Ibis (2005), **147**, 443–452

Review

Modelling relationships between birds and vegetation structure using airborne LiDAR data: a review with case studies from agricultural and woodland environments

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Airborne LiDAR (Light Detection and Ranging) is a remote sensing technology that offers the ability to collect high horizontal sampling densities of high vertical resolution vegetation height data, over larger spatial extents than could be obtained by field survey. The influence of vegetation structure on the bird is a key mechanism underlying bird–habitat models. However, manual survey of vegetation structure becomes prohibitive in terms of time and cost if sampling needs to be of sufficient density to incorporate fine-grained heterogeneity at a landscape extent. We show that LiDAR data can help bridge the gap between grain and extent in organism–habitat models. Two examples are provided of bird–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 so have the potential to predict the distribution of breeding Sky Larks in a farmed landscape. Secondly, LiDAR-retrieved canopy height and structural data are used to predict the breeding success of Great Tits and Blue Tits in broad-leaved woodland. LiDAR thus offers great potential for parameterizing predictive bird–habitat association models. This could be enhanced by the combination of LiDAR data with multispectral remote sensing data, which enables a wider range of habitat information to be derived, including both structural and compositional characteristics.

Modelling the distribution and abundance of organisms enables the identification of key areas for management and the prediction of changes in the abundance and distribution of organisms resulting from habitat change (Cowley *et al*. 2000, Manel *et al*. 2000). From a conservation perspective, predicting the effects of land-use change on biodiversity is essential to inform the decision-making process of strategic planning (e.g. Donald *et al*. 2001a).

Statistical models can be used to relate observed variation in abundance or demographic rates of birds to variation in the presence or extent of habitat variables (Fielding & Haworth 1995, Guisan & Zimmermann 2000). Ideally, the prediction accuracy of these models (and hence risk of error from those predictions) should be tested in different locations to assess their general applicability for widespread

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species (Eaton *et al.* 2002, Whittingham *et al.* 2003).

Vegetation structure

The key to the predictive ability of many species-distribution models is the incorporation of habitat variables that reflect directly the mechanism of habitat selection. There are several ways in which vegetation structure can influence habitat selection for bird species. Vegetation structure may impede the movement of foraging birds both physically (Brodmann *et al.* 1997) and behaviourally (Desrochers & Hannon 1997) and may influence foraging efficiency through its effects on the detectability and accessibility of food items (e.g. Moorcroft *et al.* 2002, Whittingham & Markland 2002). For example, the abundance of wading birds on grasslands is predicted by vegetation height which reflects ease of movement and soil penetration when feeding, and hence prey intake rate (Milsom *et al.* 2000). Cold or wet vegetation may also impose additional energetic demands via chilling effects (Dawson *et al.* 1992).

Predation risk, and hence breeding success rate, is influenced by two often inversely correlated properties of a nesting or foraging site: concealment and the view of the surroundings. The detail 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 vegetation structure as a response to weather conditions. For example, in North American prairie grasslands, McCown's Longspurs *Calcarius mccownii* and Horned Larks *Eremophila alpestris* nest early and are associated with sparse vegetation cover, while the later-nesting Lark Bunting *Calamospiza melanocorys* is associated with less-exposed sites such as overhanging shrubs and tussocky grasses (With & Webb 1993). These differences reflect the need for warmth for early nesting species and the risk of overheating for late-nesting species.

Heterogeneity in vegetation structure is an important predictor of both species richness and habitat quality for individual species, at a range of spatial scales (Hinsley *et al.* 1998, Chamberlain & Gregory 1999, Benton *et al.* 2003, Wilson *et al.* 2005). 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 *et al.* 2002, Perkins *et al.* 2002).

Measuring vegetation structure

The time and labour costs of collecting structural vegetation data manually mean that there is often a trade-off between the level of detail of observation and the size of area that can be surveyed. This is especially so at the landscape scale, which we define here to be spatial extents beyond 10 ha. If there is a need for multiple measurements of spatially heterogeneous predictor variables at the same scale, field surveys can often be applied only at a sub-landscape extent. Thus, because of the need to extrapolate, bird–habitat models based on such data often lack crucial information on the geographical generality required for management decisions affecting larger spatial extents (Eaton *et al.* 2002, Whittingham *et al.* 2003).

Remote sensing (RS) methods provide alternative means of collecting habitat data. Airborne techniques such as LiDAR (Light Detection and Ranging), Synthetic Aperture RADAR (SAR) and stereo-photogrammetry can all provide vegetation height information. LiDAR offers the ability to record variation in vegetation height at an ideal spatial resolution for parameterizing bird–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 to quantify variation in vegetation structure within those units.

Here, we review the potential of airborne LiDAR to parameterize predictive models in which bird distribution or demography is influenced by vegetation structure. The enormous potential for the use of LiDAR in ecological studies has yet to be realized (Lefsky *et al.* 2002, Turner *et al.* 2003). We use recent examples of bird–habitat models for farmland and woodland habitats to exemplify our case, although our arguments could be applied equally to many other taxa.

OVERVIEW OF LIDAR APPLICATIONS

LiDAR is an 'active' remote sensing technology. A pulse of near-infrared laser light is fired at the ground by an aircraft-borne laser. 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 return pulse, following reflection from the Earth's surface, is used to derive a measure of the distance between the sensor and the Earth's surface at that point. The laser measurements are combined with data on the aircraft's position and altitude made by a differential global positioning system (GPS) and an inertial navigation unit (measuring roll, pitch and yaw), enabling the position and elevation of each point on the ground to be identified (Wehr & Lohr 1999).

The return signal from a structurally complex surface, such as a vegetation canopy, can contain information from surfaces at varying depths within the canopy and, potentially, even from the ground. When the near-infrared radiation emitted by the LiDAR device hits a leaf or other part of a plant structure, that radiation will be partly reflected and partly absorbed, but will generally not be transmitted through the structure. Penetration of the near-infrared radiation into a vegetation layer will occur only by direct transmission through holes in the canopy structure (Gaveau & Hill 2003). The larger the footprint size the greater the likelihood that some of the near-infrared radiation emitted by the LiDAR device will penetrate through holes in the vegetation canopy and return from the ground.

The airborne LiDAR devices used in terrestrial applications record the return signal in two distinct ways. Waveform-recording devices digitize the entire return signal. Over a woodland area, for example, this can record information from signal reflection at all depths between the top of the vegetation and the ground (Lefsky *et al.* 2002). With a vertical resolution of up to 0.11 m, this provides a finely resolved measure of the vertical distribution of plant matter within each laser footprint. The area of the Earth's surface illuminated by each footprint is typically > 1 m in diameter (commonly 5–15 m). Waveform-recording devices have been used to derive forest canopy height profiles (Sun & Ranson 2000) and forest stand characteristics, such as height, basal area, above-ground biomass, volume and leaf-area index (Nelson *et al.* 1988, Lefsky *et al.* 1999, Means *et al.* 1999).

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 on the ground is typically < 1 m in diameter (commonly 0.2–0.3 m diameter). By scanning in sweeps perpendicular to the flight-line of the aircraft, an irregular pattern of spot samples is generated. With laser pulse-repetition rates of up to 100 kHz, tens of thousands of ranging points can be recorded per second, resulting in sampling densities of up to 10–20 footprints per m^2 (dependent on flying altitude). From such data it is possible to interpolate a continuous, fine spatial resolution surface, i.e. a grid-based Digital Surface Model. For a discrete-return LiDAR device recording first and last return data over a forested area the first return data will represent the top of the canopy while, typically, < 30% of the last return data will represent the forest floor, the remainder returning from a point somewhere in the vegetation canopy (Kraus & Pfeifer 1998; Næsset & Bjerknes 2001). Terrain and canopy height thus have to be modelled from the first and last return data. Discrete-return devices have been used to map tree height (Magnussen *et al.* 1999), crown diameter or depth (Næsset & Økland 2002, Næsset 2002), stem number (Næsset & Bjerknes 2001), basal area (Næsset 2002) and timber volume (Hyyppä *et al.* 2001).

In general, the larger footprint size typical of waveform-recording devices provides a better sampling of canopy vertical structure. However, their practical application for landscape-scale mapping is limited by their having a poorer horizontal sampling density than the smaller footprint size of the discrete-return devices (Lim *et al.* 2003). Currently there is no space-borne LiDAR device for terrestrial vegetation applications, so all examples of LiDAR applications for terrestrial vegetation analysis will make use of airborne systems, with the associated restrictions of targeted data-acquisition flight campaigns. The cost, availability, spatial coverage and even the nature of data recorded will vary for different countries depending on the logistics of individual data providers. However, as airborne LiDAR devices have become increasingly available to the commercial, public and academic sectors, there has been an associated decrease in the overheads associated with LiDAR data (i.e. data acquisition and processing costs and expertise in data manipulation).

Below, we review two case studies that illustrate the potential of LiDAR data from discrete-return devices to provide structural vegetation data that have potential for predicting habitat quality for birds at a landscape scale. The first example demonstrates the ability of LiDAR data to predict bird distribution in farmland, where the habitat data could be validated by field survey. The second example shows the potential of LiDAR to quantify habitat data that predict tit nestling-masses in woodland, where it would be impossible to collect the same detail of habitat data by field survey.

Case study 1. Sky Larks breeding in agricultural landscapes

The Sky Lark *Alauda arvensis* is particularly appropriate for a study evaluating the utility of airborne LiDAR for predicting bird numbers and distribution. General log-linear regression models that are underpinned by causal processes already exist for agricultural landscapes. These models explain a substantial proportion of the variation in the breeding distribution of Sky Larks, measured as territories per hectare (Wilson *et al.* 1997, 2000, Donald *et al.* 2001b). Sky Lark territory densities are highest in crops with short, sparse vegetation cover and in fields that are not surrounded by tall boundary structures or woodland. The sward variables are thought to relate primarily to the ability of the bird to access nest and food resources on the ground within fields, while the landscape variables relate probably to predator detection. Recent changes in agricultural land-use and intensity of management have reduced habitat quality for Sky Larks by developing structurally uniform, dense, fast-growing crops. Models that predict the field-by-field abundance of Sky Larks are based on variables such as crop type and field area, but their predictive accuracy is improved substantially by the inclusion of vegetation structural variables such as crop and boundary height (Donald *et al.* 2001b). Models incorporating all these variables explain a high proportion of the variance in Sky Lark numbers in fields. This is illustrated (Fig. 1) by plotting observed numbers of territories in the individual habitat units vs. the fitted values generated by the model (n = 299 fields). R^2 values cannot be 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 constructed. Overall classification success rate of the logistic regression model was very high, with presence or absence of Sky Larks in fields predicted correctly in 82.3% of cases.

To evaluate the potential of LiDAR to collect data in farmed landscapes, and hence to predict distributions of species such as the Sky Lark, we tested the ability of last return LiDAR data to provide within-field vegetation height. A discrete-return LiDAR device (Airborne Laser Terrain Mapper 1020), capable of measuring surface topography to a vertical precision of 15 cm, was used to acquire vegetation height data over two study areas of mixed arable and pastoral farmland in the UK. The first area covered 18 fields near Faringdon in Oxfordshire and the second covered 37 fields near Shrewsbury in Shropshire. The data were acquired in July 1998 and June 1999, respectively. The time between laser transmission and receipt of the last significant return signal was recorded for each laser pulse. Pulses were returned mainly from within the crop, rather than the crop canopy surface or ground. The elevation data were detrended to remove the influence of variation in surface topography (Davenport *et al.* 2000).

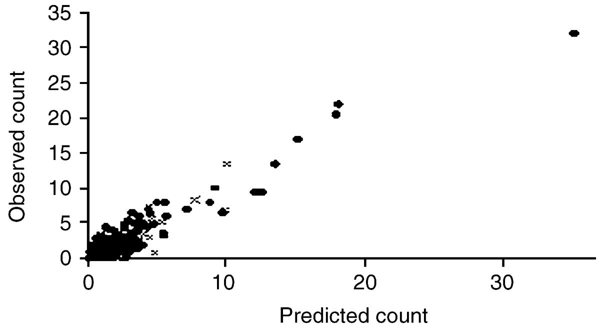


Figure 1. Relationship between fitted count (i.e. as predicted by model) and observed count of Sky Lark territories on fields. Filled circles = model 1 (based on data from 100 fields in Oxfordshire, UK in 1994, 1995 and 1998); filled squares = model 2 (based on data from 98 fields in East Anglia, UK in 1996); crosses = model 3 (based on data from 101 fields in Oxfordshire, UK in 1996). The models, based entirely on data collected in the field, include effects of crop type (categorical variables) and field area, boundary height, vegetation height, vegetation density, field slope and field shape (continuous variables). When run as a logistic regression (predicting presence or absence of any territories per field), the model predicted correctly in 82.3% of cases.

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 Figure 2 (Cobby *et al.* 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 14 cm. Measures such as heterogeneity in vegetation height and ground cover at the field scale would be extremely time-consuming and expensive for field-workers to obtain over larger areas. Such variables can be collected with airborne LiDAR at high sampling densities and over areas of 1000 hectares or more (Cobby *et al.* 2001).

An image segmentation system for LiDAR data has been devised that identifies discontinuities in height (Mason *et al.* 2003). Especially when combined with simultaneous multispectral remotely sensed data (see below), it is possible to produce maps that allocate variation in vegetation height to different

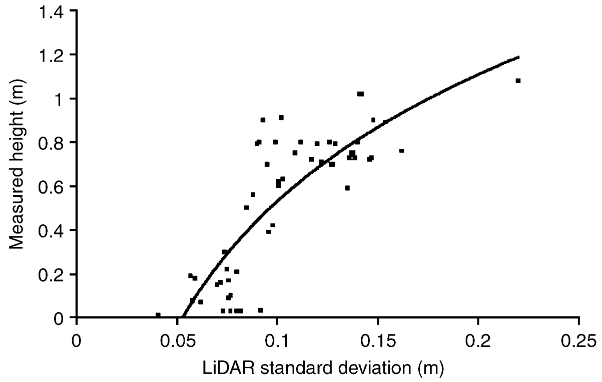


Figure 2. Regression of manually surveyed sward heights (in grass and cereal fields) against standard deviation of detrended LiDAR height differences (figure reproduced, with permission, from Cobby *et al.* 2001). Ideally, crop height would be derived as the difference between return pulses from the crop canopy surface and from the ground. However, returns from the top of the stalk are unlikely because of its small cross-section compared with the laser footprint, and ground returns are unlikely due to the dense nature of crops. Therefore, a relationship is derived between the measured crop height (h_m) and the standard deviation (σ) of 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: $h_m = 0.87 \ln(\sigma) + 2.57$.

habitat units such as crops, field margin vegetation and field boundary structures (Fig. 3).

Unfortunately, no simultaneous LiDAR data and Sky Lark territory data exist to test whether the vegetation structural data derived from LiDAR can be used to predict Sky Lark distribution. However, given that all the variables featured in Figure 3 were those used in the models from which Figure 1 was calculated, it is apparent that these data have the potential to predict Sky Lark distribution with high accuracy.

Case study 2. Habitat quality for woodland tits

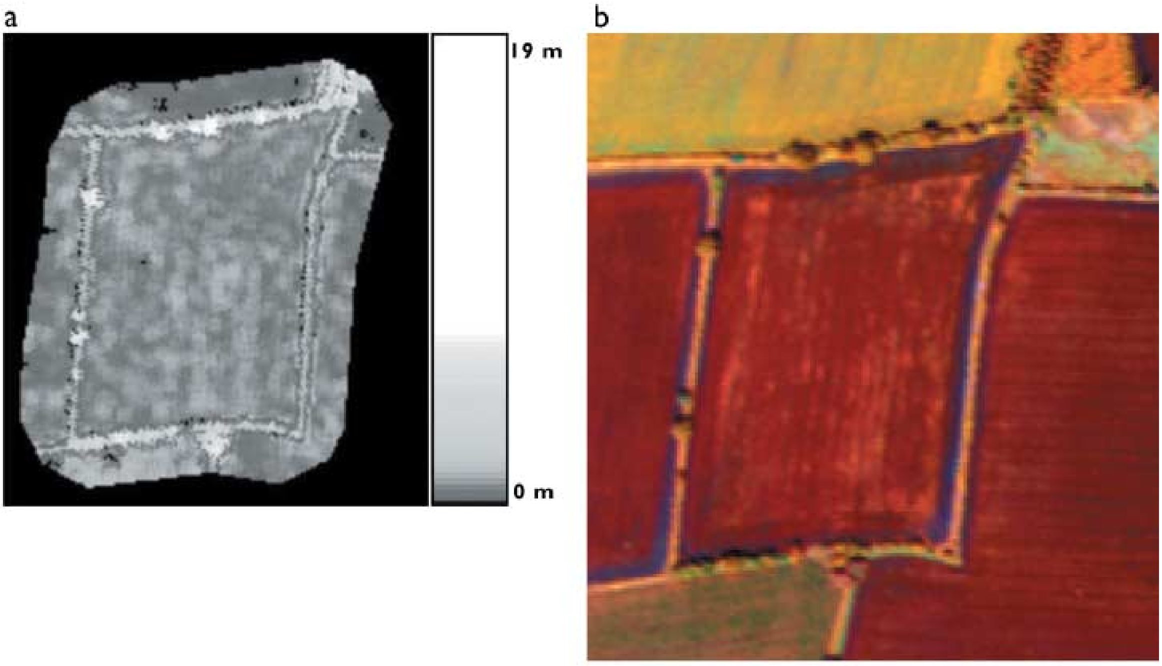
Great Tits *Parus major* and Blue Tits *P. caeruleus* are woodland birds that provision their nestlings principally with tree-defoliating lepidopteran larvae. The two species differ in body-mass and foraging behaviour (Perrins 1979). The smaller Blue Tit (*c.* 10 g) spends more time in the outer parts of the tree canopy and less time on the ground than does the larger Great Tit (*c.* 19 g).

Elevation data were collected using an Airborne Laser Terrain Mapper (ALTM 1210) for Monks Wood National Nature Reserve in Cambridgeshire, UK, in June 2000 (Hill *et al.* 2003). Both first and last return elevation data were recorded for each laser pulse, enabling canopy height to be modelled (Fig. 4 and Patenaude *et al.* 2004). Monks Wood comprises 157 hectares of deciduous woodland, dominated by Common Ash *Fraxinus excelsior* and Pedunculate Oak *Quercus robur*. Field-based estimates of a tree canopy density index (CDI) were compared with mean vegetation height calculated from the LiDAR data (LiHt) for sample areas of 54 × 54 m centred on each of 36 tit nestboxes (Fig. 4). The sample areas were assumed to be representative of the core of each territory (Hinsley *et al.* 2002). To calculate CDI in the field, the proportion of canopy in each of five density classes (range 0–4; where 0 = absence and 4 = dense, closed canopy) was estimated by eye by two independent observers. The CDI was then calculated as Σ (score × proportional coverage of sample area) and expressed as the mean of the two estimates (which were correlated significantly: $r = 0.879$, $P \leq 0.001$, $n = 36$). LiHt explained 86% of the variation in the CDI (Hinsley *et al.* 2002), and so could be used as a surrogate for the field-based estimates of canopy density.

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). Mean nestling body-mass was used as a measure of breeding performance likely to reflect territory quality (Przybylo *et al.* 2001), because it combines the effects of food abundance with the adults' abilities to find food (foraging efficiency) and to deliver it to the nestlings (travel costs). For Blue Tits, mean nestling body-mass at 11 days of age increased with LiHt in the sample area around the nestbox, but for Great Tits the relationship was negative (Fig. 5). This difference suggested that Great Tits might prefer a more varied height profile than Blue Tits, although it should be stressed that 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.* 2004a).

DISCUSSION

The collection of vegetation structure data by airborne LiDAR has several clear advantages over field survey for the construction of bird–habitat models: (i) the vertical resolution is such that data can be



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

Figure 3. Subsample of a test field, near Oxford, UK, showing (a) vegetation height map derived from LiDAR data (small black patches represent missing data), (b) false colour multispectral data (from Airborne Thematic Mapper) in which the surrounding land-cover context can be identified and (c) calculated habitat variables (manually surveyed results in brackets). Field slope is measured as the slope (degrees) between the 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.* (2003).

collected at similar precision (agricultural landscapes) or better precision (woodland) than by workers in the field; (ii) the sampling density of the data is equivalent or better than can be achieved realistically by workers in the field; (iii) data at this vertical and horizontal resolution can be collected at landscape scales; and (iv) a combination of these properties allows heterogeneity in vegetation structure to be expressed at several spatial scales, from the foraging patch or territory to the landscape.

LiDAR is not the only digital RS technology that can deliver vegetation structural data. Synthetic Aperture Radar (SAR) is an active imaging system that can be used to derive forest canopy height (Kasischke *et al.* 1997, Schmullius & Evans 1997). A variety of methods and types of SAR sensors exist, including radiometry (Imhoff *et al.* 1997), interferometry (Balzter 2001), polarimetry (Schuler *et al.* 1998), polarimetric interferometry (Cloude & Papathanassiou 1998) and tomography (Reigber & Moreira 2000). The uptake of SAR in ecology has been 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 satellite missions.

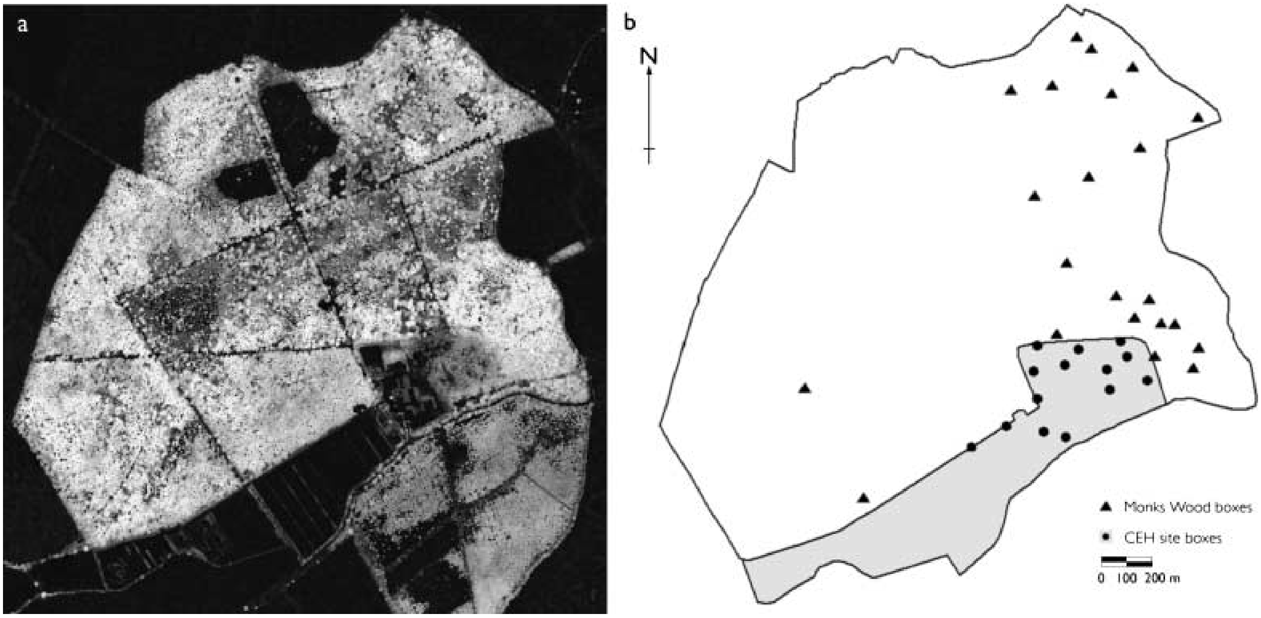

Figure 4. (a) Vegetation height map for Monks Wood National Nature Reserve, derived from LiDAR data. Map is shown as grey scale: dark tones = low vegetation height, bright tones = high vegetation height (range = 0.00 m to 23.26 m). (b) The nestbox locations across Monks Wood National Nature Reserve and the CEH Monks Wood site. Map produced with permission of NERC.

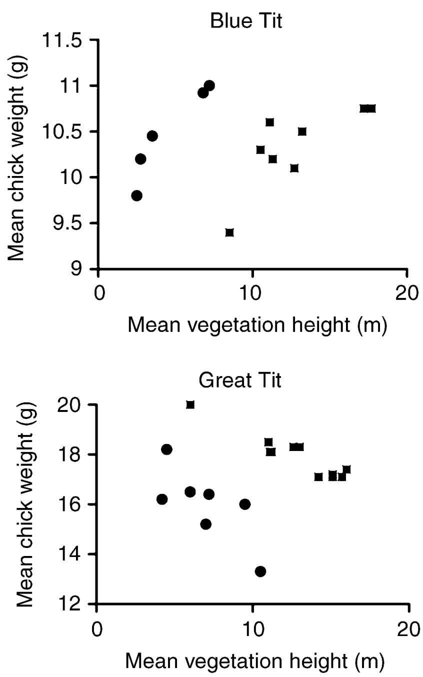

Figure 5. Blue Tit and Great Tit mean nestling body masses in relation to LiDAR-derived vegetation height around the nestbox, for 'central' Monks Wood nestboxes (squares) and 'edge' CEH site nestboxes (circles). Figure reproduced with permission from Blackwell Publishing Ltd from Hinsley *et al.* (2002).

There is a synergy in combining LiDAR data with other remotely sensed data (Searth *et al.* 2001, Hudak *et al.* 2002). Reflected radiance in the visible and infrared parts of the spectrum can supply a range of information including land-cover type (Fuller *et al.* 2002), plant species composition (Gerylo *et al.* 1998), green biomass and plant vigour (Curran 1980, Rock *et al.* 1986). The combined use of multi-spectral and LiDAR data can deliver improved habitat parcel classification (Hill *et al.* 2002, Mason *et al.* 2003, Hill & Thomsen in press) in which, for example, hedgerows and woodland can be differentiated. The spatial pattern and connectivity of habitat patches such as woodland blocks or hedgerows within the landscape can affect species–abundance models (Hinsley *et al.* 1995). Identifying such spatial patterns (Hill & Veitch 2002) can allow the movement of species through the landscape to be quantified. The simultaneous collection of data on vegetation structure and composition (Gillespie *et al.* 2004, Hill *et al.* 2004b) provides the potential to increase the proportion of variance explained by the models, beyond that explained by vegetation structural data alone.

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

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 field is impractical or impossible. Among other uses, therefore, airborne LiDAR may provide an important tool for bridging the gap between the spatial resolution and spatial extent of bird–habitat models. While aircraft-borne LiDAR data can be collected realistically only at the landscape scale defined here, it is possible that future satellite-borne LiDAR tools would be able to deliver sufficiently high resolution data at even larger spatial extents.

ALTM data were provided by the Environment Agency, the National Remote Sensing Centre Ltd (now InfoTerra Ltd, UK). ATM data were provided by the NERC Airborne Remote Sensing Facility. David Cobby helped with the development of methods for establishing crop heights for case study 1, while Richard Wadsworth advised on processing methods and David Gaveau helped with processing the LiDAR data and contributed valuable field data in case study 2. English Nature granted permission for data recording in Monks Wood NNR. We thank *ISPRS Journal of Photogrammetry and Remote Sensing, International Journal of Remote Sensing* and Blackwell Publishing Ltd for permission to reproduce Figures 2, 3 and 5, respectively. Paul Donald and Val Brown gave very useful comments on the manuscript.

REFERENCES

Balzter, H. 2001. Forest mapping and monitoring with interferometric synthetic aperture radar (InSAR). *Prog. Phys. Geog.* **25**: 159–177.

Benton, T.G., Vickery, J.A. & Wilson, J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**: 182–189.

Brock, J.C., Wright, C.W., Sallenger, A.H., Krabill, W.B. & Swift, R.N. 2002. Basis and methods of NASA airborne topographic mapper lidar surveys for coastal studies. *J. Coastal Res.* **18**: 1–13.

Brodmann, P.-A., Reyer, H.-U. & Baer, B. 1997. The relative importance of habitat structure and prey characteristics for the foraging success of Water Pipits (*Anthus spinoletta*). *Ethology* **103**: 222–235.

Chamberlain, D.E. & Gregory, R.D. 1999. Coarse and fine scale habitat associations of breeding Skylarks *Alauda arvensis* in the UK. *Bird Study* **46**: 34–47.

Cloude, S.R. & Papathanassiou, K.P. 1998. Polarimetric SAR interferometry. *IEEE Trans. Geosci. Remote Sens.* **36**: 1551–1565.

Cobby, D.M., Mason, D.C. & Davenport, I.J. 2001. Image processing of airborne scanning laser altimetry for improved river flood modeling. *ISPRS J. Photogram. Remote Sens.* **56**: 121–138.

Cowley, M.J.R., Wilson, R.J., Leon-Cortes, J.L., Gutierrez, D., Bulman, C.R. & Thomas, C.D. 2000. Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *J. Appl. Ecol.* **37** (Suppl. 1): 60–72.

Curran, P.J. 1980. Multispectral remote sensing of vegetation amount. *Progr. Phys. Geog.* **4**: 315–341.

Davenport, I.J., Bradbury, R.B., Anderson, G.Q.A., Hayman, G.R.F., Krebs, J.R., Mason, D.C., Wilson, J.D. & Veck, N.J. 2000. Improving bird population models using airborne remote sensing. *Int. J. Remote Sens.* **21**: 2705–2717.

Dawson, W.R., Carey, C. & van't Hof, T.J. 1992. Metabolic aspects of shivering thermogenesis in passerines during winter. *Ornis Scand.* **23**: 381–387.

Desrochers, A. & Hannon, S.J. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conserv. Biol.* **11**: 1204–1210.

Donald, P.F., Evans, A.D., Buckingham, D.L., Muirhead, L.B. & Wilson, J.D. 2001b. Factors affecting the territory distribution of skylarks *Alauda arvensis* breeding on lowland farmland. *Bird Study* **48**: 271–278.

Donald, P.F., Green, R.E. & Heath, M.F. 2001a. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B.* **268**: 25–29.

Eaton, M.A., Stoate, C.J., Whittingham, M.J. & Bradbury, R.B. 2002. Determinants of Whitethroat *Sylvia communis* distribution in different agricultural landscapes. In Chamberlain, D.E. & Wilson, A. (eds) *Avian Landscape Ecology: pure and applied issues in the large-scale ecology of birds*: 300–304. Garstang: Colin Cross Printers Ltd.

Fielding, A.H. & Haworth, P.F. 1995. Testing generality of bird–habitat models. *Conserv. Biol.* **9**: 1466–1481.

Fuller, R.M., Smith, G.M., Sanderson, J.M., Hill, R.A. & Thomson, A.G. 2002. The UK Land Cover Map 2000: construction of a parcel-based vector map from satellite images. *Cartogr. J.* **39**: 15–25.

Gaveau, D.L.A. & Hill, R.A. 2003. Quantifying canopy height underestimation by laser pulse penetration in small-footprint airborne laser scanning data. *Can. J. Remote Sens.* **29**: 650–657.

Gerylo, G., Hall, R.J., Franklin, S.E., Roberts, A. & Milton, E.J. 1998. Hierarchical image classification and extraction of forest species composition and crown closure from airborne multispectral images. *Can. J. Remote Sens.* **24**: 219–232.

Gillespie, T.W., Brock, J. & Wright, C.W. 2004. Prospects for quantifying structure, floristic composition and species richness of tropical forests. *Int. J. Remote Sens.* **25**: 707–715.

Götmark, F., Blomqvist, D., Johansson, O.C. & Bergkvist, J. 1995. Nest site selection: a trade-off between concealment and view of the surroundings? *J. Avian Biol.* **26**: 305–312.

Guisan, A. & Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* **135**: 147–186.

Hill, R.A., Hinsley, S.A. & Bellamy, P.E. 2004b. Integrating multiple datasets for the remote quantification of woodland bird habitat quality. In Thies, M., Koch, B., Spiecker, H. & Weinacker, H. (eds) *Proceedings of ISPRS Working Group VIII/2: Laser Scanners for Forest and Landscape Assessment*, Vol. XXXVI, Part 8/W2: 248–253. Freiburg, Germany: International Archives of Photogrammetry, Remote Sensing and Spatial Information Sciences.

Hill, R.A., Hinsley, S.A., Bellamy, P.E. & Balzter, H. 2003. Ecological applications of airborne laser scanner data: modeling woodland bird habitats. In Hyyppä, J., Næsset, E., Olsson, H., Granqvist Pahlén, T. & Reese, H. (eds) *Proceedings of the Scandlaser Scientific Workshop on Airborne Laser Scanning of Forests*: 78–87. Umeå: Swedish University of Agricultural Sciences.

Hill, R.A., Hinsley, S.A., Gaveau, D.L.A. & Bellamy, P.E. 2004a. Predicting habitat quality for Great Tits (*Parus major*) with airborne laser scanning data. *Int. J. Remote Sens.* **25**: 4851–4855.

Hill, R.A., Smith, G.M., Fuller, R.M. & Veitch, N. 2002. Landscape modelling using integrated airborne multi-spectral and elevation data. *Int. J. Remote Sens.* **23**: 2327–2334.

Hill, R.A. & Thomson, A.G. In press. Mapping woodland species composition and structure using airborne spectral and LiDAR data. *Int. J. Remote Sens.* in press.

Hill, R.A. & Veitch, N. 2002. Landscape visualisation: rendering a virtual reality simulation from airborne laser altimetry and multi-spectral scanning data. *Int. J. Remote Sens.* **23**: 3307–3309.

Hinsley, S.A., Bellamy, P.E., Newton, I. & Sparks, T.H. 1995. Habitat and landscape factors influencing the presence of individual breeding bird species in woodland fragments. *J. Avian Biol.* **26**: 94–104.

Hinsley, S.A., Bellamy, P.E. & Rothery, P. 1998. Co-occurrence of bird species-richness and the abundance of individual bird species in highly fragmented farm woods in eastern England. In Dover, J.W. & Bunce, R.G.H. (eds) *Key Concepts in Landscape Ecology*: 227–232. Preston: Myerscough College.

Hinsley, S.A., Hill, R.A., Gaveau, D.L.A. & Bellamy, P.E. 2002. Quantifying woodland structure and habitat quality for birds using airborne laser scanning. *Funct. Ecol.* **16**: 851–857.

Hudak, A.T., Lefsky, M.A., Cohen, W.B. & Berterretche, M. 2002. Integration of lidar and ETM+ data for estimating and mapping forest canopy height. *Remote Sens. Environ.* **82**: 397–416.

Hyyppä, J., Kelle, O., Lehikoinen, M. & Inkinen, M. 2001. A segmentation-based method to retrieve stem Volume estimates from 3-D tree height models produced by laser scanners. *IEEE Trans. Geosci. Remote Sens.* **39**: 969–975.

Imhoff, M.L., Sisk, T.D., Milne, A., Morgan, G. & Orr, T. 1997. Remotely sensed indicators of habitat heterogeneity: use of synthetic aperture radar in mapping vegetation structure and bird habitat. *Remote Sens. Environ.* **60**: 217–227.

Kasischke, E.S., Melack, J.M. & Dobson, M. 1997. C: The use of imaging radars for ecological applications – a review. *Remote Sens. Environ.* **59**: 141–156.

Kraus, K. & Pfeifer, N. 1998. Determination of terrain models in wooded areas with airborne laser scanner data. *ISPRS J. Photogramm. Remote Sens.* **53**: 193–203.

Lefsky, M.A., Cohen, W.B., Acker, S.A., Parker, G.G., Spies, T.A. & Harding, D. 1999. Lidar remote sensing of the canopy structure and biophysical properties of Douglas Fir/Western Hemlock forests. *Remote Sens. Environ.* **70**: 339–361.

Lefsky, M.A., Cohen, W.B., Parker, G.G. & Harding, D.J. 2002. Lidar remote sensing for ecosystem studies. *Bioscience* **52**: 19–30.

Lim, K., Treitz, P., Wulder, M., St-Onge, B. & Flood, M. 2003. LiDAR: remote sensing of forest structure. *Prog. Phys. Geog.* **27**: 88–106.

Magnussen, S., Eggermont, P. & LaRiccia, V.N. 1999. Recovering tree heights from Airborne Laser Scanner data. *Forest Sci.* **45**: 407–422.

Manel, S., Buckton, S.T. & Ormerod, S.J. 2000. Testing large-scale hypotheses using surveys: the effects of land use on the habitats, invertebrates and birds of Himalayan rivers. *J. Appl. Ecol.* **37**: 756–770.

Mason, D.C., Anderson, G.Q.A., Bradbury, R.B., Cobby, D.M., Davenport, I.J., Vandepoll, M. & Wilson, J.D. 2003. Measurement of habitat predictor variables for organism/habitat models using remote sensing and image segmentation. *Int. J. Remote Sens.* **24**: 2515–2532.

Means, J.E., Acker, S.A., Harding, D.J., Blair, J.B., Lefsky, M.A., Cohen, W.B., Harmon, M.E. & McKee, W.A. 1999. Use of large-footprint scanning airborne lidar to estimate forest stand characteristics in the Western Cascades of Oregon. *Remote Sens. Environ.* **67**: 298–308.

Milsom, T.P., Langton, S.D., Parkin, W.K., Peel, S., Bishop, J.D., Hart, J.D. & Moore, N.P. 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *J. Appl. Ecol.* **37**: 706–727.

Minot, E.O. 1981. Effects of interspecific competition for food in breeding Blue and Great Tits. *J. Anim. Ecol.* **55**: 331–350.

Moorcroft, D., Whittingham, M.J., Bradbury, R.B. & Wilson, J.D. 2002. Stubble field prescriptions for granivorous birds – the role of vegetation cover and food abundance. *J. Appl. Ecol.* **39**: 535–547.

Morris, A.J., Bradbury, R.B. & Wilson, J.D. 2002. Determinants of patch selection by yellowhammers *Emberiza citrinella* foraging in cereal crops. *Aspects Appl. Biol.* **67**: 43–50.

Næsset, E. 2002. Predicting forest stand characteristics with airborne scanning laser using a practical two-stage procedure and field data. *Remote Sens. Environ.* **80**: 88–99.

Næsset, E. & Bjerknes, K.O. 2001. Estimating tree heights and number of stems in young forest stands using airborne laser scanner data. *Remote Sens. Environ.* **78**: 328–340.

Næsset, E. & Økland, T. 2002. Estimating tree height and tree crown properties using airborne scanning laser in a boreal nature reserve. *Remote Sens. Environ.* **79**: 105–115.

Nelson, R., Krabill, W. & Tonelli, J. 1988. Estimating forest biomass and volume using airborne laser data. *Remote Sens. Environ.* **61**: 246–253.

Patenaude, G., Hill, R.A., Milne, R., Gaveau, D.L.A., Briggs, B.B.J. & Dawson, T.P. 2004. Quantifying forest above ground carbon content using LiDAR remote sensing. *Remote Sens. Environ.* **93**: 368–380.

Perkins, A.J., Whittingham, M.J., Morris, A.J. & Bradbury, R.B. 2002. Use of field margins by foraging yellowhammers *Emberiza citrinella*? *Agric. Ecosyst. Environ.* **93**: 413–420.

Perrins, C.M. 1979. *British Tits*. London: Collins.

Przybylo, R., Wiggins, D.A. & Merilä, J. 2001. Breeding success in Blue Tits: good territories or good parents? *J. Avian Biol.* **32**: 214–218.

Reigber, A. & Moreira, A. 2000. First demonstration of airborne SAR tomography using multibaseline 1-band data. *IEEE Trans. Geosci. Remote Sens.* **38**: 2142–2152.

Rock, B.N., Vogelmann, J.E., Williams, D.L., Vogelmann, A.F. & Hoshizaki, T. 1986. Remote detection of forest damage. *Bioscience* **36**: 439–445.

Schmullius, C.C. & Evans, D.L. 1997. Synthetic aperture radar (SAR) frequency and polarization requirements for applications in ecology, geology, hydrology, and oceanography: a tabular status quo after SIR-C/X-SAR. *Int. J. Remote Sens.* **18**: 2713–2722.

Schuler, D.L., Ainsworth, T.L., Lee, J.S. & DeGrandi, G. 1998. Topographic mapping using polarimetric SAR data. *Int. J. Remote Sens.* **19**: 141–160.

Searth, P., Phinn, S.R. & McAlpine, C. 2001. Integrating high and moderate spatial resolution image data to estimate forest age structure. *Can. J. Remote Sens.* **27**: 129–142.

Sun, G. & Ranson, K.J. 2000. Modelling LiDAR returns from forest canopies. *IEEE Trans. Geosci. Remote Sens.* **38**: 2617–2626.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E. & Steininger, M. 2003. Remote sensing for biodiversity science and conservation. *Trends Ecol. Evol.* **18**: 306–314.

Wehr, A. & Lohr, U. 1999. Airborne laser scanning – an introduction and overview. *ISPRS J. Photogramm. Remote Sens.* **54**: 68–82.

Whittingham, M.J. & Markland, H.M. 2002. The influence of substrate on the functional response of an avian granivore and its implications for farmland bird conservation. *Oecologia* **130**: 637–644.

Whittingham, M.J., Wilson, J.D. & Donald, P.F. 2003. Do habitat association models have any generality? Predicting skylark *Alauda arvensis* abundance in different regions of southern England. *Ecography* **26**: 521–531.

Wilson, J.D., Evans, J., Browne, S.J. & King, J.R. 1997. Territory distribution and breeding success of skylarks *Alauda arvensis* on organic and intensive farmland in southern England. *J. Appl. Ecol.* **34**: 1462–1478.

Wilson, J.D., Swetnam, R.D., Whittingham, M.J. & Bradbury, R.B. 2000. *Designing Lowland Landscapes for Farmland Birds: a Pilot Study Integrating Habitat Association Models and Geographical Information Systems*. Report to English Nature.

Wilson, J.D., Whittingham, M.J. & Bradbury, R.B. 2005. Managing crop structure: a general approach to reversing impacts of agricultural intensification on birds. *Ibis* **147**: 000–000.

With, K.A. & Webb, D.R. 1993. Microclimate of ground nests – the relative importance of radiative cover and wind breaks for 3 grassland species. *Condor* **95**: 401–413.

Received 9 March 2004;
revision accepted 18 March 2005.