Parental feeding in the Oystercatcher

(*Haematopus o. ostralegus* (L.))

By

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(Med et dansk resumé: Fodring af unger hos Strandskade.)

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INTRODUCTION

Like other wader chicks the Oystercatcher chick is nidifugous, and performs food-finding movements soon after hatching. However, it obtains all or most of its food from the parents (DEWAR 1915 and 1920, DIRCKSEN 1932, BUXTON 1939, TINBERGEN and NORTON-GRIFFITHS 1964), and the feeding of the chick takes place in a characteristic way (DIRCKSEN l.c., LIND 1958, RITTINGHAUS (in a film of Encyclopaedia Cinematographica)). This kind of behaviour is very unusual in waders, and in addition, the parental feeding-behaviour of the Oystercatcher is rather different to that of related groups, e.g. gulls and terns. It appears to be an interesting specialization.

On the basis of observations in the field, together with a few laboratory experiments, the present paper describes and discusses the parental feeding-behaviour of the Oystercatcher in more detail than attempted hitherto. The paper also deals with other behaviour patterns in adults and chicks which help to elucidate the problem of feeding as part of the parental system in this species.

Observations were carried out during three seasons (1957–59) at the Tipperne sanctuary in Ringkøbing Fjord, West Jutland. The sanctuary consists of meadows surrounded by shallow water. The nests of the Oystercatchers are found in the meadow and most food-finding activity takes place in the shallow water. In most places the meadow is bordered by rather high vegetation (mainly *Scirpus* and *Phragmites)*, which is situated partly in water and partly on land. The variations in water level are due partly to an artificial regulation in the fjord and partly to the influence of wind. There is no tidal water, but Tipperne was originally a marsh area. The water is brackish. Frequently, at a low water level, vast areas of slightly muddy sand is left drying along the coast.

The Oystercatcher population at Tipperne is not very large (about 25–30 pairs in an area of 450 hectares), but in some places they breed more closely than in others. Most of the observations were carried out in an area near the laboratory building, comprising part of the meadow and the adjacent shallow water or mud-flats. Here, three broods of different pairs were observed almost daily for periods of varying length, from the time of hatching or shortly afterwards, until some time after the chicks were fledged. When the water level was high the chicks, especially the small ones, tended to remain in the coastal vegetation; on some days, therefore, it was difficult or impossible to make any observations. Besides these rather continuous observations, the author made many sporadic observations on several other broods in the area. In most cases a telescope (35x), placed in an observation tower, was used; on a few occasions, observations were made from a hide. Some of the chicks and adults could be recognised individually (cf. below).

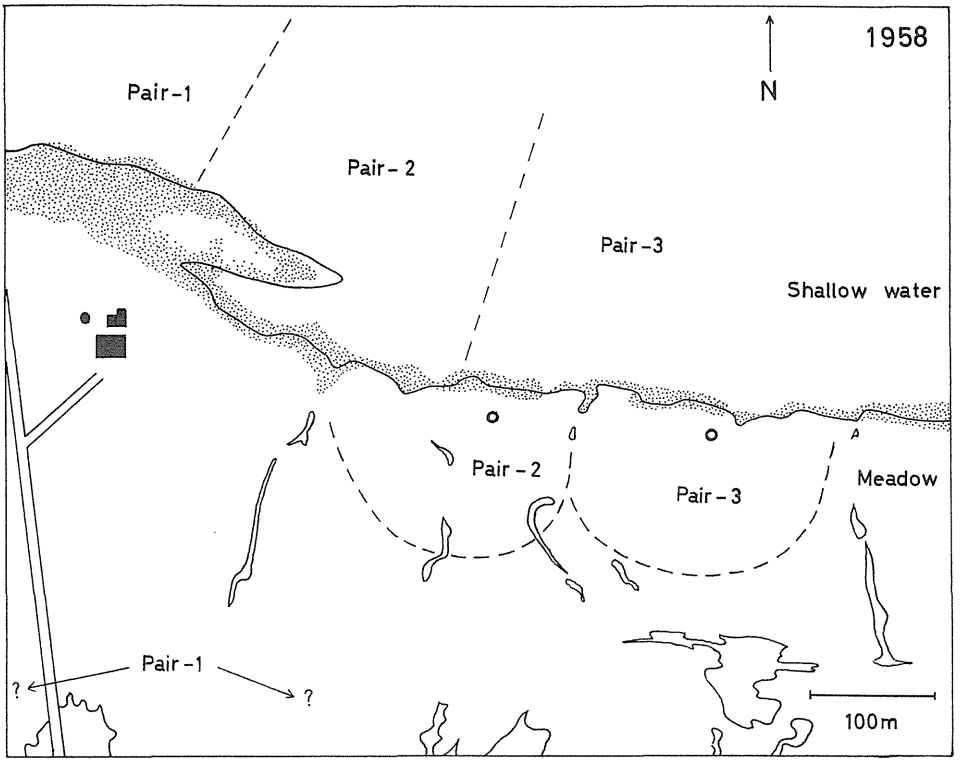
TERRITORIES

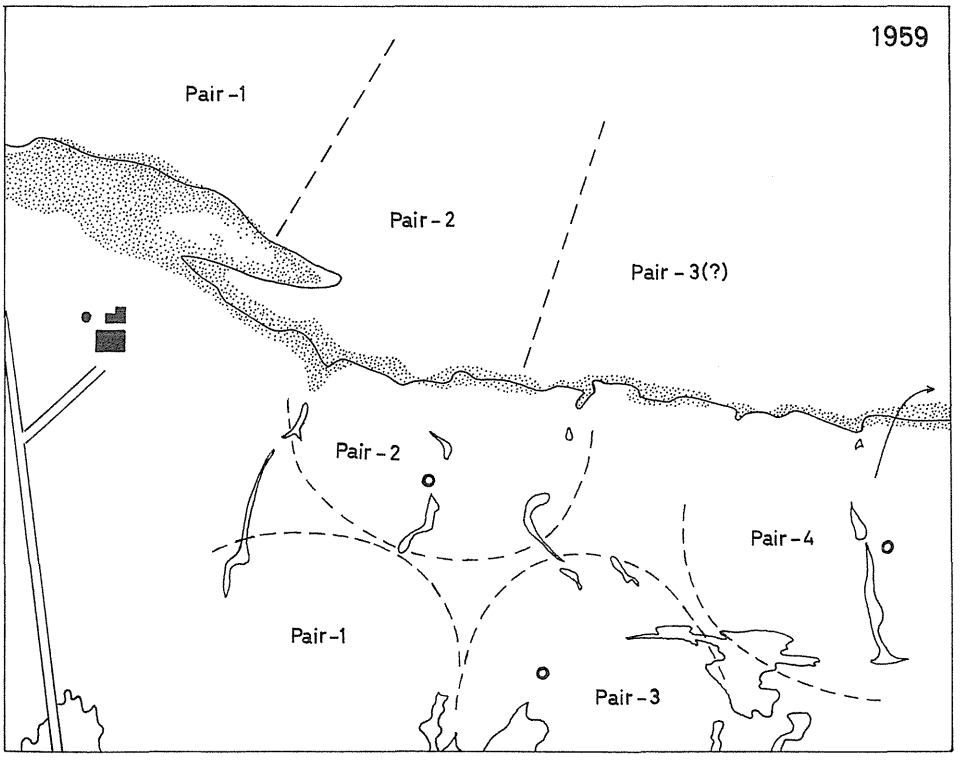
All Oystercatcher pairs inside the observation area near the laboratory building maintained typical breeding territories. In a limited area in the meadow the pair rest and find food, and here they make nest-scrapes, and finally a nest. They are so strongly attached to this place that if one nest is robbed they produce a new clutch in another nest in the same territory. All Oystercatchers are chased away and the pair perform boundary fights with neighbours. However, intruders occured only rarely, and boundary fights were mostly performed at the start of the season. The reason for this may be that the neighbours are familiar with each other, as many of the pairs are the same from one year to the next (cf. below, and JUNGFER 1954). Definite pair-forming behaviour was never observed; apparently the birds were already paired when they took up their territories.

In addition to the breeding territory a feeding territory is also maintained. Characteristics of this territory are: — 1) It is a coastal area including about 1–200 m of the shore with high vegetation and mud-flats lying outside, the area of the latter being dependent on the water level. When the flats are dry or moderately flooded, feeding and aggressive behaviour to intruders can take place at a distance of about 200 m from the coast. 2) The feeding territory may be close to the breeding territory or some distance apart. 3) Most food-finding takes place in this area. 4) Whenever strangers appear – and this happens rather often – they are chased away, and "piping fights" with neighbours frequently occur. 5) The limits between neighbouring territories are unchanged for long periods, even for the whole season, and even far from the coast where there are no landmarks, the limits

Fig. 1. The approximate situation of Oystercatcher territories in the observation area at Tipperne in the years 1958 and 1959. Dotted area: high coastal vegetation. Circles: nests. Broken lines: approximate boundaries of territories. Cf. text.

Fig. 1. Omtrentlige territoriegrænser i observationsområdet i 1958 og 1959. Prikket område: høj vegetation ved kysten. Cirkler: reder. Stiplede linjer: grænser.


1958
N
Pair-1
Pair-2
Pair-3
Shallow water
Pair-2
Pair-3
Meadow
Pair-1
?
?
100m


1959
Pair-1
Pair-2
Pair-3(?)
Pair-2
Pair-4
Pair-1
Pair-3

are fairly well respected by neighbours. 6) The chicks are brought to the feeding territory and remain here until some time after fledging; they may visit the meadow territory for short periods. 7) Some pairs, at least, maintain the feeding territory throughout the whole breeding season (e.g. pair–2 1958 and 1959, pair–1 1959, cf. below), but it is possible that others do not defend a feeding territory until after the chicks are brought there (pair–1 1958).

The situation of the territories in 1958 and 1959 is shown in fig. 1.

1958: Pair–1 appeared at the coast 22. 6., with one newly hatched chick (situation of breeding territory uncertain) and from then on maintained a feeding territory until observations were finished 30. 7., the chick still being present at that time. The male was limping a little and was, therefore, easily recognizable. Pair–2 had a breeding territory in the meadow and a feeding territory at the coast nearby. Two chicks hatched 5–6. 6. (one disappeared shortly afterwards), and the family remained in the feeding territory until about 18. 7., when they disappeared. The pair returned to the territories about 28. 7., without the chick. The male was colour-marked in 1957 (it was captured on the nest near the nesting place of 1958). Pair–3 had breeding and feeding territories like pair–2. Two chicks were hatched 17–18. 6., but disappeared shortly after. The adults stayed in their territories until at least the middle of July. One of the two was colour-marked in 1957 (captured on the nest near the nesting place of 1958).

1959: Pair–1 had a breeding territory in the meadow and a feeding territory in the same area as in 1958. They had no success in breeding, and disappeared about 8. 7. The male was identical with male–1 of 1958. The breeding and feeding territories of pair–2 were approximately the same as in 1958. The nest was robbed 18. 6. The adults stayed in their territories until about 10. 7. The male was identical with the male of pair–2 in 1958. Pair–3 (birds unmarked) had a breeding territory in the meadow some distance from the coast, and this pair, probably, maintained a feeding territory just east of the feeding territory of pair–2. No breeding success. One chick of pair–4 (birds unmarked) hatched 17. 6. The family moved to the coast farther east.

The sex of the birds mentioned was ascertained by observation of complete copulatory behaviour, in which a marked bird took part.

In 1957 two pairs had breeding and feeding territories, but it was not noticed whether they defended the feeding territories prior to the hatching of chicks.

In other places on the sanctuary the author frequently observed typical territorial disputes on breeding grounds as well as on the sands.

A pair which have chicks in the feeding territory may still maintain the former breeding territory in the meadow, e.g. pair–2, 1958; the birds of this pair sometimes found food here for themselves and the chick, and any intruders were chased away. The chick was brought to the meadow territory around fledging time, when the water level was high.

The following is an example of this behaviour: 8. 7. 1958. Late in the afternoon the adults feed the fledged chick in the feeding territory, but the water is high and the feeding rate therefore very low. The adults then fly to the territory in the meadow. One of them finds food here and brings it to the chick. It again feeds the chick in the feeding territory (only 4 times in 4 minutes, a low feeding rate). The parent subsequently flies to the meadow, followed by the chick, and the chick is fed in the territory here. Next day, the chick is back in the feeding territory.

Other pairs were also observed bringing food from the meadow territory to the chicks in the coastal territory, and occasionally, half-grown or fledged chicks were observed in the meadow territory, although they only remained here a few hours or one day at a time. The former breeding territory appears to function as a land feeding station. Pair–1 1958, which had widely separated territories, never brought the chick away from the coastal feeding territory.

In those cases where the two territories are close together and are not separated by a border of high vegetation (which is difficult for the chicks to cross), there is probably a more frequent shifting between feeding of chicks on the sands and

in the meadow. In such an instance it would be irrelevant to distinguish between two sorts of territories, there being only one which serves partly as a breeding place and partly as a feeding ground.

Pair–2 (1958) and their chick disappeared when the chick was about 40 days old. Furthermore, in a few cases it was observed that pairs fed fully fledged chicks in places where they certainly had not been before. It is, therefore, possible that the parents and their brood leave the territories (at least for periods), some time after the chicks are fledged and before parental feeding has stopped. At this stage the chicks are capable of flying, and other more profitable feeding grounds can be used.

It is remarkable that Oystercatchers which lose eggs or chicks so late in the season that a new clutch cannot be started (June–July), do not gather in flocks shortly after like many other waders, e.g. Lapwing *(Vanellus vanellus)*, Godwit *(Limosa limosa)* and Avocet *(Recurvirostra avosetta)*, but maintain pair-bond and territoriality for a month or more (cf. above). Even at the beginning of August it is not uncommon to observe pronounced territorial behaviour in pairs without young, and most of the Oystercatchers on Tipperne still occur in pairs at this time.

DEWAR (1915), observed the behaviour of Oystercatchers in an inland locality, and found that the pair will defend a breeding territory and an adjacent feeding ground giving easy access to the young; he also states that there is a more distant feeding ground where the adults go, and that here there are possibly no territories. The author's observations on Oystercatcher territoriality at Tipperne largely confirm the observations made by DEWAR half a century ago, but more or less disagree with statements made by other observers.

HUXLEY and MONTAGUE (1925) observed territorial behaviour and presume that the Oystercatcher has a breeding territory. DIRCKSEN (1932) found that it has a breeding territory and that a territory at the nesting place is maintained after the hatching of the chicks, the latter remaining here. On the coast these territories were used by the chicks as a base for excursions on the wade. He observed defence of the territory against Redshank *(Tringa totanus)* and terns, but does not mention defence against neighbours, and apparently he did not observe that the wade, where the chicks were fed, was part of the territory. BUXTON (1939) found breeding territories, where food-finding took place, and some of these territories on the rocky coast included areas which were dry only at ebb-tide. However, he states that after the hatching of chicks the territory changes, even from day to day, according to the movements of the chicks. WEBSTER (1941) – in the case of *Haematopus ostralegus bachmani* – also states that rocks exposed to the tide, which are particularly valuable for feeding, are included in the territory. MAKKINK (1942) made very detailed observations and found that the Oystercatcher is a *non*-territorial bird. This author has often been cited in handbooks and papers, but his conclusions on the territorial behaviour of the Oystercatcher (including those concerning the „piping" behaviour, cf. below) do not appear to be valid in all cases. Recently RITTINGHAUS (1964) has published a summary of his observations on territorial behaviour of the Oystercatcher at the Frisian island Oldeoog. He states that breeding as well as feeding territories are maintained throughout the season.

At present we cannot do other than guess the reason for the various disagreements on the territorial behaviour of the Oystercatcher (and some other wader species as well, cf. LIND (1961, p. 49)). It could be 1) that the territorial behaviour depends largely on how densely populated the breeding area is; 2) that the separation of breeding and feeding territories depends on the character of the locality; 3) that some observers have not recognised the existense of well defined territories on bare mud-flats far from nesting places, and have classed most of the hostile behaviour occurring here with sexual or some sort of social behaviour, and 4) that the presence of large numbers of non-breeding birds in a breeding area is likely to blot out the features of territoriality, as the hostile behaviour of non-breeding birds in flocks may have a different background from that of breeding birds. Knowledge about the behaviour in a locality like Tipperne will probably be necessary in order to understand the more complicated events occurring in places with a dense population and where flocks of non-breeding birds are present.

A few remarks should be made on *hostile behaviour patterns*.

Intruders on the territory are always met with some sort of hostile behaviour, usually the "piping performance". This behaviour is described in detail by HUXLEY and MONTAGUE (1925), DIRCKSEN (1932) and MAKKINK (1942). In encounters between two neighbours both "pipe". In two pairs, in which the sexes could be distinguished, the male proved to be by far the most active defender of the territories, but quite frequently the female joined the piping male. Thus, four birds can be piping at the same time at the boundary. Occasionally, even three pairs participate, viz., in an area where three territories meet. On one occassion four pairs formed a piping party on the sands far from the coast; they were observed before and after the performance and proved to be one intruder pair and three pairs of local territory owners. In a few cases an Oystercatcher was observed to pipe for a brief instant when meeting its mate or as a response to a begging fledged chick; otherwise, piping – on the ground and in the air – was obviously hostile behaviour only.

According to the literature, the piping performance is of a rather complicated nature. HUXLEY and MONTAGUE (1925) state that it occurs in several different situations; in courtship, in hostile behaviour and in social excitement, „apparently in all forms of strong emotional excitement except fear". MAKKINK (1942) emphasises the sexual and social nature of piping. These authors made observations in areas where flocks of non-breeding birds were present. The „social piping" was particular prominent in these flocks and seemed to be related to pair-formation. DIRCKSEN (1932) terms the piping performance a „Balzspiel" and suggests that it first and foremost serves pair-formation, but he also mentions its hostile functions. He noticed „Balzspiele" late in the season and assumes that at that time they have lost their original function (in courtship and hostility), and are often merely „asexuelle momentane Erregungsäusserungen".

At Tipperne there were rather few breeding pairs and no flocks, and the Oystercatchers already seemed to be paired when they took up their territories in spring. It may be of interest to note that under these not very complicated circumstances the piping was practically always a distinct hostile behaviour connected with the defence of territories, and this was also the case late in the season. „Social piping" was never observed. Also RITTINGHAUS (1964) states that the piping performance is a hostile behaviour.

A stranger alighting in a territory often does not pipe, but displays a sort of submissive posture (MAKKINK, 1942: "Thick-set attitude"), assuming a rounded form: the neck is withdrawn and the head is made round, without the flattened crown characteristic of the aggressive bird. Other hostile postures mentioned by HUXLEY and MONTAGUE and by MAKKINK were frequently observed, i.e., the "diplomatist attitude", "balancing" (or bobbing) and "pseudo-sleeping", and a posture resembling the upright posture of other waders (cf. LIND 1961) which is possibly the posture MAKKINK termed the "crow attitude".

Some movements which should be grouped as displacement activities occured very often during boundary disputes, viz. tail-shaking, throwing straws and pecking at the ground or the surface of the water. A bird standing in the water may perform displacement pecking followed by complete backward-throwing movements without actually throwing straws or other objects. Pecking at the ground often results in what appears to be a complete feeding action, including swallowing movements. The bird may, in some cases, swallow small food items, but in other cases (as in the following example), it obviously does not (cf. p. 14).

After a piping performance, two neighbours are together at the boundary between their feeding territories. They peck into the water at an unusually high speed; one peck follows immediately after the other and every peck is terminated by distinct swallowing. There is no searching for food items.

The birds are obviously excited (sometimes with bobbing, flattened crown). After a while one of them flies away, and then the other immediately starts normal food-finding behaviour, including searching, probing and piercing into the bottom.

"Butterfly flights" and "whirr flights" were sometimes performed in connexion with territorial disputes; the former, however, were also performed in other situations, e.g., when a bird was flying from one of its territories to the other.

FEEDING OF SMALL CHICKS

DEWAR (1920) states that the first transference of food from adult to chick takes place towards the end of the chick's first day. Observations on one brood confirm that parental feeding does not start until several hours after hatching. A chick hatched in the night (pipped egg at 9 p.m., dry chick at 7.10 a.m.) received no food until 10.20 a.m., whereas, the other chick of the brood, which hatched on the preceeding day, was fed quite a few times during the same period. The adults' feeding of the chick took place near the nest and comprised food items which the parents found in the breeding territory.

One brood arrived at the feeding territory on the coast the day after the hatching of the last chick; two other broods were observed here after a spell of two days, and in still other cases, small chicks, which could be only a few days old, were observed on the coast.

The following description concerns quite small chicks, i.e., less than 2–3 weeks old. When the chicks are about 3 weeks old the behaviour of the parents changes to some extent, as will be described later on. The changes are gradual, thus, the somewhat unprecise terms, "small" and "older" chicks.

Feeding usually takes place as follows: The adult walks forward, here and there probing the surface with the bill tip; it then jerks the bill into the sand, makes some levering movements with it, and turns on the spot; finally, the food item, usually a nereid worm, is drawn up. Holding the worm in the tip of the bill the adult runs quickly in the direction of the chick with neck withdrawn and bill pointing slightly downward. The parent stops some distance from the chick, drops the worm on the sand, and takes it up again, moving it between the mandibles. It then waits in the *feeding posture:* The adult stands motionless with the bill pointing almost vertically downward. The food is held in the tip of the bill just above the surface of the sand (fig. 2). The chick runs up to the parent and takes the food. The parent waits until the chick has swallowed the worm, then it starts searching for more. The adult always runs when bringing food, and walks when it starts searching again.

If the chick is near the adult when the latter catches the worm the adult does not run to the chick, but merely turns halfway round in the direction of the chick.

The parent always brings one food item only; collecting of food never takes place.

As long as the adult is searching for food the chick does not respond to the parent, or it follows slowly, some distance away. In some cases, the first distinct response of the chick is shown when the parent starts piercing for a worm: the chick runs quickly forward and then stops. In other cases, the first reaction comes when the adult is running in the direction of the chick; the chick then starts to move towards the adult. Finally, the chick may only respond when the feeding posture is displayed.

When the adult carries food it always stops some distance from the chick to assume the feeding posture, thus the chick has to approach the adult to receive the food. Only newly hatched chicks remaining near the nest were observed to receive food on the actual spot where they were waiting for it.

The chick calls when approaching the adult (cf. p. 12). The latter possibly calls when carrying food; during observation at a nest with newly hatched chicks it was ascertained that the parent called softly when bringing food.

The behaviour of the adult includes following specific feeding responses to the chick: Turning against or running in the direction of the chick with food, presenting the food in the feeding posture, and waiting for the chick to swallow the food. The responses of the chick are as follows: Calling and running to the adult piercing for food, approaching with food, or presenting food, and pecking at the food at the tip of the adult's bill (fig. 2).

An adult feeding a chick only a few days old presents the same food item several times when the chick does not respond at once. After the first presentation the adult walks away with the food, turns around and again assumes the feeding posture near the young. This can be repeated many times. In some cases the adult merely drops the food and takes it up again, or moves the food item between the mandibles before it again stands motionless in the posture. Sometimes the young finally eats the food, at other times the adult does. Afterwards several worms may be brought to the chick, but when the latter still refuses to take the food, the parent starts to feed itself.

The feeding of the newly hatched chick is obviously carried out with great care, but after some days, at least when the chick is one week old, some small variations in behaviour of chick and adult can frequently be observed.

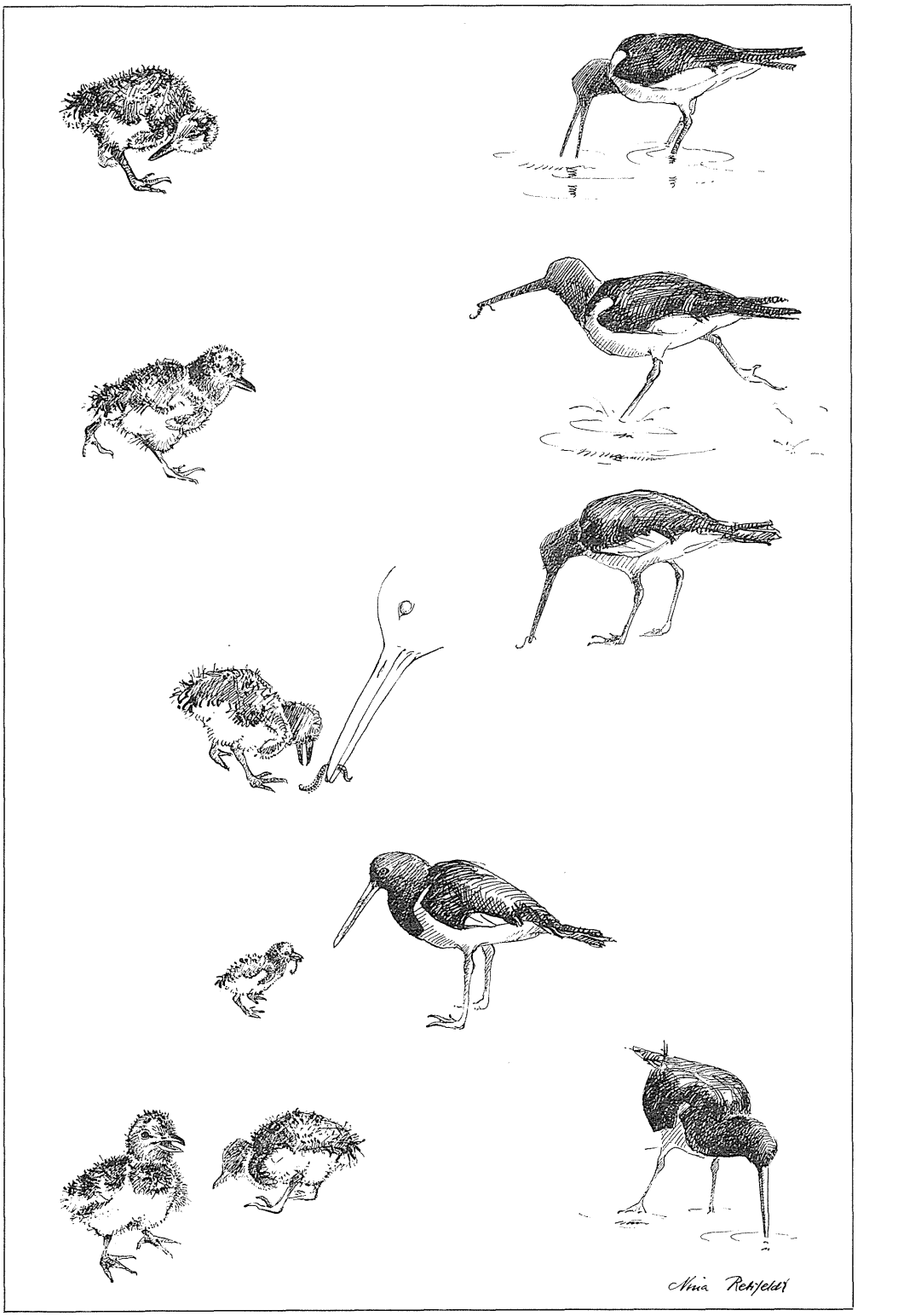
These changes certainly will increase the feeding rate. The adult's period of waiting while the chick is manipulating and swallowing the food is shortened, and sometimes the parent starts on a new search as soon as the chick pecks at the food. Repeated presentation of food now occurs more rarely. Further, the adult frequently drops the food when presenting it, so that the bill does not hold the food item but points at it, whereby the chick pecks it up from the ground.

Feeding of chicks mostly takes place in bouts, thus one adult feeds a chick many times in succession until the chick is satisfied. Sometimes an adult finding food for itself brings food only once or a few times at intervals. For instance, it may bring food from the wade far from the coast or from the meadow territory. This kind of scattered feeding sometimes occurs simultaneously with the other parent feeding the young continously.

A series of feeding can be started by the adult as well as by the chick. The parent brings a food item, the chick accepts, and feeding continues. Alternatively, the chick approaches the adult, and the adult at once starts searching for food. Pecking at the bill of the adult may possibly induce

Fig. 2. Typical sequence of behaviour during parental feeding (read from above). Chick: Waiting – running to the adult – taking food – swallowing – preening, calling, pecking at the ground, etc., during feeding pause. Adult: Catching and carrying food – presenting food in the feeding posture – waiting for the chick to swallow the food – searching for food.

Fig. 2. Typisk adfærdsrækkefølge (fra oven og nedefter) ved fodring. Unge: Venter – løber til den voksne – tager fødeemnet – sluger – piller sig, hakker mod jorden, osv., i pausen. Den voksne: Fanger et fødeemne – løber med det i retning af ungen – indtager fodringspositur – venter til ungen har slugt – søger ny føde.


Nina Rehfeldt

	Pair–1 1958		Pair–2 1958	
	♂	♀	♂	♀
Number of obs.-periods with "scattered feeding" *Antal perioder med spredt fodring*	2	3	7	3
Number of observed feeding bouts *Antal fodringsserier*	5	6	3	22

Table 1. Participation of male and female in feeding their chicks.
Tabel 1. Hannens og hunnens deltagelse i fodringen af ungerne.

parental feeding during the chick's first days. This behaviour was observed in newly hatched chicks near the nest, but produced no immediate reaction from the parent. The reason why it was not observed more often may have been that the chicks were usually hidden in the coastal vegetation during their first days, and therefore difficult to observe. DEWAR (1920) mentions that small chicks peck at the bill of the parent when hungry. The readiness of the parent to start feeding as soon as the chick approaches indicates that this kind of begging only plays a role in connection with brooding. Older chicks beg in another way (p. 15).

When not disturbed, the parent will continue to bring and present food until the chick refuses to take more or leaves the place to take cover in the vegetation, i.e., the termination of feeding depends on the behaviour of the chick, which then appears to be satiated (p. 18).

When the adult has started self-feeding after a bout of feeding the young, it sometimes adopts the feeding posture for a short while before eating, and now and then a worm may be brought to the young. This behaviour demonstrates the strong tendency of the parent to feed the chick.

During self-feeding on the sand the adult frequently takes the food to the nearest water, where it is washed before eaten. Likewise, when feeding chicks, the parent sometimes washes the worm before presenting it in the feeding posture.

Both parents feed the chicks. In one pair the mates shared feeding equally, but in another pair the female did most of the feeding (table 1).

Chicks of a brood of 3 were usually fed separetely. In a few cases the transition from feeding one chick to feeding the other was observed; the new chick starts following the adult, the other staying behind. If two chicks follow, the one reaching the parent first receives the food. Only older chicks were observed to threaten each other (p. 19), but small chicks probably also do so. DEWAR (1920) states that rivalry for food already appears on the third day of a chick's life. It may depend on the amount of food and the frequency of feeding. HEINROTH (1928) reared Oystercatcher chicks and says that "die Geschwister von Anfang an untereinander sehr unverträglich sind; sie beissen sich, namentlich wenn sie Hunger haben, beim Füttern wütend, und einer unterdrückt gleich den andern" (l.c. p. 17). HEINROTH observed that one chick of a brood killed the others.

THE "PECKING RESPONSE"

The behaviour of chicks and parents on the sands indicates that a set of releasers and learned or unlearned responses are functional in parental feeding. An important part of the feeding procedure is the manner in which the chick pecks at the food in or under the tip of the parent's bill. In order to investigate the pecking

response to the adult bill experiments with newly hatched chicks taken from nests were carried out in 1958 and 1959. The chicks were brought to the laboratory and presented to various models of the adult bill.

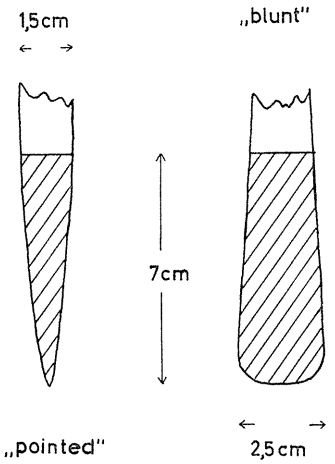


Fig. 3. Form and dimensions of bill models used in the experiments.
Fig. 3. Næbmodellernes form og størrelse.

The chicks showed a number of responses to the models and frequently pecked at them. To obtain these responses it was necessary to use young less than about 10 hours old, otherwise they would be too timid. Furthermore, the chicks had to be brooded artificially at intervals, since cold proved to suppress pecking responses to a large extent. Various other factors also influence the behaviour; e.g., after a number of tests, the chick would not respond anymore. Sometimes the chicks seemed to be somewhat frightened or confused. The limitations in the usefulness of the chicks, and the difficulties in obtaining nestlings greatly limited the number of successful tests.

Two types of cardboard bill-models were used, the pointed and the blunt model (fig. 3), and each of them were made in 3 colours, red, white and black. The chick was tested several times, and in each series of tests all 6 models were presented successively at short intervals and in random order. The models were held in a vertical position, 2 cm above the ground, and at a distance of 7 cm from the chick. 40 successful series of tests were carried out with 6 chicks (a total of 240 tests). A series of tests was regarded successful when at least one test included a pecking response; series of tests without pecking responses were rejected.

All the chicks were probably unacquainted with food (cf. p. 7), but certainly familiar with the adult bill. However, one of them was taken shortly after hatching when it was still wet, i.e., before it had received food from the parents or had begun to peck. Its reaction to the models after artificial drying did not differ from that of the other chicks.

More detailed experiments on the responses of wholly inexperienced chicks are in progress.

In a typical response the chick starts calling and goes up to the model; the bill is directed towards the lower part of the model, and the chick then makes several pecks at this area (fig. 4 and 5).

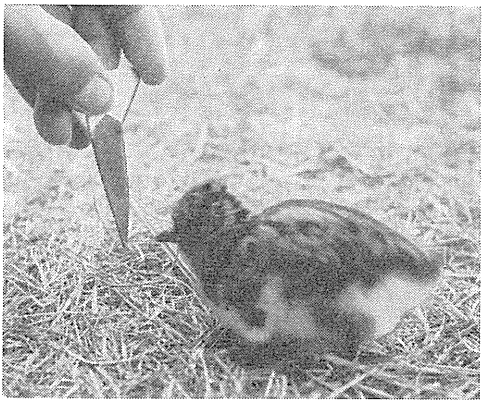


Fig. 4. Chick orienting its bill towards a model of the adult bill prior to pecking (this kind of model was not used during the laboratory experiments).
Fig. 4. En unge retter næbbet mod modellen, før den hakker.

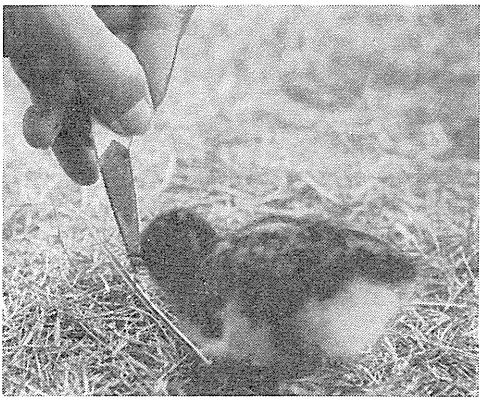


Fig. 5. Chick pecking at the tip of a model of the adult bill.
Fig. 5. En unge hakker mod modellens spids.

The calling response is a series of rapidly repeated short calls. This was always the first response, and sometimes the only one. The chick frequently uttered the same calls when something was moving nearby, and it seemed to be a rather unspecific social response. In pauses between two tests the chick uttered single calls of varying strength and of quite another quality.

The chick continues to call while going to the model, but is silent during pecking. Moreover, when the model is presented at a distance of half a metre or more, the chick may run to it calling eagerly the whole time.

Table 2 shows the number of presentations of the different models which released a pecking response. The proportion of presentations with positive responses is much higher for red models than for the other colours. The difference is highly significant for pointed as well as for blunt models (pointed, red-white: N = 78, $\chi_c^2 = 29{,}47$, $p < 0{,}001$). The difference between white and black pointed models is not significant at the 5% level (N = 34, $\chi_c^2 = 1{,}99$, $p < 0{,}20$ and $\chi^2 = 3{,}11$, $p < 0{,}10$). The pointed model is significantly more effective than the blunt model (red models: N = 80, $\chi_c^2 = 19{,}27$, $p < 0{,}001$, and white/black models: N = 118, $\chi_c^2 = 7.91$, $p < 0{,}005$).

In 1957 some preliminary experiments were carried out with three pointed wooden models, one red, one unpainted and one black. These experiments included 59 successful series of tests with a total of 177 presentations. They showed the same preference for the red colour (proportion of positive presentations: red 91,5%, unpainted light wood 52,5%, black 16,9%). These experiments were, however, less standardized than the 1958–59 experiments.

Fig. 6 shows the number of pecks made towards the different models during the 1958–59 and the 1957 experiments.

We find that among the models used the red and pointed model, which has the

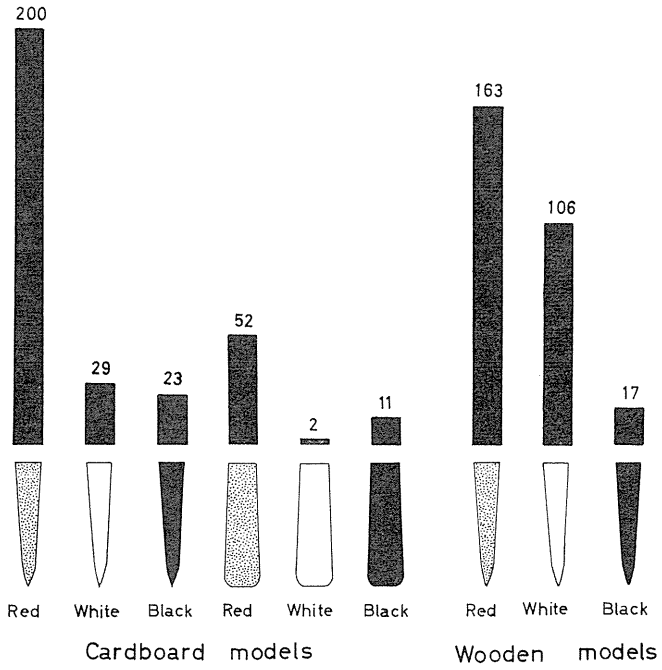


Fig. 6. Number of pecks made towards models during the 1958–59 experiments (cardboard models, number of presentations 6 × 40), and the 1957 experiments (wooden models, number of presentations 3 × 59).

Fig. 6. Antal hak rettet mod næbmodellerne i to eksperimentserier med papmodeller (1958–59) og træmodeller (1957).

	Pointed models *Spidse modeller*			Blunt models *Afrundede modeller*		
	Red *Rød*	White *Hvid*	Black *Sort*	Red *Rød*	White *Hvid*	Black *Sort*
Number of presentations with pecking response *Antal positive præsentationer*	37	13	8	21	1	6
Percentage of positive presentations *Samme i procent*	92,5	32,5	20,0	52,5	8,8	

Table 2. Frequency of pecking responses to different bill models. 40 presentations of each model.
Tabel 2. Kvaliteten af forskellige næbmodeller som udløsere for ungens hakkereaktion udtrykt ved antallet af præsentationer, der fremkaldte en reaktion. Hver model blev afprøvet 40 gange.

greatest resemblance to the adult Oystercatcher bill, is the most successful in inducing pecking. The red colour is preferred rather than the white and black, and the pointed model is more successful than the broad and rounded model.

Pecking was nearly always directed at the lowest centimetre of the model; when pecking at the blunt model, the chick nearly always aimed at the vertical edges, never at the lower edge, and only rarely at the flat side (fig. 7). Apparently, a vertical edge releases pecking, and this may be the reason why non-red and non-pointed models sometimes are effective.

The downward position of the model is of great importance to the pecking response. A few tests confirmed the general impression that a red pointed model presented in a way corresponding to the position of the bill when the adult Oystercatcher is standing in a "normal" attitude does not release pecking in small chicks (fig. 8).

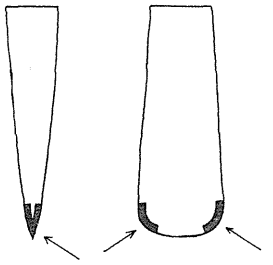


Fig. 7. Areas of the bill model at which the chicks most often directed pecking.
Fig. 7. De steder på modellerne, som ungerne oftest hakkede efter.

Sometimes the chick did not at first react to the model, but if the model was then moved slightly up and down and from side to side and again held quietly in position, the response could be released. The adult Oystercatcher performs corresponding movements of the bill during repeated presentation of food to chicks.

The manner of orienting the bill to the model prior to pecking shows a very distinctive behaviour pattern. The head is put forward and the bill tip points at the model at a distance of one centimetre or less, the head being held stationary for a short while in this position. The peck then follows (fig. 4).

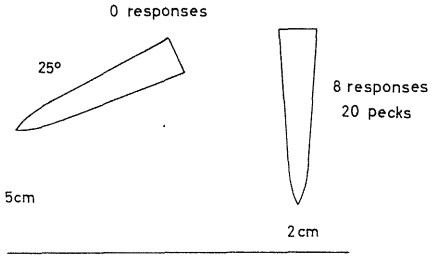


Fig. 8. Influence of position of bill model with regard to pecking response. 9 × 2 tests with two chicks.
Fig. 8. Betydningen af næbmodellens stilling for hakkereaktionens udløsning.

Normally, pecking is released and oriented by the model, but now and then the orienting part of the response does not work, some pecks being made in a rather careless manner and not hitting the model. On some occasions, the chick, when standing at the model, makes some wholly undirected pecks away from it.

In addition to pecking at the model, the chick quite often makes pecks at the ground underneath; sometimes this is done in a curious, convulsive manner with widely opened bill and strongly bent neck, the chick biting and tearing at anything on the ground. When not presented to a model the chick walks around pecking at the ground here and there, sometimes distinctly pecking at small objects. Thus, beside the specific pecking response to the tip of the vertical adult bill the newly hatched chick performs pecking in many rather unspecific situations, which is also evident in natural behaviour on the sands.

Pecking at the model and at the ground is often followed by distinct swallowing movements and sometimes by bill-shaking, even if the chick was never observed to obtain anything in the bill (cf. swallowing after displacement pecking in the adult, p. 6).

The above-mentioned experiments and observations suggest that the adult Oystercatcher bill, as demonstrated in the feeding posture, releases and directs a pecking response in the chick. Among the releasing stimuli are colour, form and position of bill. The pecks are directed at the tip of the bill, where the adult holds the food. Whether, under natural circumstances, the inexperienced chick pecks directly at the bill tip or at the object being held in the tip, is not known, and has still to be investigated.

FOOD

According to observations by telescope the main food of the adult Oystercatcher on the sands is clam worms *(Nereis diversicolor)*, which occur here in large numbers. It sometimes takes small bivalves. These food items are caught by piercing into the dry or shallow sea-bed. In addition, quite small food objects are taken directly from the surface of the sand or from the water. In the meadow, *Tipula* larvae probably constitute the main part of the food.

Sea-bed samples, taken by cand. mag. K. H. KLAUSEN in June 1960 on the sands in the observation area, contained large numbers of *Nereis diversicolor* and *Pygospio elegans* (order Polychaeta), Tubificid and Enchytraeid worms (order Oligochaeta), *Hydrobia* sp. (order Prosobranchia), and *Corophium volutator* (order Amphipoda). Additionally, there were a few rather small bivalves, viz. *Mya arenaria*, length 13–30 mm, and *Cardium edule*, length 4–22 mm (order Eulamellibranchia).

The small food items taken without piercing are probably mainly *Corophium*. The chicks also sometimes peck up small food objects from the sand, possibly *Corophium* and insects.

Apparently, all sorts of food taken by the adults are given to the chicks, but observations by telescope have shown that clam worms constitute the main part of food given to chicks staying in feeding territories on the coast.

It frequently happens that a parent, while searching food for a chick, finds small food items which it eats itself, whereas all larger worms and bivalves are brought to the chick; only when the young is in very close vicinity is it frequently given small food items too. Thus, the adult selects food items according to size, and this selection depends on the distance to the chick. This kind of selection is also evident in other situations; a few examples should be mentioned:

An adult having finished a feeding bout now finds food for itself. It eats most of the worms immediately (including those of a size usually given to the chick during a series of feeding), but now and then it obtains a particularly large one, and this is brought to the chick.

In a similar situation an adult obtains a big worm, it takes it in the bill and runs in the direction of the young. The worm breaks and only a small piece is left in the bill. The bird stops, swallows what is left of the worm and walks away to begin searching again.

Still in the same kind of situation, an adult swallows all the small worms immediately, whereas the larger ones are held for a moment in the feeding posture before they too are eaten.

An adult several times brings large food-items to the chick from some distance away, whereas it eats small food items itself. On one occassion, the chick had received a worm and the adult walked away as usual, but a few steps from the chick it catches a small food item, which is hardly visible in the telescope; it turns around and presents it to the chick.

From a functional point of view selecting food items of a certain size for feeding chicks is very important. For a bird like the Oystercatcher, which does not collect food, it will be advantageous not to waste time and energy by bringing food objects of minimal value. Only when the chick follows the food-finding parent closely is it possibly "worthwhile" to feed with small objects.

Whenever an adult searching for food for a chick catches a bivalve this is brought to the chick, sometimes in an opened condition, sometimes not. It is presented to the chick in the same way as when feeding with a worm. But the chick very often refuses to take the bivalve in spite of repeated presentations, even though it might accept worms immediately prior to and just afterwards. Apparently, the chick does not like bivalves (perhaps because of the shell); the parents, however, do not make any distinction between this kind of food and other large food items like worms and *Tipula* larvae when bringing food.

FEEDING OF OLDER CHICKS

When the chicks are about 3 weeks old the parental feeding pattern changes somewhat: 1) The adult more frequently stops presenting food and starts self-feeding when the chick does not at once react to the feeding posture; 2) the adult often stops feeding chicks before they have shown signs of being satisfied; 3) the adult often does not react to the approaching chick by feeding it. These changes of adult behaviour show that the readiness to find food for the chicks now decreases. However, the adults' behaviour does not change completely; they sometimes behave in one way, sometimes in the other way, and therefore the feeding of chicks still, in some cases, takes place in exactly the same way as previously.

About the same time the chicks start to show distinct begging behaviour, and the adults may or may not respond by feeding them.

In two different broods the first begging behaviour was observed when the chicks were 22 days old, and in a third brood begging also started when the chick was in its 4th week. If feeding is restricted to certain periods of the day (cf. TINBERGEN and NORTON-GRIFFITHS 1964), or if food is scarce, begging possibly appears at an earlier date.

When begging, the chick assumes a posture similar to the submissive posture of the adult; the neck is withdrawn, the head is held at or below the level of the back, and the body is puffed out (fig. 9). The chick approaches the parent very closely. It usually rubs its head and neck against the flanks and, especially, the breast of the adult. It moves from one side of the parent

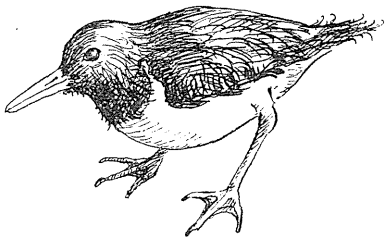


Fig. 9. Submissive posture of fledged chick.
Fig. 9. Posituren hos en flyvefærdig unge under fodringen.

to the other, passing in front. Sometimes the chick jerks its head upwards at intervals, and very frequently it pecks at the adult, particularly at its head, bill, legs and toes. In between, the chick may peck at the ground below or in front of the adult or it makes unoriented pecks in the air. The chick calls while begging.

The parent avoids the chick with raised head, but the chick continues begging and keeps close to the parent. The adult may behave aggressively by piping for a moment, or it flies away, or after some time it starts searching for food. In the latter case, the chick stops begging immediately, but it will start again if the parent even for a moment interrupts searching. Food-searching of the adult, rather than presentation of food, seems to be the consummatory situation for begging.

The submissive posture is used not only during begging, but is frequently employed when the chick follows the parent and is fed.

Because of the decreasing tendency of the parents to feed their chicks the latter are sometimes left hungry for, maybe, hours. This, however, does not mean that the parents soon discontinue feeding altogether. The fledged chicks still receive the essential part of their food from the parents.

Two broods were still fed frequently at an age of 40 days (at this time observations on them were interrupted). This also applied to another brood of approximately the same age. Chicks in juvenile plumage, and able to fly with ease – perhaps 50–60 days old – were observed to partly find food in the manner of adults and partly begging and receiving food from the parents.

Until the chicks are about 5–6 weeks old the transference of food from adult to chick takes place in essentially the same way as previously. Then some new variations of parental feeding-behaviour can be observed; these variations alternate with normal feeding procedures. The feeding posture may be incomplete or wholly absent. Frequently, the adult draws up a worm and then immediately continues searching without waiting in the feeding posture for the chick; or the parent only half draws up the worm, and standing in the posture it holds the worm until the chick arrives; or the parent bores the bill into the sand and then goes away, after which the chick pecks up food from the hole. Such variations suggest that a final break down of the feeding mechanism is approaching.

EFFICIENCY OF PARENTAL FEEDING

The parental feeding behaviour ensures that the chick receives the same high quality of food as the adult.

Apart from the quality of the food the efficiency in feeding will depend on successful transference of food and feeding rate. Successful transference demands careful feeding; a high feeding rate demands a quick way of feeding. These two demands are in conflict. Thus, we should expect the parental feeding behaviour to be balanced, ensuring that speed in feed-

ing is not increased to such an extent that transference is likely to fail. Actually we find evidence of this:

Newly hatched chicks are fed from the bill and the parent waits until the chick has swallowed the food, but later on this occurs less frequently (p. 8) and is, in fact, no longer necessary, as the chick can easily find food items dropped on the sand. As soon as food is dropped the parent is prepared to start searching again. Pointing at the food, however, still occurs and seems to be necessary. Thus, in a few cases the adult started searching for new food before the young arrived, or the adult did not assume the feeding posture because of some disturbance, and subsequently, the chick did not always find the food. As a rule, the adult does not start searching again before the chick arrives, at least not until the latter is about 5–6 weeks old.

When feeding takes place in shallow water the food would be easily lost if dropped in the same way as on the sand. In these circumstances feeding from the bill would be of advantage. Table 3 shows that the adult actually tends to keep the food in the bill when feeding in water. Furthermore, when the food is dropped into water, it is only done just before the chick arrives. In a few cases it was observed that the adult dropped the food too early (as when feeding on sand) and the chick was not able to retrieve it.

Several factors may influence the feeding rate. The most important are amount of accessible food, water level on the sands, and behaviour of the chicks.

The parent frequently finds food without difficulties, e.g. at only slightly flooded sand or on the sand just inside the water's edge. In rather high water and sometimes on dry sand food-finding is much more difficult, and envolves extensive searching. Further, it appears that food-finding in the meadow is not usually as easy as on the sands.

The transference of food is very quickly accomplished when the chick follows its parent closely and receives food on the spot as soon as it is caught. It takes longer when the adult has to bring the food to a chick hiding in the coastal vegetation, or one that cannot follow in deep water, and in cases where the chick will not accept the food at once.

	Feeding on sand *Fodring på sand*	Feeding in water *Fodring i vand*	Total
Holding food in bill *Fødeemnet holdes i næbbet*	27 (38,0%)	139 (69,8%)	166
Dropping food *Fuglen lader fødeemnet falde*	44 (62,0%)	60 (30,2%)	104
Total	71	199	270

Table 3. Feeding method in relation to feeding place. Pair–2 1958. Age of chick 17–28 days. The table gives number of observations and (in brackets) the frequency of feeding method.
Tabel 3. Fodringsmetodens afhængighed af fodringsstedet. Antal obs.

Below is given the feeding rate (number of feedings per minute) during a number of feeding bouts of a minimal length of 5 minutes, in which an adult was feeding a chick more than one week old:

Feeding on the sands near the water's edge, the chick following the adult: 10,6 – 10,0 – 9,3 – 7,1 – 5,3 – 4,3. Mean 7,8.

Feeding in water, the chick following the adult: 5,2 – 4,2 – 4,2 – 3,9 – 3,6 – 3,4 – 3,2 – 3,0 – 2,6. Mean 3,7.

Feeding in water, the food being brought to the chick: 1,4 – 1,3 – 1,2 – 1,0. Mean 1,2.

The differences between the means are highly significant ($t = 4{,}46$ and 6,15 resp., $p < 0{,}001$).

As the Oystercatcher does not collect food, as e.g. gulls, it seems to be important that under normal conditions the food-searching parent is followed by the chick ensuring that the feeding takes place at the spot where the food is found, thus wasting the minimum amount of time in bringing the food items.

DIRCKSEN (1932), who observed the Oystercatchers at the wadden sea island Norderoog, found that adults with chicks in the inner part of the island where conditions for food-finding were bad, could not bring a sufficiant amount of food from the wade a long distance away.

WEBSTER (1941) found that chicks of Black Oystercatchers *(Haematopus ostralegus bachmani)*, breeding on rocky islets, did not follow the parents until the 3rd–5th week, depending on the difficulty of descent to the feeding areas. There was a short distance between feeding ground and breeding place, and the adults often brought large food items like mussels and limpets which were offered to the chicks in small fragments. TINBERGEN and NORTON-GRIFFITHS (1964) also observed successful feeding of chicks by adults bringing food items such as Nereid worms, crabs and, especially, mussels from some distance away. The feeding interval for each parent was about five minutes. It is very likely that the success of parental feeding in such cases depends on the high quality and quantity of food present and the tendency of the adults to select large food items.

In some cases number of feedings per uninterrupted feeding bout could be counted:

A 1 day old chick was fed 5 times (+ 4 times when food was not accepted) in 18 minutes, 2 adults feeding.

A 9 day old chick was fed 31 times in 8 minutes, 1 adult feeding.

A 14 day old chick was fed 74 times in 8 minutes, 1 adult feeding.

An 18 day old chick was fed 30 times in 7 minutes, 1 adult feeding.

A 27 day old chick was fed 114 times in 33 minutes, 2 adults feeding.

In several other cases, feeding bouts were found to comprise about a hundred or more feedings, but it was usually not possible to keep a constant watch on the birds because of the high vegetation at the coast.

It appears from this that the chick usually consumes quite an astonishing amount of food during a feeding bout, and no doubt is wholly satisfied when it does not accept more. Little wonder, therefore, that the duration of feeding bouts are much shorter than the intervening feeding pauses. In several cases, feeding pauses lasting more than one hour could be observed. TINBERGEN and NORTON-GRIFFITHS (1964) also observed long feeding pauses; during high-tide the chicks were not fed, and during low-tide there were two feeding periods separated by a resting pause of some hours duration.

DEVELOPMENT OF VARIOUS BEHAVIOUR PATTERNS

Some observations on the development of food-finding behaviour and hostile behaviour are mentioned below, and references made to corresponding observations made by DEWAR (1920). His observations took place in an inland locality where the chicks lived mainly on insects and earthworms.

Pecking: Appears soon after hatching. Chicks on the sands very frequently peck at the ground and at various objects lying there, but in the beginning they do not catch any food. In one chick swallowing after pecking was observed for the first time at an age of 9 days. As small chicks spend most of their time – especially when they are not fed by the parents – in or near the coastal vegetation where they are difficult to observe, it is likely that they catch some food, at least, at an earlier stage of life. DEWAR observed a 5 day old young catching food.

Initial piercing: The chick places the bill tip close to the ground and then moves the bill up and down in the muddy sand a few times. In two chicks of different broods this behaviour was observed for the first time at an age of 9 and 13 days respectively. DEWAR states that "testing the soil" starts at the end of the first week.

Levering movements of the bill during initial piercing was in one chick observed

for the first time at an age of 18 days (DEWAR: in second week). Only rarely did this behaviour result in swallowing a small food object.

Investigating objects: For several minutes the chick pecks at an object, e.g., plant material, from different directions, pulling at it and moving it with small movements of the mandibles.

Turning objects, e.g., pieces of plants and small stones, was observed in chicks older than 17 days. The chick places its bill at the base of the stone, and after a moment quickly turns the stone over, in a manner reminiscent of the Turnstone *(Arenaria interpres)*. DEWAR (1940) has described how the adult Oystercatcher uses this method when feeding on Limpets *(Patella vulgata)*, but did not observe the same behaviour in the chicks.

It is characteristic that all these food-finding activities in chicks younger than about 4 weeks only very rarely result in actual catching of food. They are carried out in a curiously hesitating, "automatic", sometimes playful way, and without the eagerness typical of food-catching activities. They provide good examples of fixed motor patterns performed without any immediate function. The initial food-finding behaviour does not seem to be motivated by hunger, as its frequency is the same before and after a period when the chick is fed by the parents.

In one chick the first rather complete *piercing* for food was observed at an age of 37 days. The chick pierced for worms in the same way as the adult (vertical movements, levering and turning) and obtained food items. The same was observed in another chick of about the same age, or perhaps a little older (capable of flying fairly well). According to DEWAR, complete piercing occurs from the 5th week, but with only slight success. At this age feeding on small food items at the surface of the sand has also gradually become rather effective.

Washing of food received from the parent was, in two chicks, observed for the first time at an age of 9 and 14 days respectively, later on, it occurred very frequently. When the food has already been washed by the adult, it is not rewashed by the chick, and when feeding takes place in low water no distinct washing behaviour can be observed. Washing, therefore, is most probably a response to dirty food. The chick washes the food in the same way as the adult bird.

Fledgling time: One chick 29 days old rose high in the air when flapping its wings, and another was observed flying at an age of 32 days. DEWAR observed fledged chicks at the end of the 4th week. The chicks reared by v. FRISCH (1959) were fledged at an age of 31–32 days.

Hostile behaviour: Chicks of all ages perform bobbing movements when on the alert, and just before escaping into the vegetation. Attacks, e.g., on Redshanks *(Tringa totanus)* and terns, occur when the chicks are only a few days old. On one occasion it was observed that an attack of this kind was abruptly interrupted, and the chick immediately assumed the sleeping attitude, which was, apparently, a displacement activity. A chick 29 days old in the vicinity of its piping parents assumed an attitude very much like the piping posture, and still in that posture took up parallel orientation to one of the parents and made the abrupt turnings of 180° so characteristic of the piping performance of adults. In a brood of three fully fledged chicks one was observed to threaten another chick away from the feeding parent by assuming an attitude reminiscent of the piping posture.

During bill model experiments chicks only a few hours old made several movements, which looked like displacement activities, viz., preening of breast, a distinct "looking downward" (cf. GOETHE 1957: "Herabstarren"), and, immediately after pecking, lifting the head and making

drinking movements with the mandibles. The "looking downward" attitude can sometimes be observed in resting or preening adults, but it never has the character of a displacement movement. It was also noted by MAKKINK (1942), who termed it "pointing downward with the bill" and classified it in "Nesting and breeding activities".

PROTECTION OF CHICKS AGAINST PREDATORS

Chicks a few days old stay most of the time in or very close to the high coastal vegetation. Later on the chicks can be seen moving about on the sands during and also sometimes after a series of feedings, but they do not move too far away from the vegetation (usually less than 15–20 metres) and they return there after a short interval.

The following are typical examples: The chick is near the vegetation and repeatedly runs outwards to the adult, receiving food and returning to the cover every time. Or, the chick follows the parent on the sands, receiving food many times; after a while it is obviously satisfied and runs back to the vegetation. The parent brings food a few times, but the chick does not follow it out again.

The tendency to keep to the vegetation is still present in fledged chicks.

The coastal vegetation serves as a hiding place. This is clearly demonstrated when a disturbance occurs; at such times a chick on the sands either crouches on the spot or – sometimes after crouching – runs very quickly to the vegetation and takes cover there.

The wade proper is clearly an ideal feeding ground for Oystercatchers. It has, however, in comparison with the meadow, an important drawback, viz., the absence of hiding places for chicks. Therefore, an important feature of the feeding territory seems to be that it always includes part of the coastline with hiding places (RITTINGHAUS (1964) also observed that chicks were led to that part of the wade which was close to the coastline or other places, where they could hide), and the pronounced tendency to seek hiding places is an important feature of chick behaviour. The high feeding rate on the sands helps to shorten dangerous exposure on the bare flats (p. 18).

Adult Oystercatchers attack predators (big gulls and birds of prey) coming near the territory. Non-predatory birds, e.g., Black-headed Gull *(Larus ridibundus)*, Curlew *(Numenius arquatus)* and Redshank *(Tringa totanus)*, are chased away if they approach the chicks closely (distance about 3–5 m).

The hostile response of adults to predators includes alarm calls, and the chicks respond to this by taking cover or by crouching on the sand or in low water. A chick running to the hide ducks its head. The crouching chick holds its head close to the ground. If the alarm is due to intrusion of other Oystercatchers on the territory the chicks will respond in the same way. They also respond to alarm calls given by Oystercatchers other than their parents, and, e.g., alarm calls by Redshanks; this sometimes happened when the parents were close by and were not reacting to the calls.

In two cases an adult was seen to swoop on a chick (exactly like an attack) running away from a predator in the direction of a hiding place. Such attacks on their own chicks in a dangerous situation has also been observed in adults of the Gull-billed Tern *(Gelochelidon nilotica)* and they are mentioned here and there in the literature for other species of Charadriiformes. It could be that these attacks play a rôle in

the way the chick learns to respond to alarm calls and other danger stimuli.

Sometimes the parents lead the chicks in a certain direction by presenting food and calling softly, e.g., leading the chicks away from an observation tent. When the adult brings food for a chick standing near the boundary of the territory it does not usually go directly towards the chick but turns obliquely away from the boundary, thus causing that the chick runs away from the neighbouring territory.

A newly fledged chick escapes a pursuer by running a zig-zag course; from the author's own experience it is very difficult to catch!

DISCUSSION

Origin of feeding posture.

The feeding posture of the parent Oystercatcher can be considered a ritualized attitude, as 1) its form is variable to only a very small degree, 2) it is maintained without motion for several seconds, 3) it evokes a running-to response in the chicks, 4) its bill-component releases a pecking response in the chick, and 5) it functions in transfering food from parent to chick. It might, therefore, be pertinent to discuss the origin of this posture.

The feeding posture shows some similarity with the piping posture, viz., in the downward-pointing bill, which is a very important component of both postures. There are, however, several very significant differences between these postures, e.g., position of feathers on head and back, position of mandibles, calls and orientation, and it is obvious, therefore, that they are not linked by any phylogenetic relationship.

In the food-finding behaviour of the adult we find an attitude very similar to the parental feeding posture. When the bird has caught a food item by piercing in the ground, it draws it up, drops it on the ground, pecks it up again, frequently moving it between the mandibles, and then eats it. The attitude of the bird when taking up the food or when dropping it is exactly the same as in the feeding posture; the only difference is that the feeding posture is maintained without motion for a considerable length of time, the eating attitude only for a fraction of a second. Further, both of these attitudes occur in the same context – after the capture of food. Since parental feeding takes place on the food-finding grounds, it is very likely that the feeding signal has evolved from self-feeding behaviour.

Consequently, there is probably no doubt that the parental feeding posture is a ritualized attitude of normal food-finding behaviour.

The habit of transporting food from one place to another is not characteristic to parental behaviour, as this also takes place during self-feeding of the adult. The Oystercatcher frequently runs some distance with the food before dropping it and then eating it, and when food is washed, it is carried to the nearest water. The attitude of the adult is the same when carrying food during self-feeding and bringing food to a chick.

Some components of parental feeding behaviour.

An adult feeding a chick, and followed closely by the chick, usually turns halfway round before presenting the food. This "half-turn" may be important, since it causes that an essential part of the feeding posture, i.e., the motionless, downward-pointing bill, becomes visible to the chick. Normally, the chick follows some distance behind, and the parent, when turning, displays the posture at a lateral or frontal

orientation to the chick. It sometimes happens during quickly repeated feedings that the half-turn does not take place, or that the chick is on the "wrong side"; in these exceptional cases the chick is behind the posturing parent, and it does not usually react until the parent has moved the bill or has turned.

Since transitions between turning and approaching the chick can be observed, turning most probably indicates the intention of bringing food.

Small movements of bill or mandibles performed for a short while, apparently increase the value of the bill posture for releasing the "running-to" of the young and the pecking response (p. 13). These movements are performed by the adult when the chick does not respond at once. As the adult makes similar movements before eating during self-feeding, this behaviour may be considered an intention behaviour of the adult to feed itself. The same may apply to "going away" from the chick during repeated presentation of food. In the absence of a response in the chick two tendencies of the adult most probably come into conflict, viz., the tendencies of continued presentation and of eating the food. The variability of the behaviour which follows confirms that such a conflict does exist: The adult will sometimes eat the food itself, sometimes it presents the food again, and sometimes it eats only after repeated presentations.

Both of these intention movements of self-feeding cause the feeding posture to be resumed, i.e., a transition from movements of the bill, or movements of the whole body, to immobility in posture takes place again. Whether this particular change or the movements proper are important to the release of a response in the chick should be investigated experimentally.

Development of self-feeding in chicks.

Pecking at, and fondling all sorts of objects on the ground is not only found in small chicks, but continues for at least four weeks of a chicks life; it can be observed even in fledged chicks. The amount of food found in this way is very small and can be of no importance compared with the quantities of food the chick receives from the parents. Similarly, DEWAR (1920) observed no regular search for surface food at any stage of the chick's development. Gull chicks also "play with objects" rather than seriously catch food items (GOETHE 1955).

In other wader chicks food-catching develops very early. For instance, BERGMAN (1946) states that chicks of the Turnstone *(Arenaria interpres)* direct pecking at any distinct object for the first few hours of their life; when 8–12 hours old they usually peck at moving objects, and when one week old, they only peck at food items.

The "food-finding" behaviour of the Oystercatcher chick is also carried out when the chick is obviously satiated. This is reminiscent of the "feeding" behaviour observed in Flamingoes kept in zoos. These birds, which receive their food in concentrated form, and are therefore more quickly satisfied than they would be under natural conditions, perform their characteristic feeding movements – frequently in the air – independent of hunger and presence of food (H. POULSEN, pers. comm.).

The very efficient parental feeding of the Oystercatcher is probably responsible for the fact that the food-finding behaviour of the chicks remains in an initial stage for a long period of time.

Owing to the parental feeding-mechanism, pecking at objects in or under the parent's bill will be associated with eating and satisfaction, whereas pecking at various objects on the ground will only occasionally be associated with eating, and never with satisfaction. Theoretically, this implies that no connexion between hunger and the behaviour of pecking at something on the ground is established through a process of learning, and, consequently,

that this behaviour does not develop into a distinct pecking at food objects, as in other wader chicks.

Another explanation would be that there are innate differences between Oystercatcher chicks and chicks of other waders as to the development of self-feeding behaviour.

The information given by v. FRISCH (1959), who himself reared Oystercatcher chicks, is very interesting in this connexion. These chicks took food from the hand only during the first three days of life; already by the second day they had started self-feeding, and they quickly became wholly independent. In this case, plenty of food was present, and it is possible that feeding by hand did not take place as often as parental feeding, and not at the precise time when the chicks were hungry. Further, according to v. FRISCH, the chicks became timid, which must have had a detrimental effect on hand-feeding.

Under such, very special, circumstances self-feeding behaviour develops very quickly, as in other wader chicks. Therefore, the differences in development of self-feeding between chicks of the Oystercatcher and of other waders cannot be due to innate differences in behaviour control.

Whether chicks, under natural conditions, sometimes start successful self-feeding at an early stage of their life, whereby becoming wholly or partly independent on parental feeding, is very doubtful.

About fledging time the chick's food-finding behaviour gradually becomes more effective. It is probably no accident that the increased tendency towards self-feeding corresponds with the decreasing tendency of the parents to feed their young. At this stage the chicks rather frequently perform food-finding behaviour during periods of hunger, and, theoretically, the conditions necessary for establishing an association between hunger, eating and pecking at certain objects on the ground are now present.

The cessation of parental feeding is a very slow and gradual process, and even chicks capable of efficient self-feeding are still fed by the parents (p. 16). In localities where food for the chicks is scarce or difficult to obtain, it is probably of importance that parental feeding does not stop abruptly, and at an early stage.

According to WEBSTER (1941), chicks of *Haematopus ostralegus bachmani* cannot open mussels and barnacles or loosen limpets and chitons until they are 3–4 months old. As the Oystercatchers in WEBSTER's observation area largely depended on these food items, parental feeding was probably necessary for a considerable length of time.

It is probable that the time at which Oystercatcher chicks become independent of their parents depends on the sort of food found in the breeding area. A simple, adaptive mechanism responsible for the cessation of parental feeding would, therefore, be a slow-down of the feeding rate due to the behaviour of the adults (cf. above) and final stop due to the behaviour of the chick and regulated by the success in self-feeding; the latter is wholly hypothetic. This mechanism would ensure that parental feeding does not stop until the chick is able to catch the type of food present in the area.

On the parental system.

Parental feeding and the maintenance of the feeding territory, in which the chicks stay, are two very prominent characteristics of parental behaviour in the Oystercatcher, as compared with that of typical waders. Consequently, the question must arise, what is the significance of these behaviour patterns in the life of the Oystercatcher, are they functionally interrelated, and how are they adapted to natural circumstances?

Most considerations on such complicated functional interactions are, at present, rather hypothetical and certainly very

fragmentary. However, a large number of field observations have now been made on the Oystercatcher and they do support some ideas on functional relationships, which may be useful for further research on the parental system in this species as well as in others.

In their study of egg shell removal as a component of the anti-predator system in the Black-headed Gull, TINBERGEN *et. al.* (1962) have shown the usefulness of studies on entire functional systems, especially in throwing light on the problem of adaptive evolution in behaviour. Parental feeding in the Oystercatcher seems to include several adaptations of first, second and even higher orders, and parental feeding itself is merely a component of the entire parental system.

The mode of parental feeding in the Oystercatcher implies that the chicks are supplied with food in a very efficient way. They take advantage of the efficiency of adult food-finding, and, from the very beginning, they acquire the same type of food as eaten by adults. In e.g., the Black-tailed Godwit *(Limosa limosa)*, a species which usually finds food by piercing into the ground like the Oystercatcher, the chicks surface-feed only, and do not start searching for "adult food" until after they are fledged and the bill has become strong enough for piercing.

The number of chicks the parents can care for, however, must be strongly limited, especially under unfavourable conditions. This may be one reason for the clutch size of 3 found in the Oystercatcher; most other waders have 4 eggs.

In accordance with the dependence on food-finding activities of the parents the chicks are normally led to an area where conditions for adult food-finding are good, e.g., the sands of Tipperne. Again, comparison with the Godwit can be made. The adults of this species, like the Oystercatchers, find much of their food on the flooded sands, but they do not lead the chicks to this area; the chicks stay in the meadow, where conditions for surface-feeding are better.

The chicks are more exposed to predators on the wade than they would be in the meadow, but the high feeding rate on the sands and a strong tendency for the chicks to remain concealed during feeding pauses compensate for this disadvantage (p. 20).

The efficiency of parental feeding is increased by the chick's habit of following the adult during a feeding bout. When the chick cannot follow the adult to the feeding ground (because of water level, distance etc.), the adult brings food to the chick. In this case the tendency of the parent to select large food items fulfils the demand of efficiency in feeding, and the tendency of the chick to remain concealed fulfils the necessity for protection during the absences of the parents.

In broods of 2 or 3 the chicks are usually fed one at a time; therefore, parental feeding tends to split up the brood and make parental defence against predators difficult. This splitting of the brood is, however, only temporary, as after the chick is fed and satisfied it usually returns immediately, or within a short time, to the other chicks. This behaviour compensates for a disadvantage in the mode of parental feeding and is probably due to the existence of strong social ties between the chicks; v. FRISCH (1959) states that these ties are particularly well developed in the Oystercatcher as compared with most other waders. But how do the chicks find each other again after separation? Here the territory comes into the picture.

In several waders, e.g., Lapwing, Black-tailed Godwit and Redshank, the adults may stay for several days with their brood in a place suitable for the chicks' food-finding activities, and in at least some species, e.g., the Godwit, the parents attack not only various predators but also non-predatory birds and individuals of the

same species when they come too close to their chicks. These waders, however, do not defend a true territory after the hatching of the chicks (as far as is known). An essential difference between their behaviour and the typical territorial behaviour of the Oystercatcher is that the latter species – usually throughout the whole breeding season – defends an area to which the chicks are taken and where they stay, whereas other waders defend the area where the brood happens to be.

It is possible that the Kentish Plover *(Charadrius alexandrinus)*, has a feeding territory similar to that of the Oystercatcher. On this species RITTINGHAUS (1956) writes that on the wadden sea island, Oldeoog, the chicks are led by the parents to the wade soon after hatching, "meist an solche Stellen, die von diesen schon vorher mit Vorliebe aufgesucht worden waren. Hinfort verteidigen die Eltern einen weiten Raum im Umkreis ihrer Jungen und "drohen" an dessen Grensen" (l. c. p. 143).

The maintenance of a true feeding territory in the Oystercatcher is in several respects significant in relation to parental feeding:

1) It secures hiding places (cf. p. 20). Here the chicks are protected against predators when the parents are absent. This happens under two circumstances, viz., when the adults find food for the chicks some distance away (cf. TINBERGEN and NORTON-GRIFFITHS 1964), and when the adults have to find food for themselves during pauses of feeding chicks.

2) It helps to hold the chicks together. As parental feeding takes place on the territory the adult and the chick about to be fed never move far away from the other chicks, and it is probable that the chicks are familiar with the situation of the hiding and resting places in the territory.

3) It helps in establishing contact between chicks and adults. The chicks' concealment during feeding pauses, and the parents' need to find food for themselves during these pauses or to find food for the chicks some distance away, implies that parents and chicks lose contact with each-other for a time. Contact is re-established by the adults coming to the hiding place or the territory, or the chicks running out to the parents on the feeding ground in the territory close to the hiding places.

4) It secures a suitable feeding ground. The importance of this function is demonstrated by observations made by DIRCKSEN (1932), on the wadden sea island Norderoog. He found that the food supply on the wade plays a decisive role in the feeding of the chicks. Many of the chicks hatched in the inner part of the island died from malnutrition. "Der Grund hierfür wird in der Abgeschlossenheit dieses Biotopes nach dem Wattenmeer und damit zur Hauptnahrungsquelle liegen. Ein "Wandern" der Paare mit ihren Jungen über den Dünenrand zu den für die Nahrungsaufnahme günstigeren Stellen konnte nicht beobachtet werden. Auch hier schienen die Tiere Reviergrenzen innezuhalten, vielleicht zwangsläufig, weil die übrigen Plätze auf der Düne "vergeben" waren. Die Nahrungsverhältnisse waren für Haematopus im Innern der Insel sehr ungünstig, –" (l. c. p. 475). It seems very likely that in such localities, e. g., sandy islands, where the breeding population is often large and most feeding takes place along the coast, there must be pronounced competition for feeding grounds.

Owing to parental feeding, the ability to reproduce under unfavourable feeding conditions is probably much greater in the Oystercatcher than in other waders. When food is scarce and consequently, the rate of feeding low, the Oystercatcher chick able to follow the parent most persistently, and threaten away other chicks of the brood (p. 10), will get most of the food, and in many cases, a sufficient amount of food. Thus, the strongest chick will have a greater change of survival.

In other waders, the chicks of a brood under correspondingly bad feeding conditions will have more or less the same slight chance of survival. In the Oystercatcher at least one chick will survive, irrespective of the number of chicks in the brood. In typical waders none will survive, or, the more chicks in the brood, the greater the chance one will survive. The influence of predation is not considered.

The relatively good possibility for one Oystercatcher chick to survive under unfavourable feeding conditions may be one functional reason why the Oystercatcher continues the brooding of one egg when the other eggs of the clutch have been robbed; whereas, other waders in the same situation will stop brooding and start a new full clutch (cf. LIND 1961, p. 129).

Scarcity of food in Oystercatcher breeding areas is mentioned by DIRCKSEN (1932), cf. above, and DEWAR (1915). The latter states that drought reduces the supply of food, and that the adults work feverishly and for long periods of time to supply the necessary quantity of food for the young. "Occasionally, young have been seen to manifest signs of more than passing hunger owing to the drought-induced dearth of earthworms and the difficulty of getting other supplies. But in no observed instances have the young appeared to suffer permanently in consequence of the shortage" (l. c. p. 383). Dangerous shortage of food, however, was observed by DIRCKSEN, as mentioned above.

v. FRISCH (1959) found that his hand-reared chicks quickly started self-feeding and he concludes: "So scheint es nicht einleuchtend, dass im Freien oft nur ein Junges überleben soll, weil die Alten nicht genug Futter herbeischaffen können" (l. c. p. 549). Apart from the question whether small chicks living in natural conditions make any contribution to food-finding (p. 23), there may, in typical Oystercatcher localities, be a temporary scarcity of food for adults as well as for chicks.

A dangerous shortage of food was never observed on Tipperne, but food-finding was evidently impeded during periods of high water level.

Parental feeding in gulls and terns implies that these species can select breeding places which are protected against predators (e. g., on small islets, in marshes), and form large colonies, which also offer protection against predators, there being no necessity for the young to acquire food locally.

In the Oystercatcher the adaptive value of parental feeding may be that it allows this species to breed in areas with ideal feeding conditions for adults and e.g., good protection against predators, but in which food available for chicks is scarce, and in areas where temporarily unfavourable conditions for food-finding are likely to occur. Without parental feeding breeding would be difficult in such localities. Examples are the following:

1) Several islands in the Frisian Wadden-sea, where the Oystercatcher breeds in greater numbers than any other wader. Here food-finding mainly depends on bottom animals on the wade, where, further, the conditions for feeding depend on the tide and therefore are not constant.

2) A small sandy island, Bjerggård Pold, on the Tipperne reserve. Here about 10 pairs of Oystercatchers breed, together with terns and gulls. Some years small colonies of Avocets *(Recurvirostra avosetta)* are present, but nesting of other waders is rare. Owing to the character of the island, and the large Laride colonies, wader chicks have to mainly depend on food from the surrounding shallow water.

3) Rocky islands such as described by WEBSTER (1941) as a breeding place for *Haematopus ostralegus bachmani*. Firstly, the main source of food is various molluscs, which can only be obtained by adults, and, secondly, the character of the ground

makes it difficult for the chicks to move about.

The Oystercatcher frequently breed together with other waders on, e. g., meadows and beaches, but breeding places of the kind mentioned above are to some degree typical to this species.

Parental feeding in related species.

The Oystercatcher is usually placed in a family of its own, Haematopodidae, close to the family Charadriidae, or as a member of the latter. The closest relatives of the Oystercatcher should probably be found among the Charadriidae. The only member of this family in which parental feeding is known to occur is the Snipe *(Gallinago gallinago)* (e. g., v. FRISCH 1959). The strongly restricted occurrence of this behaviour pattern suggests a specialisation rather than a primitive feature. The following facts also support this assumption:

Chicks of the Oystercatcher and the Snipe are nidifugous, as are chicks of other waders; chicks of the Oystercatcher (and probably also of the Snipe) perform food-finding behaviour – however unsuccessfully – shortly after hatching; under special circumstances this behaviour can develop into effective self-feeding behaviour at an early stage (p. 23), the chicks becoming independent like other wader chicks; finally, nidifugous self-feeding chicks most likely constitute a primitive condition, as compared with nidifugous, semi-nidifugous or nidicolous chicks fed by the parents.

Parental feeding is found in two other species which are probably more distantly related to the Oystercatcher, viz., the Stone Curlew *(Burhinus oedicnemus)* and the Pratincole *(Glareola pratincola)* (v. FRISCH 1959, 1961). Furthermore, highly developed parental feeding is found in the Laridae. From the above, it seems that parental feeding has most probably evolved independently in all these groups.

In the following, the parental feeding behaviour of the Oystercatcher is compared with that of the Herring Gull *(Larus argentatus)*, cf. TINBERGEN and PERDECK (1951) and TINBERGEN (1953).

Chicks of both species peck at objects on the ground soon after hatching, without finding food (cf. GOETHE 1955). They respond to the parental bill by pecking, and the sign stimuli which release this behaviour, seem to be of the same kind, e. g., a certain colour, shape and position. In both species, pecking is directed at the tip of the bill (in case of the Herring Gull at the contrasting red spot on the lower mandible), where the food is held.

In the Herring Gull, pecking at the adult bill functions as begging behaviour, causing the parent to regurgitate food. In the Oystercatcher, pecking at the bill is probably of minor importance in begging behaviour, because the parent has such a strong tendency to bring food, that no request is needed other than the approach of the chick, and because the chick's acceptance of food is sufficient to induce new feeding; it may also play a role that the Oystercatcher does not regurgitate and therefore cannot respond immediately to the pecking by feeding. In the Gull-billed Tern *(Gelochelidon nilotica)*, which also does not regurgitate, the chick's pecking functions mainly in transferring food as in the Oystercatcher (LIND 1962). However, QUINE and CULLEN (1964) found that in the Arctic Tern *(Sterna macrura)* the pecking of the chick often functions as begging behaviour.

The begging behaviour of older chicks is different in the Oystercatcher and the Herring Gull, that of the latter being highly ritualised (head-tossing).

In the Oystercatcher, but not in the Herring Gull, there is a special feeding posture, which serves as a long-distance releaser. This is important with regard to the feeding of single food items at the place where the food is found. This posture

would be of no importance to the gull, which always brings the food to the chick.

The Herring Gull selects food of a special kind for the chicks, while the Oystercatcher rather selects food items of a certain size. Selection according to size is important in the Oystercatcher because it feeds with single food objects, but this has no significance in a gull which collects and regurgitates food.

Both species defend territories where the chicks are staying and hiding, but the Herring Gull has no feeding territory.

Thus, it can be seen that some basic patterns of the feeding mechanism are similar in the Oystercatcher and the Herring Gull, in spite of the fact that they have probably developed independently of each other. The reason for these similarities probably is that the demand of transferring food to a chick with an inborn ability to peck at something are the same. There is some convergence in the evolution of territorial behaviour due to similar demands in connexion with parental feeding (fixed hiding places for chicks). In other respects the evolution of parental feeding patterns have taken different direction in accordance with principal differences in biology, first and foremost, that the Oystercatcher is a non-colonial bird feeding the chicks at the place where food is found, whereas, the Herring Gull feeds the chicks in the colony, far from the place where food can be found.

SUMMARY

The Oystercatcher maintains – usually throughout the whole breeding season – a feeding territory which is close to or some distance away from the breeding territory. The young stay for about 6 weeks or more in the feeding territory and receive nearly all food from their parents.

The adult feeds the chick in a special posture which includes an almost vertical position of the bill. Experiments suggest that the bill (colour, form and position) releases a pecking response in the chick. The feeding posture is most probably a ritualised food-finding attitude.

Single food items are presented to the chick, usually in the area where the food is found. There is some selection of food items as to size, depending on the distance to the chick, and the feeding behaviour is balanced between the demands of successful transference of food and high feeding rate. Therefore, under normal circumstances great efficiency in parental feeding s secured.

Self-feeding in chicks develops late, and very slowly, and for a considerably length of time initial food-finding behaviour seems to be performed independent of hunger. Factors influencing development in the self-feeding of chicks are discussed.

The functional system of parental behaviour of the Oystercatcher is compared with that of other waders. Territoriality is found to be of great importance to parental feeding. It is suggested that parental feeding behaviour in the Oystercatcher is adapted to the breeding of this species in localities to which it is characteristic, e.g., sandy islands in the wadden-sea and rocky islands and coasts.

In spite of an obviously independent evolution of parental feeding in the present species and gulls we find great similarities in the basic patterns. Some differences reflect adaptations to different biological demands.

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DANSK RESUMÉ

Fodring af unger hos Strandskade.

Strandskaden har som andre vadefugle redeflyende unger, der forlader reden kort tid efter klækningen og kan løbe frit omkring. Ungerne udfører forskellige former for fødesøgningshandlinger ligesom andre vadefugleunger, men i modsætning til disse fanger de næsten intet. De modtager næsten al føde fra forældrefuglene, og fodringen foregår på en meget karakteristisk måde. Den foreliggende treårige undersøgelse på Tipperne skal tjene til at belyse nogle problemer i forbindelse med denne for vadefugle ret enestående adfærd.

Strandskaden er strengt territorial og opretholder både et yngleterritorium og et fødesøgningsterritorium. De to territorier kan være mere eller mindre adskilt (fig. 1.). På Tipperne omfattede fødesøgningsterritoriet den tætte vegetation ved kysten og den udenfor liggende del af fladvandet, der ofte er mere eller mindre tørlagt.

Strandskadens karakteristiske »pippe«-adfærd, der nogle steder i litteraturen er omtalt som parringsspil eller en art socialt spil, var på Tipperne

altid en rent aggressiv adfærd, der forekom i forbindelse med territorieforsvaret.

1–2 dage efter klækningen føres ungerne til fødesøgningsterritoriet, hvor de bliver i hvert fald de følgende 6 uger. Når vandstanden her er høj, kan de i korte perioder vende tilbage til territoriet på engen.

Fodringen af en unge foregår normalt på den måde, at den gamle fugl ved at bore i sandet finder et fødeemne, på Tipperne i de fleste tilfælde børsteorme *(Nereis diversicolor)*; den tager det i næbspidsen og løber mod ungen. I nogen afstand standser den op og præsenterer nu ormen i en særlig fodringspositur. Ungen kommer løbende til og tager ormen fra næbspidsen. Forældrefuglen venter til ungen har slugt og går så bort til ny fødesøgning (fig. 2).

Fodringspositurens er ritualiseret, d.v.s. den er udviklet til et signal, og kan sandsynligvis afledes fra den stilling, som fuglen indtager, når den bearbejder et fødeemne efter at have trukket det frem.

Fødeemnerne bringes altid enkeltvis uanset størrelsen.

Både han og hun fodrer (tabel 1).

Som regel fodres en unge mange gange i løbet af en ret kort periode (se side 18), og den følger herunder forældrefuglen, for så vidt forholdene tillader det. Derefter indtræder en ret langvarig fodringspause, i hvilken ungen oftest holder sig skjult i vegetationen.

En serie fodringer kan indledes af ungen, ved at den nærmer sig den gamle fugl, som så straks begynder at søge føde til den, eller den indledes af den gamle, der bringer føde til ungen. Perioden afsluttes af ungen, ved at denne ikke mere reagerer på fodringspositurens og søger skjul.

I eksperimenter undersøgtes nyklækkede ungers hakkereaktion på forskellige modeller af det voksne næb. Heraf fremgår, at såvel næbbets form som farve spiller en rolle for udløsningen af hakkereaktionen. Rød farve (svarende til den voksne fugls næbfarve) udløser bedre end sort og hvid, og en spids model (svarende til Strandskadens næbform) er bedre end en bred og nedentil afrundet model (tabel 2 og fig. 6). En lodret stilling af modellen svarende til næbstillingen i fodringspositurens er mere effektiv end en stilling svarende til en »normal« næbstilling (fig. 8). Ungen hakker overvejende efter den nederste del af modellen (fig. 7), svarende til den voksne fugls næbspids, hvor fødeemnet findes under fodringen.

Fodringsadfærden er tilpasset de vilkår, hvorunder fodringer ofte finder sted, således at der sikres den højst mulige frekvens af effektive fodringer.

Nogle eksempler skal nævnes:

Når ungen er nogle dage gammel, øges fodringshastigheden, ved at forældrefuglen oftere undlader at vente, til ungen har slugt; den starter ny fødesøgning, så snart ungen hakker efter ormen.

Meget hyppigt lader den gamle føden falde til jorden, så den peger på den i stedet for at holde den, og ungen finder den her uden vanskelighed. Når derimod fodringen foregår i vand, holdes føden meget oftere (tabel 3), og hvis forældrefuglen lader den falde, sker det først umiddelbart før ungen ankommer. Var adfærden den samme som ved fodring på sandet, ville fødeemnet ofte gå tabt.

Da Strandskaden ikke samler føde, men bringer hvert enkelt fødeemne, er det af stor betydning for fodringshastigheden, at ungen følger den fodrende fugl. Fodringsfrekvensen er da også under gunstige forhold meget høj, omkring 8 fodringer pr. minut (se side 17).

Nar imidlertid ungen under ugunstige forhold ikke kan følge den fødesøgende forældrefugl, bringer denne føden til ungen. Det viser sig da, at når afstanden til ungen er stor, udløses fodringsaktiviteten hos den voksne kun af forholdsvis store fødeemner, små fødeemner sluger den selv. Der spildes med andre ord ikke tid og energi på transport af føde af minimal værdi.

Når ungerne i et kuld er omkring tre uger gamle, synes de voksne fugles fodringstendens at aftage. Ungerne begynder nu at tigge og i mange tilfælde reagerer forældrefuglene end ikke på det. Det sker nu også hyppigt, at den voksne afbryder fodringen på eget initiativ, d.v.s. inden ungen har vist tegn på mæthed. Selv lang tid herefter modtager ungerne dog størsteparten af føden fra forældrefuglene, og selv fuldt flyvedygtige unger, måske 8–9 uger gamle, kan man se blive fodret.

Meget taler for, at den meget sene udvikling af effektiv fødesøgningsaktivitet hos strandskadeungen i sammenligning med andre vadefugleunger skyldes manglende indlæring i adfærden som følge af den særdeles effektive fodring. Først når forældrefuglenes fodringstendens er begyndt at aftage, bliver ungernes fødesøgningsaktivitet gradvis mere effektiv, og det sker samtidig med, at næbbet antager en størrelse, der muliggør en fødesøgningsadfærd svarende til de voksnes.

Det formodes, at fodringsadfærden hos Strandskaden oprindelig er udviklet som en tilpasning til specielle ynglelokaliteter som f. eks. sandede øer i vadehavsområder og klippefulde øer eller kyster, hvor der er ideelle forhold for de voksne fugles fødesøgning, men hvor på den anden side små ungers muligheder for at finde føde er dårlige.

Ud over selve fodringsadfærden er der adskillige træk i de voksnes og ungernes adfærd, der kan opfattes som tilpasninger til ungefodringen, f. eks. følgende:

Hos strandskadeunger er den sociale tilknytning inden for kuldet bedre udviklet end hos de fleste

andre vadefugleunger, og den bevirker, at de søger sammen efter adskillelse. Det er af stor betydning, da fodringen medfører, at kuldet splittes op, idet ungerne normalt fodres en ad gangen.

Vaden er et ideelt fødesøgningsområde, men har den ulempe, at ungerne her er stærkt udsat for fjendeangreb. Strandskadeungen har imidlertid en højt udviklet tendens til at søge skjul uden for fodringsperioderne, hvorved denne fare mindskes. I modsætning til andre vadefugleunger er strandskadeunger ofte overladt til sig selv, dels fordi de gamle fugle til tider må hente føden i nogen afstand, og dels fordi de må udnytte fodringspauserne til selv at finde føde. Det er derfor også af denne grund betydningsfuldt, at ungerne søger skjul.

Det er i denne forbindelse væsentligt, at fødesøgningsterritoriet altid omfatter egnede skjulesteder (vegetationen ved kysten).

Opretholdelsen af et territorium i ungetiden (noget der er karakteristisk for Strandskaden) sikrer endvidere, at de voksne kan finde ungerne efter fourageringsudflugter, og at skjule- og hvilesteder er de samme hele tiden, så ungerne let finder hinanden efter adskillelse.

Endelig sikrer territorialiteten en tilstrækkelig fødemængde til ungerne i umiddelbar nærhed af deres opholdssted.

Fodring af unger forekommer inden for nærtstående grupper hos Dobbeltbekkasin, Triel og Braksvale samt hos mågefugle. Det anses for sandsynligt, at der er tale om en indbyrdes uafhængig specialisering hos de enkelte arter og grupper.

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