THE ENERGETICS OF FORAGING BY REDSHANK, *TRINGA TOTANUS*

J. D. GOSS-CUSTARD[1]

ABSTRACT.—Redshank, *Tringa totanus,* in Britain feed in many places on the amphipod crustacean *Corophium volutator* and the polychaete worms *Nereis diversicolor* and *Nephtys hombergi.* When feeding on *Corophium,* redshank spent most time where prey density and the net rate at which they obtained energy were highest. When feeding on worms, redshank preferred the large ones and took very few small ones unless large ones were scarce. Simulation experiments with a mathematical model of the bird's feeding behavior suggested that this preference for large worms maximized the gross, and perhaps net, rate at which energy was collected. However, when *Corophium* and worms occurred together in the mud, redshank selected the amphipod even though taking worms would have enabled them to collect energy at a much greater net rate. It is unlikely that redshank selected *Corophium* for their nutrient content. The results are discussed in relation to some models of foraging by predators.

This paper summarizes the results of a field study on the selection of feeding places and prey types by redshank, *Tringa totanus,* outside the breeding season (Goss-Custard 1970, 1977a, b, c). These birds take a wide variety of prey species from estuarine flats, but in many places in Britain feed on the small amphipod crustacean *Corophium volutator* and two species of polychaete worms, *Nereis diversicolor* and *Nephtys hombergi* (Burton 1974, Goss-Custard 1969, 1977a, b, Goss-Custard, Kay and Blindell 1977, Prater 1972). The questions asked were: (i) Do redshank feed where prey is most abundant? (ii) Do redshank select between the different size classes of the same prey species? (iii) Do redshank select between the amphipod and the worms when they occur together in the mud? And (iv), if selection occurs in any of these situations, does it maximize feeding profitability, i.e., the net rate at which energy is obtained?

METHODS

Redshank were studied in a number of muddy sites on several estuaries in southern England and on the Ythan estuary in northeast Scotland. Using mainly observational techniques, I counted the numbers of small prey and worms in each of several size classes (based on the length of the bird's bill) that were swallowed per minute. By means of analyses of pellets and gizzard contents, small prey were identified and measured. The density of the various prey types in the mud was measured by standard core sampling techniques.

The preference of redshank for areas of different prey density was studied on the Ythan where the main food was *Corophium.* Five areas were marked out with stakes at different levels of a beach. The number of birds feeding in each zone was recorded when the tide was fully out during five study periods in two winters. *Corophium* density in each zone was measured during each period and related to bird density. The ranges in the values of both redshank and *Corophium* densities varied between periods. They were converted to a common scale by expressing each zone value of redshank density as a proportion of the sum total of bird densities in all zones during the period. The same procedure was applied to *Corophium* density and ingestion rate, i.e., the biomass of prey taken per minute by redshank.

The preference for prey types was studied in 30 sites in southern England. The numbers of each prey type taken were plotted against their own density in the mud. By definition, a preferred prey is one where the numbers taken depend mainly on their own density. In contrast, feeding rate on less preferred prey depends not only on their own density (few can be taken if few are present), but also on how many preferred prey are found. When the preferred prey is abundant and taken at a high

---

[1] Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset, England.
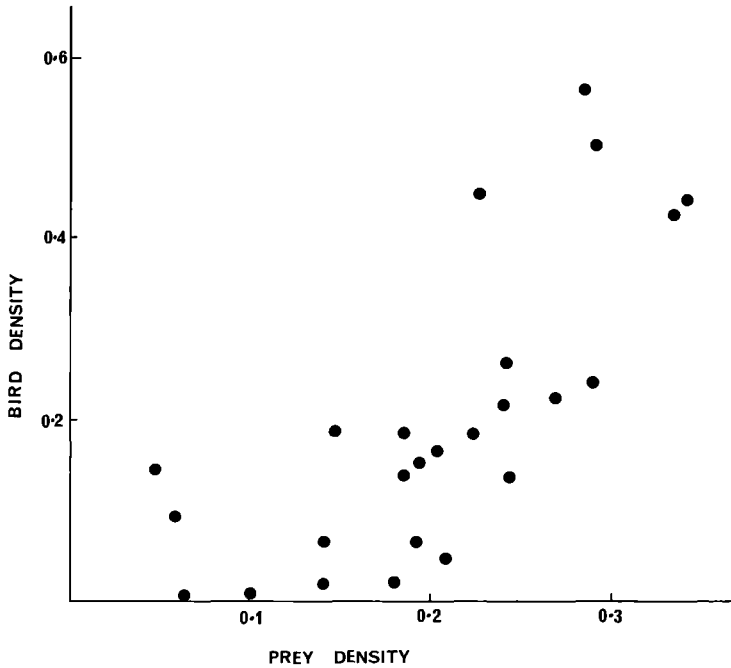
FIGURE 1. Relative density of redshank in relation to the relative density of *Corophium*.

rate, few of the less preferred ones will be taken even when they are numerous. The birds' response to the less preferred prey should be inversely related to the abundance of the preferred prey.

SELECTION FOR FEEDING PLACES

Individual redshank ranged over the whole beach but fed most where *Corophium* was densest (Fig. 1). Ingestion rate was correlated with prey density (Goss-Custard 1970, 1977c) so the birds spent most time feeding where their ingestion rate was highest (Fig. 2). Redshank also made fewer pecks and paces to collect a unit of prey biomass where *Corophium* was most abundant. Therefore, the birds preferred to feed most where they collected energy at the greatest net rate.

SELECTION BETWEEN SIZE CLASSES OF PREY

Most *Corophium* taken by redshank were over 4 mm long (maximum 10 mm) but, within this range, the numbers of small ones taken did not depend on the density of large ones (Goss-Custard 1977a). Although redshanks took more large ones than small ones overall, it is not clear whether this involved active selection or whether the birds took all they found and large ones were simply more noticeable.

The size composition of the worm populations in the different sites varied enormously and so provided a good opportunity for testing whether the birds preferred certain sizes (Goss-Custard 1977b). Using data from sites where few prey other than worms were taken, feeding rate (expressed for technical reasons as numbers taken per meter searched) on large worms (>30 mg dry weight) was quite closely correlated with their density in the mud (Fig. 3). However, the
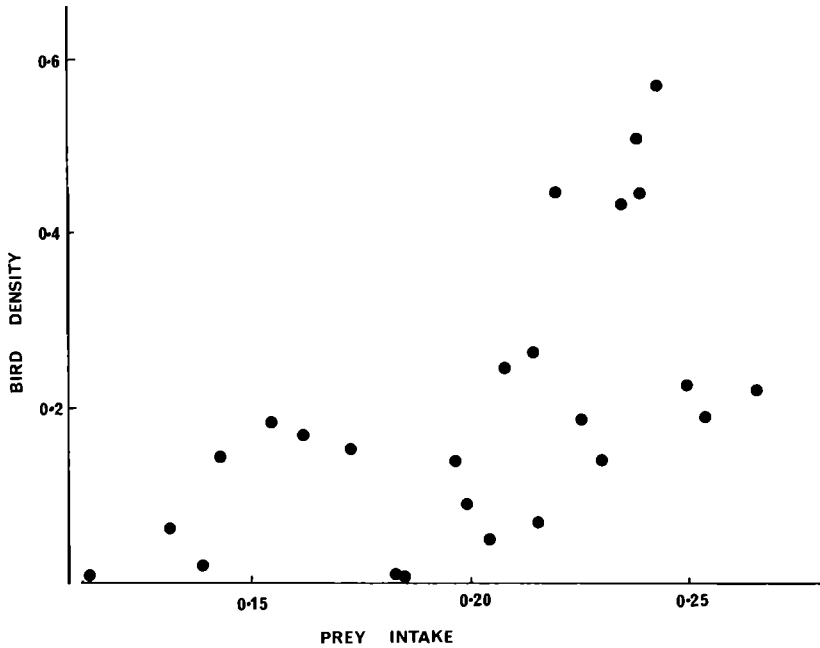
FIGURE 2.   Relative density of redshank in relation to the relative rate of collecting *Corophium* biomass.

feeding rates on the medium (10–30 mg) and, particularly, small (<10 mg) ones were poorly correlated with worm densities. Feeding rate on these size classes depended more on the quantity of large worms taken because the probability that a redshank would take a small worm decreased sharply as the biomass of large
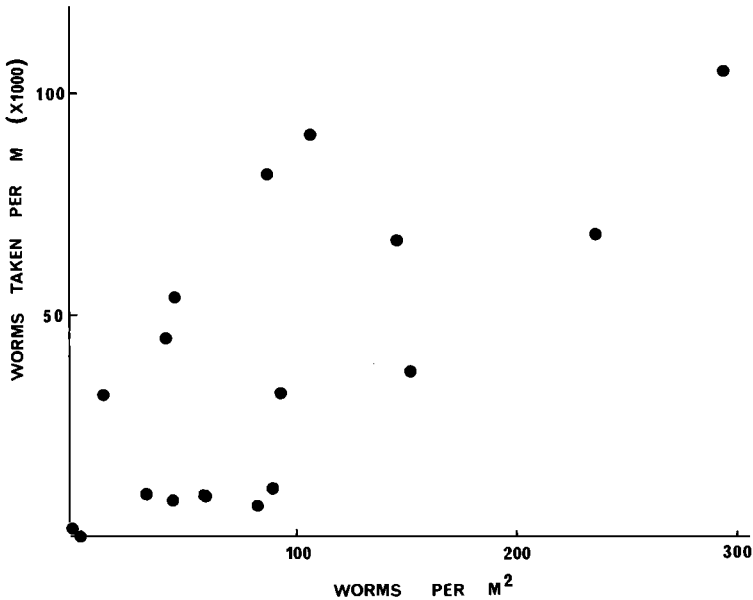

FIGURE 3.   Feeding rate on large worms (>30 mg dry weight) in relation to worm density.
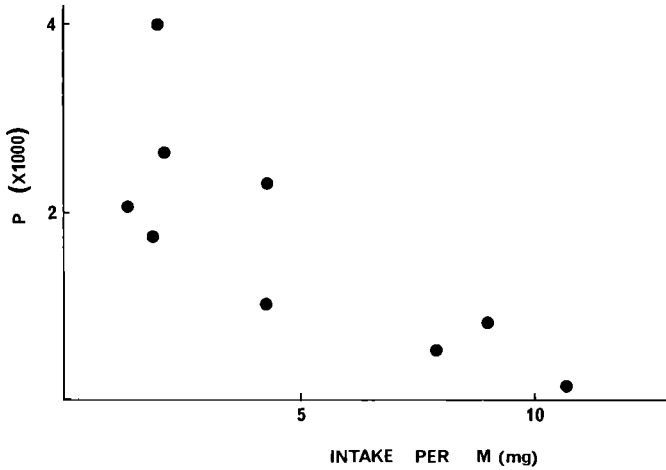
FIGURE 4. The probability (P) that redshank would take a small (<10 mg) worm it encountered in relation to the amount of food ingested from large worms (>10 mg). Data from sites where the density of small prey varied from 70–170 per m^2.

worms consumed increased (Fig. 4). Since the biomass intake of large worms depended on the biomass of these worms in the mud (Fig. 5), redshank were least likely to take small worms where large ones were abundant. The results suggest that redshank preferred large worms and took very few small ones unless large ones were scarce.
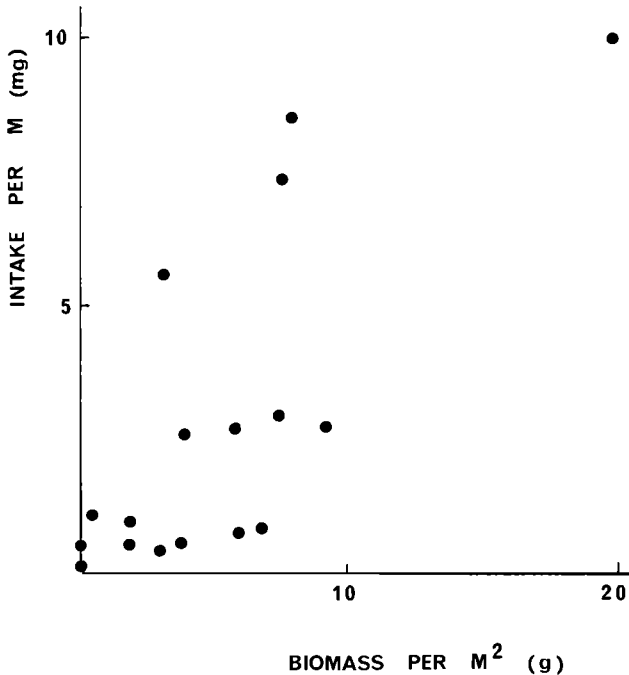

FIGURE 5. The biomass of large worms (>30 mg) taken per meter searched in relation to the biomass density of these worms in the mud.
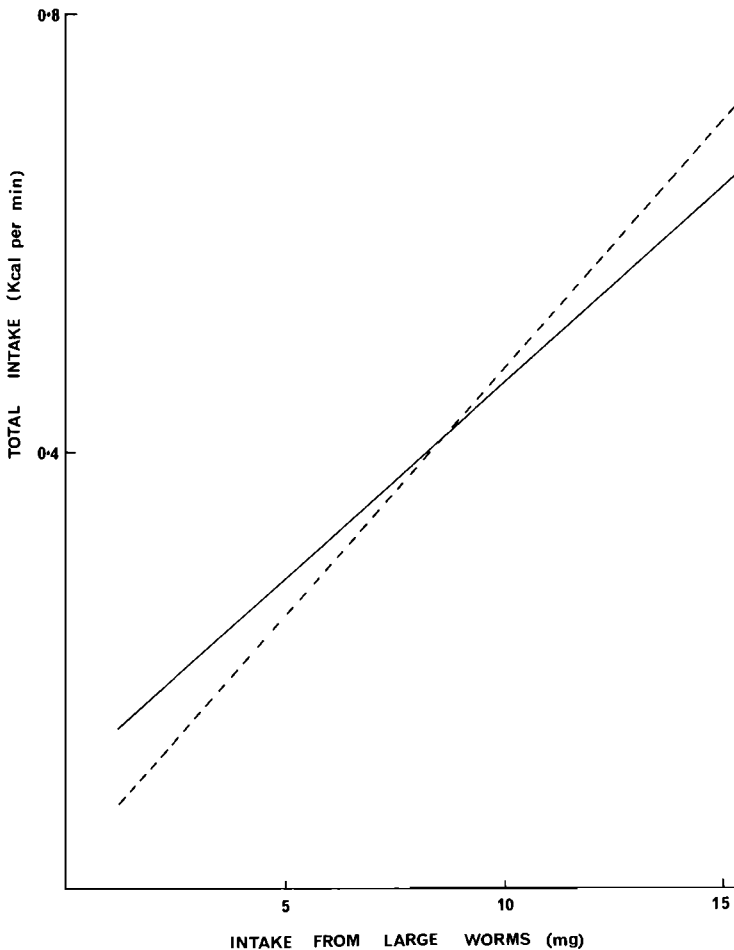
FIGURE 6.   The rate of intake of energy attained by redshank taking either many (——) or a few (– – –) small worms in relation to the biomass obtained per meter from large worms. Calculated for hypothetical sites from the model.

ENERGETICS OF WORM SIZE SELECTION

This section compares the actual rates at which redshank obtained energy from worms with the potential rates obtained by selecting different sizes. Simulation experiments were carried out using a mathematical model of redshank feeding on *Nephtys* and *Nereis*. The model (Goss-Custard 1977b) consisted of a series of relationships obtained from the field data from southern England and was in two parts. First, the relationships between the numbers of each of four size classes of worms taken per meter searched and (i) their densities in the mud, and (ii) the biomass ingested per meter from larger worms, were described by regression equations. This enabled the numbers (and thence biomass) of each size class taken per meter in a particular site to be estimated from the density and mean weight of each size class in the mud. Second, the time taken per meter to search for, find and then swallow the worms of each size class was estimated from a
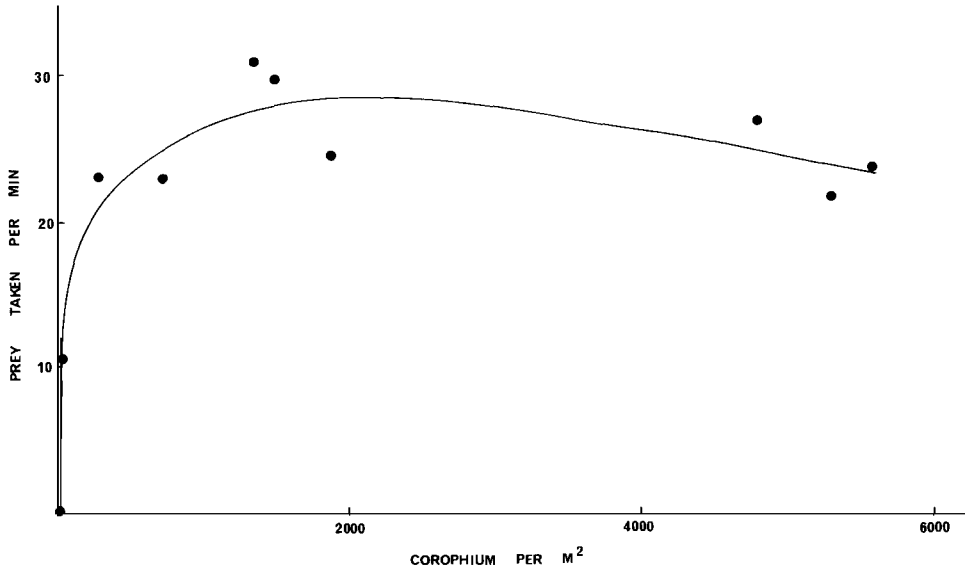
FIGURE 7.   Feeding rate of redshank on small prey (mainly *Corophium*) in relation to the density of *Corophium* in the mud.

series of curves relating time expenditure on each of these activities to the size and numbers of worms taken per meter. The total biomass of worms of all sizes taken per minute, i.e., ingestion rate, was then calculated by dividing the total biomass consumed per meter by the time taken to forage that meter. Biomass intake was converted to energy intake from the calorific values of the worms.

The model was used in the following way to explore the energetics of a preference for large worms. The densities and mean weights of each size class were varied over the typical range in a series of hypothetical sites. For each site, the model gave predictions of ingestion rate for redshank feeding in the normal way. The behavior of the birds in the model was then changed as if the birds had altered their responsiveness to the small worms. In sites where large worms were numerous so the birds would actually take very few small worms, the number of small worms taken was increased by up to tenfold. The effect of this was to reduce the rate that energy was obtained from all size classes because the extra time spent stopping and taking small worms more than outweighed the extra energy obtained. In sites where large worms were scarce so the birds would actually take many small worms, the number of small ones taken was decreased by up to tenfold. Again, the effect was to reduce the overall rate at which energy was obtained because the slightly greater rate of finding large worms achieved by ignoring small ones did not compensate for the reduced amount of energy obtained from small worms.

The results are summarized in Figure 6. This compares the overall rates of energy intake achieved by two hypothetical birds feeding in a series of sites with different densities of large worms. Both birds take medium and large worms in the normal way, but one feeds by taking many small worms irrespective of the amount of large worms ingested while the other always takes very few small worms. The former approach provided the higher overall rate of intake when
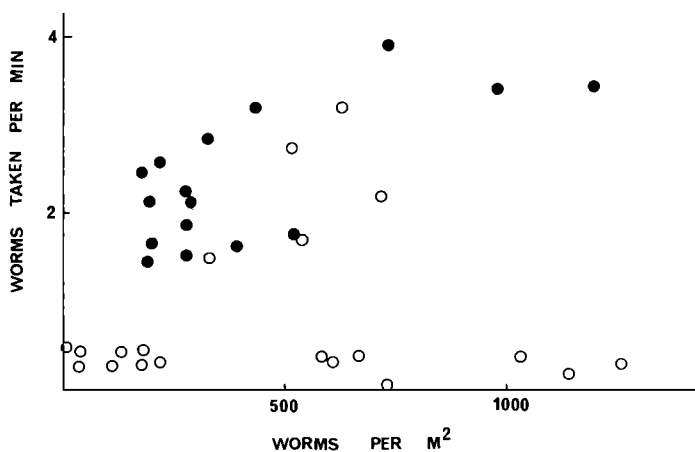
FIGURE 8. Feeding rate of redshank on worms (over 4 mg dry weight) where *Corophium* was absent (●) and present (○).

large worms are scarce but not when they are abundant. This suggests that it is more profitable for redshank to take small worms when large ones are scarce but to ignore them when large ones are numerous and this, of course, is precisely what the birds actually did. Hence it is concluded that in nature redshank took either a few or many small worms according to which was the more profitable. (Note that the results refer to gross rather than net rates of intake. The effort expended by birds behaving in the alternative ways was difficult to compare. A change from the actual to the potential response to small worms did not affect the numbers of paces and pecks made to collect a unit of energy and the time spent handling prey in similar directions. Since it is not yet possible to compare the energy expended in each of these activities, the overall effect of a change in feeding behavior on energy expenditure cannot be assessed. However, it is likely that increases in one aspect of foraging to some extent cancel out decreases in another so that the relative profitabilities of taking either many or few small worms may be similar whether expressed in gross or net terms.)

SELECTION BETWEEN PREY SPECIES

Using data from all sites, the number of small prey taken (mainly *Corophium*) was highly correlated with the density of *Corophium* in the mud (Fig. 7). Feeding rate rose rapidly but at a decelerating rate as prey density increased and then to a large extent levelled off. No site was found where *Corophium* was abundant but few were taken. This kind of Holling (1959) type-2 functional response is to be expected of a predator feeding on a preferred prey in places where prey density is uniform.

Data for feeding rates on worms produced a different pattern. Although there was a general tendency for the numbers of worms taken to increase as worm density increased, there were several sites where few were taken even though worms were very abundant (Fig. 8). This happened when *Corophium* was present because if all the sites where the amphipod occurred are excluded, there is a reasonable correlation between feeding rate and worm density. Furthermore, the
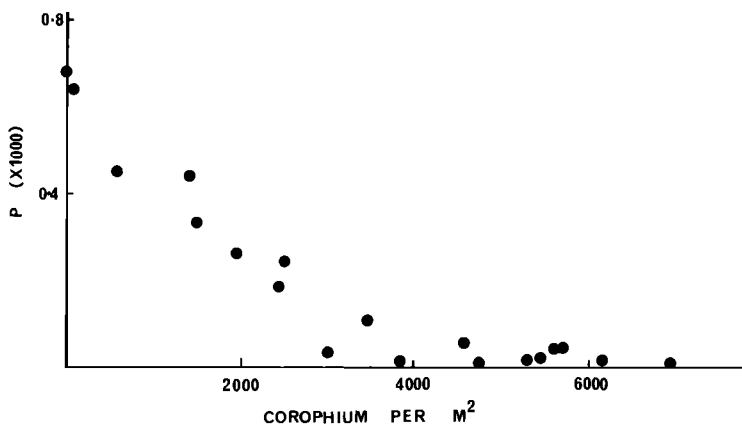
FIGURE 9. The probability (*P*) of a redshank taking a worm it encounters in relation to the density of *Corophium* in the mud.

probability that a redshank took a worm it encountered was inversely correlated with the density of *Corophium* in the mud (Fig. 9). So, rather surprisingly, it seems that the small prey *Corophium* was preferred to the much larger polychaete worms.

ENERGETICS OF PREY SPECIES SELECTION

Did taking *Corophium* yield a higher rate of energy intake than eating worms would have done? The mathematical model was used to estimate the rates of intake that would have been achieved had the birds taken worms instead. The comparison was made for the three sites in southern England where worms were abundant but the birds actually fed on *Corophium*. The values for the density and mean weight of each size class of worm recorded in each site during the sampling were put into the model and the ingestion rates calculated. The results show that, contrary to expectation, redshank would have obtained energy between two and three times faster had they taken worms rather than *Corophium* (Table 1). Table 1 also shows that birds taking worms would have made fewer pecks and paces and spent much less time in handling prey, although swallowing worms might be more costly than swallowing *Corophium*. Since the digestibilities of worms and *Corophium* are unlikely to differ enough to affect the results seriously, it appears that a preference for the amphipod did not maximise the net rate at which redshank obtained energy.

DISCUSSION

A number of authors have suggested that animals may prefer food items which can be collected most profitably (Charnov 1973, Emlen 1966, MacArthur and Pianka 1966, Pulliam 1974, Schoener 1971). By doing this, they would seem able (i) to increase their chances of collecting food at a rate sufficient for maintenance, (ii) to maximize the time spent on other essential activities, such as caring for young and avoiding predators, and (iii) to accumulate nutritional reserves for provisioning the maximum number of young. The idea has also been applied to animals choosing between alternative places in which to feed. A number of the-

TABLE 1

ACTUAL RATES OF ENERGY CONSUMPTION AND EXPENDITURE OF EFFORT BY REDSHANK FEEDING PREDOMINANTLY ON *Corophium* COMPARED WITH POTENTIAL RATES IN THE SAME SITES BUT ON WORMS

	Calories consumed per minute		Effort expended in collecting 1 Kcal:					
			Distance searched (m)		Number of pecks		Time spent handling prey	
Site	Actual	Potential	Actual	Potential	Actual	Potential	Actual	Potential
9	88	234	103	42	470	165	62	48
10	70	224	150	44	671	167	121	49
11	93	185	106	56	543	198	79	48

oretical models have been developed which attempt to describe the behavior of animals making these choices and they have become known collectively as optimal foraging theory. The word "optimal" often leads to confusion because it appears that the models claim to portray the best means by which an animal should forage for its fitness to be maximized. Actually, an organism only needs to feed better in some sense than its competitors and there may be many considerations other than maximizing the net rate of energy or nutrient gain which contribute to its ability to do so. In fact, the models make no such claim and merely explore theoretically the various means by which an animal may make the more profitable choices while feeding. Nonetheless, to avoid confusion, it may be advisable to use alternative terms, such as profitability, which do not have the same connotations.

All the models of diet selection assume that the predator is able to assess the profitabilities associated with alternative food items. Profitability may be defined in terms of the rate of net gain of either energy or some scarce nutrient. While herbivores may often select for nutrient content, it is widely believed that carnivores are more likely to select for energy content. As Ellis et al. (1976) point out, carnivores consume food items which not only contain a wide variety of biochemical substances but are also likely to be relatively constant in nutrient composition across a variety of prey items. However, when selecting between *Corophium* and the worms, redshank took the amphipod even though feeding on worms would have enabled them to collect energy at a greater net rate. Nor is it likely that redshank selected *Corophium* for its nutrient content. The numbers of worms consumed did not depend on the biomass of *Corophium* taken (Goss-Custard 1977a) as would be expected if the birds simply took sufficient worms to make up a nutrient deficiency in their diet when *Corophium* was scarce. Therefore, it is doubtful if redshank assessed the food values of *Corophium* and worms and selected accordingly.

Although not depending on the biomass or numbers of *Corophium* consumed, the numbers of worms taken decreased markedly as the numerical density of *Corophium*, and presumably the birds' frequency of encounter with them, increased (Goss-Custard 1977a). Perhaps redshank hunt by search image (Tinbergen 1960, Dawkins 1971) and concentrate increasingly on the amphipod as its density increases. But why do they form search images for *Corophium* rather than for the worms which could be collected more profitably? One possibility is that *Corophium* is simply more noticeable and would be taken preferentially by any

visually searching polyphagic shorebird that hunts by search image. However it is more likely that redshank have evolved a special sensitivity to the visual stimuli given out by *Corophium* but, if so, this also needs to be explained. No research has yet been done but perhaps a preference for *Corophium* (i) evolved as a consequence of competition with other species, (ii) provides the birds with a more widespread and dependable food source, or (iii) is associated with an evolved metabolic adaptation by redshank to different kinds of toxins or nutrients in the alternative prey species.

Although the models of profitable foraging do not predict the behavior of redshank selecting between worms and *Corophium* they predict quite well the behavior of birds choosing between alternative sizes of worms and places in which to feed. This suggests that a distinction should be drawn between the basis for selecting between some prey species and the way in which prey are exploited once they have been chosen. Having evolved a preference for *Corophium* for whatever reason, the birds' methods in exploiting it (and other prey species when forced to take them) may indeed be to choose the size classes and places in which to feed that maximize the net rate at which energy is consumed.

It is interesting that an immediate shortage of food was not required to provoke birds into choosing the more profitable means of exploiting their food niche. Redshank chose the profitably exploited prey sizes and feeding places in autumn when shorebirds appear to have little difficulty in obtaining food (Goss-Custard 1969, this volume, Heppleston 1971). Perhaps profitable foraging has a strong selective advantage when food is scarce but little disadvantage when food is abundant and so may be maintained at other times of year simply because it does not actually reduce fitness. Alternatively, there may be an advantage at all times of year in minimizing the time taken to collect energy so that more time can be spent looking for danger, for example. Again, heavy rain and strong winds can bring about a rapid deterioration in feeding conditions (Goss-Custard 1969) so that it may always be an advantage to collect energy as quickly as possible while it is available. But it is also possible that profitable foraging may simply reflect a general tendency in animals to behave economically whatever the activity, whether feeding or simply walking from place to place (Williams 1966).

LITERATURE CITED

BURTON, P. J. K. 1974. Feeding and the Feeding Apparatus in Waders. British Museum, London.

CHARNOV, E. L. 1973. Optimal foraging: some theoretical explorations. Unpublished Ph.D. thesis, University of Washington.

DAWKINS, M. 1971. Perceptual changes in chicks: Another look at the 'search image' concept. Anim. Behav. 19:566–574.

ELLIS, J. E., J. A. WIENS, C. F. RODELL, AND J. C. ANWAY. 1976. A conceptual model of diet selection as an ecosystem process. J. Theor. Biol. 60:93–108.

EMLEN, J. M. 1966. The role of time and energy in food preference. Amer. Nat. 100:611–617.

GOSS-CUSTARD, J. D. 1969. The winter feeding ecology of the redshank, *Tringa totanus*. Ibis 111:338–356.

GOSS-CUSTARD, J. D. 1970. The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. J. Anim. Ecol. 39:91–113.

GOSS-CUSTARD, J. D. 1977a. The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density. J. Anim. Ecol. 46:1–19.

GOSS-CUSTARD, J. D. 1977b. Optimal foraging and the size selection of worms by redshank, *Tringa totanus*. Anim. Behav. 25:10–29.

GOSS-CUSTARD, J. D. 1977c. Predator responses and prey mortality in redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). J. Anim. Ecol. 46:21–35.

GOSS-CUSTARD, J. D., D. G. KAY, AND R. M. BLINDELL. 1977. The density of migratory and overwintering redshank, *Tringa totanus* (L.), and curlew, *Numenius arquata* (L.), in relation to the density of their prey in south-east England. Est. Coast. Mar. Sci. 5:497–510.

HEPPLESTON, P. B. 1971. The feeding ecology of oystercatchers (*Haematopus ostralegus* L.) in winter in Northern Scotland. J. Anim. Ecol. 40:651–672.

HOLLING, C. S. 1959. Some characteristics of simple types of predation. Can. Ent. 91:385–398.

MACARTHUR, R. H., AND E. R. PIANKA. 1966. On the optimal use of a patchy environment. Amer. Nat. 100:603–609.

PULLIAM, H. R. 1974. On the theory of optimal diets. Amer. Nat. 108:59–74.

PRATER, A. J. 1972. The ecology of Morecambe Bay III. The food and feeding habits of knot (*Calidris canutus* (L.)), in Morecambe Bay. J. Appl. Ecol. 9:179–194.

SCHOENER, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369–404.

TINBERGEN, L. 1960. The natural control of insects in pine woods. 1. Factors influencing the intensity of predation by songbirds. Arch. Néerl. Zool. 13:265–343.

WILLIAMS, G. C. 1966. Adaptation and Natural Selection. A critique of some current evolutionary thought. Princeton University Press, Princeton.