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THE PARENT-CHICK FEEDING RELATIONSHIP OF THE PUFFIN, FRATERCULA ARCTICA

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SUMMARY

(1) The feeding relationship between the puffin parent and chick was studied to examine whether the parent or its chick determines the duration of feeding and the quantity of food the chick receives.

(2) The quantity of food brought to wild chicks decreases prior to their fledging. Artificially reared chicks did not reject additional food until the day before fledging implying that chicks do not influence the decrease in the parents feeding rate. Nevertheless, when large quantities of fish were available chicks did reject progressively more food before fledging.

(3) Chicks that received additional food did not fledge either earlier or heavier than control chicks.

(4) A series of chick-exchange experiments were conducted to examine the way in which adults determine the number of feeds the chicks receive. When chicks of the same age were exchanged foster parents continued to feed the chick at the normal rate. When chicks of different ages were exchanged the parents tended to feed according to their previous schedule rather than the age of the foster chick. Thus, adults appear to determine the quantity of food chicks receive. All chicks fledged at a similar age to control chicks and were not deserted by their foster parents, implying that chicks may determine the duration of the feeding schedule.

INTRODUCTION

How much effort should parents invest in their offspring? This question confronts all sexually reproducing animals whether they be woodland birds caring for a nest of chicks or a lion hunting for her cubs. In the terms of evolutionary theory each parent should solve this problem in order to maximize its own fitness (Hamilton 1964) or more simply to maximize the number of surviving offspring it produces within its lifetime. This ‘effort’ may take many forms but among the semi-precocial birds a large amount of energy will be expended by the adults searching for and collecting food for their offspring.

Trivers (1974) has demonstrated theoretically that the parents and chick can be expected to disagree over the duration and quantity of parental investment given to each chick. Parental investment is defined as ‘anything done by the parent for the offspring that increases the offspring’s chance of surviving while decreasing the parent’s ability to invest in other offspring’ (Trivers 1974, p. 249.). In most seabird species adult survival is high (greater than 90%) and so longevity and the number of chicks produced in a lifetime will be greatly reduced by only a slight decrease in the survival chances of the adult. Strain on the adults during the breeding season may well influence their future survival chances (Wooller & Coulson 1977), so the parental investment an adult gives to each
chick should be such that the adult produces the maximum number of surviving offspring in its lifetime. Hence, the effort invested in each chick will probably influence the quantity of food and duration of time the parents feed their chicks, within the structure and limitations of the existing type of chick development.

The feeding mechanism of the puffin (*Fratercula arctica* Linn.) is particularly interesting as the quantity of food the parent brings to the chick initially increases and later decreases prior to the chick fledging (Ashcroft 1979). There has been some controversy as to whether or not the puffin chicks are deserted by their parents a few days before fledging (Myrberget 1962, 1976; Lockley 1934; Harris 1976; Ashcroft 1976) and the observed decrease in feeding rate may be associated with the idea that chicks are starved into fledging. The adult must therefore determine the number of feeding visits to make to the chick each day and, if the chicks are starved into fledging, for how long the chick should be fed.

In this paper I concentrate on two aspects of this feeding behaviour; firstly the decrease in feeding rate and whether such a change is due to the behaviour of the chick or of the adult and secondly whether the chick or adult determine the number of feeds the chick receives. Since these two aspects require different experimental approaches this paper is divided into two parts dealing with each in turn.

**PART 1: THE DECREASE IN THE AMOUNT OF FOOD BROUGHT TO CHICKS**

Adult puffins bring loads of fish to their chicks which consist mostly of *Ammodites marinus* Linn. (56%) and *Sprattus sprattus* Linn. (39-7%). This study was concentrated on Skomer Island, Wales in 1977 where Ashcroft (1976) found the mean weight of ninety-six fish loads was 8 g (SE = ±0.76) and the weight and content of these loads did not differ significantly throughout the season. The number of feeding visits to the chick increases with the age of the chick until the chick is about 26 days old and then steadily decreases until the chick fledges at about 40 days of age (Ashcroft (in press), Fig. 1). This change in the feeding rate raises two questions:

1. Is the decrease in the amount of food brought to the chick the result of a change in the chick’s behaviour?
2. Would it be advantageous to the chick to receive more food prior to fledging than the adults bring?

**Methods**

Fifteen chicks were removed (under licence) from their burrows after brooding had ceased (about 9 days old) and reared artificially. The chicks were divided into three groups of five and introduced into artificial burrows about 1 m long. The chicks were fed four times a day at 4 h intervals with freshly thawed sprats (*Sprattus sprattus*) plus a drop of abidec vitamin solution. One group of five chicks were fed the maximum amount of food the adults would normally bring to the chick (maximum group; 80 g per day), a second group was fed *ad lib* (*ad lib* group; 120 g per day) and the third group received the amount of food the chicks in the wild normally receive, as shown in Fig. 1 (control group). Adult puffins usually leave fish for their chicks by dropping the food on the floor of the burrow and leaving immediately. The food offered to the captive chicks was left in a similar manner but was placed on a plastic sheet so the quantity of food remaining at the end of each day could be recorded. Other bird species (Laridae and Corvidae)
Fig. 1. Number of feeds brought to chicks according to chick’s age. Mean values are given ± 1 S.E. and each point is for chicks within a 4-day age group. After Ashcroft (in press) by permission.

Fig. 2. Quantity of food eaten by maximum group of chicks (■) and ad lib group of chicks (○) compared with the quantity eaten by wild chicks (●) according to chick’s age. Mean values are given ± 1 S.E. of each mean where this is greater than the range covered by the symbol.
have been observed stealing fish from puffin burrows (personal observation) and this was prevented by placing a wire mesh grid over the burrow entrance. The weight and wing length of each chick was measured every day prior to the chicks feed at 16.00 hours to monitor the chicks growth rate and fledging weight.

**Results**

*Is the decrease in the amount of food brought to the chick the result of a change in the chick's behaviour?*

If the chick determines the decrease in the feeding rate when 26 days of age then we can expect the chicks fed the maximum amount (maximum group) to reject food when they are older than 26 days in order to consume the same amount as the control group of chicks.

The maximum group did not reject food until the day before fledging and the control group ate all the fish they were given (Fig. 2). Therefore the decrease in the amount of food the chick receives is not the result of the chick actively rejecting food but due to the adults bringing less food than the chick is capable of eating. Nevertheless it is interesting to note that the *ad lib* group did reject food soon after the 26th day but still ate much more than chicks in the wild receive.

**Fig. 3.** Weight growth curves of artificially reared puffin chicks. Mean values are given for *ad lib* group of chicks (○), maximum group of chicks (■) and control chicks (●). Standard errors excluded for clarity and analysis summarized in text.
Is it advantageous for the chicks to receive more food?

The post-fledging survival of manx shearwater chicks (Puffinus puffinus Brunnich) is dependent on the chicks' fledging date and weight (Perrins, Harris & Britton 1973). An early fledging date and a high fledging weight is believed to assist the shearwater chicks when travelling to their winter feeding quarters. Similarly, a high fledging weight or an early date of fledging could increase the chances of the young puffins surviving, as a high fledging weight will provide the chick with ample fat reserves while learning to feed and an early date of fledging will enable the chick to learn how to feed when foraging conditions are favourable. Thus an increase in the amount of food the chick receives may be advantageous to the chicks' fledging weight, or rate of growth.

The weight increase of the three groups of chicks is shown in Fig. 3. The weight increase of the control chicks was very similar to that of wild chicks (P. J. Hudson in preparation). The chicks fed ad lib were significantly heavier than the chicks in the other two groups, from 24 to 39 days of age (Analysis of variance, \( P < 0.05, F > 3.9, \) d.f. = 2, 12). However, despite the faster growth rate of the ad lib fed chicks there was no significant difference in the age or weight of the chicks at fledging. The ad lib group rejected food prior to fledging (Fig. 2) and this resulted in a fall in the chicks' weight, so at fledging all three groups of chicks had similar weights (Analysis of variance, \( P > 0.1, F = 1.81, \) d.f. = 2, 12). The growth of the wing was similar in all three groups and is shown in Fig. 4. Thus there appears to be no apparent advantage to the chicks' fledging weight, date or wing size when fed additional food. Nevertheless, prior to the ad lib fed chicks rejecting some food they were eating more than twice the amount of food chicks

![Fig. 4. Wing length growth curves of artificially reared puffin chicks. Symbols as in Fig. 3.](image-url)
in the wild receive. I can only speculate about the consumption of this additional energy; some may have been used for the greater body maintenance requirements of larger chicks, or with a high rate of food intake the chicks may have decreased their digestive efficiency.

PART 2:
HOW DO ADULTS DETERMINE HOW MUCH TO FEED THEIR CHICKS?

The parents need to determine the quantity of food to bring their chicks each day. The methods by which they could determine this amount are either (or perhaps a combination of both) of the following:

(1) Time: the adult determines how much to feed the chick according to how long it has been feeding the chick; so the adult increases the number of feeds it brings each day until it has been feeding for 26 days and then reduces the feeding rate until the chick fledges.

(2) Chick’s age: the adult determines the amount of food to bring the chick by estimating the chick’s age from certain cues (such as the chick’s size or behaviour); so the adult increases the number of feeds it brings each day until the chick is 26 days old and then reduces the feeding rate according to the age of the chick.

Methods

To distinguish between these two methods, two chick exchange experiments were conducted, where a chick replaced another, either of a similar or different age, and then the subsequent feeding behaviour of the foster parents was recorded. In the first experiment ten puffin chicks of the same age were exchanged and the feeding behaviour of the foster parents during the next 3 days recorded to determine if exchanging chicks may influence the subsequent feeding behaviour of the adults. In the second experiment seven old chicks (about 20 days old) were exchanged for seven young chicks (about 12 days old) and the feeding behaviour of the foster parents during the next 3 days recorded. If the foster parents determine the feeding rate by a time schedule (first method) then they will feed the chick according to the parents’ previous feeding schedule, whereas if the feeding rate is determined by certain cues from the chick (second method) then the foster parents will feed the chick according to the chick’s age. So, when a chick is exchanged for either an older or a younger chick the adult must determine how much to feed the chick and whether or not to feed the chick to fledging.

After the chicks had been exchanged the number of feeds the foster parents brought to their host chick during all daylight hours were recorded. Observations were made from a hide constructed close to the study colony and a feed to the chick was scored each time an adult entered its burrow with fish and left not carrying fish. Observations were repeated and burrows checked at frequent intervals through the breeding season to determine the chicks’ fledging date.

Results

Adult feeding rate

Experiment 1. When chicks of the same age were exchanged the foster parents accepted the chicks and fed them. Chicks received the same quantity of food as wild chicks of the same age receive from their parents (Table 1, Wilcoxon test, \( P > 0.1 \)).
TABLE 1. Number of feeds brought over 3 days after control chicks were introduced to foster parents compared with the number of feeds brought to wild chicks of the same age

<table>
<thead>
<tr>
<th>Chick number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed number of feeds to exchanged chicks</td>
<td>34</td>
<td>26</td>
<td>28</td>
<td>31</td>
<td>19</td>
<td>15</td>
<td>26</td>
<td>30</td>
<td>18</td>
<td>15</td>
</tr>
<tr>
<td>Expected number of feeds (wild chicks)</td>
<td>21.9</td>
<td>24.3</td>
<td>24.3</td>
<td>20.1</td>
<td>20.1</td>
<td>24.3</td>
<td>24.3</td>
<td>21.9</td>
<td>24.3</td>
<td>24.3</td>
</tr>
</tbody>
</table>

(1) Significance level > 0.1 and determined by Wilcoxon matched pairs sign test to determine if exchanged chicks were fed more or less than wild chicks.
(2) Data for number of feeds brought to wild chicks from Fig. 1.

Experiment 2. When old chicks replaced young chicks all the foster parents accepted their introduced chick and fed them. Chicks received less food than control chicks of the same age (Table 2, Wilcoxon test, \( P < 0.05 \)). The foster parents brought their introduced chicks the same quantity of food as their own chicks could expect to receive (Table 2, Wilcoxon test \( P > 0.1 \)). Thus when an old chick replaced a young chick the parents fed the chick according to their previous feeding schedule and not according to the chick's age.

TABLE 2. Number of feeds brought over 3 days after older chicks were introduced to foster parents compared with expected from chick age and time methods respectively

<table>
<thead>
<tr>
<th>Chick number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed number of feeds to exchanged chicks</td>
<td>33</td>
<td>19</td>
<td>26</td>
<td>23</td>
<td>25</td>
<td>20</td>
<td>21</td>
<td></td>
</tr>
<tr>
<td>Expected number of feeds (chick age method)</td>
<td>35</td>
<td>25</td>
<td>23.8</td>
<td>30.7</td>
<td>28.4</td>
<td>28.4</td>
<td>24</td>
<td></td>
</tr>
<tr>
<td>Expected number of feeds (time method)</td>
<td>30.3</td>
<td>12.7</td>
<td>30.3</td>
<td>27.5</td>
<td>27.5</td>
<td>12.7</td>
<td>30.3</td>
<td></td>
</tr>
</tbody>
</table>

(1) Significance levels determined by Wilcoxon matched pairs sign test to determine whether exchanged chicks were fed more or less than the chick age and time methods respectively.
(2) The expected for the chick age method was calculated as the amount introduced chicks could expect to receive (with respect to their age) and was based on the number of feeds brought to control chicks (Table 1) and by their own parents before the chicks were exchanged.
(3) The expected for the time method was calculated as the amount of food parents would bring their own chicks and was based on the number of feeds brought to control chicks (Table 1) and the foster parents feeding rate before the chicks were exchanged.

When young chicks replaced old chicks all the foster parents accepted their introduced chick and fed them. Chicks received more food than control chicks of the same age (Table 3, Wilcoxon test, \( P < 0.1 \)). The foster parents brought their introduced chicks the same quantity of food as their own chicks could expect to receive (Table 3, Wilcoxon test, \( P > 0.1 \)). Thus when a young chick replaced an old chick the parents fed the chick according to their previous feeding schedule and not according to the chicks' age.

Chicks' fledging age

All the control (experiment 1) and experimental (experiment 2) chicks were fed to fledging and there was no desertion by the parents. When old chicks replaced young chicks then the introduced chicks fledged at a similar age to the control chicks' fledging
TABLE 3. Number of feeds brought over 3 days after younger chicks were introduced to foster parents compared with expected from chick age and time methods respectively

<table>
<thead>
<tr>
<th>Chick number:</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observed number of feeds to exchanged chicks</td>
<td>19</td>
<td>40</td>
<td>19</td>
<td>22</td>
<td>32</td>
<td>31</td>
<td>25</td>
<td></td>
</tr>
<tr>
<td>Expected number of feeds (chick age method)</td>
<td>12.7</td>
<td>27.5</td>
<td>27.5</td>
<td>12.7</td>
<td>30.3</td>
<td>30.3</td>
<td>12.7</td>
<td>( T = 3, P &lt; 0.1 )</td>
</tr>
<tr>
<td>Expected number of feeds (time method)</td>
<td>23.8</td>
<td>28.4</td>
<td>23.8</td>
<td>28.4</td>
<td>24</td>
<td>35</td>
<td>20</td>
<td>( T = 12, P &gt; 0.1 )</td>
</tr>
</tbody>
</table>

(1) Notes as in Table 2.

age (Table 4, Wilcoxon test, \( P > 0.1 \)) and significantly earlier than the foster parents own chicks were expected to fledge (Table 4, Wilcoxon test, \( P < 0.05 \)). Similarly when young chicks replaced old chicks they fledged at an age similar to the control chicks (Table 4, Wilcoxon test, \( P > 0.1 \)) and significantly later than the foster parents’ own chicks were expected to fledge (Table 4, Wilcoxon test, \( P < 0.05 \)). Thus the chick rather than the adults determine the date of fledging.

TABLE 4. Fledging dates of experimental chicks and expected fledging dates according to chicks’ age and foster parents

<table>
<thead>
<tr>
<th>Chick number:</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Older chicks introduced</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed fledging date</td>
<td>43</td>
<td>43</td>
<td>46</td>
<td>46</td>
<td>51</td>
<td>44</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td>Date chick expects to fledge</td>
<td>41</td>
<td>42</td>
<td>46</td>
<td>45</td>
<td>48</td>
<td>47</td>
<td>44</td>
<td>( T = 6, P &gt; 0.1 )</td>
</tr>
<tr>
<td>Date adult expects chick to fledge</td>
<td>51</td>
<td>53</td>
<td>53</td>
<td>50</td>
<td>50</td>
<td>53</td>
<td>51</td>
<td>( T = 1, P &lt; 0.05 )</td>
</tr>
<tr>
<td>(b) Younger chicks introduced</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Observed fledging date</td>
<td>51</td>
<td>48</td>
<td>51</td>
<td>55</td>
<td>43</td>
<td>53</td>
<td>46</td>
<td></td>
</tr>
<tr>
<td>Date chick expects to fledge</td>
<td>53</td>
<td>51</td>
<td>51</td>
<td>53</td>
<td>51</td>
<td>51</td>
<td>55</td>
<td>( T = 4, P &gt; 0.1 )</td>
</tr>
<tr>
<td>Date adult expects chick to fledge</td>
<td>46</td>
<td>47</td>
<td>45</td>
<td>47</td>
<td>44</td>
<td>41</td>
<td>43</td>
<td>( T = 1, P &lt; 0.05 )</td>
</tr>
</tbody>
</table>

(1) Numbers indicate day number where day 1 = 1 July.
(2) Significance levels determined by Wilcoxon matched pairs sign test to determine if chicks fledge earlier or later than the chick or foster parents expect respectively.

DISCUSSION

These data provide some insight into the feeding relationships between puffin adults and their chicks. Artificially reared chicks that were fed additional food (maximum amount parents bring) did not actively reject food until the day before fledging. This suggests that the observed reduction in the number of feeds brought to wild chicks older than 26 days is the result of adults bringing less food than the chicks are capable of eating. However this experiment only tested whether or not chicks older than 26 days would eat additional food and did not eliminate the possibility that the chicks could ‘discourage’ their parents from bringing more food. Although the additional food fed to chicks did not influence the chicks’ weight or age at fledging Harris (1978) reported that underweight puffin chicks on St Kilda fledged at a greater weight when given additional food. Despite there being no difference in the fledging weight of reared chicks the peak weight of chicks fed ad lib was significantly greater, and it is possible that a high peak weight could be advantageous to a chick’s future survival chances.
When I exchanged puffin chicks of a different age the foster parents accepted the introduced chick and fed it the quantity they would have fed their own chick. This was different from the amount of food the chick would have received from its own parents. These results imply that the adults determine the quantity of food brought to chicks from their previous feeding schedule rather than from any cues the adult may use to estimate the chicks’ age. However, this work concentrated on the feeding rates of the adults soon after the chicks were exchanged and it may be possible that adults slowly adapt to the chicks’ requirements. Trivers (1974) has demonstrated theoretically that each offspring should try to acquire more parental investment than their siblings receive. Hence, if parents determine the quantity of food to bring the chick from begging behaviour or certain ‘age-cues’ then the chicks could trick the parents into bringing more food, and perhaps donating more parental investment than the parents give their other offspring. In this respect, the feeding mechanism described here can be considered more adaptive than a feeding mechanism that depends on the chicks’ behaviour. Nevertheless a rigid feeding schedule with no feedback from the chick to the parent could result in chick fatality if feeding conditions were poor or either parent died. Nettleship (1972) observed the growth of twelve puffin chicks each fed by a single parent and reported that all chicks died or disappeared before fledging.

Chicks used for the exchange experiments all fledged at a similar age and were not deserted by their parents, even when the adults fed their foster chicks for longer than they would have fed their own chicks. Hence there was no desertion of puffin chicks by their parents similar to that described by Lockley (1934) and Myrberget (1962) which suggests that the chicks may determine the duration of the feeding schedule. Nettleship (1972) found that the puffin chicks on Great Island, Newfoundland that remained longer in the burrows than the normal chicks were fed until they fledged and were not deserted. Similarly Harris (1969) exchanged young audubons shearwater chicks (Puffinus lherminieri, Lesson) for old chicks and found that adults continued to feed their chicks for as long as the chicks remained in the burrows.

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