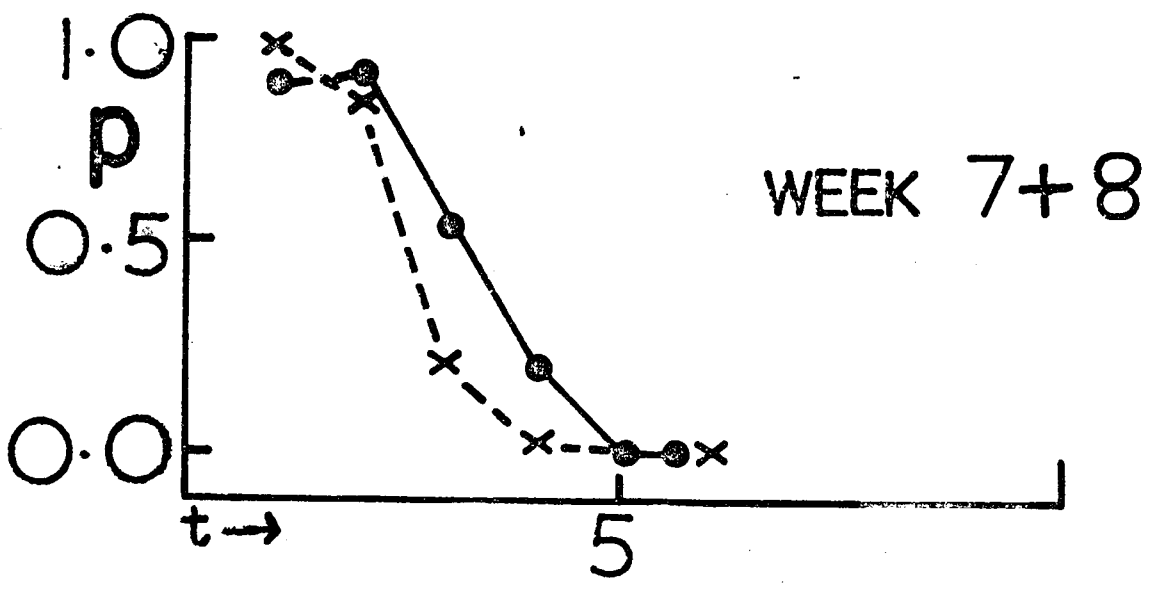
Fig. 13 Probability (p) of waiting-times of increasing length being immediately followed by the parent presenting more food .




1·0
p
0·5
WEEK 1+2
t→(SECS)
20
40
60


1·0
p
0·5
WEEK 3+4
t→
10
20


1·0
p
0·5
WEEK 5+6
0·0
t→
5
10


1·0
p
0·5
WEEK 7+8
0·0
t→
5

more food after a waiting-time longer than the threshold level, but in general begging does not seem to have much effect on the parent. The young often beg after being fed (see Lind 1965 for description) and the parents often then go and fetch more food, but it is very probable that the parents would have done this anyway. Indeed, begging only seems to be effective when the parent is motivated to feed the young, and it is not effective when the parents are not motivated to feed the young, i.e. during high tide or low tide pause from feeding activities. I rarely saw begging in the free-living families, but I frequently saw it in the fenced-in families whose young were always near to starvation. Begging in very small young occasionally seems to be effective in stimulating the parent to present food, and Tinbergen (pers. comm.) has seen a brooding Oystercatcher stimulated to dig up and present a tiny stone in response to the frantic bill tip begging of a one-day old Black-headed Gull chick (Larus ridibundus) which had been hatched out under it.

3. One behaviour of the young which has an immediate effect on the parent is the brooding call. This is sometimes very intense (and merges into the distress call) and it causes the parent to immediately come to the young and to brood it, even if the parent is feeding another young or itself.

These three types of behaviour of the young can all have an effect on the parent. Those described in 1 and 2 seem to override the effect of a waiting-time longer than

the threshold level, while the behaviour described in 3 overrides everything and causes the parent to brood the young. Unfortunately, in the case of 1, I cannot say what specific aspect of the behaviour of the young it is that the parent responds to.

3/2 Changes in the Organisation of Parental Feeding as the Grow Older

3/2/I Introduction

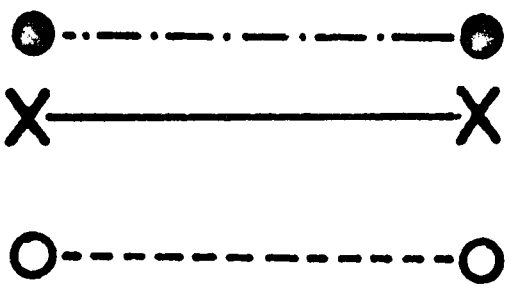
We can now see that there are two components which make up the control system of parental feeding. The first is mainly under internal control and organises the return of the parent on its own initiative with food to the non-feeding young. The second component (Waiting-Time Threshold) is dependent upon the behaviour of the young to maintain and break off the feeding trains. The two components are linked together in that some aspects of the general behaviour of the young (i.e. approach or nearness to the parent) can elicit food-presentation from the self-feeding parent and thus can initiate a feeding train.

By the time the young are 4-6 weeks old they are becoming more and more independent from their parents and are starting to forage for food by themselves. Correlated in time with this, there is a very marked change in the organisation of parental feeding, especially in the role that the parent plays, which eventually leads to the break-down of parental feeding and to the splitting up of the family.

3/2/II Evidence for a Motivational Change in the Parent

I have already described how the parents transport less and less food to their young (Fig. 2). At the same time, the parents initiate fewer feeding trains (Fig. 14).

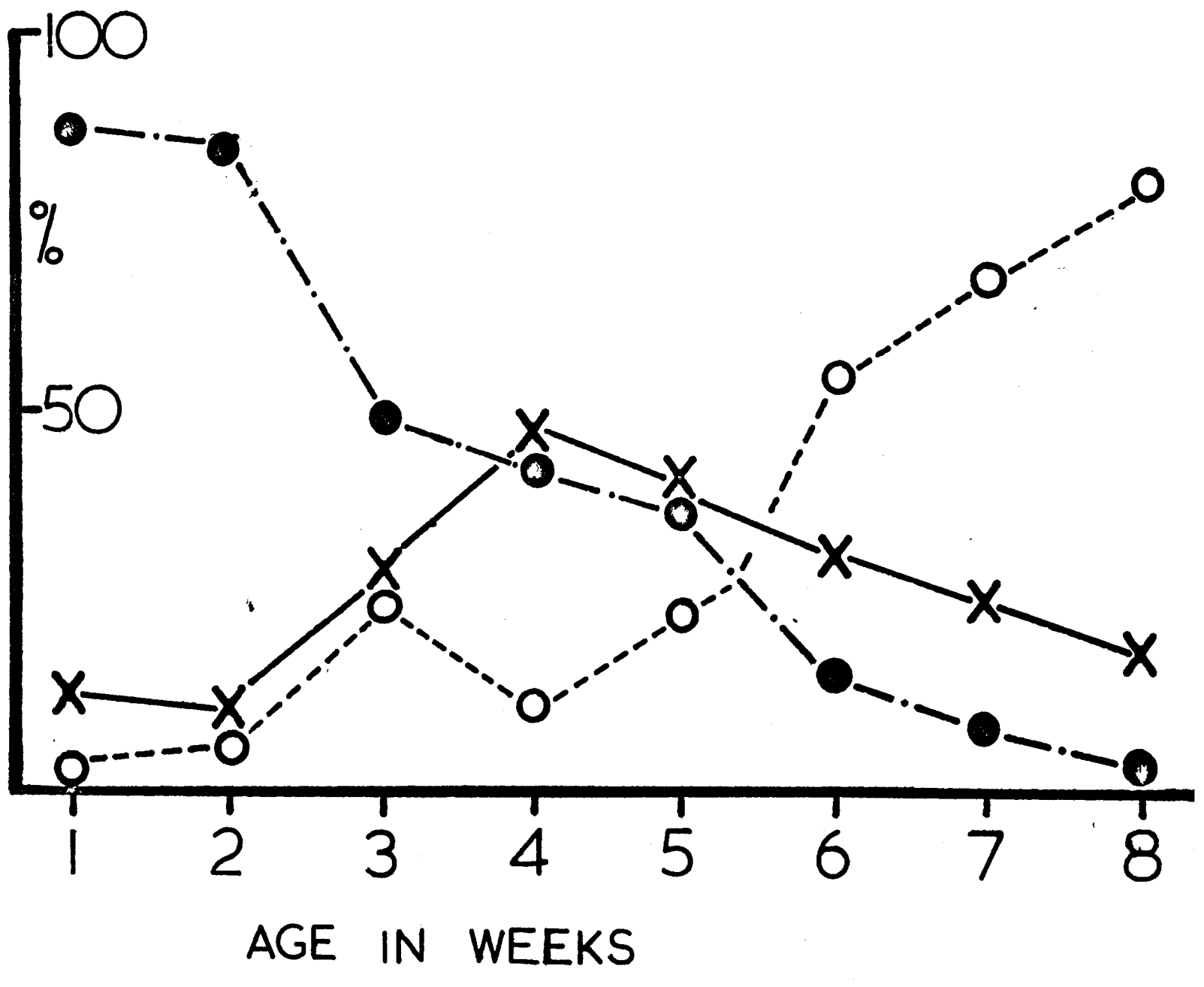
Fig. 14 % of feeding trains initiated by the parent as the young grow older



initiated by the parent

initiated by the young being alongside the parent

initiated by the young running up to the parent

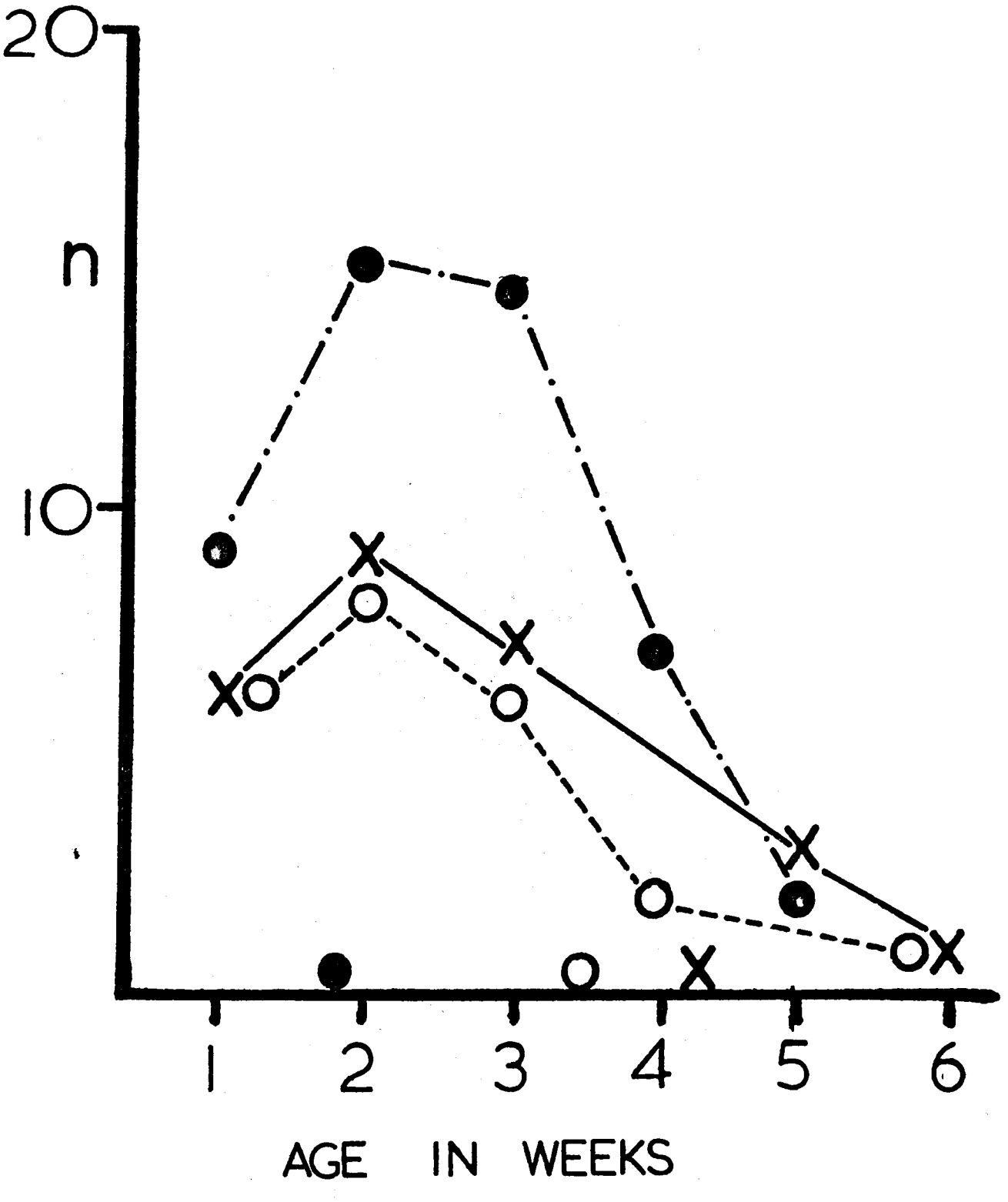


Up to the fourth week most of the feeding trains are initiated by the parent bringing food to the non-feeding young, but after this most of the feeding trains are initiated by the young eliciting food-presentation from self-feeding parents (1/C/II). This change in the behaviour of the parent could be due either to a change in the behaviour of the young (i.e. the parent would initiate more feeding trains if the young did not) or it could be due to a long term motivational change within the parent.

In the fenced-in nests the parents have to feed the young almost entirely on their own initiative, for the young are unable to initiate food-presentation from self-feeding parents since the young are restrained within the fences. Fig. 15 shows the combined average amount of food items brought to the young by both parents during the active phases of the feeding cycle in each of the three families studied. There is an increase in the feeding rate up to the end of the second week but the feeding rate then declines to a very low level in the face of an increasing need for food by the young. Whenever the parents did bring food the young immediately seized it and often begged intensely after eating it, yet this did not stimulate the parents to maintain a higher feeding rate. Each family started with two young, but in no case was enough food provided for both to survive, and when the surviving young were released at 5-6 weeks of age they were unable to fly although the young of free-living families were by then fully fledged.

This drop in the parent initiated feeding rate in the fenced-in families is similar to the drop in the frequency of parent initiated presentations in the free-living families already referred to. This suggest that there is a gradual change in the motivation of the parents to present food to the young on the parents' own initiative,

Fig. 15 Combined ~~number~~ average number of food items (n) flow in by both parents of each fenced-in family (isolated symbols show age at which first young died)



this motivational change being independent from any overt change in the behaviour of the young.

Correlated in time with this change in the behaviour of the parent is the very marked and obvious drop in the length of the Waiting-Time Threshold, i.e. the parent will not wait so long for the young to take and eat the food presented. This is also indicative of a fundamental change in the general motivation of the parent to feed the young.

3/E/III Changes in the Organisation of the Feeding Trains

Although the waiting-times are of great importance in maintaining the feeding trains of older young, these trains are not so rigidly maintained as are the feeding trains of smaller young. If the older young do not instantly react to and seize the presented food then the parent will eat the food itself, although the parent will present the next item of food if the young is still nearby. There are, thus, isolated self-feedings of the parent during a feeding train, this never being seen in the feeding trains of small young. In addition, the breaking off of a feeding trains becomes almost entirely due to the young wandering off from the parent to feed itself rather than to the parent ceasing from presenting food to the young. If a small young wanders off from the parent during a feeding train then the parent will invariably take the next item of food to it and present it, provided that the young has not previously exceeded the Waiting-Time Threshold. This is rarely seen with older young.

3/E/IV Breakdown of Parental Feeding

As the young grow older, there is a marked change in

the relative importance of the parent and the young in the general organisation of parental feeding. With small young it is the parent who initiates most of the food-presentations and most of the feeding trains, but the influence of the parent gradually decreases while the role of the young in initiating, maintaining and breaking off feeding trains becomes more and more important, and this change in the relative importance of the parents and young in the initiation of feeding trains foreshadows the final breakdown of parental feeding.

The age of the young at which parental feeding ceases is very variable but it seems to depend upon how soon the young become self-sufficient, and this itself is dependent upon what food the young is learning to eat. In environments where the parents are feeding their young almost entirely on subterranean invertebrates (i.e. annelid worms of dunes, meadows and mud flats), parental feeding stops soon after fledging, while in environments where the parents are feeding their young on marine bivalve molluscs or crabs, parental feeding may continue for months. It seems that the young can become self-sufficient more quickly in the former environment than in the latter, and my observations on the development of feeding behaviour in young Oystercatchers (in prep.) show that whereas a six-week old young is nearly as efficient as an adult in probing for annelid worms, a similar aged young is hopelessly inefficient at opening bivalves.

Thus, Dare (pers. comm.) reports that inland breeding Oystercatchers in the Scottish Highlands split up from their young at about 6-8 weeks after hatching. Mercer (pers.comm.) reports the same for dune feeders at Newborough Warren in

Anglesey, and Safreil (1967) and Harris (1967) report the same for the meadow feeders on the island of Skokholm in Pembrokeshire. At Ravenglass I have observed only one breeding pair which fed entirely on mud flat annelids, and in both years that I have studied this pair the family split up 6-7 weeks after the chicks hatched.

With bivalve or crab eating breeding pairs the pattern is entirely different. Mercer (pers. comm.) reports one family from Anglesey in which the parents fed their young on Cardium edulis, and parental feeding was continuing after 12 weeks. At Ravenglass, all the families which I observed to feed their young on Mytilus edulis or Carcinus were continuing with parental feeding for at least 12 weeks (the earliest split up being at 12 weeks), the others splitting up between 18 and 26 weeks. I have eight observations of families feeding their young on Mytilus for at least 26 weeks, the record being a family with a 38-week old young which were still feeding together as a family group although parental feeding had apparently ceased. I also have three observations of families feeding their young on Carcinus for at least 22-26 weeks, the record being a family which was still feeding their young 43 weeks after hatching. (N.B. In all these cases either the parents or the young or both were individually colour ringed).

This last family was very interesting to watch, for the organisation of parental feeding was very chaotic. I observed the family while the young was 22 weeks, 39 weeks and 43 weeks old. At 22 weeks of age there were still well defined feeding trains, and some of them were even initiated by the parents, both of whom were feeding the young (this also being the case for the other families referred to which

were feeding young of this age). By 39 weeks of age, the male had stopped feeding the young and the female only fed the young on her own initiative twice out of 83 observations of food presentation. There were no well defined feeding trains, and food presentation was being initiated entirely by the young running up to the female and seizing the food from her bill. By the time the young was 43 weeks old, the male was attacking the young and driving it away from their feeding territory. The female was not attacking the young, but neither was she presenting food on her own initiative. I observed the young take food from her on 50 occasions and in each case the young had to almost pull the food from the female's bill.

These observations show that the breakdown of parental feeding occurs in two stages. The first is the gradual reduction in the parent's role in initiating feeding trains which occurs around the third week. The second stage is dependent upon how long the young demands food from its parents, and this seems to be correlated in time with how long the young take to learn to feed themselves. This demand by the young can keep parental feeding going for as long as 43 weeks (although this must be an extreme case). An interesting sideline from this observation is the effect of the young on the migration of the parent. Normally, as soon as the family splits up, the parents migrate away from their breeding grounds (Safriel 1967, Dare pers. comm.) this being noticable at Ravenglass where colour-ringed young were observed to be feeding themselves when there was no sign of their parents in the area. However, in the cases when constant demand by the young maintained parental feeding, the parents did not migrate although parents which had split up from their young were migrating.

Observations of parental feeding in other species of Oystercatchers also show the same pattern. Webster (1941) reports that the young of Haematopus bachmanii are not self-sufficient on marine molluscs until 16 weeks of age and are fed by their parents up to that age (see also Williams 1927 for the same species). Bancroft (1927) similarly reported that in Haematopus palliatus frazari, parental feeding continues 'well after fledging', the parents in this case were feeding their young on marine bivalves.

3/F A Model of the Motivation and Control of Parental Feeding (Fig.16)

3/F/I Introduction

From the data and observations presented in the preceding sections it is now possible to construct a model which will describe both the motivation and control of the parental feeding system as seen in the Oystercatcher. The function of the model is mainly to describe the simplest causal system that will account for the observed behaviour of the parents, but the model may also be useful in describing a basic control system for parental feeding which is applicable to other avian species.

3/F/II Self-Feeding

The observations on both non-breeding and breeding birds (3/B) show that there is a pause from all feeding activities during the low tide period and that during the active phase of the feeding cycle the birds tend to feed at a constant rate. This data is undoubtedly simplified but it is the best available.

It is therefore assumed that the basic motivation for self-feeding is controlled by a central nervous feeding system which gives a continuous output signal (OS). The appropriate motor activities of food-searching, food-preparation and food-ingestion are primarily organised by

this OS on all-or-nothing basis. At the start of the first active phase of the feeding cycle the level of the OS is high, and feeding activities are observed. Feedback from the consequences of these activities, acting through both peripheral receptors (crop distension may be important, see Wood-Gush 1968) and central receptors, gradually reduce the level of the OS until OS = 0. When the OS reaches this subliminal level all feeding activities will cease. According to this hypothesis, the OS must remain at this subliminal level during the low tide pause, which necessitates the assumption of a second central nervous 'satiety system' which inhibits the output from the feeding system until, perhaps, the crop is once more empty. Once the crop is empty, the OS will once again be at a high level, and feeding activities will recommence.

3/F/III Presentation of Food Initiated by the Parent

Observations show that presentation of food does not occur unless there is some motivation for self-feeding (i.e. OS > 0), and observations also show that at the beginning of each active phase of the feeding cycle the parents always feed themselves first before presenting food to their young (see also Safriel 1967). These observations suggest that the switch from food-ingestion to food-presentation is determined by the level of the OS. It is therefore proposed that there is an output signal threshold (OST) set at a certain level which switches the on-going self-feeding behaviour from food-ingestion to food-presentation when OS = OST.

It is observed that the frequency of parent-initiated presentations decreases as the young grow older, and this can be accounted for by a gradual, long-term reduction of the

level at which the OST is set. When the OST is set at a high level (i.e. when the young are small) then the frequency of parent-initiated presentations will also be high, but as the setting of the OST decreases then so will the frequency of the parent-initiated presentations.

The factors which might affect the long term setting of the OST must be independent from those factors which affect the level of the OS at any particular moment, for the observed decrease in the frequency of parent-initiated presentations is not accompanied by any observable decrease in the amount of self-feeding. It is therefore proposed that the OST is controlled by a factor (K) which acts independently from those factors controlling the level of the OS.

The proposed operation of the switch is as follows. K sets the OST at a certain level. Feedback from self-feeding gradually reduces the level of the OS until OS = OST. The motor activities will then be switched from food-ingestion to food-presentation. K gradually wanes as the young grow older with the result that the OST setting is gradually reduced and thus the frequency of parent-initiated presentations is also reduced.

3/F/IV Presentation of Food Initiated by the Young

Observations show that the approach or nearness of the young can elicit food presentation from self-feeding parents. Operationally this has the same effect as that of the OST switch in that the parent's self-feeding activities are switched from food-ingestion to food-presentation.

The approach, nearness and general behaviour of the young will be called the D factor, and it is assumed that

the parent can compute D and give it some value. It is proposed that D operates the OST switch by raising the level of the OST so that OS = OST. As long as D remains high (i.e. during a feeding train) then the OST will remain raised and food-presentation will continue. As soon as D falls (i.e. the young leave the parent) then the OST will fall with the result that OS > OST, and self-feeding will continue. D therefore has a very short term effect on the OST.

There are many observations which support this interpretation of D, for example, by comparing the behaviour of the parent in young initiated feeding trains and in parent initiated feeding trains when the young leave the parent. In the young initiated feeding trains the OST has been raised by the D factor, so when the young leaves the parent the OST will rapidly fall so that OS > OST, and the parent should not subsequently follow the young and and present more food but should revert to self-feeding. However, in the parent initiated feeding trains the opposite should happen, for when the young leaves the parent, then the OS should still be at the OST level (i.e. OS = OST) and the parent should follow the young and present more food.

This is in fact what happens (Table 10), for in young initiated feeding trains the parents follow the young and present more food significantly less often than in parent initiated feeding trains.

TABLE 10 Behaviour of the Parent when the Young Breaks Off a Feeding Train

	Parent follows young and presents food	Parent does not follow young
Feeding Train initiated by parent	28	53
Feeding Train initiated by young	16	73

$$\chi^2 = 5.25,\ p = <0.02>0.01$$

As K wanes, D will become more important in the initiation, maintenance and breaking off of feeding trains, as is observed. This must mean that D acts directly on the OST and does not act through K (see also 3/F/V), for the waning of K occurs independently from any effects of D.

3/F/V The Waiting-Time Threshold (WTT)

From 3/D/VIII it has been shown that the WTT is unaffected by who initiates a feeding train (i.e. it is unaffected by D) and that it is unaffected by the number of YTs in the feeding train (i.e. it is unaffected by the level of the OS). The WTT must therefore operate independently from the OST. However, since the decrease in the frequency of parent-initiated presentations is correlated in time with the decrease in the length of the WTT, it is proposed that the WTT is set by the K factor.

Although D does not affect the WTT, D can override the effect of a waiting-time longer than the WTT by its action on the OST.

3/F/VI Behaviour of the Parent Subsequent to YL, Yi or PA

Subsequent to a YL, Yi, or PA the parent usually reverts to self-feeding and, for this to happen, then OS > OST. In the case of feeding trains or presentations which were initiated by the young the OST will fall as soon as the young leave the parent so then OS > OST and self-feeding can continue. However, in the case of feeding trains or presentations which were initiated by the parent (i.e. when OS = OST) it is difficult to understand how OS > OST so soon after the feeding event.

The YL, Yi and PA have in common the fact that the WTT is exceeded, and this in itself could have the effect of depressing the OST so that subsequently the OS > OST and and self-feeding can continue. A third factor, the L factor, is therefore proposed which acts to depress the OST if the WTT is exceeded. It is assumed that the value of L is dependent upon by how much the waiting-time (T) exceeded the WTT, i.e. L = T - WTT. It is also proposed that L has a longer term effect on the OST than does the D factor.

3/F/VII The Pause from all Feeding Activities

This can only happen when OS = O, but before this can happen the OS will reach the OST level and so a presentation will occur. There are two rather clumsy ways out of this paradox: (1) repeated depressing of the OST by the L factor and (2) in conjunction with this, on-going digestive processes might reduce the OS to zero during either a self-feeding train or a parental feeding train.

3/F/VIII The Final Hypothesis

1. The basic motivation for all feeding activities is

controlled by a central nervous feeding system which gives a continuous output signal (OS). This OS organises the appropriate feeding activities, and feedback from these activities gradually reduces the level of the OS. When OS = 0 all feeding activities cease.

2. Linked to the OS is a threshold operated switch which switches the motor activities from food-ingestion to food-presentation at a certain level of OS. This output signal threshold (OST) is set by the K factor.

3. The K factor also sets the Waiting Time Threshold (WTT) which operates independently from the OST. The gradual wanting of K as the young grow older reduces the setting of the OST and therefore the frequency of parent initiated presentations, as well as reducing the length of the WTT.

4. Aspects of the general behaviour of the young, the D factor, act directly upon the OST by raising it so that OS = OST, thus initiating food-presentation. The effect of D is short term.

5. The effect of exceeding the WTT is to lower the OST by the L factor, the value of L being proportional to the amount by which the waiting-time (T) exceeded the WTT. D, however, can override the effect of the L factor.

3/F/IX The Structure of the Model (Fig. 16)

The model is made up of 'decision points', 'computation orders' and 'motor output orders' which are linked in certain ways. Each decision point can have the value 'true' or 'false', and the sequences of behaviour generated by the model depends on these values. The computation orders

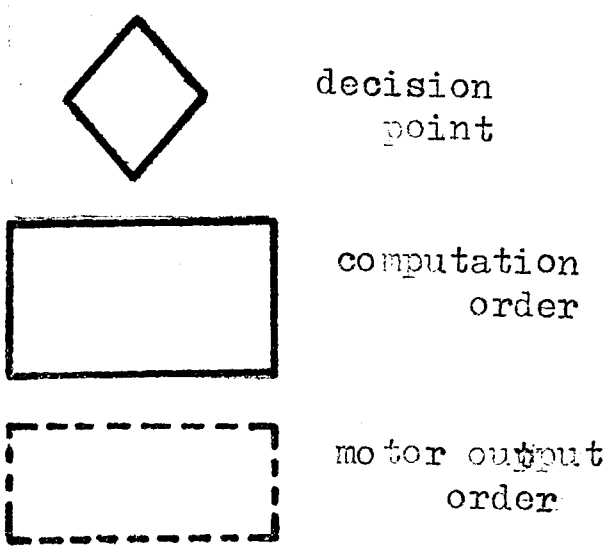
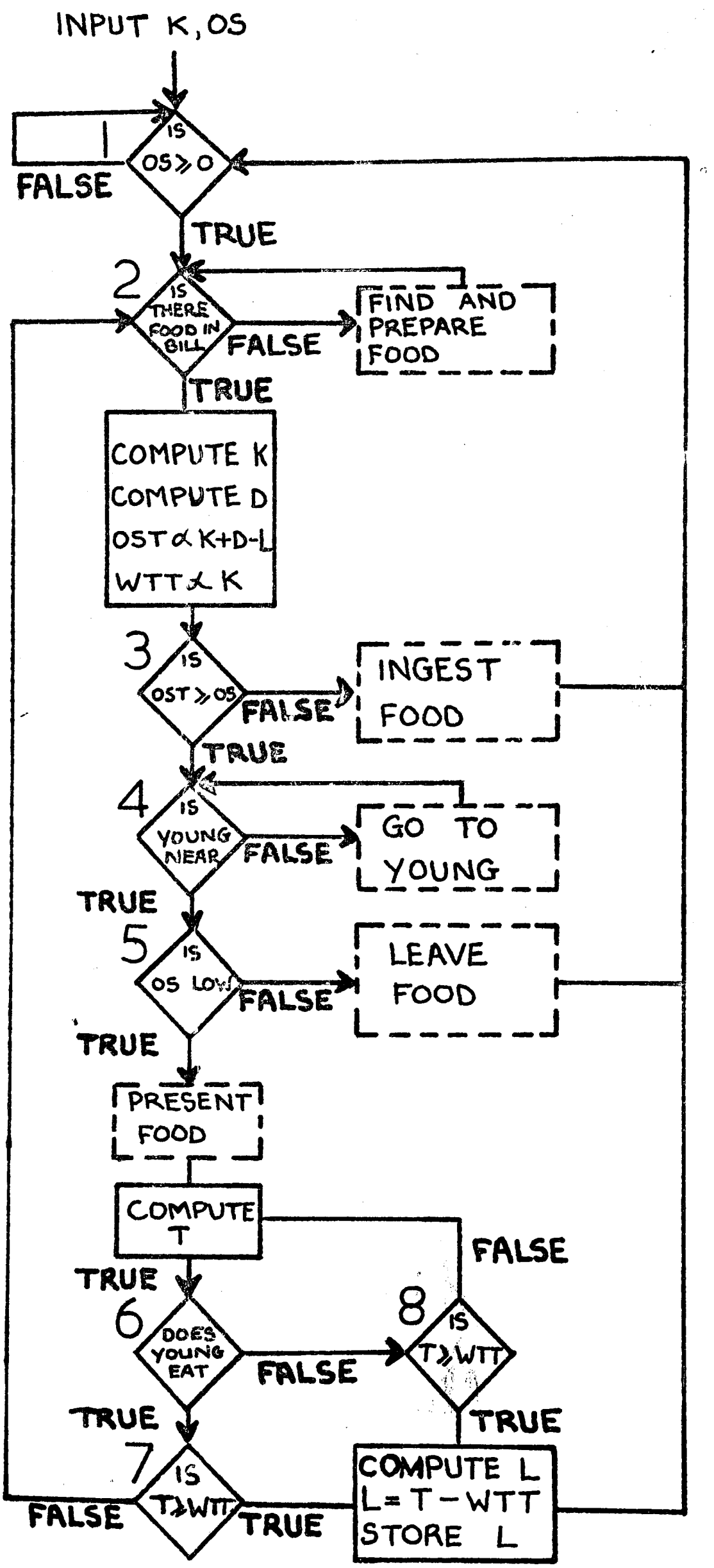


Fig. 16 Model of the Motivation and Control of Parental Feeding in the Oystercatcher



compute the values of the variables K, D and L which are required for setting the levels of the two thresholds OST and WTT. The model is represented in Fig. 16.

3/F/X The Generation of Sequences of Parental Feeding Behaviour

1. Self-Feeding Train: 1→2→3

The parent will continue feeding itself until either Point 1 becomes False (i.e. OS = 0) or Point 3 becomes True. In the first case it will stop feeding, in the second case it will transport or present food.

2. Isolated Feed of the Young (Yi): 1→2→3→4→5→6→8→7

Point 3 becomes True. Food is presented to the young, but the WTT is exceeded (i.e Point 7 is True). L is therefore computed and stored so that when OST is next computed the level of OST will be depressed. Point 3 will thus become False, and the self-feeding train will continue. Note: the same sequence, or with Point 8 becoming True, will generate a PA.

3. Initiation of a Feeding Train (YF):

The same sequence as 2. above, only Point 7 becomes False. The feeding train will be maintained for as long as Point 7 remains False, or for as long as D can override any effect of Point 7 becoming True. Note: Point 3 can become True either by the OS falling to the OST level, or by D raising the OST to the OS level. Note: the maintenance of the feeding train will not be affected by OS becoming zero.

4. Breaking Off a Feeding Train (YL)

Either Point 7 or Point 8 become True. L will depress OST so that self-feeding can continue. In feeding trains initiated by the young, the departure of the young will immediately cause the OST to fall as the value of D falls, so making Point 3 False.

5. Parent Leaves Food for the Young

Point 5 becomes False. The operation of Point 5 is proposed because observations show that (1) Leaving tends to occur in those feeding trains initiated by the young and that (2) Leaving occurs most when the young are well grown. These observations suggested that Leaving occurs when the OB is high.

3/F/XI Discussion of the Model

The model works quite efficiently at the purely descriptive level but its main weakness lies in its inability to give quantitative predictions. In order to make quantitative predictions, much more would have to be known about the digestion rates and crop capacity of both the parents and the young, as well as the size, wet weight and dry weight of the food items being eaten. However, the basic assumptions of the model could be tested by opening the feedback loops between the parents and young. This could be done by trapping either the parent or the young and artificially eating them by force-feeding. Thus, the model would predict that an artificially eated parent would cease from all feeding activities even if the young intensely begged, and similarly, that a parent faced with a continually eated young would still keep returning at random moments in time with food. Experiments along these lines could reveal much information about the interactions between self-feeding and parental feeding, and about the interactions between the parents and the young, but unfortunately, I have not had the opportunity to carry them out.

3/G Discussion of the Control System

The control system of parental feeding in the Oystercatcher is made up of two separate components. The first

organises the return of the parent on its own initiative with food to the non-feeding young, and is closely linked to the factors that control self-feeding. The output from this component is largely unaffected by the behaviour of the young in that the time elapsing between the parent-initiated presentations is not affected either by when the young last took food from the parent, or by how long the young maintained a feeding train. This component of the parental feeding system is therefore mainly under internal control. The second component of the system controls the behaviour of the parent subsequent to the presentation of the food and is almost entirely dependent upon the behaviour of the young. The parent will continue to present food items for as long as the young eats the food within the threshold time, and, as soon as the young fails to do this, the parent will stop presenting food. The two components of the control system are linked together in that the general behaviour of the young (i.e. approach or nearness to the parent) can elicit food presentation from the parent by activating the first component of the control system. In this way the demands of the young for food will be exactly met by the parent.

There are unfortunately few studies of the control system of parental feeding of other avian species with which the Oystercatcher's control system can be compared, for it would be interesting to see how the control system differed with factors like the amount of food brought at each visit and whether or not the young accompanied the parent. However, von Haartman (1953) studied the Pied Flycatcher (Muscicapa hypoleuca) which, like the Oystercatcher, feeds its young on numerous small items of food, although the young are unable to accompany the parents while being fed.

Von Haartman showed that the frequency with which the parents bring food to the brood is determined by the strength of the response of the young to the parent. By reducing a brood of seven young to two young and then by continually replacing these two young (once they had been fed) with two new hungry young, von Haartman showed that the parents brought food at the same rate as if there were seven young in the brood. Similarly, by placing six hungry young in auditory but not visual contact with a nest containing but one young, the parents brought food at a very high rate, even though the only young which the parents could actually feed was sated. These data suggest that there might be a threshold system (analogous to the sTT in the Oystercatcher) which controls the frequency of feeding. Von Haartman does not indicate whether the parent Flycatcher feeds the young in bouts separated by longer absences (analogous to the feeding trains), or whether the increase in feeding rate is due to longer bouts or to a general shortening of intervals between feeds, nor does he indicate how self-feeding of the parent relates to feeding the young, so it is difficult to make closer comparisons.

Hailman (1967) in his study on the Laughing Gull (Larus atricilla) showed how regurgitation of food by the parent was controlled by the pecking and begging of the young, but unfortunately quantitative and qualitative details are lacking.

CHAPTER 4 THE EVOLUTION OF PARENTAL FEEDING IN THE OYSTERCATCHER

4/A Functional Interpretation of Parental Feeding

Both the general organisation and control of parental feeding show specific adaptations to feeding relatively small items of food in large quantities to rapidly growing young for a long period of time.

For example:

1. The successful rearing of the young depends upon the young following the parents out onto the feeding grounds. When the young are very small the parents can in fact support them by transporting all the food, but we have seen from the fenced-in nests that the parents are unable to support their young in this way once the young are more than two weeks old. Indeed, the parents gradually stop transporting the food to the young under these conditions even though the young need more and more food and beg more and more intensely. Safreil (1967) also fenced-in some nests and found the same phenomenon. Of more interest are Safreil's observations on free living families who are feeding their young on marine food. Many of these families had territories on the meadows on top of Skokholm Island, and the young were unable to follow their parents down onto the shore because of the steep cliffs. Consequently, the parents had to transport much food to the young, and Safreil observed that these young grew more slowly than did the young of parents who were feeding entirely on terrestrial invertebrates. Safreil also observed that the predation rate was higher on the young of these shore feeders than on the young of the terrestrial feeders, for the shore feeders had to be away from their young on numerous occasions in order to collect food.

2. In 2/D I described various differences between the ontogeny of parental feeding in Oystercatchers and Laughing Gulls, and these can be interpreted in terms of the totally different forms of parental feeding shown in these two species. In the Laughing Gull the first regurgitation of food is in response to the pecking of the young and there is a high probability that the parent will have food in its crop since the temporal patterning of incubation shift is closely related to foraging behaviour (Drent 1967). In the Oystercatcher no such process can occur because the Oystercatcher is only able to produce one item of food at a time, and each item must be gathered separately. It would be highly disadvantageous if bill tip pecking of the young would stimulate the brooding parent to search for food because the brood would be left unguarded, so instead the on-coming parent at brood relief brings food and the off-going parent after brood relief returns with food. In this way the young are fed without both parents being away at any one time. There are also differences between the development of behaviour in the young for the young Oystercatcher does not show such a marked pecking response to the parent's bill but instead develops a marked orientation response which may be an adaptation for following the parent.

3. The Oystercatcher also maintains a feeding territory which it defends against other Oystercatchers. This feeding territory may be the same area as the breeding territory (Safriel 1967), or it may be an adjoining area of mud flat (Lind 1965) or it may be an area on a

mussel bed some distance away (over 3 Km in extreme cases). In these latter cases the parents cannot take their young to these feeding territories until the young can fly, so that the parents may have another feeding territory adjoining or nearer to the breeding territory.

4/B Possible Selection Pressures

The function of parental feeding is obviously to feed the young, but this gives little indication as to why it has evolved in the Oystercatcher. Lind (1965) suggests that the evolution of parental feeding is highly advantageous for the Oystercatcher can now breed in areas away from the main feeding grounds and in areas rich in food for the adults, but where food for the young is scarce. In addition, Lind suggests that in time of severe food shortage, the Oystercatcher might be able to raise at least one young whilst other waders might be totally unsuccessful. Safriel (1967) expresses essentially the same views. Although these may be important secondary advantages from the evolution of parental feeding, they still do not explain why parental feeding evolved in the Oystercatcher rather than in any other wader.

Lack (1967) has pointed out that breeding adaptations shown by many marine birds are closely inter-related. The examples which he quotes are (a) most intertidal feeders have nests accessible to predators but widely dispersed, with cryptic eggs and cryptic nidifugous young; (b) most offshore feeders and some inshore feeders have large colonies in inaccessible sites and nidicolous non-cryptic young; and (c) many inshore feeders have more accessible colonies, with cryptic eggs and cryptic young which, though active, stay in the colonies, where the adults attack intruders.

Of these three groups, (b) and (c) have parental feeding, an obvious necessity if the young are tucked away in colonies far from the breeding grounds. The Oystercatcher is basically an intertidal feeder and shows all the group (a) breeding adaptations with the exception that it has evolved parental feeding. The Oystercatcher has in common with the offshore and inshore feeders a highly specialised feeding behaviour in that the Oystercatcher has evolved a skilled method of eating bivalve molluscs and other hard shelled marine organisms, as well as retaining the basic wader feeding behaviour of probing with the bill for buried food. The evolution of such a specialised feeding behaviour, and especially of a feeding behaviour which the young are unable to employ, entails difficulties during the raising of young, for the parents must either abandon their specialised feeding behaviour and feed in a manner, or an area, where the young can also feed, or the parents must feed their young. In the case of the Oystercatcher, the specialised feeding behaviour on bivalves possibly became species-typical through competition with other waders for food which could be found simply by probing. This competition with other waders would be fiercest during the breeding season, yet this would be precisely the time when parent Oystercatchers, prior to the evolution of parental feeding, would have been unable to exploit their specialisation on bivalve foods because there would not be enough food of a type which could be found by probing for the young to eat on the bivalve beds. The parents would therefore have had to abandon their specialisation in order to raise their young. The only way in which this source of food could be exploited by the parents would be for them to take their young out onto the

bivalve beds and feed them themselves, and selection would have favoured the young of parents who behaved in this manner.

The next point to consider is why the Oystercatcher feeds its young in such a peculiar way when the inshore and offshore feeders have not only developed some form of colonial nesting but have also developed the ability to carry large amounts of food to the young at each visit. Those inshore or offshore feeders which carry small amounts fo food on each trip (i.e some of the Sterni) have small young so that the size of the food item is large in comparison with the size of the young. The Oystercatcher has, in fact, one advantage over the inshore and offshore feeders in that the parents can take the young to the feeding grounds and thus protect it from predators while feeding it. The inshore and offshore feeders are unable to do this, and thus selection might favour colonial nesting as antipredator behaviour. The greater distance then travelled by the parents to and from the feeding grounds might then also favour the ability to carry large amounts of food on each trip.

The parental feeding of present day Oystercatchers has a second and very important function, for it is through the process of parental feeding that young Oystercatchers learn from their parents not only to recognise bivalves (or other hard-shelled organisms) as food, but also the technique of eating them (Norton-Griffiths 1967, Norton-Griffiths in prep.). This learning process depends upon the young following their parents out onto the feeding grounds, and there practising on the food which the parents leave for them to eat. In this way the young acquire the specialised feeding behaviour as soon as they are physically capable of doing so and they can also become fully efficient at this specialised feeding behaviour while still being supported and protected by their parents. This means that when they

finally split up from their parents they are not in competition with other waders for food. During the evolution of parental feeding, selection would therefore favour the retention of the basic wader breeding adaptations of having cryptic nidifugous young who accompany their parents onto the feeding grounds.

APPENDIX 1

Significance levels arising out of the analysis of the control of parental feeding presented in 3/D. The heading of each Table indicates the waiting-times that are being ra against each other. Two-tailed probabilities associated with Mann-Whitney z are given in each case. Note that:

a. A (-) indicates that the first member of the ranked pair is significantly shorter than the second member of the pair.

b. A (o) indicates that there is no significant difference between them.

c. In Tables K and L: t(YFy) indicates the t(YF) of young feeding trains
t(YLy) indicates the t(YL) of young initiated feeding trains
t(YFp) and t(YLp) indicate the t(YF) and t(YL) of parent initiated feeding trains

d. Tables I and J give values of the Spearman Rank Correlation Coefficient (r_s)

e. Wk. 1 ..... 8 indicate the age of the young.

	(A)			(B)		
	t(PA) : t(Yi)			t(YF) : t(PA)		
Wk. 1	(o)	z = 0.45	p = 0.66	(-)	z = 2.37	p = 0.02
2	(o)	z = 1.34	p = 0.18	(-)	z = 3.95	p = 0.0001
3	(o)	z = 1.59	p = 0.14	(-)	z = 2.14	p = 0.04
4	(o)	z = 1.92	p = 0.066	(-)	z = 2.00	p = 0.04
5		----------			----------	
6		----------			----------	
7		----------			----------	
8	(+)	z = 2.03	p = 0.04	(-)	z = 2.80	p = 0.006

the (+) indicates that t(PA) is longer than t(Yi)

(C)

t(YT) : t(PA)

Wk. 1	(-)	z = 2.90	p = 0.004	
2	(-)	z = 3.80	p = 0.0001	
3	(-)	z = 2.26	p = 0.02	
4	(-)	z = 2.17	p = 0.04	
5		————		
6		————		
7		————		
8	(-)	z = 2.04	p = 0.04	

(D)

t(PA) : t(YL)

	(o)	z = 1.59	p = 0.12	
	(o)	z = 0.61	p = 0.54	
	(o)	z = 1.11	p = 0.26	
	(o)	z = 1.46	p = 0.14	
		————		
		————		
		————		
	(o)	z = 0.84	p = 0.40	

(E)

t(YF) : t(YL)

Wk. 1	(-)	z = 2.70	p = 0.008	
2	(-)	z = 2.85	p = 0.004	
3	(o)	z = 1.26	p = 0.20	
4	(-)	z = 2.32	p = 0.02	
5	(-)	z = 2.49	p = 0.01	
6	(o)	z = 0.72	p = 0.52	
7	(o)	z = 0.00	p = 1.00	
8	(o)	z = 1.10	p = 0.92	

(F)

t(YP) : t(Yi)

	(-)	z = 2.53	p = 0.01	
	(-)	z = 3.65	p = 0.0002	
	(-)	z = 2.72	p = 0.006	
	(o)	z = 1.48	p = 0.14	
	(o)	z = 1.70	p = 0.10	
	(o)	z = 0.85	p = 0.40	
	(o)	z = 0.96	p = 0.34	
	(-)	z = 3.32	p = 0.001	

(G)

t(YT) : t(YL)

Wk. 1	(-)	z = 4.32	p = 0.00006	
2	(-)	z = 4.96	p = 0.00006	
3	(-)	z = 2.87	p = 0.004	
4	(o)	z = 1.54	p = 0.12	
5	(-)	z = 3.12	p = 0.002	
6	(o)	z = 0.55	p = 0.58	
7	(o)	z = 1.36	p = 0.18	
8	(o)	z = 0.43	p = 0.66	

(H)

t(YT) : t(Yi)

	(-)	z = 4.35	p = 0.00006	
	(-)	z = 6.09	p = 0.00006	
	(-)	z = 3.37	p = 0.001	
	(o)	z = 1.89	p = 0.06	
	(o)	z = 0.36	p = 0.72	
	(o)	z = 0.26	p = 0.78	
	(-)	z = 2.10	p = 0.04	
	(-)	z = 3.70	p = 0.0002	

(I)

correlation between t(YF) and number of YTs in the feeding train

Wk. 1	r_s = - 0.74	p = 0.01	
2	r_s = - 0.15	ns	
3	r_s = - 0.43	ns	
4	r_s = - 0.03	ns	
5	r_s = - 0.20	ns	
6	r_s = - 0.28	ns	
7	r_s = - 0.18	ns	
8	r_s = - 0.08	ns	

(J)

correlation between t(YL) and the number of YTs in the feeding train

	r_s = - 0.38	ns
	r_s = - 0.29	ns
	r_s = - 0.28	ns
	r_s = - 0.31	ns
	r_s = - 0.12	ns
	r_s = - 0.11	ns
	r_s = - 0.39	ns
	r_s = - 0.03	ns

	(K) t(YFy) : t(YFp)		(L) t(YLy) : t(YLp)	
Wk. 1	(-)	z = 2.61 p = 0.003	(o)	z = 0.36 p = 0.70
2	(o)	z = 1.50 p = 0.14	(o)	z = 1.22 p = 0.22
3	(o)	z = 1.57 p = 0.12	(o)	z = 1.73 p = 0.08
4	(o)	z = 1.80 p = 0.07	(o)	z = 1.27 p = 0.20
5	(o)	z = 0.00 p = 1.00	(o)	z = 0.72 p = 0.48
6	(o)	z = 1.35 p = 0.18	(o)	z = 0.00 p = 1.00
7	(o)	z = 1.60 p = 0.10	(o)	z = 0.26 p = 0.68
8	(o)	z = 0.33 p = 0.74	(o)	z = 0.65 p = 0.50

	(M)		(N)	
Wk. 1	(o)	z = 1.49 p = 0.14	(o)	z = 0.89 p = 0.38
2	(o)	z = 1.63 p = 0.10	(o)	z = 0.02 p = 0.98
3	(o)	z = 0.86 p = 0.38	(o)	z = 1.55 p = 0.12
4	(o)	z = 1.32 p = 0.18	(o)	z = 0.43 p = 0.66
5	(o)	z = 0.86 p = 0.40	(o)	z = 0.19 p = 0.84
6	(o)	z = 0.00 p = 1.00	(o)	z = 0.00 p = 1.00
7	(o)	z = 0.35 p = 0.72	(o)	z = 0.67 p = 0.50
8	(o)	z = 0.09 p = 0.92	(o)	z = 0.79 p = 0.44

APPENDIX 2

The Technique of Fencing-In Nests

The nests were fenced-in to prevent the young being led away by the parent and so that close observations could be made on the development of the behaviour of the young.

Previous experience had shown that the fence had to be opaque so that the parents were unable to see the young through the fence. If this is not done, the parents do not feed or brood the young but attempt to lure the young through the fence for day after day until the young die from exposure.

The fence was made in prefabricated sections of 3 m in length and 1.7 m high. The basic construction was of chicken wire with five thicknesses of hessian sacking pinned to the wire. The hessian was 1 m high. Each section was supported by bamboo poles and, when placed in position, the bottom 15 cm were dug into the ground and the ends of each section overlapped by some 10 cm.

The first section was dug in some 15 m away from the nest, and each day it was moved a little nearer until it was some 6 m from the nest. Observations were made from a hide at each stage to make sure that the bird returned to the nest. Once the first section was in place, every day another section was placed next to it and dug in. The nest was thus gradually encircled until there was room for only one more section (7 sections were used in all at each nest).

The final section was first laid flat on the ground in position so that the bird had to walk over it to get to the nest. The end nearest the nest was then raised some 10 cm off the ground so that the bird had to walk up a slight slope and then jump down. A nest relief was allowed between each stage, so that both members of the pair became used to the obstacle. The fence was then raised 0.5 m off the ground

so that the bird, after walking up the slope, had to fly down to the arena. Finally, the end nearest the nest was raised 1 m off the ground so that the bird had to fly over the section. Once this had happened the section could be fully erected and dug into position. A hide was then moved up alongside the fence, and all the overlapping pieces of the sections securely fixed.

Note: The parents are unable to keep their chicks alive by flying food to the nest. After the first week food should be placed in the arena for the young to eat, and this should be done during the high water period when parental feeding stops.

SUMMARY

1. The transport and presentation of food to the young Oystercatcher is described. The parents will present food to the young either on their own initiative or in response to the approach of the young.

2. The auditory and tactile interactions between the hatching eggs and the incubating parents are described. As hatching proceeds, both the parents and young become more responsive to each other, and both show marked selective responsiveness. These pre-hatch interactions lead to the transition from incubation behaviour to brooding behaviour and to the onset of parental feeding. It is suggested that the young may learn to respond to the call of the parent before hatching.

3. Both non-breeding and breeding birds show the same cyclical pattern of total feeding activities and it is suggested that self-feeding and parental feeding are part of the same motivational system. Once the food has been presented to the young, the subsequent behaviour of the parent is dependent upon the speed with which the young seizes and eats the food. If the young reacts within a certain time (the Waiting-Time Threshold), then the parent will present more food, and will continue to do so for as long as the young reacts within the threshold time. In this way, feeding trains are initiated and maintained. The feeding train is broken off once the young fails to react within the threshold time.

As the young grows older the parent plays an increasingly minor part in the initiation of feeding trains, the role of the young becoming more important. This leads

to the eventual breakdown of parental feeding which is closely correlated in time with how long it takes the young to learn to feed itself.

A model of the motivation and control of parental feeding is described.

4. It is suggested that parental feeding evolved in the Oystercatcher subsequent to the evolution of a specialised feeding behaviour which very small young were unable to employ. The parental feeding system shows specific adaptations to feeding nidifugous young on numerous small items of food, and it is suggested that selection has maintained this system because (1) the parents can take their young out onto the feeding grounds and protect them whilst feeding them and because (2) the young acquire the techniques of the specialised feeding behaviour from their parents during the parental feeding.

PART 2

PART II

SOME ECOLOGICAL ASPECTS OF THE FEEDING BEHAVIOUR OF THE OYSTERCATCHER (Haematopus Ostralegus) ON THE EDIBLE MUSSEL (Mytilus Edulis)

(Reprint from IBIS 109 1967)

INTRODUCTION

Descriptions of the behaviour of the Oystercatcher (Haematopus ostralegus) when feeding on the Edible Mussel (Mytilus edulis) have been published by Dewar (1908), Drinnan (1954, 1958, 1958), Tinbergen & Norton-Griffiths (1964) and Hulscher (1964). I studied the feeding behaviour of Oystercatchers on the mussel beds in the estuary of the River Esk and Ravenglass, Cumberland and on the Barnscar mussel bed at Drigg, Cumberland, and it appeared that the birds were feeding differently both on these two mussel beds and on different parts of the same bed. In addition, their feeding behaviour in these places differed strikingly from the published observations made elsewhere. The present study was aimed at finding out how these various mussel beds differed from one another, how the differences affected the bird's feeding behaviour and the extent to which individual birds could modify their behaviour to deal with different situations. The observations were made through a large telescope from a Land Rover which was driven out onto the mussel beds.

CHAPTER 1 METHODS OF OPENING MUSSELS

The Oystercatcher has two methods of gaining entry into a mussel shell. The first is used against mussels which are exposed to the air and which are therefore tightly closed, and consists of hammering the shell until it breaks with the bill. The second method is used against mussels which are under water and slightly open. Here the bill is stabbed into the mussel between the gaping valves.

1/A The Hammering Method

When Oystercatchers hammer mussels, they select patches of hard sand in a way similar to that described by Drinnan (1957) when they hammer Cockles (Cardium edulis). Should the mussel sink into the sand while being hammered the bird will carry it to another patch of sand, and repeat the process until sand of sufficient firmness is found. It will then tend to return to that area repeatedly with other mussels to hammer open. Before hammering, the mussel is orientated with its flat ventral surface upwards; although this is rather an unstable position, the bird maintains it by re-positioning the mussel if it falls over. The blows are delivered on the mid-ventral region of the shell (rarely anywhere else) with the bill held vertically downwards, the neck held stiff, and the body pivoting from the pelvis. The toes tightly grip the sand to maintain purchase. Anything between one and twenty-six blows may be delivered before the shell is fractured, the average for 55 observations being five blows. The usual effect of the blows is to break off a semi-circular chip from one or both of the ventral valve margins which is then driven inside the shell.

Sometimes, however, the dorsal part of the shell shatters into small fragments leaving the ventral part intact, giving the misleading appearance that the shell has been struck from the dorsal side and not from the ventral. In some cases a fracture line runs from the point of impact on the ventral margins to the dorsal margins so that the whole of the posterior part of one, or both, valves breaks off. The blows often seem to have the effect of "knocking out" the mussel, for occasionally a mussel will spring open after only a few blows and before the valves are damaged. Once a hole has been made in the shell, the Oystercatcher thrusts its bill up into the posterior region of the shell and cuts through the adductor muscle. It then prises the valves apart and removes the flesh.

The great majority of those shells collected by Dewar, Drinnan and by myself, which had been hammered open by Oystercatchers, had been attacked through the ventral margins (Dewar 100%, Drinnan 95%, present study 92%), and both Dewar and Drinnan commented on the orientation of the mussel prior to hammering and on the restriction of the attack to the valve margins. A similar orientation of the shell, or restriction of attack to a particular part of the shell, of other molluscs has been described by Dewar (1908), Drinnan (1957), and Tomkins (1948). Drinnan (1958) suggested that the ventral valve margins of the mussel might be the weakest part of the shell because of the persistent gape and because of the obtuse angle between the valve edges which therefore lend each other little support. I decided to test this idea by cracking the shells of live mussels under controlled conditions to see whether different regions of the shell varied in strength.

The apparatus used was an adaptation of a Fletcher's Trolley. The basis of the machine (Fig.1) is a wheeled trolley (A) running in grooves down a smooth plane (B). The mussel is held in a clamp (D) and is struck with a brass rod (C) which is attached to the trolley. The last 10 mm. of the brass rod was shaped to correspond with the bill tip of a stuffed adult Oystercatcher in the University Museum, Oxford. The trolley was released by a simple mechanism (F). The mussel was held in the clamp between plastic moulds so that, while being firmly supported, the shell could not derive additional strength from the valves being pressed together. The clamp could be moved both up and down, and forwards and backwards, so that it was possible to orientate the mussel with its dorsal-ventral axis parallel to, and continuous with, the longitudinal axis of the "bill". The weight (ω) of the trolley, the length (l) of the run and the angle (α) of the slope were kept constant throughout the tests so that the blows delivered to the mussels were always the same. Only two regions of the shell were tested, the mid-ventral region, and the highest point on the dorsal margins. These were chosen because they could be exactly located on every shell. Blows were delivered to the shell until the shell fractured and the tip of the bill penetrated inside the shell, and thus the number of blows necessary to penetrate the different regions give a measure of their relative strengths. Mussels of the following lengths were tested: 20 mm., 25 mm., 30 mm., 35 mm., 40 mm., 45 mm., 50 mm., 55 mm., and 60 mm. The mussels were picked at random off the mussel bed at Ravenglass and were kept alive in sea-water prior to testing. Mussels from the different size classes were tested in a random order and only one test was done on each mussel.

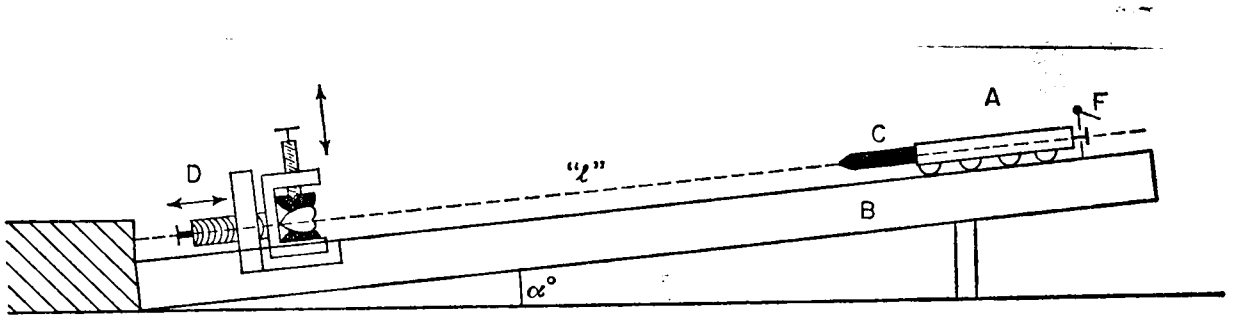


FIGURE 1. Mussel cracking machine. (A) Wheeled trolley; (B) smooth plane; (C) brass Oystercatcher bill; (D) clamp for holding mussel; (F) release mechanism.

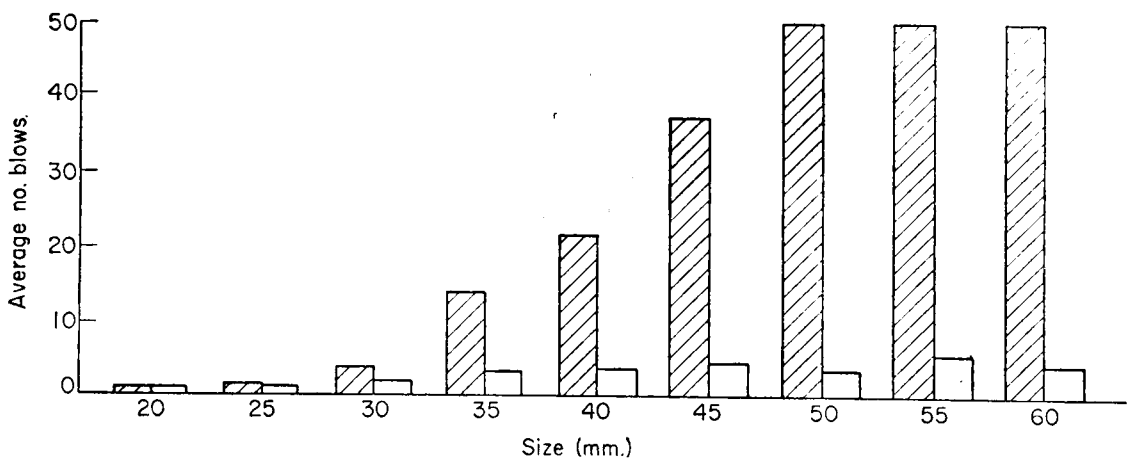


FIGURE 2. Ventral and dorsal scores tested against one another using a one-tailed Wilcoxon matched-pairs signed-ranks test where

$$Z=\frac{T-\frac{N(N+1)}{4}}{\sqrt{\left[\frac{N(N+1)(2N+1)}{24}\right]}}.$$

$N=36$, $T=23$ so $Z=-3{\cdot}6$, $P=<0{\cdot}001$.

////, Dorsal margin; □, ventral margin.

The average number of blows taken to penetrate the different regions of the different sizes of mussel is shown in Fig.2. The difference between the strength of the dorsal and ventral margins is at once apparent, and it is interesting that, while the scores for the ventral margin remain low and relatively constant, those for the dorsal margin increase sharply with size until, with shells larger than 50 mm., 50 blows to the dorsal margin produced no effect at all (the tests were stopped at this stage). The functional significance of the orientation of the mussel shell by the Oystercatcher prior to hammering can now be fully seen, for not only is the ventral margin of a mussel absolutely weaker than the dorsal margin, but also the ventral margins of even the largest shells are relatively weak. In addition, the ventral margin offers an almost flat surface at which to hammer while the dorsal surface is usually sharply pointed and so a much more difficult target.

The damage done by the machine to the ventral margins of the shells was almost indistinguishable from that done by Oystercatchers (see Plate (a)). Usually a semi-circular chip was knocked out from one of the valve margins, but in some cases either the dorsal region collapsed in fragments or a fracture line ran from the point of impact to the dorsal region so that the whole of the posterior part of one of the valves would be broken off. The "knocking out" effect was observed, usually after three of four blows, and only when the blows were to the ventral region. The valves would suddenly gape 1 or 2 mm. and the following blow would always break the shell, thus demonstrating the additional strength gained by the valve margins from being tightly held together by the force of the adductor muscle.

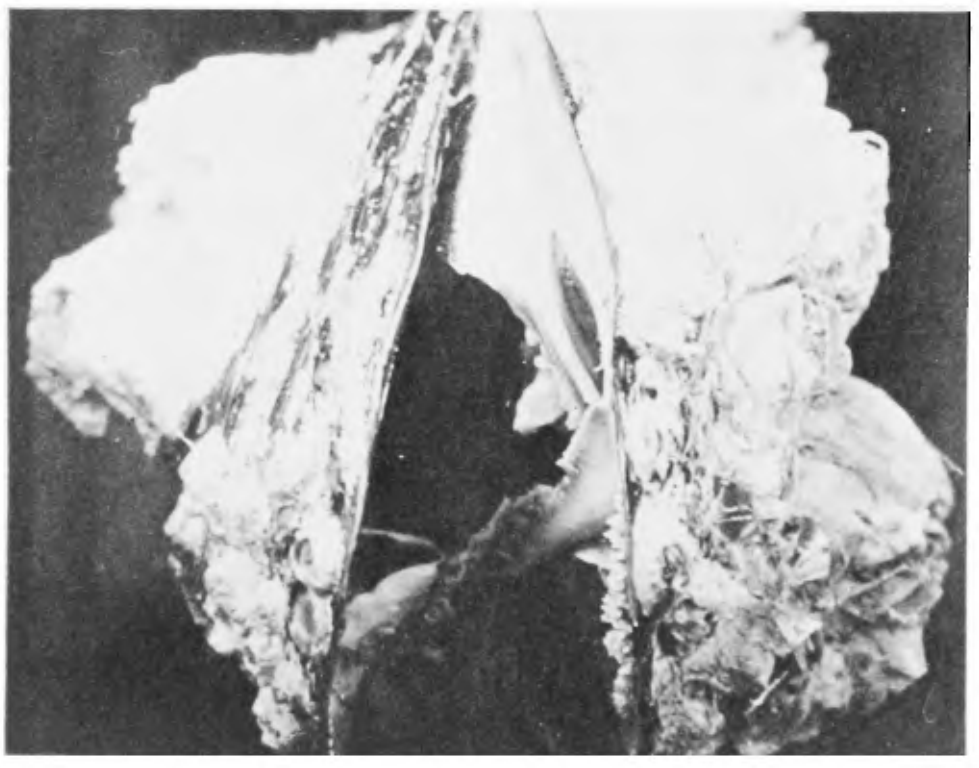
PLATE 1



(a)



(c)



(b)

[redacted] (a) Damage done to the ventral margins of mussel shells by Oystercatchers and cracking machine. Top row: semi-circular chip broken from valve edge. Bottom row: fracture line running from point of impact to dorsal margin. (Shells on the left were damaged by Oystercatchers, those on the right by the cracking machine.)

(b) Large mussel stabbed by an Oystercatcher photographed from the posterior-dorsal aspect.
The torn mantle attachment just below and to the left of the siphon indicates the direction of entry of the bill.

(c) The same mussel photographed from the ventral aspect. The cleanly severed posterior adductor muscle is clearly seen.

1/B <u>The Stabbing Method</u>

The stabbing method is used against mussels which are covered with sea-water and therefore slightly open. A hard downward stab with the bill, accompanied by rapid levering and twisting of the neck and head, serves to gain entry into the shell. The rapid levering and twisting may serve either in forcing the bill between the valves or in tearing the mussel off the substrate once entry has been gained. The fact that (1) the mussels are open under water and that (2) they are gaping when brought to the surface by the Oystercatcher suggests that the stab enters between the open valves and severs the posterior adductor muscle, thus preventing the mussel from closing. On three occasions Oystercatchers were chased away from mussels which they had just stabbed but which they had not yet fully opened, and each time it was found that the posterior adductor muscle was cut through. Plate (b) and (c) show details of the damage to the largest of these mussels. The torn attachment in Plate (b) shows that the bill must have entered from just below the siphon and between the posterior valve margins, where the gape of an open mussel is widest. Plate (c) shows that the bill cut through the adductor and ended up against the left-hand valve where it tore the mantle.

The posterior margins of mussels which have been opened are sometimes very slightly chipped, but there are never any other signs of damage to the shell. Once the gaping mussel is brought to the surface the valves are prized apart and the flesh removed.

The different conditions under which these two methods are used are clearly shown from a collection of freshly opened mussel shells from two nearby areas of the Barnacar mussel beds at Brigg. Only those shells were collected

which still had traces of fresh meat inside them and which were surrounded with Oystercatcher footprints. The shells were classified as "fractured" (i.e. they had been hammered) or as "undamaged" (i.e. they had been stabbed). In Area A (see Table 1) the birds were hammering open mussels which had been left exposed by the tide, while in area B, some 40 yards away, the birds were stabbing mussels which were still covered with water.

TABLE 1 Damage to mussel shells opened by Oystercatchers (Haematopus ostralegus) on the Barnacar Beds.

	% FRACTURED	% UNDAMAGED
AREA A (totally exposed at low tide)	85·5% (231)	14·5% (39)
AREA B (covered with water at low tide)	10·1% (46)	89·9% (411)

CHAPTER 2 THE FEEDING BEHAVIOUR ON THE RAVENGLASS MUSSEL BED

2/A Oystercatchers were observed feeding on the largest of the mussel beds on the Esk, which is situated well out towards the mouth of the estuary. It is about half a mile long and some 200 yards wide, with a substrate of rocks and hard sand. The bed can be divided up into two regions: the Upper bed is flat with numerous small pools of water and occasional rocky lumps, and is covered with a dense unbroken carpet of small mussels of average size 20·1 mm. (s=4·2 mm.); the Lower bed consists of a strip twenty yards wide along the low water mark and is broken up by ridges of large rocks festooned with mussels, as well as by expanses of bare sand. There are many mussels on the Lower bed of a much larger size, up to 65 mm., the average size being

22·5 mm. (s=12·2 mm.). At low tide, the Upper bed is always completely exposed, while the Lower bed, except at low water spring tides, is covered with water to a greater or lesser extent.

The empty shells of mussels which had been opened by Oystercatchers were collected off the Upper and Lower beds, classified as "fractured" or "undamaged", and also measured. From Fig.3, it can be seen that the birds had fed differently on the Upper and Lower beds; on the former most mussels had been hammered open (Table 2), while on the Lower bed, most had been stabbed.

TABLE 2 Methods used by Oystercatchers (Haematopus ostralegus) to open mussel shells on the Upper and Lower beds at Ravenglass.

	FRACTURED	UNDAMAGED	
UPPER BED	97	35	$\chi^2 = 13.6$
LOWER BED	43	165	$P = < 0.001$

This can perhaps be explained by the fact that on the Upper bed the birds have to hammer open the mussels (except for a few caught open as the tide recedes, or in the small pools), whereas on the Lower bed they can feed on either exposed or covered mussels. If, however, the average size of all the mussels taken by Oystercatchers on both the Upper and Lower beds is used to distinguish between "large" and "small" mussels, then it appears that the Oystercatchers are only hammering open the "small" ones (Table 3).

TABLE 3 Methods used by Oystercatchers (Haematopus ostralegus) at Ravenglass to open "large" and "small" mussels (mean size of all mussels opened (35 mm.) is used to distinguish "large" from "small").

	FRACTURED	UNDAMAGED	
SMALL MUSSELS	129	72	$\chi^2 = 117.6$
LARGE MUSSELS	9	165	$p = < 0.001$

In addition, as Fig.3 shows, mussels larger than 40 mm. do not seem to be hammered at all. This is difficult to understand, in view of the cracking tests (described above), on mussels off this same bed, which showed that the ventral margins of mussels of all sizes are almost equally easy to break.

2/B Comparisons between the feeding behaviour at Ravenglass, in the Firth of Forth and the Conway

Dewar, working in the Firth of Forth, and Drinnan, working in the Conway estuary, also collected shells which had been opened by Oystercatchers and their results indicate that the birds are feeding differently in each of these places (see Table 4).

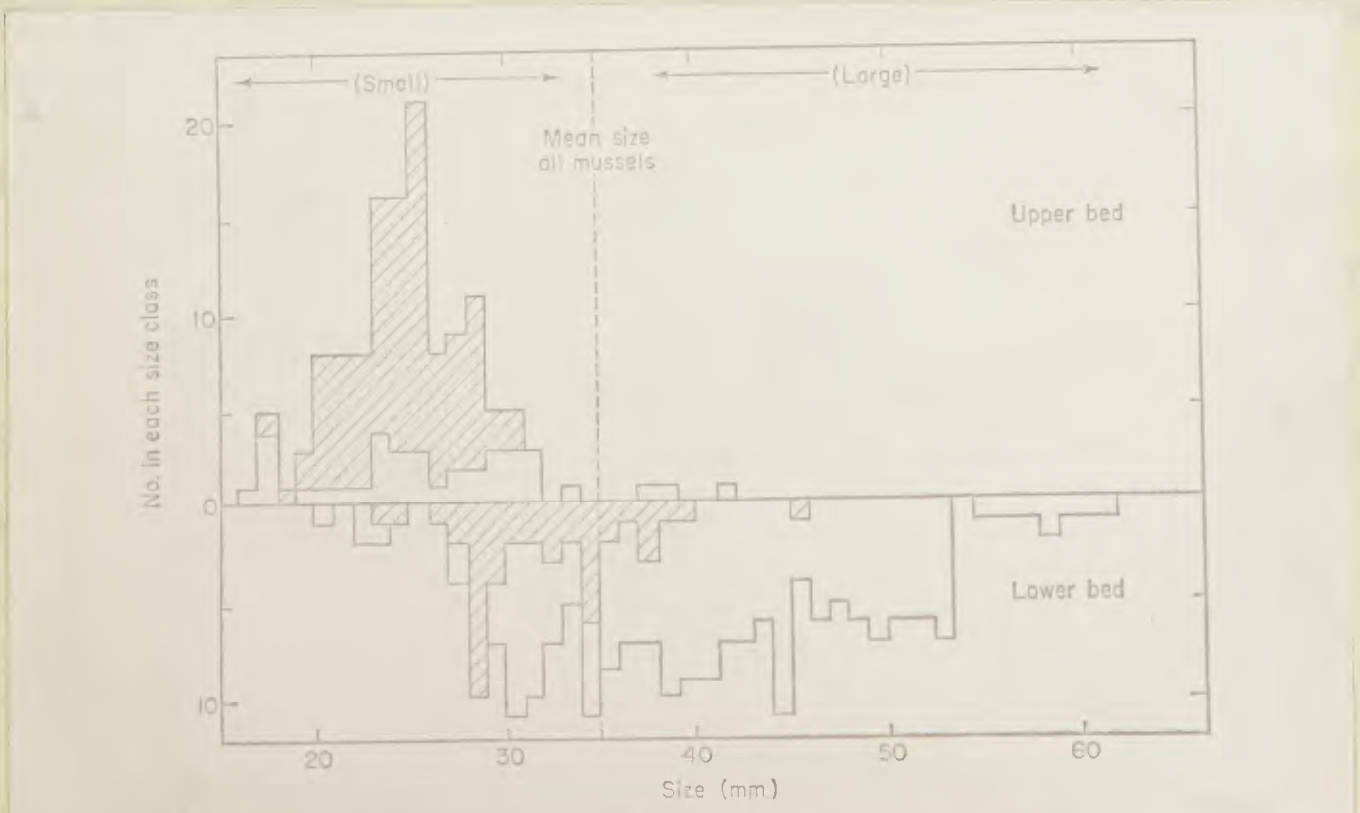


FIGURE 3. Distribution by size of mussels opened at Ravenglass. ▨, Fractured shells; □, undamaged shells.

TABLE 4 Methods used by Oystercatchers (Haematopus ostralegus) to open mussels at Ravenglass, Conway and Firth of Forth.

AUTHORITY	Drinnan	Norton-Griffiths	Drinnan	Norton-Griffiths	Dewar
LOCALITY	Morpha (Conway)	Ravenglass Upper Bed	Pensarn (Conway)	Ravenglass Lower Bed	Firth of Forth "All sizes"
SIZE RANGE	10-35mm.	10-35mm.	20-60mm.	20-60mm.	
NO.IN SAMPLE	500	132	350	208	Not given
UNDAMAGED	12%	26.5%	21%	79.3%	91%
FRACTURED	88%	73.5%	79%	20.7%	9%
	$\chi^2 = 16.1$		$\chi^2 = 179.2$		
	$p = < 0.001$		$p = < 0.001$		

RAVENGLASS UPPER BED; MORPHA BED AT CONWAY

Here the birds are feeding in essentially the same way except that the proportion of shells hammered at Morpha is significantly larger than the proportion hammered on the Upper Bed.

RAVENGLASS LOWER BED; PENSARN BED AT CONWAY; FIRTH OF FORTH

The birds seem to be feeding in the same way on the Lower bed as they are in the Firth of Forth, except that the proportion of stabbed shells is higher at the Firth. The birds are, however, feeding very differently at the Pensarn bed in the Conway. Here, not only are the majority of shells hammered open, but also shells of all sizes are treated in this way. This is in complete contrast to the situation on the Lower bed at Ravenglass where, on a bed similarly exposed at low tide, the majority of shells are stabbed, and shells longer than 40 mm. are not hammered at all.

2/C The Substrate of the mussel beds

One important factor which might cause the difference in feeding behaviour on the different mussel beds is the nature of the substrate. Drinnan (1957) stressed the dependence of Oystercatchers on areas of hard sand on which they can hammer open cockles, and he showed also that birds select patches of hard sand to which they carry cockles. Oystercatchers similarly select hard sand to which they carry mussels too, so they must be dependent on a firm substrate for success with this prey.

Dewar did not give an adequate description of the mussel beds in the Firth of Forth, but his frequent references to "sand and mud" indicate that the substrate may be rather soft. If this is so, it could explain why so few shells were found hammered open there, since the only way possible for the birds to open the mussels under these circumstances would be to stab them while they were still covered with water.

Drinnan described the substrate of the Penmarn bed in the Conway as ranging from soft mud with occasional stones, to sand, sand and rocks, and rocks; in general, therefore, it is very firm. The mussels are exposed (and closed) at low tide, as in the Firth of Forth, but at Penmarn the birds are able to hammer them open as well, because of the firm substrate. There is, however, one area on the Penmarn bed which is so muddy that the birds do not feed there at all.

At Ravenglass, the substrate of both the Upper and Lower beds is very hard indeed, for the whole mussel bed is formed on packed rocks. All the mussels are firmly attached to this substrate, for they are continually swept by strong waves and currents. There is, therefore, a very firm substrate, and mussels are therefore found hammered open. Yet on the

Lower bed, in a similar situation to the Pensarn bed, relatively few mussels are found hammered open, and certainly no large ones. There is, however, one important difference between the Lower and Pensarn beds. Thus while the former lies at the mouth of the estuary and is continually swept by strong currents the Pensarn bed lies almost as far upstream as it is possible for marine animals to live, and where the mussels are protected from strong tidal currents.

It has already been shown that the ventral margins of a mussel shell are weaker than the dorsal ones and for this reason Oystercatchers have to tear a mussel off the substrate before hammering it. Thus while the very hard substrate at Ravenglass provides ideal condition for hammering, these favourable feeding conditions could be to some extent countered if the mussels were difficult to detach. I therefore carried out some tests to see whether the larger mussels on the Lower bed were more firmly attached to the substrate than were the small mussels, and whether the mussels on the Lower bed were in general more firmly attached than were the mussels on the Pensarn bed. The apparatus used was a simple spring balance with a sliding scale attached to a clamp made from a small test tube holder. Mussels were chosen at random on the two beds and the clamp was attached around the shell, great care being taken not to damage any of the byssal threads. The mussel was then pulled off the bed with a smooth vertical pull and the force needed to detach it read off the sliding scale. Figure 4 shows the force needed to detach mussels of different sizes from the two beds.

The data for the Lower bed shells, taken separately and tested with a median test, show a good correlation

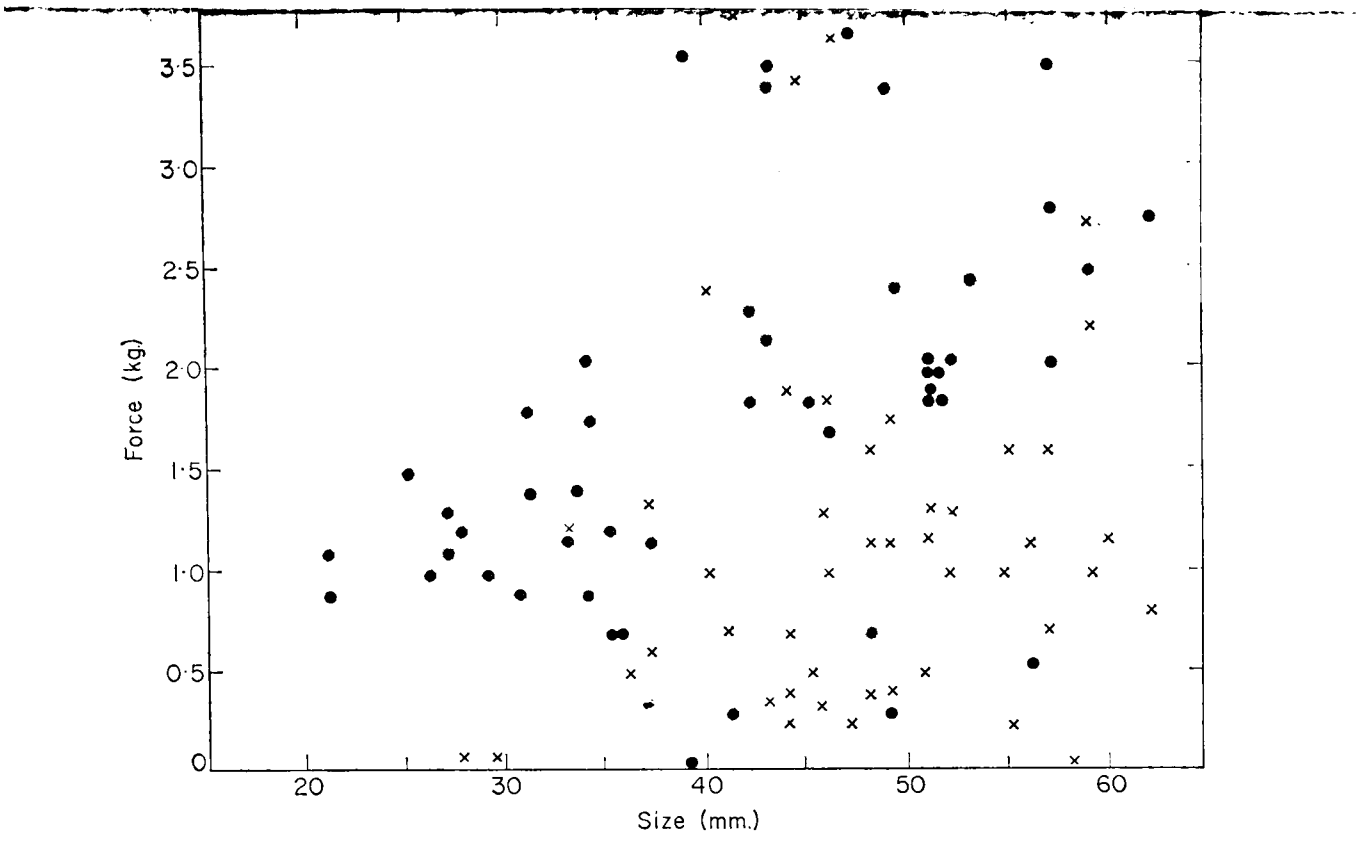


FIGURE 4. Force (kg.) needed to detach mussels of different sizes from the Lower and Pensarn beds. (X) Pensarn shells; (●) Lower bed shells.

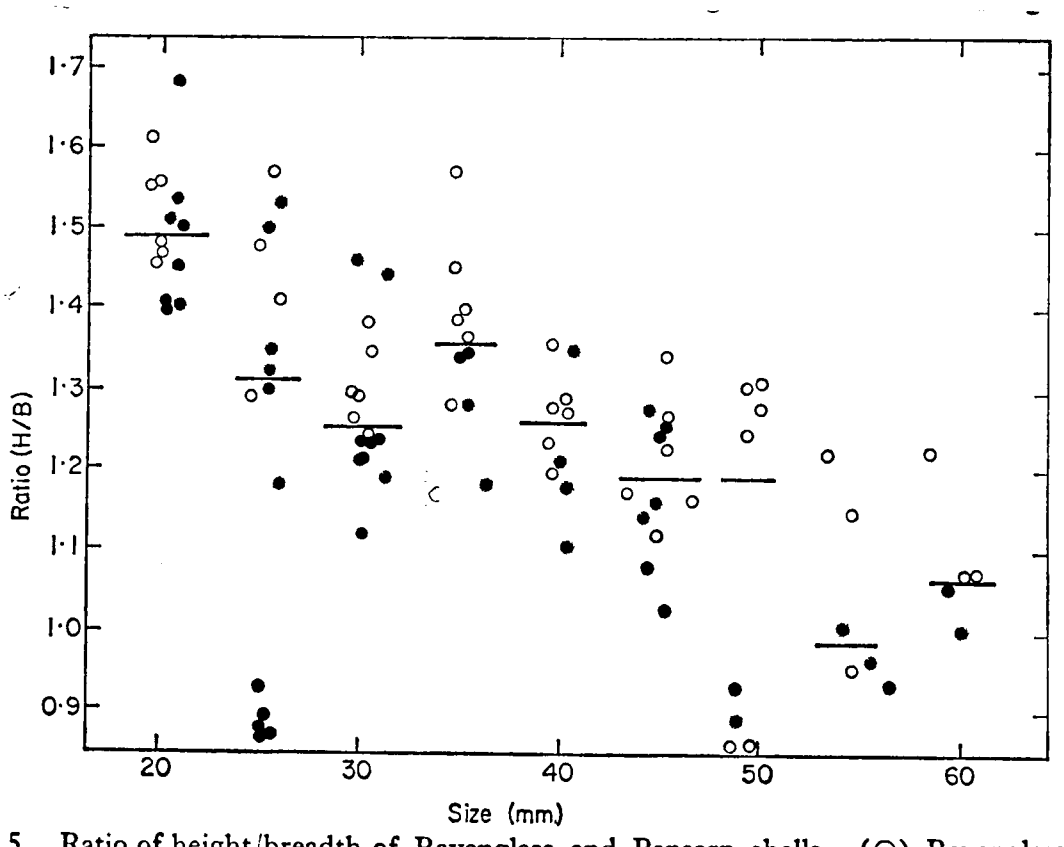


FIGURE 5. Ratio of height/breadth of Ravenglass and Pensarn shells. (○) Ravenglass shells; (●) Pensarn shells. (Median lines for each size class marked.)

between an increase in size of the shell and an increase in the force needed to detach it (χ^2=22.3, p = <0.001). A median test on the combined data from the Lower and Fensarn beds shows that the Lower bed shells are more firmly attached than are Fensarn shells of equivalent size (χ^2=85.0, p =<0.001). These results could well account for the fact that while mussels of all sizes are found hammered open on the Fensarn bed, only small ones are found hammered on the Lower bed, the large ones being too firmly attached. From Fig.4, it can be calculated that the average force needed to detach mussels of 35-45 mm. from the Lower bed is 1.7 kg., and further that 80% of the Fensarn shells were detached with less effort. One might therefore predict that 80% of the mussels eaten on the Fensarn bed would be hammered and that 20% would be stabbed. Table 4 shows that the observed figures are 79% hammered and 21% stabbed. This therefore suggests that both the observed difference between the feeding behaviour of the Oystercatchers on the two mussel beds and the difference in the size range of mussels found hammered can be accounted for by the varying strength with which the mussels are attached to the two beds.

2/D Ecological Factors affecting the mussel shells

There is considerable evidence that the laying down of calcium in the shell of marine shellfish is susceptible to ecological conditions. Orton (1925), Fox & Coe (1943), Robertson (1941), Bevelander (1948), Wilbur & Jodrey (1952) and Rao & Goldberg (1954) all reported that the calcium incorporated into marine molluscan shells was taken directly from the sea-water. Collip (1920), Dugal (1939), Dugal & Fortier (1941) and Baird & Drinnan (1957) reported that marine bivalves, exposed to the air (or to fresh water) and tightly closed, respire

anaerobically; the resulting acidity in the body tissue fluids is buffered by Ca^{+} ions which are released from the shell. Finally, Fox & Coe (1943) reported that exposure of mussels to wave action results in a stunting of shell growth and in thick shells.

The conditions of the Lower Ravenglass bed and the Pensarn bed differ in many ways. The mussel bed in the Ravenglass estuary is exposed to high wave action and the sea-water covering the beds is little diluted by fresh water from the river. Indeed, the mussels close only when they are exposed by the tide, so here the loss of calcium from the shell due to anaerobic respiration is at a minimum. The protected position of the Pensarn bed, on the other hand, means that wave action is at a minimum; but since it lies far upstream the sea-water covering the bed is more diluted by river flow. The salinity at low water drops to a very low level (especially after long rainfall), so tidal exposure to both air and fresh water is much longer. It therefore seemed possible that the shells of the two populations of mussels would differ in strength.

The first factor to be investigated was the effect of wave action on mussel shells. A sample of mussels from the Lower and Pensarn beds was taken and the height, breadth and length of each shell was measured. The ratio of height to breadth was plotted against length (Fig.5), a ratio of more than one indicating that the shell was higher than it was broad. For any given length of shell, a Pensarn shell has a higher ratio of height to breadth than does a Lower bed shell ($\chi^2 = 12.58$ $p = < 0.001$). Unfortunately, the opportunity to weigh the shells and measure their thickness was overlooked, but it seemed by inspection that the Ravenglass shells were thicker. The stunting of growth

and thickening of the Lower bed shells is most likely an effect of strong wave action, which might result in the Lower bed shells being stronger than the Pensarn ones.

A sample of shells from the Pensarn bed was therefore tested with the same cracking apparatus to see if they were weaker than the Lower bed shells. The same nine size classes were used and tested in the same way. In Fig.6 the average number of blows taken to crack the ventral margins of the Ravenglass and Pensarn shells is compared, and it shows that the Ravenglass shells are in fact significantly stronger than the Pensarn ones. In Fig.7, the difference is even more striking, for even the largest of the Pensarn shells were fractured by blows to the dorsal margin. The difference in strength could, of course, greatly influence the feeding behaviour of the birds. There is unfortunately no way of relating either the force needed to detach the mussels from the substrate or the force needed to crack the shells to the physical strength of the Oystercatchers, and this makes it difficult to assess which of these two factors is the more important in affecting the feeding behaviour.

CHAPTER 3 THE PROBLEM OF SIZE SELECTION.

There is presumably an "optimum" size of mussel which gives Oystercatchers maximum return for minimum expenditure of energy, and if Oystercatchers had evolved some mechanism for size selection it would show up by their selecting mussels of a particular size range, irrespective of the mussel population on which they were feeding. Such a mechanism would, however, be highly disadvantageous, for not only does the frequency of occurrence of mussels of a particular size vary in different populations, but also, as we have seen, mussels of the same size in different

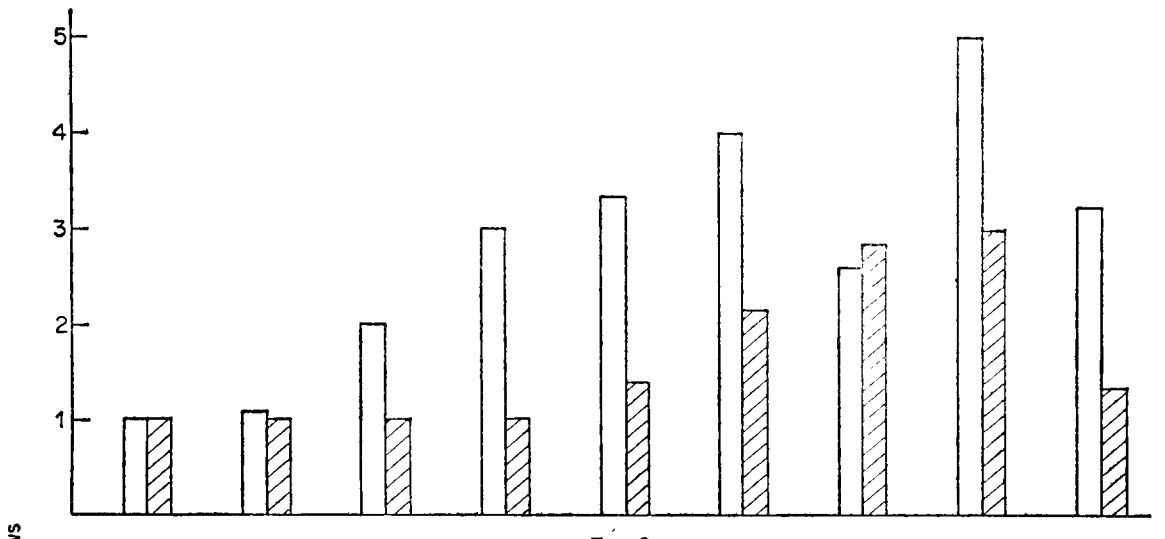


FIG. 6

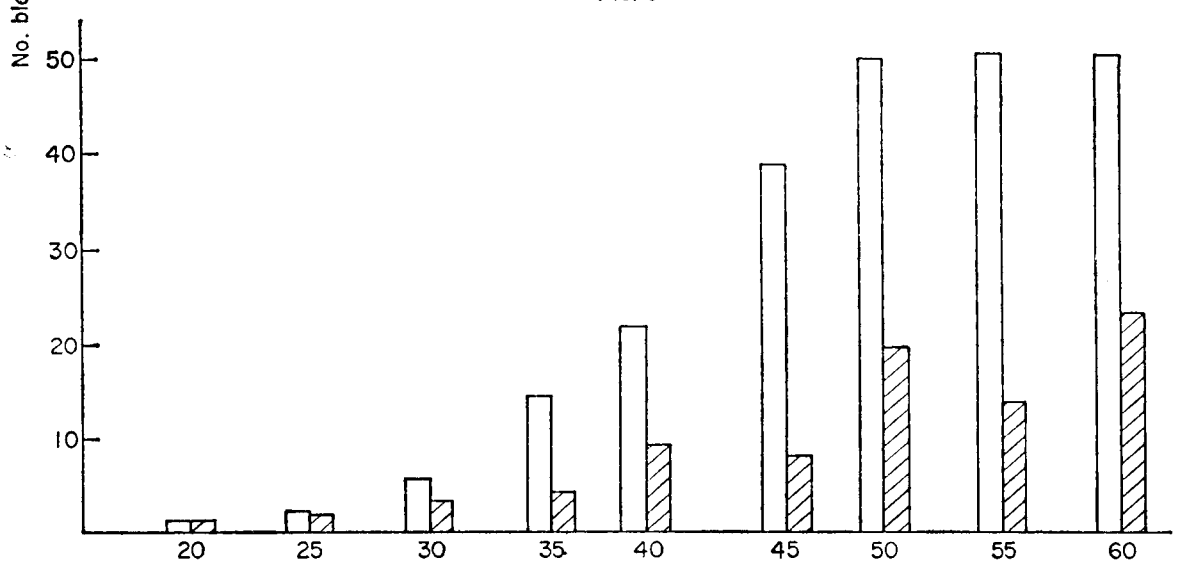


FIG. 7

FIGURE 6. Average number of blows to crack ventral margin of Ravenglass and Pensarn shells. ▨, Pensarn shells; ▭, Ravenglass shells. $Z = -3{\cdot}6$; $P = <0{\cdot}001$.

FIGURE 7. Average number of blows to crack dorsal margin of Ravenglass and Pensarn shells. ▨, Pensarn shells; ▭, Ravenglass shells. $Z = -4{\cdot}1$; $P = <0{\cdot}001$.

populations vary in the strength of their shells and, in addition, in the amount of meat they contain.

The references to size selection by Oystercatchers in the literature present a rather confused picture. Dewar (1908) reported that on the Morpha bed Oystercatchers "prefer" mussels of 35 mm. Drinnan (1958a) found that on the Morpha bed, too, 35 mm. mussels were taken more than any other (35 mm. being the largest available there), while on the Penearn bed the birds took the various sizes in proportion to their occurrence in the population. Hulscher (1964) studied breeding birds which were taking mussels from the beds to their young. He found apparent size selection when comparing those mussels taken with the mussel population of the whole bed, but no selection when comparing those taken with the population on the restricted part of the bed on which the birds were feeding. These observations suggest that the Oystercatchers are taking whatever is available, with perhaps a bias against small mussels. At Ravenglass, on both parts of the bed the birds seem to be selecting the larger mussels (Figs. 8 and 9), this preference being more marked on the Lower bed. The general morphology of the two beds must, however, be taken into consideration. It has already been described how, on the Lower bed, the mussels are clumped together in large masses on the rocks, with the larger mussels on the outside of the clumps. In order for an Oystercatcher to take the small mussels, it would first have to pull the clump t pieces. It is much more reasonable to suppose that it would instead feed on the outer mussels because of their great accessibility, in which case the population at risk would be very different to the population of the bed as a whole. On the Upper bed, the mussels are evenly spread so all sizes are equally



FIGURE 8. Apparent size selection on the Ravenglass Upper bed.

Mussel population (—●—●—): mean size 20·1 mm.
s. 4·2 mm.
Taken by Oystercatchers (—Δ—Δ—): mean size 25·39 mm.
s. 3·86 mm.

$d = 14{\cdot}52$; $P < 0{\cdot}001$.

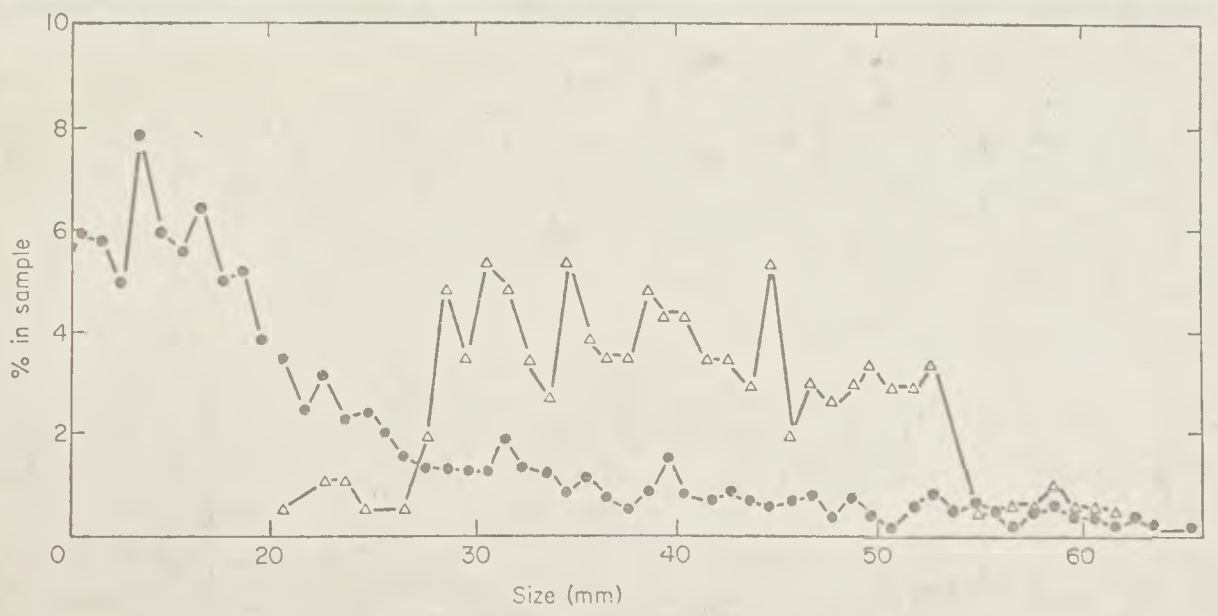


FIGURE 9. Apparent size selection on the Ravenglass Lower bed.

Mussel population (—●—●—): mean size 22·49 mm.
s. 12·16 mm.
Taken by Oystercatchers (—Δ—Δ—): mean size 39·08 mm.
s. 8·49 mm.

$d = 23{\cdot}95$; $P < 0{\cdot}001$.

available, yet here again, the larger mussels are taken more frequently. Of all the shells which have been opened by Oystercatchers on the Ravenglass beds, none have been smaller than 16 mm. in length. There thus seem to be two factors operating to produce the size selection on the Ravenglass beds: first the way in which the mussels are arranged on the bed, and second their size, in that th very small mussels may not present the correct stimuli to elicit feeding behaviour on the part of the Oystercatcher.

DISCUSSION

To fully understand the feeding behaviour of the Oystercatcher on mussels it is as important to take the mussels into consideration as it is to study the behaviour of the birds. This can be shown in two ways. The feeding methods are adapted to the structure of the mussels. For instance, the hammering is not directed at random against the shell but only at the weakest part, and the bird first positions the shell accordingly. The stab, on the other hand, is directed towards the posterior region where the gape is widest and is so aimed that it passes straight through the main posterior adductor muscle. Secondly, the way in which the mussels are grouped on the mussel bed, the strength of their shells and the firmness with which they are attached to the substrate can influence the way they are taken. On the Ravenglass Lower bed, for example, the mussels have strong shells, are firmly attached to a hard substrate and are grouped in large clumps; here few are hammered and the larger mussels are apparently preferred. In contrast, the mussels on the Ponsarn bed have weaker shells, are more loosely attached and more evenly spread; here the greater portion are hammered open and there is no apparent size selection.

This, however, presupposes that any individual Oystercatcher is able to both hammer and stab mussels, and that the conditions prevailing on any mussel bed determine which method it will use. This indeed was my belief, until I started to work with individually marked adults, when it then appeared that this was not the case at all: an individual bird will either hammer mussels or stab them, but will not do both. This throws an entirely new light on the problem for it means that individual birds select mussel beds, or parts of mussel beds, which have conditions suitable for their particular feeding method. However, two new problems are now raised: how do individuals become hammerers or stabbers, and how do they find suitable feeding grounds?

By individually colour ringing breeding adults and their young, it has been shown that young Oystercatchers develop the same feeding technique as their parents. In other words, young whose parents stab mussels develop the stabbing technique while those whose parents hammer mussels develop the hammering technique. My detailed work on this is still in progress (see Part IV), but it seems most unlikely that this is due to genetic differences. While the young are developing their feeding technique they are fed by their parents and accompany them onto the mussel beds. In this way they can learn at least one locality which is suitable for their particular feeding technique, but what happens to them when they migrate at the end of their first summer is still not clear. The large scale ringing studies sponsored by the Ministry of Agriculture, Fisheries and Food, at Conway may soon produce information on this point.

SUMMARY

Oystercatchers have two methods of opening mussels, both neatly adapted to the structure of the prey. To open mussel exposed by the side, the bird hammers a hole along the ventral margin of the shell, whereas to open mussels under water, the bird stabs its bill into the gape of the valves to cut through the posterior adductor muscle. Large and strong-shelled mussels can be opened by stabbing but not by hammering.

Feeding methods of Oystercatchers vary from mussel-bed to mussel-bed. These variations in behaviour are attributable to differences in the strength of the shells of the prey and to the firmness of their attachment to the substrate.

Diversity of ecological conditions on the mussel-beds causes an apparent size selection of prey by Oystercatchers.

PART 3

PART III THE FEEDING TECHNIQUES OF THE ADULT OYSTERCATCHER

INTRODUCTION

The European Oystercatcher (Haematopus ostralegus) has a very versatile feeding behaviour. A check list compiled by Dare (1966) records the following prey:

> 10 species of Lamellibranchiata, at least 5 species of Gastropoda, 3 species of Decapoda, 2 species of Amphipoda, 3 species of Polychaeta, many species of Oligochaeta, as well as Holothuria, numerous Insecta and even some Teleosts (Ammodytes and Anguilla).

This plethora of prey species falls into two categories when considered from the point of view of the technique employed by the Oystercatcher to eat them. Firstly, there are the 'soft-bodied - invertebrates' (annelids, insects etc.) all of which live on or near the surface and which are located simply by probing with the bill and which are then eaten whole: secondly, there are the lamellibranchs, gastropods and decapods which present a hard-shelled exterior to the Oystercatcher and which the Oystercatcher eats by employing skilled techniques to penetrate the hard shell and to remove the flesh. The feeding techniques on soft-bodied - invertebrates will only be dealt with briefly (Chapter 1) for they are essentially the same as those employed by any other wader which probes for food. The main analysis will deal with the techniques employed against the hard-shelled prey.

When observing Oystercatchers feeding on lamellibranchs, gastropods and decapods, it can be seen that their feeding techniques are made up from a number of motor patterns, each one having a different form and a different function, and each one occurring in a definite sequence. My analysis of the different feeding techniques will take the following form:

1) the description of the form of the motor patterns and of the sequence in which they occur.
2) the analysis of the function of each motor pattern and of the sequence in which they occur, and of the way in which the motor patterns and their sequence are adapted to the structure of the various prey.
3) a causal analysis of the stimuli eliciting each motor pattern, of the factors controlling the duration of each motor pattern, and of the factors controlling the sequence in which the motor patterns occur (i.e. the transition from one motor pattern to another).
4) a comparison of the different feeding techniques and an analysis of the remarkable versatility and skill of the techniques.

The most detailed analysis is on the feeding techniques on two bivalve molluscs, Mytilus edulis and Cardium edulis, both staple foods of the Oystercatcher, although the feeding techniques of Scrobicularia, Tapes, Littorina, Patella and Carcinus are also analysed.

METHODS OF OBSERVATION

Most of the data were obtained by direct observations on Oystercatchers on their natural feeding grounds. The observations were tape recorded so that both qualitative and quantitative analysis could be made. Relatively few observations were made on captive adult Oystercatchers due to the difficulty of reconstructing the natural environment of the prey species and due to the difficulty of sufficiently taming the birds in the short period of time available to me during the field season.

CHAPTER 1. THE TECHNIQUES OF PROBING FOR SOFT-BODIED INVERTEBRATES

The Oystercatcher has two techniques of probing for such prey, and which one it uses depends upon the ecological conditions of the prey.

The Dart-Probe

The dart-probe is used in areas where there are visual signs on the surface that indicate the precise location of the buried prey. An Oystercatcher who is hunting for annelids on a mud flat, for example, will steadily criss-cross the area, looking intently at the ground. Every now and then it will suddenly probe the bill deep into the ground and emerge with a worm. The bird will often run two or three paces before dart-probing.

The Follow-Up-Probe

This is used in areas where there are no such surface visual signs. An Oystercatcher who is hunting for insect larvae on a sand dune, for example, will deliver bouts of many rapid, shallow probes into the sand. Each bout of probes may cover an area of some 3 cm, and between each bout the bird moves forward a little. Suddenly, one of these shallow probes will be followed-up (the bird bores the bill deep into the sand) and a larva is extracted.

In both cases the prey must be located by touch (presumably the bird has a 'feeling image', for it is very rare to see an Oystercatcher dig anything up that is not edible), but the dart-probe is elicited by visual stimuli while the follow-up-probe is elicited by tactile stimuli.

Hunting Strategies

The hunting strategies of the birds are very different and depend on the technique used. With the dart-probe technique, the hunt is area-restricted only in the sense that the bird hunts over a mud flat and avoids stony areas. The

whole area is covered at a steady pace, and a large area is covered per unit time. With the follow-up-probe technique, the hunt is also area-restricted in the sense that the bird is hunting along dunes, but in addition each bout of probes may be restricted to particular targets, i.e. the base of marram grass plants where larvae are wont to lie. The total area covered per unit time is quite small, but the area is covered more intensively.

The possession of these two hunting strategies and two techniques of locating buried prey enable the Oystercatcher to find food in many different areas.

Opportunistic Techniques

The Oystercatcher is a great opportunist and sometimes employs curious techniques for catching prey. Mercer (pers. comm.) has seen an Oystercatcher plunge diving into a shoal of Ammodytes and catch quite a few. I have watched Oystercatchers hunt for Talitrus by picking up and shaking great clumps of seaweed and then running about and catching the animals which had fallen out. I once trained an adult Oystercatcher to shake a nettle three times and then turn through 180° and wait for a reward. I did this by blowing meal worms out of a hide window. It took me no more than 15 minutes to train the bird to do this, and the behaviour persisted for three days after I had run out of mealworms.

CHAPTER 2 THE TECHNIQUES OF FEEDING ON MUSSELS (MYTILUS EDULIS

2/A The Structure of the Mussel (Fig. 1)

Before considering what an Oystercatcher does to a mussel it is first necessary to understand the problem which the mussel presents to the Oystercatcher. The mussel is a bivalve mollusc which shows extreme adaptations to an intertidal way of life. It has a strong, laminated shell, and lives on a hard and often rocky substrate to which it firmly attaches itself by the byssal threads (which emerge from between the ventral valve margins). It can thus withstand severe battering from waves and tidal currents without being swept away. At low tide the mussel is exposed to the air and the valves can be clamped tightly together by sustained contraction of the enlarged posterior adductor muscle. Internally, there is a much smaller anterior adductor muscle near the hinge, while the foot and gut are suspended from the cruciform ligament. This cruciform ligament is attached to the dorsal region of the shell in four places, two just anterior to the posterior adductor muscle and two just posterior to the anterior adductor muscle. The mantle attachments lie around the edges of the valve margins.

There are therefore three problems facing an Oystercatcher: (1) gain entry into the shell, (2) open up the valves and (3) detach the flesh.

The Oystercatcher has two techniques of gaining entry into the shell of a mussel. The first is used against mussels which are under shallow water (and whose valves are therefore slightly open) and consists of Stabbing the bill between the gaping valves. The second technique is used against mussels which are exposed to the air and whose valves are therefore tightly closed. Here the bill is Hammered against the shell until the shell fractures. These two techniques will be considered separately.

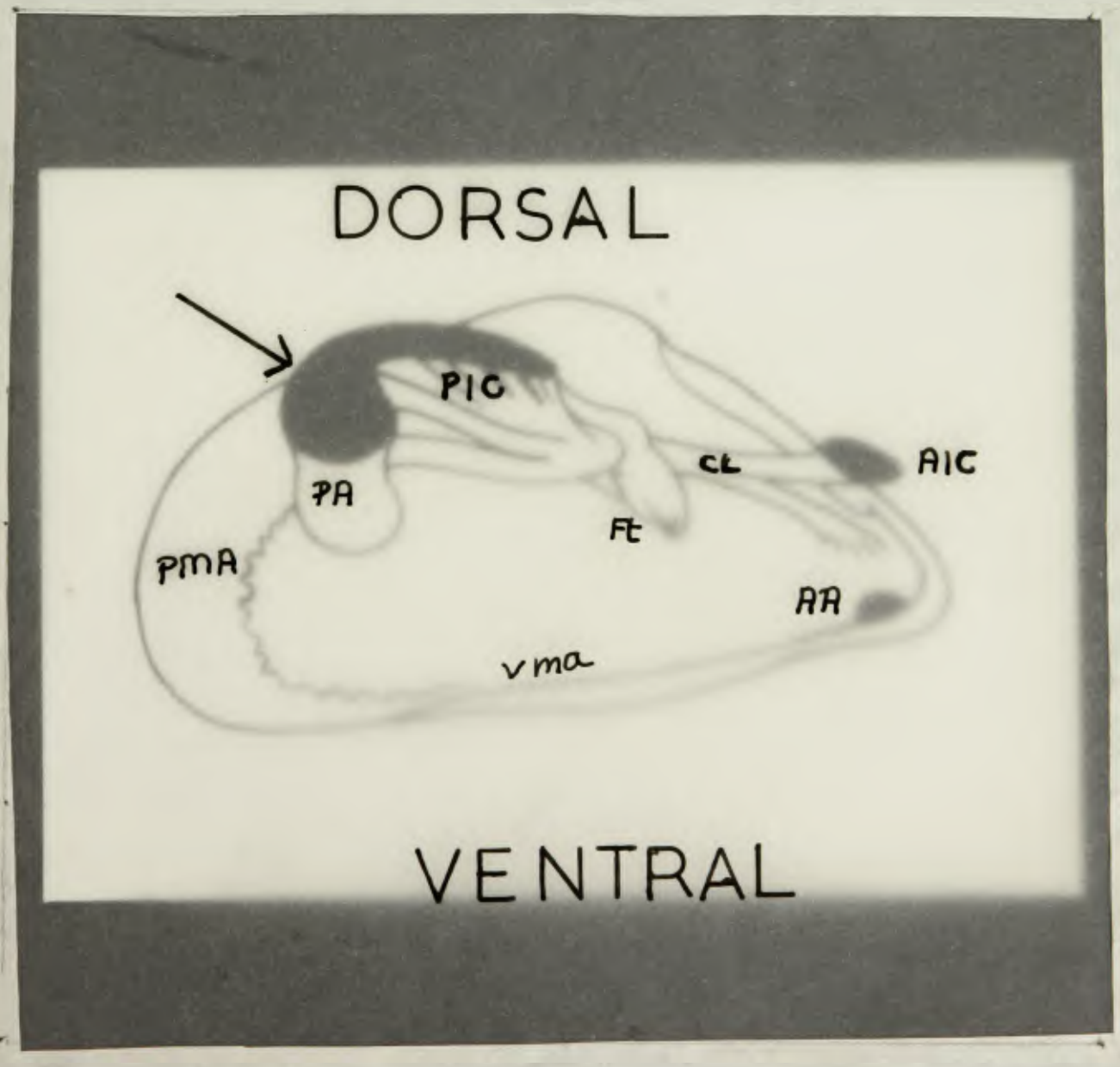
Fig. 1

The Internal Anatomy of a Mussel

the mussel is viewed from the right hand side , and the right hand valve is removed

PMA = posterior mantle attachment
PA = posterior adductor muscle
PIC = posterior insertion of the cruciform ligament
AIC = anterior insertion of the cruciform ligament
AA = anterior adductor muscle
FT = foot
CL = cruciform ligament

arrow indicates the position of the ~~squirt~~ siphon





2/B <u>The Stabbing Technique</u>

2/B/I The Form of the Motor Patterns

The Stab — A single swift and downwards movement of the bill, tips opening slightly as the bill moves downwards (Fig. 2i). Prior to the Stab the bill is some 3-4 cm above the substrate and at an angle of about 45° from the vertical. This angle is very variable.

Levering — A series of lateral side-to-side movements of the bill (Fig. 2ii) often incorporating a twisting component.

Prise — From a closed position, the mandibles are opened wide apart (Fig. 2iii).

Chiseling — The bill tip is moved to-and-fro very rapidly (some 6 times per second), the bill tip moving some 3-4 mm on each stroke (Fig. 2iv). The bill tips may open and close slightly (up to 4 mm), opening as the bill moves forward and closing as the bill is withdrawn.

Eating — The food is gathered into the bill tips and ingested.

2/B/II The Sequence of Motor Patterns

132 observations of Oystercatchers Stabbing mussels were broken down into sequences of the various motor patterns and the transition probabilities between all pairs of motor patterns were calculated (see Introduction to Appendix 1). From Appendix 1 A.a it can be seen that the observed probabilities are highly significantly different from random expectation. The Stab, which always comes first in the sequence, is always followed by Levering. Levering is followed equally by Prising or Chiseling, and Chiseling is followed by Eating. Prising is followed by Chiseling. Appendix 1.a also gives the frequency with which each motor pattern occurs in the sequences, and by inspection it can be seen that Prising is far less frequent than any of the others. The basic

Fig. 2 **The Form of the Motor Patterns**

The STAB

(side view of the bill)

LEVERING

(the bill is vertical : viewed from in front of the bird)

(a) the lateral side-to-side component

(b) the twisting component

PRISING

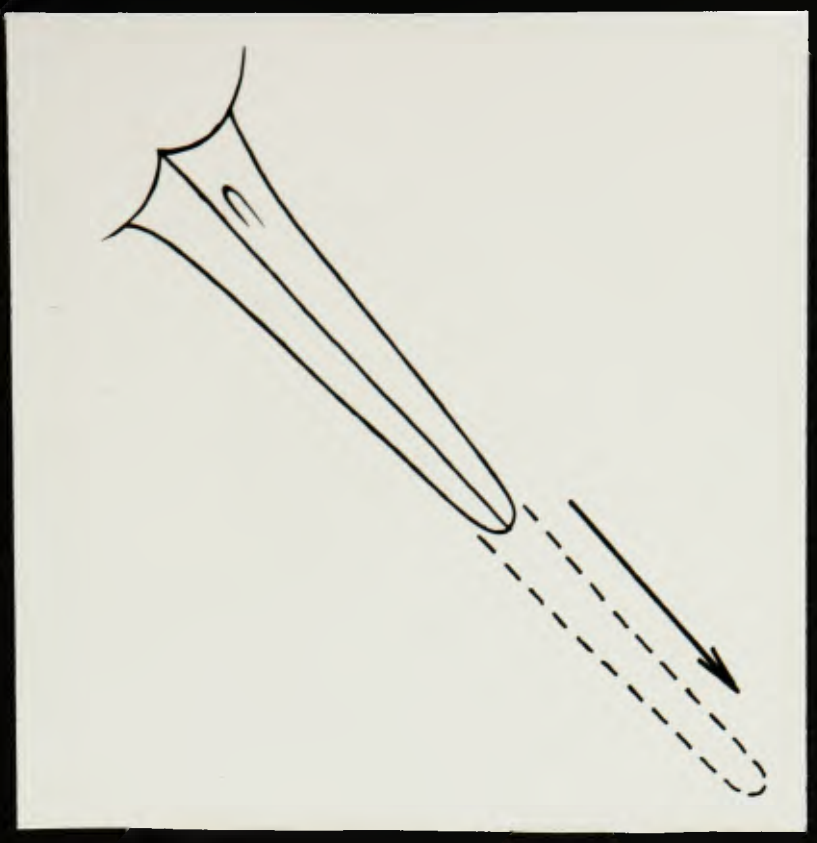
from a closed position ..... the mandibles are forcibly opened

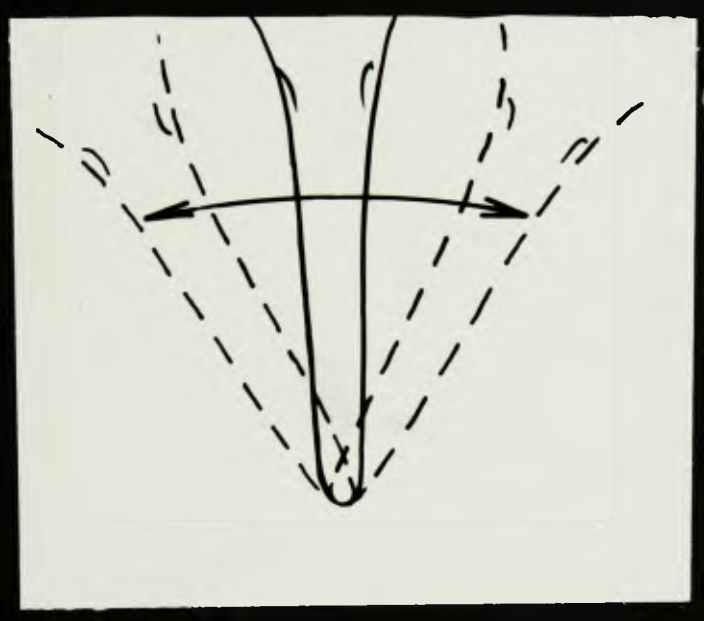
CHISELING

rapid to-and-fro movements of the bill tips

1.

STAB





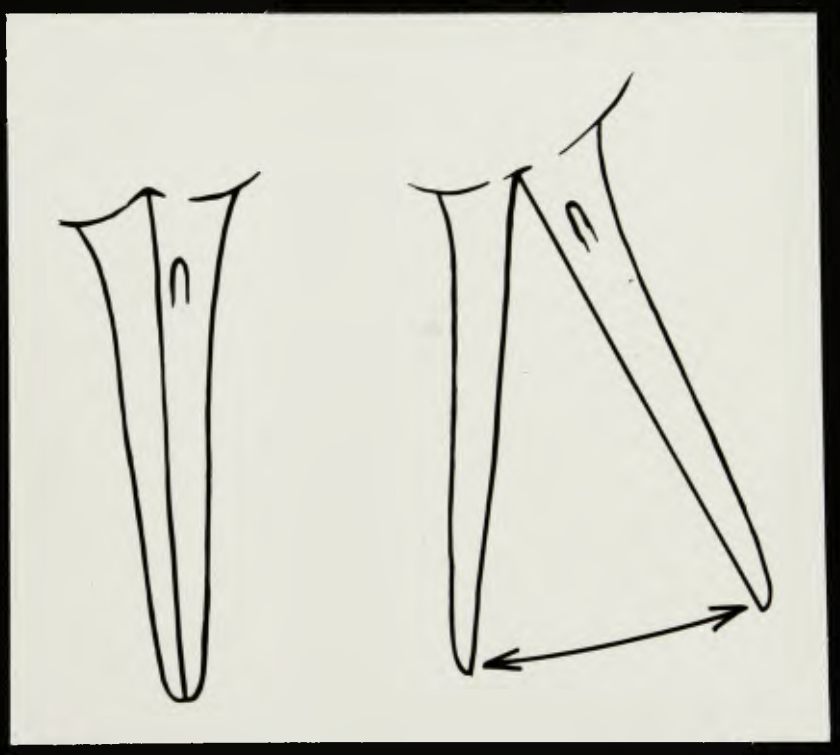
2.
a b

LEVER



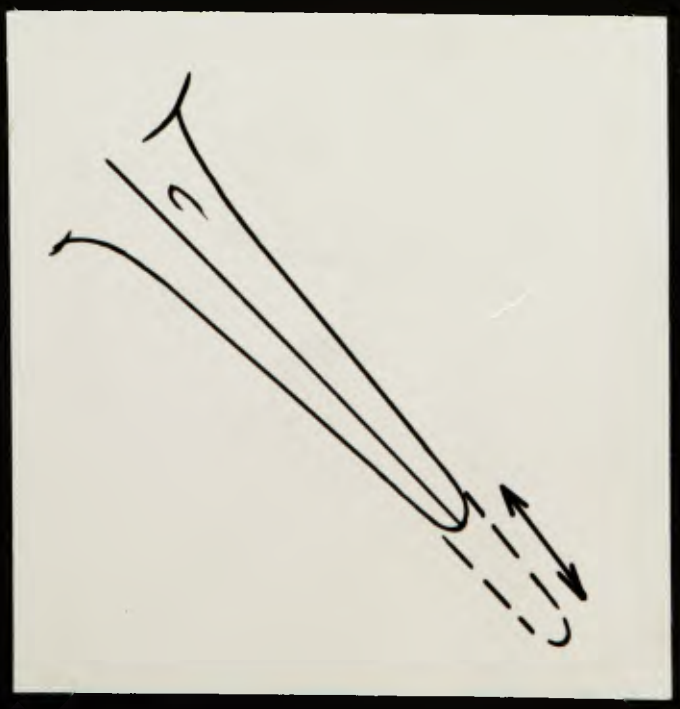
3.

PRISE



4.

CHISEL



sequence is therefore

Stab → Lever → Chisel → Eat

with Prising often occurring between Levering and Chiseling, and infrequently occurring during Chiseling.

2/B/III The Function of the Motor Patterns and of Their Sequence

Armed with what we know of the structure of the mussel, the form of the motor patterns and the sequence in which the motor patterns occur, it is possible to analyse both the function of each motor pattern and the function of the sequence in which they occur.

The Stab

A mussel is normally attached to the mussel bed by its ventral surface so that its dorsal surface is uppermost. The fact that (1) the valves are slightly open when the mussel is under water and that (2) they are gaping to a much wider degree when the mussel is brought to the surface suggests that the Stab is so orientated that the bill passes between the posterior valve margins and severs the posterior adductor muscle which lies immediately anterior to the posterior margins (Fig. 3). When the Oystercatcher brings a Stabbed mussel to the surface it can be seen that one mandible is inside the shell between the posterior valve margins and in a dorsal/posterior - anterior orientation. Very infrequently the Stab is not quick enough and the mussel clamps tight onto the Oystercatcher's bill tip, and in these cases it is clearly seen that the bill tip is just inside the posterior margins. On three occasions it was possible to chase an Oystercatcher away from a mussel which it had just Stabbed, and in each case the posterior adductor muscle was found to be cut through (see Part II, p. 80a for photographs of the damage). Other internal injuries to the mussels showed that the bill had entered from a dorsal/posterior direction.

The Oystercatcher thus aims the Stab at the posterior

valve margins of the gaping shell (where the gape is widest) and, by forcing the bill between the valve margins, cuts through the posterior adductor muscle which effectively disables the mussel. The Stab thus serves to gain initial entry into the shell.

Levering

Levering always occurs after the Stab, when the bill is deep inside the mussel. The vertical axis of the bill is parallel to the lateral axis of the mussel (Fig. 3) and the bill is Levered and twisted against the posterior margins of the valves. The mussel is then detached from the substrate and reorientated with the ventral side uppermost. More Levering may then follow with the bill thrust into the anterior region of the shell and Levered and twisted against the ventral valve margins (Fig. 3). In relatively few cases (9% of observations) no Levering is seen prior to detaching and reorienting the mussel and all the Levering is carried out with the bill in the anterior region of the shell.

Mussels which are reoriented after the Levering are seen to be gaping widely, and in those cases when Levering occurs after the reorientation of the mussel, the Levering movements are seen to force the valves apart. Levering therefore functions to open the valves of the mussel once initial entry has been gained by the Stab, and the Levering movements most probably destroy any muscular attachments inside the shell which are undamaged by the first Stab.

Prising

Prising only occurs once the mussel has been considerably damaged by the Stab and Levering. The closed bill is turned at right angles to the valve margins and then the mandibles are forcibly opened (Fig. 3). The effect of this is to open the valves of the shell as wide apart as possible.

Fig. 3

The Orientation of the Motor Patterns in the Mussel

The STAB

the bill enters between the posterior valve margins (direction of arrow) and severs the posterior adductor muscle (dotted circle)

LEVERING

the mussel is oriented with the ventral side up and the bill is Levered across the ventral valve margins , as well as being twisted between the margins

PRISING

the mandibles are forcibly opened against the ventral valve margins , thus forcing apart the valves

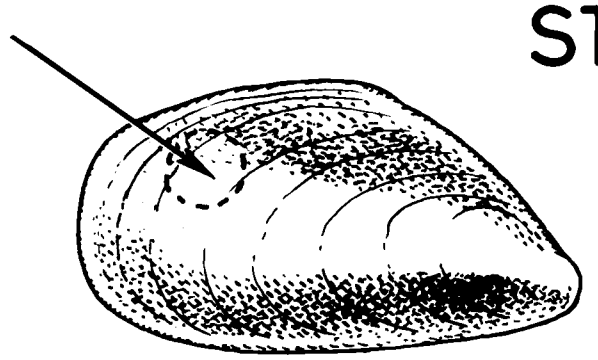
CHISELING

(a) only the left valve of the mussel is shown (viewed from the dorsal side) and only the posterior adductor stump is shown. Note how the bill is turned flat against the valves so that the broad cutting edge of the bill tip has the most effect

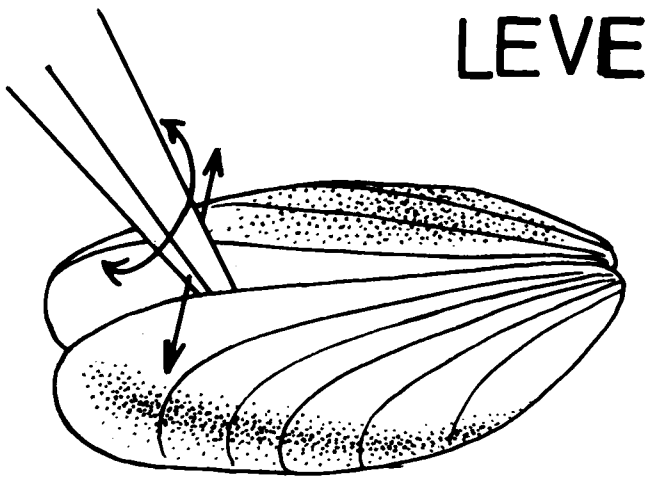
(b) a longitudional cross section through the valve. The posterior adductor stump is shown in cross section , and the bill (solid lines) is in the same orientation as in (a) . The adductor stump can be easily cut and pared away from the shell by an attack from this orientation.

The dotted line shows an attack mounted from the anterior. This attack will merely shred the adductor , and not cut it cleanly away .

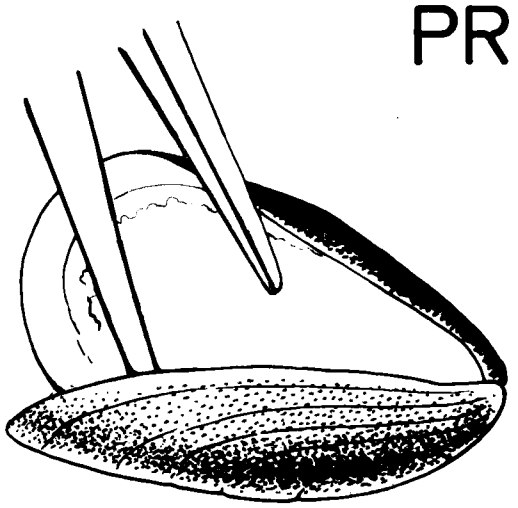
STAB



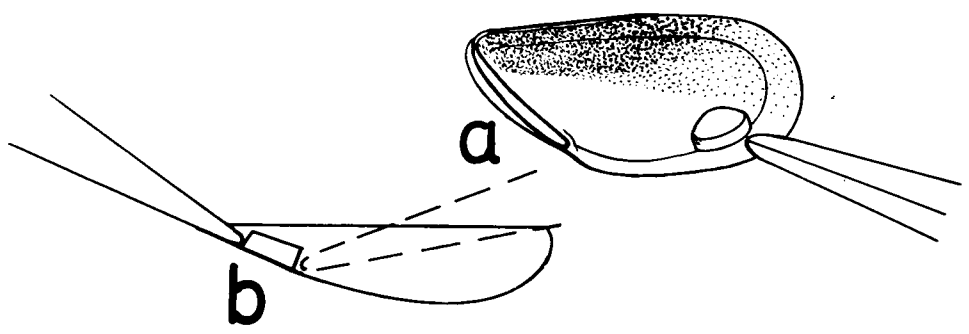
LEVER



PRISE



CHISEL



Chiseling

The Chiseling movements are directed at the stumps of the posterior adductor muscle, the insertions of the cruciform ligament and at the mantle attachments which lie around the valve margins. The bill is oriented so that the broad bill tip lies flat against the valves (Fig. 3) and so that the to-and-fro movements of this broad 'cutting edge' are directed between the muscular and mantle attachments and the shell. In this way the various attachments are cut and pared away from the shell so that the flesh becomes free.

The various muscular attachments are not attacked in a random order (for more details see Chapter 3/F). The Oystercatcher always Chisels from posterior to anterior and this is the most efficient orientation of the attack for two reasons. Firstly, the shell is asymmetrical, and the anterior attachments cannot be easily reached from any other direction. Secondly, the shell is markedly concave in the posterior region, and it is only from a posterior direction that the posterior attachments can be cleanly cut away. A Chiseling attack from any other direction would merely shred them.

Thus, starting from the posterior end of one valve, the bird Chisels down into the anterior region of the valve, cutting away the posterior mantle attachments, posterior adductor stump, posterior insertion of the cruciform ligament and anterior attachment of the cruciform ligament in that order. The process is then repeated in the other valve. Once all these attachments are cut, the flesh is shaken free and this usually tears free the ventral mantle attachments which are rarely specifically attacked.

During the Chiseling attack, the shell often skids about over the surface of the sand, yet the Oystercatcher is able to maintain its bill in contact with the shell, and in the correct orientation, by remarkably adroit contortions of the neck.

The function of Chiseling is thus to free the flesh of the mussel from the shell by cutting the attachments between the flesh and the valves.

It will be remembered that there are three problems facing an Oystercatcher who wants to eat a mussel: (1) gain entry into the shell, (2) open up the valves and (3) detach the flesh. The functional significance of the sequence of the motor patterns is now clear. The Stab serves to gain initial entry into the shell, Levering and Prising serve to open up the valves and Chiseling serves to cut the flesh free.

2/C The Hammering Technique

The Hammering technique is used against mussels which are exposed to the air and which are therefore tightly closed. The Oystercatcher breaks into the mussel by cracking the shell.

2/C/I The Form of the Motor Patterns

Hammering a series of hard, downward blows with the bill tip. The neck is held stiff, the bill points vertically downwards and the body pivots from the pelvis (Fig. 4).

Levering, Prising, Chiseling as described for the Stabbing technique, there being no discernible difference between the form of these motor patterns and those in the Stabbing technique.

2/C/II The Sequence of Motor Patterns

138 observations of Oystercatchers Hammering mussels were broken down into sequences of the various motor patterns and the transition probabilities between all pairs of motor patterns were calculated (Appendix 1 B.). The basic sequence is

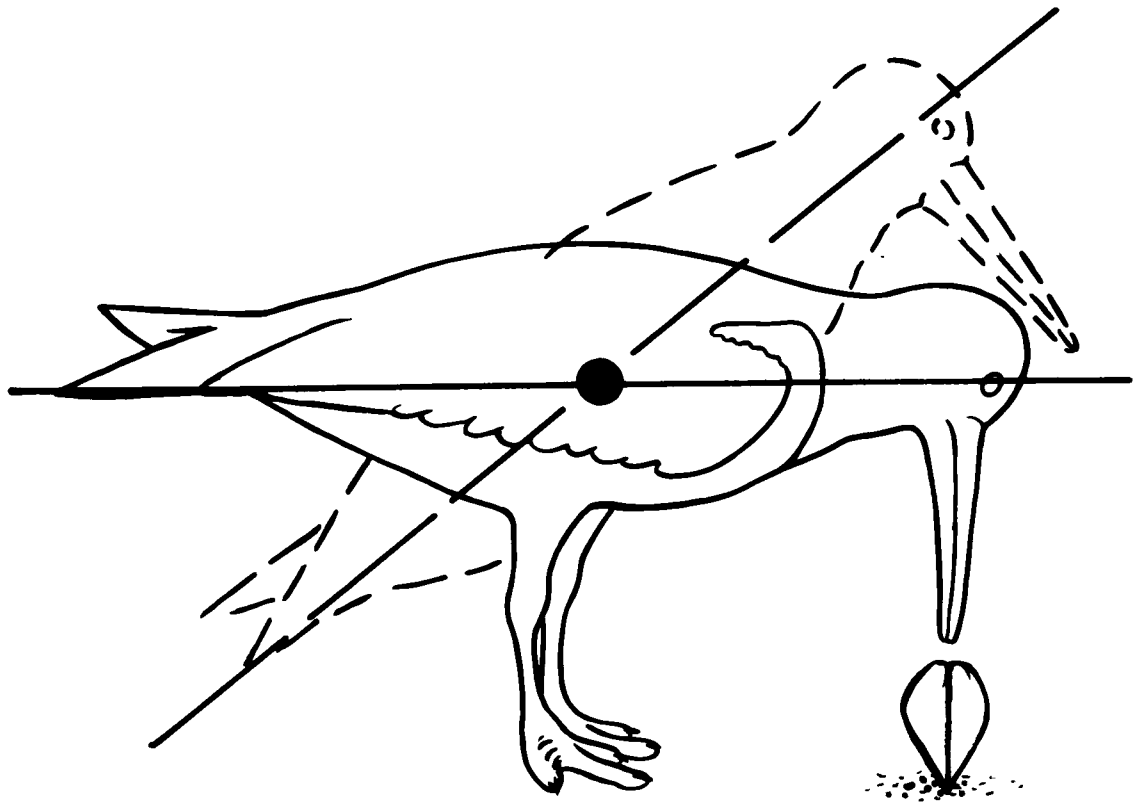
Hammering → Levering → Chiseling → Eating

with Prising sometimes occurring between Levering and Chiseling.

Fig. 4

The Hammering Attack

The mussel is oriented with the flat ventral side uppermost , and the blows are directed at this surface . The body pivots from the pelvis .



2/C/III The Function of the Motor Patterns

Hammering

The exposed mussel is firmly attached to the mussel bed by the byssal threads which emerge from between the ventral valve margins. The first action of the Oystercatcher is to detach the mussel and then carry it to a patch of firm sand. The Oystercatcher then orientates the mussel so that the flat ventral surface is uppermost and directs the Hammer blows at this region until the shell fractures. If the mussel falls over during the Hammering attack then the Oystercatcher will reorient it, and if the mussel sinks into the sand (i.e. the sand is too soft) then the Oystercatcher will remove the mussel to a different patch of sand and try again there. On the whole, individual Oystercatchers tend to take successive mussels to the same place to Hammer.

From direct observations and by collecting the shells of mussels which had been Hammered open it was seen that the Hammer blows damage the shell in various different ways:

(a) a semi-circular chip is broken off from one or both of the ventral valve margins (66% of 406 damaged shells).

(b) the whole dorsal region of the shell collapses in fragments (4% of shells).

(c) a fracture line runs from the point of impact of the blows to the dorsal margins so that the posterior end of one, or both, valves is completely broken off (21% of the shells).

(d) sometimes the Oystercatcher attacks the shell in situ, i.e. the bird Hammers at the posterior or dorsal margins. This damages the shell in a very characteristic fashion, and shells damaged in this way are readily distinguishable from those described in (b) above. Only very tiny mussels are attacked in this fashion (9% of the shells).

(e) very infrequently I have observed that the Hammer blows 'knock out' the mussel, for the mussel is seen to gape widely before the valves are fractured and only after a

very few blows. Since these shells are undamaged they are difficult to distinguish from those undamaged shells which have been Stabbed, so it is impossible to estimate accurately with what frequency this occurs, but I would estimate it is less than 1%.

It can be seen from the above data that 91% of all the damaged shells had been attacked through the ventral side and tests designed to measure the relative strength of different regions of a mussel shell to Hammer blows showed that this ventral region was by far the weakest (Part II p. 79-A) The Hammering attack is thus restricted to the weakest part of the shell, and the shell is specifically oriented so that this weakest part is exposed. Hammering thus functions to gain initial entry into the shell by fracturing the valves.

Levering

The function of Levering is the same as that described in the Stabbing technique, but there are however slight differences in the orientation of the Levering movements. For a start, the mussel is already oriented with its ventral side up so that the reorientation seen in the Stabbing technique is not seen. The Levering movements themselves are often directed into the posterior region of the shell and the bill is Levered and twisted against the posterior valve margins. The function of this is probably to destroy the posterior adductor muscle which is relatively undamaged by the Hammering attack. Mussels damaged in fashions (a) and (e) will have their posterior adductors completely undamaged, while mussels damaged in fashions (b), (c) and (d) will have posterior adductor effectively put out of action by the damage done to the shell. Unfortunately, my observations are not detailed enough to show if the Levering movements are more frequently directed into the posterior

region of the shell in the former cases than in the latter cases, but I predict this to be so.

Prising, Chiseling and Eating

The orientation and function of these motor patterns in the Hammering technique are the same as described for the Stabbing technique.

2/D Comparisons between the two Techniques

Inspection of the Tables in Appendix 1 Aa and 1 Bb show that the general organisation of the sequence of the motor patterns is very similar. One striking difference is that Prising is more frequent and is more variable in position in the Stabbing sequences. However, this difference is due entirely to bias in the observations. The areas of the mussel bed on which Oystercatchers Hammered mussels was very rocky and uneven and it was extremely difficult to observe the birds clearly. There was only one area where I I could consistently make clear observations, and unfortunately this area of the bed was entirely covered with small mussels. The areas of the bed where the birds were Stabbing mussels were more flat and open and I was able to collect observations on Oystercatchers opening a wide range of sizes of mussels. In the causal analysis of Prising (2/D/V) I show that Prising is less frequent and less variable in position when small mussels are opened than when larger mussels are opened, so this apparent difference between the frequency of Prising in these two techniques is not a real difference.

The function of the motor patterns in these two techniques is exactly the same. Stabbing or Hammering serve to gain initial entry into the shell, Levering and Prising serve to open the valves wide apart, and Chiseleing serves to cut the flesh free.

The form of each of the motor patterns is specifically

adapted to a particular function, yet this function (and the efficiency and skill of the techniques) is dependent upon the correct orientation of each motor pattern with respect to the mussel. The Stab is aimed at the posterior region of the shell (where the gap is widest) and therefore severs the posterior adductor muscle; the Hammering attack is restricted to the weakest part of the shell and the shell is specifically oriented so that this weakest part is uppermost; the Levering movements are made against the valve margins and they would be less effective in any other orientation; the Prise is made against the valve margins and would also be less effective in any other orientation; the Chiseling movements are directed from posterior to anterior and would similarly be less effective in any other orientation. The orientation of the motor patterns is crucial - and is adapted to the structure of the mussel.

CHAPTER 3 THE INTEGRATION OF THE MOTOR PATTERNS IN THE MUSSEL TECHNIQUES

3/A Introduction

The similarity of the strength of association between the different motor patterns in the Stabbing and Hammering sequences suggests that the factors which control the sequence in which the motor patterns occur are the same in each case. There are two main problems to be considered. Firstly, what stimuli elicit each of the motor patterns and secondly, what factors determine the duration of each motor pattern. The answers to these questions should explain what determines the transition from one motor pattern to another.

The analysis presented in this Chapter is based primarily on tape recorded observations of Oystercatchers Stabbing and Hammering mussels. From these records both the sequence and duration (measured in seconds) of the motor patterns could be measured. The size of the mussel being eaten was classified as 'small', 'medium' or 'large' as compared with the Oystercatcher's bill, but I do not know how exactly these size categories compare with the actual size of the mussel (i.e. as measured in millimetres). From section 3/F/I it seems that a 35 mm mussel is midway between 'small' and 'medium'.

3/B The Stab

The Oystercatcher has two different methods of hunting for mussels and which one it uses is dependent upon where the mussel is on the mussel bed.

In those areas where the mussels are either under shallow sea water or are buried in soft and soggy sand (as often happens as a conseque ce of tidal shifts in the sand ridges), the Oystercatchers walk slowly over the mussel bed and then suddenly dart forward and Stab the bill under the

water or into the sand. These dart-Stabs must be elicited by visual stimuli for the bird will often run forwards a few paces before Stabbing. The stimuli from a mussel covered with shallow water is most likely to be from the gaping valves, but the stimuli from a mussel which lies buried in soggy sand are more difficult to imagine. I have sat in vain looking at patches of soggy sand which I knew contained buried mussels and yet have never seen any sign or movement on the surface to indicate their position. Yet the Oystercatcher is able to see some visual signal which indicates the precise location of the mussel and is able to Stab the bill - first time - accurately between the valves. It could be that mussels buried in soggy sand occasionally 'cough' to try and clear their gills and that the Oystercatcher reacts to this slight movement. I have kept mussels buried in a sand-lined aquarium and there was a very obvious movement of sand particles around the siphons. When I drained out the water so that the mussels were in soggy sand, I occasionally could detect a slight movement of sand particles on the surface which indicated the position of the mussels' siphon.

The second method of Stabbing mussels is used in those areas of the mussel beds where there are mussels buried in hard sand (i.e. sand ridges from which the excess water has drained). A completely different behaviour is shown, for here the Oystercatchers move slowly over the sand making bouts of many shallow rapid probes. Suddenly, one of these probes is 'followed-up' and the bill is forced deep into the sand. A mussel is then brought to the surface transfixed through the posterior margins. When I dug up mussels which were buried in hard sand, many of them were found to be moribund and gaping (very few of those buried in soggy sand were moribund). This suggests that the Oystercatcher locates these mussels by touch, distinguishes whether or not the mussel is gaping, and then Stabs the bill between the valves.

TABLE 1 SPECIFICITY OF STABBING TECHNIQUES TO THE ECOLOGICAL CONDITIONS OF THE MUSSELS

	Location of the Prey		
	Exposed under water	Buried in wet sand	Buried in dry sand
Dart-Stab	38	164	0
Follow-up-Stab	0	5	40

Table 1 shows the specificity of these hunting methods to the ecological conditions of the mussels. Of interest is the fact that there is no significant difference between the percentage success of these two methods (dart-Stab 13% unsuccessful; follow-up-stab 15% unsuccessful; $chi^2 = 1.9$).

The similarities between these two hunting methods and those described for soft-bodied invertebrates are immediately apparent. In both cases it seems that, in the absence of visual stimuli on the surface indicating the precise location of the food, the Oystercatcher hunts by touch.

The Stab can thus be elicited either by visual (dart-Stab) or by tactile (follow-up-stab) stimuli.

3/C The Hammering Attack

The Hammering attack consists of detaching the mussel, orienting the mussel with the ventral side up and directing the Hammer blows at this ventral region, and there is nothing to suggest that this behaviour is not entirely controlled by visual stimuli.

The series of Hammer blows is elicited once the mussel has been oriented and it stops as soon as the shell fractures and the bill penetrates between the valves, the larger the mussel the more blows being necessary to fracture the shell (small mussels 4.0 blows on average, medium mussels 7.6 blows on average, Mann-Whitney $z = 3.38$, $p = 0.0005$). I have only

eight observations of Oystercatchers abandoning a mussel before the shell fractured, and in each case the number of blows given prior to abandoning it were well within the normal range of successful Hammering attacks. I have also once seen an Oystercatcher deliver 63 blows to a mussel-shaped stone (though normally they can decide before Hammering whether or not they have a stone instead of a mussel).

The number of Hammer blows given is therefore determined by the size of the mussel, and there is no evidence that once the Hammering is elicited it continues for a pre-set number of blows. The Hammering attack is therefore both elicited and terminated by external stimuli.

3/D Levering

3/D/I The Stimuli Eliciting Levering

Both Stabbing and Hammering are followed by Levering, and observations show that:

1. after a successful Stab the bill ends up deep inside the mussel and Levering is elicited.
2. this transition from Stabbing to Levering happens even if the mussel is completely hidden in sand.
3. after a successful Hammering attack the bill ends up deep inside the mussel and Levering is elicited.
4. if the Stab is not quick enough the mussel will clamp tightly onto the end of the bill tip; the Oystercatcher then does everything possible (i.e. stabing and scratching at it) to remove the mussel and will then abandon it without Levering.
5. if, during Chiseling, the valves of the mussel inadvertently close, a Prise will be elicited and not Levering.

These observations suggest that Levering is primarily elicited by tactile stimuli (although visual stimuli cannot be

entirely ruled out) in the form of the amount of pressure around the bill tip. It seems that 'tight' pressure elicits bill-withdrawal, 'firm' pressure elicits Levering and 'loose' pressure elicits Prising.

An experiment was set up to try and demonstrate if this was so. The rationale of the experiment was to present captive adult mussel-eating Oystercatchers with mussels which gave the same visual stimuli (slightly gaping valves) but which were damaged internally (by myself) in various different ways so as to offer different degrees of resistance when opened. The mussels were presented to the birds with the ventral side uppermost and with the posterior valve margins gaping some 4 - 5 mm. All the mussels were 35 mm in length, and 5 different types were used.

Type 1 the posterior adductor and all other internal muscular attachments were destroyed. The mussel was fixed in position by being lightly pressed into the sand of the cage.

Type 2 damaged and presented in the same way as Type 1, but an elastic band was placed around the valves so that the valves promptly closed every time the Oystercatcher attempted to open them.

Type 3 only the posterior adductor muscle was cut through, all other internal muscular attachments being undamaged.

Type 4 the mussels were completely undamaged inside and the valves were wedged open with a piece of wood.

Type 5 damaged in the same way as Type 1, but presented with the valves fully open. This was the normal food of the captive birds.

The results of this experiment (summarised in Table 2) are not very conclusive for the two Oystercatchers which I possessed proved to be very uncooperative when presented with mussels other than Type 5 (their normal food in captivity).

TABLE 2 EXPERIMENT WITH MUSSELS OF TYPES 1 - 5

	Type 1	Type 2	Type 3	Type 4	Type 5
Number eaten	20	10	12	0	88
LEVERING					
No. mussels in which Levering occurred	1	2	12	-	0
Median Duration of Levering (Sec)	0.8	1.2	7.8	-	-
PRISING					
Total number of Prises	3	41	9	-	2
Position of Prise					
a) 1st motor pattern	2	24	0	-	0
b) after Lever	0	2	6	-	0
c) during Chisel	1	15	3	-	2
CHISELING					
Median Duration of Chiseling (sec)	14.1	22.3	15.4	-	13.8

Duration of Levering: Type 3 > Type 2 = Type 1 (Mann-Whitney z = 2.8; p = 0.005 : Mann-Whitney z = 1.13, p = 0.26)

Duration of Chiseling: Type 2 > Type 1 = Type 3 = Type 4 (Mann-Whitney z = 2.63, p = 0.008 : Mann-Whitney z never > 1.86, p never < 0.06)

Type 1: all internal attachments between the valves are cut

Type 2: as above, but an elastic band is placed around the valves

Type 3: only the posterior adductor muscle is cut

Type 4: no internal damage, valves wedged open

Type 5: all internal attachments cut, mussel presented with the valves fully open

Neither bird would attempt the Type 4 mussels, and it was only after much food deprivation that I could persuade them to eat mussels of Types 2 and 3. Mussels of Type 1 they initially ate very readily. The quantitative data from these experiments should therefore be treated with reservation and should not be compared with the data collected from free living birds eating mussels under more natural conditions.

The initial response of the birds when presented with mussels of Types 1, 2, 3 and 4 was to push the bill in through the gaping ventral margins (technically a Stab?). The Type 1 mussels immediately flopped open and no Levering was elicited, except for 3 mussels which did not entirely open and from which a negligible amount of Levering was elicited in one case, and a Prise in 2 cases. The Type 2 mussels remained loosely closed around the bill and there was similarly a neglibible amount of Levering but instead much Prising. The Type 3 mussels remained firmly closed around the bill and a great deal of Levering was elicited, while the Type 4 mussels were abandoned because the birds could not (or would not) push the bill between the valves.

The data from mussels of Types 2 and 3 were collected from one individual in each case, and both these individuals had experience with Type 1 mussels prior to their experience with Types 2 or 3. These data, therefore, strongly suggest that the stimulus that elicits Levering is the amount of pressure around the bill tip.

3/D/II The Duration of Levering

From tape-recorded observations of Oystercatchers Stabbing and Hammering mussels the duration of Levering (measured in seconds) could be measured. Analysis of these records showed that:

1. the larger the mussel the longer is the duration of Levering (Table 3).

TABLE 3 MEDIAN DURATION OF LEVERING (IN SEC) IN STABBED AND HAMMERED MUSSELS

a) Comparisons between Stabbed and Hammered Mussels

	Small Prey	Medium Prey	Large Prey	
Stabbed	3.0	3.4	6.1	(small < medium < large: z never < 2.06, p never > 0.02)
Hammered	2.6 (z = 1.32 p = 0.18)	3.8 (z = 0.42 p = 0.67)	-	(small < medium: z = 2.32 p = 0.02

b) Comparisons between dart-Stabbed and follow-up-Stabbed prey

	Small Prey	Medium Prey	Large Prey
Dart-Stab	3.9	5.01	6.7
Follow-up-Stab	2.1 (z = 3.12 p = 0.002)	2.9 (z = 3.07 p = 0.002)	4.0 (z = 2.9 p = 0.004)

c) The Transitions from Lever → Prise and from Lever → Chisel

	Small Prey	Medium Prey
Lever Prise	3.0	3.9
Lever Chisel	2.6 (z = 1.22 p = 0.22)	3.5 (z = 0.97 p = 0.97)

z is calculated from Mann-Whitney: all p values are two-tailed

2. mussels which are dart-Stabbed elicit significantly more Levering (size for size) than those which are caught by follow-up-Stabs (Table 3b). This suggests that the mussels which are buried in hard sand are indeed more moribund (and therefore offer less resistance to Levering) than are those buried in soggy sand or those covered with water.

3. there is no significant difference between the amount of Levering elicited from Stabbed and from Hammered mussels of the same size (Table 3a). This is an unexpected result for since the posterior adductor muscle is undamaged by a Hammering attack I would have expected that more Levering would be elicited from the Hammered mussels. Of course, when the posterior end of one of the valves splits off or when the whole dorsal region of the shell collapses the adductor is effectively disabled, but this only happens 25% of the time(2/C/II).

4. there is no correlation between the number of blows necessary to fracture the shell and the duration of Levering following the Hammering attack (small mussels, $r_s = + 0.03$, $n = 67$: medium mussels, $r_s = + 0.19$, $n = 19$: r_s is the Sperman Rank Correlation Coefficient).

In both the Stabbing and Hammering sequences, Levering is followed by Prising or by Chiseling and these transitions can obviously not occur unless the stimuli eliciting these motor patterns are present. The crucial point therefore is whether Levering is terminated by the stimuli eliciting Prising or Chiseling overriding those eliciting Levering, or whether Levering continues until the stimuli eliciting it are no longer present, at which time the bird switches its attention to the stimuli which will elicit Prising or Chiseling.

If the duration of Levering in the transition Levering Prising is compared with the duration of Levering in the

transition Levering → Chiseling, no significant difference can be found (Table 3c). If the duration of Levering was controlled by the stimuli eliciting Prising or Chiseling overriding those eliciting Levering, then it seems most unlikely that the duration of Levering prior to these two different transitions would be the same. These data therefore show that Levering continues for as long as the eliciting stimuli are present, or in functional terms, the duration of Levering depends only upon the size of the mussel.

3/E Prising

3/E/I The Stimuli Eliciting Prising

The data from mussels of Types 2 and 3 (Table 2) suggest that Prising is elicited by 'loose' resistance around the bill. When presented with these mussels the birds' initial response was to push the bill in through the ventral margins. With mussels of Type 2 the bill was then immediately reoriented with the dorsal-ventral axis at right angles to the mussel's median axis and a Prise was elicited, the mandibles opening against the ventral valve margins. With mussels of Type 3 there was no reorientation of the bill, and Levering was immediately elicited. The subsequent behaviour of the birds is of great interest.

Type 2 mussels: With the first three mussels eaten there was initially a series of Prises. After each Prise the valves closed again and another Prise was elicited. The bird then attempted to Chisel and there were many Prises during the Chiseling as well as two instances of Levering. The rubber band eventually slipped off (due to the rounded shape of the mussel shell) and the valves flopped open. While eating the next three mussels the bird learnt that by Prising in the 'wrong' orientation (i.e. longitudionally instead of laterally) the rubber band could be speedily removed, and in the last two mussels eaten the bird needed but one

longitudional Prise to remove the rubber band.

Type 3 mussels: 9 Prises were observed in the 12 mussels eaten. 6 of these occurred after Levering, and 3 during Chiseling when the valves inadvertently closed.

Type 1 mussels: only 3 Prises were observed in the 20 mussels eaten. 2 of these followed the initial insertion of the bill when the valves did not fully flop open, and one occurred during Chiseling.

Type 5 mussels: 2 Prises were observed in 88 mussels eaten, in each case when the valves closed during Chiseling.

From these data, and from Appendix 1a and 1b it can be seen that Prising is elicited in two situations, (a) following Levering and (b) during Chiseling. Tactile stimuli seem to be the most important in the first case, but visual stimuli may also be important in the second case.

3/E/II The Position of Prising in the Sequences

Analysis of the Stabbing and Hammering sequences show that:

1. the larger the mussel the more likely is a Prise to occur somewhere in the sequence (Table 4a).
2. in small mussels most of the Prises occur immediately after the Levering, while in larger mussels the position of the Prise is more variable (Table 4b).

Prises which occur during Chiseling are due to the valves inadvertently closing during the Chiseling process. Unfortunately, I do not have the necessary 'control' data as to how many times Prising did not occur when the valves closed, so not much more can be said about this. The main problem is why should a Prise sometimes be elicited after Levering and sometimes not, and why should this happen less frequently in small mussels than in larger mussels. The answer may lie in the final orientation of the bill inside the mussel when Levering stops, or it may be due to where the bird was Levering inside the mussel (it may even be an

TABLE 4 PRISING IN THE MUSSEL TECHNIQUES

a) The frequency of Prising in Small and Medium sized mussels

	Small Prey	Medium Prey	
Sequences with Prise	30%	82%	
Sequences without Prise	70%	18%	$chi^2 = 49.7$
			$p = <0.001$
Number of sequences	177	93	

b) The Position of Prising in the Sequences

	Small Prey	Medium Prey	
Prise immediately after Levering	85%	65%	
Prise during Chiseling	15%	35%	$chi^2 = 5.6$
			$p = <0.02$
			>0.01
Number of sequences	53	76	

TABLE 5 MEDIAN DURATION OF CHISELING (IN SEC) IN SEQUENCES WITH AND WITHOUT A PRISE

	No Prise in sequence	Prise immediately after Levering	Prise during Chiseling
Small Prey	6.6	7.1	7.0
Medium Prey	14.8	14.0	14.2

small prey: Mann-Whitney z never >1.22, p never <0.22

medium prey: Mann-Whitney z never >0.96, p never <0.34

individual trait). My observations are not detailed enough to give any indication.

Yet it seems fairly certain that Prising is elicited primarily by tactile stimuli in the form of 'loose' resistance around the bill, but the factors that control whether or not it will occur, or even where it will occur in the sequence, are still not clear. The best that can be said is that Prising is an opportunistic behaviour which functions to open the valves wide apart if and when necessary. The effectiveness of the Prise is seen from the data in Table 5 for no significant difference can be found between the duration of Chiseling in mussels in which (a) no Prise occured in the sequence, (b) a Prise occurred before the Chiseling and (c) a Prise occurred during Chiseling. In contrast, the Prises in mussels of Type 2 (Table 2) were mainly ineffective because the rubber band closed the valves after each Prise. The duration of Chiseling in the Type 2 mussels was significantly longer than in any of the other types.

3/F Chiseling

3/F/I Introduction

Chiseling is the most complex motor pattern in the Oystercatcher's repertoire. Analysis of the tape recorded observations show that:

1. in both Stabbed and Hammered mussels the duration of Chiseling in small mussels is significantly shorter than it is in larger mussels (Table 6).
2. there is no significant difference between the duration of Chiseling (size for size) in mussels which have been either Stabbed or Hammered (Table 6)

TABLE 6 MEDIAN DURATION OF CHISELING IN STABBED AND HAMMERED MUSSELS

	Small Prey	Medium and Large Prey
Stabbed Mussels	6.2	15.0 ($z = 6.46$, $p = 0.00001$)
Hammered Mussels	7.5 ($z = 1.12$, $p = 0.26$)	15.2 ($z = 3.55$, $p = 0.00004$) ($z = 1.7$, $p = 0.10$)

3. there is no correlation between the duration of Levering and the duration of Chiseling in the same mussel (Stabbed mussels: small, $r_s = + 0.19$, $n = 35$; medium $r_s = + 0.21$, $n = 35$: Hammered mussels, small, $r_s = - 0.01$, $n = 67$, medium, $r_s = + 0.25$, $n = 19$).

These data suggest that the duration of Chiseling is dependent upon some aspect of the size of the mussel, and a plausable hypothesis is that it is the actual size of the muscular attachments that determines the duration of Chiseling.

The Number of Bouts of Chiseling per mussel

A bout of Chiseling is here defined as a series of Chiseling movements which terminate directly in the removal of a piece of flesh from the valves. More bouts of Chiseling are recorded from larger mussels than from smaller mussels (Table 7a). Most usually a large piece of flesh is removed after the first bout, and small pieces after the second and subsequent bouts (Table 7b). In addition, the first pieces are usually preceded by a 'Shake', i.e. the bird Chisels and then grabs and Shakes the flesh free before eating it. This is so for both small, medium and large mussels. The first Chiseling bout is much longer than the subsequent bouts (Table 7c). The general pattern of the Chiseling attack is thus one long bout of Chiseling (terminating in a large piece of flesh being removed) followed by further shorter bouts (each terminating in small

TABLE 7 GENERAL PATTERN OF THE CHISELING ATTACK IN MUSSELS

a) Number of Chiseling Bouts

	Small Prey	Medium Prey	Large Prey
Number of Observations	175	81	13
1 Chiseling bout only	88%	32%	15%
More than 1 Chiseling bout	12%	68%	85%

b) Size of pieces of flesh removed after the Chiseling bouts, and the frequency of Shaking (data from all sizes of mussels)

	Small Piece	Medium Piece	Large Piece	Number of Shakes	Totals
After 1st bout	1%	8%	91%	250	269
After 2nd & subsequent bouts	94%	3%	3%	18	144

c) Median duration (in sec) of Chiseling bouts

	Small Prey	Medium Prey
1st bout	6.9	12.6
2nd and subsequent bouts	2.8	3.0

(in both small and medium prey, 1st bout > 2nd bouts, p never > 0.001)

pieces of flesh being removed).

The basic sequence in which the various muscular and mantle attachments are cut has already been mentioned in 2/B/III. During the first long bout of Chiseling the posterior mantle attachments, posterior adductor stump and anterior adductor stump in each valve are cut free after which the majority of the flesh is removed. The bird then cleans up any small pieces of flesh which may be left in the shell. The basic problems are therefore to determine what stimuli elicit the Chiseling movements and what factors control the duration of Chiseling and the sequence in which the various attachments are attacked.

For this more detailed analysis it was necessary to use my one remaining captive Oystercatcher. This animal was presented with Type 5 mussels of exactly 35 mm in length (Type 5 mussels have the posterior adductor muscle cut and the mussel is presented with the valves fully open). Although Oystercatchers do not usually come across mussels in this condition the general pattern of the Chiseling attack was very similar to that observed in the wild birds (Table 8).

TABLE 8 CAPTIVE ADULT CHISELING IN 35 mm TYPE 5 MUSSELS

(DATA FROM 51 OBSERVATIONS)

		1st bout	2nd bout	3rd bout	4th bout
Number of bouts		51	51	37	12
Median duration		9.0	2.7	2.4	2.3
Size of piece of flesh removed	Sm.	0	51	37	12
	Med.	1	0	0	0
	Large	50	0	0	0
Shake before eating		49	18	3	0

There is one long bout of Chiseling (terminating in a large piece of flesh being removed) followed by further shorter bouts (each terminating in small pieces of flesh being removed). By comparing Tables 7c and 8 it appears that 35 mm mussels

are midway between the size classes 'small' and 'medium'.

3/F/II The Chiseling Motor Patterns

Up to now Chiseling has been considered as one single motor pattern, an oversimplification necessary to determine the overall function of Chiseling. However, from my observations on free living birds I suspected that Chiseling had more than one component, and I was able to confirm this with my observations on the captive bird. Three separate components could be distinguished:

1. Rapid Chisel Pecking (RCP): as already described for the Chiseling motor pattern. A series of to-and-fro movements of the bill tip, the bill tip moving some 4 - 6 mm on each stroke at a frequency of about 6 strokes per second. The bill tips may open and close about 4 mm. The force is applied on the forward movement of the bill tip.
2. Rapid Grab Pecking (RGP): in form the same as RCP. The bill tips open more widely (often up to 6 - 7 mm). The force is applied as the bill is withdrawn.
3. Shaking (SH): flesh, which has been gathered into the bill tips is Shaken free from the shell.

Twenty observations of the bird Chiseling in 35 mm Type 5 mussels were recorded as sequences of RCP, RGP and SH, and the observed transition probabilities between them are shown in Table 9a. The basic sequence is

RCP → RGP → SH → Eat

although SH is not always present (i.e. sometimes RGP → Eat).

The bout lengths of RCP and RGP were also measured (Table 9b). Before the first Eat there is a long bout of RCP followed by a short bout of RGP. Subsequently, the bout length of RCP becomes much shorter it is always longer than that of RGP. The bout length of RGP does not alter.

TABLE 9 ANALYSIS OF RAPID CHISEL PECKING (RCP), RAPID GRAB PECKING (RGP) AND SHAKE (SH)

a) Transition Probabilities between RCP, RGP and SH (based on 20 records)

	RCP	RGP	SH	Eat	Totals
RCP	x	1.00 + (0.41)	0.00 - (0.19)	0.00 - (0.40)	58
RGP	0.03 - (0.30)	x	0.48 + (0.23)	0.49 (0.47)	60
SH	0.00 - (0.24)	0.00 - (0.38)	x	1.00 + (0.38)	29
Eat	0.95 + (0.29)	0.05 - (0.48)	0.00 - (0.23)	x	38

Expected probabilities in ( ):

+ and - show that observed probabilities are more (+) or less (-) frequent than random expectation, p never $>$ 0.05:

b) Median duration (in sec) of RCP and RGP (based on 20 records)

		1st bout	2nd bout	3rd bout	4th bout
Median RCP		7.4	1.8	1.6	1.4
Median RGP		1.1	1.1	1.0	1.0
Size of piece of flesh removed	Small	0	19	13	5
	Medium	1	1	0	0
	Large	19	0	0	0

Duration of RCP: 1st bout $>$ 2nd = 3rd = 4th z = never $<$ 3.39, p never $>$ 0.001

Duration of RGP: 1st bout = 2nd = 3rd = 4th z never $<$ 0.78 p never $>$ 0.44

RCP always $>$ RGP, z never $<$ 3.32, p never $>$ 0.001

The functions of RCP, RGP and SH were abundantly obvious. RCP cuts the flesh free, RGP gathers the flesh into the bill tips and SH breaks free any remaining tenuous attachments.

3/F/III The Intergration of RCP, RGP and SH

From the data already given a reasonable hypothesis is that RCP is elicited by resistance from the muscular attachments to the bill movements and that it continues until all resistance ceases (i.e. everything is cut free). RGP and SH are then elicited by the loose flesh. To test this hypothesis I presented my Oystercatcher with Type 5 mussels which differed in various ways.

a) all attachments were cut except for the posterior adductor stumps and the posterior insertions of the cruciform ligament which lie immediately anterior to them (PAC mussels). Two sizes were given, 35 mm and 45 mm in length. These mussels therefore differed only in the size of these two attachments.

b) all attachments were cut, and the loose flesh lay in one piece in the valves (LF mussels). Only 35 mm mussels were given.

The mussels were given three at a time, and there was one of each type at each presentation. 20 presentations were made, and the results are shown in Table 10.

In all cases the bill was first oriented at the posterior region of the shell and the bird attacked one of the adductor stumps.

<u>PAC mussels</u>:

A long bout of RCP was followed by a shorter bout of RGP, and a large piece of flesh was then removed. There then followed a shorter bout of RCP and a RGP bout, and smaller pieces were removed. The first bout of RCP was significantly

TABLE 10 MEDIAN DURATION (IN SEC) OF RCP AND RGP IN PAC AND LF MUSSELS

	1st bout		2nd and subsequent bouts	
	RCP	RGP	RCP	RGP
35mm PAC mussels	4.6	1.1	1.3	0.9
45mm PAC mussels	5.8	1.2	1.5	0.8
35mm LF mussels	0.14	0.9	-	-

longer in the 45 mm mussels than in the 35 mm mussels, (z = 2.23, p = 0.02) but there was no measurable difference in the length of the first RGP bouts. The second and subsequent RCP and RGP bouts in the 45 mm were not different in length from those in the 35 mm mussels.

LF mussels:

A total of 2.4 sec of RCP was recorded from the 20 mussels eaten, and usually the RCP was so short that I was unable to measure it (i.e. it was less than 0.2 sec). The bout length of the RGP was not significantly different from the RGP in the PAC mussels.

The Elicitation and Duration of RCP

These data show that RCP is not elicited unless there is some resistance to the bill movements, and that the duration of RCP depends upon the actual size of the attachments, i.e. RCP is maintained for as long as the eliciting stimuli are present, or, in functional terms, the duration of RCP depends upon the amount of work to be done. However, the eliciting stimulus is not simply 'resistance', for RCP stops when either the attachment is cut free (i.e. the resistance suddenly gives way) or when the bill ends up against the shell (i.e. the resistance becomes 'total'). The eliciting stimulus is thus a complex one in that the resistance must yield slightly to the RCP

movements. RCP stops when this resistance becomes 'none' or 'total'.

The Elicitation of RGP

RGP is always preceded by RCP (Table 9a), and this is also true in these PAC mussels. At the end of an RCP bout the flesh is lying loose in the valves, so it seems that the stimuli eliciting RGP have something to do with 'loose flesh'.

The Integration of RCP and RGP

When the bird is presented with PAC mussels (or with normal Type 5 mussels) it cuts the attachments in both valves before any RGP is elicited - even though there is much loose flesh available after the attack in the first valve. This suggests an inhibitory relationship between RCP and RGP. This inhibition could operate in two different ways:

1) the RGP-eliciting stimuli are not attended to until a certain mount of RCP has been performed (or until the bird has performed RCP in each valve).

2) RGP-eliciting stimuli are not attended to if there are any RCP-eliciting stimuli present

The second alternative seems to be the most plausable for the following reasons:

(a) the duration of RCP in the 35 mm and 45 mm PAC mussels was significantly different

(b) the duration of RCP in the LF mussels was often so short that I was unable to measure it

(c) in the LF mussels there was no sign that the bird 'tried' first one valve and then the other before RGP was elicited

(d) there is no sign of any inhibitory relationship once the first large piece of flesh has been removed and eaten, for each RCP bout is immediately followed by an RGP bout

The integration of RCP and RGP is therefore as follows:

1) the stimuli eliciting RGP have something to do with

'loose flesh'

2) these stimuli are attended to as soon as the RCP bout finishes

3) after the attack in one valve there must be some residual resistance from the flesh which indicates that it is still attached in the other valve. The stimuli eliciting RGP are not attended to until the attachments in the other valve have been cut.

In this way the stimuli eliciting RCP can inhibit RGP. The function of this inhibitory relationship will be discussed in 3/F/IV (p. 131).

Shaking

From Tables 7b and 8 it appears that the stimuli eliciting SH are connected with the size of the piece of flesh being removed, for SH precedes the removal of large pieces of flesh but not that of smaller pieces. However, size alone cannot be the most important stimulus, for I noticed that SH was less frequent in LF mussels than in FAC mussels although the size of the piece removed was roughly the same in each case.

I therefore presented my Oystercatcher with LF mussels of the following kind and recorded the frequency of SH before eating.

35 mm length LF flesh as one large piece

35 mm length LF flesh cut into 4 equal pieces

35 mm length LF flesh as one large piece, but remaining attached by a single anterior insertion of the cruciform ligament

The mussels were presented three at a time (one of each kind being present) and 10 presentations were made. Only in those mussels in which the flesh was still attached was there any SH, and each time a SH occurred before eating. This shows that SH is elicited by some slight resistance to the RGP, i.e. SH functions to free the flesh from any remaining tenuous attachments.

In Summary

The functional motor pattern of Chiseling can be broken down into the three sub-units of RCP, RGP and SH. RCP functions to cut the attachments between the flesh and the valves, RGP functions to gather the loose flesh into the bill tips and SH functions to break any remaining tenuous attachments.

The overall pattern of attack is one long bout of RCP followed by a short bout of RGP and SH, and a large piece of flesh is removed. Any remaining pieces are then cleaned out with short bouts of RCP followed by RGP.

RCP is elicited by resistance from the flesh to the bill movements and RCP continues for as long as this resistance is present. When the resistance becomes 'none' (i.e. the attachment is cut free) or 'total' (i.e the bill is up against the shell) then the RCP stops. This suggests that the resistance must yield slightly to the RCP movements in order to elicit RCP or to maintain the RCP attack.
RGP is elicited by some stimuli from the loose flesh. RCP may inhibit the elicitation of RGP in that the RGP-eliciting stimuli are not attended to when there are RCP-eliciting stimuli present.

SH is elicited if there is any tenuous resistance to the RGP.

3/F/IV The Sequence of the Chiseling attacks in mussels

We must now try to use the above data for a causal analysis of the sequence in which the various attachments of an entire mussel are attacked. I observed the captive Oystercatcher Chiseling in 35 mm Type 5 mussels and I recorded how long it spent attacking each attachment and the sequence in which the various attachments were attacked. I distinguished five different attachments within the mussel (Fig. 5),

PMA posterior mantle attachment (one in each valve)

PAC posterior adductor stump and posterior insertion of the cruciform ligament (one in each valve)

AAC anterior adductor stump and anterior insertion of the cruciform ligament (one in each valve)

VMA ventral mantle attachment (one in each valve)

VBM ventral body mass, comprising the gut, foot musculature and mantles (one in each valve)

The Number of Attacks at Each Attachment

I have distinguished between the number of attacks occurring before and after the first large piece of flesh is removed and eaten (which will be referred to as E1).

It might be expected that each attachment would be attacked twice (one attack in each valve) but this is not the case (Table 11). From the Oystercatcher's point of view the most important attachments are the PAC and the AAC for they are the main anchorages of the VBM. Once these are severed most of the flesh can be removed in one large piece.

TABLE 11 THE FREQUENCY AND MEDIAN DURATION (IN SEC) OF ATTACKS AT THE DIFFERENT ATTACHMENTS WITHIN A MUSSEL (BASED ON 31 RECORDS FROM TYPE 5 MUSSELS)

	PMA	PAC	AAC	VMA	VBM
Total Frequency of attacks	2.7	3.4	1.5	0.4	1.0
Before E1	1.0	2.0	1.4	-	1.0
After E1	1.6	1.4	0.1	0.4	0.03
Median duration of attacks					
Before E1	1.3	2.4	1.8	-	1.05
After E1	1.4	1.5	1.4	1.1	1.00

Fig. 5

The Sequence in which the Attachments are Attacked

the mussel is viewed from the ventral side

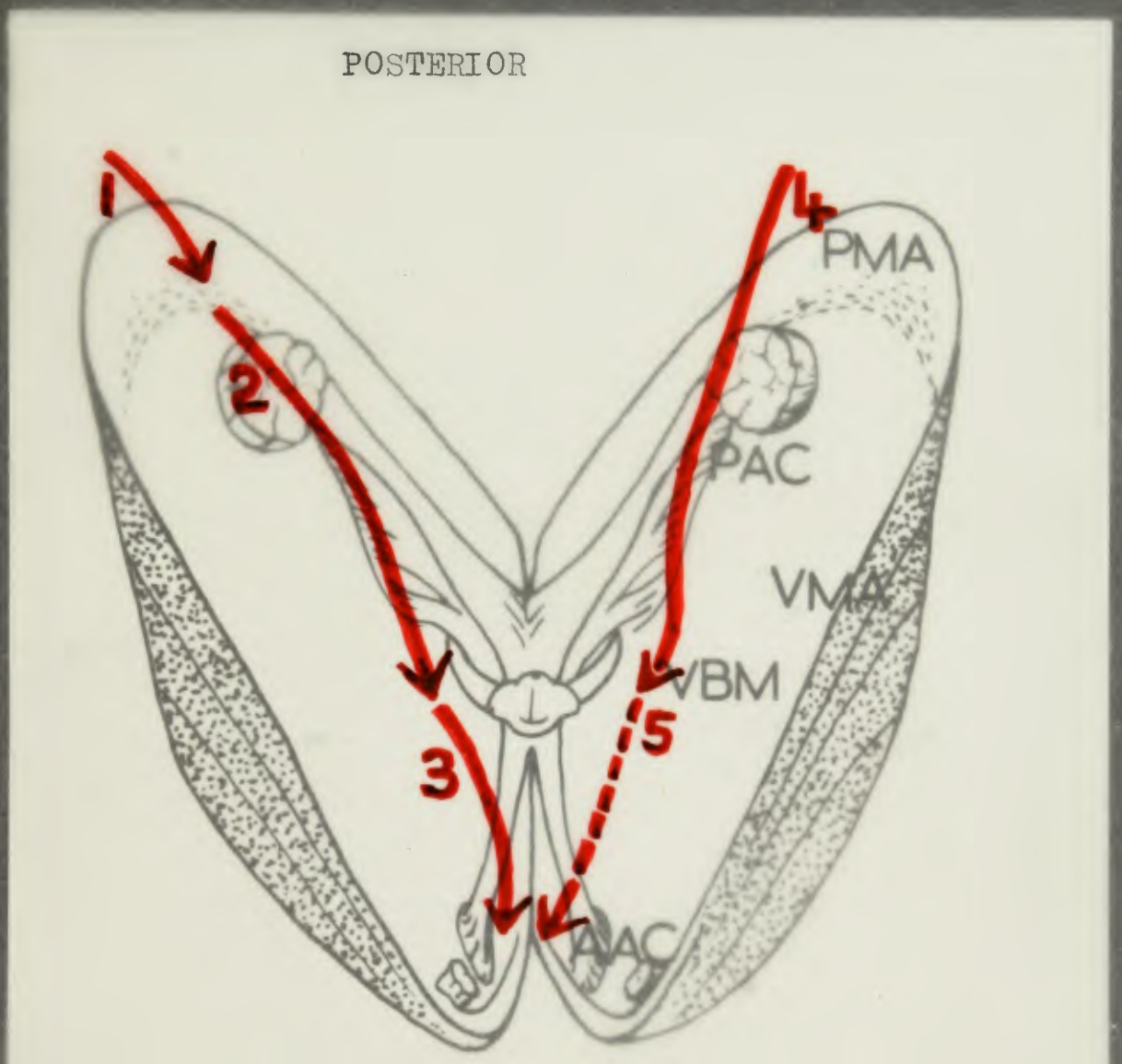
PMA = posterior mantle attachment

PAC = posterior adductor and insertion of cruciform ligament

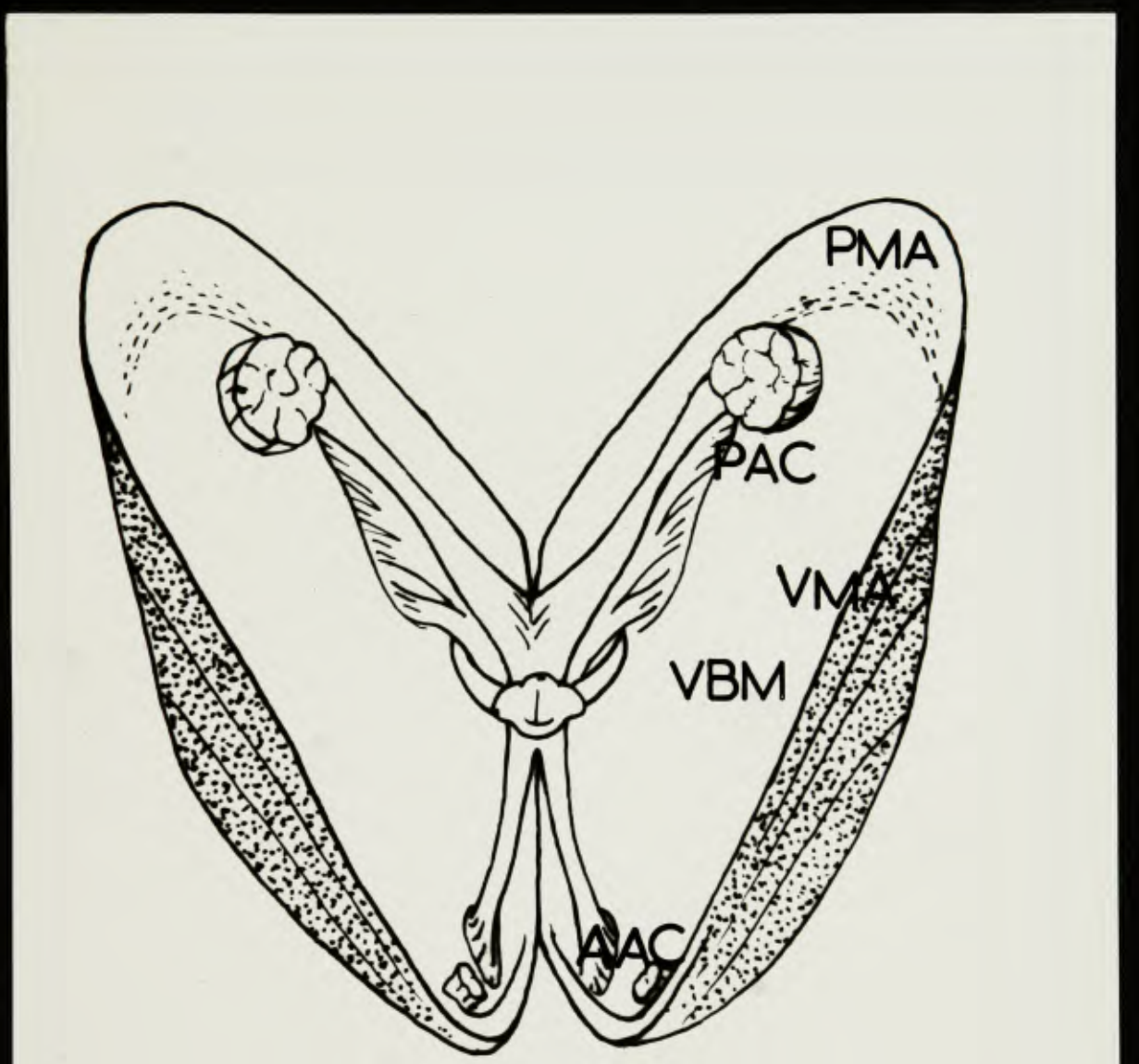
AAC = anterior adductor and insertion of cruciform ligament

VMA = ventral mantle attachment

VBM = ventral body mass



the direction of the arrows shows the order in which the attachments are attacked (before El) : the second attack at the AAC (dotted arrow) only occurs if the first attack does not manage to break both AAC attachments


PMA
PAC
VMA
VBM
AAC

Before E1:

there are always two attacks at the PAC, but this is not so for the AAC, for one attack usually suffices in breaking both anterior insertions of the cruciform ligament. A second attack is therefore only necessary if the first attack fails to sever both insertions. The PMA receive scant attention, and the VMA are not attacked (they are usually torn out when the flesh is removed). Only one attack is seen at the VBM because the VBM is removed as a whole once the PAC and AAC are severed.

After E1:

any remaining scraps are removed. The PMA (which are largely untouched before E1) are frequently attacked, as are any remaining pieces of the VMA. The PAC are attacked less frequently than before E1 for usually only scraps of the adductor stumps remain. There are usually no traces of the AAC or the VBM left, so we therefore find very few attacks at these attachments.

The general pattern is for the most important attachments (PAC and AAC) to be attacked most frequently and by doing this the main mass of the flesh (and much of the VMA) is removed. Any remaining scraps are then removed.

The Duration of the Attacks

I have again distinguished between attacks occurring before and after E1 (Table 11).

Before E1:

if the duration of the attacks at the various attachments are ranked from longest to shortest then we find that

PAC > AAC > PMA > VBM (in each case p at least < 0.05)

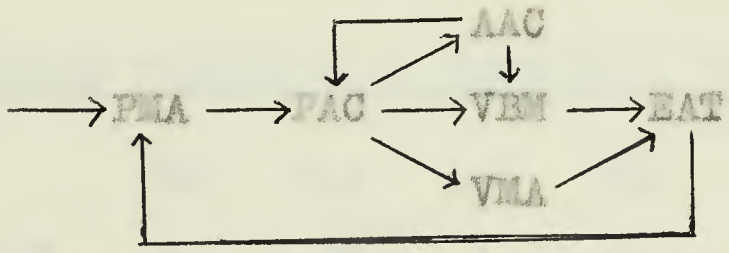
which is also the order of the attachments in decreasing size. The duration of the attack therefore depends upon the actual size of the attachment, which is expected from the data given in Table 10 .

After E1:

the attacks at the PAC are significantly shorter than they are before E1 ($p = 0.001$) but the attacks at the other attachments are the same length. This is because any remaining pieces of PMA, VMA, AAC or VBM are as firmly attached after E1 as they were before E1, while any remaining pieces of the PAC will already have been attacked at least once. This confirms the hypothesis that the duration of the attack depends upon the actual size of the attachment.

The Sequence in which the Attachments are Attacked

The observed and expected transition probabilities between all pairs of attachments were calculated from 31 observations of my Oystercatcher Chiseling in Type 5 mussels (Table 12). The basic sequence of attack is shown diagramatically below.



This does not give an accurate picture of what the Oystercatcher is doing because the observed transitions between any given pair of attachments depends upon what the bird has already done in the mussel. In Table 13 I therefore show the observed transitions from PMA, PAC and AAC before and after E1 (with PAC and AAC I also show the transitions for the first and second attacks before E1), and in each case there are highly significant differences between them. The transitions from VMA and VBM have not been included in Table 13 because attacks in these regions are always followed by Eating.

Before E1:

PMA → PAC → AAC all in one valve. Then → PAC in the other valve. This transition from AAC → PAC does not mean that the bird is Chiseling from anterior to posterior. The

TABLE 12 SEQUENCE IN WHICH THE VARIOUS ATTACHMENTS ARE ATTACKED

(OBSERVED TRANSITIONS BETWEEN ALL PAIRS OF ATTACHMENTS)

	PMA	PAC	AAC	VMA	VBM	Eat	Totals
PMA	0.00 - (0.16)	0.75 + (0.31)	0.00 - (0.15)	0.04 (0.04)	0.00 - (0.10)	0.21 (0.24)	83
PAC	0.00 - (0.15)	0.06 - (0.31)	0.41 + (0.13)	0.09 + (0.04)	0.17 + (0.09)	0.27 (0.28)	106
AAC	0.04 (0.15)	0.65 + (0.30)	0.00 - (0.13)	0.00 (0.04)	0.31 + (0.08)	0.00 - (0.30)	46
VMA	0.00 (0.15)	0.00 (0.30)	0.00 (0.15)	0.00 (0.04)	0.00 (0.06)	1.00 + (0.30)	13
VBM	0.00 (0.15)	0.00 - (0.30)	0.00 (0.14)	0.00 (0.03)	0.00 (0.09)	1.00 + (0.29)	32
Eat	0.84 + (0.15)	0.13 - (0.31)	0.03 - (0.14)	0.00 (0.03)	0.00 - (0.09)	0.00 - (0.28)	61

expected transition probabilities in ( ): + or - show that observed probabilities are greater than (+) or less (-) than random expectation, p never > 0.05:

TABLE 13 OBSERVED TRANSITIONS FROM PMA, PAC and AAC

		PMA	PAC	AAC	VMA	VBM	Eat	
PMA	Before E1	0	32	0	0	0	0	$chi^2 = 17.3$
	After E1	0	30	0	3	0	18	$p = <0.001$
PAC	1st bout before E1	0	0	31	0	0	0	$chi^2 = 16.6$
	2nd bout before E1	0	0	12	0	17	0	$p = <0.001$
	After E1	0	0	1	10	1	28	$chi^2 = 61.7$ df = 3 $p = <0.001$
AAC	1st bout before E1	2	24	0	0	6	0	$chi^2 = 4.05$
	2nd bout before E1	0	5	0	0	8	0	$p = <0.05$ >0.02
	After E1	0	1	0	0	0	0	

bill is first reoriented into the posterior region.

The transition from PAC now depends upon the effectiveness of the first AAC attack. If this attack severs both anterior insertions of the cruciform ligament then

PAC → VBM → Eat

but if both insertions were not severed then

PAC → AAC → VBM → Eat

After E1:

The transitions from PMA and PAC are much more variable and depend upon what remains inside the mussel.

In only 12 records was I able to record at the same time the sequence of RCP and RGP (and even then I was only able to do this up to E1). In these 12 dual records, RCP was directed at the PMA, PAC and AAC, and RGP was directed only at the VBM.

The causal factors that control the sequence in which the attachments are attacked are therefore basically concerned with the elicitation and integration of RCP and RGP. The bird Rapid Chisel Pecks from posterior to anterior cutting the PMA, PAC and AAC in one valve and then the PAC (and AAC if necessary) in the other valve. The RCP attack at each attachment is maintained until the attachment is cut free (i.e. each attachment is attacked only for as long as is necessary) and not until then does the bird move on to the next attachment. Once the four main attachments have been cut, RGP is elicited and the flesh is gathered (by the VBM) and removed.

The function of the inhibitory relationship between RCP and RGP is clearly seen from these records for it not only causes the switch in attack from one valve to the other but also causes a second attack at the AAC only if necessary. This total dependence on outside stimuli makes the Chiseling process both very efficient and very flexible.

3/G Discussion of the Integration of the Motor Patterns

The Stimuli Eliciting the Motor Patterns

Each of the motor patterns is elicited by a particular external stimulus. Hammering and dart-Stabbing are elicited by visual stimuli, while follow-up-Stabbing is elicited by tactile stimuli. Levering is elicited by some aspect of pressure around the bill tip. Prising, too, seems to be elicited by pressure around the bill tip which may differ merely in degree from the Levering stimulus. Of the three components of Chiseling, RCP is elicited by some quantitative aspect of resiistance to the RCP movements, while RGP is elicited by 'loose flesh'. SH is elicited by resistance to the flesh being gathered by the RGP.

The Duration of the Motor Patterns

In every case the duration of the motor patterns depends solely upon some aspect of the size of the mussel and there is no indication anywhere that once a motor pattern is elicited it continues for a pre-set length of time. The duration of each motor pattern is thus under continuous external control.

The Integration of the Motor Patterns

The sequence in which the motor patterns occur show a clear example of a simple chain response in which the performance of each motor pattern brings out the stimuli necessary for the elicitation of the next motor pattern in the chain. The stimuli eliciting Levering are brought about as a consequence of Stabbing and Hammering. The stimuli eliciting Chiseling are brought about as a consequence of Levering. Similarly, the stimuli eliciting RGP and SH are brought about as a consequence of RCP. It seems that Prising occurs so irregularly because the stimuli eliciting it occur almost by chance - but only after Levering.

There is no evidence that the integration of the motor patterns is even partly under internal control, i.e. that once Stabbing or Hammering have been elicited the sequence

continues irrespective of the stimulus situation at any particular moment. The transition from one motor pattern to another is in every case due to external stimuli alone. This explains why the sequence does not need to pass through every link in the chain. For example, the Prise is often absent and is variable in position when it is present. Levering may be missed out when, for instance, I presented my captive birds with mussels of Types 1, 2, and 5. I similarly have observations of wild birds stealing opened mussels from one another in which the bird immediately starts with Chiseling.

Of course, some internal control must be present to set off, for example, the initial hunting behaviour that precedes the elicitation of Stabbing and Hammering. This hunting behaviour is probably mainly under internal (deprivation) control (although external cues may be important, i.e. tidal rhythms, or the behaviour of other birds in flying off to the feeding grounds), and internal factors also probably cause the cessation of hunting (see Part I). However, once a mussel has been found, the elicitation, duration and integration of the motor patterns is under the control of external stimuli, each stimulus resulting from the effect of the preceding act.

The function of this type of control is immediately obvious for it imparts a remarkable degree of flexibility to the feeding behaviour. Each motor pattern is performed only for as long as is necessary, and only if necessary. This is not only economic but also of great advantage when dealing with an animal like a mussel which is itself extremely variable in size, strength of shell etc.

CHAPTER 4 THE TECHNIQUES OF FEEDING ON COCKLES (*CARDIUM EDULIS* L.)

4/A The Structure of the Cockle

The cockle is a bivalve mollusc of essentially the same structure as a mussel but there are a number of anatomical differences between them which greatly affect the feeding behaviour of the Oystercatcher. The cockle is adapted to living buried just under the surface of the sand so it does not show the extreme adaptations of the mussel to withstand exposure to tital currents and to the air. The cockle shell is heavily ribbed and, unlike the mussel shell, is almost shperical. There is a very recognisable persistent gape in the posterior region of the shell (Fig. 6) through which the siphons emerge. Internally, the cockle is more symmetrical than is the mussel. The posterior and anterior adductors are of the same size and both are situated dorsally near the hinge. They are thus unable to exert as much leverage on the valve margins as can the enlarged posterior adductor muscle of the mussel. Finally, the cockle's shell is of a 'crystalline' structure unlike the laminated structure of the mussel's shell.

The Oystercatcher employs both the Stabbing and Hammering techniques to gain entry into the cockle's shell.

4/B The Form of the Motor Patterns

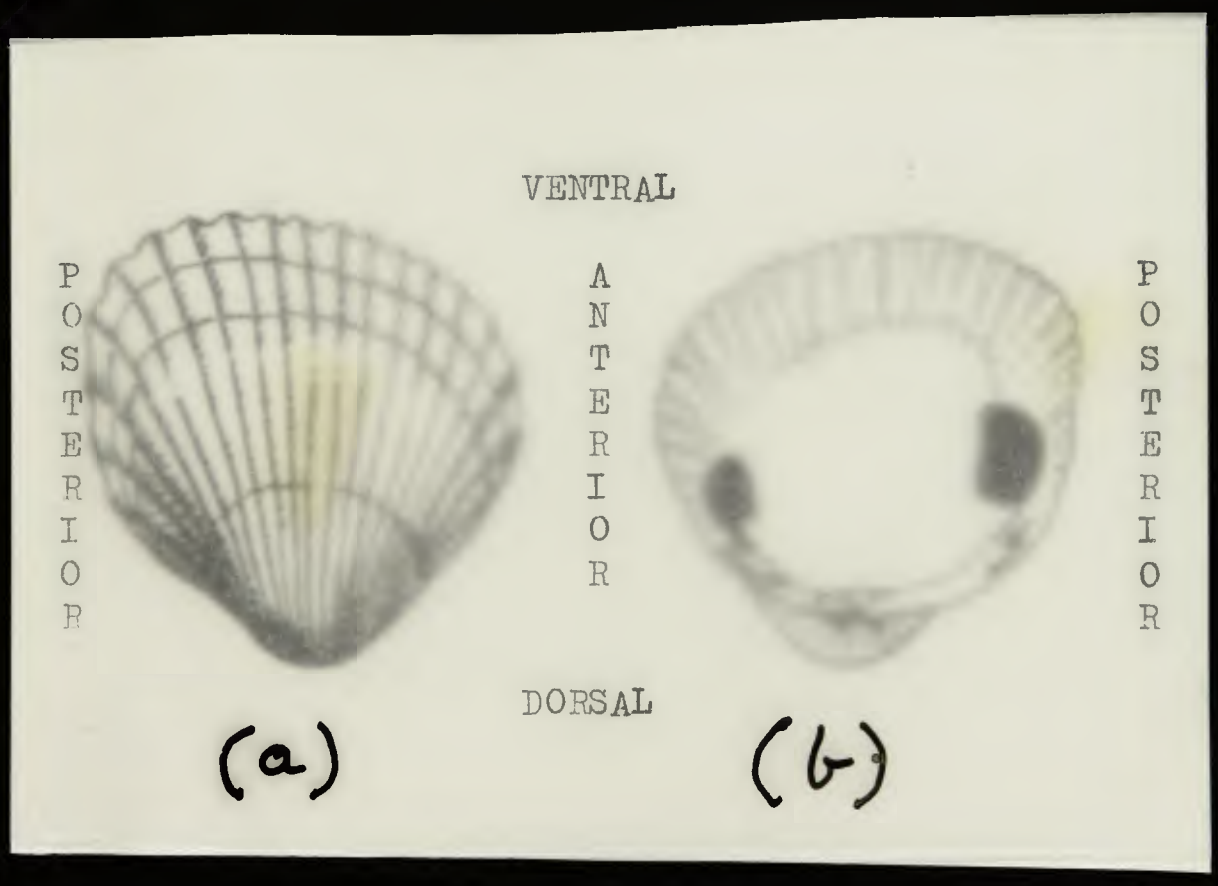
Stabbing, Hammering, Levering, Prising, Chiseling and Eating are observed, and they do not differ in form in any way from those described in the mussel Stabbing and Hammering techniques.

Fig. 6

The Structure of the Cockle

(a) external view of the shell

(b) internal view of the shell : note the position of the anterior and posterior adductor muscles (black areas)



4/C The Sequence of Motor Patterns

4/C/I The Stabbing Technique

The observed transition probabilities between all pairs of motor patterns were calculated from 93 observations of Oystercatchers Stabbing cockles (Appendix 1 C.c). The basic sequence is

Stab → Lever → Prise → Chisel → Eat

although the Prise is sometimes not present.

4/C/II The Hammering Technique

The same calculations were made from 99 observations of Oystercatchers Hammering cockles (Appendix 1 D.d). The basic sequence is

Hammer → Lever → Chisel → Eat

with the Prise often occurring between the Levering and the Chiseling.

Note: Prising is much less frequent in the Hammering sequences than in the Stabbing sequences (of the mussel sequences) but this is again entirely due to bias in the observations in that the Hammering observations consist almost entirely of small cockles (see 5/D).

4/D The Function of the Motor Patterns

4/D/I The Stab

The cockle usually lies in the sand with the posterior region (i.e. the persistent gape) uppermost, although it may also lie with the ventral margins uppermost. After the Stab has been elicited, the Oystercatcher emerges with the bill transfixing the cockle through either the persistent gape or through the ventral valve margins, and the cockle is seen to be gaping widely. The bill is usually deep inside the cockle where it undoubtedly severs, or greatly damages, the adductor muscles.

The Stab thus serves to gain unitial entry into the shell by passing through the posterior or ventral valve margins, thus damaging the adductor muscles and disabling the cockle.

4/D/II Hammering

Prior to the Hammering attack the cockle is oriented with either the posterior, ventral or anterior valve margins uppermost and the Hammering attack is directed at whichever valve margin is so oriented. There is no significant difference between the number of blows necessary to fracture these different valve margins in cockles of the same size (Table 14).

TABLE 14 THE HAMMERING ATTACK AGAINST COCKLES

a) Median number of blows necessary to fracture different regions of the shell

	Posterior Margin	Ventral Margin	Anterior Margin	
Small Prey	2.0	3.0	2.0	(z never >0.41 p never <0.68)
Medium Prey	3.2	4.0	3.0	(z never >0.82 p never <0.42)

b) Median number of blows necessary to fracture the shells of mussels and cockles

	Small Prey	Medium Prey
Mussels	4.0	8.0
Cockles	2.0	4.4
	(z = 4.43 p = <0.00001)	(z = 2.58 p = 0.01)

The Hammering attack is therefore not so restricted to one area of the shell as is the Hammering attack on mussels. Cockles need far fewer blows to fracture the shell then do mussels of comparable size (Table 14b) and unless one imagines that cockle-Hammering Oystercatchers posess greater physical strength than do mussel-Hammering Oystercatchers, this shows that

cockle shells must be more friable than are mussel shells (the cause of this is probably due to the difference between the actual structure of the shell of these two animals). This explains why the Hammering attack on cockles is less restricted to one particular area of the shell. The flat ventral area of a mussel is by far the weakest point of the shell(Fig. 2 p. 79-4) while the data in Table 14a suggests that all the valve margins of the cockle's shell are equally weak. Note however that the attack on the cockle shell is area restricted in the sense that the birds do not Hammer at either the hinge region or at the sides of the valves.

Hammering therefore functions to gain initial entry into the shell by fracturing the valve margins.

4/D/III Levering and Prising

The Levering movements are made against the ventral or posterior valve margins and are seen to force the valves apart. The Prise is made laterally across the valve margins and opens the valves as far apart as possible.

4/D/IV Chiseling

The bill is so oriented that the broad cutting edge of the bill tip lies flat against the valves, and the cutting movements are directed between the shell and the attachments. Due to the dorsal position of the hinge, the symmetrical shape of the valves and the marked curvature of the shell, the Oystercatcher can only Chisel from the ventral side of the cockle, although the bill may be oriented from either the anterior or posterior side of the ventral margins. The adductors of one valve are cut first, and then the adductors of the other valve, and it is rare to see the bird Chiseling at any other attachments. Undoubtedly the main body mass is dislodged when the adductors are cut and the mantles

and most of the mantle attachments are torn free when the ventral body mass is removed.

The function of Chiseling is therefore the same as it is in the mussel eating techniques, but the orientation of the attack and the sequence in which the attachments are cut are entirely different.

4/E Comparisons with the Mussel Techniques

4/E/I The Form and Function of the Motor Patterns

The form, function and sequence of the motor patterns is the same in the mussel and cockle techniques. Stabbing and Hammering gain initial entry into the shell, Levering and Prising serve to open the valves apart, and Chiseling cuts the flesh free.

4/E/II The Orientation of the Motor Patterns

In both cases the function of the motor patterns depends upon their correct orientation with respect to the mussel or cockle and differences between the orientation of some of the motor patterns can be directly linked to anatomical differences between mussels and cockles. The Hammering attack against mussels is more restricted than the attack against cockles, and there is good evidence that a cockle's shell has more vulnerable regions than does a mussel's shell. The Chiseling attack in cockles is very differently oriented than it is in mussels, and this again is due to differences between the shape of the shells of these two animals. In each case, therefore, the functional orientation of the motor patterns is adapted to the structure of the prey.

CHAPTER 5 THE INTEGRATION OF THE MOTOR PATTERNS IN THE COCKLE TECHNIQUES

5/A The Stab

Oystercatchers hunt for cockles in essentially the same way as they hunt for mussels which are buried under sand. The bird criss-crosses the cockle bed and dart-Stabs into the wet sand to catch the cockle. The dart-Stab must therefore be elicited by visual stimuli as in the mussel dart-Stabbing technique. I have never observed Oystercatchers to hunt for cockles using the follow-up-Stab technique and in fact Stabbing Oystercatchers seem to avoid those areas of the cockle beds where the sand has dried out and has become firm. Instead, they stay entirely on those areas where the sand is either soft and soggy or is still covered with shallow water. This difference in hunting technique may be due to the cockle's adaptations to living buried in sand, for mussels which are buried in firm sand are often moribund and gaping while a cockle will be very much alive and firmly closed.

Indeed, a cockle is a much more difficult animal to Stab than is a mussel, for 34% of cockles which are dart-Stabbed are abandoned because the cockle manages to clamp tight onto the bill tip and thus prevent the bill from entering between the valves, while only 13% of mussels are abandoned because of this (the difference is highly significant, $chi^2 = 33.1$, $p = 0.001$). This difficulty in Stabbing cockles may also be due to the cockle being in its natural habitat when buried under sand for perhaps the cockle is able to close its valves very quickly in response to the Stab. In addition, the ribbing around the valve margins may greatly increase the pressure that the adductors can bring to bear on the valve margins.

Cockles which the Oystercatchers abandon are left lying around on the sand, and eventually they open slightly. Some Oystercatchers seem to specialise in hunting for these cockles for they will go from cockle to cockle and will attempt to Stab the gaping ones. However, 85% of the Stabs are unsuccessful (n = 144) so this does not seem to be a very efficient technique of hunting.

5/B Hammering

The Hammering attack on cockles is a much more complex process than is the Hammering attack on mussels. First of all the cockles are buried under the sand (instead of being exposed) and the Oystercatcher has to search for them and dig them up. It does this by making bouts of many shallow rapid probes in the sand and digging up a cockle when it finds one (presumably by touch). 47% of cockles are found in this way, 15% being already exposed, and 29% being located under the sand apparently by sight for the bird will just pull the cockle out of the sand without first probing (n = 223).

Once the cockle has been picked up it may be taken to a feeding pile. A feeding pile is an area to which Oystercatchers repeatedly take cockles and huge piles of broken shells build up (see photographs in Drinnan 1953 and Davidson 1967). 67% of the cockles are taken to the pile and all sizes are taken there with equal frequency. This carrying behaviour is not so marked when Oystercatchers are Hammering mussels but why this is I do not know.

Almost every mussel which an Oystercatcher detaches prior to Hammering is in fact attacked but this is certainly not the case with cockles. A great many are rejected by the bird as soon as they are dug up (even though these same cockles may be later successfully Hammered open by the same bird), others are rejected after the shell has been oriented but before the

shell has been attacked and still more are rejected once they have been Hammered at a few times but before the shell has broken (Table 15a). There is however no detectable difference between the number of blows given before rejecting the cockle and the number of blows given in a successful attack. The effect of this behaviour is to reject the larger sized cockles (100% of the large cockles, 68% of the medium sized cockles and 45% of the small sized cockles are rejected). I find it difficult to understand the function of this behaviour because mussel-Hammering Oystercatchers do not show any sign of such a size selection even though mussels are harder to fracture than are cockles.

TABLE 15 THE HAMMERING ATTACK AGAINST COCKLES

a) Size selection of cockles before Hammering

	immediate rejection	reject after orientation	reject during Hammering	successful attacks
Small Prey (n = 122)	21%	14%	10%	55%
Medium Prey (n = 91)	30%	21%	17%	32%
Large Prey (n = 10)	100%	-	-	0%

b) Median number of blows necessary to fracture cockles in situ or on the feeding piles

	in situ	feeding pile	
Small Prey	2.3	2.8	(z = 1.47, p = 0.14)
Medium Prey	4.8	4.0	(z = 1.81, p = 0.08)

The carrying of cockles to feeding piles is also rather puzzling because both large and small sized cockles are taken there with equal frequency and there is no significant difference between the number of blows necessary to fracture a cockle in situ rather than one which has been carried to the

feeding pile (Table 15b). Perhaps there is a difference early in the tidal cycle when the sands are still soft and waterlogged, but I have no evidence that this is so (but see Drinnan 1957).

The cockle-Hammering attack is thus basically similar to the mussel-Hammering attack in that the stimuli eliciting the blows are undoubtedly visual and that the attack is maintained until the shell fractures, the larger the cockle the more blows being needed to fracture the shell (small cockles 2.0 blows on average, medium cockles 4.0 blows on average, Mann-Whitney z = 2.94, p = 0.004). However, Oystercatchers show a marked tendency to carry cockles to the feeding piles and there is a very marked selection of the size of cockle to be attacked.

5/C Levering

5/C/I The Stimuli Eliciting Levering

Levering is elicited after Stabbing and Hammering when the bill is deep inside the cockle. Unsuccessful Stabs (i.e. when the cockle clamps onto the Oystercatcher's bill) are not followed by Levering, and instead the bird shakes the cockle off the bill and then abandons it. If, during Chiseling, the valves inadvertently close, then a Prise is elicited and not Levering.

There thus seems little reason to suppose that the stimuli eliciting Levering in a cockle are in any way qualitatively different from those eliciting Levering in mussels.

TABLE 16 MEDIAN DURATION OF LEVERING (IN SEC) IN THE COCKLE TECHNIQUES

a) size of prey and technique of gaining entry to shell

	small prey	medium prey	
Stabbed cockles	2.2	3.2	(z = 3.04, p = 0.002)
Hammered cockles	1.3 (z = 4.7 p = 0.0001)	2.4 (z = 3.8 p = 0.0002)	(z = 3.49, p = 0.0004)

b) orientation of Levering after the Hammering attack

	posterior	ventral	anterior	
Small Prey	1.3	1.2	1.4	(z never >1.7, p never <0.1)
Medium prey	2.4	1.8	2.3	(z never >1.1, p never <0.28)

c) Transitions from Lever → Prise and from Lever → Chisel

	small prey		medium prey	
	Stabbed	Hammered	Stabbed	Hammered
Lever → Prise	2.1	1.2	2.4	2.2
Lever → Chisel	2.5 (z = 0.42 p = 0.68)	1.0 (z = 1.47 p = 0.14)	3.4 (z = 1.79 p = 0.08)	2.2 (z = 0.72 p = 0.48)

5/C/II The Duration of Levering (Table 16)

Analysis of the Stabbing and Hammering sequences show that:

1. the larger the cockle the longer is the duration of levering (Table 16a).

2. there is less Levering in Hammered cockles than in Stabbed cockles (Table 16a). This could be due to the damage done to the shell by the Hammering attack, for most usually half of one of the valves breaks away thus disabling the adductors (Drinnan 1953).

3. Subsequent to a Hammering attack, Levering is carried out with the bill in the same orientation as it was during the Hammering attack. There is no significant difference between

the duration of Levering with the bill in these various orientations within the cockle's shell (Table 16b).
4. Levering is followed either by Prising or by Chiseling. There is no significant difference between the duration of Levering in the transitions Levering → Prising and Levering → Chiseling (Table 16c).

These data show that, as in mussels, the duration of Levering depends solely upon some aspect of the size of the cockle and that Levering continues until the eliciting stimuli are no longer present. Both the elicitation and duration of Levering are therefore under the control of external stimuli.

5/C/III Comparisons with mussels

Less Levering is seen in cockles than in mussels of comparable sizes (from Tables 3 and 16: Stabbed prey, small $p = 0.008$, medium $p = 0.28$, large $p = 0.02$: Hammered prey, small $p = 0.0006$, medium $p = 0.006$). This difference is understandable when the anatomical differences between mussels and cockles are considered. The cockle has relatively small adductors which are dorsally situated and which are therefore easily damaged by Levering against the valve margins, while the mussel has much larger adductors and many muscular attachments around the hinge. However, even though there is less Levering overall in cockles than in mussels, the factors controlling the elicitation and duration of Levering are the same in each case.

5/D Prising

5/D/I The Occurrence and Position of Prising

Although Prising seems to occur less frequently in the Stabbing sequences than in the Hammering sequences (Appendix 1 C.c and 1 D.d) this difference is again due to bias in the observations (in this case because the Oystercatchers reject the larger sized cockles before Hammering them). Size for size, Prising is as frequent in both techniques. Analysis of the sequences shows that:

1. the larger the cockle the more likely is a Prise to occur (Table 17a).
2. almost all the Prises occur after Levering, irrespective of the size of the cockle (Table 17b).

Prising is therefore as enigmantic in the cockle techniques as it is in the mussel techniques. Its function in both cases is the same, and the stimuli that elicit it are most probably the same, yet the causal factors determining its occurrence and position in the sequence are still not clear. All I can suggest is that there may be some correlation between the final orientation of the bill after Levering and the presence or absence of Prising. The effectiveness of the Prise is seen from Table 17c for there is no significant difference between the duration of Chiseling in cockles in which (a) no Prise occurred and (b) a Prise occurred before the Chiseling.

TABLE 17 PRISING IN THE COCKLE TECHNIQUES

a) Frequency of Prising and size of prey

	Small Prey	Medium Prey	
Sequences containing a Prise	48%	78%	
Sequences not containing a Prise	52%	22%	$chi^2 = 4.5$ $p = <0.05 >0.02$
Totals	93	99	

b) Position of Prise in the sequences

	Small Prey	Medium Prey	
Prise immediately after Levering	100%	95%	
Prise during Chiseling	0%	5%	exact p = 0.32
Totals	45	80	

c) The effectiveness of the Prise: median duration of Chiseling (in sec) in sequences with or without a Prise

	Small Prey	Medium Prey
Stabbed Prey		
No Prise in sequence	7.1	16.1
Prise in sequence	6.4 (z = 0.34 p = 0.74)	14.6 (z = 0.97 p = 0.34)
Hammered Prey		
No Prise in sequence	5.0	9.2
Prise in sequence	4.8 (z = 0.24 p = 0.82)	8.8 (z = 0.86 p = 0.40)

5/D/II Comparisons with Mussels

Prising is as frequent in the mussel-Stabbing sequences as it is in the cockle-Stabbing sequences, and in the mussel-Hammering sequences as it is in the cockle-Hammering sequences. However, it is significantly more frequent in small cockles (both Stabbed and Hammered) than in small mussels (Table 18a), although there is no difference in the frequency in medium prey. The position of the Prise is less variable in cockles than in mussels for almost all the Prises in cockles occur immediately after the Levering (Table 18b). The reason for these differences are obscure, and I can think of no reasonable explanation.

TABLE 18 COMPARISONS BETWEEN PRISING IN THE MUSSEL AND COCKLE TECHNIQUES

a) Frequency of Prising and size of prey

	Totals	Sequences containing Prise	Sequences without Prise	
small cockles	93	48%	52%	$chi^2 = 49.7$, $p = <0.001$
small mussels	177	30%	70%	
medium cockles	99	78%	22%	$chi^2 = 0.1$, $p = 0.70$
medium mussels	93	82%	18%	

b) Position of Prising in the sequences

	Totals	Prising after Levering	Prising during Chiseling	
small cockles	45	100%	0%	exact $p = 0.035$
small mussels	53	85%	15%	
medium cockles	80	95%	5%	$chi^2 = 32.7$, $p = <0.001$
medium mussels	76	65%	35%	

5/E Chiseling

5/E/I The Duration of Chiseling

In both the Stabbing and Hammering sequences, the larger the cockle the longer is the duration of Chiseling (Table 19). However, for both small and medium sized cockles, the duration of Chiseling is shorter in Hammered cockles than in Stabbed cockles. This may again be due to the damage done by the Hammering attack which, as already mentioned, usually breaks away half of one valve. This may allow the Oystercatcher to orient the bill more exactly for Chiseling.

These data show that the duration of Chiseling, as in mussels, depends upon the size of the cockle.

TABLE 19 MEDIAN DURATION OF CHISELING (IN SEC) IN THE COCKLE TECHNIQUES

	small prey	medium prey	
Stabbed	7.0	12.8	(z = 5.75, p = <0.001)
Hammered	4.9 (z = 4.02 p = <0.001)	8.8 (z = 5.08 p = <0.001)	(z = 6.81, p = <0.001)

5/E/II Comparisons with Mussels

There is no significant difference between the duration of Chiseling in mussels and cockles which have been Stabbed (from Tables 6 and 19: small prey p = 0.58, medium prey p = 0.52) but the duration of Chiseling in Hammered cockles is significantly shorter than in Hammered mussels (from Tables 6 and 19: small prey p = 0.001, medium prey p = 0.02). This may again be due to one half of a cockle's valve breaking off as a result of the Hammering attack.

5/F Comparisons between the Integration of the Motor Patterns in the Mussel and Cockle Techniques

The elicitation, control and integration of the motor patterns in the cockle techniques is basically the same as it is in the mussel techniques. Each motor pattern is elicited by a particular external stimulus and there seems little reason even to suppose that these stimuli are qualitatively different from those eliciting the motor patterns in the mussel techniques. The duration of the motor patterns similarly depend solely upon some aspect of the size of the cockle, i.e. they are under continuous external control. Quantitative differences between the duration of some of the motor patterns in the cockle and mussel techniques (for example, the number of blows necessary to break the shell, the duration of Levering, the duration of Chiseling in Hammered cockles) can be attributed to anatomical differences between the two food animals and this underlines the external control of the motor patterns. The integration of the motor patterns in the cockle techniques is also seen to be a simple chain response in which the performance of one motor pattern brings about the external stimuli necessary to elicit the next motor pattern.

CHAPTER 6 THE TECHNIQUES OF FEEDING ON TAPES PULLASTRA AND SCROBICULARIA PLANA

6/A The Structure of Tapes and of Scrobicularia

Tapes and Scrobicularia are bivalves which are adapted to living buried deeper than the cockle.

Tapes: lives buried in muddy sand. The external shape of the shell is very similar to that of the cockle except that laterally it is slightly more flattened, and the shell is not ribbed. Internally, the anatomy is very similar to a cockle except that the animal is 'slighter', i.e. size for size the adductors seem to be smaller.

Scrobicularia: shows extreme adaptations for living buried deep in soft mud. The shell is very flattened laterally and is very thin. The siphons are exceptionally long and emerge from between the posterior valve margins. Internally the anatomy is much reduced. The adductors are very small, but there is a large and well developed foot mechanism (which it uses to quickly escape backwards down its burrow if surprised by an Oystercatcher).

I have only observed Oystercatchers Stabbing Tapes and Scrobicularia, but there seems no reason why they should not Hammer them, especially Tapes.

6/B The Form of the Motor Patterns

Stabbing, Levering, Prising, Chiseling and Eating are observed, and their form differs in no way from that already described.

6/C The Sequence of Motor Patterns

From Appendix 1 E.e and 1 F.f it can be seen that the basic sequence in each case is

Stab → Levering → Chiseling → Eating

with Prising occuring very infrequently between Levering and Chiseling in Tapes, and only once (during Chiseling) in Scrobicularia.

6/D The Function of the Motor Patterns

The Stab

only dart-Stabs were observed in each case. In Tapes it was clearly seen that the Stab entered the posterior or ventral valve margins and ended up deep inside the animal. In Scrobicularia it was usually impossible to see the orientation and effect of the Stab due to the large encrustation of mud which always surrounds the shell, but in 8 clear observations the bill was seen to be deep inside the animal through the ventral valve margins, and the valves were seen to be gaping widely.

Levering

in both cases the shell is always brought to the surface after the Stab and is then oriented ventral side up. The bill is thrust deep into the animal through the ventral margins and is levered and twisted against them. The valves can be seen to be forced apart.

Prising

is very infrequent in both Tapes and Scrobicularia. In both cases the bird prises laterally across the ventral valve margins and opens the valves wide apart.

Chiseling

the orientation of the attack is the same as in cockles. It similarly functions to cut the flesh free.

From the functional viewpoint the feeding techniques are organised in the same way as in cockles and mussels. The Stab serves to gain initial entry into the shell, Levering and Prising open the valves apart and Chiseling cuts the flesh free.

6/E The Integration of the Motor Patterns

I have very little quantitative data for these two feeding techniques.

6/E/I The Stab

Only dart-Stabs are observed, and the hunting behaviour is exactly described for Oystercatchers dart-Stabbing cockles and mussels. The Stab must therefore be elicited by visual stimuli. In Tapes I have no idea what the particular stimulus is, but Scrobicularia have a very obvious hole in their burrow which is surrounded by small troughs fanning out from the burrow (these troughs are caused by the hoovering of the long siphon). On very soft wet mud the tips of the siphons are sometimes visable at the entrance of the burrow and, when the animal is disturbed, the siphons are withdrawn. This could be the stimulus to which the Oystercatcher responds.

6/E/II Levering

Levering is elicited once the bill is deep inside the animal, and I see no reason to suppose that the eliciting stimuli are different from those in cockles and mussels.

I only have quantitative data from Scrobicularia on the duration of Levering, and the most striking aspect is that Levering is very short. Levefing is longer in larger Scrobicularia than in smaller ones, and in all sizes is much shorter than in either cockles or mussels (Table 20). This is most likely due to the much reduced anatomy of Scrobicularia when compared with cockles and mussels.

The general organisation of Levering in Scrobicularia is thus the same as in cockles and mussels. It is elicited by an external stimulus and continues for as long as the external stimulus is present (in functional terms the bird

Levers for as long as necessary). Levering therefore lasts longer in larger Scrobicularia than in small ones, and, due to the reduced anatomy of Scrobicularia, lasts for a shorter time than in either cockles or mussels.

TABLE 20 MEDIAN DURATION OF LEVERING AND CHISELING (IN SEC) IN THE SCROBICULARIA TECHNIQUE

	small prey	medium prey	large prey	
Levering	0.8	1.1	1.6	(small < medium < large z never < 2.2, p never > 0.02)
Chiseling	3.6	5.2	6.2	(small < medium < large z never < 2.62, p never > 0.008)

6/E/III Prising

Prising is very infrequent in both Tapes and Scrobicularia when compared with cockles and mussels (Table 21). In Tapes the Prise always occurred after the Levering and before Chiseling, while with Scrobicularia the one Prise observed occurred during Chiseling (when the valves inadvertently closed). It is easy to understand why Prising is so infrequent in Scrobicularia because Levering is seen to open the valves almost as wide as they can be opened and thus the stimulus to elicit a Prise is unlikely to be ever present. But in Tapes the Prise is as enigmatic as it is in cockles and mussels.

6/E/IV Chiseling

In Scrobicularia, the larger the animal the longer is the duration of Chiseling (Table 20), and in all cases duration is shorter than in either cockles or mussels. This is again understandable in terms of the much reduced anatomy of Scrobicularia, for the adductors and attachments around the

6/F Discussion of the Bivalve Techniques

The four bivalves which I have described range from those that live exposed to those that live buried deep in mud, yet fhe form and function of the motor patterns in the Oystercatcher's feeding techniques is the same for all, as is the sequence in which the motor patterns occur. The interesting differences lie in the fine orientation of the motor patterns (for example, the restriction of the Hammering attack, the orientation of Chiseling) for in each case this functional orientation is adapted to the anatomy of the animal under attack. I have also stressed the importance of external stimuli in the control of the elicitation, orientation, duration and integration of the motor patterns. The quantitative differences between the feeding techniques correspond to anatomical differences between the food animals (for example, the number of blows necessary to fracture the shell, the duration of Levering and of Chiseling, and even the overall frequency of Prising) and therefore are consistent with this interpretation.

CHAPTER 7 THE TECHNIQUES OF FEEDING ON GASTROPODS

7/A Littorina

Littorina is a small intertidal gastropod with a very hard shell and a tough operculum that closes the opening of the shell.

7/A/I The Form of the Motor Patterns

Hammering, Levering, Chiseling and Eating are seen, and their form is as described. Prising is never observed.

7/A/II The Sequence of Motor Patterns

From Appendix 1 G.g it can be seen that the basic sequence is

Hammering → Levering → Chiseling → Eating

although there is often a second Hammering attack after the first Levering. This second Hammering attack may go to Chiseling instead of to Levering.

7/A/III The Function of the Motor Patterns

Hammering: the attack is restricted to the operculum of the shell, and the shell is oriented before the Hammering attack so that the operculum is uppermost. The attack can be seen to break the operculum.

Levering: the bill is Levered between the operculum and the collar of the shell. The function can not always be clearly seen but in some cases Levering removes the operculum, and in other cases Levering seems to tear some of the body out of the shell.

Chiseling: the movements are directed around and inside the edges of the collar. It functions to cut free the head and foot region of the animal.

7/B Patella Vulgata

Patella is adapted to living clamped tight to rocks when exposed by the tide to the air. The shell is conical and strong. Internally, the massive central foot is attached around the edges of the shell.

Oystercatchers hunt for exposed limpets, and there are the equivalent of the Stabbing and Hammering techniques. The Stabbing technique is used against limpets which are sitting 'relaxed' on the rocks so that there is a very obvious gap between the shell margins and the rock. The Hammering technique is used against Limpets which remain firmly attached to the rocks.

7/B/I The Form of the Motor Patterns

Hammering, Stabbing, Levering, Chiseling and Eating are seen, and their form is as described. Prising is never observed.

7/B/II The Sequence of Motor Patterns

The Stabbing Technique:

The basic sequence (Appendix 1 H.h) is

Stab → Levering → Chisel → Eat

although Levering is infrequent and often does not occur (Table 21).

The Hammering Technique:

From Appendix 1 I.i the basic sequence is

Hammer → Levering → Chiseling → Eating

although again Levering may not occur (Table 21).

7/B/III The Function of the Motor Patterns

The Stab

is aimed at the gap between the side walls and the rock, and one hard blow suffices to dislodge the limpet or to knock it right off the rock. Oystercatchers seem to hunt

specifically for these limpets in that they walk around the rocks 'looking' at the limpets and then suddenly Stabbing one. The Stab is thus the equivalent of the dart-Stab used against bivalves. Oystercatchers also hunt for limpets in a more random fashion. They will approach a rock that is covered with sea weed and 'rake' the bill through the seaweed a number of times. Often a limpet will be dislodged and will fall down. This behaviour is analogous to the follow-up-Stab used against bivalves.

Hammering

the Hammering attack is directed against the lateral wall of the limpet and at the junction between the mantle edges and the rocks. The attack is maintained until the limpet is either knocked off, or is dislodged, or a hole is made in the mantle edge. Safreil (1967), using a spring-fired bolt, has shown that a limpet is most easily dislodged by an attack on the lateral walls (the area which the Oystercatchers attack).

Levering

The bill is inserted between the shell and the rock and the Levering movements completely remove the limpet.

Chiseling

The limpet is oriented with the ventral side up and the Chiseling movements are directed around the edges of the shell. The shell muscle and mantle retractor are cut through and the flesh is removed (see Safreil 1967 for full description).

7/C Discussion of the Gastropod Techniques

These gastropods are anatomically very different from the bivalves and yet the form, function and sequence of the motor patterns show the same features as in the bivalve techniques.

There are two interesting features in the gastropod techniques:

The Orientation of the Motor Patterns

We see again that the functional orientation of the motor patterns is adapted to the structure of the food animal (i.e. the restriction of the Hammering attack to the lateral walls of the limpet).

The Frequency of the Motor Patterns

Levering : Levering is significantly less frequent in the limpet-Stabbing technique than in the limpet-Hammering technique ($chi^2 = 6.24$, $p = <0.02$) and in both techniques Levering is often not present at all. This is because both the Stabbing and Hammering attacks often knock the limpet off the rock (this happens more frequently with the Stabbing attack) and therefore the stimuli eliciting Levering are not present.

Prising : Prising is absent from the feeding techniques on Littorina and limpets, again because the animals are so constructed that the eliciting stimuli can not be present.

The importance of these features are that they again underline the essential role of external stimuli in the elicitation and integration of the motor patterns.

CHAPTER 8 THE TECHNIQUE OF FEEDING ON CARCINUS MAENAS

8/A The Structure of the Crab

The crab is a very complex animal from the Oystercatcher's point of view in that it is capable of determined attempts to defend itself against attack. However, its anatomy (also from the Oystercatcher's point of view) is very similar to that of a bivalve mollusc. It has one very vulnerable part (the mouth), and the carapace is joined to the cephalothorax in such a way that it can be cracked free and levered open. Herein lies the Oystercatchers' technique.

8/B The Form of the Motor Patterns

Hammering, Levering, Prising, Chiseling and Eating are observed, and their form is as described.

8/C The Sequence of Motor Patterns

From Appendix 1 J.j the basic sequence is

Hammering → Levering → Prising → Chiseling →
→ Eating

although it can be seen that both Levering and Prising sometimes loops back to Hammering, and that Prising often loops back to Levering.

8/D The Function of the Motor Patterns

Hammering

Oystercatchers hunt for crabs by making bouts of probes in and around seaweed clumps under which crabs are wont to lie during low tide. Once located (presumably by touch) the crab is dug up. Very small crabs are then Hammered into

a mash and are ingested whole, no Levering, Prising or Chiseling being observed. Medium and large sized crabs usually run away and are chased. They put up a spirited defence and may even scare off the Oystercatcher (although they are speedily jumped on by roving Herring Gulls). The Oystercatcher eventually flips the crab onto its back and then Hammers into the mouth of the crab. This breaks a hole and kills the crab by destroying the supra- and sub-oesophageal ganglia. The Hammering attack is always restricted to the mouth region.

Levering (Fig. 7a)

Once the bill is inside the crab, the Oystercatcher Levers both laterally and dorso-ventrally between the carapace and the cephalothorax. The twisting component is often seen. This functions to split the carapace free from the cephalothorax.

Prising (Fig. 7b).

The Prise is in a dorso-ventral orientation between the carapace and cephalothorax. It functions to open up the crab so that the cephalothorax is once more standing on its legs while the carapace remains upside down. The interesting point is that more than one Prise is usually necessary for the body keeps falling back onto the carapace (cf Type 3 mussels with an elastic band around them). There may therefore be a whole series of Prises (four or five in a row) which is never seen in the feeding techniques on other prey.

Chiseling

The Chiseling movements are directed mainly around the edges of the cephalothorax and carapace. The flesh is then grasped, pulled out and eaten.

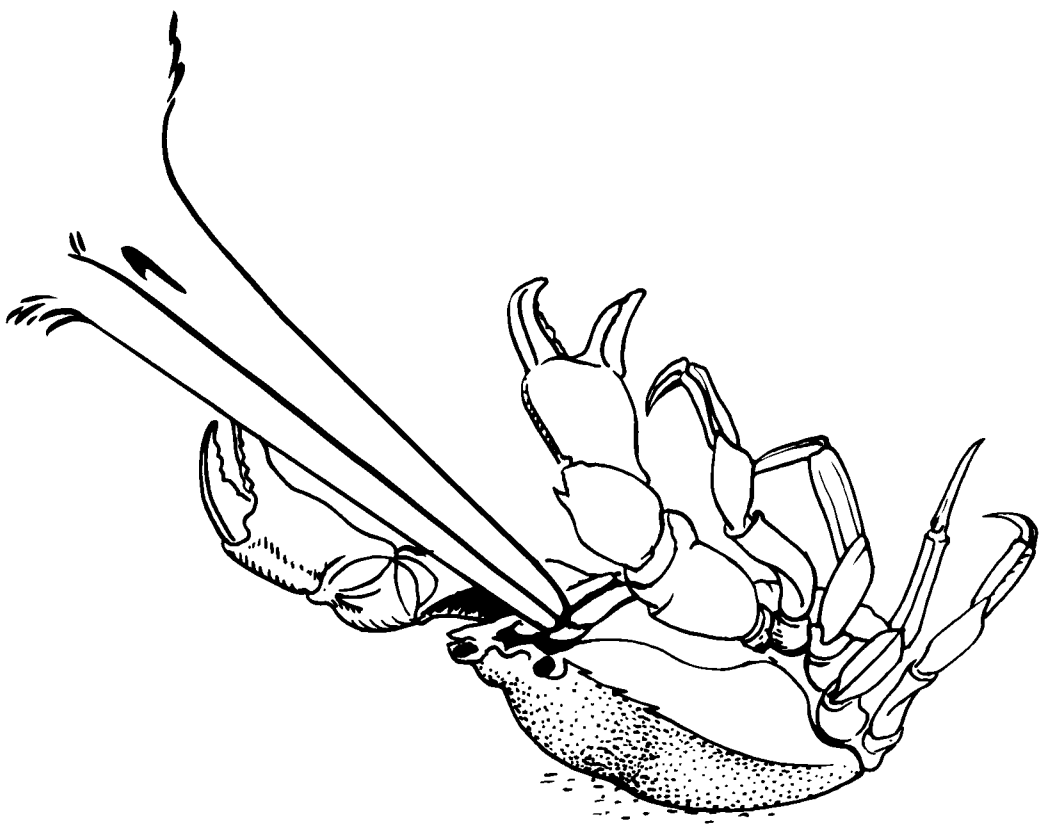
Fig. 7

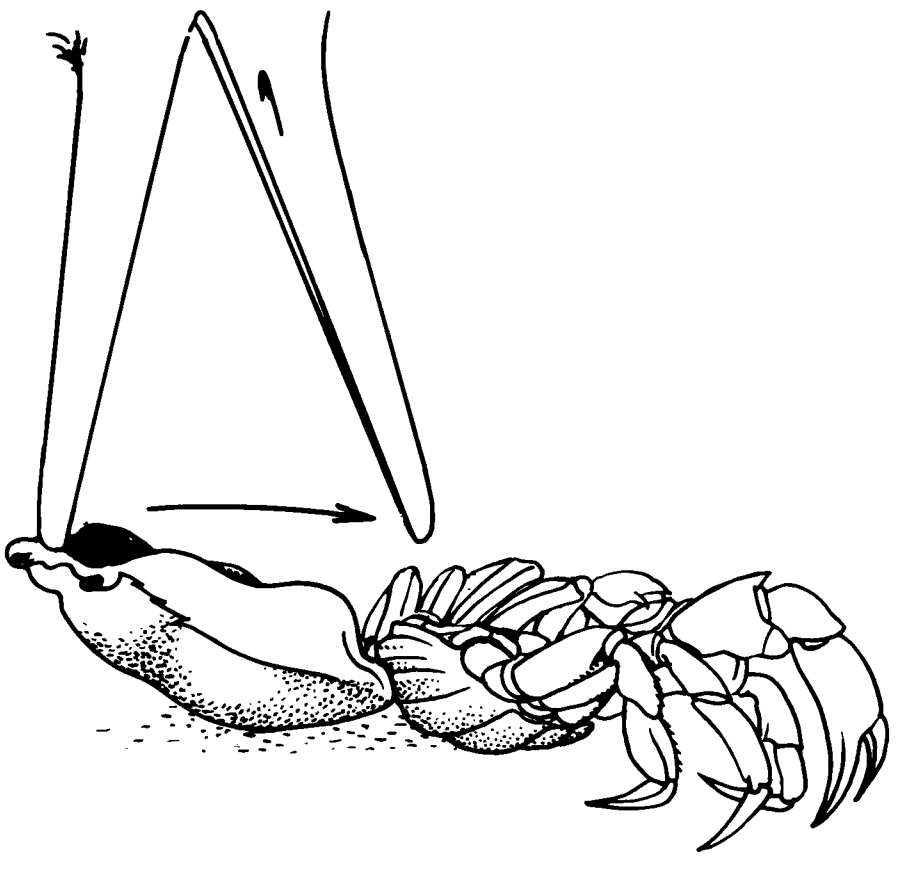
The Orientation of the Hammer Patterns in the Crab

(a) Hammering: the crab is flipped onto its back, and the Hammer blows are directed at the mouth region.

the bird then levers between the carapace and the cephalothorax until the carapace splits away.

(b) Prising: a Prise between the carapace and the cephalothorax then opens up the crab.


a


b

CHAPTER 9 DISCUSSION OF THE FEEDING TECHNIQUES

In this analysis of the feeding techniques I have concentrated on the form and function of the motor patterns, the functional orientation of the motor patterns, and the control of their organisation (i.e. elicitation, duration and integration). The evidence must now be considered together to understand the skill, efficiency and versatility of the entire feeding behaviour.

The Oystercatcher has a basic repertoire of motor patterns whose form and function are the same in all these feeding techniques. Hammering breaks, Levering tears apart, Prising separates, Rapid Chisel Pecking cuts and Rapid Grab Pecking gathers. The form of each particular motor pattern is adapted to a very generalised function.

However, the function of each motor pattern, as well as the skill and efficiency of each technique, entirely depends upon the orientation of each motor pattern with respect to the prey. The clearest examples are the orientation of the Hammering attack (to the ventral margins of mussels, to the postererior, ventral or anterior margins of cockles, to the lateral walls of limpets and to the mouth of crabs) and the orientation of the Chiseling attack. In each feeding technique the orientation of each motor pattern is precisely adjusted to the structure of the prey. This is one of the most important factors in understanding the skill and versatility of these techniques, for the Oystercatcher is able to adjust the orientation of motor patterns which have very generalised functions so that they acquire very precise functions in each prey.

Each motor pattern is elicited by qualitatively different external stimuli and, where quantitative data have been collected,

the duration of each motor pattern is seen to be under continuous external control. The evidence for this is clearly seen by the quantitative variation within the techniques which is due to the size of prey under attack (i.e. the duration of Chiseling in small, medium and large sized mussels) and by the quantitative variation between techniques which is due to anatomical differances between the prey (i.e. the duration of Levering in mussels and Scrobicularia). There is no evidence at all that a motor pattern continues for a pre-set length of time once it has been elicited. The function of this continuous external control is that it imparts great efficiency and economy of effort to the techniques, for each motor pattern is performed only for as long as is necessary.

TABLE 21 FREQUENCY OF THE MOTOR PATTERNS IN THE VARIOUS TECHNIQUES

Prey	Techn.	N	Hm/St	Lever	Prise	Chisel	Eat
Mussels	St	757	1.00	1.03	0.73	1.63	1.40
	Hm	679	1.00	1.01	0.37	1.30	1.20
Cockles	St	605	1.00	1.01	0.85	1.80	1.80
	Hm	532	1.00	1.00	0.48	1.50	1.50
Tapes	St	70	1.00	1.00	0.27	1.20	1.00
Scrobic.	St	214	1.00	1.00	0.02	1.02	1.00
Littorina	Hm	154	1.70	1.40	0.00	1.30	1.30
Patella	St	123	1.00	0.38	0.00	1.90	1.90
	Hm	67	1.00	0.72	0.00	1.00	1.00
Carcinus	Hm	320	1.08	1.40	2.80	1.80	1.80

St = Stabbing technique; Hm = Hammering technique; N = total of motor patterns

The integration of the motor patterns is also seen to be under the control of external stimuli, and the sequences in which the motor patterns occur are seen to be simple chain responses in which the performance of one motor pattern brings about the external stimuli necessary to elicit the next. There is no evidence at all that once one motor pattern has been elicited the others follow it irrespective ofthe stimulus situation at any particular moment. The function of this external control is extreme economy of effort, for motor patterns are performed only if necessary. Clear evidence of this is seen by the variability of Prising and of Levering in the different techniques (Table 21).

The skill, efficiency and versatility of the Oystercatchers' feeding techniques are therefore due to these three basic elements:

1. a repertoire of motor patterns which are adapted to very generalised functions.
2. the ability to adjust the orientation of each motor pattern to the anatomy of any one prey so that each acquires a precise function.
3. the completely external control of the elicitation, duration and integration of the motor patterhs, so that each one is only performed if and when necessary, and only for as long as is necessary.

An important question which must now be raised is the degree of quantitative and/or qualitative difference between the stimuli from these different prey which elicit the motor patterns and which control their orientation. In the case of Levering, Prising and Chiseling, I feel sure that the eliciting stimuli are qualitatively the same although they

may differ quantitatively. However, the orienting stimuli are not only undoubtedly quantitatively different, but may also in many cases be qualitatively different. For example, compare the orientation of the bill for Levering after Stabbing a mussel and after Hammering a hole in a limpet.

It is with the stimuli controlling the orientation and elicitation of Stabbing and Hammering that the most obvious differences are apparant. For example, the areas in which to hunt (i.e. mud flats, mussel beds, cockle beds, exposed rocks, seaweed clumps) are very different, and so too are the physical appearance of the prey. With Stabbing and Hammering it is almost impossible to disentangle the orienting stimuli from the eliciting stimuli.

The importance of these considerations is that in spite of the basic elements of each feeding technique being the same, individual Oystercatchers show a surprising degree of specialisation not only on one particular prey but also on one particular technique of eating it (the evidence for this is given in Chapter 9). This suggests that there may be considerable differences between the orienting and eliciting stimuli from the different prey, especially between those of Stabbing and Hammering.

CHAPTER 10 THE DEGREE OF INDIVIDUAL SPECIALISATION

10/A Individual Specialisation on Prey

10/A/I Introduction

The Oystercatcher shows strong attachment to mates, to breeding territories and to winter feeding grounds (Harris 1968 and references cited, Safriel 1969). This will obviously affect any estimation of individual food specialisations because all possible Oystercatcher foods will not be available on one spot where any particular individual may be. A careful distinction must therefore be made between apparant specialisation due to the unavailability of some possible prey, and true specialisation. The best evidence for true specialisation must come from observations on known individuals who persistently select only one of a possible range of known Oystercatcher prey from the immediate area in which they are feeding.

10/A/II The Breeding Population at Ravenglass, Cumberland

From 1965-1968 I studied the breeding population of Oystercatchers on the dunes of the Nature Reserve in the Esk estuary at Ravenglass in Cumberland. The total breeding population was around 30 pairs, of which I studied 16 pairs, 8 of them intensively. These 16 pairs were marked individually by uniquely colour ringing one member of the pair or their chicks, or both. When I studied a pair for a number of years, I assumed that the unringed mate was always the same individual. This is a reasonably safe assumption since

Oystercatchers are known to be faithful to both mates and breeding territories (Harris 1968, Safreil 1967).

I studied the birds before, during and after the breeding season, and I found that they often changed their feeding area within the estuary. For example, a pair might feed entirely on the mussel beds until their eggs hatched and then feed almost entirely on the mud flats until their chicks fledged. They would then return again to the mussel beds, taking their chicks with them. I have therefore estimated for each individual the total range of possible prey in all the areas in the estuary in which the individuals were feeding during their stay. I have also indicated (very roughly) the relative abundance of the various prey.

The possible foods were 'soft bodied invertebrates', mussels, crabs, cockles, limpets, Scrobicularia and Littorina (Table 22). The category 'soft bodied invertebrates' includes everything from annelid worms to insect larvae, and I have lumped them together because the birds obtain them with the same basic technique (as described in Chapter 1). All the Oystercatchers relied at some time on this source of food (usually when the chicks were just hatched) and I can not imagine that there is a single Oystercatcher in existence who is unable to utilise it. It is the basic wader feeding behaviour which Oystercatchers have retained in spite of their specialisation.

TABLE 22 FEEDING HABITS OF INDIVIDUAL BREEDING OYSTERCATCHERS AT RAVENGLASS, CUMBERLAND

Identity of birds	SBI	MS	CR	CO	LM	SC	LT	Yrs Obs	Approx Hrs Obs
cr 1)	a +					a		2	2
2)	a +					a			
cr 3)	a +					a +		1	1
4)	a +					a			
5)	a +	a +		s				1	3
6)	a +	a +		s					
cr 7)	a +	a +	a				s	2	21
8)	a +	a +	a				s		
cr 9)	a +	a +	a		s		s	4	150
10)	a +	a +	a		s		s		
cr 11)	a +	a +	s		s(+)		s	3	150
12)	a +	a +	s		s		s		
cr 13)	a +	a +	a		s		s	3	150
14)	a +	a +	a		s		s		
cr 15)	a +	a +	a		s		s	2	2
16)	a +	a +	a		s		s		
cr 17)	a +	a +	a(+)	s	s	a(+)	s	3	300
18)	a +	a +	a	s	s	a	s		
cr 19)	a +	a +	s	s	s	a	s	3	10
20)	a +	a +	s	s	s	a	s		
cr 21)	a +	a +	s	s	s	a	s	2	10
22)	a +	a +	s	s	s	a	s		
cr 23)	a +	a +	s	s	s		s	1	1
24)	a +	a +	s	s	s		s		
cr 25)	a +	a +	a	s		a(+)	s	1	6
26)	a +	a +	a	s		a(+)	s		
cr 27)	a +	a	a +	s		s	s	3	100
28)	a +	a	a +	s		s	s		
cr 29)	a +	a	a +	s (+)		a	s(+)	2	80
30)	a +	a	a +	s		a	s(+)		
cr 31)	a +	a	a +	s		a	s	1	1
32)	a +	a	a +	s		a	s		

Notes: 1. members of breeding pairs are bracketed: cr = colour ringed individual:

2. SBI = soft bodied invertebrates : MS = mussels : CR = crabs : CO = cockles : LM = limpets : SC = scrobicularia : LT = littorina :

3. a = prey was abundant in the individuals' feeding areas :
s = prey was scarce in the individuals' feeding areas :

4. + = major food supply for individual :
(+) = occasional food supply for individual :

5. Yrs Obs = number of breeding seasons observed for each pair :

6. Approx. Hrs Obs = approximate number of hours spent observing each pair :

7. "mussel" specialists and "crab" specialists are boxed in.

Table 22 shows that individuals of the population were indeed true food specialists in that, apart from taking 'soft bodied invertebrates', they showed individual food preferences. These were:

Individuals 1 - 4

Scrobicularia were very abundant in their feeding areas, yet only one bird took them.

Individuals 5 - 26

All persistently ate mussels, irrespective of what else was present. One individual occasionally ate limpets, two occasionally took Scrobicularia and one had an occasional crab and Scrobicularia in its diet.

Individuals 27 - 32

All persistently ate crabs. One pair also took Littorina and occasional cockles, but no Scrobicularia.

Of these 32 individuals, 9% seemed to have no specialisations at all (individuals 1, 2, 4), 69% specialised on one prey (individuals 3, 5, 6, 7, 8, 9, 10, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 23, 24, 27, 28, 31, 32) and 22% were mixed feeders (i.e. they took more than one type of prey (individuals 11, 17, 25, 26, 29, 30).

Table 23 shows the association between the number of different prey (excluding soft-bodied-invertebrates) in each individual's feeding areas and the number of different prey in each individual's diet.

TABLE 23

		number of prey in each individual's feeding areas					
		1	2	3	4	5	6
number of different prey in each individual's diet	0	3					
	1	1	2	2	7	6	5
	2				1	3	
	3					1	1
	4						
	5						
	6						

Although the data in Table 23 shows a significant correlation ($r = +0.69$, $n = 32$, $p = <0.001$) this correlation is highly significantly different from the expected value of $r = +1.0$ if the individuals had been showing no specialisations at all (i.e. if they had been eating all available prey).

10/A/111 Data from Other Sources

Other workers in this field do not seem to have been very aware of this problem of prey specialisation in the Oystercatcher, so it has been difficult to find corraborating evidence.

Dr. P.J.Dare (M.A.F.F. Conway) has kindly allowed me to use his data which he collected from observing individually colour ringed Oystercatchers wintering in Conway Bay, North Wales. During the winters of 1966/67 and 1967/68 he regularly observed where these individuals were feeding. There were two main feeding areas, the mussel beds and the sand flats immediately adjoining them (which contained Macoma balthica and cockles). Table 24 indicates a high degree of food specialisation for only

21% of the birds are classed as mixed feeders (compared with 22% of the Ravenglass population).

TABLE 24 INDIVIDUAL PREY SPECIALISATION BY OYSTERCATCHERS WINTERING IN NORTH WALES (DATA SUPPLIED BY P.DARE, M.A.F.F. CONWAY)

	Feeding areas			
	mussel beds only	sand flats only	feeds in both areas	Totals
number of colour ringed individuals	55	68	33	157
% of total	33%	44%	21%	
median number of observations per individual	14	4	9	

Davidson (1967) made an entensive study of the winter population of Oystercatchers in the Bury Inlet, South Wales. Here the main foods were huge beds of cockles and Macoma, and there was a mussel bed situated at the mouth of the estuary below Whiteford Burrows. Colour ringing showed that the cockle-eating winter population was made up of the same birds year after year, and also that this cockle-eating population was descreet (discrete?) from the mussel-eating population which frequented the Whiteford mussel beds. These two populations did not even roost together.

Safreil (1967) studied the breeding population of Oystercatchers on Skokholm Island, South Wales. The breeding pairs were made up of terrestrial feeders (eating invertebrate foods on the meadows), shore feeders (eating mainly limpets) and mixed feeders (eating both). This data is difficult to interpret in terms of specialisations because it is not clear whether the terrestrial feeders were shore feeders who took up terrestrial feeding to raise

their young. Indeed, a reservation must be made about all these data from Dare, Davidson and Safreil in that feeding site attachment (with as a consequence the birds taking the food most easily available) can not be excluded.

I have made some incidental observations on Skomer Island where there is a plentyful supply of limpets and, in at least one area, some 'scrub' mussel. In this area I observed an unringed bird to be eating only the mussels, while around and nearby were other birds eating only limpets. On the cliff tops overlooking this area I found two areas some 200 yards apart where the ground was littered with old shells. One area had only limpet shells and the other had only mussel shells (these were the shells from food flown up to the young in previous years). I also found on the island three more 'limpet' territories (but there were no mussels nearby). These observations indicate the presence of a mussel specialist among the limpet eaters.

Reduction of Normal Food Supply

Another good indication of true individual food specialisation is to observe what happens to an individual when it either migrates to an area where its usual food is not present, or when some ecological disaster seriously reduces its normal food.

The Ravenglass Population

I have no idea where most of the Ravenglass breeders go during the winter (except that they leave the breeding grounds). However, the pair 29/30, who were crab specialists, spent the whole winter of 1967/68 in the Ravenglass estuary feeding their chick (see Part 1, p. 50). Crabs are unavailable during the winter, and these birds relied entirely on soft bodied invertebrates and Littorina

for food. They did not switch to eating the mussels over which they walked in order to obtain the Littorina.

Data from Other Sources

Dare (1966) records a switch in feeding behaviour of the Oystercatcher population in Morecambe Bay during the severe winter of 1963/64. The intertidal cockle stocks were devastated, and the birds switched first to Macoma and then moved inland to feed on terrestrial foods. They did not switch to the nearby mussel beds and feed there. Feeding site-attachment can again not be excluded here.

In this same winter the cockle stocks of the Bury Inlet were also devastated, although there was a good spat settlement in the nearby Taf-Towy estuary (Davidson 1968). The cockle-eating population moved to the Taf-Towy estuary and not to the adjactent Whiteford Burrows mussel beds, so site-attachment was more easily broken than specialisation.

Although all the above edidence is not as conclusive as one could wish, it leaves little doubt that there is a surprising degree of specialisation. Certainly, when one actually observes these birds feeding, the impression that they are true specialists is very strong. For example, one often sees two birds working over the same area of mud flat, one of them only taking annelids and the other taking both annelids and Scrobicularia. Similarly, I have often observed a crab specialist and a mussel specialist working over the same area of mussel bed, but one only hunting for crabs and totally ignoring the mussels, the other hunting mussels and positively avoiding any crabs which it might dig up. The general points that emerge from the above

data are that:

1. all Oystercatchers can probe for 'soft bodied invertebrates'.
2. most, if not all, show one major specialisation on either a bivalve, crabs or limpets.
3. a few, circa 20%, seem to be able to take more than one of these specialised foods.
4. switches from one food to another have been recorded, especially from cockles to Macoma (a burrowing bivalve with essentially the same anatomy as a cockle and which lives in the same habitat). The switch from cockles to mussels, or from crabs to mussels, does not seem to occur.

10/B Individual Specialisation on one Technique

I was even more suprised to find that individuals who shared the same food preference also specialised in their technique.of catching it. Of the 22 adults in the Ravenglass population who persistently ate mussels, 4 used the Hammering technique only, while the other 17 exclusively used the Stabbing technique. There was but one bird, a Stabber, who was once observed to Hammer mussels - although the rest of the time (more than 20 observation periods) it always used the Stabbing technique (Table 25). A further 18 non colour r nged adults were each observed for one standard period of 30 min. 5 of these confined themselves to the Hammering technique, the other 13 exclusively used the Stabbing technique.

In the Burry Inlet I similarly recorded the technique used by 23 non colour ringed adults who were eating cockles. The observation period on each bird was much shorter (15-20 min.), but 9 individuals used the Hammering technique only, the other 14 exclusively used the Stabbing technique (Table 25).

TABLE 25 INDIVIDUAL SPECIALISATION IN THE TECHNIQUES OF EATING COCKLES AND MUSSELS

	number of individuals	total number obs. periods	Feeding technique: Stab only	Hammer only	Both
individually known Ravenglass birds eating mussels	22	400	17	4	1
unknown birds eating mussels	18	18	13	5	0
unknown birds eating cockles in Bury Inlet	23	23	14	9	0
TOTALS	63	441	44	18	1

These individuals were definitely specialising in one technique. A second point of interest is that the technique seems to be prey-specific. For example, the crab specialist No. 29 ate crabs by Hammering at them, but it Stabbed cockles. Similarly, the mussel specialist No. 17 Stabbed mussels and Scrobicularia yet Hammered at crabs. However, the mussel specialist No. 11 was the one who both Stabbed and Hammered mussels, and it also both Stabbed and Hammered limpets. Indeed, all the limpet eating birds that I observed on Skomer Island were able to both Stab and Hammer their prey.

10/C Discussion

These data, indicating a high degree of individual specialisation not only on one particular prey but also in one technique of eating it, raise the twin problems of causation and survival value, for at first sight it seems paradoxical that an animal which possesses the capacity to eat a wide range of foods with more than one technique should restrict itself to only one of each and thus cut itself

off from a large potential food supply, and should, so to speak, deny itself part of its potential skills.

I suggested in Chapter 8 that there may be great quantitative and qualitative differences between the stimuli from these different prey that elicit the initial Stabbing or Hammering attack. This could account for the observed individual specialisations.

1. Oystercatchers seem to be able to switch quite easily from eating cockles to eating Macoma, and both these animals are very similar and live in the same habitat. The changes which might have been expected but did not occur (i.e. from crabs to mussels in the Ravenglass pair No. 29/30 during the winter months, and from cockles to mussels in the Bury Inlet birds when the cockle stocks were devastated) would have required switches to drastically different stimuli.

2. The technique specialisations seem to be prey specific, with the exception of limpets, which individuals both Stab and Hammer. However, there is less difference between the two techniques when applied to limpets than when they are used against mussels or cockles. The limpet is always exposed on the rocks and to dislodge it it needs either a single blow (very similar to a Stab) or a series of blows (a Hammering attack), both of them aimed at the lateral walls. With cockles and mussels the Stabbers and Hammerers locate their prey in different ways and in different parts of the beds, and there is a tremendous difference between the form and orientation of the Stab and the Hammering attack.

The question remains as to how these birds become specialists in the first place. This is a problem in ontogeny and is dealt with in some detail in Part IV of this thesis. The main points may be summarised here:

1. Young Oystercatchers learn one particular prey and one technique in catching it, and they stick to this

specialisation after they split up from their parents.
2. Which prey and technique the young bird learns depends upon the specialisation of its parents. From Table 22 it can be seen that of each breeding pair the male and female showed the same major specialisation in both prey and technique. Of the 11 pairs of mussel specialists, 2 were Hammerers and 9 were Stabbers. How this correspondence between males and females originates remains unsolved.

My studies on the ontogeny of these feeding techniques have shown that they take a long time to perfect (3 years for the mussel Stabbing technique for example). The survival value of specialising might therefore be that it is better to be very good at one technique and one prey than to be bad at a large number, and the loyalty of Oystercatchers to breeding grounds and to winter feeding grounds may be connected with this. It must also be remembered that Oystercatchers have retained the basic wader feeding behaviour of probing for worms and suchlike, so that they always have an additional feeding method to rely on should their particular food become scarce.

APPENDIX 1 THE TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE DIFFERENT FEEDING TECHNIQUES

Introduction

A series of a single motor pattern (i.e. a bout of many Levering movements or Chiseling movements) is scored as one occurrence of the motor pattern. Thus, the following observation Stab - - 4 sec of Levering - - Prise - - 12 sec of Chiseling - - Eat is scored as Stab - - Lever - - Prise - - Chisel - - Eat. This protocol is used even if the ongoing motor pattern is interrupted by other behaviour

not associated with the motor patterns (i.e. a bout of Chiseling being interrupted by the Oystercatcher having to run off with a mussel when chased by a marauding Herring Gull).

TABLES A - J

Diagramatical representation of the observed transition probabilities. The thickness of the arrows indicates the probability with which one motor pattern is followed by the one to which the arrow leads.

Note: the absolute frequency of each motor pattern in the sequence is not given.

Tables a - j

Note that:

(a) the absolute frequency (f) of each motor pattern in the sequences is given

(b) figures in ( ) are the transition probabilities expected if the motor patterns were occurring in a random order

(c) + or - indicate that the observed transition probabilities occur more (+) or less (-) frequently than random expectation; p = never 0.05

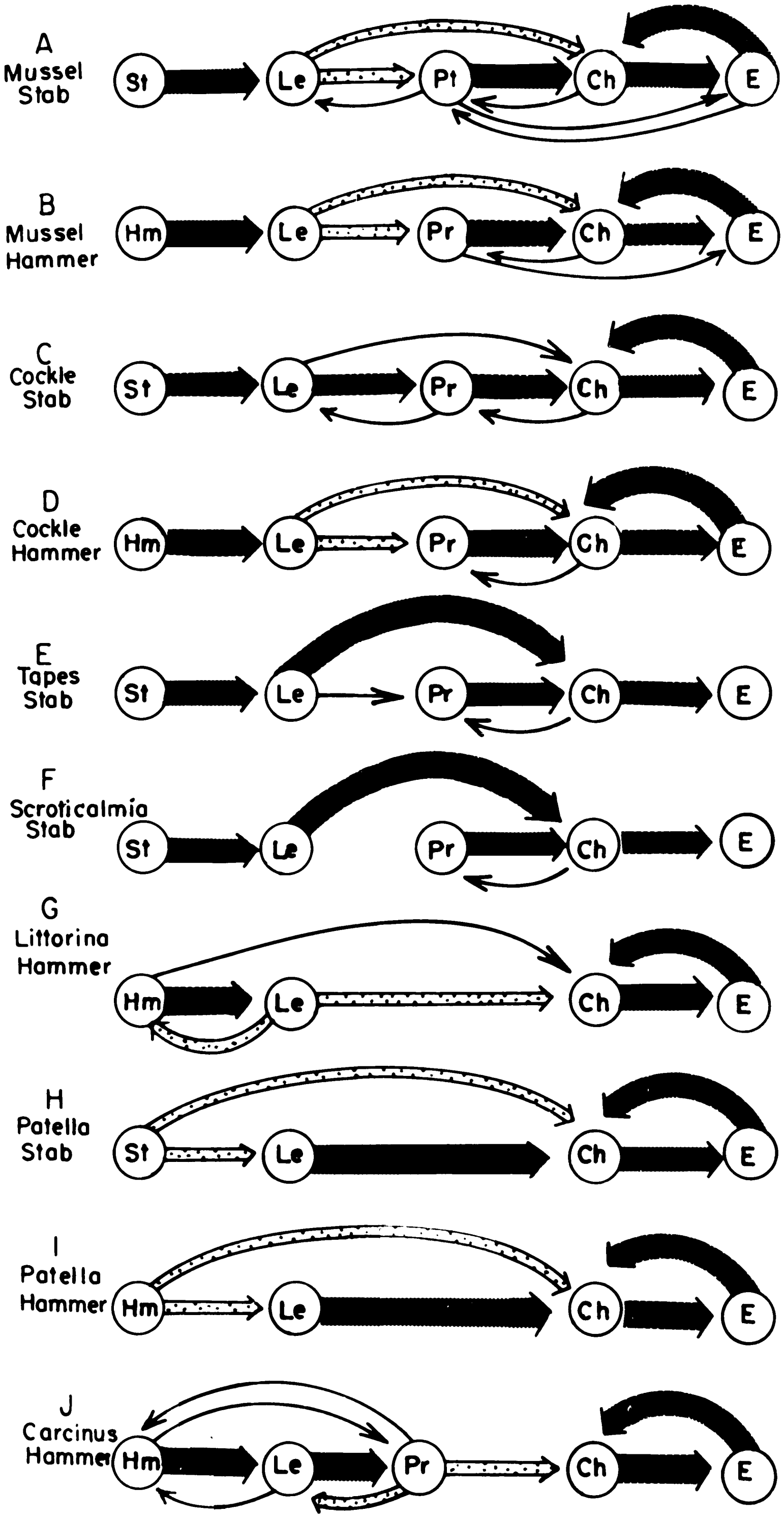

A
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TABLE a OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE MUSSEL STABBING TECHNIQUE (132 OBSERVATIONS)

	Following						
	Stab	Lever	Prise	Chisel	Eat	Totals	f
Preceding							
Stab	X	1.00 + (0.21)	0.00 - (0.15)	0.00 - (0.35)	0.00 - (0.29)	132	1.0
Lever	0.00 (0.00)	X	0.42 + (0.19)	0.58 + (0.44)	0.00 - (0.37)	136	1.03
Prise	0.00 (0.00)	0.02 - (0.26)	X	0.95 + (0.44)	0.03 - (0.30)	96	0.73
Chisel	0.00 (0.00)	0.01 - (0.33)	0.18 (0.24)	X	0.81 + (0.43)	215	1.63
Eat	0.00 (0.00)	0.00 - (0.30)	0.01 - (0.22)	0.99 + (0.48)	X	45	1.33

TABLE b OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE MUSSEL-HAMMERING TECHNIQUE (138 OBSERVATIONS)

	Following						
	Hammer	Lever	Prise	Chisel	Eat	Totals	f
Preceding							
Hammer	X	1.0 + (0.25)	0.00 - (0.10)	0.00 - (0.34)	0.00 - (0.31)	138	1.0
Lever	0.00 (0.00)	X	0.30 + (0.13)	0.70 + (0.42)	0.00 - (0.45)	139	1.0
Prise	0.00 (0.00)	0.00 (0.28)	X	0.96 + (0.37)	0.04 - (0.35)	51	0.37
Chisel	0.00 (0.00)	0.01 (0.39)	0.05 (0.14)	X	0.94 + (0.47)	180	1.30
Eat	0.00 (0.00)	0.00 - (0.36)	0.00 - (0.15)	1.00 + (0.49)	X	33	1.20

TABLE c OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE COCKLE STABBING TECHNIQUE (93 OBSERVATIONS)

	Following						
	Stab	Lever	Prise	Chisel	Eat	Totals	f
Preceding							
Stab	X	1.00 + (0.18)	0.00 - (0.16)	0.00 - (0.34)	0.00 - (0.32)	93	1.0
Lever	0.00 (0.00)	X	0.81 + (0.19)	0.19 - (0.43)	0.00 - (0.39)	94	1.01
Prise	0.00 (0.00)	0.01 - (0.22)	X	0.99 + (0.39)	0.00 - (0.39)	79	0.85
Chisel	0.00 (0.00)	0.00 - (0.28)	0.02 - (0.23)	X	0198 + (0.49)	171	1.80
Eat	0.00 (0.00)	0.00 - (0.28)	0.00 - (0.23)	1.00 (0.49)	X	75	1.80

TABLE d OBSERVED TRANSITION PRO ABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE COCKLE HAMMERING TECHNIQUE (99 OBSERVATIONS)

	Following						
	Hammer	Lever	Prise	Chisel	Eat	Totals	f
Preceding							
Hammer	X	1.00 + (0.22)	0.00 - (0.10)	0.00 - (0.34)	0.00 - (0.34)	99	1.0
Lever	0.00 (0.00)	X	0.47 + (0.13)	0.53 (0.44)	0.00 - (0.43)	99	1.0
Prise	0.00	0.00 -	X	1.00 +	0.00 -	47	0.48
Chisel	0.00 (0.00)	0.00 - (0.34)	0.07 - (0.16)	X	0.93 + (0.50)	144	1.4
Eat	0.00 (0.00)	0.00 - (0.34)	0.00 - (0.16)	1.00 + (0.50)	X	44	1.4

TABLE e OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE TAPES STABBING TECHNIQUE (15 OBSERVATIONS)

	Following						
	Stab	Lever	Prise	Chisel	Eat	Totals	f
Preceding							
Stab	X	1.00 + (0.27)	0.00 (0.13)	0.00 - (0.33)	0.00 - (0.27)	15	1.0
Lever	0.00 (0.00)	X	0.07 (0.13)	0.93 + (0.47)	0.00 - (0.40)	15	1.0
Prise	0.00 (0.00)	0.00 (0.33)	X	1.00 + (0.33)	0.00 (0.33)	4	0.27
Chisel	0.00 (0.00)	0.00 - (0.45)	0.17 (0.10)	X	0.83 + (0.45)	18	1.2
Eat	-	-	-	-	X	-	1.0

TABLE f OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE SCROBICULARIA STABBING TECHNIQUE (53 OBSERVATIONS)

	Following						
	Stab	Lever	Prise	Chisel	Eat	Totals	f
Preceding							
Stab	X	1.00 + (0.32)	0.00 (0.02)	0.00 - (0.34)	0.00 - (0.32)	53	1.0
Lever	0.00 (0.00)	X	0.00 (0.01)	1.00 + (0.49)	0.00 (0.50)	53	1.0
Prise	0.00 (0.00)	0.00 (0.33)	X	1.00 (0.34)	0.00 (0.33)	1	0.02
Chisel	0.00 (0.00)	0.00 - (0.50)	0.02 (0.01)	X	0.98 + (0.49)	54	1.02
Eat	-	-	-	-	X	-	1.0

TABLE g OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE LITTORINA HAMMERING TECHNIQUE (27 OBSERVATIONS)

	Following: Hammer	Lever	Prise	Chisel	Eat	Totals	f
Preceding:							
Hammer	X	0.81 + (0.34)	-	0.19 - (0.32)	0.00 - (0.32)	46	1.7
Lever	0.50 + (0.20)	X	-	0.50 (0.40)	0.00 - (0.40)	38	1.4
Prise	-	-	X	-	-	0	0.00
Chisel	0.00 - (0.23)	0.00 - (0.40)	-	X	1.00 + (0.37)	35	1.3
Eat	0.00 (0.24)	0.00 (0.38)	-	1.00 + (0.38)	X	8	1.3

TABLE h OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE PATELLA STABBING TECHNIQUE (24 OBSERVATIONS)

	Following: Stab	Lever	Prise	Chisel	Eat	Totals	f
Preceding:							
Stab	X	0.37 + (0.08)	-	0.63 (0.46)	0.00 - (0.46)	24	1.0
Lever	0.00 (0.00)	X	-	1.00 + (0.50)	0.00 - (0.50)	9	0.38
Prise	-	-	X	-	-	0.00	0.00
Chisel	0.00 (0.00)	0.00 - (0.18)	-	X	1.00 (0.82)	45	1.9
Eat	-	0.00 - (0.19)	-	1.00 (0.81)	X	21	1.9

TABLE i OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE PATELLA HAMMERING TECHNIQUE (18 OBSERVATIONS)

	Following						
	Hammer	Lever	Prise	Chisel	Eat	Totals	f
Preceding							
Hammer	X	0.72 + (0.28)	-	0.28 (0.36)	0.00 - (0.36)	18	1.0
Lever	0.00 (0.00)	X	-	1.00 + (0.50)	0.00 - (0.50)	13	0.72
Prise	-	-	X	-	-	0.00	0.00
Chisel	0.00 (0.00)	0.00 - (0.44)	-	X	1.00 + (0.56)	18	1.30
Eat	-	-	-	-	X	-	1.30

TABLE j OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF MOTOR PATTERNS IN THE CRAB HAMMERING TECHNIQUE (36 OBSERVATIONS)

	Following						
	Hammer	Lever	Prise	Chisel	Eat	Totals	f
Preceding							
Hammer	X	0.98 + (0.23)	0.02 - (0.23)	0.00 - (0.27)	0.00 - (0.27)	39	1.08
Lever	0.02 (0.01)	X	0.98 + (0.29)	0.00 - (0.35)	0.00 - (0.35)	52	1.4
Prise	0.04 (0.01)	0.27 (0.29)	X	0.69 + (0.35)	0.00 - (0.35)	52	2.80
Chisel	0.00 (0.02)	0.00 - (0.30)	0.00 - (0.30)	X	1.00 + (0.38)	64	1.80
Eat	0.00 (0.02)	0.00 - (0.30)	0.00 - (0.30)	1.00 + (0.38)	X	28	1.80

APPENDIX 2 COMPARISONS WITH MOTOR PATTERNS DESCRIBED BY OTHER AUTHORS

Many other accounts of the feeding behaviour of Oystercatchers have been published (see Part II, Introduction, p. 76), but the authors have been mainly concerned with more ecological aspects of the feeding behaviour. The more detailed analysis of the technique, as I have attempted, have not been made.

The published accounts of the actual techniques of catching the various prey differ in no major way from my own observations. Dewar (1908) and Drinnan (1958) described both the Stabbing and Hammering techniques against mussels, as well as the restriction of the Hammering attack to the ventral valve margins. Drinnan (1957) also describes the Stabbing and Hammering techniques against cockles, but in none of these reports was a totally clear distinction made between these two techniques. Dewar (1913) describes both Stabbing and Hammering at Tapes. I have never seen Oystercatchers Hammering at Tapes, but I was observing the feeding in a muddy estuary (in Southern Portugal) where, perhaps, the Hammering technique could not be applied. Safriel (1967) originally distinguished between Stabbing and Hammering at limpets, and Hulscher (1964) describes the Hammering attack at the mouth of crabs.

The other motor patterns of the feeding techniques have not been recorded so consistently. Levering is mentioned by all these authors as occurring after the initial attack, and its function is also given.

Prising is not mentioned at all. This is difficult to understand because the Price is such a very obvious

part of the techniques. However, the analysis of cine films of Oystercatchers eating mussels shows that the Prise is usually very quick (about 1 second or less from start to finish). I think that N. Tinbergen was the first person to recognise the Prise as an integral part of the Oystercatcher's technique (Tinbergen and Norton-Griffiths 1964), so that when I started to observe the feeding techniques I was looking out for the Prise. It is therefore possible that the earlier authors either did not see the Prise at all or that they saw it but failed to recognise its importance.

The Chiseling process is not specifically mentioned either, except by Safreil (1967) and by Dewar (1908) who, in passing, mentions '... snapping motions of the mandibles...'.

SUMMARY

1. The feeding techniques of the Oystercatcher on Mytilus, Cardium, Scrobicularia, Tapes, Littorina, Patella and Carcinus are analysed.
2. Each feeding technique is made up of a number of discrete motor patterns, each of which has a different form and a different function.
3. The form of each motor pattern is adapted to a very generalised function, and the function of each motor pattern is the same in all the feeding techniques.
4. The skill and efficiency of each feeding technique depend upon the precise orientation of each motor pattern with respect to the prey, and this orientation is exactly adjusted to the anatomy of each prey.
5. The functional integration of the motor patterns is the same in all the feeding techniques. With bivalves, for example, Stabbing and Hammering serve to gain initial entry into the shell, Levering and Prising serve to open the valves, and Chiseling (rapid chisel pecking and rapid grab pecking) serves to cut the flesh free from the shell.
6. Each of the motor patterns is elicited by a particular external stimulus, and the duration of each motor pattern (i.e. the number of Hammer blows, the number of seconds spent Levering) is likewise under continuous external control. The sequence in which the motor patterns occur can thus be seen to be simple chain responses in which the performance of one motor pattern brings about the external stimuli necessary to elicit the next. It is this total dependence on external control which imparts the remarkable efficiency and economy of effort to the technique, for each motor pattern is performed only if and when necessary, and only for as

long as is necessary.

7. There is strong evidence that individual Oystercatchers specialise not only on one particular prey (i.e. on mussels or on crabs) but also on one technique of eating it (i.e. Stabbing mussels or Hammering mussels).

8. The causation of these specialisations is twofold:

   (a) there may be considerable differences between the stimuli that elicit the initial Stabbing or Hammering attack at the different prey.

   (b) young Oystercatchers learn to specialise on one particular prey and one technique of eating it; which prey and which technique the young bird learns depends upon the specialisations of its parents (both parents of each breeding pair show the same specialisations). The young retain these specialisations after they have become independent from their parents.

PART 4

PART IV

THE DEVELOPMENT OF SKILLED FEEDING TECHNIQUES IN YOUNG OYSTERCATCHERS

INTRODUCTION

I have already stated in Part 1 (p.67), Part II (p.93) and Part III (p.181) that young Oystercatchers develop the same feeding specialisations as their parents'. The evidence for this is given in Table 1. In every single case, the young had developed the same feeding specialisations (on both prey and technique) as those of their parents' by the time that they had become independent from their parents. In addition, those individuals which I was able to observe in their second and third years were still feeding with the same techniques.

Since both members of a breeding pair share the same feeding techniques (Part III, p.172), it is possible that major genetic differences between the young of different specialists could account for their particular specialisations. I therefore attempted a cross-fostering experiment in which the eggs of known, colour-ringed specialists were interchanged. The following interchanges were made:-

Specialisations of Original Parents		Specialisations of Foster Parents
mussel-Stab	raised by	mussel-Hammer
mussel-Stab	" "	crab-eater
crab-eater	" "	mussel-Stab
mussel-Hammer	" "	mussel-Stab

Two interchanges of each type were made. Control interchanges (i.e. mussel-Stabber's eggs raised by different mussel-Stabbers, etc.) were not carried out because there were not enough

colour-ringed specialist pairs. The complete clutch of eggs was interchanged in every case, for this greatly increased the probability of at least one young surviving.

The young of five of the eight foster-families were devoured by predators before fledging and only one young of each of the three remaining families survived. Each of these young developed the same specialisations as those of their foster parents (Table 2).

The foster-parents and the original parents of these three young had raised their own broods in previous years, and their young had similarly developed the specialisations of their parents. Even though my sample is very small, the data in Tables 1 and 2 must mean that the young had the potential to develop any one of these three specialisations, but that some interaction with the parents (or with the environment in which the parents raise the young) channelled the development system so that only one of the potential specialisations developed.

In my analysis of the development of these skilled feeding techniques I am going to concentrate on four main problems:

1) how do the young acquire the skilled techniques? This raises a host of problems, for example, what are the developmental origins of the motor patterns, how do the young come to recognise the prey as food, how do the motor patterns acquire their adult function, how are the sequences of motor patterns developed? If learning is involved - what are the rewards at each stage?
2) how is the developmental system itself adapted to teaching these skilled techniques to young Oystercatchers?
3) what is the basis of the flexibility of the developmental system?

TABLE 1 THE FEEDING TECHNIQUES DEVELOPED BY YOUNG OYSTERCATCHERS

Parents' specialisations	feeding techniques of the young: just independent from parents	2nd year	3rd year
mussel-Stab (a)	mussel-stab	not seen	mussel-stab
mussel-stab (c)	mussel-stab	mussel-stab	not seen
mussel-stab	mussel-stab	mussel-stab	mussel-stab
mussel-stab	mussel-stab	not seen	not seen
mussel-hammer (b)	mussel-hammer (2 young)	mussel-hammer (1 young)	not seen
mussel-hammer	mussel-hammer	mussel-hammer	not seen
crab-eater	crab-eater	not seen	not seen
crab-eater (d)	crab-eater	not seen	not seen

note: (a), (b), (c), (d) refer to parents used in cross-fostering experiment, see Table 2.

TABLE 2 THE FEEDING TECHNIQUES DEVELOPED BY CROSS-FOSTERED YOUNG OYSTERCATCHERS

Parents' specialisations	Foster-parents' specialisations	feeding techniques of the young: just independent from parents	2nd year
mussel-stab (a)	mussel-hammer (b)	mussel-hammer	mussel-hammer
mussel-stab (c)	crab-eater (d)	crab-eater	crab-eater
mussel-hammer (b)	mussel-stab (a)	mussel-stab	not seen

note: (a), (b), (c), (d) refer back to Table 1.

4) I try to show that the Oystercatcher has evolved a developmental system which has the potential to produce a number of different 'end results', and that the particular end result produced depends upon how the system is channelled by the parent. This leads to a discussion of the co-adaptation between the parental feeding system and the requirements of the developmental system.

The main specialisations shown by the Ravenglass breeding population are mussel-Stabbing, mussel-Hammering and crab-eating (Part III, Table 22, and p.173), so I can only deal with the development of these three techniques. Even with this restriction my data covers only a very few individuals, for my main difficulty throughout this study has been to get close enough to the young birds to make consistent, detailed observations. The parents lead the young away from the immediate vicinity of the nest soon after hatching, and it is then very difficult to approach them. This is true even after the young have fledged and are feeding with their parents on the estuary feeding grounds. The number of individuals that I was able to observe was further reduced by the2heavy predation of young Oystercatchers in the Ravenglass population (due to a nearby gull colony attracting numerous mammalian and avian predators).

I have studied young Oystercatchers under three conditions; "Free-Living" (i.e. with their parents on the beach), "Fenced-in" (when the young were confined to the immediate vicinity of the nest by a high fence encircling the nest, see Part 1, Appendix 1, p.72) and "Hand-Raised" (raised from the egg by myself), and I have had to rely heavily on the data obtained from the Fenced-in and Hand-Raised young.

CHAPTER 1 THE OPPORTUNITIES FOR THE YOUNG TO GAIN EXPERIENCE WITH THE PREY

The young are not taken to the estuary feeding grounds by their parents until they are about 3-4 weeks of age, and during the first three weeks the opportunities to gain experience with prey are naturally limited. However, the parents do occasionally bring mussels and crabs from the estuary, and a very small proportion of these are brought 'unprepared' (i.e. the prey is brought complete with shell or carapace and with all the flesh inside, see Part I, p. 9). The parents open up and remove the flesh from these unprepared prey in the immediate presence of the young before feeding the flesh to the young. The remains of the prey (mussel shells and crab carapaces) are left lying about, and the young by themselves sometimes find scraps of flesh in them. These scraps are Chiseled out and eaten.

When the young accompany their parents to the estuary feeding grounds they have much greater opportunity to gain experience with the prey.

1) the parent now hunt, open up and empty almost every prey in the immediate presence of the young.
2) the young participate more actively in the preparation of the prey; they often Lever or Chisel at the same time as the parent, or, as frequently happens, the young and the parents 'take it in turn' to Lever and Chisel in the prey.
3) all over the feeding grounds numerous prey-remains are lying about in which the young find scraps of flesh, and from which they Chisel the flesh free.
4) as the young grow older, the parents leave unprepared prey for the young. The parents can either -
   (a) leave the prey <u>fully opened</u> (i.e. the parent has Levered and Prised open the prey but has not removed the flesh); the young then Chisels out the flesh: or -
   (b) leave the prey <u>partly opened</u> (i.e. the parent Stabs or

Hammers the prey, but does not Lever and Prise it open);
the young Levers and Prises before Chiseling at the flesh.

5) There are large numbers of undisturbed prey which the young attempt to catch and open for themselves.

At no stage during development is the opportunity for only one of these forms of prey experience exclusively available, for all the opportunities are continuously present. The one (obvious) exception is that the young do not meet undisturbed prey until they accompany their parents to the feeding grounds. One important point to remember is that the young of mussel-eating parents (both Stabbers and Hammerers) and of crab-eating parents all have the same opportunities for gaining these forms of prey experience.

CHAPTER 2 THE INDEPENDENT FEEDING ACTIVITIES OF THE YOUNG

INTRODUCTION

Within a few hours of hatching the young perform Independent Feeding Activities (which will in future be referred to as IFA). The IFA consist of investigating - especially with the bill - "anything and everything" lying around in the immediate environment of the young bird (see 2/C). The data given in this Chapter is based mainly on observations on young of less than 3 weeks of age belonging to the fenced-in nests.

2/A The IFA Motor Patterns

The IFA is made up of a number of discreet motor patterns which are very similar in form to the motor patterns seen in the adults' feeding techniques.

Peck: young birds aim simple Pecks at objects, sometimes grasping the object; they also 'Hammer Peck' (a series of hard Pecks at an object) and 'Probe' (Pecks in which the bill is forced deep into the substrate, usually sand). Since it was difficult to distinguish sharply between Pecks, Hammer Pecks and Probes, these are for the time being lumped together as Pecks.

Rapid Grab Pecks (RGP):

a series of Pecks with the bill opening and closing widely. The bill is opened wide on the forward lunge, and is closed on the withdrawal.

Rapid Chisel Peck (RCP):

a series of Pecks (4 or 5 per second). The bill tips hardly open at all. A bout of RCP may last for many seconds, and the bill is kept in contact with the object (which often moves about) by adroit contortions of the neck.

Mandibulate:

objects are Mandibulated between the bill tips.

Lever: lateral side-to-side movements of the bill, often incorporating a twisting component.

Prise: from a closed position, the mandibles are opened wide apart.

I have observed the IFA behaviour of 25 individual free-living Oystercatcher young of less than three weeks of age, and I particularly recorded whether or not they performed all the IFA motor patterns. By the time they were 3 weeks old, all 25 individuals were performing the full repertoire of IFA motor patterns, irrespective of the environment in which they were growing up, and irrespective of the specialisations of their parents (11 of the young had mussel-Stabbing parents, 4 of the young had mussel-Hammering parents, 3 of the young had crab-eating parents, the specialisations of the parents of the other 7 young were unknown). In addition, the 8 young from the five fenced-in nests all showed the complete repertoire of motor patterns (the parents of three of these fenced-in families were mussel specialists, and the parents were crab specialists), and so too did all my hand raised-young (Appendix 2).

These IFA motor patterns therefore make up a basic repertoire of bill movements which is common to all Oystercatcher young, and which is common to all the adult feeding techniques.

2/B The Cycles of IFA and Other Behaviour of the Young

The full analysis of the cycles of sleeping, preening, feeding from the parent, IFA and intense begging is contained in Appendix 1. The basic conclusion is that IFA are performed when the young is motivationally midway between being hungry (when it goes to the parent for food) and being sated (when it goes to sleep). There is therefore some degree of feeding motivation during the IFA.

2/C The Objects Eliciting the IFA Motor Patterns

The arenas inside the fences were littered with a wide variety of objects which included straws, twigs, dried seaweed, small stones, tiny specks on the sand, large stones, bits of wood, various forms of plant growth, fragments of many different types of shells, and the remains of mussels and crabs which the parents had brought from the estuary. I recorded what kinds of objects elicited the various IFA motor patterns, but the wide variety of objects made it difficult to make meaningful categories. I finally grouped all these objects into 9 categories, and in Table 3 I show the percentage of each motor pattern that was elicited by these nine categories. I have lumped the data from all 8 young from the five fenced-in nests together, for I could find no consistent difference between individuals from the same nest or between individuals from different nests.

The various IFA motor patterns are elicited by a very wide range of objects and there is much overlap between them. I have unfortunately no idea of the relative frequency of the various categories of objects inside the arenas, so Table can give no indication of the overall selective responsiveness of the young. In addition, it is impossible to decide what are the precise stimuli from these various objects that elicit the different motor patterns, but some of the stimuli bear some similarity to those eliciting the motor patterns in the adult feeding techniques.

Pecks are elicited most by ' small' and 'thin' objects. Rapid Chisel Pecking shows the same general pattern in that 'small' and 'thin' objects elicit more RCP than do 'large' or 'thick' objects, but 'thin straws' and 'cracks' are the most effective. All these objects offer a firm resistance which 'gives' a little to the RCP movements in that the objects are pushed across the sand while the young Rapid Chisel Pecks at

TABLE 3 THE DISTRIBUTION OF EACH IPA MOTOR PATTERN OVER 9 CATEGORIES OF OBJECTS LYING IN THE ARENAS OF THE FENCED-IN NESTS (IN % OF EACH MOTOR PATTERN ELICITED BY EACH OBJECT CATEGORY)

	Peck	RCP	RGP	Mandib	Lever	Prise
specks on the sand	40	-	-	-	-	-
small stones or shell fragments	13	18	-	21	12	-
large stones or shell fragments	5	3	8	10	4	-
thin straws	36	40	-	66	14	-
thick straws	4	5	-	-	4	-
prey-remains	1	13	2	-	6	18
cracks	1	21	-	3	56	21
sand	-	-	73	-	-	38
vegetation masses	-	-	17	-	2	23
Totals	2574	917	455	336	118	58

Lumped data from 8 young from 5 fenced-in nests. Young all less than three weeks of age.

them. I have previously suggested that this is a most important factor in maintaining RCP in the adults when they are Chiseling flesh free (Part III, p.128), and it can be seen from Table 3 that 79% of the RCP bouts of the young are directed at objects that 'give' a little to the RCP movements. The stimulus 'firm resistance that gives a little' may therefore be as important in eliciting and maintaining RCP in the youngs' IFA behaviour as it is in the adults' Chiseling.

Rapid Grab Pecking is totally different to RCP, for it is elicited by 'sand' (i.e. the young Rapid Grab Pecks through the loose sand) and by 'vegetation masses' (i.e. RGP at a mass of dried seaweed). These stimuli may be very similar to the 'loose flesh' that elicits RGP in the adults' Chiseling (Part III, p.129).

Mandibulations, Lever and Prise are basically very different in that they are not elicited directly by these objects but only <u>after</u> Pecking, RCP or RGP (see 2/D). Mandibulations are elicited only when there is something between the bill tips, and 'thin straws' seem to be most effective. Levering is elicited in two different situations. Firstly, when the bill is 'in between' something (i.e. prey remains or 'cracks') and when there is some resistance to Lever against. In these situations the eliciting stimuli may also be very similar to those eliciting Levering in the adults feeding techniques (i.e. Levering against the valves of a mussel or a cockle). Secondly, Levering is also elicited when the bill tips are merely 'in contact' with something (i.e. Levering at a thin straw). This is not seen in the adults. However, from Table 3 it can be seen that 64% of Levering was elicited when there was some resistance to Lever against.

TABLE 4 THE RESPONSE OF THE YOUNG TO 9 DIFFERENT CATEGORIES OF FOOD OBJECTS (IN % OF TOTAL RESPONSE TO EACH OBJECT CATEGORY MADE UP BY THE DIFFERENT MOTOR PATTERNS)

	Peck	RCP	RGP	Wand	Lever	Prise	TOTALS
specks on the sand	100	-	---	-	-	-	1300
small stones or shell fragments	52	28	-	12	8	-	584
large stones or shell fragments	55	12	16	15	2	-	231
thin straws	60	24	-	14	2	-	1531
thick straws	67	30	-	-	3	-	154
prey-remains	15	70	5	-	6	4	170
cracks	8	60	-	3	20	9	323
sand	-	-	85	-	-	15	402
vegetation masses	-	-	83	-	3	14	93

Lumped data from 8 young from 5 fenced-in nests : young all less than 3 weeks of age.

Prising (as in the adults' feeding techniques) is only elicited when there is some resistance to Prise against. I suggested (Part III, p.118) that the difference between the Lever-eliciting stimuli and the Prise-eliciting stimuli in adults is of a quantitative nature. This also seems to be the case for the stimuli that elicit Lever and Prise in the IFA behaviour, for from Table 3 it can be seen that 61% of the Prises are elicited by 'sand' or 'vegetation masses' (which probably offer a very 'loose' resistance to the bill) while only 2% of Levering is elicited by these objects. Conversely, 'cracks' (which probably offer a very firm resistance to the bill) elicit 56% of the Levering but only 21% of the Prising. It is therefore possible that even at this early stage in development there is a quantitative difference between the Lever and Prise eliciting stimuli.

In general, therefore, the various IFA motor patterns are elicited by a very wide range of objects. In many respects the eliciting stimuli are fairly similar to the stimuli eliciting the motor patterns in the adult feeding techniques, and, although this undoubtedly biases which particular motor pattern is elicited by each of the nine different categories of objects (see Table 4), there is no evidence that this by itself causes bias towards particular objects.

2/D The Integration of the Motor Patterns

I also recorded from the 8 fenced-in young the sequences in which the motor patterns occurred. I first distinguished between single motor patterns (i.e. a motor pattern which was neither preceeded nor followed within one second by another motor pattern) and integrated motor patterns (i.e. a motor pattern which was preceeded or followed within one second by another motor pattern). The great majority of the motor patterns were single (Pecks 62%, RGP 76%, RCP 68%) while mandibulations,

Lever and Prise were always integrated. I could find no consistent trends for these motor patterns to become more integrated as the young grow older, or for various stable cominations of motor patterns to be developed. In addition, I could find no consistent differences between the various young in the ways in which the motor patterns were integrated. I have therefore lumped the data from all eight young together.

In Table 5 the observed transition probabilities between all pairs of IFA motor patterns are shown.

The first point to make is that Mandibulations, Lever and Prise are always, in the first instance, preceeded by Peck, RGP or RCP, presumably because these three motor patterns bring the bill into contact with an object. Secondly, there are three almost independent groupings of motor patterns:

(a) Peck and Mandibulate are closely associated together and rarely with the other motor pattern, i.e. an object elicits a peck, then it is very unlikely that any other motor pattern (except Mandibulation) will occur.

(b) RGP, Lever and Prise occur together when RGP is elicited. Most of the RGP is directed into the loose sand (Table 3), and the young Grab Pecks through the sand. Occasionally it locates an object buried in the sand, and then Lever or Prise (or RGP) may be elicited.

(c) RCP, Lever and Prise form a very closely associated group of motor patterns. 65% of Levering, and 80% of Prising are elicited after a bout of RCP.

I attempted to categorise the objects that elicited sequences of motor patterns, but no consistent patterns could be found. For example, a thin straw might on one occasion elicit RCP alone, and on another occasion elicit RCP $\longrightarrow$ Lever $\longrightarrow$ RCP. There was no sign at all of the development of stable sequences as seen in the adults' feeding techniques, even when the young were investigating prey remains. The important point is that there is no sign of internal linking (i.e. once one

TABLE 5 THE OBSERVED TRANSITION PROBABILITIES BETWEEN ALL PAIRS OF IFA MOTOR PATTERNS

	Peck	Mand	RGP	RCP	Lever	Prise	other behav.	TOTALS
other behav.	0.62+ (0.58)	0.00- (0.08)	0.15+ (0.10)	0.23+ (0.20)	0.00- (0.02)	0.00- (0.02)	-	3010
Peck	0.27- (0.34)	0.11+ (0.04)	0.00- (0.06)	0.00- (0.12)	0.01- (0.02)	0.00- (0.01)	0.61+ (0.41)	2574
Mand.	0.00- (0.35)	0.01- (0.04)	0.00- (0.05)	0.04- (0.10)	0.01 (0.01)	0.00 (0.01)	0.94+ (0.44)	336
RGP	0.00- (0.35)	0.03 (0.04)	0.00- (0.06)	0.12 (0.12)	0.04+ (0.01)	0.04+ (0.01)	0.77+ (0.41)	455
RCP	0.00- (0.34)	0.04 (0.04)	0.02- (0.06)	0.11 (0.12)	0.10+ (0.02)	0.04+ (0.01)	0.69+ (0.41)	917
Lever	0.00- (0.35)	0.00- (0.05)	0.00- (0.06)	0.26+ (0.12)	0.00 (0.02)	0.01 (0.01)	0.73+ (0.39)	118
Prise	0.00- (0.34)	0.00 (0.05)	0.00 (0.06)	0.26+ (0.13)	0.00 (0.01)	0.00 (0.01)	0.74+ (0.39)	58

Note: 'other behaviour' indicates that the motor pattern was not preceeded or followed within one second by another IFA motor pattern.

figures in ( ) indicate the transition probabilities expected if there was random association between the motor patterns.

+ or - indicate that the observed transition probability occurs more frequently (+) or less frequently (-) than random expectation.

motor pattern is elicited then no other one automatically follows it). The observed patterns of integration are very variable and seem in every case to depend upon the stimuli (whatever they may be) peculiar to the eliciting object.

2/E The Development of the IFA motor patterns

2/E/I The Individual Motor Patterns

Pecking, Mandibulating, RGP and RCP all appear on the day of hatching, while Prising was not seen until Day 5 and Levering not until Day 10 (Table 6). I did not make detailed observations of the development of each motor pattern (i.e. as Hailman, 1968, made on the development of the various components of Pecking of gulls), with the exception of Rapid Chisel Pecking. This was the only motor pattern to show any marked change as the young grew older. Two changes were noticable:

(a) the young become more 'skillful'. By this I mean that the young were able to keep the bill in contact with the object by adroit contortions of the neck, even though the object usually skidded wildly over the sand.

(b) probably as a result of this, the length of the RCP bouts became longer.

2/E/II Trends in the Frequency of the Motor Patterns

I estimated the percentage frequency of the various IFA motor patterns shown by the young from each fenced-in nest (Table 6), and I calculated trends in the frequency of each motor pattern by correlating the percentage frequency of each motor pattern against the age of the young (Speerman Rank Correlation r_s). This was done separately for nests 1, 2 and 3 (from which I had most data) and for all the nests taken together (Table 7).

TABLE 6 % FREQUENCY OF THE IFA MOTOR PATTERNS SHOWN BY THE YOUNG FROM FIVE FENCED-IN NESTS

	Age of the young in days																
NEST	1	2	4	5	7	8	9	10	11	13	14	15	16	17	19	21	23
PECKING																	
1 (m)	90			87		65			60		53			49		42	
2 (c)		94	79		76			55		47			45		43		
3 (c)			89		86		78					61					57
4 (m)			88				65						62				
5 (m)		91			71					79			70				
RAPID CHISEL PECKING																	
1 (m)	7			2		7			24		28			30		44	
2 (c)		1	5		13			23		29			33		42		
3 (c)			3	-	7		9					15					23
4 (m)			5				13						26				
5 (m)		2			4					10			11				
MANDIBULATE																	
1 (m)	2			5		10			9		9			11		5	
2 (c)		4	14		6			8		6			7		1		
3 (c)			7		2		9					7					6
4 (m)			5				10						6				
5 (m)		3			15					4			5				
RAPID GRAB PECKING																	
1 (m)	1			5		18			7		8			6		7	
2 (c)		1	2		4			10		12			8		7		
3 (c)			1		5		4					12					9
4 (m)			2				6						2				
5 (m)		4			8					5			11				
PRISE																	
1 (m)	0			1		0			0		1			1		1	
2 (c)		0	0		1			2		4			1		0		
3 (c)			0		0		0					1					1
4 (m)			0				1						1				
5 (m)		0			2					1			2				
LEVER																	
1 (m)	0			0		0			0		1			3		1	
2 (c)		0	0		0			2		2			6		7		
3 (c)			0		0		0					4					4
4 (m)			0				5						3				
5 (m)		0			7					1			1				

Note: (m) indicates that the parents were mussel specialists

(c) indicates that the parents were crab specialists

Pecking: there is an overall significant decrease in the frequency of Pecks. All the records show this decrease, although there is much variation between the nests.

Rapid Chisel Pecking:

there is an overall significant increase in the frequency of RCP which is shown in all the records.

Mandibulating:

no significant trends are shown by any of the young. There is no overall trend.

Rapid Grab Pecking:

Although the young from nest 3 show a significant increase in frequency, none of the other young shown a significant trend, and there is no overall significant trend.

Lever and Prise:

there is an overall significant increase in frequency of both these motor patterns. The young from nests 1 and 2 show significant increases.

There therefore seem to be two basic changes, a decrease in the frequency of Pecking and an increase in the frequency of RCP. The increase in the frequency of Lever and Prise is most likely caused by the increase in RCP, for Table 5 shows that Lever and Prise are closely associated with RCP. The important point to consider is to what extent this change in frequency is environmentally induced. Since the arenas did not noticeably loose any of their Peck-eliciting objects, it is possible that there is an endogenous change in the selective responsiveness of the young. In support of this hypothesis we see that all the young show the same basic changes (Table 6), irrespective of the specialisations of their parents and irrespective of the local environment in which they are growing up. An endegenous change of this kind might be biologically relevant, for a high

TABLE 7 SPEERMAN RANK CORRELATIONS (r_s) CALCULATED FROM THE DATA GIVEN IN TABLE

Motor Pattern	Nest 1(m)	Nest 2(c)	Nest 3(c)	Overall trend
Pecking	-0.96 p=<0.01	- 1.00 p=<0.01	- 0.90 p=0.05	- 0.82 p=<0.01
Rapid Chisel Pecking	+ *1.00 p=<0.01	+1.00 p=<0.01	+*0.90 p=0.05	+*0.84 p=<0.01
Mandibulate	+0.52 ns	-0.25 ns	-0.05 ns	-0.03 ns
Rapid Grab Pecking	+0.04 ns	+0.68 ns	+*0.95 p=<0.05	+0.48 ns
Prise	+0.47 ns	+0.37 ns	+0.87 ns	+0.47 p=<0.05
Lever	+0.84 p=<0.05	+0.95 p=<0.01	+0.87 ns	+0.72 p=<0.01

selective responsiveness to Peck-eliciting stimuli would be advantageous to the young when establishing the first feeding responses to the parent. A switch to RCP-eliciting stimuli (or a waning to Peck-eliciting stimuli) might then be retevant to the development of feeding skills. However, from Table 6 it can be seen that there is much variation between the frequencies of the motor patterns in the IFA behaviour of the different young, and especially in the rate of change of these frequencies. Most noticeable is that the young from nests 1 and 2 are consistently Pecking less and Rapid Chisel Pecking more than are the young from the other nests. These consistent differences can be attributed to an environmental effect. The parents of nests 1 and 2 brought a reasonably consistent supply of food to their young (although the supply was not enough to prevent the young from eventually starving) while the parents of nests 3, 4 and 5 were bringing a very erratic food supply (especially by the second week). The young of these three parents were always

near to starvation, and they spent most of their IFA in Pecking at (and eating) tiny specks on the sand (see Appendix 1). This suggests that the change in frequency of Pecking and Rapid Chisel Pecking is perhaps due to a waning to Peck-eliciting stimuli, and that environmental effects can greatly alter the rate of this change. This problem will be discussed further in Chapters 3, 4 and Appendix 3.

2/F Summary

1) the IFA are the incipient adult feeding equipment of young Oystercatchers. They consist of a repertoire of six discrete Motor patterns which are very similar in form to the motor patterns seen in all the adults' feeding techniques. All Oystercatcher young possess this full pepertoire irrespective of the feeding specialisations of their parents and irrespective within the range observed, of the environment in which they are growing up.
2) the various IFA motor patterns are elicited by a very wide range of stimuli which are similar in many respects to the stimuli that elicit the motor patterns in the adult techniques.
3) the integration of the motor patterns is very variable, and there is no evidence of internal linking. Both the elicitation and initial integration of the motor patterns seems to be under the control of external stimuli.
4) there is a basic change in the relative frequency of the motor patterns in that Pecking decreases in frequency while RCP, Lever and Prise increase in frequency. Environmental effects can alter both the extent and the rate of this change.
5) the IFA are performed when there is some feeding motivation.

CHAPTER 3 THE FIRST INTERACTIONS WITH THE PREY

I have already mentioned (Chapter 1) that the parents of free-living young occasionally bring unprepared mussels or crabs from the estuary, and that these prey are opened up in the immediate presence of the young. The remains of these prey are left lying around, and, during their IFA, the young occasionally investigate them and find scraps of flesh inside. These scraps are then Chiseled free and eaten. The young are also very occasionally left to deal with fully opened or partly opened prey.

The parents of the fenced-in nests also brought unprepared prey into the arenas, and gradually a large collection of prey remains collected inside. The young occasionally investigated these prey remains during their IFA, and they removed and ate any scraps of flesh that they found. Three things were then very noticeable:

1) the scraps of flesh are Chiseled free by RCP and RGP.
2) the young spend more and more time in investigating these prey remains. In Table 8a I show the percentage of all IFA motor patterns that were elicited by these prey remains correlated against the age of the young. The young from all five nests show a marked increase, irrespective of whether the prey remains were those of crabs or those of mussels.
3) the prey remains mainly elicit RCP - even when there are no scraps of flesh present, and the percentage of RCP bouts elicited by prey remains greatly increases (Table 8b). There is also a marginal increase in the percentage of Pecks elicited by the prey remains (Table 8c).

These observations suggest three possible hypotheses about the function of the IFA and the effect of the interaction between the IFA and the prey remains.

TABLE 8 THE RESPONSE OF THE FENCED-IN YOUNG TO PREY REMAINS LYING ABOUT IN THE ARENAS

a) the % of all IFA motor patterns elicited by the prey remains

time rank:	1	2	3	4	5	6	7	r_s	
nest 1(m)	1	1	2	5	6	15	17	+0.98	p=<0.01
nest 2(c)	0	0	6	10	14	17	21	+0.99	p=<0.01
nest 3(c)	0	0	3	6	9			±0.97	p=<0.05
nest 4(m)	0	6	16						
nest 5(m)	0	1	8	6					

overall trend r_s = +0.73 p=<0.01

b) the % of all RCP bouts elicited by the prey remains

time rank:	1	2	3	4	5	6	7	r_s	
nest 1(m)	0	12	16	19	34	26	41	+0.91	p=<0.01
nest 2(c)	0	0	24	30	31	29	33	+0.90	p=<0.01
nest 3(c)	0	3	6	14	11			±0.90	p= 0.05
nest 4(m)	0	10	23						
nest 5(m)	0	0	30	28					

overall trend r_s = +0.85 p=<0.01

c) the % of all Pecks elicited by prey remains

time rank:	1	2	3	4	5	6	7	r_s	
nest 1(m)	0	0	3	5	9	5	8	+0.86	p=<0.05
nest 2(c)	0	0	4	0	6	5	4	+0.59	ns
nest 3(c)	0	0	0	3	3			+0.72	ns
nest 4(m)	0	6	2						
nest 5(m)	0	5	1	2					

overall trend r_s =+0.65 p=<0.01

Note: (m) or (c) indicates that the parents were mussel or crab specialists.

the age of the young at each time rank are the same as in Table 6.

1) the responsiveness of the IFA motor patterns to a very wide range of objects and stimuli results in the eventual investigation of prey remains. Food reward from the remains then conditions the young to the remains as a potential source of food, and the young spends more and more time investigating the remains (Chapter 4).
2) the IFA motor patterns (in this case RCP and RGP) acquire their adult functions by practice at removing the scraps of flesh. In addition, perhaps practice with inedible objects (i.e. RCP at thin straws) leads to the acquisition of fine control over the motor patterns (Appendix 4).
3) the food reward from prey remains might reinforce a change in selective responsiveness from Peck eliciting stimuli to RCP eliciting stimuli. This might contribute to the observed change in the frequency of Pecking and RCP (Appendix 3).

It must be realised that finding scraps of flesh in the remains is not the only prey experience that the young have at this stage. The unprepared prey are opened up in the immediate presence of the young, and very occasionally the young are left to deal with fully opened and partly opened prey. These prey-experiences may all contribute to the observed change in the behaviour of the young. However, if these hypotheses can be supported then we see the first indications of the flexibility of the developmental system, in that (a) the young will become conditioned to the particular prey that the parent is feeding them on and (b) the young will acquire through practice with this prey the precise functions and orientation of the motor patterns appropriate to that particular prey.

CHAPTER 4 CONDITIONING TO THE PREY AS A POTENTIAL SOURCE OF FOOD: EXPERIMENTS WITH HAND RAISED YOUNG

INTRODUCTION

The experiments with hand-raised young were designed to answer three questions: (a) whether the young become conditioned to the prey as a potential source of food through finding scraps of flesh in the prey remains, (b) whether this experience effects the rate of change in the frequency of the various IFA motor patterns, and (c) whether practice at removing the flesh contributes to the acquisition of the adult functions of the motor patterns.

Young Oystercatchers are not easy to raise in large numbers, so I had to design an experiment which would (a) give data to answer all these problems, (b) produce some results even in the face of massive mortality of the young, and (c) withstand the unavoidable variations and disasters inherent in any long term hand-raising experiment carried out under field conditions.

The experiment was therefore very simple. I hatched out 34 Oystercatcher eggs, divided the young into 3 groups, and gave a different daily regime of experience with mussels from which the young had to remove the flesh. The young were raised in an environment containing a wide variety of different objects which included empty mussel shells. When the young were performing IFA I recorded the frequency of the different motor patterns and the number of IFA motor patterns directed at these empty mussel shells. In addition, when I gave the young experience with mussels containing flesh, I recorded various aspects of their Chiseling. The experiment ran for 54 days.

4/A Rearing and Living Conditions

The young birds were raised together in a small hut (measuring 3m x 2m). There was one large internal living cage (see Fig. 1) with an external run extending out of the window. There was also a large external aviary (measuring 15m x 30m x 2m high) in which the young spent much of their time and in which they could fly around. The young were constantly handled, and were exceptionally tame.

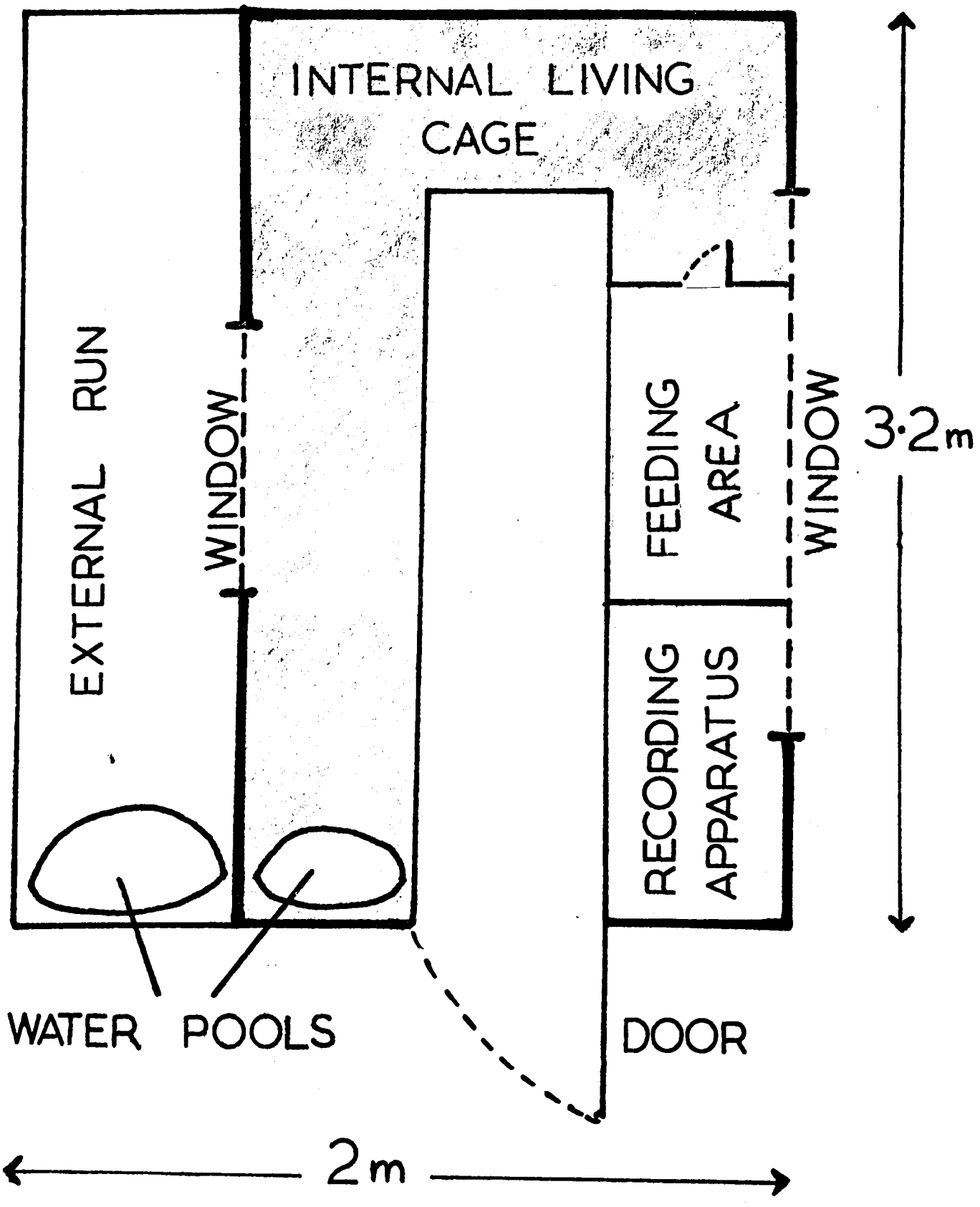
One section of the internal living cage (the feeding area) was reserved entirely for feeding, and the young were only fed in this area. They were fed at least 6 times a day (on a mixture of fresh meat, fresh mussel flesh, and various annelids when these were available), and they were always fed by hand (from tweezers). The only occasions when the young found food by themselves was when they emptied the flesh from mussels. Each young was fed once a day completely alone, otherwise they were fed en masse.

4/B The Environment of the Internal Living Cage

The young had a wide variety of objects at which they could direct their IFA behaviour. The floor of the internal living cage and of the external run was covered with sand to a depth of some 4 cm, and the sand was littered with a very wide range of objects (straws of different thickness and length, bits of wood, stones, seaweed etc). It was impossible to maintain these different objects at the same relative frequency, but I always ensured that the same range of objects was present. Small stones and shell fragments had to be carefully excluded because the young persisted in eating them.

The internal living case always contained 12 mussel shells of exactly 35mm in length which were completely free from any trace of flesh. All other shells were excluded.

Fig. 1 Plan of the Internal Living Cage of the hand-raised young (the floor of the cage was at window sill height)



4/C The Daily Schedules of Experience with Mussels Containing Flesh

The young were assigned to one of three groups as soon as they hatched.

Group 1 from Day 18 onwards, each young was given daily 10 mussels containing flesh. The mussels were exactly 35mm in length, and were presented fully opened (i.e. the adductors were cut and the valves were opened as far apart as possible). The flesh of these entire mussels (EM) was attached to the shell and the young had to Chisel out the flesh and eat it. The mussels were presented one at a time in the feeding area of the cage (the young was by itself), and the young had as much time as it needed to eat the ten mussels.

Group 2 from Day 18 onwards, each young had 10 mussels a day of exactly the same size and presented in the same way. However, the flesh of these mussels had previously been removed and then placed back in the shell (loose flesh mussels, LM). The young merely had to pick up the flesh and eat it. The total amount of food obtained from the mussels was therefore the same as for the Group 1 young, but the Group 2 young did not have to perform any Chiseling.

This schedule was continued until Day 39. From Day 40 onwards, each young received 10 EM, presented in the same way as the Group 1 young.

Group 3 They had no experience at all with mussel shells containing flesh until Day 40. Each young then received 10 EM per day, presented in the same way as for Groups 1 and 2.

These different schedules of mussel experience are shown in Table 9.

TABLE 9 SCHEDULES OF EXPERIENCE WITH MUSSEL SHELLS CONTAINING FLESH

EM = entire mussels : LM = loose flesh mussels

	age of the young in days			
	1	18	40	54
Group 1:	no mussel experience	EM.....		
Group 2:	no mussel experience	LM.....	EM.....	
Group 3:	no mussel experience.....		EM.....	

4/D Testing Conditions

4/D/I The Behaviour Recorded

At weekly intervals I recorded the IFA behaviour of the young when they were in the internal living cage. I recorded on a multi-event recorder the total number of Pecks, Mandibulations, RGP bouts, RCP bouts, Lever and Prise, as well as the length of each individual bout of Mandibulation, RGP and RCP. I also recorded the number of Pecks and RCP bouts (and their length) directed at the empty mussel shells lying on the floor of the internal living cage.

4/D/II Conditions of the Tests

The young were fed some 30 min before recording commenced (see Appendix 1). At a moment convenient to myself, I started to record the IFA behaviour, and I continued recording until the young had performed 50 IFA motor patterns.

I have carefully checked to see if I can detect any bias in the data due to this recording regime. For each group of young, and then for all the young taken together, I correlated the number of each motor pattern recorded, in turn, with the time taken by the individual over the test. I made these correlations for each test. No consistent correlations could be found, which shows that no great bias was introduced by this method of collecting the data.

4/D/III The Age at which the young were tested.

The IFA behaviour of each young was recorded on Day 3, Day 6 and then at weekly intervals (Table 10). There was heavy mortality among the young, especially during the time of fledging so the number of young in each group dwindled towards the end of the series of tests.

TABLE 10 THE AGE OF THE YOUNG WHEN TESTED, AND THE NUMBER OF YOUNG IN EACH GROUP

age in young in Days:	3	6	13	20	27	34	41	48
test number:	1	2	3	4	5	6	7	8
number of young in each group								
Group 1:	7	7	7	7	5	4	3	3
Group 2:	8	9	10	8	8	3	3	3
Group 3:	4	4	4	2	1	1	(1)	1

note: the young in group 3 was not tested on Day 41 due to ill health. N. Gull ? or Oystercatcher?

4/D/IV The Criteria for Infering a Conditioning to Mussels

In order to test whether or not finding flesh in prey remains (in this case mussel shells) conditions the young to investigate prey remains as a potential source of food, I analysed the data to see whether those young which had experience of obtaining food from mussel shells (Groups 1 and 2) were more responsive to empty mussel shells during their IFA behaviour than the young which had not had this experience (Group 3). For each group of young I therefore analysed (a) the number of Pecks directed at the empty mussel shells, (b) the number of RCP bouts and (c) the length of these RCP bouts directed at the empty mussel shells.

4/D/V Statistical Analysis

I calculated regression coefficients to estimate trends in these three behaviours. Two time periods were used : (a) up to Test 6 (day 34), for this was the last test before Groups 2 and 3 had experience with EM, and (b) over the whole series of tests (Table 11).

The Mann-Whitney U Test (z, two-tailed) was used for comparing the performance of each Group against the others on each test day. From Test 4 onwards, the scores of Groups 2 and 3 were combined together because there were so few young remaining in Group 3.

4/E Results

4/E/I Pecking at Mussel shells

There is no trend at all for the number of Pecks directed at mussels to increase. The Mann-Whitney tests revealed no significant differences between the number of Pecks by each Group except for:

(a) Test 4 Group 1 > Group 2 combined with Group 3 ($z = 2.7$, $p = 0.006$):

(b) Test 7 Group 2 > Group 1 ($z = 1.98$, $p = 0.046$):

This indicates that there may be an initial increase in the number of Pecks directed at mussel shells immediately after the first experience with EM, but this effect soon wanes.

4/E/II RCP at mussel shells

Up to Test 6, Group 1 alone showed a significant increase. Over the whole test series both Group 1 and 2 showed a significant increase, but Group 3 did not.

The Mann-Whitney tests showed that:

(a) up to Test 3: Group 1 = Group 2 = Group 3 (z never > 1.79, p never < 0.08)

(b) Tests 4 - 6: Group 1 > Group 2 combined with Group 3 (z never < 2.0, p never > 0.04)

(c) Tests 7 - 8: Group 1 = Group 2 combined with Group 3 (z never > 1.3, p never < 0.20).

TABLE 11 THE RESPONSE OF EACH GROUP OF HAND RAISED YOUNG TO EMPTY MUSSEL SHELLS DURING THEIR IFA

a) the average number of Pecks

age of young (days) :	3	6	13	20	27	34	41	48
Test No. :	1	2	3	4	5	6	7	8
Group 1	0.1	0.1	1.6(EM)	2.7	1.4	1.5	1.0	1.3
Group 2	0.6	0.1	0.4(LM)	0.3	0.7	0.0(EM)	2.3	1.3
Group 3	0.0	0.3	0.7	1.0	1.0	0.0(EM)		1.0

b) Average number of RCP bouts

Group 1	1.0	1.0	1.0(EM)	12	12	10	16	18
Group 2	1.0	1.0	1.0(LM)	3.0	2.0	4.0(EM)	13	14
Group 3	1.0	1.0	3.0	1.0	0.0	0.0(EM)		19

c) Average bout length (sec) of RCP bouts

Group 1	1.2	1.4	1.6(EM)	2.1	2.4	2.6	3.2	3.2
Group 2	1.0	1.5	1.7(LM)	1.6	1.2	1.1(EM)	2.1	2.7
Group 3	1.0	1.2	1.2	1.0	-	-(EM)		4.6

d) regression coefficients

Group 1	no. of pecks	+ 0.94 $p = > 0.05$ ns	+ 1.94 $p = > 0.05$ ns
Group 2	" " "	+ 0.72 $p = > 0.05$ ns	+ 1.63 $p = > 0.05$ ns
Group 3	" " "	+ 1.86 $p = > 0.05$ ns	+ 0.46 $p = > 0.05$ ns
Group 1	no. of RCP	+ 2.4 $p = < 0.05 > 0.02$	+ 2.45 $p = < 0.001$
Group 2	" " "	+ 0.6 $p = > 0.05$ ns	+ 1.89 $p = < 0.01$
Group 3	" " "	- 0.29 $p = > 0.05$ ns	+ 1.31 $p = > 0.05$ ns
Group 1	bout length RCP	+ 3.00 $p = < 0.001$	+ 3.73 $p = < 0.001$
Group 2	" " "	- 0.29 $p = > 0.05$ ns	+ 1.51 $p = > 0.05$ ns
Group 3	" " "	- 0.23 $p = > 0.05$ ns	+ 2.81 $p = > 0.05$ ns

Note: (a) (EM) and (LM) indicate age at which young had mussel-experience

(b) underlined figures are significantly larger than those of the other groups (mann whitney z, p never > 0.05)

4/E/III Bout length of RCP at mussel shells

Up to test 6, and over the whole series of tests, only Group 1 showed a significant increase in bout length.

The Mann-Whitney tests showed that:

(a) up to Test 3: Group 1 = Group 2 = Group 3 (z never >1.1, p never <0.3)

(b) Tests 4 - 6: Group 1 > Group 2 combined with Group 3 (z never <2.4, p never >0.01)

(c) Tests 7 - 8: Group 1 = Group 2 combined with Group 3 (z never >1.6, p never <0.11)

4/F Discussion

These data show conclusively that obtaining food from mussels is not enough by itself to produce a conditioning effect. Group 1 and Group 2 obtained exactly the same amount of food from mussels, yet, up to Test 6, only the Group 1 young showed any increase in the number and length of the RCP bouts directed at mussel shells. Group 2, however, showed by Test 7 a striking increase in the number and length of RCP bouts directed at mussel shells, even though they had by then only Chiseled in 20 mussels. By Test 8, there were no significant differences between the behaviour of the three Groups. The conditioning effect is therefore extremely rapid, and it only occurs if the young have to Chisel out the flesh. RCP in mussels without obtaining food (this happened during the IFA behaviour of Groups 2 and 3), or RGP in mussels plus food reward (Group 2 when fed from mussels) does not lead to the conditioning effect. It is the performance of the functional response (RCP) linked to the appropriate reinforcement (food) that causes the observed conditioning effect.

This prerequisit for conditioning is functionally very important:

(a) it ensures that the young become conditioned only to prey remains and not to other inedible objects that elicit RCP (i.e. RCP at thin straws will not result in the young

becoming conditioned to thin straws).

(b) it is the basis of the flexibility of the developmental system RCP linked to a food reward will cause the young to become conditioned to whatever prey the parents are bringing (i.e. to mussels or to crabs) or to other Oystercatcher prey). This is admitedly a broad generalisation from my data, and it should be tested experimentally using different prey (as well as mussels) with the same schedules of experience as I have used. However, we have seen from Table 8 that young become conditioned to both mussels and crabs, and in the cross-fostering experiments the young must have similarly become conditioned to prey which they would not normally have come across. In Appendix 2 I compare the behaviour of those of my hand raised young whose parents were known to be mussel or crab specialists. Their parentage made no difference to whether or not they became conditioned to mussels - it was the schedule of experience that was important.

These data raise a more general point. The response of the conditioned young (both hand raised and fenced-in) to the mussel shells is mainly RCP, although there also seems to be a short-term increase in the number of Pecks. The conditioning had thus not only increased the responsiveness of the young to mussel shells but has also changed the selective responsiveness of the young to these shells. I have suggested previously (Chapter 3) that the conditioning to prey-remains in the fenced-in young might reinforce a change in selective responsiveness from Peck eliciting stimuli to RCP eliciting stimuli, and that this might contribute to the observed change in the frequency of Pecking and RCP. This point is discussed in Appendix 3.

CHAPTER 5 EXPERIENCE WITH PREY WHEN THE YOUNG ARE MORE THAN THREE WEEKS OF AGE

The young have much greater opportunity for prey-experience once they accompany their parents to the estuary feeding grounds, and it must be remembered that by the time this happens the young have, almost certainly, become conditioned to prey-remains. Prey-experience occurs under two different situations:-

1) While the young is fed by the Parent
   (a) almost every prey is hunted, opened up and emptied in the immediate presence of the young.
   (b) the young often actively participate in the preparation of the prey, and they may Lever or Chisel at the same time as the parent.
   (c) the young often remove scraps of flesh from the prey remains after the parent has emptied them.
   (d) the parent leave fully opened and partly opened prey for for young to deal with.
2) During the IFA of the Young
   (a) numerous prey remains are lying all around the feeding grounds in which the young find scraps of flesh.
   (b) undisturbed prey abound in large numbers. The young attempt to catch and prepare them by themselves.

The next step in my analysis is to try and sort out the effects of each type of prey-experience on the development of the feeding techniques. There are three major effects:

   (a) the acquisition of the function and orientation of the motor patterns (from 1b, 1c, 1d, 2a). Some details of the development of Chiseling in mussels is given in Appendix 4.
   (b) the acquisition of the correct sequence of motor patterns (from 1d).
   (c) the development of hunting behaviour, which seems to greatly depend on 1a.

Two points must be reiterated here. First, the young of both mussel specialists (Stabbers and Hammerers) and crab specialists have the same type of prey-experience, and second, all these different types of prey-experience are present at all stages in the development of the feeding techniques (Table 12).

TABLE 12 PREY-EXPERIENCE OF YOUNG OF DIFFERENT AGES

	specialisation of parents	age of young in weeks 1-4	5-8	9+
% of prey left partly opened or fully opened	mussel parents	7%	16%	22%
	crab parents	5%	3%	17%
% of prey from which the young remove scraps of flesh after the parent has empted it	mussel parents	34%	48%	55%
	crab parents	26%	71%	68%

note: (a) lumped data from 7 'mussel families' and 3 'crab families'.

(b) the crab parents consistently leave unprepared prey less frequently than do the mussel parents. This may be in response to marauding gulls which are very quick to pounce on any unattended crab. The gulls do not seem to be so interested in mussels.

CHAPTER 6 THE DEVELOPMENT OF THE SEQUENCES OF MOTOR PATTERNS

INTRODUCTION

In Appendix 3 I describe the development of Chiseling from the first confrontation between 2/3 week old young with prey remains to the well organised Chiseling seen in independent young of 16/20 weeks of age. Over this same time period the young interact frequently with the partly opened prey that the parents leave for them, and in which they Lever and Prise as well as Chisel.

The data presented below were obtained from (a) fenced-in young of 2/3 weeks of age; (b) free-living young of 4/5 weeks of age; (c) free-living young of 6/7 weeks of age who were just starting to successfully catch and open prey; (d) fully independent young of 16/20 weeks of age; (e) adults.

6/A The Development of Levering and Prising in mussels

6/A/I Fenced-in young of 2/3 weeks of age

I have 8 observations of young of this age attempting to open up and empty out partly opened mussels which the parents had left in the arenas.

Sequence of Motor Patterns

The mussels had usually been left lying with the ventral side up. The young first Chiseled out as much flesh as possible through the gape between the ventral valve margins and only then attempted to Lever and Prise apart the valves. There was much Levering and Prising mixed up with the Chiseling, and no coherent sequence could be seen. Table 13a shows that the transition from Lever to Chisel is the only transition that occurs more frequently than random expectation. The transitions between Prise and Lever, Prise and Chisel, Chisel and Lever, and Chisel and Prise were random. Table 13b shows that the frequency of Lever, Prise and Chisel per mussel eaten is much

greater than in older young or in adults.

The Orientation of Lever and Prise

Most of the Lever and Prise were in the 'wrong' orientation (Table 13c), i.e. they were not oriented laterally <u>across</u> the valves.

The Stimuli Eliciting the Motor Patterns

Most of the Lever and Prise were elicited by the flesh of the mussel rather than by the valve edges. The young would often Lever in the ventral body mass, or between the cruciform ligament and the shell. Prising, too, was frequently elicited when the young Chiseled at the flesh of the mussel. It was very noticable that a Prise was elicited when, for example, the young managed to Chisel free a muscular attachment. It seemed that tactile stimuli from the flesh around the bill was responsible for the elicitation of both Lever and Prise.

6/A/II Older Young with Partly Opened Mussels

By 4/5 weeks of age the sequence of Lever, Prise and Chisel had considerably changed. Firstly, the young start by Levering, and they do not Chisel until they have Levered. The frequency of Levering is therefore much less (Table 11b). Prising has become very rare, and it always occurrs during Chiseling. The orientation of both Lever and Prise are now mainly across the valve edges (Table 11c), and both these motor patterns are now elicited by contact between the bill and the valve edges, rather than by stimuli from the flesh of the mussel.

6/A/III First successful attempts at opening mussels (6/7 weeks old).

By the time that the young start to catch and open mussels the sequence of motor patterns is stabilised. Levering always occurs after Stabbing and Hammering, and only very occasionally is there a second bout of Levering. Prising is still

TABLE 13 THE DEVELOPMENT OF THE SEQUENCE OF LEVER, PRISE AND CHISEL IN THE MUSSEL OPENING TECHNIQUES

(a) 2/3 week old fenced-in young. Observed transition probabilities between Lever, Prise and Chisel in partly opened mussels.

	Lever	Prise	Chisel	Eat	Totals
Lever	x	0.05- (0.22)	0.95+ (0.56)	0.00- (0.22)	56
Prise	0.06 (0.11)	x	0.94 (0.82)	0.00- (0.07)	122
Chisel	0.16 (0.18)	0.40 (0.39)	x	0.44 (0.43)	298
Eat	0.00- (0.11)	0.00- (0.25)	1.00+ (0.64)	x	131

from 8 observations on 3 young: figures in ( ) indicate the transition probabilities expected if there was random association between the motor patterns: (+) or (-) indicates that the observed transition probability occurs more frequently (*) or less frequently (-) than random expectation:

(b) the frequency of occurrence (per mussel opened) of Lever, Prise and Chisel

	Lever	Prise	Chisel	number of observations	no.of individs.
Fenced-in young of 2/3 weeks, opening partly opened prey	7.0	15.3	37.3	8	3
Free-living young of 4/5 weeks, opening partly opened prey	1.1	0.17	6.0	23	7
Free-living young of 6/7 weeks, opening prey by themselves	1.2	0.10	4.2	20	4
free-living young of 16/20 weeks, independent from parents	1.02	0.16	4.5	153	c. 15
Adults	1.01	0.5	1.4	242	?

(c) the orientation of Lever and Prise. Figures give the % of all Lever and Prise oriented <u>laterally across</u> the valve margins.

	Lever	Prise
Fenced-in young of 2/3 weeks opening partly opened prey	23%	2%
Free-living young of 4/5 weeks opening partly opened prey	90%	(25%)
Free-living young of 6/7 weeks opening prey by themselves	100%	(100%)

very infrequent, although now some of the Prises are occurring after the Levering as well as during the Chiseling (see Appendix 4). Lever and Prise are oriented across the valve margins, and they are elicited by contact between the valve edges and the bill.

6/A/IV Possible Causes of the Observed Changes in Behaviour

There are three main changes in organisation during the development of the sequence of motor patterns in mussels:

(a) Lever (and Prise) occur before Chiseling.

(b) Lever and Prise are oriented across the valve margins rather than in any other orientation.

(c) Lever and Prise are elicited by contact between the bill and the valve margins rather than by stimuli from the flesh of the mussel.

All these changes can be accounted for by trial-and-error learning through this experience with partly opened prey, for they will be reinforced by the flesh being extracted from the shell more quickly and with less expenditure of effort. However, it must be remembered that, as well as dealing with these partly opened prey, the young are constantly Chiseling both in prey remains and in fully opened prey. By 4/5 weeks of age the organisation of Chiseling is well developed, and one of the most important changes in the organisation of Chiseling has been that the young starts by Chiseling at the posterior end of the mussel. The young can not Chisel at the posterior end of a partly opened mussel until the valves have been Levered and Prised apart, The attainment of the Chisel-eliciting stimuli may therefore also reinforce the development of the correct sequence and orientation of Lever and Prise.

Normal growth processes may also be a very important factor in the development of the sequence of motor patterns.

Young of 2/3 weeks of age are not very strong, their bill is short and thin, and it was very noticeable that even correctly oriented Levering had little effect in forcing the valves apart. In the case of Prising, the bill is so short that even a correctly oriented Prise across the valve margins would be unable to open the valves fully. Even if the young did Lever and Prise before Chiseling it is unlikely that the valves would have been fully opened. It will be remembered that when an adult bird opens a mussel, the Lever-eliciting stimuli are no longer present once Levering has been performed (because the valves are then wide apart). With these very small young, the Lever-eliciting stimuli may still be present after a bout of Levering because the young is just not strong enough. It is therefore not surprising to find much Levering (and Prising) while these small young are attempting to open up a mussel. Young of 4/5 weeks of age are much stronger, and their bills are longer and stouter, and so Levering (or Prising) in any orientation will be more effective in damaging the mussel, and this will be itself reduce the frequency of Levering (and Prising) without any learning being involved. In addition, Lever and Prise in older young and in adults are elicited by contact between the valve margins and the bill. Small young of 2/3 weeks of age can insert their bill between the ventral valve margins of a partly opened mussel without contacting both valve margins, so Lever and Prise are unlikely to be elicited at the appropriate moment in the behaviour. The bill of older young comes into contact with both valve margins as as soon as it is inserted into the partly opened mussels, and this by itself makes it more likely that Lever and Prise will be elicited at the appropriate moment (i.e. before Chiseling).

I have described how the stimuli eliciting Lever and Prise seem to change as the young grow. Much of the Levering and

Prising of 2/3 week old young is elicited by the flesh of the mussel, while the Levering and Prising of older young are elicited instead by contact between the valve margins and the bill. I suggested (Part III, p. 114) that Lever and Prise in the adults is elicited by pressure around the bill tips, and that the difference between the Lever-eliciting stimuli and the Prise-eliciting stimuli of a quantitative nature. I feel sure that this is also true for Lever and Prise in 4/5 week old young and 2/3 week old young, as well as for Lever and Prise elicited during the IFA behaviour. It seems, however, that the tactile stimuli from the flesh of a mussel that elicit Lever and Prise in the small young are quantitatively less than the tactile stimuli from the valve margins that elicit Lever and Prise in 4/5 week old young. It is therefore possible that the thresholds of pressure around the bill tips at which Lever and Prise are elicited become greater as the young grow (this may be an integral part of the normal growth of the bill). The young would therefore respond more to stimuli from the valve margins than to stimuli from the mussel's flesh, and this would give <u>directionality</u> to any trial-and-error learning process.

Finally, it is possible that there is a separate feedback from Lever and Prise that is totally unconnected with gaining food reward, in that Levering or Prising against a firm resistance (i.e. across the valve margins) is in itself reinforcing when compared with Levering or Prising against anything else (i.e. in the flesh). This would bias the young towards Levering and Prising in the correct orientation, as well (perhaps) towards responding to the appropriate stimuli (i.e. stimuli from the valve margins rather than to stimuli from the flesh). This bias would also give directionality to any trial-and-error learning process.

Conclusion: three major changes in organisation are observed during the development of the sequence of motor patterns in mussels: (a) Lever and Prise occur before Chiseling, (b) Lever and Prise are oriented across the valve margins, and (c) Lever and Prise are elicited by the appropriate stimuli. Experience with partly opened prey offers the opportunity for trial-and-error learning, for all of these changes in organisation will be reinforced by the flesh being removed more quickly and with less expenditure of effort. However, I have suggested three other factors which may be of great importance:

1) normal growth processes which result in the body becoming stronger and in the bill becoming longer and stouter. This by itself will reduce the frequency of Levering and Prising (because they become more effective in damaging the mussel) and increase the probability of Lever and Prise occurring before Chiseling (because the bill of the older young immediately contacts both valve margins) without any learning being involved.
2) the thresholds at which Lever and Prise are elicited may change, and this may bias the young towards responding to stimuli from the valve margins.
3) Levering and Prising against a firm resistance may in itself be reinforcing. This may bias the young towards Levering and Prising in the correct orientation, as well as to responding to the appropriate stimuli.

(a) and (3) will lend directionality to any trial-and-error learning process in that they may speed up the process as well as biasing what is learned.

6/B The Young of Stabbing and Hammering Parents

I have no observations of the behaviour of 2/3 week old young of Hammering parents for the fenced-in young of this age all had Stabbing parents. However, when comparing the

behaviour of 4/5 week old young of Stabbing and of Hammering parents who were dealing with partly opened prey, I could find no significant differences in either the sequence, frequency or orientation of the motor patterns. From 6/7 onwards, the only noticeable difference was in the frequency of Chiseling (the Hammering young had significantly fewer Chiseling bouts per mussel, see Appendix 4) but this was almost certainly due to the difference in size of the mussels being eaten by the young. The behaviour of the young of Stabbing and Hammering parents is therefore developing in the same way at this stage.

6/C <u>The young of Crab-eaters</u>

Fenced-in young of crab-eating parents show exactly the same pattern of behaviour when dealing with partly opened crabs. They first Chisel out as much flesh as possible through the hole around the mouth of the crab, and only then Lever and Prise. Lever, Prise and Chisel occur in a very chaotic sequence. Much of the Levering and Prising is in the wrong orientation, and much of it is elicited by the flesh of the crab rather than by tactile stimuli from the hole in the crab's mouth. It was also very noticeable that the young were too weak, and their bills were too short, to be able to open up the crab.

I have no detailed observations of older free-living young of crab-eating parents dealing with partly opened prey. They do have experience with this type of prey, and a well organised sequence of motor patterns has been developed by the time that the young catch and open up crabs for themselves. I see no reason why the same developmental processes suggested for the young of mussel-eating parents should not produce these same changes in behaviour in the young of crab-eating parents.

CHAPTER 7 THE DEVELOPMENT OF HUNTING BEHAVIOUR

7/A The environment of the young

We must now take into account the environment in which the young of mussel-Stabbing parents, mussel-Hammering parents and crab-eating parents are growing up. I will refer to these young as Stabbing young, Hammering young and Crab young.

7/A/I Stabbing and Hammering Young

I made detailed observations on the young of two different Stabbing families and the young of one Hammering family. There is some degree of ecological isolation between the Stabbing and Hammering young due to the position of their parents' territories on the mussel beds. Both types of territory contained mussels which could be Stabbed and mussels which could be Hammered, for in the pre-breeding season I observed adults to successfully Stab mussels on the eventual feeding territory of the Hammering parents, and vice versa. However, the Stabbing territories were more suitable for Stabbing than for Hammering (there were many pools and areas of soft soggy sand) while the Hammering territory was on slightly higher ground where the sand was harder and there were fewer pools of water. Fortunately for me, the young from these three families often intermingled away from their parents on an area of neutral ground which contained mussels suitable for both Stabbing and Hammering. It was on this neutral ground that I made most of my observations. In general, therefore, although the immediate mussel bed environment in which the Stabbing and Hammering young were growing up were either more suitable for Stabbing or more suitable for Hammering, this difference was by no means absolute.

The Stabbing territories contained few crabs, as did the neutral area, but the Hammering territory had very few crabs, if any.

7/A/II The Crab Young

Crabs abounded on the area of the mussel bed where the crab-eaters held their territory. Since this was an area of the mussel bed, there were naturally immense numbers of mussels suitable for both Stabbing and Hammering. Other birds were successfully Stabbing mussels in this area of the bed although I never observed Hammering birds to operate in this area.

7/B <u>The IFA behaviour of young of 4/5 weeks of age</u>

At this age the IFA behaviour consists mainly of investigating prey remains, of hunting for prey, and of attempting to open up any prey discovered.

I recorded the frequency of the motor patterns in the IFA behaviour of Stabbing, Hammering and Crab young, irrespective of what the motor patterns were directed at (but I excluded the motor patterns envolved in removing flesh from prey remains and in opening up partly opened prey left by the parents). At this stage the young had not started to successfully catch and open prey.

There was no significant difference between the frequencies of Mandibulate, RGP, Lever and Prise (Table 14). However, the Crab young had a significantly higher frequency of RGP than did the Stabbing or Hammering young (the Hammering young had avvery low frequency of RGP), while the Hammering young had a very high frequency of Pecking.

These differences have much significance for the development of hunting behaviour. RGP in sand develops into the shallow rapid probing with which buried crabs (and mussels) are located, while Pecking develops into Hammering

TABLE 14 THE FREQUENCY (%) OF THE MOTOR PATTERNS IN THE IFA BEHAVIOUR OF FREE LIVING YOUNG OF 4/5 WEEKS OF AGE

	Number of Crab-young (1)	Number of Stabbing-young (4)	Number of Hammering-young (2)
Peck	14	18	23+
Mandibulate	0.5	0.0	0.0
RGP	30+	22	15-
RCP	40	42	48
Lever	15	17	14
Prise	0.5	1	0.0
Total motor patterns	111	332	331

(+) or (-) indicated that the observed frequency of the motor pattern is greater (+) or less (-) than the expected mean frequency, p never > 0.05.

and Probing. These young are therefore showing a high frequency of the motor pattern appropriate to their particular hunting behaviour. The Crab young shows a high frequency of RGP, the Hammering young show a high frequency of Pecking (Hammering and Probing were in this analysis scored with Pecking), while the Stabbing young seem to be intermediate in that they show both Pecking (Probing) and RGP (locating buried mussel by touch). The differences between these young are thus already consistent with the hunting methods which they will eventually employ, even though at this age they have not yet started to successfully catch and open prey by themselves.

7/C The Development of Hunting in the Crab Young

At 4/5 weeks of age most of the RCP is directed at crab remains and other extraneous objects lying around, while most of the RGP and Lever are directed around seaweed clumps and rocks. Eventually the young manages to locate buried crabs, and these are dug up. By 6/7 weeks of age the young are

successfully opening them. The only response to mussels made by the crab young was the occasional peck or RCP at exposed mussels on rocks. I never observed the crab young to make consistent attempts to open them, or even to pay very much attention to them. They certainly did not show the type of behaviour described below for the Stabbing and Hammering young.

7/D The Development of Stabbing and Hammering at Mussels

7/D/I Methods of Finding Mussels

The young have four methods of locating a mussel before they attempt to do anything to it. These are (a) attend to an exposed mussel lying on the sand, (b) lever a mussel off a rock, (c) locate a mussel by a follow-up-probe and (d) locate a mussel by a dart-Stab. Table 15a shows the frequency of these four methods shown by Stabbing and Hammering young. Both young show the same amount of interest in exposed mussels. However, the Stabbing young show significantly more dart-Stabs and follow-up-Stabs than do the Hammering young, while the Hammering young lever more mussels off rocks (the first part of the Hammering attack).

7/D/II Attempted Attacks on the Mussels after Location

The following behaviours are seen: (a) RCP over the outside of the closed shell, (b) Lever at the shell, either at the ventral or dorsal valve margins, (c) Hammer at the shell, (d) peck at it, (e) do nothing to it. In Table 15b I show the frequency of these behaviours shown by Stabbing and Hammering young. Overall, both young show the same amount of Pecking and RCP at the closed mussel, but the Stabbing young Lever more at the shells, while the Hammering young Hammer more.

TABLE 15 THE DEVELOPMENT OF HUNTING BEHAVIOUR IN STABBING AND HAMMERING YOUNG OF 4/5 WEEKS OF AGE

(a) Methods of finding mussels

	Lever off rock	Lying exposed	Dart-Stab	Follow-up-Stab	TOTALS
Stabbing young (4)	6%-	28%	16%+	50%+	131
Hammering young (2)	36%+	47%	0.0%-	17%-	92

(+) or (-) indicates that the observed frequency is greater (+) or less (-) than the expected mean frequency, p never >0.05.

(b) Attempted attacks on the mussels after location

	Hammering	Peck	Lever	RCP	Nothing	TOTALS
Stabbing young	2%-	3%	71%+	16%	8%	131
Hammering young	36%+	11%	10%-	24%	19%	92

(+) or (-) indicates that the observed frequency is greater (+) or less (-) than the expected mean frequency, p never >0.05.

(c) the orientation of the Hammering attack

	Hammering at the ventral valve margins	Hammering at other parts of the shell
Stabbing young	0	3
Hammering young	18	15

exact p = 0.11

(d) the orientation of the Levering attack

	Levering at the ventral valve margins	Levering at the dorsal valve margins
Stabbing young	65	28
Hammering young	7	2

exact p = 0.48

7/D/III The Orientation of Hammering and Levering

Hammering: 55% of the Hammering attacks of the Hammering young were directed at the ventral valve margins (Table 15c), while none of the Hammering attacks of the Stabbing young were so oriented.

Levering: Both the Hammering and Stabbing young Lever mainly at the ventral valve margins (Table 15d).

7/E Discussion

Both the Stabbing and Hammering young are showing the elements of both hunting behaviours in an environment (mainly the neutral area) in which both can be performed, yet the most frequent behaviours shown in each case are those of their parents' hunting techniques. As far as I know, the young at this age had not yet been successful in catching and opening prey. It therefore seems that this difference between the pre-hunting behaviour of Stabbing and Hammering young is a direct effect of parental example, for these young are constantly having mussels caught and opened with one particular technique in their immediate presence. The Hammering young see mussels levered off rocks, oriented and then Hammered, while the Stabbing young see mussels caught by dart-Stabs and follow-up-Stabs. I do not see why the Stabbing young Lever more at mussels than do the Hammering young, for both are used to Levering open partly opened prey in order to remove the flesh. Levering, however, is a very integral part of the Stabbing technique used by the parents, so this might cause the difference.

Another difference between the young is in the areas in which they hunt. The Crab young hunt mainly around rocks and seaweed covered clumps, but the Stabbing young (who are also searching for buried food) hunt more in the areas of soft

soggy sand. The Hammering young tend to spend most of their time on rocky outcrops to which mussels are festooned. The areas in which the young hunt might also be due to parental example.

This must remain a very hypothetical explanation for the differences between the behaviour of the young, and it should be tested experimentally. I feel, however, that ecological isolation alone (i.e. the Stabbing young being in an environment where there are mainly 'Stabbing' stimuli, and vice versa) is not enough to produce these differences in behaviour, for there is just not that much difference between the Stabbing and Hammering territories.

CHAPTER 8 COMPARISONS BETWEEN THE MUSSEL-FEEDING TECHNIQUES OF NEWLY INDEPENDENT YOUNG AND ADULTS

8/A Introduction

In this Chapter I first describe the final development of the hunting techniques of the Stabbing and Hammering young, and then compare the feeding techniques of young just independent from their parents (12/20 weeks of age) with the feeding techniques of adults. An analysis of the organisation of the feeding behaviour of these young is given in Appendix 5. I also discuss why it takes the young three years to become fully efficient at eating mussels.

8/B The Final Development of the Stabbing and Hammering Techniques

By 6/7 weeks of age the young are successfully Stabbing and Hammering mussels.

The Stabbing Young (Tables 16a and 16c):

At 6/7 weeks of age the young are mainly employing the follow-up-Stab technique. 28% of the follow-up-Stabs are successful, while only 13% of the dart-Stabs are successful. The young still attempt to Lever apart the valves of closed mussels (only 15% of these attempts are successful), but no Hammering attacks at exposed mussels are seen.

The young use only the dart-Stab and follow-up-Stab techniques by the time that they are feeding completely independently from their parents, and their skill at both these techniques has greatly increased. They use the follow-up-Stab more than the dart-Stab, and their success with the follow-up-Stab is significantly greater (65% as compared with 51%, $chi^2 = 4.14$, $p = <0.05 > 0.02$). They no longer attempt to Lever apart the valves of closed mussels.

TABLE 16 THE FINAL DEVELOPMENT OF THE STABBING AND HAMMERING TECHNIQUES

(a) The Techniques used by the Stabbing Young (as % of total attacks)

	Hammering	dart-Stab	follow-up-Stab	Lever	TOTALS
4/5 weeks old	2%	16%	50%	16%	131
6/7 weeks old	0%	17%	54%	29%	91
Independent young	0%	30%	70%	0%	240

(b) The Techniques employed by the Hammering young (as % of total attacks)

	Hammering	dart-Stab	follow-up-Stab	Lever	TOTALS
4/5 weeks old	36%	0%	17%	10%	92
6/7 weeks old	82%	0%	4%	14%	43
Independent young	100%	0%	0%	0%	13

(c) The Success of the Techniques (as % of attempts)

	Hammering	dart-Stab	follow-up-Stab	Lever
Stabbing Young				
6/7 weeks old	—	13%	28%	15%
Independent	—	51%	65%	—
Hammering Young				
6/7 weeks old	21%	—	0%	0%
Independent	100%(?)	—	—	—

The Hammering Young (Tables 16b and 16c)

At 6/7 weeks of age the young are mainly Hammering at mussels, and there are very few attempted follow-up-Stabs or Levering attacks. 21% of the Hammering attacks are successful, while none of the follow-up-Stabs or Levering attacks were observed to be successful.

The young use only the Hammering technique by the time they are independent. It was extremely difficult to observe Hammering young of this age, and my sample is so small that I am unable to estimate the success rate of the Hammering attacks.

There are, therefore, two basic changes that occur during the final development of the Stabbing and Hammering techniques:

(a) a gradual increase in the skill of the techniques. The skill of the Stabbing techniques shows a marked improvement by the time that the young are independent from their parents, while the skill of the Hammering technique (estimated by the average number of blows taken by the young to fracture a mussel shell) shows a similar improvement (6/7 week old young take 8.5 blows on average, n = 35: independent young take 5.4 blows on average, n = 13).

(b) by the time that the young are independent, the Stabbing young employ the Stabbing techniques exclusively and do not attempt to Lever or Hammer open mussels, while the Hammering young use the Hammering technique and do not attempt to Lever or Stab mussels.

8/C <u>The Stabbing Technique of Independent Young and Adults</u>

8/C/I The Hunting Behaviour of the Young

The Stabbing technique of the independent young is in many respects very inefficient when compared to the Stabbing technique of the adults. Although the young are hunting for

mussels in the same areas as the adults (Table 17a), they use the follow-up-Stab technique rather than the dart-Stab technique (Table 17b). The young are considerably less skillful at both these techniques than adults (Table 17c)

TABLE 17 THE HUNTING BEHAVIOUR OF NEARLY INDEPENDENT YOUNG COMPARED WITH ADULTS

(a) The Areas in which the young hunt for mussels (as % of mussels taken from the different areas)

	water pools	soggy sand	dry sand	TOTALS
Independent young	11%	78%	11%	240
Adults	16%	68%	16%	279

$chi^2 = 5.05$, df = 2, $p = > 0.05$

(b) The Technique used by the Young (as % of all mussels taken)

	follow-up-Stab	dart-Stab	TOTALS	
Independent young	70%	30%	240	$chi^2 = 53.8$
Adults	18%	82%	279	$p = < 0.001$

(c) The Success of the Techniques used by the Young (as % of attempts)

The success of dart-Stabs	Successful	Unsuccessful	TOTALS
Independent young	51%	49%	71
Adults	88%	12%	229

$chi^2 = 44.3$, $p = < 0.001$

The success of follow-up-Stabs

	Successful	Unsuccessful	TOTALS
Independent young	65%	35%	169
Adults	90%	10%	50

$chi^2 = 9.97$, $p = < 0.01 > 0.001$

8/C/II The time taken by the young to open and clean out the mussels

From Table 18a and 18b it can be seen that the young are as quick as adults in Levering open small mussels, but they are taking significantly longer to Lever open medium-sized mussels. The Chiseling of the young (in both small

TABLE 18 TIME TAKEN BY THE NEWLY INDEPENDENT YOUNG TO OPEN UP AND CLEAN OUT MUSSELS

(all figures are median values: z is calculated from Mann-Witney U : p is two-tailed probability association with z)

(a) Stabbing small mussels

	duration of Levering	duration of Chiseling	number of Chiseling bouts	number of pieces of flesh	TOTAL OBS.
Independent young	3.9	13.9	4.7	3.6	97
Adults	3.0	6.2	1.2	1.1	65
	z= 1.65	z= 5.92	z= 9.96	z= 8.96	
	p= 0.10	p= 0.001	p= 0.001	p= 0.001	

(b) Stabbing medium sized mussels

	duration of Levering	duration of Chiseling	number of Chiseling bouts	number of pieces of flesh	TOTAL OBS.
Independent young	5.1	31.1	6.1	5.6	53
Adults	3.4	15.0	2.3	1.6	44
	z= 2.79	z= 5.23	z= 6.36	z= 7.46	
	p= 0.005	p= 0.001	p= 0.001	p= 0.001	

(c) Hammering small mussels

	number of blows	duration of Levering	duration of Chiseling	number of Chiseling bouts	number of pieces of flesh	TOTAL OBS.
Independent young	5.4	3.5	16.5	2.5	2.5	13
Adults	4.0	2.6	7.5	1.2	1.1	110
	z= 1.89	z= 1.97	z= 3.89	z= 4.1		
	p= 0.058	p= 0.49	p= 0.001	z= 0.001		

and medium mussels) is much less efficient than adults, for the young take much longer to remove all the flesh, there are more bouts of Chiseling and the flesh is removed in many small pieces rather than in one large piece.

8/D The Hammering Technique of Independent Young and Adults

I have only very few observations of independent young Hammering mussels. However, from Table 18c it can be seen that they are as efficient as adults at Hammering and that they take only marginally longer to Lever open the mussel. However, as with the Stabbing young, the Chiseling of the Hammering young is much less efficient than the adults. The young take longer to remove the flesh, there are more bouts of Chiseling, and the flesh is removed in many small pieces rather than in one large piece.

8/E The Stabbing Technique of Juveniles

Juvenile Oystercatchers are those in their second and third years, and they can be readily distinguished from adults by their smaller size, brownish plumage, broad white collar around the neck and wishy-washy colouring of the bill and legs. I was able to observe juveniles Stabbing mussels on the Ravenglass mussel beds.

From Table 19a it can be seen that the juveniles are still using the follow-up-Stab technique rather than the dart-Stab. However, they are as successful with the follow-up-Stabs as with the dart-Stabs (Table 19b), and they are as skillful as the adults at both these techniques.

The juveniles are as quick as adults at Levering open both small and medium sized mussels, but they are still not as efficient at Chiseling. They take longer to remove the flesh (Table 19c and 19d), there are more bouts of Chiseling, and the flesh is removed in a number of small pieces rather than in one large piece.

TABLE 19 THE STABBING TECHNIQUE OF JUVENILE BIRDS

(a) The Techniques used by Juveniles (as % of all mussels taken)

	follow-up-Stab	dart-Stab	TOTALS	
Juveniles	59%	41%	44	$chi^2 = 38.3$ $p = 0.001$
Adults	18%	82%	279	

(b) The Success of the Techniques (as % of attempts)

	follow-up-Stab (% successful)	dart-Stab (% successful)	
Juveniles	77%	72%	$chi^2 = 0.89$ $p = 0.05$
Adults	90%	88%	
	$chi^2 = 1.85$ $p = 0.05$	$chi^2 = 0.85$ $p = 0.05$	

(c) Stabbing Small Mussels

	duration of Levering	duration of Chiseling	Chiseling bouts	number of pieces of flesh	TOTAL OBSERVATION
Juveniles	2.9	8.4	2.1	1.9	36
Adults	3.0	6.2	1.2	1.1	65
	$z = 0.63$ $p = 0.52$	$z = 2.1$ $p = 0.04$	$z = 2.4$ $p = 0.02$	$z = 2.6$ $p = 0.001$	

(d) Stabbing Medium Mussels

	duration of Levering	duration of Chiseling	Chiseling bouts	number of pieces of flesh	TOTAL OBSERVATION
Juveniles	3.8	19.3	4.2	2.8	8
Adults	3.4	15.0	2.3	1.6	44
	$z = 1.3$ $p = 0.20$	$z = 2.18$ $p = 0.04$	$z = 2.63$ $p = 0.008$	$z = 3.4$ $p = 0.0006$	

8/F Discussion

Oystercatchers therefore take at least three years to become fully efficient at eating mussels. The Hammering technique seems to be very easy to acquire, for newly independent young take the same number of blows as adults to Hammer open small mussels (however, it must be remembered that my sample is very small). The two Stabbing techniques take longer to become fully efficient, and it is not until the young are 2/3 years old that they are as efficient as adults. It is the Chiseling process that takes longest to perfect, and this slow increase in skill could be due to the need for long practice, for Chiseling is the most complex part of the mussel-feeding techniques. The efficiency of Chiseling may, however, be affected by the very low frequency of Prising in the feeding behaviour of both independent young and juveniles (Appendix 5). The Prise, in the adult feeding behaviour, functions to open the valves of the mussel wide apart, and the effectiveness of the Prise is demonstrated by the fact that there is no significant difference between the duration of Chiseling in mussels in which (a) there was no Prise, (b) a Prise occurred before the Chiseling, and (c) a Prise occurred during the Chiseling (Part III, p. 121). In my experiments with captive adults I reduced the effectiveness of the Prise by placing a rubber band around the mussel shell, and this greatly reduced the efficiency of Chiseling (the adults took very much longer to Chisel out the flesh). In Appendix 4 I show that the duration of Chiseling in medium sized mussels is significantly reduced when the young Prise (there is no significant difference when the young Chisel in small mussels), i.e. the absence of a Prise decreases the efficiency of Chiseling. The long time taken over learning to Prise may therefore prevent the development of fully efficient Chiseling.

There is another factor which may be of the greatest importance in the development of Chiseling. Young Oystercatchers have very sharply pointed bill tips which by itself may well make Chiseling more difficult, for the effectiveness of Rapid Chisel Pecking depends upon the broad edge of the bill tip cutting free the attachments between the flesh and the shell. The bill tips of Oystercatchers become progressively worn down, and, by the time they are 3/4 years old, the adults have well blunted bill tips. This in itself will greatly increase the efficiency for Chiseling, for the adult will be Chiseling with a broader cutting edge than will the young or the juveniles. It is therefore very possible that Chiseling takes three years to become fully efficient because it takes that long for the bill tips to become blunted.

To test this hypothesis I used two of my hand-raised young which, aged 54 days, had reached a certain known efficiency of Chiseling. I recorded the time taken by each young to Chisel out the flesh from 10 mussels of 35mm in length (with the same experimental procedure as described in Appendix 3), and I then amputated their bill tips so that they had blunted bills instead of sharply pointed ones. Next day, I gave each young another 10 mussels to empty out. One young showed a 15% decrease in the time taken (from 13.1 sec to 9.7 sec, Mann-Whitney U = 18, $p = <0.01 > 0.001$) and the other an 11% decrease (from 14.8 sec to 13.2 sec, Mann-Whitney U = 24, $p = <0.05 > 0.025$). Blunting of the bill tip can therefore cause an immediate increase in the efficiency of Chiseling.

This immediately poses the question of why young Oystercatchers are not 'born' with a blunter bill tip? There are two possible explanations for this. Firstly, it must be remembered that Oystercatchers have retained the basic wader feeding behaviour of probing for buried invertebrate

foods, and a sharply pointed bill tip may make it much easier for young Oystercatchers to probe in sand and earth. Probing for soft-bodied invertebrates is a very important part of the feeding behaviour of both adults and young. Some young birds are born in areas where they never have the opportunity to acquire any of the specialised feeding techniques on mussels, crabs etc. (i.e. those young born in the highlands of Scotland) and they have to maintain themselves by probing for invertebrates. Similarly, when young which have acquired a specialised feeding skill migrate away from the breeding grounds, they may also have to maintain themselves by probing until they can find a suitable winter feeding ground. The young birds at Havenglass had all started to successfully probe for food by the time they were 4 weeks old (i.e. well before they started to successfully catch and open crabs or mussels), and some individuals were successfully probing at 2 weeks old. I have a little data on the development of the efficiency of probing in the young of two families who often hunted for annelid worms on a large mud flat near their nest sites (these were the two families used in the analysis of parental feeding presented in Part I). By the time that the young were 10 weeks old they were still less efficient at probing than their parents (both the young and the parents were using the dart-probe technique), but they had a much higher success rate than when hunting for mussels (Table 20). It is interesting to note in this context that my hand-raised young also probed successfully in the turf of their outside aviary, and they often dug up larvae etc. Probing can therefore develop without the direct influence of the parent, so in this respect Oystercatchers are like other waders.

TABLE 20 THE DEVELOPMENT IN THE EFFICIENCY OF DART-PROBING OF YOUNG OYSTERCATCHERS HUNTING FOR MUD-FLAT ANNELIDS

Age of young (weeks)	% of successful dart-probes	total number of dart-probes observed	number of individuals in sample
4	18%	647	4
6	23%	359	2
8	31%	180	3
10	42%	348	2
Efficiency of the parents	65%	892	4

Secondly, a sharply-pointed bill tip may make it much easier to learn to Stab prey, and any increase in the difficulty of Stabbing due to the slow blunting of the bill tip may well be offset by an increase in the skill of Stabbing.

CHAPTER 9 SOME ECOLOGICAL ASPECTS OF THE PROTRACTED DEVELOPMENT OF FEEDING SKILLS

9/A Delayed Breeding In Oystercatchers

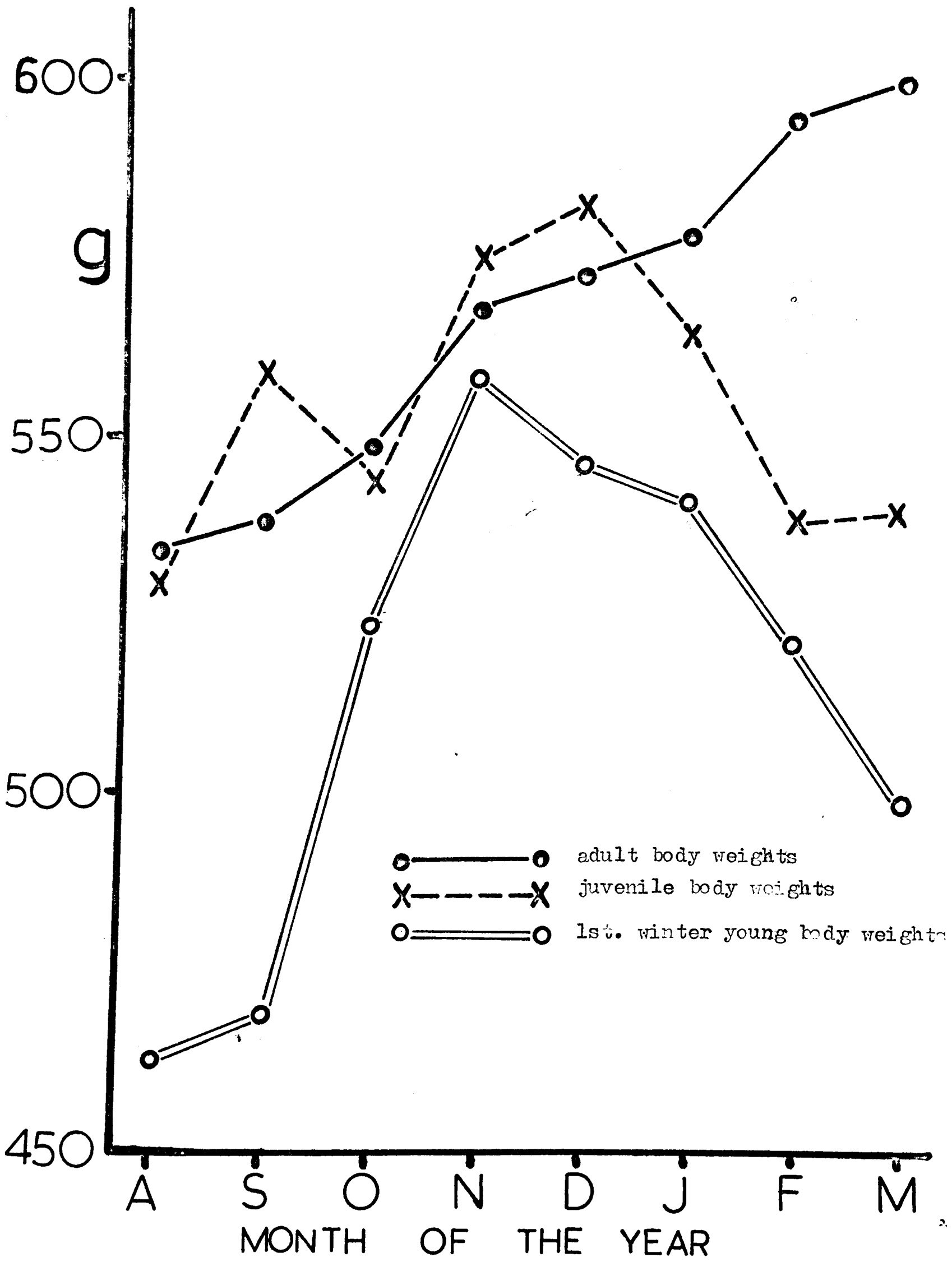
We have seen that it takes an Oystercatcher at least three years to develop the fully efficient mussel feeding skills, and that it is the Chiseling process that takes longest to perfect. I have suggested that this is due to (a) the need for long practice at Chiseling, (b) the slow development of Prising, and particularly (c) the time taken for the bill tip to become blunted. Although strictly speaking my data applies only to the mussel Stabbing technique, it is likely that the other feeding skills also take a very long time to become fully efficient, for Chiseling (and Prising) are common to all of them.

Dr. P. Dare (M.A.F.F., Conway) has kindly allowed me to present his unpublished data on the body weights of Oystercatchers wintering in and around Morecambe bay. The Oystercatchers were shot (or netted) as they left their feeding grounds, and freshly eaten food was removed from the oesophagus before they were weighed.

Fig. 2 shows the average body weights of adults, juveniles and 1st. winter young sampled at various times during the winter months. It can immediately to seen that the body weight of the adults steadily increases over the whole winter period, while those of the juveniles and 1st. winter young shown an initial increase followed by a drastic decrease during the latter part of the winter. The juveniles begin to loose weight from December onwards, while the 1st. winter young start to loose weight from November onwards.

These data have not yet been analysed in any great detail. For example, the samples include both males and females, and the females are on average always heavier that the males. In addition, the samples are made up from individuals who eat different foods (mussels, cockles, or inland or terrestrial

Fig. 2 Body weights (g) of Adult , Juvenile and 1st. Winter Young wintering in the Morecambe Bay Area



number of young in each sample:

adults:	155	34	126	139	205	231	309	257
juveniles:	70	10	34	59	64	53	59	86
1st. winter.	39	25	42	95	99	49	67	51

invertebrates). However, the overall trends in body weight are consistent with the observed differences in feeding efficiency between adults, juveniles and newly independent young, and it seems that the juveniles and 1st. winter young are just not efficient enough even to maintain their body weight during the latter part of the winter. The annual mortality of Oystercatchers is interesting from this respect. In a sample of 115 young Oystercatchers who fledged and split up from their parents, 55% had died by the end of their first winter (i.e. by March 31st). There was a 34% mortality among the survivors over the next two years (i.e. while they were immature juveniles), and the annual mortality dropped further to 21% when these survivors became adult (data from P. Dare). Dare has not yet analysed these data in detail, but the heaviest mortality among both juveniles and adults occurs during the period February - April (there are no details available yet for the 1st. winter young). 19.5% of juveniles die during the period November - January, while 45.5% die during the period February - April (provisional figures from a sample of 77). The adult mortality during these two periods is 26.8% and 33.6% respectively (provisional figures from a sample of 220).

The significance of these data is shown in a study by Mercer (1968) who weighed adult Oystercatchers which were breeding on Angelsey, North Wales. The adults averaged 616 g when they first arrived on the breeding grounds in early April (This compares well with the March weights of the Morecambe Bay adults), but, by the time that the clutch of eggs was completed in early May, the adults averaged only 520 g. This loss of body weight was probably due to territorial behaviour and egg laying. There was a further loss of weight during the first part of incubation (the adults averaged 480 g by mid-term incubation) but this was made up by the time that the eggs hatched (530 g). The adults again lost weight during the first two weeks of chick rearing (when they fell to 490 g), but they had regained

weight (520 g) by the time that the young had fledged.

Oystercatchers do not start to breed until they are 3 years old, and most of them do not even breed until 4 or 5 years old (Harris 1968). I suggest that this delayed breeding is an evolutionary consequence of the long time required by individuals to become fully efficient at these skilled feeding techniques. It must be supposed that the pre-breeding weight of c. 600 g is necessary to withstand the massive weight losses which occur during the breeding season - in spite of the possession of fully efficient feeding skills. We have seen that neither the 1st. winter young nor the juveniles are able to achieve this body weight by the end of the winter (due to their still inefficient feeding skills), and it is therefore highly unlikely that they would be able to maintain both themselves and their young if they attempted to breed.

I have unfortunately been unable to locate any data on the age at which other wading birds, of the same size as Oystercatchers, begin to breed, especially data on those waders which do not possess such skilled feeding techniques. In order to establish a causal connection between the possession of specialised or skilled feeding techniques which take a number of years to perfect and delayed breeding, three separate lines of evidence are required: (1) do species which possess skilled feeding techniques also have delayed breeding? (2) do the young of these species take an equivalent length of time to become fully efficient at these techniques? and, (3) do the sub-adults and adults show similar weight changes during winter and the breeding season? There is of course no way of quantifying the 'skill' of a feeding technique except, perhaps, by reference to how long it takes an individual to acquire it. The Oystercatchers' feeding skills could therefore by quantified as 'three year skills', and this might be a method of comparing the skills of the different feeding techniques of different species.

However, although the relevant data are in most cases totally lacking, some less direct evidence is available. Lack (1968) has some very revealing data on the age at which individuals of many different species and groups of birds start to breed, and in general there is a positive correlation between delayed breeding and the possession of skilled feeding techniques. For example, among the Anatidae, the surface feeding species tend to breed when two years old while the diving species tend to breed when three or four years old. Among the Procellariformes and the Pelecaniformes, the species that feed inshore start breeding earlier than those that feed offshore. A particular example from the Larinae is afforded by a comparison between the Black-Headed gull (Larus ridibundus) and the Kittiwake (Rissa tridactyla). The scavenging and inshore-feeding Black-Headed gull first breeds when two years old, while the offshore, plunge-diving Kittiwake does not begin breeding until three or four years old.

It would be interesting to know how long it takes individuals of these different species to become fully efficient but there is unfortunately no published data, and there is precious little data of the feeding efficiency of the young of other specialised feeders. Ashmole (1968) has observed that the young of Fregata aquilla are less efficient than adults at hunting the young chicks of Sterna fuscata. Adult terns of many different species have been observed to feed young-of-the-year on migration and at the winter feeding grounds (Ashmole, 1968, in the Royal Tern Thalasseus maximus: Monroe, 1956, in the Elegant Tern T. elegans: Pyle and Small, 1951, in the Sandwich Tern T. sandvicensis: and Palmer, 1941, in the Common Tern Sterna hirundo). These observations suggest that the young of these species take quite some time to learn how to feed themselves, but here again there is no direct data on the feeding efficiency of the young-of-the-year, or of sub-adults.

I am not suggesting that every example of delayed breeding in species that possess skilled feeding techniques is due to the time taken by the young to become fully efficient, for the age at which any species begins to breed is affected by a host of other variables (for example, body size, availability of best sites and mates etc., see Lack 1968). However, species that possess skilled feeding techniques share many breeding characteristics, i.e. a small clutch size, a long period of parental care (Ashmole 1968) and delayed breeding. We have seen that in the Oystercatcher the period of parental care is determined by how long the young take to become self sufficient (Part I, Chapter III), and there is good evidence that the age at which Oystercatchers start to breed is determined by how long the juveniles take to become fully efficient feeders. These factors may also be of great importance in other species which have skilled feeding techniques.

9/B Maintaining Specialisations over a number of Years

Both adults and young maintain their specialisations on both prey and technique over a number of years (Part III, Table 22; Part IV, Table 1). The long time taken to become fully efficient at a technique may play an important part in this:

(a) by the time that an individual has become fully efficient in a technique it may have such a strong fixation with regard to both the areas in which to hunt and to a particular set of 'prey stimuli', that it will neither hunt in different areas nor attend to the relevant stimuli from other prey.

(b) any individual who attempts to acquire a new technique will initially have very little success, and will expend much energy for meagre returns. This would probably make the individual revert either to its original technique or to probing for soft bodied invertebrates.

These two points will be discussed further in the general discussion in Chapter 10. I can also mention, in passing, that

this protracted development of the techniques may underly the loyalty of Oystercatchers to both breeding grounds and winter feeding grounds. It may initially be very advantageous for juveniles to return to areas which they know contain the appropriate prey, and this habit may then be maintained even once they have become fully efficient.

9/C The Acquisition of Additional Skills

Some adults possess more than one specialisation (Part III, Table 22). In addition, many young are brought up in areas where no specialisations can be acquired (i.e. in the Faröe Islands and in the Highlands of Scotland), and yet these young have been observed feeding on mussel beds and cockle beds in their winter quarters (Dare, pers.comm.). There is in fact no reason why both adults, and young such as these, can not acquire additional or new techniques through essentially the same process as the young who acquire a technique from their parents. There are three major steps in the development of the feeding skills: (a) the initial conditioning to the prey as a potential source of food, (b) practice with the prey, through which the orientation and sequence of Lever, Prise and Chisel is developed, and (c) the acquisition of the hunting techniques.

I have frequently observed independent young, juveniles and even adults to clean out scraps of flesh from prey remains (in these cases cockles and mussels). In this way an 'nninitiated' bird could at any time become conditioned to a new prey as a potential food source. Safreil (1968) has observed a 1st. winter young (who was brought up on the Island of Skokholm) feeding in a muddy estuary on the nearby mainland. This young was following behind some adults who were feeding on Scrobicularia, and it was removing scraps of flesh from the discarded shells. The young could not have had experience with Scrobicularia on Skokholm Island (they do not grow there) and it was not attempting to catch Scrobicularia for itself.

Furthermore, Oystercatchers of all ages constantly steal food from one another (I have once observed a mussel to change 'hands' 4 times before it was finally devoured), andsuch behaviour too would afford the opportunity for an uninitiated bird to acquire the orientation and sequence of motor patterns appropriate to the prey. Finally, if, as I have suggested, the young acquire the hunting techniques through parental example, then there seems little reason why an uninitiated bird should not acquire the hunting techniques from the other members of the flock who are feeding all around it. In this way an uninitiated bird could acquire a new feeding technique on a new prey.

This is admitedly very hypothetical, and it should be tested experimentally. I have very little data on know individuals who have acquired new techniques, but this has happened with two colour ringed young. One of these was the crab-young who stayed with its parents on the breeding grounds all through one winter and into the next breeding season Part I, p its parents were Pair 29/30, Table 22, Part III). The young had learnt to eat crabs by the end of the summer, but, by the following spring, it was eating Littorina. The parents were also eating Littorina (for there were no crabs during the winter months), and they were also feeding Littorina to the young. The young might therefore have acquired this second technique from its parents at a relatively late stage. The second young was a mussel-Stabber who had also acquired the Littorina technique by its second year, but this bird had acquired the new technique after it had split up from its parents. Many individuals in the flock were also feeding on Littorina, so this young may have acquired the technique from them. However, Littorina moves about in a very obvious fashion in pools of water, and this may have initially attracted the attention of the young bird.

In conclusion: although there are some very strong ecological pressures against acquiring a new feeding technique, the ability to switch is present, and may on occasions be invaluable. What little evidence there is suggests that the required flexibility is retained (latently) throughout an Oystercatcher's life.

CHAPTER 10 A GENERAL DISCUSSION OF THE DEVELOPMENT OF THE FEEDING SKILLS

Introduction

The general aims of this part of my study has been to understand the basis of the remarkable flexibility of the development system. In doing this I have found it rewarding to approach the problem from both the causal and the functional viewpoint. The results have strengthened my belief that a full understanding of any behaviour requires an understanding of the function of both the overt behaviour and the details of the behavioural "machinery", and in addition that this dual approach is fertile with respect to the development of the behaviour as well.

I shall deal first with the initial, wide potential for development found in each young Oystercatcher, and its subsequent narrowing-down, or channeling into one out of the initial multiple possibilities. I shall next discuss the various learning processes by which the channeling is achieved, and then with the functional aspects of this channeling, which happens in such a way that the resulting feeding behaviour fits the requirements of the adults environment. Finally, I shall discuss briefly the coadaptations between the development system, the parental feeding system and the skilled feeding techniques of the adults, and the ecological consequences of these coadaptations.

10/A <u>The Observed Changes in Behaviour During Development</u>

There are three main stages in the development of the feeding skills:-

1) the progressive <u>narrowing down</u> of the objects at which the young direct their IFA. The young initially respond to 'anything and everything' lying in their immediate environment, but they progressively respond more and more

to prey remains until eventually they respond only to the 'prey stimuli' that elicit hunting behaviour.

2a) the acquisition of the functions of the adult motor patterns, particularly of the functional orientation of Lever, Prise and Chisel.

2b) the acquisition of the efficient sequence of the motor patterns.

3) the development of hunting behaviour.

These stages are not rigidly separated in time, and there is much overlap between them. Yet, since slightly different learning processes occur at each stage, and since in some cases the development of the later stages depend on what has been learned during the earlier stages, the distinction between these stages is a valid one.

10/B Causal Analysis

10/B/I The Progressive restriction of the responsiveness of the young to prey remains.

The initial stage occurs when small young (of 2-3 weeks of age) Chisel in prey remains and remove scraps of flesh; subsequently there is a progressive narrowing down of the range of objects responded to, and the young respond more and more to the prey remains. My experiments with the hand-raised young (Appendix 3) showed that this channeling is not the consequence of the finding of food by itself, nor of Chiseling without a food reward, nor even of the performance of any other motor patterm than Chiseling - with or without a food reward. The channeling only occurred through the elicitation and performance of RCP followed by food reinforcement as a result of the RCP movements.

This channeling is a simple example of Type II instrumental conditioning, but the interesting point is that the

conditioning is <u>totally dependent</u> on the performance of only one out of many possible responses linked to food reinforcement as a consequence of that response. The progressive channeling of the total responsiveness of the IFA to the prey remains is probably reinforced by all the later stages in the development of the feeding skills.

10/B/II The Acquisition of the Functions and Sequence of the Motor Patterns

Three separate steps are involved here: learning to respond to the appropriate stimuli, learning the precise orientation of the motor patterns, and learning the sequence in which to perform the motor patterns.

Trial-and-error (i.e. true practice) can account for most of the observed changes, and certainly the randomness of the initial Chiseling behaviour and of the initial orientation and sequences of Levering and Prising are good 'starting points' for such learning processes to occur.

To me the most interesting aspects are the possible reinforcements involved inthe learning. I have suggested (Appendix 4) that the development of Chiseling is based on the ability of the young to differentiate between the time spent working from one of a number of orientations and the food reinforcement. The relevant time measure could be either the time and/or effort spent working at a particular attachment or the time and/or effort spent working in the whole mussel. Of course, both of these may be important, the first for learning the best orientation for the attack at each particular attachment, the second for learning the best sequence in which to attack the attachments. The learning of both the orientation and the sequence of Lever and Prise are almost certainly based on similar reward differentials. For example, the young may be able to differentiate between Levering and Prising in one of many possible orienta ions and the speed with which

the flesh is Chiseled out or between the speed with which the Chiseling stimuli are attained (Chapter 6). Incidentally, this may be an example of the dependence of the later stages of development on the earlier stages. For example, if the reinforcement for Levering and Prising in the correct orientation (i.e. across the valve margins) is dependent upon the young differentiating between how long it takes to Chisel after Levering in one orientation rather than in another, then the ability to make this differentiation may depend upon the existing efficiency of Chiseling. At a stage when the young are very inefficient at Chiseling, Levering in the correct orientation may take so little difference to the total time taken over Chiseling that there is little reinforcement for it. However, as soon as the young becomes more efficient than Levering in the correct or incorrect orientation will have a relatively greater effect on the Chiseling performance, and the reinforcement for the correct orientation will become stronger.

I have also suggested that there may be other reinforcements apart from food. For example, in the development of Chiseling (Appendix 4) cutting through an attachment may have reinforcing properties, and the young may learn the best orientation of an attack by differentiating between the time taken to Chisel through an attachment from a number of different orientations. The performance of the RCP movements may in itself be reinforcing, and certainly the initial switch from RGP at the 'soft parts' of the mussel to RCP at the 'hard parts' (which occurs without any increase in Chiseling efficiency) must in part be due to these kinds of reinforcement. In the case of Levering and Prising I suggested that perhaps the orientation against a firm resistance (i.e. the valve margins) rather than loose resistance (i.e. in the flesh of the mussel) may in

itself be reinforcing. Reinforcements of this nature have been shown in other developmental studies. Wells (1962) demonstrated in Sepia a decrease in the latency of the response to prey which was dependent only upon the previous performance of the response, and Henty (1965) has suggested that the ability of young thrushes (Turdus ericetorum) to respond selectively to hard anvils when learning to smash snails depends on the immediate feedback from hitting hard rather than soft anvils, and not on the successful performance of smashing. In addition, studies on the development of bird song (Thorpe 1961, Konishi 1965) have shown the existence of perceptual "templates" (both innate and learned) that guide the development of vocalisations into certain patterns. The importance of these kinds of reinforcement is that they will bias and speed up what is learned. Finally, 'somatic' growth may be very important, for the effectiveness of the various motor patterns will increase merely as a result of increased strength and length of the bill and irrespective of their orientation or sequence. This would lead to an increase in efficiency without any learning.

10/B/III The Development of the Hunting Behaviour

I have suggested that the observed differences between the pre-hunting behaviour of the young of different specialist pairs is due to parental example, for the young constantly see their parents hunt and open prey in one particular fashion. This raises the problem of whether this is ducase of imitation. Thorpe (1964) defines imitation as 'the copying of a novel or otherwise improbable act or utterance, or some act for which there is clearly no instinctive tendency'. On this definition the young are clearly not imitating their parents, because the motor patterns envolved in hunting are already present in their IFA and they develop without patent parental example. What is being biased by the parent is the

responsiveness of the young to various 'prey stimuli', and the parents must be directing the attention of the young to particular prey stimuli. Of course, the difference between this example of 'social facilitation' or 'local enhancement' and true imitation is one of degree only, for what can or can not be imitated is going to be biased by the capabilities of the organism. The difference may be merely in the number of potential 'channels', and the Oystercatcher may be showing a very simple form of imitation: the choice of one out of a very limited number of possible channels.

10/C The Functional Aspects of the Developmental System.

The entire developmental system shows specific adaptations to retain flexibility so that potentially a number of different skills can be developed and yet, once the system has been channeled, the particular skill selected will be developed in as efficient a manner as possible. The IFA are made up of a repertoire of motor patterns which are similar to the motor patterns of the adults. All Oystercatchers young possess this full repertoire irrespective of the specialisations of their parents, and irrespective (within the range observed) of the environment in which they are growing up. In addition, the motor patterns are elicited by stimuli which are very similar to those that elicit the same motor patterns in the adults. This, so to speak, is the basic 'equipment' of the young Oystercatcher.

The initial conditioning to the prey remains is totally dependent upon the performance of RCP followed by food reward as a result of the RCP. This has two functional aspects: firstly, the young will become conditioned only to prey remains and not to any other objects at which it directs its IFA, and secondly, the young will become conditioned to whatever prey the parents are feeding to it.

In Appendix 4 I describe the initial development of Chiseling, and I point out that the first task facing a young Oystercatcher is to learn the precise location of the 'hard parts' of the prey. This learning occurs through the initial switch from RGP at the soft parts to RCP at the hard parts, and this switch too is dependent upon the RCP+food reward link described above. Here again we see the flexibility in the developmental system, for the young will learn in this way the precise location of the hard parts in whatever prey it is Chiseling.

The precise orientation and sequence of the motor patterns are learned during a long period of trial-and-error or practice with the prey. Here again, the same learning processes based on the same reinforcements (as mentioned above) will lead to the development of the orientation and sequence demanded by the anatomy of any particular prey.

Finally, in the development of the hunting behaviour, we see that the flexibility is retained up to the last moment.

I believe that these learning processes are definite adaptations ensuring that a whole range of feeding skills can be developed. Each skill develops through the same learning processes at each stage, yet totally different adaptive feeding skills can result. It is this adaptation for flexibility that distinguishes the developmental system of the Oystercatcher from that of other birds who also employ skilled feeding techniques. For example, studies on the development of snail smashing in the Thrush (Henty 1965) and on the development of spearing prey by various species of Shrike (Lanius sp., Lorenz and St. Paul, 1968) have shown that practice as such is of relatively little importance. However, in each case some parts of the skills have to be learned through practice (the selection of hard anvils by the Thrush, and the pressure necessary to impale the prey by the Shrike). In many respects the development of these

/development of

feeding skills in Oystercatchers is similar to the speech from the rudimentary babbling of young children (Carrol 1961).

Both Henty (1965 and references cited) and Dawkins (1968) have considered the analogy between developmental systems and learning machines with preset programmed instructions. The advantage of this analogy is that the adaptations shown by the developmental system both to environmental variables and to the nature of the behaviour being developed can be expressed in terms of the 'programming strategy'. Thus Dawkins points out that the programming strategy for the development of pecking preferences by domestic chicks shows some precise instructions (i.e. how to use the data from surface shading cues to estimate depth) as well as some less specific instructions which can be altered by data fed in from the environment (i.e. the establishment of pecking preferences are conditional upon reinforcement). The precise instructions are adapted to a very 'predictable' aspect of the environment (i.e. the light always comes from above) while the less specific instructions are adapted to the 'unpredictable' range of edible and inedible objects that the chick will find in its immediate environment. Henty (1965) considers that the instructions for the development of snail smashing are precise, and he makes the interesting point that the quantitative nature of the instructions must in this case change with age irrespective of the performance of smashing behaviour.

The programming strategy of the Oystercatcher also shows both precise and less specific instructions. For example, the RCP+food link that causes the initial conditioning to prey-remains is a very precise instruction, while the trial-

and-error instructions are much less specific. Here again we see that the precise instructions are adapted to a very predictable part of the environment (i.e. to the fact that all prey remains will have scraps of flesh in them) while the less specific ones are adapted to dealing with many different types of prey. The interesting point is that on the one hand none of the instructions are adapted specifically to any particular prey, but that on the other hand they are such that learning 'fits' several distinct types of prey. Two clear examples of this are shown by the results of the cross-fostering experiment in which young Oystercatchers successfully learnt the techniques of dealing with prey that they would normally never pay any attention to, and by the data presented in Appendix 2 which show that the young of crab-eating parents become as quickly and as firmly conditioned to mussel shells (given the correct reinforcement) as do the young of mussel-eating parents. I have already shown (Part III) how the basic organisation of the feeding behaviour of the adult Oystercatcher is adapted to dealing with an unpredictable environment (i.e. to a wide range of potential prey), and we can now see that the programming strategy of the developmental system is just as well adapted to the wide range of prey species as is the 'finished' feeding machinery of the adults. In other words, the flexibility of the developmental system has evolved as a coadaptation to the flexible adult feeding behaviour.

We can now see the full scale of the intricate co-adaptations between the developmental system, the parental feeding system and the flexible - yet specialised - adult feeding system. The parents are instrumental in the initial chaneling of the developmental system of the young, for, since both members of a pair share the same specialisations, the young will only have the opportunity to practice on one particular type of prey. Indeed, there are specific changes in the organisation of parental feeding as the young grow

older which result in the parent leaving the partially opened prey which the young require for practice.

One striking aspect of the development of these techniques is the long period of time necessary to become fully efficient. The ecological consequences of this protracted development have already been discussed (Chapter 9) but I want to mention again that this may underly the stability of the specialisations shown by the adults. Individuals may have to become totally fixated on one particular prey and one particular technique and will therefore not respond to the relevant stimuli from other prey. The loyalty of Oystercatchers to breeding grounds and to winter feeding grounds amay also be a result of this protracted development. This may be relevant to the problem of how individuals who share the same skills manage to mate with each other, for there will be some slight ecological separation between the different kinds of specialists.

APPENDIX 1 THE MOTIVATION OF THE YOUNG DURING IFA

A. Introduction

The general behaviour of theyoung can be grouped into the 5 basic activities of sleeping, Preening, Feeding from the parent, IFA and Intense begging. The young alternate between these activities during the course of the day, and it was very noticeable to me as an observer that these activities occurred in definite cycles. For example, a period of time when the young spend most of the time asleep would be followed by a period when the young spent most of the time at IFA. Feeding from the parent seemed to have little effect on which activity occurred - except for the few occasions when the parent brought such a large peice of food that the young was stupified after eating it and immediately went to sleep. However, Intense Begging was only seen after long periods of time when the parent had not been bringing food, and bouts of Intense Begging seemed to continue until the parent had fed the young a number of times in succession.

I became interested in these cycles of activities during my observations on the parental feeding, and I was particularly interested in what effect - if any - feeding from the parent (i.e. hunger level) had on the occurence of these various activities. In other words, I have attempted to analyse the cycles and occurence of these behaviours in terms of the level of food deprivation of the young.

My basic data came from three young from different fenced-in nests, and on various days I made continuous (minute by minute) records of which activity was occuring. I obtained 22 records from these young at various ages from 1-21 days of age, and the records varied from 4 - 12 hours in length.

B. Description of the Activities

Sleeping (Sl): I have classified as 'sleeping' all those occasions when the young were asleep or were doing nothing,

i.e. just sitting still. Although small young (less than 1 week) usually sleep under th parent, sleeping is by no means dependent on the presence of the parent, for even at this stage the young will sleep on its own initiative when the parent is away. Older young of course are not brooded so frequently, and they sleep almost totally independently from the parent.

Preening (Pr): all preening and comfort behaviour has been classified as Preening.

Feeding from the Parent (Fd): this consists of all feeding interactions with the parents, i.e. excited running about in response to the approach weep, approach and ingestion of food, following the parent, begging to the parent, begging after the parent has flown out of the arena after feeding the young. Begging was only classified as 'feeding activities' if performed in the presence of a parent, or if performed during the first minute after the parent has flown from the arena (begging usually stops within one minute of the parent leaving.) Begging which occurs for more than one minute after the parent has flown is classified as 'Intense Begging'.

Intense Begging (IB): the young runs around the arena giving the begging call and the distress call. This is only counted as Intense Begging if it occurs in the absence of the parents. Although this activity is probably an artefact of the starvation conditions of the fenced-in young, it could nevertheless be readily distinguished from more normal begging.

Independent Feeding Activities (IFA): these have already been described in some detail in Chapter 3. It can be seen that some of these activities should in fact be further subdivided, but this broad classification must be used, due to basic inadequacies in the original records.

C. The Frequency of the Activities

The proportion of time spent at each acticity changes as the young grow older (Table 22). All the young show the

TABLE 22 THE PROPORTION OF TIME SPENT SLEEPING, PREENING, FEEDING, IFA AND INTENSE BEGGING (as % of total time)

(records from one young from three different fenced-in nests, all young less than 21 days old).

SLEEPING

Time rank:	1	2	3	4	5	6	7	8	Spearman Rank Correlation
nest a	88	68	44	49	24	38			- 0.89 p= 0.05
nest b	87	75	62	56	37	45	53	59	- 0.77 p= 0.01
nest c	87	68	63	42	49	33	49	53	- 0.74 p= 0.05
							overall trend		- 0.79 p= 0.01

PREENING

Time rank:	1	2	3	4	5	6	7	8		
nest a	1	1	1	5	4	3			+ 0.70	ns
nest b	1	1	4	5	4	3	4	2	+ 0.21	ns
nest c	2	1	2	2	6	3	1	2	+ 0.34	ns
						overall trend			+ 0.42	p= 0.05

FEEDING

Time rank:	1	2	3	4	5	6	7	8		
nest a	9	27	50	31	25	24			+ 0.03	ns
nest b	3	14	19	15	15	12	8	6	- 0.29	ns
nest c	6	21	25	13	14	17	12	6	- 0.44	ns
						overall trend			- 0.29	ns

IFA

Time rank:	1	2	3	4	5	6	7	8		
nest a	2	4	5	15	31	23			+ 0.94	p= 0.01
nest b	9	10	15	24	27	29	35	33	+ 0.82	p= 0.01
nest c	5	10	10	27	17	33	38	37	+ 0.91	p= 0.01
						overall trend			+ 0.88	p= 0.01

Intense Begging

Time rank:	1	2	3	4	5	6	7	8		
nest a	-	-	-	-	16	12			+ 0.78	ns
nest b	-	-	-	-	17	11			+ 0.51	ns
nest c	-	-	-	14	16	14	14	2	+ 0.56	ns
						overall trend			+ 0.60	p= 0.01

same basic change in that they become more and more active. There is a reduction in the time spent sleeping and a corresponding increase in the time spent at IFA. Preening and Intense Begging also increase, but they are always at a low frequency. The proportion of time spent feeding from the parent shows no significant trend.

D. The Sequential Organisation of the Activities

The first step in [redacted] was to analyse the sequential organisation of the activities by calculating the first and second order transition probabilities between the activities. In this analysis I have scored bouts of a single activity as a single occurrence of that activity. For example, the observation...32 min of IFA followed by 60 min Sleep followed by 4 min Feeding from the parent... was scored as IFA→Sl→Fd,' There is, therefore, no time base to these calculations.

The results of these calculations appear in Tables 23 and 24. In each case I have also calculated the transition probabilities expected if the association between the activities was due only to their overall frequency (i.e. if there was random association between them). In Table 24 I show only those 'triplets' that occurred more less frequently than random expectation.

1st order transition probabilities (Table 23)

Sleeping is often followed by Feeding, but it is not associated with IFA. Preening is of interest because it precedes both Sl and IFA, i.e. it occurs in the transition from an active state to a passive state and vice versa. IFA tends to occur after Fd, and Sl follows IFA. Intense Begging (IB) is not associated with Sl or Pr, but is more often associated with Fd and IFA.

Table 23 reveals little about the organisation of the behaviour except that there seem to be two separate groupings of activities; (a) Sleep, Preen, Feeding, IFA and (b) Intense

TABLE 23 FIRST ORDER TRANSITION PROBABILITIES BETWEEN ALL ACTIVITIES - Sl = Sleeping ; Pr = Preening; IFA = Independent Feeding Activities ; IB = Intense Begging - BASED ON 22 RECORDS FROM THREE DIFFERENT YOUNG

	Sl	Pr	Fd	IFA	IB	
Sl	x	0.17 (0.14)	0.58 + (0.42)	0.20 - (0.38)	0.05	436
Pr	0.56 + (0.31)	x	0.01 - (0.34)	0.42 + (0.30)	0.01 - (0.05)	159
Fd	0.35 (0.40)	0.04 (0.15)	x	0.54 + (0.39)	0.07 (0.06)	474
IFA	0.43 + (0.38)	0.15 (0.14)	0.38 (0.41)	x	0.04 (0.07)	421
IB	0.02 - (0.29)	0.02 - (0.12)	0.79 + (0.33)	0.17 (0.26)	x	72

figures in ( ) are the transition probabilities expected if there was random association between the activities : + and - indicate that the observed transition probability occurred more (+) or less (-) frequently than random expectation, p never > 0.05.

Begging, Feeding and IFA.

Second Order Transition Probabilities (Table 24)

A diagramatical representation of those second order transition probabilities which occurred more frequently than expected is shown in Fig.3.

Firstly, observe the activities Sl, IFA and IB (see Fig.3). If these are interrupted by Fd (i.e. the parent flies in with food), then, after the Fd, the young continues in those same activities and does not switch to a different activity. This means that feeding from the parent has little immediate effect on the activity of the young. Secondly, observe the strong association between Sl:IFA:Sl and IB:IFA:IB. The young will oscillate between Sleep and IFA, and between Ib and IFA, but not directly between Sl and IFA. Thirdly, note that Pr occurs in the transition from Sl to IFA and vice versa. Finally, note that Fd is strongly associated with Pr:Sl, i.e. Fd can lead immediately to Sl.

The basic organisation of the activities is now much more evident. The young can oscillate between Sl and IFA, and between IB and IFA, but not directly between Sl and IB. However, the transition from IB to Sl can occur through the IFA:Pe:Sl link. Fd has no immediate effect on switching the ongoing activity, but the association between Fd:Pr:Sl suggests that it may have a longer term effect.

E. A Working Hypothesis on the Effect of Food Deprivation on the Activities

From the results of the calculation of second order transition probabilities I constructed a working hypothesis as to the effect of food deprivation on the occurrence of the various activities. A representation of this hypothesis is shown in Fig. 4 A.

The hypothesis is that the three main activities of Sleep, IFA and Intense Begging occur at different thresholds of food deprivation: Sleep occurs at a very low level of deprivation (i.e. the young sleep when sated), while Intense

TABLE 24 SECOND ORDER TRANSITION PROBABILITIES BETWEEN ALL ACTIVITIES

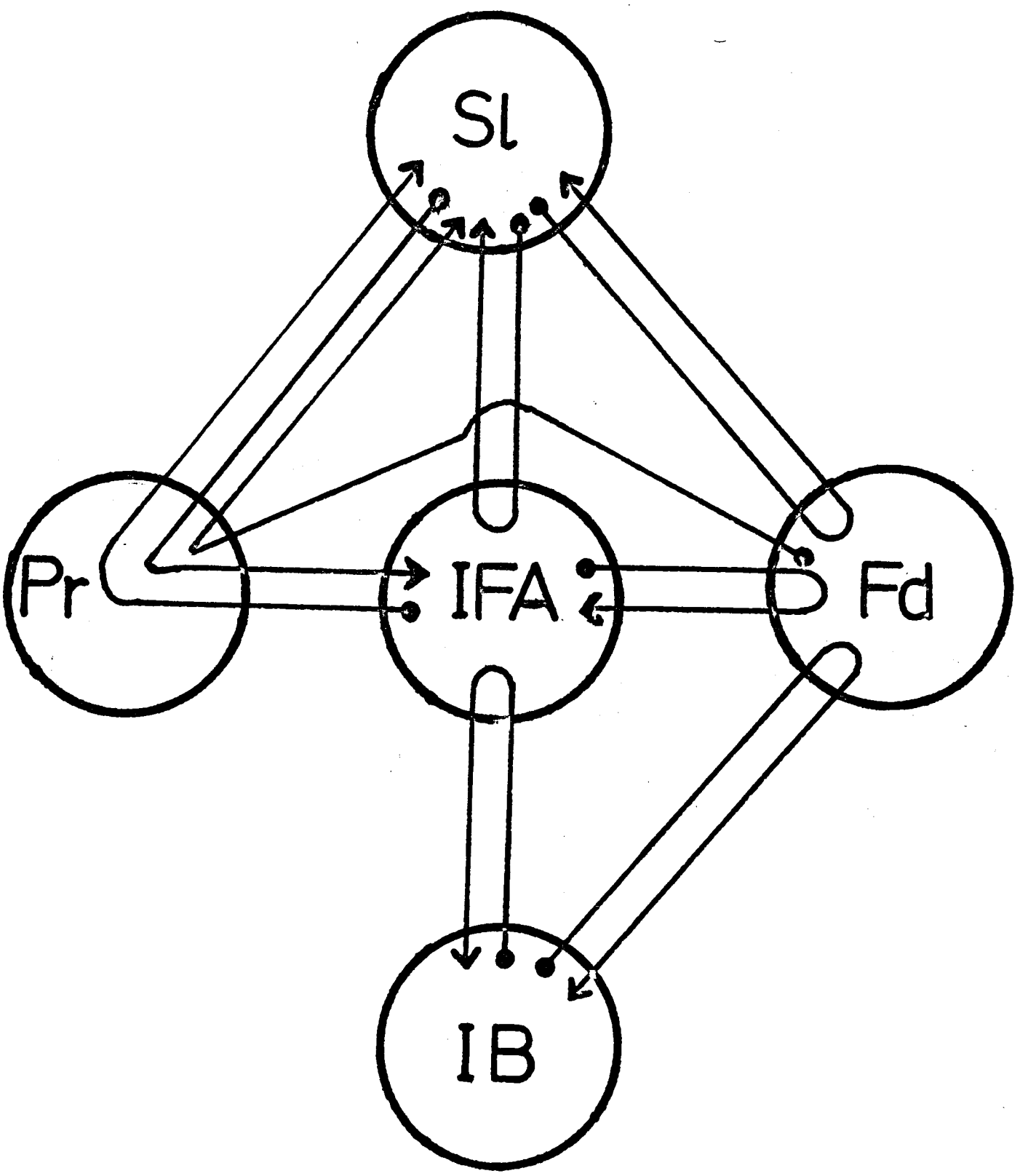
The table shows all possible triplets: + or - indicates that the triplet occurred more (+) or less (-) frequently than expected if there was random association between the activities, p never > 0.05.

Sl	Pr	Fd	IFA	IB	
x					Sl:Pr
x					Sl:Fd
x					Sl:IFA
x					Sl:IB
-	x	+	+		Pr:Sl
	x				Pr:Fd
+	x		-		Pr:IFA
	x				Pr:IB
+	x	-		-	Fd:Sl
	x				Fd:Pr
-	x	+			Fd:IFA
-	x			+	Fd:IB
+	-	x			IFA:Sl
		x			IFA:Pr
-		x			IFA:Fd
		x		+	IFA:IB
				x	IB:Sl
				x	IB:Pr
				x	IB:Fd
				x	IB:IFA

Fig. 3 Diagramatical representation of the second order transition probabilities that occurred more frequently than random expectation .

Sl = sleep : Pr = Preen : IFA = Independent Feeding Activities : Fd = Feeding from the Parent : IB = Intense Begging :

the sequence of each triplet is shown by ●——→



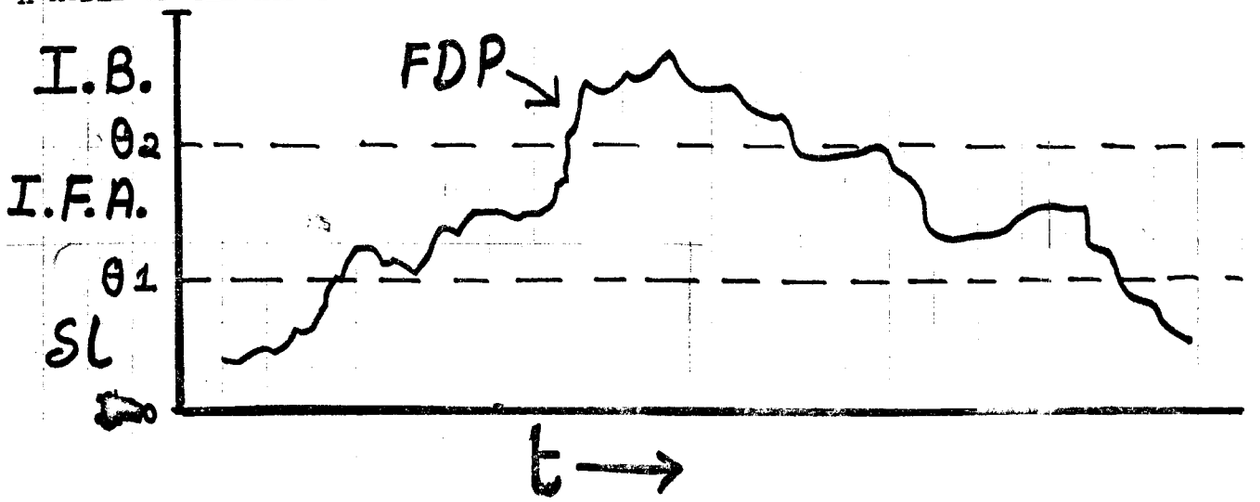
Begging occurs at high levels of food deprivation (i.e. when the young are very hungry). IFA occurs at a level mid-way between the two: the various thresholds at which these activities occur are shown in Fig. 4A (Theta 1 and Theta 2), and, as the level of food deprivation (FDP) changes, so the occurrence of the different activities become more or less probable. Thus, as the level of FDP rises the occurrence of Sleep becomes less probable while that of IFA becomes more probable, and as FDP approaches and passes Theta 2, IFA becomes less probable while IB becomes more probable. The FDP curve in Fig. 4 is shown as changing relatively slowly, for Table 24 shows that feeding has no immediate effect on the ongoing activities. This suggests that any effect of feeding is delayed by other processes, probably digestion and absorption.

The initial testing of this hypothesis has been carried out by making predictions about the temporal correlations between the various activities and then examining my data to see if these predictions are upheld. I have therefore analysed my records in a different way: each record was divided up into successive 10 minute time chunks, and the amount of each activity recorded in each time chuck was measured.

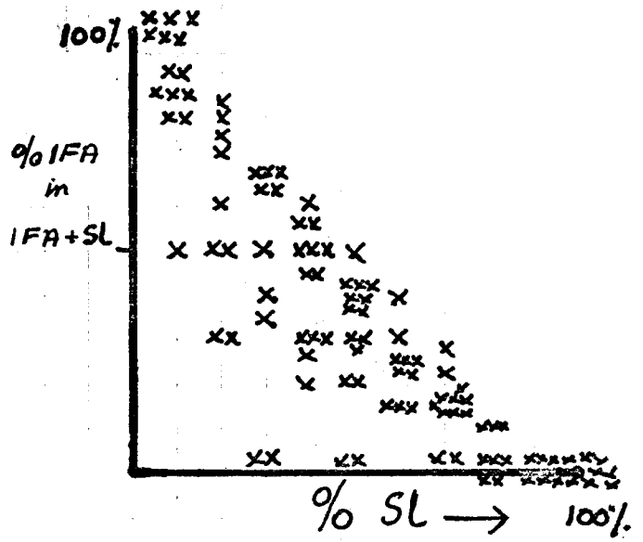
Prediction 1: When no IB occurs, the level of FDP is below Theta 2. There should therefore be a strong negative correlation between the occurrence of Sleep and IFA; Fig. 4b shows how the % of IFA in IFA+ Sleep alters as the % of Sleep changes (all these measurements are based on the amount of each activity that occurs in all the 10 minute time chunks of the 22 records). There is a very strong negative correlation (N.B. those 10 minute periods when neither Sl nor IFA occurred have not been included in this correlation).

Prediction 2: This is not an independent check on the hypothesis, for the prediction is that in periods when no Sleep occurs (i.e. the level of FDP is somewhere about Theta 1),

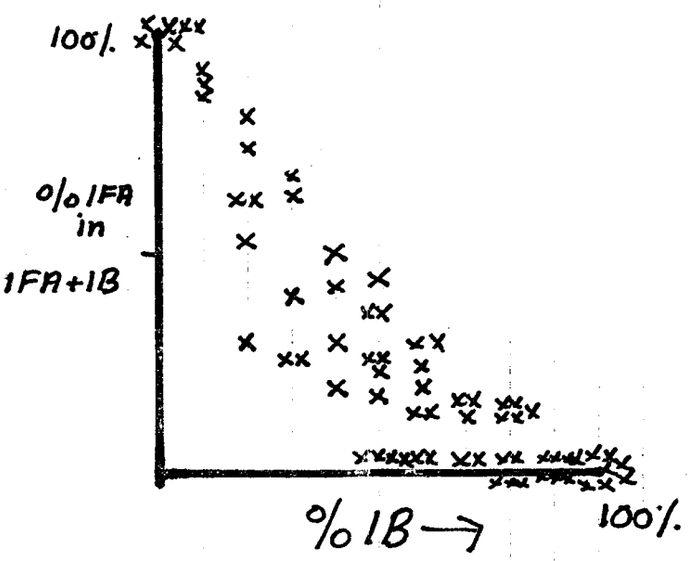
A] A MODEL OF THE HYPOTHESIS



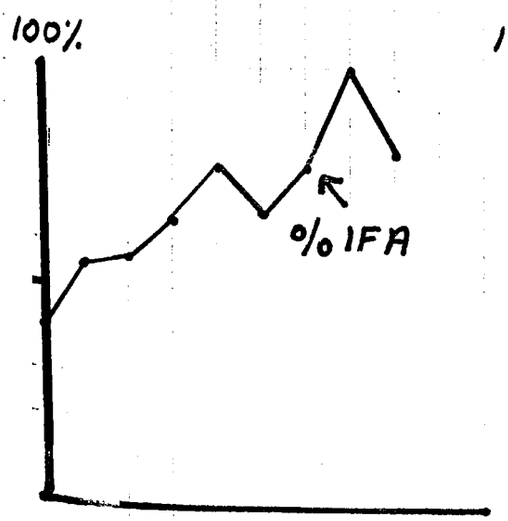
B] % OF IFA in IFA + Sl when no IB



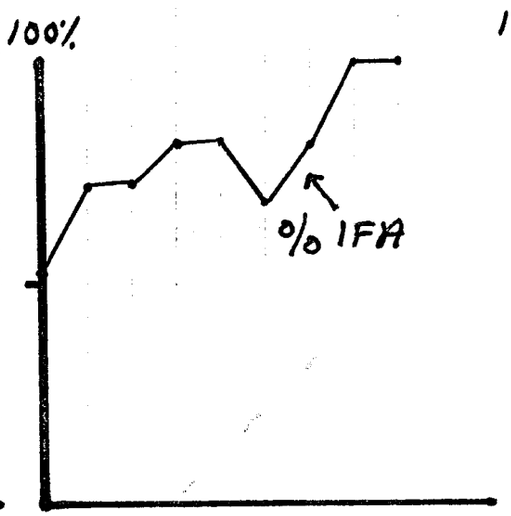
C] % of IFA in IFA + LB when no Sl



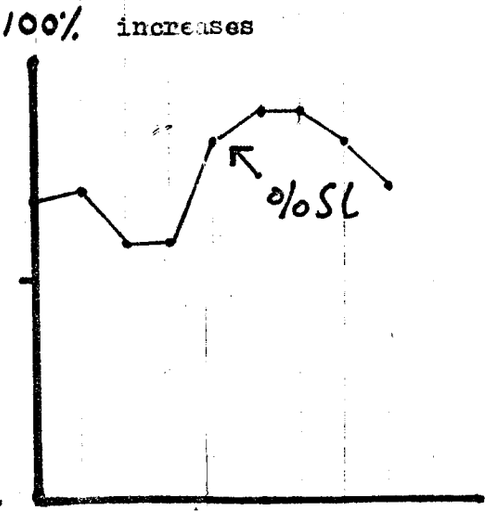
D. % of IFA in IFA + Sl as % IB increases



E. % of IFA in IFA + IB as % Sl increases



F. % of Sl in Sl + IB as % IFA increases



there sho ld be a negative correlation between IFA and IB. Fig. 4c shows that this is so (here again, time periods when neither IFA nor IB occurred have not been included).

Prediction 3: As the level of FDP rises so the proportion of IFA in the behaviour not taken up by IB should rise, for the occurrence of IFA becomes more probable as Theta 2 is approached. Fig. 4d shows that the % of IFA in IFA+Sl increases as the % of IB increases (i.e. as FDP rises) until, of course, IB alone is occurring.

Prediction 4: This is not independent from Prediction 3. As the level of FDP falls (i..e as Sleep becomes more probable), so the % of IFA occurring in the time not taken up by Sleeping should increase. Fig. 4 f shows that this is so.

Prediction 5: As the proportion of IFA increases, the % of Sleep and IB that occur in the time not taken up by IFA should not show any marked changes. This is because IFA can occur at a low level when either FDP is high or when FDP is low. Fig. 4f shows that this is so. The % of Sleep in Sleep+IB shows no marked change as the % of IFA increases. The relatively high level of Sleep suggests that either the distances between Theta 1 and Theta 2 are unequal, or that FDP tends to both rise and fall steeply as it approaches and crosses Theta 2.

Time has prevented me from proceeding further with this analysis. However, the hypothesis has held up well at this simple level of analysis, so it seems worthwhile to pursue it. The failing of this hypothesis and analysis is that it can give no indication as to the speed with which FDP changes, or of the immediacy of a change in FDP and a change in the occurrence of an activity.

F. Auto- and Cross-correlation Functions

The second order transition probabilities suggested that the young oscillates between Sleep and IFA, and between IFA and Intense Begging, and that the patterning of these activities were relatively unaffected by feeding over a short time period (although there may be longer term effects). The data presented in Fig. 4 gives the same picture, as well as showing how the frequencies of these activities change with the level of FDP. Since I am dealing with cycles of different activities, I have used the techniques of auto- and cross-relation, which are ideally suitable for analysing the interdependence of such cycles.

These techniques are discussed by Bendat and Peirsol (1966), and their relevance to behavioural data have been discussed by Delius (1968 MS in prep, and pers. comm.). The basic data for the analysis were the frequencies of each activity in the successive ten minute time chunks of all my records, and auto- and cross-correlationsfunctions were calculated for all the activities in all of the 22 records. I found such enormous variation between different individuals when analysing the data that I have had to throw out a great deal. For example, young of less than 7 days in age do almost nothing but Sleep, so all these records have been discarded. On days when there was very cold weather and heavy rain the young again did little but huddle for shelter, so these records have also been discarded. This left me with 6 records from young of 8 - 14 days of age, and 4 records of young of 15 - 21 days of age.

The data presented in Figs. 5 and 6 were obtained by plotting out the auto- and cross-correlations for all the records, and then averaging the correlation coefficients at each lag. The maximum variation around the means are shown for every other lag (showing them for every lag made the figures almost unreadable).

The data were then pruned further. Firstly, Preening occurs at such a low frequency that it was ignored from the analysis. Secondly, feeding from the parent is not under the 'control' of the young, and the behaviour of the young is not influencing the parents' feeding rates (see Part I of this Thesis). The cross-correlations between Sleep, IFA, and IB on Feeding are therefore meaningless, have been ignored from the analysis.

F/1 Some General Comments on Figs. 5 and 6

The auto-correlations for each activity can be read diagonally from top left to botton right (as they are also marked a/c). The cross-correlations are read from left to right. Thus, Fig. 5B shows the cross-correlation function for Sleep on IFA, while Fig. 5F shows the cross-correlation function for IFA:Sl.

Auto-correlations necessarily assume the value of r=+1.0 for zero lag, but this is not the case for the cross-correlations.

In all cases, I show the correlations from zero lag to + lage24 (240 minutes).

F/2 The Simplest Situation: Sl, Fd, and IFA in Young aged 15-21 Days

Fig. 5 shows the auto- and cross-correlations for Sleeping, Feeding from the parents and IFA, based on the records from 4 young aged 15-21 days. No Intense Begging occurred.

The Autocorrelations

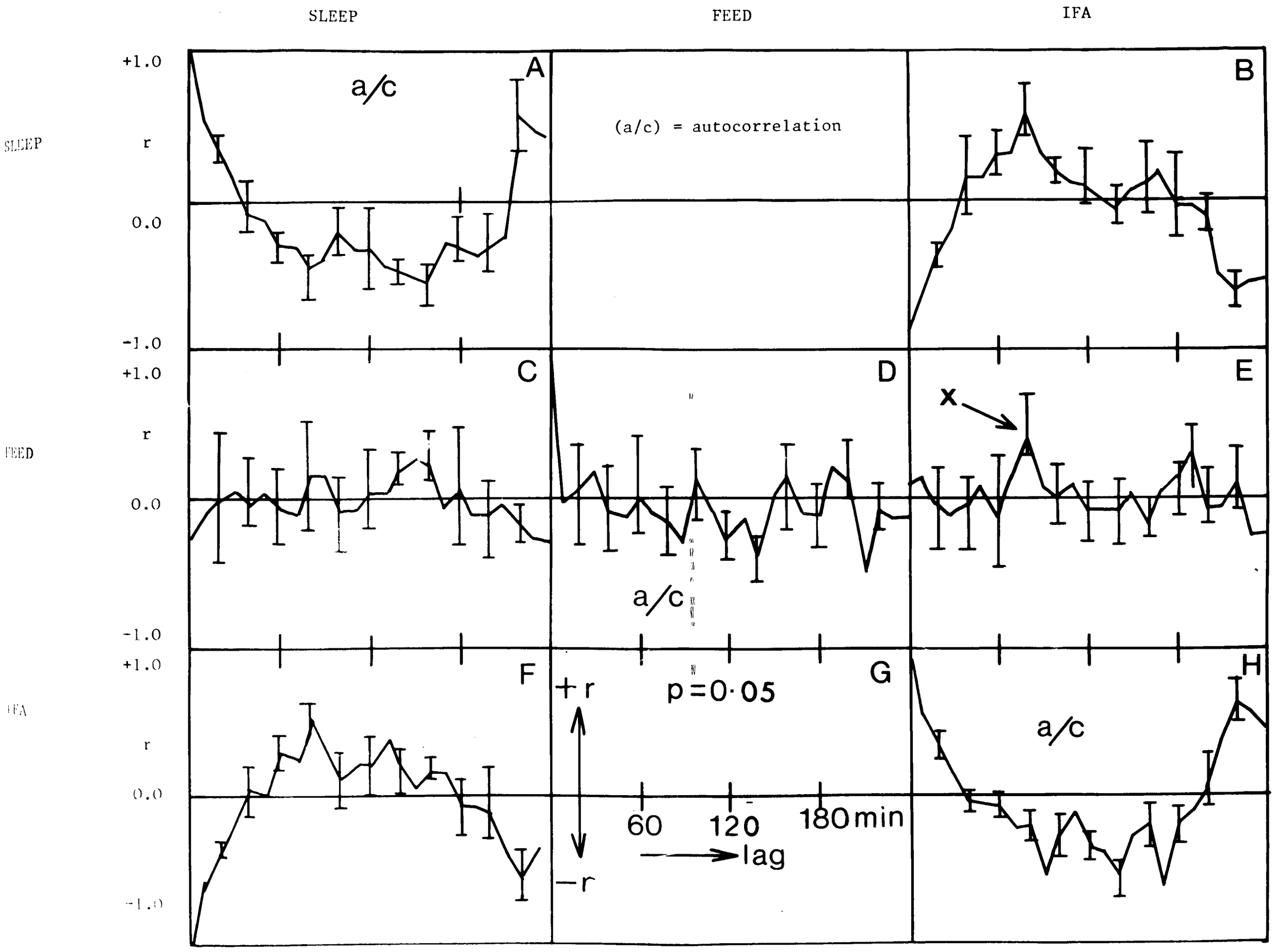
Both Sl and IFA show a marked periodicity of 240 mins, and the bouts of both Sl and IFA last for some 20 - 30 minutes (positive correlations up to lag 3 or 4). Note, that not only does the average value of the correlation change with increasing lag but also that there is little variation around the average values.

Fd however, shows no such periodicity. Note the extreme variation around the means. The auto-correlation of Fd is typical of what Bendat and Piersol (1966) call 'narrow band

Fig 5.

AUTO - AND CROSSCORRELATION FUNCTIONS FOR SLEEP, FEED, IFA :

4 RECORDS OF YOUNG AGED 15 - 21 DAYS



random noise'.

The Cross-correlations

S1 and IFA are almost exactly out of phase. At zero lag there is a strong positive correlation between them, but at +lag 6 there is a strong positive correlation between them. Note again how little variation there is around the average points. These cross-correlations show that the young are oscillating between S1 and IFA.

The Fd:S1 cross-correlation shows no periodicity at all, and there is tremendous variation around the average points. Feeding from the parent is therefore having relatively little effect (at least over 240 minutes) on the occurrence of S1.

The Fd:IFA cross-correlation similarly shows no periodicity and much variation around the means. However, there is one striking positive correlation at +lag 8 (80 minutes), and, although there is much variation around this point, all the records are showing a strong positive value (point X, Fig. 5E).

I am very tempted to deduce an entrainment effect on the S1:IFA oscillation from this one correlation because (a) all the young show a strong positive correlation at this point, (b) it occurs at the peak of the S1:IFA oscillation and (c) it is a delayed effect (i.e. it occurs 80 minutes after feeding from the parent) and we have seen from the earlier analyses that f eding has a delayed effect on the occurrence of the activities. However, I also fully realise that this may be a totally random result, and I have been advised on good authority that it is a random result. I will return to this point after discussing the data from the other records.

F/3 A More Complex Situation: young aged between 8 & 14 days

Fig. 6 shows the auto- and cross-correlations for S1, Fd, IFA and IB calculated from 6 records of young aged 8 - 14 days (these were the same individuals as used in the previous analysis).

The Auto-correlations

Sleep has a marked periodicity with peaks occurring

roughly every 50 minutes, and the periodicity is radically different from that obtained whenethe young were a week older. Feeding has again no sign of any periodicity, while IFA also seems to have no periodicity. Intense Begging has a marked periodicity up to +lag 11, but the cycles seem to break down with larger lags.

The Cross-correlations

These are difficult to interpret because, unlike the cross-correlations seen in Fig. 5B, they are markedly asymetrical.

IFA:Sl this shows a very pronounced periodicity (Fig. 6H), but there is little evidence for periodicity in the Sl:IFA cross-correlation (Fig.6C)

IB:Sl there is no sign of periodicity (Fig. 6K) and there is much variation about the means. However, the Sl: IB cross-correlation (Fig. 6C) shows a very marked periodicity with little variation between the different records up to +lag 13, after which the cycles break down.

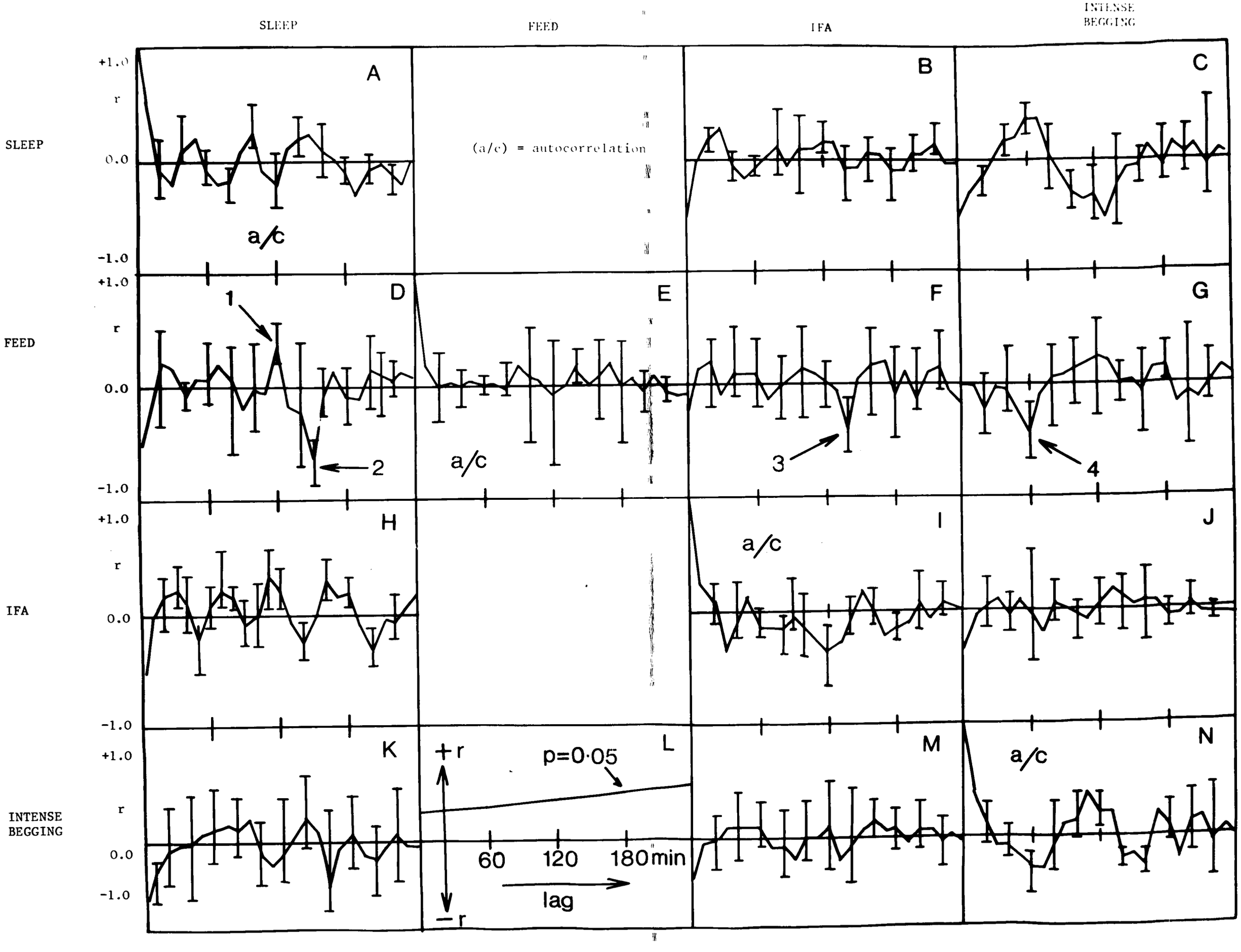
IB:IFA These cross-correlations show no periodicities at all.

These cross-correlations indicate that Sleep is strongly influencing the amount of Intense Begging coming 60 minutes later, but that Intense Begging is having little influence on the occurrency of Sleep. Similarly, IFA seems to be having a marked effect on the amount of Sleep occurring later, but Sleeping seems to be having little effect on the occurrence of IFA. It seems that Sleeping is oscillating with Intense Begging at 60 minute intervals, while IFA are oscillating with Sleep every 30 minutes, (i.e. a period of IFA will occur between each bout of Sleep and Intense Begging).

The Feeding Cross-correlations

All the cross-correlations (Fig. 5D, F, G,) show no sign of periodicity, but in every case there is at least one strikinglycorrelation (labelled from 1-4). These not only

Fig 6



AUTO - AND CROSSCORRELATION FUNCTIONS FOR SLEEP, FEED, IFA, INTENSE BEGGING :

6 RECORDS OF YOUNG AGED 7 - 14 DAYS

occur at quite large lags, but they also occur in phase with the S1:IB and the IFA:S1 cycles. I am again aware that these may be purely random effects, but they might also indicate a delayed entraining effect of feeding on the cycles of activities.

I have again not had time to carry this analysis very far, but this approach in general seems to be quite promising. The drawback to these auto- and cross-correlation techniques is that they yield descriptive data rather than show causal relationships.

APPENDIX 2

Individuals of Known Parentage

Among the eggs that I collected to hatch out and hand-raise were the eggs from a pair of colour ringed crab specialists and from a pair of colour ringed mussel specialists (I was unable to take the eggs from other known specialists because I was carrying out the egg-fostering experiment at the same time).

These six young were divided among the three groups in the following way:

Group 1 2 'mussel' siblings, 1 'crab' young

Group 2 1 'mussel' young, 2 'crab' siblings

I have analysed the responsiveness of these 'mussel' young and 'crab' young to mussel shells during their IFA to see whether there were any consistent differences over and above the differences caused by the conditioning. On each Test day I therefore compared (a) the % of Pecks directed at the mussel shells and (b) the % of rapid RCP directed at mussel shells during the IFA behaviour of the young. The results are shown in Tables 25 and 26.

The % of Pecks Directed at Mussel Shells (Table 25)

There were no consistent differences between the mussel and crab young in Groups 1 and 2. During Test 5, the Group 1 crab young directed a very high percentage of pecks at mussel shells, but otherwise there were no significant differences.

The % of RCP Directed at Mussel Shells (Table 26)

There were again no consistent differences between the mussel and crab young of the same groups. On Test 4 the Group 1 mussel young directed more RCP bouts at mussel shells than did the Group 1 crab young, but this was reversed on Test 5, and apart from this there were no differences between their behaviour. On Test 4 the mussel young of Group 2

TABLE 25 THE % OF PECKS DIRECTED AT MUSSEL SHELLS DURING THE IFA BEHAVIOUR OF 'MUSSEL' YOUNG AND 'CRAB' YOUNG

Table (a) shows the % of Pecks and the total number of Pecks

Table (b) shows the significance levels

p values calculated from Chi^2 or Fisher exact p test:

M = mussel young, C = crab young: (1) or (2) = Group 1 or Group 2:

(a) The % of Pecks directed at Mussels

		Test Number							
		1	2	3	4	5	6	7	8
M(1)	total pecks	31	24	16	11	6	10	3	6
	% at mussels	2%	0%	5%	3%	16%	0%	43%	16%
M(2)	total pecks	29	—	15	6	—	—	8	5
	% at mussels	0%	—	0%	0%	—	—	0%	20%
C(1)	total pecks	21	16	14	6	5	10	—	—
	% at mussels	0%	0%	0%	0%	80%	0%	—	—
C(2)	total pecks	27	20	20	16	10	11	—	3
	% at mussels	3%	0%	5%	0%	10%	0%	—	33%

(b) Comparisons between Mussel and Crab Young

comparisons between:	Test Number							
	1	2	3	4	5	6	7	8
M(1) : C(1)	ns	ns	ns	ns	p=0.05	ns		
M(1) : M(2)	ns	-	ns	ns	-	-	ns	ns
M(1) : C(2)	ns	ns	ns	ns	ns	ns	-	ns
C(1) : M(2)	ns	-	ns	ns	-	-	-	-
C(1) : C(2)	ns	ns	ns	ns	p=0.25	ns	-	-
M(2) : C(2)	ns	-	ns	ns	-	-	-	ns

TABLE 26 THE % OF RCP BOUTS DIRECTED AT MUSSEL SHELLS DURING THE IFA BEHAVIOUR OF 'MUSSEL' AND 'CRAB' YOUNG

(a) The % of RCP bouts directed at mussels

		Test number 1	2	3	4	5	6	7	8
M(1)	total RCP	10	12	20	28	30	26	33	30
	% at mussels	0%	0%	23%	57%	30%	77%	42%	63%
M(2)	total RCP	11	-	26	35	-	-	30	29
	% at mussels	0%	-	0%	17%	-	-	40%	52%
C(1)	total RCP	16	20	24	31	36	25	-	-
	% at mussels	0%	5%	20%	30%	58%	77%	-	-
C(2)	total RCP	14	18	18	25	26	27	-	32
	% at mussels	21%	6%	12%	2%	0%	0%	-	60%

(b) Comparisons between mussel and crab young

comparisons between:

	Test Number 1	2	3	4	5	6	7	8
M(1) : C(1)	ns	ns	ns	p = 0.03	p = 0.01	ns	-	-
M(1) : M(2)	ns	-	ns	p = 0.001	-	-	ns	ns
M(1) : C(2)	ns	ns	ns	p = 0.001	p = 0.001	p = 0.001	-	ns
C(1) : M(2)	ns	-	ns	p = 0.05	-	-	-	-
C(1) : C(2)	ns	ns	ns	p = 0.03	p = 0.001	p = 0.001	-	-
M(2) : C(2)	ns	-	ns	p = 0.046	-	-	-	ns

also directed more RCP bouts at mussel shells than did the crab young of Group 2, but again this was the only Test in which there was a difference between their behaviour.

There was no difference between the behaviour of the young in the two Groups up to Test 3. From Tests 4 to 6, the mussel and crab young of Group 1 directed more RCP bouts at mussels than did the mussel and crab young of Group 2, but there was again no difference between their behaviour during Tests 7 and 8.

CONCLUSION: Although these samples are very small, this analysis shows that there is no consistent difference between the behaviour of mussel young and crab young towards mussel shells. The only apparent differences are those caused by the conditioning. This is an important detail, because it shows that crab young can become as quickly and as firmly conditioned to a prey (which they normally would never come into contact with) as do the mussel young. This underlines the flexibility of the developmental system.

APPENDIX 3 CHANGES IN THE FREQUENCY OF THE MOTOR PATTERNS IN THE IFA BEHAVIOUR OF THE HAND RAISED YOUNG

This analysis is aimed at describing (a) any changes in the frequency of the IFA motor patterns, (b) effect of Chiseling experience on this change, (c) the precise effect of the Chiseling experienc on the selective responsiveness of the young and (d) the effect of practice on the length of the RCP bouts in the IFA behaviour.

The data were collected in the manner described in Chapter 4/D. To reiterate, I recorded (on a multi-event recorder) the number of Pecks, Mandibulates, RGP bouts, RCP bouts, Lever and Prise, as well as the bout lengths of Mandibulate, RGP and RCP. I also recorded the number of Pecks and the number of RCP bouts (and their length) which were directed at the empty mussel shells. Each Test consisted of recording 50 IFA motor patterns from each young.

The data have been analysed by using (a) regression coefficients to estimate trends in time, and (b) the Mann-Whitney U test (two-tailed) to compare the behaviour of each Group of young with the other Groups on successive test days.

A Overall Trends in the Frequency of the Motor Patterns

Table 26 shows the frequency of the various motor patterns in the IFA behaviour of the three Groups of young, as well as the median bout lengths of Mandibulate, RGP and RCP.

I calculated the regression coefficient over the whole series of tests for the frequency of each motor pattern as well as for the median bout lengths of Mandibulate, RGP and RCP for (a) all the young lumped together, (b) each Group of young, and (c) those individuals in the various Groups from whom I had enough data. In Table 27 I show the results of this analysis.

TABLE 26 THE FREQUENCY (%) OF THE IFA MOTOR PATTERNS IN THE BEHAVIOUR OF THE HAND-RAISED YOUNG

TEST NUMBER	1	2	3	4	5	6	7	8
% of Pecks								
Group 1 :	64	40	36(EM)	26	12	16	14	10
Group 2 :	56	46	34(LM)	22	16	24(EM)	16	12
Group 3 :	60	44	38	30	20	22(EM)	-	12
% of Mandibulate								
Group 1 :	7	15	10(EM)	8	10	12	4	6
Group 2 :	12	13	7 (LM)	11	9	4(EM)	8	8
Group 3 :	11	12	9	13	14	8(EM)	-	2
% of RGP								
Group 1 :	9	10	8(EM)	8	9	19	18	11
Group 2 :	12	10	11(LM)	10	11	12(EM)	12	10
Group 3 :	9	12	8	8	10	12(EM)	-	12
% of RCP								
Group 1 :	20	30	42(EM)	54	66	58	66	62
Group 2 :	22	28	40(LM)	52	58	54(EM)	60	60
Group 3 :	18	34	44	48	52	54(EM)	-	64
% of Lever + Prise								
Group 1 :	0	5	4(EM)	4	3	4	8	11
Group 2 :	0	1	8(LM)	5	66	6(EM)	4	10
Group 3 :	2	0	1	1	4	10(EM)	-	10
Median bout length of Mandibulate (sec)								
Group 1 :	0.8	0.9	0.8(EM)	0.8	0.9	0.8	0.8	0.9
Group 2 :	0.8	0.9	0.8(LM)	0.7	0.8	0.8(EM)	0.6	0.9
Group 3 :	0.6	0.9	0.7	0.7	0.7	0.7(EM)	-	0.8
Median bout length of RGP (sec)								
Group 1 :	0.9	1.1	1.1(EM)	1.2	1.0	1.0	1.2	1.4
Group 2 :	0.7	1.1	1.1(LM)	1.0	1.0	1.2(EM)	0.7	1.3
Group 3 :	0.7	1.2	0.8	0.8	0.8	1.0(EM)	-	1.5
Median bout length of RCP (sec)								
Group 1 :	1.2	1.5	1.6(EM)	1.6	2.0	2.0	3.1	2.6
Group 2 :	1.0	1.5	1.5(LM)	1.6	1.7	1.7(EM)	2.0	2.4
Group 3 :	1.0	1.5	1.3	1.1	1.4	1.8(EM)	-	3.5

TABLE 26 (contd.)

(EM) and (LM) show when each group had daily experience with entire mussels (EM) or loose-flesh-mussels (LM).

underlined scores are significantly larger than the scores of the other groups (Mann-Whitney z, p never >0.05)

TABLE 27 REGRESSION ANALYSIS OF DATA PRESENTED IN TABLE . THE REGRESSION COEFFICIENTS WERE CALCULATED OVER THE WHOLE SERIES OF TESTS. +, - or o shows the sign of the regression coefficient: ( ) shows that the coefficient was not significant (p never 0.05, t test)

	Pe	Ma	Ma(bt)	RGP	RGP(bt)	RCP	RCP(bt)	Lev	Pr
GROUP 1:									
a	-	(-)	(-)	(+)	(-)	+	+	+	(-)
b	-	(+)	(+)	(+)	(+)	+	(+)	+	(+)
c	-	(-)	(-)	(-)	(-)	+	+	+	(+)
d	-	(-)	(-)	(-)	(-)	+	+	+	o
all young	-	(-)	(+)	(+)	(+)	+	+	+	(+)
GROUP 2:									
a	-	-	(+)	(+)	(+)	+	(+)	(+)	(+)
b	-	(-)	(-)	(-)	(-)	+	+	(+)	(+)
c	-	(-)	(+)	(+)	(-)	(+)	+	(+)	o
d	(-)	(-)	(+)	(-)	(+)	+	(+)	+	(+)
e	-	(-)	(-)	(-)	(+)	+	(+)	(+)	(+)
f	-	(-)	(-)	(-)	(+)	+	(+)	(+)	(+)
all young	-	(-)	(+)	(-)	(+)	+	+	+	(+)
GROUP 3:									
a	-	(-)	(+)	(-)	(+)	+	(+)	+	(+)
all young	-	-	(+)	(+)	(+)	+	(+)	(+)	(+)
ALL GROUPS TOGETHER:									
	-	(-)	(+)	(+)	(+)	+	+	+	+

Note: in each group, a-f represent different individuals

Pe = no. pecks; Ma = no. mandibulate; etc;

Ma(bt), RGP(bt), RCP(bt) = bout length of Ma, RGP, RCP :

The same basic changes are seen in each case. The frequency of Pecking significantly decreases, while the frequencies of RCP, Lever and Prise significantly increase. The frequencies and bout lengths of Mandibulate and RGP show no significant trends. It will be seen that these changes in the frequency of the motor patterns are basically the same as those observed in the IFA behaviour of the fenced-in young (Chapter 2/E/II).

These regression coefficients were calculated over the whole series of tests, during which all the young had Chiseling experience in mussels (i.e. they had Chiseled out the flesh from EM). For comparison, I then made the same calculations (for each Group of young) using the data from Tests 1-6 (i.e. Group 1 had Chiseling experience, Group 2 had LM experience, Group 3 had n experience of obtaining food from mussel shells). The results are shown in Table 28.

TABLE 28 REGRESSION ANALYSIS OF THE FREQUENCY OF THE MOTOR PATTERNS IN THE IFA BEHAVIOUR OF GROUPS 1, 2 AND 3. TESTS 1-6 ONLY

ƒf	Group 1	Group 2	Group 3	All young
Pe	-	-	-	-
Ma	(+)	(-)	(-)	(-)
Ma(bt)	(+)	(-)	(-)	(o)
RGP	(+)	(+)	(+)	(+)
RGP(bt)	(+)	(+)	(+)	(+)
RCP	+	+	+	+
RCP(bt)	+	+	(+)	+
Lever	(+)	(+)	(+)	(+)
Prise	(+)	(+)	(+)	(+)

Note: Pe, Ma(bt) etc. as for Table 27.

+, - and o show the sign of the regression coefficient:

( ) show a non significant coefficient, $p > 0.05$, t test:

The same basic changes in the frequency of Pe and RCP are seen in all three Groups. Group 3 did not show a significantly positive trend in the bout length of RCP, but this may be due to the small numbers of young in this Group (see section C of this appendix).

In general, therefore, there is a basic change in the selective responsiveness of the young in that they respond progressively less to Peck-eliciting stimuli and more to RCP-eliciting stimuli. There is also an increase in responsiveness to Lever and Prise stimuli. This change in selective responsiveness is not dependent upon Chiseling experience, nor is it dependent upon gaining food reward from mussels. This is clear from the data in Table 26, which contains the results of the Mann-Whitney analysis. On each Test day I compared the frequency (and bout length) of each motor pattern in the behaviour of the three Groups of young. There are very few significant differences between them, in fact the only consistent differences are in the bout length of RCP shown by Group 1 on Tests 5, 6 and 7. In other words, although the Chiseling experience in Entire Mussels strongly conditions the young to mussels (Table 11), this does not effect the overall frequency of the IFA motor patterns.

B <u>The Precise effects of Chiseling experience on the IFA Motor patterns</u>

B/I The Rate of Change in the Frequency of Pe and RCP

Chiseling experience speeds up the rate of change in the frequencies of Pe and RCP (Table 29).

TABLE 29 COMPARISONS BETWEEN THE REGRESSION COEFFICIENTS OF Pe, RCP AND RCP(bt) FOR GROUPS 1, 2 AND 3

Up to Test 6	Pe	RCP	RCP(bt)
Group 1 v Group 2	+	+	+
Group 1 v Group 3	+	+	+
Group 2 v Group 3	o	o	+

result : Group 1 > Group 2 = Group 3

Whole Test Series			
Group 1 v Group 2	+	+	+
Group 1 v Group 3	o	-	o
Group 2 v Group 3	-	-	-

result : Group 1 = Group 3 > Group 2

Notes: + and - indicate significant differences: + means that the coefficient of the first member of a pair is > the second member: - means that the coefficient of the first member of the pair is < the second: o means no significant difference: + and - are significant at $p < 0.05$: p calculated from t or d:

The rate of change in Group 1 up to Test 6 is greater than the rate of change in Groups 2 and 3. Over the whole series of tests, Group 1 still changes faster than Group 2, but Group 3 changes as fast as Group 1.

B/II Changes in Selective Responsiveness to Mussels

Table 30 shows the regression coefficients of RCP and RCP(bt) for (a) all RCP bouts, (b) RCP bouts directed at objects other than mussel shells, and (c) RCP bouts directed at mussel shells.

TABLE 30 REGRESSION COEFFICIENTS OF RCP BOUTS

	Up to Test 6		whole series of Tests	
All RCP bouts	% f	bout length	% f	bout length
Group 1:	+	+	+	+
Group 2:	+	+	+	+
Group 3:	+	(+)	+	(+)
RCP at other objects				
Group 1:	+	(+)	(+)	+
Group 2:	+	+	(+)	+
Group 3:	+	(+)	+	+
RCP at mussels				
Group 1:	+	+	+	+
Group 2:	(+)	(-)	+	(+)
Group 3:	(-)	(-)	(+)	(+)

Note: + and - show the sign of the coefficient: ( ) shows coefficient is not significant at $p \ll 0.05$, t test:

All Groups are showing a significant increase in the frequency of RCP bouts by Test 6. Group 1 shows a significant increase in the frequency of RCP bouts directed at mussels. Over the whole series of Tests, Group 1 and 2 do not show a significant increase in RCP bouts directed at 'other objects', but they show a significant increase in RCP bouts directed at mussels. Group 3 (over the whole series of Tests), however, shows a significant increase of RCP bouts at 'other objects' but does not show a significant increase in RCP bouts at mussels.

We have seen that there is a basic change in the selective responsiveness of the young, and that this change can be speeded up by Chiseling experience. Here we see the precise effect of this Chiseling experience. As the young become more responsive to RCP-eliciting stimuli, the Chiseling experience conditions them to respond selectively to the RCP stimuli from the mussel shells rather than to the RCP stimuli from other objects lying around. The same sort of process is

occurring with the Pecking response. Tables 27 and 28 show that the frequency of Pecking significantly decreases in all Groups of young. From Table 11 we see that all Groups show a positive (though not significant) trend to Peck more at mussels, i.e. the young are tending to respond selectively to the Peck-eliciting stimuli from mussel shells rather than to the Peck stimuli from other objects.

One other interesting point must be mentioned here. When the young Chisel in Entire Mussels, they use Rapid Grab Pecking to remove the pieces of flesh that they have Chiseled free. Similarly, the Group 2 young used Rapid Grab Pecking to remove the flesh from the Loose Flesh Mussels. However, there is no sign of any increase in the frequency of RGP in the IFA behaviour (Table 26), and from this we must conclude that food has no reinforcement value for RGP (although it does have reinforcement value for RCP). The appropriate reinforcement for RGP seems to be 'locating and digging something out of the sand' (see Chapter 7/B).

C <u>The Effect of Practice on the Bout Length of RCP</u>

This is a difficult question to answer for I have no data from young who have had no experience at RCP in mussel shells, nor from young who have had no experience at performing RCP (though how this could be arranged I do not know). However, up to Test 6, we see that the bout length of RCP increase significantly in Group 2 (Table 30) even though these young had had no Chiseling practice. Admittedly, the Group 3 young did not show a significant increase in bout length but they showed a positive trend. This uncertainty might well be due to the small number of individuals in Group 3). The conclusion is that the performance of functional Chiseling (i.e. RCP in a mussel to cut the flesh free) is not necessary for the development of skill at RCP during the IFA, and that perhaps RCP

practice with the various objects lying around leads to the acquisition of fine control over RCP movements.

D Conclusions

1. There is a basic change in the selective responsiveness of the young. They respond progressively less to Peck stimuli, and more to RCP, Lever and Prise stimuli.
2. These changes do not depend upon Chiseling experience, or on any interaction with the prey that leads to food reward.
3. However, Chiseling experience will speed up the rate of change in selective responsiveness.
4. Chiseling experience conditions the young to respond selectively to the RCP stimuli from mussels rather than to the RCP stimuli from other objects. RCP in mussels without food reward does not lead to this effect.
5. Food reward does not reinforce the performance of RGP (see Appendix 4).
6. RCP at objects may lead (through practice) to the acquisition of fine control over the RCP movements).
7. The function of this change in selective responsiveness is not immediately apparent. I suggested in Chapter 2/E/II that a high responsiveness to Peck-eliciting stimuli might be advantageous to the small young in establishing the first feeding responses to the parent. A change in responsiveness to the stimuli that elicit RCP, Lever and Prise might then be relevant to the acquisition of feeding skills in which these motor patterns will be employed.

APPENDIX 4 THE DEVELOPMENT OF CHISELING

A Introduction

Chiseling is the most complex motor pattern in the Oystercatcher's repertoire and the young take a very long time to become fully efficient at it (see Chapter 8). Chiseling is first seen when small young remove scraps of flesh from prey remains and from fully opened and partly opened prey. The Chiseling is at first very inefficient, but observations made on free-living young of various ages show that the efficiency of Chiseling slowly improves. In Table 31 I show some basic data on the Chiseling efficiency of free-living young of different ages. There is a rapid decrease in total time spent

TABLE 31 CHANGES IN THE EFFICIENCY OF CHISELING IN MUSSELS
(data from fenced-in and free living young)

age	state of mussel	size	Total time (sec)	number of: bouts	Pieces	Obs
2/3 week old fenced-in	FO	small	c.180	28	13	3
	PO	small	c.250	31	16	8
4/5 week old free-living	FO	small	18	5	4	12
	PO	small	22	6	5	23
6/7 week old free-living	self	small	25	4	4	20
Newly-independent	self	small	14	5	4	97
	self	medium	31	6	6	53
Juveniles	self	small	8	2	3	36
	self	medium	19	4	2	8
Adults	self	small	6	1	1	65
	self	medium	15	2	2	44

Notes: 'state of mussel', FO = fully opened by parent, PO = partly opened by parent, self = opened by the young :

Chiseling, in the number of Chiseling bouts and in the number of pieces in which the flesh is removed by the time the young

are 4/5 weeks of age. After then the improvement is slower.

The following analysis is aimed at describing the changes in the organisation of Chiseling that lead to greater Chiseling efficiency.

B <u>The Organisation of Chiseling in 2/3 week old Fenced-in Young</u>

B/I Chiseling in Prey Remains (Mussels)

The Chiseling is well organised when the young remove scraps of flesh from prey remains. The RCP bouts are directed at the flesh, and, once the flesh comes free, RGP and SH follow. Table 32 shows the observed transition probabilities between RCP, RGP, SH and Eat.

<u>TABLE 32 THE OBSERVED TRANSITION PROBABILITIES BETWEEN RCP, RGP, SH AND EAT</u>

(2/3 week old young young removing scraps of flesh from mussel shells)

	RCP	RGP	SH	EAT	Totals
RCP	x	0.81+ (0.38)	0.10 (0.24)	0.09- (0.38)	21
RGP	0.10 (0.30)	x	0.50+ (0.28)	0.40 (0.42)	20
SH	0.21 (0.28)	0.07 (0.36)	x	0.72+ (0.36)	14
EAT	0.84+ (0.33)	0.16 (0.42)	0.00 (0.25)	x	12

Note: figures in ( ) are the transition probabilities expected if there was random association between the motor patterns: + means that O > E, - means that O < E, p = 0.05:

B/II Chiseling in Fully Opened and Partly Opened Prey (Mussels)

The Chiseling is still hopelessly disorganised. Table 33a shows the observed transition probabilities between RCP, RGP,

SH and Eat, and it can be seen that only the transition between RCP and RGP, and between SH and Eat occur more frequently than random expectation. Indeed, RCP, SH and Eat occur randomly after an RGP bout. Table 33b compares the transition probabilities observed from the young with the transition probabilities observed when adults Chisel in mussels (see Part III, Chapter 3/F/III, p. 126). The differences are very striking, and the transitions RCP → RGP and RGP → SH are the only ones which are not significantly different.

With the one and only exception that Shaking (followed by eating) follows an attack at the VMB with a greater frequency than random expectation, the sequence in which the various attachments are attacked is totally random. There is not even a general trend at this age to Chisel from the posterior end of the mussel to the anterior end (Table 33c).

What the young are in fact doing is to first remove all of the 'soft parts' of the mussel (i.e. the mantles, gut etc), and they do this almost entirely with RGP. It is not until the soft parts are removed that the young attack the 'hard parts' (i.e. the mantle attachments and the posterior adductor stump) with RCP. Each piece of flesh is shaken free and eaten as soon as it become loose, with the result that the flesh is removed in many tiny pieces - obviously an ineffecient proceedure

TABLE 33 THE ORGANISATION OF THE CHISELING OF 2/3 WEEK OLD PENCED-IN YOUNG IN PARTLY OPENED AND FULLY OPENED MUSSELS.

(a) The observed transition probabilities between RCP, RGP, SH and Eat compared with the transition probabilities expected if there was random association between them, expected figures in ( ).

	RCP	RGP	SH	EAT	Totals
RCP	x	0.84+ (0.48)	0.08- (0.26)	0.08- (0.26)	56
RGP	0.36 (0.35)	x	0.39 (0.31)	0.25 (0.34)	87
SH	0.09 (0.25)	0.42 (0.50)	x	0.49+ (0.25)	45
Eat	0.37 (0.27)	0.50 (0.46)	0.13 (0.27)	x	41

(b) The Observed transition probabilities between RCP, RGP, SH and Eat compared with the observed transition probabilities in the adult Chiseling, expected figures in ( ).

	RCP	RGP	SH	EAT	Totals
RCP	x	0.84 (1.00)	0.08+ (0.00)	0.08+ (0.00)	56
RGP	0.36+ (0.03)	x	0.39 (0.48)	0.25- (0.49)	87
SH	0.09+ (0.00)	0.42+ (0.00)	x	0.49- (1.00)	45
Eat	0.37- (0.95)	0.50+ (0.05)	0.13+ (0.00)	x	41

(c) The Observed transition probabilities between Chiseling bouts occurring in the posterior and anterior of the mussel.

	Post	Ant	Sh/Eat	Totals
Posterior	0.14 (0.21)	0.38 (0.34)	0.48 (0.45)	42
Anterior	0.19 (0.22)	0.19- (0.33)	0.62+ (0.45)	69
SH/Eat	0.27 (0.21)	0.44 (0.33)	0.29 (0.46)	84

Note: expected figures in all tables in ( ): + means that O > E.

- means that O < E, at p = 0.05

C Changes in the Organisation of Chiseling in Older Young

In addition to the observed changes in the organisation of Chiseling listed in Table 31, there are two important additional changes. Firstly, the young Chisel from the posterior end of the mussel to the anterior end (i.e. the sequence in which the attachments are attacked has slowly changed). Secondly, the young no longer remove every piece of flesh as soon as it comes free but progressively extend the Chiseling attack until a large piece of flesh is loose. This large piece is then Shaken out and eaten.

D Experiments with Hand Raised Young

D/I Introduction

My experiments with the hand raised young were aimed at (a) describing these basic changes in organisation in more detail and (b) analysing what role (if any) practice had to play in the development of efficient Chiseling.

I have already described the daily schedules of mussel-experience of the three Groups of young (Chapter 4/C, Table 9, p. 218). Each young had to Chisel in 10 mussels every day, and every third day I recorded the following behaviour:

With 5 of the 10 mussels: the sequence of RCP, RGP, Sh and Eat, the size of each piece of flesh removed, and the length of each bout of RGP and RCP.

With the other 5 mussels: the sequence in which the various attachments were attacked, the length of each attack at each attachment, and the size of each piece of flesh removed.

These data were recorded on my multi-event recorder. The event recorder operated in the following way: there were nine electronic counters each operated by a separate button. Some of the counters recorded single events (i.e. the counter recorded '1' every time the button was pushed) while others recorded

the length of time for which the button was pushed (in units of 0.2 sec). The readings of all nine counters were photographed every time a button was released (i.e. after each item had been recorded). The whole operation was therefore:- press button A for 2 sec - counter A records for 10 units of time - release button A - all the counters are photographed - press button B for 6 sec - counter B records for 30 units of time - release button B - all the counters are photographed - etc. These photographic records enable me to analyse, for each mussel eaten, both the sequence in which the various behaviour occurred as well as the bout length of each behaviour. Unfortunately, I accumulated 2400 feet of film to analyse, and I have not yet had time to even start on this task. However, I also made separate records of the total amounts of behaviour recorded on each counter after the young had finished Chiseling in each mussel, so I can present a very simplified analysis of the changes in the organisation of Chiseling.

D/II The Series I and Series 2 Tests

A complication must now be explained. My original experimental programme was to have <u>two</u> Groups of young which had experience of Entire Mussels from Day 18 onwards. One of these groups was to have 10 EM per day in which only the adductor muscle was cut and in which all the other attachments were left undamaged. The other Group was to have 10 EM per day in which <u>all</u> the attachments except for the adductor stumps were to be cut free. The rationale for this was that the second Group had an 'easier' task to learn, and I wanted to see whether it learnt it in the same way as did the first Group. Unfortunately all the young designated for the first Group of EM died before Day 18 (their behaviour has been excluded from all the previous analysis), but after the second Group of EM young had already started on their schedules of experience.

My Group 1 young were therefore having 10 EM per day in which all the attachments except the adductor stumps were cut free. At day 40, when Groups 2 and 3 were to have experience with Entire Mussels, I therefore decided to give all the young (including Group 1) Entire Mussels in which the attachments were undamaged. The observations made on the Group 1 young from Day 18 to Day 39 will therefore be referred to as Series 1 Tests, and the observations made on Group 1, 2 and 3 from Day 40 - 54 will be referred to as Series 2 Tests.

Finally, when analysing the Series 2 tests, I have lumped Group 2 and 3 together because (a) there was no obvious difference between their behaviour, and (b) there was only 1 individual in Group 3, and this made comparisons very difficult.

D/III Group 1, Series 1 (Chiseling in mussels in which the flesh is attached only at the adductor stumps)

Table 34 shows the changes in organisation of RCP and RGP that I was able to extract from the data. There is a gradual increase in efficiency up to Test 6, after which there is little further change. The changes are of the same kind as shown in Table 31. The total time spent Chiseling in each mussel decreases. there are fewer bouts, and the flesh is removed in fewer and larger pieces. These changes are of the same kind as those shown to occur in the free living young (Table 31). Note, however, the rapid and stable decrease in time spent RGP and in the number of RGP bouts, and that the length of the RGP bouts does not alter. The number of RCP bouts also decreases (as does the time spent at RCP), but note that the bout length increases.

TABLE 34 GROUP 1, SERIES 1: CHANGES IN THE ORGANISATION OF CHISELING(LUMPED DATA FROM ALL THE YOUNG)

	test number								regr. coeff.	t test p =
	1	2	3	4	5	6	7	8		
TT spent	54	40	30	27	17	19	15	15	-5.3	<0.001
TT RCP	35	36	26	24	16	18	14	14	-3.4	<0.001
TT RGP	19	4	4	3	1	1	1	1	-1.8	<0.05 >0.02
Total Bouts	31	18	15	13	7	6	5	5	-3.3	0.002
RCP bouts	14	13	10	10	5	5	4	4	-1.6	<0.001
RGP bouts	17	5	5	3	2	1	1	1	-1.7	<0.05 > 0.02
Bout length										
RCP	2.4	2.7	2.6	2.4	3.2	3.6	4.2	4.6	+3.2	0.002
RGP	1.1	0.9	0.8	1.0	0.7	0.8	0.7	0.8	-0.4	>0.05 ns
Number of pieces in which flesh was removed	12	11	7	6	4	4	2	2	-1.4	<0.001

TT = total time : all figs are averages : time in sec :

D/IV Group 1, Series 2 (Chiseling in mussels in which all the attachments are undamaged)

The behaviour was initially highly disorganised (Table 35) but there was a rapid improvement by Test 5(the last Test in the series). The same basic changes in organisation were seen (Table 36), but note that the time spent at RCP, the bout length of RCP and the number of pieces in which the flesh was removed did not show significant changes.

D/V Groups 2+3, Series 2

From Table 35 we see that exactly the same changes in organisation occur (see also Table 36), with the one exception that the time spent at RCP at first markedly increases and then only slowly decreases.

D/VI Comparisons between Group 1 and 2+3, Series 2

I compared the performance of these two Groups on each Test day (Mann-Whitney U test), and Table 35 shows the results of

TABLE 35 GROUP 1 AND GROUPS 2+3, SERIES 2: CHANGES IN THE ORGANISATION OF CHISELING

	1	2	3	4	5	regr. coeff.	t test, p =
Total Time Spent (sec)							
Group 1	45	42	43	32	28	-4.4	< 0.05 > 0.02
Groups 2+3	67	61	43	42	26	-8.7	0.002
TT RCP....							
Group 1	36	36	38	29	26	-2.7	> 0.05 ns
Groups 2+3	28	39	33	35	22	-0.4	> 0.05 ns
TT RGP....							
Group 1	9	6	5	3	2	-1.7	< 0.01 > 0.002
Group 2+3	39	22	10	7	4	-8.3	< 0.05 > 0.02
Total Number of Bouts							
Group 1	22	15	16	11	10	-2.8	< 0.05 > 0.02
Group 2+3	44	35	23	21	13	-7.1	< 0.02 > 0.01
RCP bouts...							
Group 1	12	9	9	7	5	-1.6	< 0.01 > 0.002
Group 2+3	14	15	13	11	6	-3.1	< 0.01 > 0.002
RGP bouts...							
Group 1	10	6	7	4	5	-1.3	< 0.05 > 0.02
Group 2+3	30	20	10	10	7	-5.7	0.01
Bout length (sec)							
RCP bouts...							
Group 1	3.2	4.0	4.3	4.4	4.7	+3.1	0.05
Group 2+3	2.3	4.3	3.7	5.0	4.4	+3.3	< 0.01 > 0.002
RGP bouts...							
Group 1	0.9	0.8	0.8	0.8	0.8	-0.2	> 0.05 ns
Group 2+3	1.3	1.1	1.0	0.7	0.8	-1.8	> 0.05 ns
Number of pieces in which flesh was removed							
Group 1	8	7	8	5	5	-0.8	> 0.05 ns
Group 2+3	20	17	10	9	4	-3.8	0.01

note: all figures are averages: underlined figures indicate that Group 2+3 > Group 1 on that test day, Mann-Whitney z, two-tailed; note however that this test could not be applied to the estimated bout lengths.

these comparisons (the underlined figure is significantly larger, p never 0.05). The basic result is that Group 2+3 were much less efficient than Group 1 on Test 1, but, by Test 5, there was very little difference between them.

TABLE 36 THE BASIC CHANGES IN THE ORGANISATION OF CHISELING IN THE YOUNG OF GROUP 1 AND GROUPS 2+3

	Group 1 Series 1	Group 1 Series 2	Groups 2+3 Series 2
total time spent (sec)	-	-	-
time RCP	-	(-)	(-)
time RGP	-	-	-
total number of bouts	-	-	-
RCP bouts	-	-	-
RGP bouts	-	-	-
bout length RCP	+	(+)	+
bout length RGP	(-)	(-)	(-)
number of pieces in which flesh was removed	-	(-)	-

Note: - and + show the sign of the regression coefficient:
( ) indicates the coefficient was not significant at
p = 0.05, t test :

E Discussion

We can draw the obvious (and not surprising) conclusion that Learning plays a very important part in the development of efficient Chiseling. However, the speed with which the Group 2+3 young learnt to Chisel shows that other factors must be operating as well. 'Somatic' structural growth processes may again be very important, for, as the young grow stronger, the effectiveness of any RCP, RGP or SH in removing flesh will become greater, and there will be a

corresponding decrease in the time taken over emptying out the flesh. In addition, the Group 2+3 young may have acquired fine control over the RCP movements through experience with inedible objects (see Appendix 3/C).

The two most interesting problems are (a) what are the young learning to do? and (b) how are they learning to do it?

Table 36 shows the basic changes that occur in the organisation of Chiseling, but, until I have analysed the individual records in detail, it is difficult to tell which are the most important changes that lead to the increase in efficiency. The increase in efficiency could be due to learning to Chisel in the correct orientation, or to maintaining an attack until all the attachments are cut free, or to ignoring small, loose pieces of flesh and only removing large pieces, or to a combination of all of these.

I am also unable to say very much about the second of these problems until the data have been fully analysed. However, any increase in Chiseling efficiency will lead to the flesh being extracted in a shorter time, so any general change in behaviour which leads to this result may well be reinforced. There will undoubtedly be short-term reinforcing effects as well. For example, the young may be able to distinguish between the time spent Chiseling at a given attachment from a number of different orientations, and then choose to Chisel in the orientation in which a food reward is received in the shortest time. The ability to differentiate between food reward per time spent Chiseling (either in the mussel as a whole or in a particular part of a mussel) will probably be an important part of the learning machinery. The possibility also exists that the ability to differentiate between reward per time spent Chiseling may increase with age, and perhaps with experience. Of course, food reward as such may not in fact be all that important, for

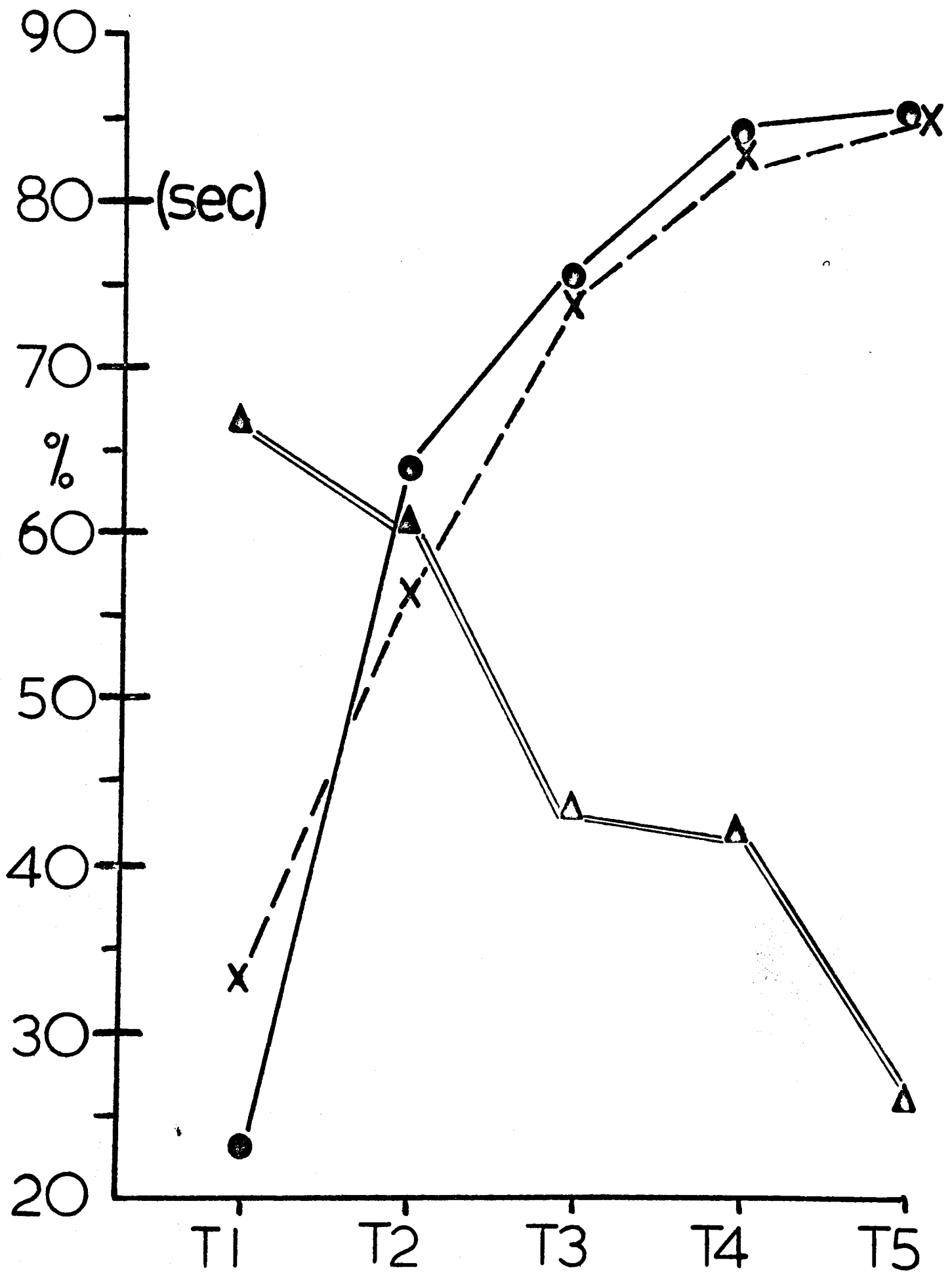
it is possible that merely cutting an attachment free has reinforcing properties. The possibilities are endless, and it will be interesting to see which of them, if any, prove to be correct. Certainly, the almost total randomness of the Chiseling behaviour of small young is a good starting point for such learning to occur.

There is, however, one particular change in organisation which I believe is fundamental to the development of efficient Chiseling. I have already described how the fenced-in young first removed all the soft parts of the mussel (i.e. mantles, gut, foot musculature etc.) by Rapid Grab Pecking, and only then removed the hard parts (i.e. the mantle attachments, the adductor stumps, etc.) by Rapid Chisel Pecking. This same behaviour was also shown by both Groups of hand raised young during their first experiences with the series 1 and series 2 mussels.

The clearest example is shown by the Group 2+3 young. From Table 35 it can be seen that, between Test 1 and Test 2, the time spent at RCP increased while the time spent to RGP decreased. Fig. 7 shows these changes in more detail. There is a persistent increase in both the percentage of time spent at RCP and in the percentage of time spent in attacking the hard parts of the mussel, with the increase being very marked between Test 1 and Test 2. Note, however, that there is no corresponding increase in efficiency between the first two tests, i.e. neither the total time spent removing the flesh nor the number of pieces in which the flesh is removed shows a marked change. In other words, this change in organisation (from mainly RGP at the soft parts to mainly RCP at the hard parts) occurrs initially <u>without</u> any marked increase in efficiency.

Group 1 also showed this same basic change between Test 1 and Test 2 of series 1 (Table 34). Note that the time spent at RCP does not change, while the time spent at RGP shows a marked decrease. It is interesting that the Group 1 young do

Fig. 7 Changes in the organisation of Chiseling in the young of Groups 2+3



not show this basic change during Tests 1 and 2 of series 2 (Table 35), and this is probably due to their previous experience at Chiseling in mussels.

Although this may at first seem to be a minor point, I feel that it is one of the most crucial steps in the development of Chiseling. We must first consider what is the function of this change.

The mussel is so constructed that the 'soft' parts are attached to the 'hard' parts, which are in turn attached to the shell. One of the problems facing the young Oystercatcher is to learn where these hard parts are positioned inside the shell. If the soft parts are first removed by RGP, only the hard parts will remain, and these can then be attacked with RCP. The young thus has the opportunity to learn the precise location of the hard parts within the shell. The importance of this is that the problem of learning the precise position of the hard parts is relevant to <u>any</u> prey in which a young Oystercatcher is learning to Chisel. My observations on the fenced-in young of crab eating parents showed that these young were behaving in exactly the same way when they first attempted to Chisel out the flesh from a crab. They started by removing all the soft parts (by RGP) and only then attacked the hard parts with RCP.

Two problems are now raised: (a) why do the young initially perform RGP instead of RCP? and (b) why does the change occur?

The first response of both the fenced-in young and the hand raised young when they first had experience with prey containing flesh was to perform RGP. This was equally so in the hand raised whether the flesh was attached in the mussel (Group 1) or was lying loose in the shell (Group 2 with LM). The soft flesh therefore elicits RGP (note the similarity between 'soft flesh' and the stimuli that elicit RGP in the IFA behaviour). RGP is performed until all of the soft flesh is removed, and only then is RCP elicited (by the hard parts). This, of course, will only happen if there are hard parts present to elicit the RCP, for the Group 2 young never showed any RCP when they emptied out the

Loose Flesh Mussels. Thus, the initial elicitation of RGP followed by the elicitation of RCP can be understood in terms of the stimuli from the soft and hard parts of the mussel.

Why, then, does the behaviour change so that RCP is elicited <u>instead</u> of RGP? I think that this occurs for the s me reasons that young who have Chiseling experience become conditioned to mussel shells while young who have merely to pick up the flesh do not. I have already shown that food does not have reinforcing properties for RGP, while it does for RCP. The young will therefore become conditioned only to the RCP eliciting stimuli from the mussel (i.e. to the hard parts) and they will not become conditioned to the RGP stimuli (i.e. to the soft parts). This will lead to a gradual change in behaviour so that the young will respond <u>first</u> to the RCP stimuli, i.e they will begin by attacking the hard parts and they will largely ignore the soft parts. This change will occur <u>without</u> there being any immediate increase in the overall efficiency of the Chiseling, although such a change may well occur.

We see here another example of the flexibility of the developmental system. The first problem facing a young Oystercatcher who is attempting to Chisel in any prey species is to learn the precise location of the hard parts (the location of these parts will of course be different for each prey species). RGP will be initially elicited by the soft flesh of the prey, followed by RCP once this soft flesh has been removed. The young will ignore the RGP eliciting stimuli (because food has no reinforcing properties for RGP) but instead will become conditioned to attend to the RCP eliciting stimuli. In this way they will learn the precise location of the hard parts. This conditioning will cause a gradual change in the behaviour of the young so that they will begin by attacking the hard parts of the prey, and this change can occur without the overall efficiency of the Chiseling process being necessarily improved. Once the location of the hard parts has been learnt, the young can then develop (in the ways suggested above) the precise orientation and sequence of attack relevent to the particular prey species.

APPENDIX 5 THE ORGANISATION OF THE MOTOR PATTERNS IN THE MUSSEL TECHNIQUES OF NEWLY INDEPENDENT OYSTERCATCHERS

This is a brief analysis of the factors that control the elicitation and integration of the motor patterns, and is of the same kind as that made on the organisation of the motor patterns in the adult mussel-techniques (Part III, Chapter 3): I draw some comparisons with the adult organisation.

5/A The Frequencies of the Motor Patterns

Table 37 shows the frequency (per mussel opened) of the motor patterns in the techniques of the newly independent young compared with the frequencies in the adult techniques. The most striking differences are between the frequencies

TABLE 37 THE FREQUENCIES OF THE MOTOR PATTERNS IN THE TECHNIQUES OF NEWLY INDEPENDENT YOUNG AND ADULTS

(a) The Stabbing Technique

	stab	lever	prise	chisel	eat	number of sequences
young birds	1.0	1.02	0.18	4.7	3.6	139
adults	1.0	1.03	0.73	1.63	1.4	132

(b) The Hammering Technique

	Hammer	lever	prise	chisel	eat	number of sequences
young birds	1.0	1.01	0.00	2.5	2.4	13
adults	1.0	1.00	0.20	1.06	1.06	110

of Prise and Chiseling. Prising will be discussed later (section D of the Appendix), while the inefficiency of the Chiseling of the young birds has already been dealt with (Chapter 8/F).

5/B The Sequence in Which the Motor Patterns Occur

Table 38 shows the observed transition probabilities between all pairs of motor patterns in the Stabbing

technique of the newly independent young. The basic sequence is Stab → Lever → Chisel → Eat, with the Prise occasionally occurring after the Levering or during the Chiseling. Prising is almost always followed by Chiseling. The sequence of motor patterns is very similar to that observed in the adult Stabbing technique - with the exception of the transition probabilities between Lever and Prise and between Lever and Chisel (see Part III, Appendix 1, Table a, p. 183). These differences are due to the low frequency of Prise in the technique of the young birds. Note, however, the similarities between the transition probabilities Prise → Lever and Prise → Chisel in the techniques of both adults and young.

TABLE 38 THE OBSERVED TRANSITION PROBABILITIES BETWEEN THE MOTOR PATTERNS IN THE MUSSEL STABBING TECHNIQUE OF NEWLY INDEPENDENT YOUNG (139 OBSERVATIONS)

Preceding:	Stab	Lever	Prise	Chisel	Eat	TOTALS
Stab	x	0.99 + (0.10)	0.01 (0.01)	0.00- (0.45)	0.00 - (0.44)	140
Lever	0.00 (0.00)	x	0.06 + (0.02)	0.94 + (0.50)	0.00 (0.48	143
Prise	0.00 (0.00)	0.04 (0.08)	x	0.96+ (0.48)	0.00 - (0.44)	25
Chisel	0.00 (0.00)	0.005- (0.18)	0.025 (0.03)	x	0.97 + (0.79)	654
Eat	0.00 (0.00)	0.00 - (0.00)	0.002 - (0.03)	0.998+ (0.80)	x	497

note: figures in () are the transition probabilities expected if the motor patterns were occurring in a random order: + and - indicate that O>E (+) or O<E (-), p = never >0.05.

The transition probability matrix for the Hammering technique of the young is not worth showing because the sample is very small and because there was no Prising.

The Hammering attacks were always followed by Levering, Levering was always followed by Chiseling and Chiseling was always followed by eating (except for 3 occasions when there was a second Levering bout during the Chiseling).

The sequences are thus very similar to those observed in the adult techniques. Stabbing and Hammering are followed by Eating. The differences between the sequences are basically due to the low frequency of Prise in the young birds' techniques.

5/C The Elicitation and Duration of Levering

Levering is elicited under the same conditions as with the adults, i.e. subsequent to a Stab or a Hammering attack when the bill is inside the mussel. The young birds are also observed to withdraw the bill from Stabbed mussels that become tightly clamped onto the bill tips, and they then abandon these mussels. In addition, if the valves inadvertently close during Chiseling, a Prise is sometimes elicited but Levering is never elicited. This shows that the stimuli that elicit Levering are the same as those suggested for adults (firm pressure around the bill tips).

The duration of Levering is entirely under external control (Table 39a). There is no significant difference between the duration of Levering in Stabbed and Hammered mussels of the same size (from Table 39a, $z = 1.31$, $p = 0.21$), but larger mussels elicit more Levering than smaller mussels. There is also no significant difference between the duration of Levering in the transition Lever → Prise and Lever → Chisel. Finally, there is no correlation between the duration of Levering and the duration of Chiseling (small Hammered mussels, $r_s = + 0.29$, small Stabbed mussels $r_s = - 0.24$, medium Stabbed mussels $r_s = + 0.31$, p never < 0.05).

5/D Prising

Unlike the adults, Prising is as frequent in large mussels as it is in small ones (small mussels, 14% out of 75

TABLE 39 THE MEDIAN DURATION OF LEVERING AND CHISELING IN THE MUSSEL TECHNIQUES OF NEWLY INDEPENDENT YOUNG (all times in sec)

(a) The Duration of Levering

	total time	no. prise in seq.	prise in sequence	
small Hammered mussels	3.5	—	—	
small Stabbed mussels	3.9	3.6	3.9	z= 0.32, p > 0.05
medium Stabbed mussels	5.1	4.8	5.8	z= 1.34, p > 0.05
	z= 3.48 p <0.001			

(b) The Duration of Chiseling

	total time	no prise in seq.	prise in sequence	
small Hammered mussels	16.5	—	—	
small Stabbed mussels	13.9	15.5	14.3	z= 0.75 p > 0.05
medium Stabbed mussels	31.1	33.4	24.4	z= 2.16 p= 0.03
	z= 6.15 p <0.001			

(c) The Bout Length of Chiseling

	1st Chiseling bout	Successive Chiseling bouts	
small Hammered	10.8	3.7	z = 3.58 p <0.001
small Stabbed	7.5	2.9	z= 7.76 p <0.001
medium Stabbed	13.9	3.8	z= 7.83 p <0.001

observations: medium mussels, 21% out of 42 observations, $chi^2 = 1.13$, $p = 0.30$), and in both sizes of mussel 50% of the Prises occur after Levering and 50% during Chiseling. Overall, Prising is much less frequent than it is in the adults' techniques (adults: a Prise occurs in 30% of small mussels and in 82% of medium mussels).

I do not know why this should be so, especially since Prising initially occurs at a very high frequency when 2/3 week old young first attempt to open apart the valves of a mussel. An interesting point with the newly independent young is that the duration of Chiseling in medium sized mussels is significantly reduced when a Prise occurs (see Table 39b), although there is no significant reduction in small sized mussels. If the young are able to differentiate between the duration of Chiseling with and without a Prise, then there exists the opportunity for the young to learn to Prise if and when necessary.

5/E Chiseling

Chiseling is under continuous external control (as in the adults) for the duration of Chiseling varies only with the size of the mussel (Table 39b). The general organisation of Chiseling is also similar in that there is one long Chiseling bout followed by shorter Chiseling bouts (Table 39c).

5/F Discussion

Although these data are not as detailed as those obtained for the adults, there is nothing to suggest that the factors organising the sequence in which the motor patterns occur are not the same, i.e. the complete external control of the elicitation, duration and transition between the motor patterns. The two major differences are the inefficiency of Chiseling and the low frequency of Prising, and I have already suggested (Chapter 8) that these may be causally connected.

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