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THE SEARCHING SPEEDS OF FORAGING SHOREBIRDS: REDSHANK 
(TRINGA TOTANUS) AND OYSTERCATCHER 
(HAEMATOPOUS OSTRALEGUS)

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Abstract.—Foraging models predict terrestrial animals should maximize search speed whenever it is profitable to forage. Observations of foraging animals, however, suggest they seldom walk at their maximum speeds. Animals may walk slower than predicted because factors not accounted for in the models influence the relationship between net energy gain and search speed in a manner that makes it more profitable to forage at speeds below the maximum. Alternatively there may be a limit on the speed at which animals can search because they cannot accelerate instantaneously from a standing start to their maximum speed. A theoretical model is developed that predicts the expected searching speeds of terrestrial predators as a function of prey encounter density (number of prey encountered per unit distance searched), when they cannot accelerate instantaneously. This model predicts an inverse nonlinear relationship between speed and prey encounter density such that in most circumstances predators will search at less than their maximum possible searching speeds. Quantitative predictions were generated from the model for two charadriiform birds (redshank, Tringa totanus; and oystercatcher, Haematopus ostralegus). Observations of the walking speeds of free-living redshanks and oystercatchers had a form similar to those predicted by the model, but they deviated by being lower, particularly at low prey encounter densities. Redshank may be acceleration limited in their prey-searching behavior at high prey encounter densities, but at low prey encounter densities and for oystercatchers other factors also appear to be important.

The assumption that foraging animals have been selected to maximize the net rate of energy gain has been used extensively to derive testable predictions of various aspects of animal foraging behavior (see Krebs et al. 1983; Krebs and McCleery 1984; Stephens and Krebs 1987 for reviews; see Pierce and Ollason 1987 for critique of method). The majority of predictive models, and tests of them, have considered the problems of patch choice and diet choice (Stephens and Krebs 1987). Relatively scant attention has been focused on the problems of searching and prey-handling behavior. This article considers the searching speed of terrestrial predators under the premise of maximization of net energy gain.

Several theoretical papers have already addressed this problem by considering a hypothetical predator with a choice between two alternative search speeds; one at a high speed but with high cost and a second at a lower speed but with lower

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cost (Evans 1976; Norberg 1977; Krebs 1978). These models predict there is a critical prey density above which the animal should use the faster, high-cost method, and below which it should use the slower but less costly method. The interpretation of these models has been expanded to consider predators that have a range of potential speeds available, as is the case for most terrestrial predators, so as to suggest such predators should gradually increase speed as prey density increases.

More recently, however, it has been shown that, in cases in which the energy cost of searching increases as a linear function of search speed, as is the case for the majority of terrestrial predators (Taylor 1977; Fedak and Seeherman 1979; Kramm and Taylor 1990), the prediction that searching predators should gradually increase searching speed as prey density increases is erroneous (Pyke 1981; Speakman 1986). For these predators there is a critical search speed above which search speed should be maximized and below which the animal should stop foraging (Speakman 1986). The prediction that predators should maximize search speed in all conditions where it is profitable to continue feeding depends on the assumption that energy gain increases as a linear function of search speed (Speakman 1986). This assumption may be erroneous if the ability to detect prey declines as search speed increases (Gendron and Staddon 1983). This would lead to curvilinear gain functions, and, as a consequence, the speed maximizing net energy gain may lie somewhat below the maximum speed at which the predator is capable of traveling (Ware 1975; Gendron and Staddon 1983).

The fact that most predators search at slower speeds than they are capable of does not necessarily mean they are searching at an optimum that is lower than the maximum speed. Other factors may potentially limit the speed attained by a predator selected to maximize search speed. One factor that will affect many predators is the rate at which they encounter prey items combined with an inability to accelerate instantaneously from standing still to the maximum speed (Speakman 1986).

In this article we explore through a theoretical model the effects of this inability to accelerate instantaneously from standing still to the maximum speed. Quantitative predictions of this model are then tested by observations made in the field of searching speeds of two terrestrial foraging charadriiform shorebirds: the redshank (Tringa totanus) and the oystercatcher (Haematopus ostralegus).

THEORETICAL MODEL

Consider a predator that sets out searching from an item \( n \) that it has just handled or unsuccessfully attempted to handle. The instantaneous speed of the predator \( V_p \) is initially zero. The predator accelerates with an acceleration \( a_p \) over a time \( T_{ac} \) until it reaches its maximum speed \( V_p = V_{\text{max}} \). If the predator encounters a second prey item \( n + 1 \) before \( T_{ac} \) then its instantaneous speed will be lower than \( V_{\text{max}} \). The predator may then be described as acceleration limited in its search speed. The effects of prey density on predator search speed may be divided into two phases: when speed is, and is not, acceleration limited by prey density.
Consider first prey densities where speed is acceleration limited. The instantaneous speed of the predator is given by the equation

$$V_p = a_p \times T_s,$$  \hfill (1)

where $T_s$ is the time spent searching since leaving the item $n$. The distance traveled while accelerating ($d_a$) is given by the equation

$$d_a = 0.5 \times a_p (T_s)^2.$$  \hfill (2)

Hence,

$$d_a = (V_p)^2/2 \times a_p,$$  \hfill (3)

and

$$V_p = (2 \times a_p \times d_a)^{0.5}.$$  \hfill (4)

The distance traveled between two prey items ($d$) is the reciprocal of the prey encounter density ($E$), the number of prey encountered per unit distance searched. Since $d = d_a$, when a predator is acceleration limited, equation (4) may be rewritten to express the instantaneous search speed as the predator encounters the $n + 1$ prey item:

$$V_p = [(2 \times a_p)/E]^{0.5}.$$  \hfill (5)

Since $a_p$ is constant, the average speed ($V_{me}$) over the time spent traveling between the $n$ and $n + 1$ prey items equals $0.5 \times V_p$. Consider now prey densities in which the predator is not acceleration limited ($d > d_a$). A critical prey encounter density ($E_{CRIT}$) at the transition between being and not being limited by the ability to accelerate is defined when $V_p$ first equals $V_{max}$. Substituting $V_{max}$ into equation (5) yields

$$E_{CRIT} = 2 \times a_p/(V_{max})^2.$$  \hfill (6)

At prey encounter densities below $E_{CRIT}$, $V_p$ equals $V_{max}$ as the predator encounters the $n + 1$ prey item. As $E$ decreases below $E_{CRIT}$ the time spent searching at $V_{max}$ increases and $V_{me}$ approaches $V_{max}$:

$$V_{me} = d/[T_{ac} + [(d - d_a)/V_{max}]].$$  \hfill (7)

Substituting equations (1) and (3) into equation (7) yields

$$V_{me} = 1/[(1/V_{max}) + (E \times V_{max}/2 \times a_p)].$$  \hfill (8)

The relationship between $V_{me}$ and $E$ is defined therefore by two equations. At encounter densities above $E_{CRIT}$ the speed is defined by equation (5) and $V_{me} = 0.5 \times V_p$, and at encounter densities of prey below $E_{CRIT}$ the predator search speed is defined by equation (8). To illustrate the effects of prey encounter density on predator search speed a range of curves relating predator speed to encounter density were generated. These curves were calculated for a theoretical predator in which the following predator variables were set: $V_{max} = 1 \text{ m s}^{-1}$ and $T_{ac}$ was allowed to vary between 0 (no acceleration limitation) and 10 s (fig. 1).

Figure 1 highlights four general predictions of the acceleration-limited model. These are summarized as follows.
1. Predators that search for widely distributed prey are expected to search at speeds that approach $V_{\text{max}}$. In contrast, predators that encounter prey very frequently are predicted to search at slower speeds. The general observation that predators search at speeds lower than their maximum cannot therefore be used to reject the suggestion that animals should attempt to maximize search speed when it is profitable to continue foraging (Pyke 1981; Speakman 1986).

2. Predators that encounter prey over a range of encounter densities are predicted to exhibit a nonlinear inverse relationship between search speed and encounter density.

3. Predators capable of rapid acceleration are expected to search at speeds closer to $V_{\text{max}}$ than animals that are less capable of accelerating.

4. Since the only property pertaining to prey type in the equations (5) and (8), which define the relationship between predator search speed and prey encounter density, is encounter density, equal encounter densities of different prey types (profitabilities), under equal conditions, are predicted to result in the same predator search speed.

This model is valid for the prediction of average speeds observed as animals accelerate between two prey items. However, when observations are made of the average speed of a predator as it encounters and handles, or attempts to handle, a sequence of prey items the model as presented is too simple because it assumes that the distances between the prey are constant and hence that the prey are distributed homogenously. This assumption is likely to be violated for
many prey items that have clumped or random distributions. We have expanded this simple model to predict the expected average search speed for a predator encountering a sequence of prey distributed at random and modeled the effects on the predicted speeds as a function of prey encounter density (see the Appendix). The effects of ignoring a random prey distribution on the predicted speed across a sequence of encounters are trivial.

METHODS

In this article we consider two predictions of the model. First, the predicted nonlinear inverse relationship between search speed and encounter density was tested by generating quantitative predictions for two charadriiform birds (the redshank *Tringa totanus* and the oystercatcher *Haematopus ostralegus*) and then by comparing observed searching speeds of free-living birds in relation to encounter density with the model predictions. Second, the predicted absence of an effect of different prey types on search speed was explored in redshanks by comparing the retardant effects on search speed of increasing encounter densities with different prey.

Quantitative Model Predictions for Redshanks and Oystercatchers

Predictions were generated for the expected relationship between search speed and prey encounter density for redshanks and oystercatchers. To generate these predictions assumptions had to be made for two unknown variables: $V_{\text{max}}$ and $T_{\text{ac}}$.

McNeil Alexander (1977) defined a dimensionless speed ($\hat{u}$), where $\hat{u} = u / (gh)^{0.5}$. $u$ is the animal’s actual speed, $g$ is acceleration due to gravity, and $h$ is the height of the animal’s center of gravity, and noted the maximum speed attained by most animals is in the range 3–4 $\hat{u}$. However, such high speeds can only be achieved by exceeding aerobic scope and resorting to anaerobis (Peterson et al. 1990). Hence, there is a trade-off between maximum speed and the duration for which that speed can be sustained (Peterson et al. 1990). Since searching for food is an activity that must be sustained for protracted periods we are concerned not with the absolute maximum speed at which the animal can move but the speed that can be sustained for 10–15 h per d, which represents the typical foraging durations of the predators in the current study during winter.

There are few data on the trade-off between speed and duration of sustained performance for animals attempting to maximize speed. The best data are those for human beings in track-running competitions (McGillivery 1971). These data indicate that the maximum speed ($3.2 \hat{u} = 10$ m s$^{-1}$) can only be maintained for around 20 s. Thereafter speed declines along a complex double exponential as the duration of exercise increases. The maximum sustainable speed for a human being running for 10–15 h is 1.45 $\hat{u}$. We have assumed this speed to be the most appropriate maximum speed for the purpose of sustained foraging. The estimated $h$ in the midbody, directly between the legs, for redshanks was 0.15 m and for oystercatchers 0.18 m. This leads to predicted sustainable maximum speeds of 1.76 and 1.92 m s$^{-1}$ for redshanks and oystercatchers, respectively. These predictions closely match allometrically predicted maximum observed speeds from
body mass for mammals (redshank, 150 g, 1.86 m s\(^{-1}\); oystercatcher, 600 g, 2.15 m s\(^{-1}\)) (Garland 1983).

Capacity for acceleration is less documented than maximum speeds. The best data are for lizards performing at endothermic body temperatures at which their maximum running performance does not differ from that of endotherms (Garland 1982). At these body temperatures small lizards can achieve accelerations of about 2 m s\(^{-2}\) (Bennett 1981). This level of acceleration would lead to the study species reaching maximum speed in well under 1 s, which accords well with casual observations of burst speed performance (J. R. Speakman and D. M. Bryant, personal observation) and of other small birds (e.g., bobwhite quails [Calipepla gambeli]; R. P. Gendron, personal communication). This acceleration results in a \(T_{ac}\) to reach \(V_{max}\) of 0.88 and 0.96 s for redshanks and oystercatchers, respectively.

Clearly these assumptions may be inaccurate, with consequent inaccuracies in the predicted search speed. In particular, the accelerations discussed above refer to animals on solid substrates while our study species search in the often thick mud of an estuarine environment. This factor would likely reduce the maximum sustainable acceleration. We accordingly set tolerance limits to the estimate to include this possibility. We allowed \(T_{ac}\) to vary in the range 100%–200% of the prediction. The predicted relationships between predator search speed and prey encounter rate for redshanks and oystercatchers are shown in figure 2.

Measurement of Search Speed

The most direct method of measuring search speed is to time the predator as it searches over a known distance. In the field, however, this technique is difficult to apply since it is frequently impossible to obtain a reference distance along which the predator can be timed. Goss Custard and Rothery (1976) suggested an estimate of searching speed can be obtained by measuring the number of paces an animal takes within the time it spends searching, that is, the total time minus time spent handling prey. The implication of this “pacing rate” method is that pacing rate is directly proportional to speed, which may therefore be measured by multiplying pacing rates by the mean stride length that can also be measured in the field from footprints. This technique has been used to evaluate the walking speeds of predators in several previous studies (e.g., Goss Custard 1977). Although the pacing rate technique is more easily applied, many animals increase both the pacing rate and stride length simultaneously to cause increases in speed (Hayes and McNeil Alexander 1983; McNeil Alexander and Jayes 1983). Moreover, Hayes and McNeil Alexander (1983) indicated some birds may increase speed without increasing pacing rate at all. If the mean stride length were used but the animal increased stride length at the same time as or instead of pacing rate, the pacing rate method proposed by Goss Custard and Rothery (1976) would overestimate slow speeds but underestimate fast speeds, although it would provide an unbiased estimate of the mean speed across many unbiased observations. A relationship was sought therefore between speed measured directly, pacing rate, and stride length.
Relationship between Search Speed, Pacing Rate, and Stride Length

Six redshanks and two oystercatchers, all captured in the wild, were kept in an outdoor aviary (see Speakman 1987 for details). After several weeks in captivity the birds established a series of routes around the various objects in the aviary—stones, logs, and feeding dishes—and over a variety of substrates from hard to very soft mud, along which they walked frequently. Markers were positioned along these routes. Individuals were timed as they walked spontaneously.
between markers, and the number of paces taken was counted. Pacing rate \( R \), pace length \( L \), and walking speed \( V \) were calculated for each run as \( R = n/t \), \( L = d/n \) and \( V = d/t \), where \( n \) is the number of paces, \( t \) is the time, and \( d \) is the distance between markers.

**Field Estimates of Search Speed**

Empirical relationships between pacing rate and search speed from the birds in the aviary were used to predict the search speeds of foraging redshanks and oystercatchers at several sites on the midestuarine Firth of Forth on the east coast of Scotland, United Kingdom (56°N). In addition, since redshanks left footprints in the mud an empirical relationship between speed and pace length from birds in the aviary was used to predict search speed for this species from pace lengths measured from the footprints in the field.

**Redshank: pacing rate estimates.**—Foraging redshanks were observed from a blind at the north end of the mudflat at Skinflats (NS 923867 on U.K. ordinance survey) and from the seawall at Culross (NS 975875 on U.K. ordinance survey) at distances of 30–200 m, for periods of approximately 30 s, with a tripod-mounted telescope. In each period the number of paces taken and the number of prey items successfully or unsuccessfully ingested were recorded. Prey were allocated to one of eight classes: unsuccessful pecks and small items (either *Hydrobia ulvae* or *Corophium volutator*), small, medium, and large *Macoma balthica* (a bivalve mollusk), and small, medium/small, medium, and large polychaete worms (either *Nereis diversicolor* or *Nepthys hombergii*). The pacing rate was estimated from the time the redshanks spent searching, that is, the total observation time minus the time spent handling prey items and pecking unsuccessfully. The time spent not searching was estimated as the number of each class of prey ingested in the period multiplied by an independent mean estimate for the handling time of that prey. Unsuccessful pecks were assumed to have the same duration as the handling time for small items. Although estimating the handling times for small items, which are short, involves inevitable errors, they probably occur at random and hence the mean timings are probably not biased. Encounter densities of prey were calculated as the number of items encountered (handled successfully or otherwise) per meter of path searched. The distance searched was estimated from the empirically predicted speed (from the pacing rate with the empirical relationship derived in the aviary) multiplied by the time spent searching. This method of measuring encounter densities of prey yields the density of prey along the search path to which the predator makes a response rather than the actual total prey availability. It was necessary to use this technique since it was logistically impossible to observe an individual and then locate the search path and measure prey availabilities directly. However, because the acceleration-limited model considers only those prey that halt the animal in its searching behavior, the method used to assess encounter density is superior to measuring the total prey availability, since the predator will not respond to a proportion of the total prey available and these prey are predicted not to retard search speed via acceleration limitation of the predator. Some observations were also made of travel speeds of birds that were not foraging. These were mostly involved in aggressive interactions.
Redshank: pace length estimates.—Redshank footprints were located in the mud at both Skinflats and Culross. Pace length was measured from the apex of one print to the apex of the next. Between prints a stick 80 cm long with a tip area of 25 mm² and a ball of modeling clay attached centrally (total mass = 50 g) was dropped from a height of 30 cm into the mud. The depth of penetration was a measure of mud softness, which was a potential factor influencing the predator's ability to accelerate and, as indicated by the model, should therefore affect searching speed.

Oystercatcher: pacing rate estimates.—Foraging oystercatchers feeding on mussels (Mytilus edulis) were observed from the pier end at Culross (NS 975858 on U.K. ordinance survey) at a distance of 50–200 m using a tripod-mounted telescope. Aspects of the foraging behavior were dictated onto a portable cassette recorder that was later translated by timing directly with a stopwatch. Oystercatchers make many unsuccessful attempts to capture mussels for each successful attack (Goss Custard et al. 1984). For both successful and unsuccessful handling attempts the birds must stop searching. Since prey-handling behavior occupies such a large proportion of the foraging time budget, estimates of search speed were made for each period between prey-handling attempts. For each search period the time and number of paces were recorded and pacing rate calculated. Searching speed was then estimated from the empirical relationship, derived from the aviary observations, between pacing rate and search speed. The distance between two capture attempts was calculated from the estimate of search speed multiplied by the duration spent searching. Encounter densities of prey were calculated as the reciprocal of interattempt distance. Some estimates of travel speed were also estimated for birds involved in aggressive interactions.

RESULTS

Relationship between Search Speed, Pacing Rate, and Pace Length

In both species there were positive relationships between pacing rate and walking speed and between pace length and walking speed (fig. 3). Differences between individuals were not significant (tables 1 and 2). Oystercatchers made shorter paces than redshanks when walking at a given speed and therefore also paced at a faster rate. The major method adopted by both species to increase speed was to increase pacing rate, and hence pacing rates increased by more than five times between the slowest and fastest speeds. In contrast, pace length increased only 3.3 times and 4.2 times in redshanks and oystercatchers, respectively. Despite the fact that increases in pacing rate were the major component contributing to increased speed, the effect of pace length was still highly significant (tables 1 and 2). The assumption for the technique of evaluating speeds from pacing rates multiplied by mean pace length, namely, that pace length is independent of speed, does not therefore hold for these species. Although the birds in the aviary walked over a variety of substrates, this did not substantially affect the form of the relationship. Empirical relationships between pacing rate and speed (which take into account pace length changes) therefore explained 93.3% and 78.2% of the variability in speed in redshanks and oystercatchers, respectively.
**SHOREBIRD SEARCH SPEEDS**

**Relationship between Search Speed and Prey Encounter Rate in the Field**

**Redshanks.**—Estimates of the mean handling time for each of the prey items selected by redshanks are shown in table 3. No significant differences in handling time for each prey were observed between the two study sites. The relationship between the searching speed and total prey encounter density at 11 separate 1-ha plots across the two sites is shown in figure 4. At all but one of the study sites there was a significant negative nonlinear relationship between predator search speed and prey encounter rate (table 4). The data pooled across all sites are shown in figure 5. Although there was a significant inverse nonlinear relationship between the search speed and prey encounter density, which was qualitatively in accord with the model prediction, inspection of figure 5 reveals that despite the model prediction and observations being close at high encounter densities there was a progressive departure from the prediction as the encounter density declined. At encounter densities of less than two ($\log_{10} = 0.3$) items per meter searched all the observed search speeds were lower and outside the limits of the model prediction. Travel speeds of birds that were not foraging were considerably higher than those recorded from foraging birds and approximately equaled the prediction of $V_{\text{max}}$ (1.5 m s$^{-1}$).

Encounter densities with the different prey types were not significantly correlated with one another and were entered as independent predictors in a multiple regression analysis (tables 5 and 6). Figure 6 shows the effects of encounter densities with each prey type on the search speed. The gradient of decline in searching speed with increases in encounter densities for each of the three major prey types (small items, *Macoma*, and polychaete worms) was not significantly different (tables 5 and 6) between prey types (fig. 6). Changing encounter densities with different prey therefore exerted the same effect on redshank searching speed, in accord with the model prediction. Although encounter densities with prey explained up to 50% of the variability in search speed at individual plots (table 4), there was still a large amount of unexplained variability in search speed. If the acceleration-limited model explains the variation in search speed then this residual variability should be accounted for by local microhabitat factors that influence the salient variables of the acceleration-limited model. One such factor is mud viscosity. We have already shown the birds were capable of walking at speeds approaching $V_{\text{max}}$ in the muddy substrate, because nonforaging birds ran at these speeds. Changes in mud viscosity may, however, influence search speed by its effect on acceleration. Acceleration will be lower in soft muds because efficiency is reduced by an insufficient ground reaction to the applied force and subsequent energy loss in sinking. There was a significant negative relationship between instantaneous search speeds, evaluated from pace lengths, and mud softness (fig. 7). Local microhabitat changes in mud softness explained 27.6% of the variability in instantaneous walking speed.

**Oystercatchers.**—There was a significant negative relationship between the searching speed of foraging oystercatchers and the reciprocal of the interattempt distance (= encounter density) (fig. 8). The estimated travel speeds of nonforaging birds were considerably greater than the speeds of foraging birds and approximated the estimate of $V_{\text{max}}$ (observed mean maximum = 1.9 m s$^{-1}$). Searching
Fig. 3.—Relationships between pacing rates and walking speed and between pace length and walking speed for redshanks (A and B; n = 6) and oystercatchers (C and D; n = 2) measured directly for birds kept in an outdoor aviary. Increases in walking speed were accompanied by increases in both pacing rate and pace length for both species.
C

D

307
TABLE 1
REGRESSION ANALYSES OF PACING RATES (m s⁻¹) AND PACE LENGTHS (m s⁻¹) OF REDSHANKS AND OYSTERCATCHERS ON WALKING SPEED (m s⁻¹), POOLED ACROSS SIX INDIVIDUALS IN THE REDSHANK AND TWO INDIVIDUALS IN THE OYSTERCATCHER

<table>
<thead>
<tr>
<th>Species and Intercept</th>
<th>Slope</th>
<th>Independent</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Redshank (n = 167):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>− .957</td>
<td>1.44</td>
<td>Log₁₀ pacing rate</td>
<td>.933</td>
</tr>
<tr>
<td>1.47</td>
<td>2.26</td>
<td>Log₁₀ pace length</td>
<td>.800</td>
</tr>
<tr>
<td>Oystercatcher (n = 125):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>− 1.18</td>
<td>1.46</td>
<td>Log₁₀ pacing rate</td>
<td>.780</td>
</tr>
<tr>
<td>1.00</td>
<td>1.57</td>
<td>Log₁₀ pace length</td>
<td>.732</td>
</tr>
</tbody>
</table>

Note.—In all equations the dependent variable was log₁₀ walking speed (m s⁻¹). Both species achieved increases in speed by a combination of increased pacing rate and pace length. In both species the differences between individuals were not significant (ANCOVA).

TABLE 2
ANCOVA OF PACING RATE AND PACE LENGTH AGAINST WALKING SPEED

<table>
<thead>
<tr>
<th></th>
<th>Pacing Rate</th>
<th>Pace Length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Redshanks:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equality of slopes</td>
<td>1.493</td>
<td>.207</td>
</tr>
<tr>
<td>Equality of adjusted means</td>
<td>.758</td>
<td>.554</td>
</tr>
<tr>
<td>Oystercatchers:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equality of slopes</td>
<td>.270</td>
<td>.604</td>
</tr>
<tr>
<td>Equality of adjusted means</td>
<td>.068</td>
<td>.794</td>
</tr>
</tbody>
</table>

Note.—Data are from ANCOVA with individual as a concomitant variable

TABLE 3
HANDLING TIMES OF REDSHANKS FOR THEIR COMMON PREY

<table>
<thead>
<tr>
<th>Prey Type</th>
<th>Handling Time (s)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small items (n = 180)</td>
<td>.42</td>
<td>.14</td>
</tr>
<tr>
<td><em>Macoma balthica</em>:*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small (n = 116)</td>
<td>1.00</td>
<td>.21</td>
</tr>
<tr>
<td>Medium (n = 46)</td>
<td>2.03</td>
<td>.42</td>
</tr>
<tr>
<td>Large (n = 4)</td>
<td>12.4</td>
<td>2.3</td>
</tr>
<tr>
<td>Polychaete worms:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small (n = 82)</td>
<td>.99</td>
<td>.25</td>
</tr>
<tr>
<td>Medium small (n = 120)</td>
<td>1.75</td>
<td>.38</td>
</tr>
<tr>
<td>Medium (n = 42)</td>
<td>2.68</td>
<td>.59</td>
</tr>
<tr>
<td>Large (n = 20)</td>
<td>3.58</td>
<td>.66</td>
</tr>
</tbody>
</table>
speed between any two handling attempts was independent of the outcome of either attempt. The form of the observed relationship between speed and encounter density was very similar to that observed in the redshank (fig. 5); however, in the oystercatcher the entire curve was shifted to the left relative to the acceleration-limited prediction (fig. 8). Hence, as with redshank the most significant deviation of the observed searching speeds was at low encounter densities of prey.

DISCUSSION

Relationship between Pacing Rate, Pace Length, and Walking Speed

The physical responses of both redshanks and oystercatchers to cause increases in speed (fig. 1) were consistent with the responses of other bipedal animals (Hayes and McNeil Alexander 1983). Since most species increase both the pace length and pacing rate to increase speed the method of evaluating speed from pacing rate multiplied by mean pace length produces erroneous estimates of walking speed, particularly at low and high pacing rates. In view of these errors we suggest that the use of pacing rates combined with an evaluation of mean pace length to estimate speeds of individuals should be avoided. However, the technique will provide an unbiased estimate of mean speed across many observations as long as pace length and pacing rates are sampled fairly. Walking speeds of individuals should ideally be evaluated by timing the animal over measured distances or alternatively from empirically derived relationships between pacing rates and speed that take into account changes in pace length for the species under study.

Relationship between Searching Speed and Prey Encounter Density

Redshanks.—The similarity of the searching speed responses of redshanks to those predicted by the acceleration-limited model, in addition to the effect of microhabitat effects of mud softness on walking speed, suggests that, at least at the higher encounter densities of prey, redshanks were walking much slower than speeds that they were demonstrably capable of, because they were limited by the ability to accelerate instantaneously from standing still to their maximum speed. However, at lower prey encounter densities, at which inability to accelerate would not be expected to limit searching speed, the birds searched at a speed slower than that predicted by the acceleration-limited model. These data suggest that the assumption that prey detection ability does not decline as speed increases, an integral component of the models of prey-searching behavior (Pyke 1981; Speakman 1986), may be erroneous. Predators might not be expected therefore to maximize their search speed, as predicted by these models, but to optimize it at some level at which further increases in speed do not bring greater returns in energy gain because of reduction in the ability to detect prey (Gendron and Staddon 1983). We envisage two potential mechanisms by which increases in search speed may reduce ability to detect prey. First, effective scanning of an area may require some fixed time. As the animal increases its speed, the area that is searched effectively therefore becomes progressively narrower, and intake
Fig. 4.—Relationships between searching speeds of foraging redshanks and prey encounter density measured at each of 10 1-ha plots on the midestuarine Firth of Forth, where there was a significant relationship. Observations at an eleventh site produced no significant relation. Refer to table 4 for details of fitted regression equations.
<table>
<thead>
<tr>
<th>SITE</th>
<th>Coefficient</th>
<th>Constant</th>
<th>r²</th>
<th>df</th>
<th>p</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>-.32</td>
<td>-.402</td>
<td>.323</td>
<td>45</td>
<td>&lt;.001</td>
<td>.174</td>
</tr>
<tr>
<td>B</td>
<td>-.38</td>
<td>-.250</td>
<td>.200</td>
<td>67</td>
<td>&lt;.001</td>
<td>.176</td>
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<tr>
<td>C</td>
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<td>-.113</td>
<td>.282</td>
<td>26</td>
<td>&lt;.001</td>
<td>.167</td>
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<tr>
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<td>-.453</td>
<td>.400</td>
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<td>.159</td>
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<td>&lt;.001</td>
<td>.121</td>
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<td>G</td>
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<td>-.209</td>
<td>.447</td>
<td>13</td>
<td>&lt;.009</td>
<td>.553</td>
</tr>
<tr>
<td>H</td>
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<td>-.327</td>
<td>.462</td>
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<td>&lt;.001</td>
<td>.232</td>
</tr>
<tr>
<td>I</td>
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<td>.323</td>
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<td>&lt;.011</td>
<td>.221</td>
</tr>
<tr>
<td>J</td>
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<td>-.243</td>
<td>.222</td>
<td>17</td>
<td>&lt;.05</td>
<td>.105</td>
</tr>
<tr>
<td>K</td>
<td>-.40</td>
<td>-.128</td>
<td>.021</td>
<td>87</td>
<td>NS</td>
<td>.015</td>
</tr>
</tbody>
</table>

**Note.**—In all plots except one there was a significant negative relationship. Nonlinear regression models explained more of the variation in speed than linear models in all except one case, indicating that the relationships were nonlinear, as predicted by the acceleration-limited model.
Fig. 5.—Searching speeds of foraging redshanks summed across all study plots ($n = 683$) plotted against prey encounter density, with the limits of the predictions generated from the acceleration-limited model.

**TABLE 5**

PARAMETERS OF MULTIPLE REGRESSION EQUATION
RELATING WALKING SPEED (m s$^{-1}$) TO
ENCOUNTER DENSITY ($n$ m$^{-1}$) WITH
THREE DIFFERENT TYPES OF PREY

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Coefficient</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>-.1512</td>
<td>.0240</td>
</tr>
<tr>
<td>$\log_{10}$ (small items + 1)</td>
<td>-.454</td>
<td>.0327</td>
</tr>
<tr>
<td>$\log_{10}$ (Macoma + 1)</td>
<td>-.352</td>
<td>.1212</td>
</tr>
<tr>
<td>$\log_{10}$ (worms + 1)</td>
<td>-.872</td>
<td>.1930</td>
</tr>
</tbody>
</table>

**TABLE 6**

MATRIX OF TWO SAMPLE TESTS COMPARING REGRESSION
COEFFICIENTS IN TABLE 5 WITH RESPECT
TO INDEPENDENT VARIABLES

<table>
<thead>
<tr>
<th>Small Items</th>
<th>Macoma</th>
<th>Worms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small items</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macoma</td>
<td>$t = .66; P &gt; .05$</td>
<td></td>
</tr>
<tr>
<td>Worms</td>
<td>$t = 1.95; P &gt; .05$</td>
<td>$t = 2.3; P &gt; .01$</td>
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</tbody>
</table>
Fig. 6.—Searching speeds of foraging redshanks as functions of encounter densities with three different prey types: small items, *Macoma*, and polychaete worms. Each plot includes selected data in which at least one of the appropriate prey were selected.
Fig. 7.—Instantaneous search speeds of foraging redshanks evaluated from pace lengths plotted against the mud softness. The line equals the fitted regression curve: speed $= 0.431 - 0.119 \log_e$ mud softness ($+1$), $n = 255$, $P < .001$.

Fig. 8.—Searching speeds of foraging oystercatchers plotted against prey encounter rate (reciprocal of the interattempt distance). The limits of the predicted search speeds from the acceleration-limited model (see fig. 2) are also shown.
reaches an asymptote. A second mechanism depends on observations that as speed increases so do potential energy fluctuations in the body and head. Clark and McNeil Alexander (1975) and Davies and Green (1988) have suggested that the characteristic bobbing of the head while walking, which is exhibited by many birds, including redshanks, may reflect an adaptation to reduce these potential energy fluctuations, in which the head is kept stationary for the maximum period in each pace cycle to allow efficient prey detection. As speed increases the duration of the stationary phase declines, which may result in a reduction in detection efficiency. The extent to which the “optimum” speed will fall below $V_{\text{max}}$ will depend on the extent to which these factors become important as speed increases, which will presumably vary with the predator and prey involved. For predators that frequently encounter prey, however, the inability to accelerate instantaneously from standing still to $V_{\text{max}}$ may be of greater importance as an influence on the prey-searching speed. This is likely to be representative of many small predators that feed on abundant sources of relatively small prey, of which they must eat large numbers to cover their daily energy requirements (Gibb 1957). Since these predators commonly exhibit numerical responses to their prey they may spend much of their foraging time in the region of the curve relating walking speed to prey encounter density, at which they would be acceleration limited and not limited by the relation of prey detection to speed.

An alternative explanation for the observed data is that the relationship between speed and encounter density reflects entirely a relationship between speed and detection efficiency. Hence, as the birds walked faster the apparent prey density, measured as encounters per meter searched, would decline, even if the true density were constant. It is not possible in the current context to evaluate prey density (availability) independently of the birds’ behavior to test this hypothesis. However, this hypothesis implies that the birds were running fast and hence expending more energy to ingest fewer prey in a situation in which running more slowly would lead to a much greater net gain. We suggest this aspect of the hypothesis makes it unlikely as an explanation for the observed trends.

The absence of different effects of different prey types on the searching behavior of the redshank (tables 5 and 6; fig. 6) supports the suggestion that these predators are predominantly acceleration limited in their searching behavior and not commonly affected by changes in prey detection with speed. These data conflict with observations of Goss Custard (1977) that redshanks on the Ythan estuary, northeast Scotland, walked slower when feeding on worms than when feeding on Corophium. The discrepancy is even greater than is readily apparent since in that study encounter rates with Corophium were greater. It is possible that sediment differences between the sites at which the two species were found account for this discrepancy since Corophium generally prefer mud with a high silt fraction (Mossman 1977), which is generally less thixotropic (Chapman 1949) and therefore has a low retardant effect on search speed.

The negative relationships between search speed and prey encounter density demonstrated in this study are the opposite of the erroneous predictions of early treatments of search speed (Evans 1976; Norberg 1977; Krebs 1978) and conflict with the observations of Smith (1975) that bar-tailed godwits (Limosa lapponica)
walked slower as temperature, and hence availability of their major prey item, *Arenicola marina*, declined, which have been cited extensively to support these earlier predictions (Evans 1976; Krebs 1978; Avery 1985). However, although the availability of *Arenicola* to godwits declined as temperature fell, the birds also expanded their diet to include the less preferred prey *Scolops armiger* (Smith 1975), and consequently encounter densities with all prey increased as temperature fell. The decline in walking speed with temperature is not therefore incompatible with the acceleration-limited model presented here.

**Oystercatchers.**—In contrast to the redshank, in which, over a large range of prey encounter densities, observed speeds and those predicted by the acceleration model were similar, in the oystercatcher at all prey encounter densities the observed speeds were considerably lower than predicted. This discrepancy probably reflects the different nature of the task involved in prey selection by the oystercatcher. Oystercatchers feeding on mussels select prey from a background mosaic of similar prey items. This discriminatory task is substantially more difficult than that faced by redshanks, which select prey from a noncryptic background. Since oystercatchers must visually process many prey items to identify which are “suitable,” the searching speed may be always retarded by the effects of search speed on processing capacity, which we have indicated above is possibly also important in determining the search speeds of redshank at lower prey encounter densities. These data suggest then that, in circumstances in which the prey are particularly cryptic, search speed may be more influenced by the relationship between search speed and prey detection than the inability to accelerate instantaneously.

Finally, in both species studied here the relationship between predator search speed and prey encounter density was similar, but the precise position of the curve appeared to depend on a complex interaction of the limited ability of predators to accelerate instantaneously and the effect of speed on prey detection ability combined with the complexity of the discriminatory prey selection task. These effects have generally been neglected in previous treatments of foraging behavior. In particular the negative relationships between walking speed and prey encounter density, which are predicted by the acceleration-limited model and have been demonstrated in the field in this article, have several important implications, for studies of predator/prey exploitation relationships (see Krebs et al. 1983) and for models predicting the diet choice that maximizes net energy gain (Speakman 1984).

**ACKNOWLEDGMENTS**

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APPENDIX

EFFECT OF RANDOM, AS OPPOSED TO REGULAR, PREY DISTRIBUTION ON PREDICTED SEARCH SPEED

We consider here the predicted average speed of a predator across a sequence of prey encounters, when those prey are randomly distributed (as is known for surface distributions of benthic invertebrates selected by redshanks; J. R. Speakman, personal observation).

When a predator encounters prey distributed at random the interprey distances are distributed according to a negative exponential distribution. Given a mean prey encounter density \( (\overline{D}) \) items \( m^{-1} \), the probability of a given interprey item distance in the interval \( a \) to \( a + 1 \) is given by the equation

\[
P(d \text{ in interval } a \text{ to } a + 1) = e^{-E \times a} - e^{-E \times (a + 1)}
\]

(see Speakman et al. 1992). The mean prey encounter density \( (\overline{D}) \) across the sequence of encounters is then described as

\[
\overline{D} = \sum_{a=0}^{\infty} [P(d \text{ in interval } a \text{ to } a + 1)] \times (a + 0.5),
\]

that is, the sum across all intervals of the probability of the interprey item distance being in any particular interval multiplied by the midpoint of that interval. This probabilistic estimate of \( \overline{D} \) is equal to the unbiased estimate \( E \). However, since the relationship between \( E \) and predator search speed is not linear, then the estimated average speed of a predator accelerating between two prey items separated by \( d \) is not the same as the average speed across a sequence of items separated on the average by \( \overline{D} \) (where \( \overline{D} = d \)), where the distances between prey are distributed according to the negative exponential.

To predict the average speed across several prey encounters it is necessary to generate an expected probability density function for the predator speed \( V_{me} \) from the probability density function for interitem distances (eq. [A1]). This is achieved by substituting into either equation (6) or equation (8) the midpoint distance of any particular interval and then multiplying the predicted speed by the probability of that particular distance \( P(d) \) occurring at the mean \( E \) as defined in equation (8), and summing these products across all intervals:

\[
V = \sum_{d=d_{\text{a}}}^{d=d_{\text{a}}} P(d) \times w \times \{0.5[(2 \times a_p) d]^{0.5}\}
\]

\[
+ \sum_{d=d_{\text{a}}}^{d=d_{\text{a}}} P(d) \times w \times \{1/([1/V_{\text{max}}] + (V_{\text{max}}/2 \times a_p \times d))\},
\]

where \( P(d) \) is the probability of a given interitem distance \( d \) (midpoint of interval). The first term of equation (A3) sums across all interprey distances below \( d_{\text{a}} \) and the second at all distances above \( d_{\text{a}} \), and \( w \) is a weighting term equal to 1.0. Equation (A3), however, gives a biased estimate for the mean predicted speed across a sequence of encounters, because all interprey speeds are equally weighted in the calculation \( (w = 1.0) \). Hence very short distances, which are covered relatively quickly but during which time the animal walks slowly (because the animal is heavily acceleration limited), are weighted equally to longer interprey distances, which take longer to cover but during which the animal walks faster since it is more released from the acceleration limitation. The probability of a given interprey distance, which is used to predict the probability of a given speed between any two items (eq. [A3]), must then be weighted according to the average duration the animal takes to cover that distance. To remove this bias the \( w \) must be recalculated for each interval as \( (d/V_{me})/T \), where \( d \) is a given midpoint of an interval of interprey distances,
TABLE A1

PREDICTED AVERAGE SEARCH SPEEDS AS FUNCTION OF THE MEAN PREY ENCOUNTER DENSITY

<table>
<thead>
<tr>
<th>Mean Encounter Density (n m⁻¹)</th>
<th>Homogenous Distribution (m s⁻¹)</th>
<th>Random Distribution (m s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>.01</td>
<td>1.48331</td>
<td>1.48260</td>
</tr>
<tr>
<td>.1</td>
<td>1.34831</td>
<td>1.34757</td>
</tr>
<tr>
<td>1</td>
<td>.70711</td>
<td>.70702</td>
</tr>
<tr>
<td>5</td>
<td>.31623</td>
<td>.31622</td>
</tr>
<tr>
<td>10</td>
<td>.22361</td>
<td>.22349</td>
</tr>
<tr>
<td>20</td>
<td>.15811</td>
<td>.15809</td>
</tr>
</tbody>
</table>

$V_{me}$ is the predicted search speed for that particular distance, and $T$ is the mean time to walk between two prey items that are separated by the average interprey distance ($D$; eq. [A2]).

We calculated the mean search speeds for a hypothetical predator searching for homogeneously distributed prey and for randomly distributed prey, with the reciprocal of the prey encounter density to estimate the speeds as in the text and with the weighted probability density function as described in this Appendix. We assumed the maximum prey-searching speed was 1.5 m s⁻¹ and the maximum acceleration was 1 m s⁻². The results are shown in table A1. The difference between the predictions, under the assumptions of homogenous distribution and random prey distribution, was in all cases negligible.

LITERATURE CITED


Goss Custard, J. D., R. T. Clarke, and S. E. A. le V. Durrell. 1984. Rates of food intake and


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