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6	Modeling relationships between organisms and vegetation structure using								
7	airborne LiDAR data								
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10	Whittingham, M.J. <sup>5</sup> , Davenport, I.J. <sup>3</sup> , & Bellamy, P.E. <sup>2</sup>								
11									
12	1. RSPB, The Lodge, Sandy, Beds, SG19 2DL, UK.								
13	2. Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon,								
14	Cambridgeshire, PE28 2LS, UK.								
15	3. Natural Environment Research Council Environmental Systems Science Centre,								
16	University of Reading, Reading, RG6 6AL, UK.								
17	4. RSPB Scotland, Dunedin House, 25 Ravelston Terrace, Edinburgh, EH4 3TP, UK.								
18	5. Farmland Bird Group, Edward Grey Institute of Field Ornithology, Department of								
19	Zoology, South Parks Road, University of Oxford, Oxford, OX1 3PS, UK.								
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27									
28	Correspondence:								
29	Richard B. Bradbury								
30	RSPB								
31	The Lodge								
32	Sandy								
33	Beds. SG19 2DL. UK								
34	Tel: 01767 680551								

- 1 Fax: 01767 692365
- 2 Email: Richard.Bradbury@RSPB.org.uk
- 3 Summary
- 4
- Models that predict the distribution or demography of organisms are important tools in
   applied ecology. A key mechanism underlying many such 'organism-habitat' models is
   the influence of vegetation structure on the organism. Vegetation structure is a
   determinant of habitat quality that can influence prey abundance and availability, predator
   detection and avoidance, and organism thermoregulation.
- The collection of high sampling densities of accurate vegetation structure data over whole
   landscapes presents problems. Manual survey becomes prohibitive in terms of time and
   cost if sampling needs to be of sufficient density to incorporate fine-grained heterogeneity
   over this spatial extent.
- Airborne laser scanning (ALS) is a remote sensing technology, based on a principle of
   light detection and ranging (LiDAR). Airborne LiDAR offers the ability to collect high
   horizontal sampling densities of high vertical resolution vegetation height data, over
   larger spatial extents than could be obtained practically by field survey.
- 4. Two examples are provided of organism-habitat models that use structural habitat
  information derived from airborne LiDAR data. First, it is shown that data on crop and
  field boundary height can be derived from LiDAR data, and used to predict the
  distribution of breeding skylarks in a farmed landscape. Second, LiDAR-retrieved canopy
  height and structural data are used to predict breeding success of great tits and blue tits in
- 23 woodland.

1	5.	The combination of LiDAR data with multi-spectral remote sensing data enables a wider
2		range of habitat information to be derived, including both structural and compositional
3		characteristics. This enhances the ability to distinguish habitat parcels.
4	6.	Synthesis and applications. LiDAR offers the ability to deliver high sampling densities of
5		accurate vegetation structure data over whole landscapes. Particularly when combined
6		with multi-spectral remote sensing data, LiDAR offers great potential for parameterising
7		predictive organism-habitat association models.
8		

### 1 Introduction

2

3 It is important to be able to model the distribution and abundance of organisms, both for conservation and pest-control purposes. This enables the identification of important areas for 4 5 management and the prediction of changes in the abundance and distribution of organisms resulting from habitat change (Manel, Buckton & Ormerod 2000; Cowley et al. 2000). There are 6 proven consequences of policy-driven land-use change on biodiversity, for example the effect of 7 agricultural intensification on European bird populations (Chamberlain et al. 2000; Donald, 8 Green & Heath 2001). Thus, it is essential to be able to predict the effects of such changes before 9 decisions are taken on their implementation. 10 Models of organism-habitat relationships can help us to predict the response of animal 11 distribution or demography to land-use change. Statistical models relate surveyed variation in 12 abundance or demographic rates of organisms to variation in the presence or extent of habitat 13 variables (Fielding & Haworth 1995; Guisan & Zimmermann 2000). Ideally, the prediction 14 15 accuracy of these models (and hence risk involved in making judgements based on the predictions) should be tested in different locations if the models are to be of value to decision-16 makers considering the effect of land-use policy changes on widespread species (Eaton et al. 17 2002; Whittingham, Wilson & Donald in press). 18 Here, we explore the potential of LiDAR to parameterise predictive models in which 19 organism distribution or demography is influenced by vegetation structure. The enormous 20 potential for the use of LiDAR in ecological studies has yet to be realised (Lefsky et al. 2002). 21 We use recent examples of bird-habitat models for farmland and woodland habitats to exemplify 22

our case, although our arguments could equally be applied to many other taxa.

24

#### 1 VEGETATION STRUCTURE

2

3 The key to the predictive ability of many distribution models is the incorporation of habitat variables that reflect directly the mechanism of habitat selection. There are several ways 4 5 in which vegetation structure can influence habitat selection. Vegetation structure may impede movement of foraging birds both physically (Brodmann, Reyer & Baer 1997) and behaviourally 6 (Desrochers & Hannon 1997) and may influence foraging efficiency through its effects on 7 detectability and accessibility of food items (e.g. Moorcroft et al. 2002; Whittingham & 8 Markland 2002). For example, the abundance of wading birds on grasslands is predicted by 9 vegetation height, which reflects ease of movement and soil penetration when feeding and, 10 hence, prey intake rate (Milsom et al. 2000). Cold or wet vegetation may also impose additional 11 energetic demands via chilling effects (Dawson, Carey & Van't Hof 1992). 12 Predation risk and hence nest success rate is influenced by two often inversely correlated 13 properties of a nesting or foraging site; concealment and the view of the surroundings. The detail 14 15 of this trade-off varies between predators, as well as with the anti-predator response of the prey species (Götmark et al. 1995). Birds can also show diametrically opposed associations with 16 vegetation structure as a response to weather conditions. For example, in North American prairie 17 grasslands, McCown's longspurs Calcarius mccownii Lawrence and horned larks Eremophila 18 alpestris L. nest early and are associated with sparse vegetation cover, whilst the later-nesting 19 lark bunting Calamospiza melanocorys Stejneger associates with less exposed sites such as 20 overhanging shrubs and tussocky grasses (With & Webb 1993). These differences reflect the 21 need for warmth for early-nesting species and the risk of overheating for late nesting species. 22 Heterogeneity in vegetation structure is an important predictor of species richness and of 23 habitat quality for individual species, at a range of spatial scales (Hinsley, Bellamy & Rothery 24

1998; Chamberlain & Gregory 1999; Benton, Vickery & Wilson in press). Heterogeneity is also
important within habitat units (such as individual woods or agricultural fields). For example,
while denser swards may promote some invertebrates, birds may select adjacent sparser areas
where access is easier (Morris, Bradbury & Wilson 2002; Perkins *et al.* 2002). In addition,
structurally heterogenous swards attract a greater diversity of arable weeds and invertebrates, in
terms of both taxonomic and functional diversity and in their various relations with the
vegetation phenology (Gibson, Hambler & Brown 1992; Marshall *et al.* in press).

8

# 9 MEASURING VEGETATION STRUCTURE

The time and labour costs of collecting structural vegetation data manually means that there is 10 often a conflict between collecting less detail over landscape scales or detailed recording over 11 smaller areas. Here we define the 'landscape scale' to be spatial extents beyond 10ha. If there is a 12 need for multiple measurements of spatially heterogeneous predictor variables at the same scale, 13 field surveys can often only be applied at a sub-landscape extent. Thus, organism-habitat models 14 15 based on such data often lack crucial information on the geographical generality required for management decisions over larger spatial extents, because of the requirement for extrapolation 16 (Eaton et al. 2002; Whittingham, Wilson & Donald in press). 17

Remote sensing (RS) methods provide alternative means of collecting habitat data. Airborne LiDAR, Synthetic Aperture RADAR (SAR) and stereo-photogrammetry can all provide vegetation height information based on different techniques, of which LiDAR is the most direct. LiDAR offers the ability to record variation in vegetation height at an ideal spatial resolution for parameterizing organism-habitat models by remote means. Brock *et al.* (2002) provide an overview of the basic principles of LiDAR and among many applications, they discuss the determination of vegetation canopy structure as a key variable in mapping wildlife habitats.

LiDAR can be used to identify differently structured habitat units in the landscape and quantify
 variation in vegetation structure within those units.

3

### 4 Methods

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LiDAR is an 'active' remote sensing technology. A pulse of near infrared laser light is fired at 6 7 the ground by an aircraft-borne laser scanner. In practice, the laser pulse spreads as it descends to the ground, so that it forms a circular 'footprint' by the time it hits the ground. The timing of the 8 return pulse, following reflection from the Earth's surface, is used to derive a measure of the 9 distance between the sensor and the Earth's surface at that point. The laser scanner measurements 10 are combined with data on the aircraft's position and height made by a differential global 11 positioning system (GPS) and an inertial navigation unit (measuring roll, pitch and yaw), 12 enabling the position and elevation of each point on the ground to be identified (Wehr & Lohr 13 1999). 14

15 The return signal from a structurally complex surface, such as a vegetation canopy, will contain information from surfaces at varying depths within the canopy and potentially even from 16 the forest floor (Lefsky et al. 2002). There are two distinct ways in which the airborne LiDAR 17 devices used in terrestrial applications record the return signal from an emitted laser pulse. 18 Waveform-recording devices record information from all depths between the top of the 19 vegetation and the ground (Lefsky et al. 2002). With a vertical resolution of up to 0.11 m, this 20 provides a finely resolved measure of the vertical distribution of plant matter within each laser 21 footprint. The area of the Earth's surface illuminated by each footprint is typically > 1 m in 22 diameter (commonly 5-15 m). Waveform-recording devices have been used to derive forest 23 canopy height profiles (Sun and Ranson 2000), and forest stand characteristics, such as height, 24

basal area, biomass, volume and leaf area index (Nelson, Krabill & Tonelli 1988; Lefsky *et al.* 1999).

3 Discrete-return devices record information from fewer points within each return pulse, frequently only the first and/or last part of the return signal. The footprint size of each laser pulse 4 5 on the ground is typically < 1m in diameter (commonly 0.2-0.3m diameter). By scanning in sweeps perpendicular to the flight-line, the forward motion of the aircraft generates a saw-tooth 6 pattern of point samples. With high laser pulse-repetition rates, thousands of ranging points can 7 be recorded per second, resulting in sampling densities of up to 10 footprints per m<sup>2</sup>. From such 8 data, it is possible to interpolate a continuous, fine spatial resolution surface (i.e. a grid-based 9 Digital Surface Model), from which a Digital Terrain Model (DTM) and a Digital Canopy Height 10 Model (DCHM) can be extracted. Discrete-return devices have been used to map tree height 11 (Magnussen, Eggermont & LaRiccia 1999), crown diameter or depth (Næsset 2002; Næsset & 12 Økland 2002), stem number (Næsset & Bjerknes 2001), basal area (Næsset 2002), timber volume 13 (Hyyppä et al. 2001) and carbon content (Patenaude et al. 2002). 14 In general, the larger footprint size of waveform-recording devices provide a better 15 sampling of canopy vertical structure, but their practical application for landscape-scale mapping 16 is limited by poor horizontal sampling density compared with the smaller footprint sized 17 discrete-return devices. 18 Below, we review two case studies that illustrate the potential of LiDAR data from 19 discrete-return devices to provide structural vegetation data that predict habitat quality for birds 20 at a landscape scale. The first example demonstrates the ability of LiDAR data to predict bird 21 distribution in farmland, where the habitat data can be validated by field survey. The second 22

23 example shows the potential of LiDAR to quantify habitat data that predict nestling masses of tits

in woodland, where it would be impossible to collect the same detail of habitat data by field
survey.

3

#### 4 **Results**

5

# 6 CASE STUDY 1: SKYLARKS BREEDING IN AGRICULTURAL LANDSCAPES

7

The skylark Alauda arvensis L. is particularly appropriate for a study evaluating the utility of 8 airborne LiDAR for predicting bird numbers and distribution. General log-linear regression 9 models that are underpinned by causal processes already exist for enclosed agricultural 10 landscapes. These models explain a substantial proportion of the variation in the breeding 11 distribution of skylarks, measured as territories per hectare (Wilson et al. 1997, 2000; Donald et 12 al. 2001). Skylark territory densities are highest in crops with short, sparse vegetation cover, and 13 14 which are not surrounded by tall boundary structures or unsuitable habitats such as woodland. The sward variables are thought primarily to relate to the ability of the bird to access nest and 15 food resources on the ground within fields, while the landscape variables probably relate to 16 predator detection. Recent changes in agricultural land-use and intensity of management have 17 reduced habitat quality for skylarks by developing structurally uniform, dense, fast-growing 18 crops. Models that predict the field-by-field abundance of skylarks are based on variables such as 19 crop type and field area, but their predictive accuracy is substantially improved by the inclusion 20 of vegetation structural variables such as crop and boundary height (Donald et al. 2001). Models 21 incorporating all these variables explain a high proportion of the variance in skylark numbers in 22 fields. Figure 1 illustrates this by plotting observed numbers of territories in the individual 23 habitat units versus the fitted values generated by the model (n = 299 fields). R<sup>2</sup> values cannot be 24

estimated with log-linear regression. Hence, to quantify the predictive accuracy of the model, a
binary logistic regression (0 = territories absent, 1 = territories present) was instead constructed.
Overall classification success rate of the logistic regression model was very high, with presence
or absence predicted correctly in 82.3% of cases.

5 To evaluate the potential of LiDAR to collect data in farmed landscapes, and hence to predict distributions of species such as skylark, we tested the ability of last-return LiDAR data to 6 7 provide within-field vegetation height. A discrete-return Airborne Laser Terrain Mapper (Optech ALTM 1020), capable of measuring surface topography to a vertical precision of 15cm, was used 8 to acquire vegetation height data over two study areas of mixed arable and pastoral farmland in 9 the UK. The first area covered 18 fields near Faringdon in Oxfordshire, and the second covered 10 37 fields near Shrewsbury in Shropshire. The data were acquired in July 1998 and June 1999 11 respectively. Time between laser transmission and receipt of the last significant return signal was 12 recorded for each laser pulse. Pulses were returned mainly from within the crop, rather than the 13 crop canopy surface or ground. The elevation data were detrended, to remove the influence of 14 15 variation in surface topography. For each field, histograms of the differences in heights from the local average were approximately normally distributed about zero height difference. This allowed 16 the histograms to be parameterized by their standard deviations (Davenport et al. 2000). 17

The relationship between the standard deviation of detrended return heights within a field and the mean field crop height measured by field survey is shown in Fig. 2 (Cobby, Mason & Davenport 2001). This relationship could be used to derive crop height from LiDAR data, with an  $r^2$  value of 0.8 and a standard error of 14cm. Measures such as heterogeneity in vegetation height and ground cover at the field scale would be extremely time-consuming and expensive for fieldworkers to obtain over larger extents. Such variables can be collected with airborne LiDAR

at high sampling densities and at extents of 1000 hectares or greater (Cobby, Mason &
 Davenport 2001).

3	A range image segmentation system for LiDAR data has been devised that identifies
4	discontinuities in height and so allows measurements such as mean crop height and boundary
5	height to be allocated accurately to individual agricultural fields (Mason et al. in press).
6	Especially when combined with simultaneous multi-spectral remotely-sensed data (see below),
7	it is possible to produce maps that allocate variation in vegetation height to different habitats
8	such as crops, field margin vegetation and field boundary structures (Fig. 3).
9	Unfortunately, no simultaneous LiDAR data and skylark territory data exist to test
10	whether vegetation structural data derived from LiDAR can be used to predict skylark
11	distribution. However, given that all the variables featured in Fig. 3 were those used in the
12	models from which Fig. 1 was calculated, it is apparent that these data would be sufficient to
13	predict skylark distribution with high accuracy.
14	
15	CASE STUDY 2: HABITAT QUALITY FOR WOODLAND TITS
16	
17	Great tits Parus major L. and blue tits P. caeruleus L. are woodland birds that provision their
18	nestlings principally with tree-dwelling lepidopteran larvae. There are differences in the two
19	species' body masses and foraging behaviour (Lack 1971; Perrins 1979). The smaller Blue Tit (c.
20	10 g) spends more time in the outer parts of the tree canopy and less time on the ground than the
21	larger Great Tit (c.19 g). It is possible, therefore, that the two species will benefit from different
22	woodland vegetational structure.
23	Elevation data were collected using a discrete-return Airborne Laser Terrain Mapper

24 (Optech ALTM 1210) for Monks Wood National Nature Reserve in Cambridgeshire, UK, in

1 June 2000. Both first and last return elevation data were recorded for each laser pulse. This enabled canopy height to be modeled (Fig. 4) by a process of adaptive morphological filtering, 2 3 thin-plate spline interpolation and data subtraction (Hill, Gaveau and Spendlove 2002). Monks Wood comprises 157 hectares of deciduous woodland, dominated by common ash *Fraxinus* 4 5 excelsior L. and English oak *Quercus robur* L. Field-based estimates of a tree canopy density index (CDI) were compared with mean vegetation height calculated from the LiDAR data (LiHt) 6 7 for sample areas of 54 x 54 m centered on each of 36 tit nestboxes (Fig. 4). These boxes were distributed throughout the wood and near the Centre for Ecology and Hydrology (CEH) site at 8 the edge of the wood. The sample areas were assumed to be representative of the core of each 9 territory (Hinsley et al. 2002). To calculate CDI in the field, the proportion of canopy in each of 10 five density classes (range 0-4; where 0 = absence and 4 = dense, closed canopy) was estimated 11 by eye by two independent observers. The CDI was then calculated as  $\sum$  (score x proportional 12 coverage of sample area) and expressed as the mean of the two estimates (which were 13 significantly correlated: r = 0.879, P = < 0.001, n = 36). LiHt explained 86% of the variation in 14 the CDI (Hinsley et al. 2002). Thus, LiDAR-derived height could be used as a surrogate for the 15 field-based estimates of canopy density. 16

17 Mean nestling body mass for each brood of tits in occupied nestboxes was calculated by weighing the nestlings (excluding runts) using a spring balance on day 11 (day of hatching = 0). 18 Mean nestling body mass was used as a measure of breeding performance likely to reflect 19 territory quality (Przybylo, Wiggins & Merilä 2001), because it combines the effects of food 20 abundance with the adults' abilities to find food (foraging efficiency) and to deliver it to the 21 nestlings (travel costs). For blue tits, mean nestling body mass at 11 days of age increased with 22 LiHt in the sample area around the nestbox, but for great tits the relationship was negative (Fig. 23 5). This difference suggested that great tits might prefer a more varied height profile than blue 24

tits, but many factors could be involved, including competition for food between the two species
(Minot 1981). Using the relationship between mean nestling body masses and remote-sensed
woodland canopy height, this aspect of breeding performance (and hence, habitat quality) can be
predicted across the entire wood (Hill *et al.* in press).

5

## 6 Discussion

7

The collection of vegetation structure data by airborne LiDAR has several clear advantages over 8 field survey for the construction of organism-habitat models; (i) The vertical resolution is such 9 that data can be collected at similar precision (agricultural landscapes) or better precision 10 (woodland) than by workers in the field, (ii) the sampling density of the data is equivalent or 11 better than can be achieved realistically by workers in the field, (iii) data of this vertical and 12 horizontal resolution can be collected at landscape scales, and (iv) a combination of these 13 properties allows heterogeneity in vegetation structure to be expressed at multiple spatial scales, 14 15 from the foraging patch or territory to the landscape. LiDAR is not the only digital RS technology that can deliver vegetation structural data. 16 Synthetic Aperture Radar (SAR) is an active imaging system in the microwave spectrum that can 17 be used to derive forest canopy height (Kasischke, Melack & Dobson 1997; Schmullius & Evans 18 1997). A variety of methods and types of SAR sensors exist. Most developed are SAR 19 radiometry (Imhoff et al. 1997), SAR interferometry (Balzter 2001), SAR polarimetry (Schuler et 20 al. 1998), polarimetric SAR interferometry (Cloude & Papathanassiou 1998) and SAR 21 tomography (Reigber & Moreira 2000). Balzter et al. (2003) compare different approaches of 22 vegetation height retrieval from airborne SAR interferometry with LiDAR. The comparison 23 shows a comparable height accuracy of SAR to LiDAR at a short wavelength if two antennas are 24

mounted on an aircraft at the same time, but at a lower spatial resolution (~3 m) and with less 1 2 responsiveness to gaps in the canopy. Although current SAR systems have a coarser spatial 3 resolution (airborne SAR between 1 - 5 m, spaceborne SAR 30 - 50 m) compared with LiDAR, the present availability of SAR sensors in space gives it a high operational potential for 4 5 monitoring. Forthcoming satellite SAR missions like TerraSAR or ALOS PALSAR will have greatly enhanced sensors with multiple modes. However, the uptake of SAR in ecology has been 6 7 limited by the lack of automation of the data processing chains required to derive height data, by the limited availability of airborne SAR, and by the technological cost-induced restrictions of 8 satellite missions. 9

While the intention here is to introduce the potential of LiDAR, it is important to note 10 that several remote sensing techniques already exist which have supplied habitat data for 11 organism-habitat models (e.g. Lavers, Haines-Young & Avery 1996; Mack et al. 1997). Satellite-12 borne 'passive' sensors collect multi-spectral data, allowing different habitats to be distinguished 13 by differences in spectral reflectance. For example, the Advanced Very High Resolution 14 15 Radiometer (AVHRR) sensor on the National Oceanic and Atmospheric Administration (NOAA) series of satellites can give global coverage with horizontal resolution of 1.1 km at best, 16 while the Thematic Mapper (TM) and the more recent Enhanced Thematic Mapper (ETM) on the 17 Landsat series of satellites provides horizontal resolution of c.10-80m. AVHRR data have been 18 used to predict site occupancy by Great Bustards Otis tarda L. in steppe habitats in central Spain 19 (Osborne, Alonson & Bryant 2001), and Landsat TM data have been used to determine the 20 relationship between remotely sensed habitat classes and species distribution patterns of different 21 bird species in the Greater Yellowstone Ecosystem, USA (Debinski et al. 1999). 22 While multi-spectral data cannot provide information on vertical vegetation structure, 23

reflected radiance in the visible and infra-red parts of the spectrum can supply a range of

information including land-cover type (Fuller et al. 2002), plant species composition (Gerylo et 1 2 al. 1998), Leaf Area Index, biomass and plant vigour (Rock et al. 1986). Vegetation type and 3 fractional ground cover may be obtained from high resolution multi-spectral data from airborne sensors, such as the Airborne Thematic Mapper (ATM) and Compact Airborne Spectrographic 4 5 Imager (CASI). Therefore, there is an important role for the combined use of multi-spectral and LiDAR data (Searth, Phinn & McAlpine 2001; Hudak et al. 2002). This can deliver improved 6 habitat parcel classification (Hill et al. 2002; Mason et al. in press), in which, for example, 7 hedgerows and woodland can be differentiated. The spatial pattern and connectivity of habitat 8 patches such as woodland blocks or hedgerows within the landscape can affect species 9 abundance models (Hinsley et al. 1995). Identifying such spatial patterns (Hill and Veitch 2002) 10 can allow the movement of species through the landscape to be quantified. The simultaneous 11 12 collection of data on vegetation structure and composition gives the potential to increase the proportion of variance explained by the models, beyond that explained by vegetation structural 13 data alone. 14

15 There are many advantages of LiDAR when compared with other traditional field-based techniques or alternative remote sensing technologies. Like other remote sensing techniques, 16 LiDAR provides a means of data collection in areas of restricted or limited access. It is less 17 restricted than techniques such as aerial photography or multi-spectral scanning by weather 18 conditions and low sun incidence angle (being operational by day or night). As with all remote 19 sensing data, LiDAR can generate synoptic data rapidly and more efficiently than ground-based 20 habitat data, giving the potential to collect near-simultaneous spatially-referenced data over 21 whole landscapes (Lefsky et al. 2002). 22

In summary, airborne LiDAR has the potential to collect high precision vegetation
structural data, with a high sampling density and over spatial extents for which collection in the

1	field is impractical or impossible. Among other uses, therefore, airborne LiDAR may provide an
2	important tool for bridging the gap between spatial resolution and spatial extent of organism-
3	habitat models. While aircraft-borne LiDAR data can only realistically be collected at the
4	landscape scale defined here, it is possible that future satellite-borne LiDAR tools would be able
5	to deliver sufficiently high resolution data at even larger spatial extents.
6	
7	
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9	
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20	
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Fig. 1. Relationship between fitted count (i.e. as predicted by model) and observed count of
skylark territories on fields. Open circles = model 1 (based on data from 100 fields in
Oxfordshire, UK, in 1994, 1995, and 1998); triangles = model 2 (based on data from 98 fields in
East Anglia, UK, in 1996); crosses = model 3 (based on data from 101 fields in Oxfordshire, UK,
in 1996). The models include effects of crop type (categorical variables) and field area, boundary
height, vegetation height, vegetation density, field slope, and field shape (continuous variables).

7

8 Fig. 2. Regression of manually surveyed sward heights (in grass and cereal fields) against standard deviation of detrended LiDAR height differences (figure reproduced, with permission, 9 10 from Cobby, Mason & Davenport 2001). Ideally, crop height would be derived as the difference between return pulses from the crop canopy surface and from the ground. However, returns from 11 the top of the stalk are unlikely because of its small cross-section compared with the laser 12 footprint, and ground returns are unlikely due to the dense nature of crops. Therefore, a 13 relationship is derived, between the measured crop height  $(h_m)$  and the standard deviation  $(\sigma)$  of 14 15 LiDAR heights. This does not rely on a certain fraction of pulses hitting the ground. The relationship, from data from 55 fields, takes the form:  $h_{\rm m} = 0.87 \ln(\sigma) + 2.57$ 16

17

**Fig. 3**. Sub-sample of a test field, near Oxford, UK, showing (a) vegetation height map derived from LiDAR data, (b) false colour Airborne Thematic Mapper image in which the surrounding land-cover context can be identified, (c) calculated habitat variables (manually-surveyed results in brackets). Field slope is measured as the slope (degrees) between highest and lowest point on the field. Field shape is measured as the perimeter of the field divided by the perimeter, if a field of the same area was circular. Figure reproduced, with permission, from Mason *et al.* (in press).

- Fig. 4. Vegetation height map for Monks Wood National Nature Reserve, derived from LiDAR
   data. Map produced with permission of NERC.
- 3

Fig. 5. Blue tit and great tit mean nestling body masses in relation to LiDAR-derived vegetation
height around the nestbox, for 'central' Monks Wood nestboxes (closed circles) and 'edge' CEH
site nestboxes (open circles). Figure reproduced with permission from Blackwell Publishing
from Hinsley *et al.* (2002: Fig. 3, *Functional Ecology* 16: 851-857).







3b



3c

Variable	Estimate
Field area (hectares)	5.5
Mean vegetation height (cm)	87 (92)
Vegetation height standard	24
deviation (cm)	
Mean boundary height (m)	5.6 (5.9)
Mean slope (degrees)	0.025
Field shape	2.0
Crop type	Wheat

3a







