Apparent Absorption Efficiencies for Redshank (Tringa totanus L.) and Oystercatcher (Haematopus ostralegus L.): Implications for the Predictions of Optimal Foraging Models

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APPARENT ABSORPTION EFFICIENCIES FOR REDSHANK
(TRINGA TOTANUS L.) AND OYSTERCATCHER (HAEMATOPUS
OSTRALERUS L.): IMPLICATIONS FOR THE PREDICTIONS
OF OPTIMAL FORAGING MODELS

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Food that enters an animal’s digestive system is not completely absorbed by the
body. This occurs in part because no animals possess all the digestive enzymes
necessary to digest all substrates, and also because substrates may avoid contact
with digestive secretions because they are mechanically protected by indigestible
matter or because they move through the portion of the gut where an enzyme is
secreted too rapidly for digestion to occur fully. Estimates of apparent absorption
efficiency (A), the proportion of food absorbed, without correction for matter
passed into the gut as secretions (Harris 1966), vary between 30% and 95%
between species and food types and even between individuals in different
situations (Gibb 1957; Altman and Dittmer 1968; Moss 1973, 1975; King 1974; Ricklefs
1974; Beamish et al. 1975; Grodzinski and Wunder 1975; Lavigne et al. 1982).

Apparent absorption efficiency has important applications in estimates of re-
source exploitation and utilization (Njaa 1977) and in studies of energy balance
(King 1974; Ricklefs 1974), energy flow in ecosystems (Odum 1971), and nutrition
(Brody 1945; Graham 1977). In a recent review of energy-balance studies in
shorebirds (Charadrii), Pienkowski et al. (1984) noted that estimates of A were not
available for this family. In this paper I present estimates of dry-mass and ash-free
dry-mass A for the redshank (Tringa totanus) and the oystercatcher (Haematopus
ostrolegus), when feeding on a variety of food types. I discuss the significance of
these data for predictions of the classical models of diet choice (Schoener 1971;
Charnov 1976) and partial prey consumption (Sih 1980).

METHODS

Apparent absorption efficiencies may be measured in two ways. First, the dry
mass of food ingested by an animal (Mf) and the dry mass of feces produced (Mf)
may be measured simultaneously over a given period (Lloyd and Crampton 1955).

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Apparent dry-mass absorption efficiency ($A_{DM}$) is calculated as follows:

$$A_{DM} = (M_i - M_d)/M_i.$$  

(1)

Apparent absorption efficiencies of different substrates within food are not equal. Given the proportion of any particular component ($x$) in the food ($p_{xf}$) and in the feces ($p_{xf}$), the $A$ of that component ($A_x$) can be calculated from the dry-mass absorption efficiency ($A_{DM}$).

Generally,

$$A_x = 1 - [p_{xf}(1 - A_{DM})]/p_{xf}. \tag{2}$$

This technique is not easy to use, however, since it is difficult to ensure that all the feces have been collected unless the animal is closely confined and/or wears a collecting bag to avoid fecal loss. In addition, it is difficult to measure accurately the dry mass of food ingested, unless its water content is known accurately, since food is generally consumed wet.

Another method is to mix the food with an inert marker, which is not digested. (For a review, see Kotb and Luckey 1972.) Since the apparent absorption efficiency of the marker is negligible, it may be assumed to equal zero. Substitution of $A_x = 0$ into equation (2) yields

$$A_{DM} = 1 - [p_{xf}/p_{xf}]. \tag{3}$$

The advantage of this alternative technique is that the mass of food ingested and of feces produced need not be measured. Estimates are required of only the marker concentration in the food and in the feces. The problem associated with this technique is that, although the marker itself is not absorbed, it may influence digestion and/or absorption of other substrates. For example, Njaa (1961, cited in Njaa 1977) found a reduction in $A$ of protein in rats ($Rattus$ sp.) on the first day they were fed the marker titanium dioxide. In addition, it is difficult to mix the marker thoroughly with most food types without homogenizing the food, which probably also influences the apparent absorption efficiency.

The principle behind the marker technique is that equation (3) may be derived from equation (2) if the apparent absorption efficiency of a component of the food, the marker, equals zero. If the apparent absorption efficiency of a natural component of the food were zero, then $A_{DM}$ could be estimated from the concentration of this natural component in the food and feces using equation (3). This natural-marker method avoids the problems associated with the artificial-marker technique. This paper demonstrates the validity of using inorganic matter in food, which remains as ash after combustion under standard conditions (here, the ash equivalent), as a natural marker in the redshank. I present some estimates of apparent dry-mass and ash-free dry-mass absorption efficiencies ($A_{DM}$ and $A_{AM}$) in redshank and oystercatcher using this marker.

Ash Equivalent as a Natural Marker

Three wild-caught redshank were housed in an indoor aviary measuring 2 m by 1.5 m in surface area. The birds were fed either blowfly ($Calliphora$ sp.) larvae or sardines ($Sardina pilchardus$). On experimental days, the birds were removed
from the aviary and deprived of food for an hour. A weighed quantity of either homogenized sardines or live blowfly larvae was introduced to the aviary, the floor was covered with plastic sheeting, and the birds were reintroduced. Free access was allowed to water. When the birds were fed sardines, a second, inaccessible dish was also introduced. The percentage of mass lost from sardines in this second dish was used to correct the estimate of food mass ingested by the birds for evaporative water loss. Approximately 10 h after the birds were introduced, a small (10-g) sample of the food was collected for drying and ash analysis. A full 24 h (12 h light, 12 h dark) after introducing the birds, the food was removed; 1 h later the plastic sheeting was also removed.

All the droppings on the sheeting (henceforth, the feces) were removed. It should be noted, however, that since urine and feces are discharged together these droppings were contaminated to an unknown, but probably slight, extent by the ash-equivalent content of the urine. The feces were weighed and subsampled for drying and ash analysis. Preliminary trials suggested that the birds ate predominantly during darkness, as has been observed in other captive shorebirds (M. Kersten, pers. comm.). Since the experiments began and ended in the middle of the light period, it was unlikely that large quantities of food were eaten in the 4 or 5 h before the food was removed. The plastic sheeting was left in the aviary for an extra hour after the food was removed to collect any feces still in the gut. An hour was sufficient, since food transit time in the Charadrii is rapid. For example, the time from first feeding after emergence of tidal mud flats to time of first feces production in free-living grey plovers (Pluvialis squatarola) was between 22 and 39 min \((n = 5; \ T. \ Piersma \ and \ P. \ M. \ Zegers, \ pers. \ comm.)\).

**Apparent Absorption Efficiency**

Six wild-caught redshank were housed in an outdoor aviary measuring 6 m by 2 m in surface area. The aviary was cleared of feces and the experimental food was introduced. Water was freely available. Both water and food were replensihed daily. Samples of fresh feces were collected from the cleaned surfaces on which the birds roosted, on and after the third day after the food was first introduced. Samples of uneaten food were taken daily. All the food samples were mixed and approximately 10 subsamples taken for ash analysis. Between 30 and 150 droppings were collected for each food type. These feces were pooled, and 10–30 subsamples of the resulting homogenate weighing approximately 0.5 g each were taken for ash analysis. The foods included in the investigation were blowfly (Calliphora sp.) larvae and pupae, sardines, and laver spire snails (Hydrobia ulvae). The blowfly larvae were purchased and allowed to pupate. Sardines were purchased canned in brine and homogenized before being presented to the redshank. Live laver spire snails were collected from a large intertidal estuarine mud flat on the southern shore of the inner Forth estuary on the eastern coast of Scotland \((56^\circ N)\). The shells were sieved from the mud using a 1-mm mesh sieve. This sieve retained at least 97% of the Hydrobia snails present in the mud.

Identical procedures were used with two wild-caught oystercatchers feeding on the fresh flesh of edible mussels (Mytilus edulis). Live mussels were collected from Culross, a bay on the northern shore of the inner Forth estuary. The mussels were washed and kept alive in continuously running seawater in the aquarium of
the Department of Biological Sciences, University of Stirling. Each day, the birds were presented with 60–80 mussels with the posterior adductor muscle severed to reveal the flesh. The birds ate only the flesh.

**Ash Analysis**

Samples were weighed wet and then dried at 60°C for 14 days in aluminum crucibles. After reweighing, samples were incinerated at 450°C for 24 h, and reweighed a third time. These procedures were developed to ensure complete evaporation of water, to prevent volatilization of lipids during the drying phase (Warnes 1981), and to prevent volatilization of calcium and potassium in the ignition phase (Rees 1937). There was no mass change in the crucibles with any treatment. Ash-equivalent contents were expressed as the mass remaining after ignition as a proportion of the dry mass. The mean apparent absorption efficiencies of dry mass ($A_{DM}$) were calculated using mean ash-equivalent contents of food and feces substituted into equation (3). Apparent absorption efficiency of ash-free dry mass ($A_{AM}$), that is, absorption of organic material, was calculated for each predator-prey combination by substituting the ash-free proportions of food and feces and the appropriate mean dry-mass absorption efficiency ($A_{DM}$) into equation (2).

**RESULTS**

**Ash Equivalent as a Natural Marker**

Estimates of dry mass of food ingested, dry mass of feces produced, and the calculated $A_{DM}$ for the 6 days in which the redshank were fed sardines and the 2 days in which they were fed blowfly larvae are shown in table 1. The mean ash-equivalent content of sardines was 7.3% (SD, 2.6%; $n = 10$), whereas the ash-equivalent content of feces produced from redshank feeding on sardines was 31.0% (SD, 5.7%; $n = 10$). Substituting the proportions of ash-equivalent content in food and feces into equation (3) yields an estimated apparent absorption efficiency of dry mass of 76.5% when the birds fed on sardines. The mean ash-equivalent content of blowfly larvae was 3.8% (SD, 1.4%; $n = 9$), and the mean ash-equivalent content of feces produced from redshank equaled 33.2% (SD, 4.6%; $n = 10$). Substitution into equation (3) yields an estimated apparent absorption efficiency of dry mass of 88.5% when the birds fed on blowfly larvae. The estimates of mean apparent absorption efficiency of dry mass using the direct weighing technique and the ash-equivalent marker technique are very close, and the mean marker estimate lies well within the standard deviation of the distribution of direct weighing estimates across days for both prey types. It was concluded that ash equivalent was not absorbed and therefore could be used as a natural marker.

**Apparent Absorption Efficiency**

When feeding on blowfly pupae, redshank regurgitated pellets consisting exclusively of the chitinous exoskeletons of the prey. The chitinous exoskeleton had a significantly greater ash-equivalent content than the dissected body contents
TABLE 1

TWENTY-FOUR-HOUR DRY-MASS INTAKE OF EITHER SARDINES (Sardina pilchardus) OR BLOWFLY LARVAE (Calliphora sp.) BY REDSHANK, AND SIMULTANEOUS DRY FECES PRODUCTION WITH THE CALCULATED APPARENT ABSORPTION EFFICIENCIES

<table>
<thead>
<tr>
<th>Predator</th>
<th>Prey</th>
<th>Intake, dry (g)</th>
<th>Feces, dry (g)</th>
<th>Apparent Absorption Efficiency (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redshank</td>
<td>Sardina pilchardus</td>
<td>21.19</td>
<td>4.46</td>
<td>78.95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>19.10</td>
<td>5.13</td>
<td>73.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>16.36</td>
<td>4.53</td>
<td>72.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td>22.34</td>
<td>2.50</td>
<td>79.57</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.55</td>
<td>0.94</td>
<td>73.35</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10.31</td>
<td>2.02</td>
<td>80.40</td>
</tr>
<tr>
<td>Redshank</td>
<td>maggots</td>
<td>22.1</td>
<td>2.73</td>
<td>87.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.6</td>
<td>0.96</td>
<td>91.69</td>
</tr>
</tbody>
</table>

Note.—For redshank fed on S. pilchardus mean apparent absorption efficiency = 76.28%, SD = 3.71, n = 6; for redshank fed on maggots, mean = 89.65%, SD = 2.88, n = 2.

TABLE 2

MEAN ASH-EQUIVALENT CONTENT (% OF DRY MASS) OF THE CHITINOUS EXOSKELETON AND BODY CONTENTS OF BLOWFLY (Calliphora sp.) PUPAE

<table>
<thead>
<tr>
<th>Body Contents</th>
<th>Exoskeleton</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean ash-equivalent content (%)</td>
<td>6.73</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>1.71</td>
</tr>
<tr>
<td>n</td>
<td>7</td>
</tr>
</tbody>
</table>

Note.—The ash-equivalent content of the exoskeleton was significantly greater than the body contents (t = 7.32, P < 0.01).

(table 2). Since the body contents were the only component to pass through the alimentary canal, the ash-equivalent content of the body contents alone was used to predict the apparent absorption efficiency.

The ash-equivalent content of Hydrobia was inversely related to shell length (fig. 1). Larger Hydrobia snails had relatively more flesh. The redshank preferred to eat the larger Hydrobia snails from the distribution they received (fig. 2). The birds preferentially selected Hydrobia snails in the range of 3.2–4.4 mm long. The mean length ingested was 3.9 mm. Substituting this mean ingested length into the fitted regression of the percent of ash equivalent against mean length (fig. 1) yielded an estimate of the percent of ash equivalent in the ingested food of 58.8% (SD, $S_{yx} = 1.8$). Ash content of the flesh was not related to shell length in M. edulis.

Estimates of the mean ash-equivalent contents of the different food types, and the feces of redshank or oystercatcher when eating these foods, with the calculated mean $A_{DM}$ (eq. 3) and mean $A_{AM}$ (eq. 2) are shown in table 3. $A_{DM}$ varied between 26% and 88%. As expected, prey with high ash-equivalent contents had lower $A_{DM}$’s (fig. 3a); however, the gradient of the decline in $A_{DM}$ was greater than
Fig. 1.—Ash-equivalent content of *Hydrobia ulvae* against shell length. Larger snails had lower ash-equivalent contents. The fitted regression equation, \( \% \text{ ash-equivalent content} = 87.7 - 7.42 \times \text{ mean length ingested (mm),} \) explained 92.7% of the variability in percent ash-equivalent content. *Vertical bars,* standard deviation.

would be expected because of the indigestibility of ash-equivalent content alone. A similar nonlinear inverse relationship between \( A_{AM} \) and ash-equivalent content (fig. 3b) accounted for this discrepancy. The least-squares-fit regression equation,

\[
A_{AM}(\%) = 103.88 - 8.93 \ln (\% \text{ ash}),
\]

explained 86.9% of the variability in \( A_{AM} (F = 20.0, n = 5, P < 0.05). \)

**DISCUSSION**

Apparent dry-mass absorption efficiencies (\( A_{DM} \)) estimated in the present study were in the same wide range as estimates for mammals (Altman and Dittmer 1968; Lavigne et al. 1982) and for birds of other families feeding on a variety of plant and animal material (Gibb 1957; Moss 1973, 1975; Ricklefs 1974). The inverse relationship between \( A_{AM} \) and ash-equivalent content of the food type (fig. 3b) may arise because the inorganic matter mechanically obstructs the access of digestive enzymes to the organic, ash-free component. An inverse relationship between \( A \) of protein or energy and fiber content of plant foods (Chick et al. 1947; Saunders et al. 1972; Bhattry et al. 1974) has been attributed to mechanical obstruction of enzyme access by cellulose (Silvano 1977). Alternatively, carbonates and hydroxides, which probably make up a high proportion of the bound cations in the ash equivalent, may combine with hydrochloric acid in the stomach, increasing the gut pH and decreasing the efficiency of the protease trypsin, which is optimum in the range of pH 1.5 to 2.5 (White et al. 1964). Further research is required to distinguish between these alternative explanations.
Fig. 2.—Size distribution of *Hydrobia ulvae*: A, as presented to redshank (*n* = 157); B, remaining after 3 days (*n* = 129, corrected to 157); A − B, eaten by redshank, by inference. Redshank preferentially selected *Hydrobia* snails in the range of 3.5 to 4.4 mm long.

Fig. 3.—Relationships between apparent absorption efficiencies of dry mass (a) and ash-free dry mass (b) against ash-equivalent content of the prey. (For predator-prey combinations, refer to table 3.) b, The least-squares-fit curvilinear regression \( A_{AM}\% = 103.88 - 8.93 \log_e \) ash-equivalent content (%) explained 86.9% of the variability in \( A_{AM}\).
### TABLE 3
ASH-EQUIVALENT CONTENTS (% OF DRY MASS) OF VARIOUS PREY AND THE FECES OF REDSHANK OR OYSTERCATCHER WHEN FEEDING ON THOSE PREY, WITH CALCULATED MEAN APPARENT ABSORPTION EFFICIENCIES OF DRY MASS ($A_{DM}$) AND ASH-FREE DRY MASS ($A_{AM}$)

<table>
<thead>
<tr>
<th>Predator</th>
<th>Prey</th>
<th>Ash-Equivalent Content (%)</th>
<th>Mean Absorption Efficiencies (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Food</td>
<td>Feces</td>
</tr>
<tr>
<td>Redshank (Tringa totanus)</td>
<td>Calliphora larvae</td>
<td>3.82</td>
<td>33.21</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD</td>
<td>1.36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$n$</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>Calliphora pupae</td>
<td>6.73</td>
<td>36.75</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD</td>
<td>1.71</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$n$</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>Sardina pilchardus</td>
<td>7.28</td>
<td>31.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD</td>
<td>2.63</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$n$</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Hydrida ulvae</td>
<td>58.76</td>
<td>80.11</td>
</tr>
<tr>
<td>Oystercatcher (Haematopus ostralegus)</td>
<td>Mytilus edulis†</td>
<td>22.0</td>
<td>61.25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SD</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$n$</td>
<td>35</td>
</tr>
</tbody>
</table>

* Predicted.
† Fleshy only.

Since the observed relationship between $A_{AM}$ and ash-equivalent content was established across two species foraging on a taxonomically diverse range of prey, the relationship may be more generally applicable within the Charadrii. The regression equation presented may be used, therefore, in the absence of absorption-efficiency data for specific predator-prey interactions as a first approximation to estimate apparent ash-free dry-mass absorption efficiencies in this group.

In addition, the observed effect of ash equivalent on apparent ash-free dry-mass absorption (fig. 3b) may facilitate an interpretation of several anomalous foraging behaviors of the Charadrii within the framework of the premise of net energy maximization. For example, wading birds frequently wash their prey before eating (Goss-Custard 1977b). Superficially, this behavior appears to be energetically inefficient since it increases both the handling time and the energy expended in handling the prey but not its energy content. If, however, washing removes inorganic matter, the energetic advantages of an increase in $A_{AM}$ might offset the more obvious energetic disadvantages. Similarly, when foraging on Macoma balthica bivalves (Hulscher 1981), Cerasteroderma edule cockles (Sutherland 1982), and mussels (Dewar 1908; Norton Griffiths 1966; Goss-Custard et al. 1980; Speakman 1984), oystercatchers extract and ingest only the flesh of these prey, leaving the shells. By ingesting prey whole, the birds would achieve a greater intake of organic energy (i.e., the fibrous protein of the shell in addition to the flesh), and particularly for the smaller prey, like Macoma, ingesting prey whole
would probably be faster. Removing the flesh would consequently appear to be energetically inefficient. When compared with the flesh (Speakman 1984), bivalve shells are, however, relatively heavy, consisting almost entirely of ash-equivalent matter (>90%; Speakman 1984). The relationship between ash equivalent and \( A_{AM} \) observed in this study suggests that ingesting a large bulk of inorganic matter greatly reduces absorption efficiency of ash-free matter. Thus, removing the flesh may represent an energetically more efficient handling strategy for this species. In this context, it is interesting to note that as the shell length of the edible mussel decreases, the organic component of the shell increases and the relative mass of the shell to flesh decreases (Speakman 1984). The advantages of opening mussels and eating only the flesh would therefore be expected to decline as shells get shorter, and below some critical length it might be more profitable to eat both the shell and the flesh. In support of this hypothesis, Evans (1977) reported seeing oystercatchers eat small mussel shells whole on a mussel bank where only small shells were available.

More generally, the relationship between ash-equivalent content and \( A_{AM} \) may have important consequences for partial consumption of prey, which invariably include portions with different ash-equivalent content. These effects are ignored in a theoretical model that addresses the problem of partial prey consumption (Sih 1980). In this model the prey item is considered as a patch in which net energy returns occur at a decreasing rate with time. At a critical point, it is more profitable for the predator to leave and find another prey item than continue eating the same prey. If the rate of intake of ash equivalent, however, increases as a monotonic function of time spent feeding, such as would occur if fleshy parts were ingested before skeletal tissue, then the effects of ash equivalent on \( A_{AM} \) would be expected to cause the predator to leave the prey earlier and leave more behind than predicted by the simple patch model (Sih 1980).

Diet choice may be most profoundly affected by the aforementioned relationship, particularly if the mode of reduction in \( A_{AM} \) was a result of elevation of stomach pH. This result occurs because ash ingested in one prey would influence the energy absorbed from another. The effects are most important for diet choice when two prey are available, one with a high profitability but a high ash-equivalent content, and the other with a lower profitability but a low ash content. The predictions of classical models of diet choice, formulated under the premise of net energy maximization (Schoener 1971; Charnov 1976; Elner and Hughes 1978), would be to select exclusively the item of higher profitability and to include the item of lower profitability only below some critical density of the high-profitability items. If there is an inverse nonlinear relationship between \( A_{AM} \) and ash-equivalent content of the prey mix in the gut of the form of figure 3b, however, at low densities of the high-profitability item, the predator may maximize its net rate of energy gain by selecting exclusively the item of low profitability. This unexpected prediction occurs because although the predator ingests more energy when feeding on both prey than when feeding on the low-profitability item alone, the reduction of \( A_{AM} \) by the high ash-equivalent content of the high-profitability item means less energy is actually absorbed by the gut.

The effect on diet choice depends critically on the form of the relationship
between $A_{AM}$ and ash-equivalent content. To illustrate the effects of the relationship presented in figure 3b on diet choice, consider the following hypothetical example. Prey A weighs 2 g and comprises 50% ash-equivalent content. Prey B weighs 0.61 g and comprises 1.64% (0.01 g) ash-equivalent content. The handling time of both items equals 10 s and the ash-free mass of both items has an energy density of 20 kJg$^{-1}$. It is assumed that the rate costs of searching for and of handling both prey are equal and can therefore be ignored in this analysis. Therefore, the profitability of A equals 2 kJs$^{-1}$ and that of B equals 1.2 kJs$^{-1}$. Since A has a greater ash-equivalent content, the absorbed energy is much lower than that ingested. Using the fitted regression equation for the data in figure 3b, absorption when feeding on A alone equals 69% and absorption when feeding on B alone equals 99%. The true profitabilities, therefore, based on the energy absorbed per second of handling, are $A = 1.38$ kJs$^{-1}$ and $B = 1.18$ kJs$^{-1}$. Even accounting for this effect, therefore, A remains more profitable than B.

The energy gained by foraging exclusively on item A varies inversely with the time required to search for an item of that type (fig. 4). If the density of B is fixed at, say, one item discovered every 5 s spent searching, the energy gain when foraging exclusively on that item is 0.78 kJs$^{-1}$, independent of the time spent searching for (and, hence, the density of) item A (fig. 4). The classical interpretation of this graphic model (Schoener 1971; Charnov 1976; Elner and Hughes 1978) generated by interpolating the profitability of B on the gains of A would be to forage exclusively on item A when it requires less than 2.2 s to find an item of that type and to include both items when it takes longer (fig. 5a).

The actual gains from this mixed diet can also be calculated, against changes in the density and hence the time spent searching for items of type A. This calculation takes into account the changing proportion of the two items in the gut, which influence the ash-equivalent content of the gut and hence $A_{AM}$. Gains with the mixed diet against density of A are also shown in figure 4. This figure illustrates that when a relationship of the type in figure 3b is found and the prey have characteristics similar to those of A and B, the predictions of the classical diet-choice model do not hold. In particular, the shift to a mixed diet should be made at lower densities of A than predicted because the high ash content of item A effectively reduces the energy absorbed from item B. In practice, the profitability of item B is lowered when it is eaten in combination with item A. In addition, at low densities of item A, it becomes profitable to switch to a diet comprising exclusively the low-profitability item B. The relatively large amount of ash in a few items of A reduces the energy absorbed from the more abundant item B to a greater extent than the energy in A increases absorption.

By generating similar graphic predictions and varying the density and search time for item B, it is possible to picture how the predicted diet changes with shifts in the density and time spent searching for both prey items (fig. 5b). A similar figure (fig. 5a) shows the expected diet changes predicted by the classical optimal foraging models (e.g., Charnov 1976). Figure 5b shows that at high densities of item B it is most profitable to switch directly from specialization on A to specialization on B as the density of A declines. At lower densities of B, it is more profitable to include a period when both items are taken as the density of A
declines. The range of densities of A over which this mixed diet is profitable increases as the density of B declines. This prediction is similar to the predictions of frequency-dependent selection and switching (Visser 1981), but it depends entirely on the inverse relationship between $A_{AM}$ and ash-equivalent content described in figure 3b.

One further point from figure 5b is that the expansion in area of the mixed-diet zone results predominantly from change at the boundary where the diet is mixed and item B is excluded, rather than at the boundary where the diet is mixed and item A is excluded. The latter boundary varies little with changes in density of either item. This is important because an interpretation of diet-choice observations in this situation would undoubtedly lead to the conclusions that the animal exclusively ingested item B more often than it exclusively ingested item A and that inclusion of item A in the diet depended on the density of item B. The item of lower profitability would consequently appear to be "the preferred item," and ipso facto the predator would not appear to be maximizing energy gain in its diet.

The potential effects of intraspecific differences in ash-equivalent content (or cellulose content) on absorption efficiency and hence diet choice should be considered when interpreting diet choice with mixed-prey species or where age and size differences influence prey composition. One example of this effect may be the observation that redshank feed preferentially on Corophium volutator (Pallas), a small amphipod crustacean that occurs at high densities, and not on Nereis
Fig. 5.—Effects of density of two prey items on the diet that maximizes energy gain. Item A is of greater profitability but of greater ash-equivalent content that item B. a, The ash-free dry-mass absorption efficiency is independent of ash-equivalent content of the prey. The pattern of diet choice is that predicted by the classical optimal foraging models. b, The nonlinear inverse relationship between ash-free dry-mass absorption efficiency and ash-equivalent content is of the same form as that in figure 3b. The pattern of diet choice that maximizes net energy gain differs markedly from the prediction of the classical model. In particular, at high densities of the lower-profitability item, B, net energy gain is maximized by selecting that item exclusively.
dversicolor (Muller), a polychaete worm of greater profitability (Goss-Custard 1977a). Estimates of ash-equivalent content of these two prey do not differ sufficiently to account for the preference (Speakman 1984). In the field, however, ingested ash equivalent in Nereis may be much greater than that estimated in the laboratory, since large amounts of inorganic mud may be trapped between the parapodia. Further observations that redshank frequently wash Nereis worms (pers. obs.; Goss-Custard 1977b), possibly to remove this matter, and occasionally reject worms after they have been removed from the substrate (Goss-Custard 1977a) are not incompatible with the above hypothesis. These observations are more difficult to interpret if other explanations for the Corophium preference are accepted (e.g., a selection for complementary resources; Krebs 1978). It is certain that redshank do ingest matter from the substrate since it is a principal component of regurgitated pellets in the wild (pers. obs.). Whether more is ingested with Nereis than with other prey and whether this is sufficient to account for the Corophium preference require further investigation.

SUMMARY

Apparent absorption efficiencies of dry mass for redshank (Tringa totanus) feeding on blowfly (Calliphora sp.) larvae and pupae, sardines (Sardina pilchardus), and laver spire snails (Hydrobia ulvae) and for oystercatcher (Haematopus ostralegus) feeding on the flesh of mussels (Mytilus edulis) varied from 27% to 88%. Prey with high indigestible ash-equivalent contents had lower apparent absorption efficiencies of dry mass and also lower apparent absorption efficiencies of ash-free dry mass. These relationships suggest that several superficially energetically inefficient foraging behaviors performed by the predators—for example, washing prey items and partial prey consumption—may maximize net energy gain. The relationships have wider implications for foraging models that predict partial prey consumption and optimal diet. With respect to partial consumption of prey, the relationships, in combination with a monotonic increase in ash-equivalent content during the time spent eating a prey item, would lead the predator to leave the prey earlier and to leave more prey than previously predicted. In combination with variations in ash-equivalent content between prey types, the relationships may also lead to frequency-dependent shifts in prey preference.

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