

Prey detectability: significance and measurement using a novel laser pen technique

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Understanding foraging behaviour requires measurement of three aspects of prey: abundance, availability and detectability. Few techniques exist for measuring detectability on the appropriate scale and many models subsume variation in detectability within availability. However, there is great potential for detectability to differ markedly between patches with the same prey distribution. This paper describes a new method using a laser pen to simulate prey detection under field conditions in order to determine how small-scale variation in soil surface topography, crop type and crop growth might affect foraging behaviour of Northern Lapwings *Vanellus vanellus* on arable fields.

INTRODUCTION

A thorough knowledge of the behaviour of individuals can give insights into population dynamics (Hassell & May 1985) which are essential when one is concerned with predictions. In this context, the ecology of shorebirds has received much attention with the parallel development of theoretical and empirical studies and models of foraging behaviour, especially using functional response curves, depletion rates and aggregative responses (e.g. Gill *et al.* 2001; Stillman *et al.* 2001). These behavioural processes are influenced by three aspects of the prey: abundance, availability and detectability. There may be few or many prey items present in an area (*Abundance*), but some or all may be difficult or impossible to obtain (*Availability*). Finally, prey may be both abundant and available but must be also *detectable*. That is, the degree to which the predator notices that a prey item is present, either through visual, auditory, olfactory or tactile cues.

Detectability may be influenced by prey behaviour, which itself may interact with environmental conditions. Grey Plovers *Pluvialis squatarola* and Great Ringed Plovers *Charadrius hiaticula* detect their intertidal invertebrate prey from brief periods of caste production, water outflow from burrows and swimming movements, but these activities slow or cease at low temperatures (Pienkowski 1983a, b). Therefore, although still available, low activity renders these prey undetectable to foraging plovers. At the opposite extreme, high temperatures can decrease availability and detectability as invertebrates move deeper, away from the drying substrate surface (e.g. Batty 1988). Detectability may be directly influenced by the environment in which the predator is searching. Eriksson (1985) showed how water transparency reduced fish detectability with depth in different ways for surface-feeding birds (e.g. mergansers *Mergus*) and for plunge-diving birds (e.g. terns *Sterna*). Quammen (1982) showed that the substrate in which a tactile-searching wader was feeding could interfere with prey detection if the substrate particles were of similar size to the prey items.

Typically, detectability is subsumed within prey availability. For instance, the probability of prey detection is incorporated within the attack constant a' in Holling's (1959) disk equation which combines the area or volume of substrate searched, the probability of detection and the probability of prey capture within the area or volume (Sutherland 1996). However, as the examples above show, detectability has the potential to vary widely between patches, and independently of prey availability, so estimates of a' are likely to differ between patches. Thus foragers on patches with similar prey abundance and prey distribution yet differing substrate or vegetation structure may not be expected to have similar intake rates or conform to the same generalised functional response. Abundance is relatively straightforward to measure, availability less so, but few studies have directly examined prey detection and the effect of environmental variation and habitat structure on prey detectability.

This study examines the effect of environmental variation in the form of soil surface topography and vegetation growth on the foraging behaviour of Northern Lapwings *Vanellus vanellus* foraging on arable fields. Lapwings are pause-travel foragers (O'Brien *et al.* 1990): in a stationary phase they scan for prey, before making a series of paces to a new scanning location, with or without making a peck. Metcalfe (1985), Getty & Pulliam (1991) and Anderson *et al.* (1997) have provided a theoretical framework for understanding pause-travel foraging. Metcalfe (1985) hypothesised that a forager should move to the edge of the area it has just scanned; if it moves a shorter distance it will waste time by scanning the same ground; if it moves a greater distance it risks missing prey in unscanned ground. Furthermore, Anderson *et al.* (1997) predicted that, to maximise prey intake, pause-travel foragers should pause more often and move shorter distances when their ability to see distant objects degrades. However, how can one measure a Lapwing's ability to see distant objects? This paper describes a novel method, giving examples from a field study on arable fields.



METHODS

Field technique

Prey detection was simulated using a laser pen mounted at plover-eye height such that wherever the laser beam contacted the substrate was a point at which a prey item would be detectable – Getty & Pulliams’ theoretical “spotlight of attention” (2001). Rather than use mounted specimens in which the feeding posture may be misrepresented, photographs of foraging plovers (scaled from bill measurements) were measured which showed that the eye was approximately 20 cm above the ground during the stationary phase of foraging. The laser pen was mounted on a photographic tripod adapted so that the pan and tilt head was inverted between the legs. In this way the laser pen could move freely and point at the ground at varying distances whilst remaining at 20 cm above the ground surface (Fig. 1).

Initial observations showed that wintering Lapwings pecked almost exclusively at the ground (rather than vegetation). Thus visibility of the ground as opposed to vegetation was likely to be most important in determining foraging success. Visibility was quantified along a 2.5 m long transect by aiming the pen at the ground in increments of 10 cm distance. At each distance, visibility was scored at five points, 2.5 cm apart and perpendicular to the transect. Scores were 0 = no red spot of light visible on the ground surface, 1 = incomplete red spot, 2 = complete well-defined red spot. In this way, scores summed across the five points gave an aggregate visibility score ranging from 0 (nil visibility) to 10 (complete visibility) at each distance. When plotted against distance these values gave a ‘Visibility Profile’. Visibility profiles were measured at three random locations in each of five fields with differing cover to measure the range of variation in visibility: three cereal crops, one cereal stubble and one sugar beet stubble. Initial measurements were made in December 2001 and January 2002 with repeat measurements made in two cereal fields in mid March 2002 following significant crop growth. In all cases vegetation height was measured every 50 cm along the visibility transect. In addition to height, the structure of the cereal seedlings was classified as either Upright Stage: individual leaf blades are short and remain upright, forming a neat row of near vertical vegetation along the drill line; or Spreading Stage: leaves extend and droop downwards.

Analysis

Relationships between visibility and distance and differences between fields or growth stages were tested using logistic regression. Logistic regression was performed using the SAS procedure PROC GENMOD using a logit link function and binomial error distributed to give a function of the form:

$$V = 100 \times \frac{e^{c+mr}}{1 + e^{c+mr}} \quad \text{Eqn. 1}$$

where c is the intercept and m the gradient of the distance–visibility relationship on a logit scale and V the predicted percentage visibility. Using logistic regression ensured that the predicted values were bounded by 0 and 100%. Data were entered in the events-trials syntax with events = visibility score and trials = 10.

To ascertain the importance of a given change in visibility on the effective foraging range of a plover, a plover was

assumed to search a semi-circular area, centred on and in front of the bird. It is worth noting that the visual field of a plover probably extends more than 180° but since virtually all prey attacks were in a forward direction (pers. obs.), a semi-circular area was deemed appropriate for this study. The area can be visualised as comprising narrow concentric rings to which the percentage visibility for the midpoint of each band can be predicted from the logistic regression equations relating distance to visibility (equation 1). An estimate of A_d , the total ground area visible (cm²) within a radius of D centimetres can be derived by summing the product of band area and band visibility. This can be simplified to the following integral:

$$A_d = \int_0^D \pi r \left(\frac{e^{c+mr}}{1 + e^{c+mr}} \right) dr \quad \text{Eqn. 2}$$

where r is the radius (cm) of a distance band and c and m are the intercept and gradient respectively of the logit-transformed visibility function as in equation 1. Field observations of foraging Lapwings showed that 95% of movements between scanning locations involved 12 paces, and that a pace was on average 10.8 cm (Gillings 2003). Therefore, Lapwings travelled c. 130 cm between scanning locations, which can be considered the limit of prey detection (Metcalf 1985) and this value was used for D in equation 2 to estimate the area of ground visible from the scanning point.

RESULTS

In all fields, visibility declined with increasing distance (Fig. 2). The rate of decline varied not only between fields but between transects within the same field. Each visibility transect was therefore treated as independent. Note that only two of the three transects in each of the revisited cereal fields could be re-measured because the canes marking their locations disappeared. Furthermore, in Cereal field 2 no seeds germinated along one transect (Fig. 2Bii, 2nd transect).

For each of the 19 Visibility Profiles logistic regression showed that there was a significant negative relationship (at least $P < 0.01$) between distance and visibility (Table 1). Individual visibility transects differed in the rate at which visibility declined as can be seen from the variation in m values in Table 1. The most rapidly declining curves, and the visibility transects with the largest negative m values were in the cereal stubble field (Fig. 2) and on the second measurement of visibility transect A of the cereal crop field 2 (Fig. 2Bii). When the tabulated m and c values were substituted into equation 2 to give A_{130} , the ground area visible within a semi-circle of radius 130 cm (12 paces), values ranged from 0.25 m² to 2.06 m² out of a possible 2.65 m². Consistent with the hypothesis that vegetation height is one factor likely to influence visibility and thus A_{130} , there was a significant negative relationship between ground visibility and mean vegetation height on visibility transects in bare and cereal fields ($r_s = -0.67$, $n = 16$, $P = 0.004$, Fig. 3). The sugar beet field was excluded here since it differed in structure and did not possess live vegetation. However, total vegetation height did not explain all of the variation in visibility. For instance, some visibility transects with short vegetation had greater A_{130} values than the bare (pre-emergent) fields. This must be due to fine scale differences in soil surface topography or changes in the structure of seedlings.

By comparing the results from the re-measured visibility transects the effect of changing vegetation height and struc-



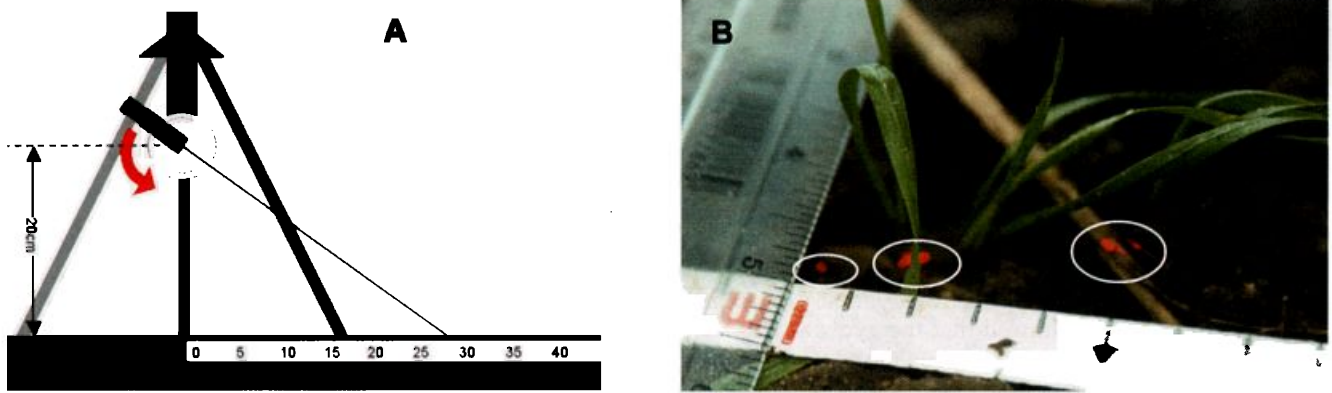


Fig. 1. Diagram (A) shows the equipment used to measure visibility profiles. The pan and tilt head of the tripod was inverted so that it was positioned below and between the legs and was adjustable up or down until the laser pen was 20 cm above the ground. The laser pen was mounted such that it rotated without changing height. A tape measure was extended 2.5 m from below the laser pen to act as the transect. Photograph (B) showing a close-up of the laser light point hitting the ground. The laser pen is mounted 1 m to the right and the laser beam (circled in white) is being broken and scattered by a piece of straw, a clod of soil and only a fraction of the point is hitting the ground at the 1 m mark. This would have been scored as '1'.

ture can be examined more closely. In cereal field 2 measurements were made three months apart. On transect A the intercept parameter decreased from 1.8 to 0.6 and the gradient parameter changed from -0.02 to -0.04 (Table 1) indicating that visibility was generally reduced and declined with distance more rapidly on the second measuring (Fig. 2). This resulted in ground area visibility decreasing from 1.30 m^2 to 0.25 m^2 (Table 1). During the intervening three months vegetation height increased significantly from $6.5 \pm 0.3 \text{ cm}$ to $10.4 \pm 1.0 \text{ cm}$ (paired t-test, $t = -3.0$, $df = 5$, $P < 0.03$) and had changed from Upright to Spreading stage. However, results from cereal field 2 transect B suggested that ground visibility increased from 1.82 cm^2 to 2.03 cm^2 . This transect fell where a seed-drill line had largely failed to germinate so

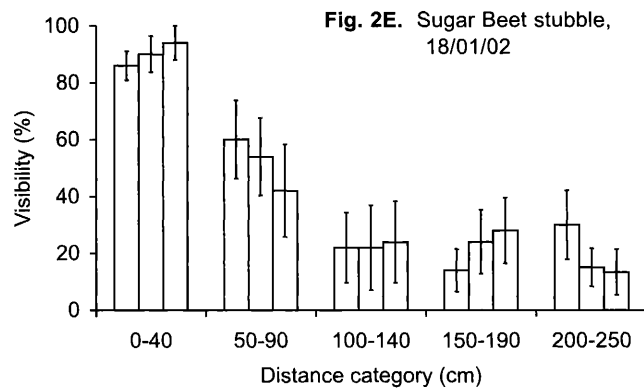
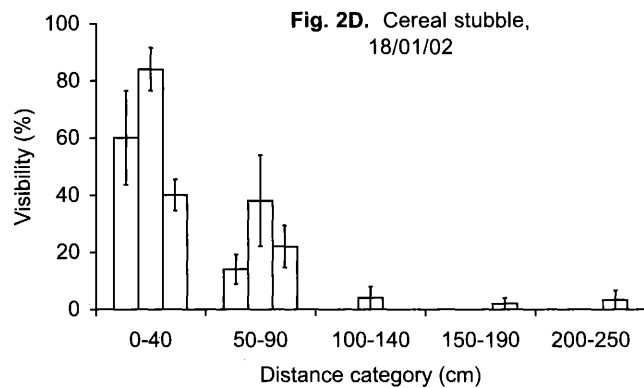
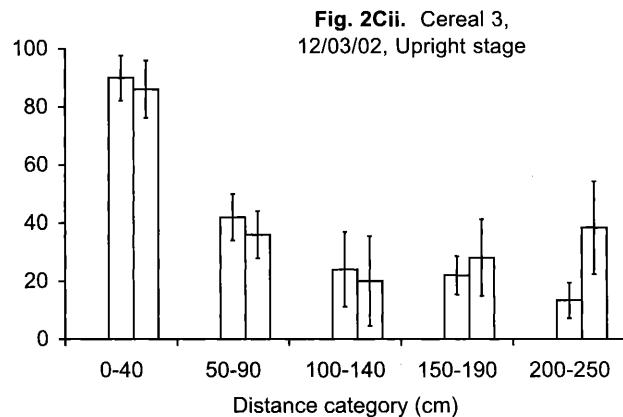
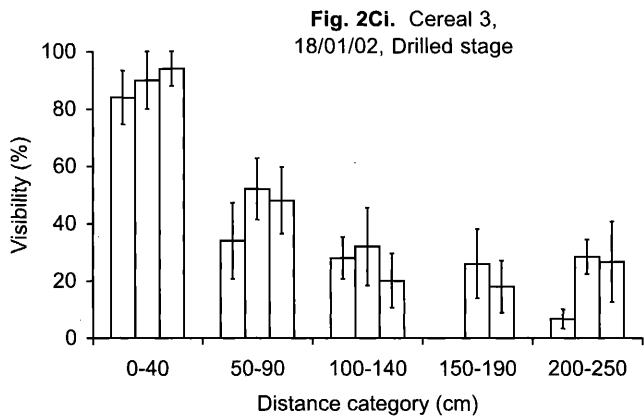
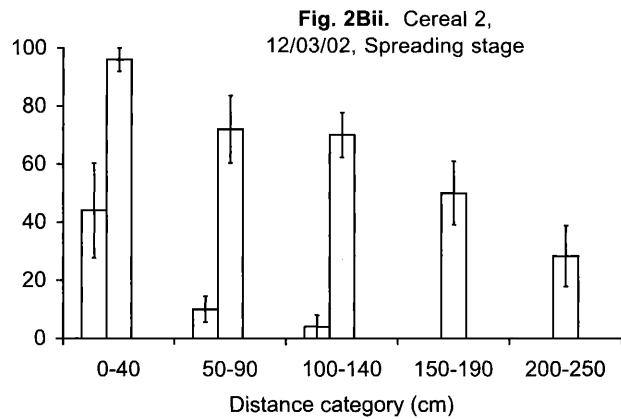
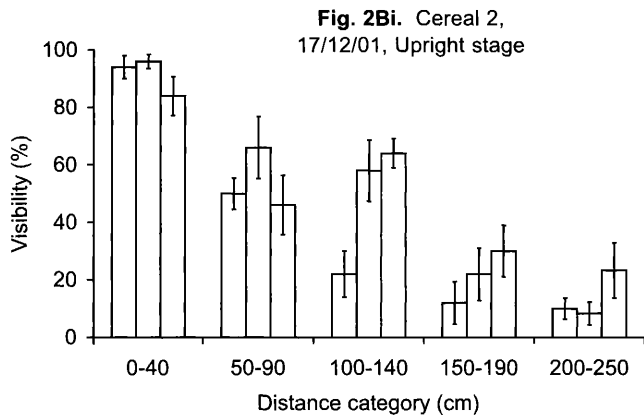
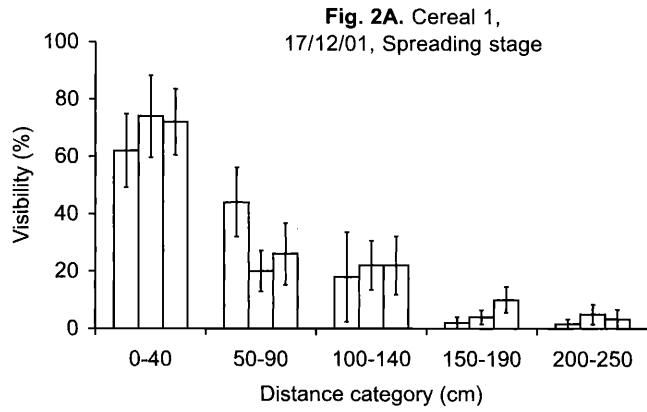
there was virtually no cereal vegetation and hence no large decrease in visibility. The apparent small increase in visibility may be attributed to changing position of the few cereal leaves present, ground flattening due to heavy rain and snow cover during the intervening period, or measurement error. Measurements in cereal field 3 were repeated after a period of two months. On the first visit, the field had been drilled with cereal seeds but no seedlings had emerged. On the second visit, seedlings had emerged to the Upright stage and were $5.3 \pm 0.5 \text{ cm}$ tall. This change in height had relatively little effect on ground area visibility with changes on the two transects from 1.48 m^2 and 1.37 m^2 to 1.30 m^2 and 1.27 m^2 respectively.

Table 1. Results of logistic regression of visibility against distance (cm) on each visibility transect. Subscript values indicate visibility transects in which repeat measurements were made. Logistic regression results are shown in the form of the intercept c and the gradient m of the logit-transformed function and the chi-square test of the significance of distance in explaining variation in visibility. $A_{1.30}$ is the area of ground searchable (m^2) within a 1.3 m radius semi-circle centred on the bird (Equation 2). (** $p < 0.01$, *** $p < 0.001$)

Field	Transect	c	m	χ^2_1	$A_{1.30}$
Cereal 1	A	1.209	-0.0243	90.2***	0.82
	B	1.037	-0.0225	81.1***	0.80
	C	1.058	-0.0212	79.0***	0.87
Cereal 2	A	1.842	-0.0217	100.0***	1.30
	A _{repeat}	0.590	-0.0400	51.4***	0.25
	B	2.808	-0.0223	118.7***	1.82
	B _{repeat}	2.579	-0.0155	63.7***	2.03
Cereal 3	C	1.441	-0.0121	45.3***	1.58
	A	1.692	-0.0255	107.9***	1.02
	B	1.355	-0.0128	49.2***	1.48
	B _{repeat}	1.493	-0.0177	77.0***	1.30
Cereal stubble	C	1.292	-0.0141	56.2***	1.37
	C _{repeat}	0.560	-0.0074	18.3***	1.27
	A	1.546	-0.0525	62.6***	0.30
	B	2.988	-0.0507	85.5***	0.72
Sugar Beet stubble	C	-0.432	-0.0101	8.8**	0.58
	A	1.211	-0.0129	48.8***	1.39
	B	1.859	-0.0197	91.8***	1.41
	C	1.444	-0.0162	69.0***	1.35



Fig. 2. Visibility profiles for five fields and for initial and repeat measurements (where performed). The legend includes the field number, date of measurements and habitat or vegetation stage. In each chart three bars represent the three visibility transects (except Bii and Cii where only two could be re-measured). Measurements have been summarised as mean visibility (\pm SE) in categories of distance from the origin for each transect.



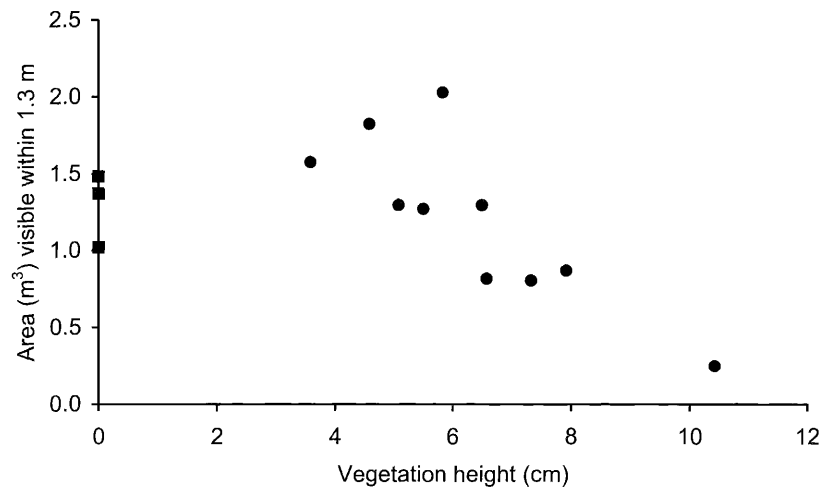


Fig. 3. Relationship between mean vegetation height on a visibility transect and the area of ground within a semi-circle of 1.3 m (maximum of 2.6 m²) that a Lapwing can search within 12 paces (A_{130}). Circles = cereal crops, squares = drilled soil (pre-emergent, hence vegetation height = 0 cm).

DISCUSSION

The novel laser pen method described here for measuring visibility through different habitats shows promising results for application to a range of studies. It is capable of detecting the effect of small differences in soil surface topography and the changing influence of vegetation as it develops. It demonstrated how the visibility in a field drilled with cereal crop had ground area visibility within 1.3 m of *c.* 1.4 m² which declined by about 10% when the cereal crop emerged to a height of 5 cm. As vegetation increased from only 6.5 cm to 10.4 cm, visibility declined from 1.3 m² to 0.3 m² – a decrease of 81%. The temporal decline in visibility is largely due to changes in vegetation height and the structure of individual cereal plants. Gallagher (1979) showed how the rate of leaf emergence and leaf extension is due to thermal time (time integral of temperature above 0°C). When lamina length first reaches 5 cm only one leaf is present but when leaf length first reaches 10 cm there are six leaves (Gallagher 1979). Furthermore, field observations showed how, as leaves lengthened, they tended to droop downwards, thus causing more visual obstructions to either side of the plant. These effects combined to greatly reduce visibility in the later stages of crop development. It is probably this marked decline in ground visibility which accounts for the preference by Lapwings (and Eurasian Golden Plovers *Pluvialis aprinaria*) of short turf (e.g. Milsom *et al.* 1998) and abandonment of cereal fields with tall vegetation (e.g. Gregory 1987). The low visibility within cereal stubble fields may partly explain why these habitats were rarely used in this study area despite containing abundant prey (Gillings 2003). Additionally, physical resistance to movement in structurally complex stubbles may also be important (e.g. Butler & Gillings in press).

Clearly the next stage is to directly relate Lapwing foraging behaviour to visibility profiles. This was attempted in the present study but the Lapwing distribution in the study area changed during the course of experiments and birds infrequently occupied measured fields. Initial work quantifying the distance between scans and to successful pecks gave qualitative support to gross differences in detectability

between crops but insufficient data were collected to relate behaviour directly to visibility. Nonetheless some clear hypotheses can be made. In the absence of differences in prey density between patches, 1) individuals should move further in smoother or structurally less complex habitats; 2) a threshold density must occur at some distance beyond which prey cannot be detected adequately; 3) visibility at the edge of the scanned area should be constant across fields; 4) foragers not responding to changing visibility will suffer increased frequency of aborted/failed pecks and decreased intake rates (perhaps below critical thresholds for survival). Knowing in detail the relationships between prey abundance, prey detectability, sward structure and predator searching activity, it should be possible to estimate the number of detectable prey items in different habitats and estimate give-up densities. If behavioural responses to visibility can be measured alongside relationships between visibility and vegetation growth there is potential for inter-disciplinary predictive modelling using plant physiological models for wheat such as the ARCWheat model (Porter 1984; Weir *et al.* 1984) which would allow changes in prey detectability to be modelled as functions of climatic conditions and management regimes. Furthermore, for those species, or seasons where predators glean prey from leaf surfaces, incorporating plant models that predict lamina area may allow the relative costs (reduced visibility) and benefits (greater phytophagous insect density) of sward structure to be assessed. Where there are likely to be large spatial or temporal differences in prey detectability (and therefore the effective area searched) such process need to be included in conjunction with functional response relationships if foraging models are to correctly predict future responses of bird populations.

This method may be applicable to a wide variety of species and systems: several species are pause-travel foragers, from ground-based species such as plovers and thrushes to perching species such as chats, shrikes and owls. It may be possible to turn the apparatus round, and assess predation risk from the prey's perspective by, for instance, mounting the laser pen in a nest-cup, and determining the range of angles from which the nest can be seen, or an approaching predator detected. The power of this laser pen technique is



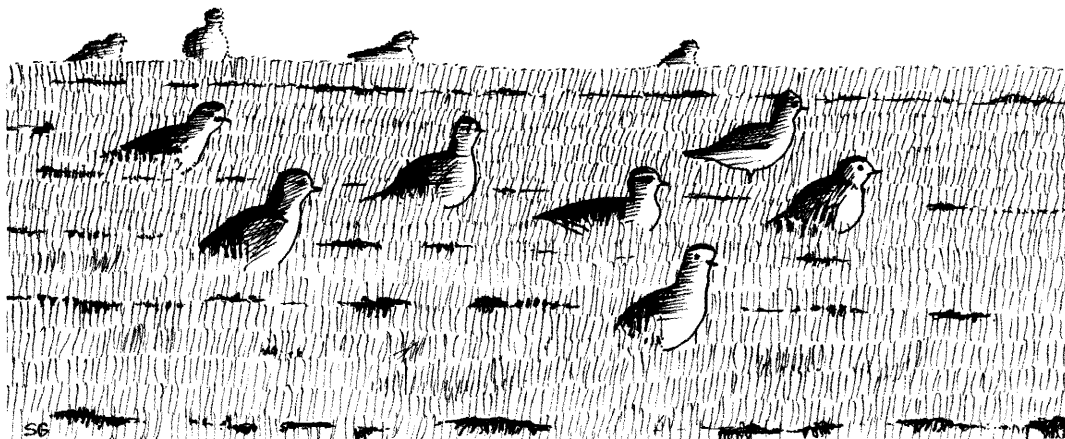
to allow quantitative predictions involving visibility and detectability to be made and tested. Moreover, it affords a new bird's eye view of the environment that can aid scientists to realise the scale and magnitude of environmental factors that impact upon bird behaviour.

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