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RESEARCH ARTICLE

Nest site use by crested ibis: dependence of a multifactor model on spatial scale

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Abstract The crested ibis (*Nipponia nippon*), a species at the brink of extinction in 1981, remain restricted to a small (25 km radius) area of temperate forests in central China. To improve the chances of successful reintroduction into new areas we developed a multifactor logistic regression model of habitat association at multiple scales. Using habitat variables, i.e. vegetation, human impact, elevation, and wetland, we compared occupied and unoccupied sites at grain sizes ranging from 1 to 6400 ha. The goodness-of-fit of the habitat suitability model depended on grain size, with the best fit (most information) at a grain size of 2 ha. Semivariograms showed the habitat variables at control sites have a gradient pattern, yet the crested ibis had their specific habitat preferences, and only selected a narrow range from the available gradient. Our results indicated that spatial scale needs to be considered in developing habitat models for applications such as conservation planning.

Keywords Habitat · Logistic regression · Multiscale analysis · Nest site use · *Nipponia nippon* · Geographic information system · Reintroduction · Scaling · Semivariogram

Introduction

Spatial scale has been believed to be a major concept in ecology (Levin 1992; Wu and Qi 2000; Schneider 2001). Understanding landscape structure and functioning requires multiscale information (Wu 2004). As to wildlife, Johnson (1980) distinguished four levels of habitat selection responsible for scale-dependent habitat use: first-order selection of the geographical distribution of a species; second-order selection of individual home ranges within the geographical distribution; third-order selection of habitat components within home ranges; and fourth-order selection of a specific site, for example, a nest site within a feeding area.

Other than Johnson's ecologically meaningful discrimination on the four scale levels, studies on

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Modifiable Areal Unit Problem (MAUP) provided the most comprehensive treatments of the sensitivity of analytical results to the spatial scales (Openshaw and Taylor 1979; Jelinski and Wu 1996). MAUP is the problem of results from analyses potentially differing due to the size or location of artificially imposed sampling units, rather than ecologically meaningful differences. The MAUP has two related but distinctive components: the scale problem and the zoning (or aggregation) problem (Openshaw and Taylor 1979). The scale problem is that the sizes of sample plots cause difference in results; the zoning problem is that the location and shape of sample plots cause difference in results. Most MAUP studies dealt with each landscape feature or index separately. The animal distribution associated with any one habitat variable typically decreases at small scales as they become locally decoupled from habitat (Schneider and Piatt 1986; Rose and Legget 1990; Veit et al. 1993; Schneider 1994). Multifactor models of habitat association can also be expected to depend on spatial scale. Recent studies (e.g. Bevers and Flather 1999; Mackinnon et al. 2001; Hatten and Paradzick 2003; Robinson et al. 2004) have shown that multifactor models differ in structure when compared at a few (2–4) arbitrarily chosen scales. The strength of association with multiple habitat variables as a function of scale remains unknown.

The crested ibis is an endangered species (BirdLife International 2003) that was thought to be extinct until a population of seven birds was discovered in 1981 (Liu 1981). By July 2004 the population had grown to about 360 (wild population, not including captive individuals) (Zhai personal communication). Despite its intrinsic rate of increase ($r = \ln(360/7)/23 = 17\%$/year) the species remains at risk because it is confined to a small (25 km radius) area of temperate forests in Yang county, Shaanxi province, in central China. The typical habitat is temperate forest mixed with rice paddy or other wetland (Liu 1981). Population dynamics of the crested ibis depends on habitat quality (Shi et al. 1991a; Wang et al. 1994, 1995), which has been quantified in a GIS database (Li et al. 2002a). Habitat use (Wang et al. 1985; Shi et al. 1991c; Wang 1993), nest site preference (Li et al. 2001), and wintering-site selection (Ma et al. 2001) have been described relative to elevation, wetland accessibility, vegetation, human disturbance, and other habitat variables.

To reduce the risk of extinction new breeding populations need to be established at other sites in the former habitat of this species. The success of reintroduction efforts will rest on accurate assessment of habitat requirements, which needs to solve modifiable area unit problem. The objective of our study was to analyze the nest site preference of the crested ibis at the landscape level using a multifactor model, taking into account dependence on spatial scale, in order to identify the most appropriate levels of scale for estimating nest site suitability in current and potential habitat of the crested ibis. The zoning problem of MAUP was not addressed in this paper.

Methods

Since the term ''scale'' may refer to different concepts such as grain, extent, lag, and cartographic ratio (Wu 2004), we restrict the meaning of ''scale'' to grain in this study. A number of quantitative models have been developed for detecting scales at which regular and irregular patterns occur in the landscape (Marceau 1999), and here we used the blocking technique that involves iterative aggregation of contiguous quadrats, and analysis of average and variance of habitat variables at each aggregation level. Four habitat variables (vegetation, human impact, elevation, and wetland accessibility) were measured at 35 occupied and 45 unoccupied sites. These habitat variables were known to be biologically significant to crested ibis (Li et al. 2001). They were digitized from satellite images as four raster layers in GIS software ArcGIS, which allowed us to resample the variable values using the blocking technique. We used logistic regression to estimate the odds of a site having a nest by taking account of the four habitat variables at grain sizes ranging from 1 to 6400 ha.

Study area

A field survey was conducted in Yang county, Shaanxi province, China in 1999 (Fig. 1). Yang county lies on the southern slope of Qinling Mountain. The landscape changes from gently rolling croplands in the south to forested foothills and steep mountains in the north. We located 35 nest sites in forest stands in mountain valleys at 680–1200 m above sea level (Fig. 1). The breeding region for the entire species is

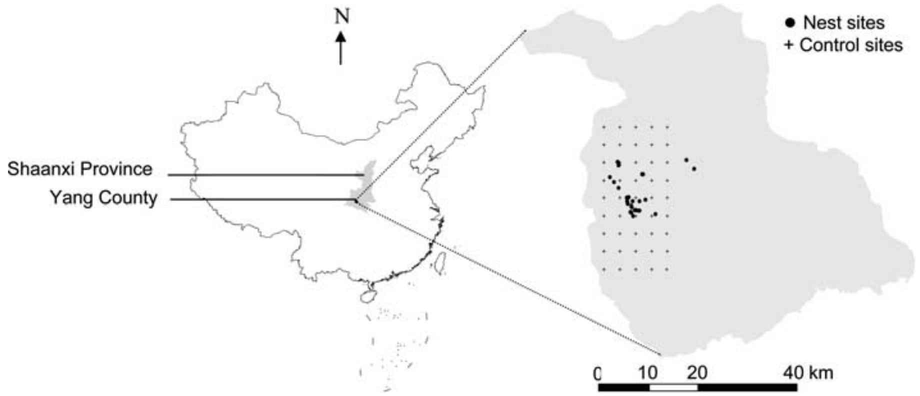

Fig. 1 Nest sites of the crested ibis from 1984 to 1999 and the control sites in Yang County, Shaanxi province, China

currently no more than a 2000 km^2 area between 33°18′39.9″–33°24′47.64″ N and between 107°23′ 15.12″–107° 28′59.82″ E.

Within the breeding area, the crested ibis build nests in tall trees, usually half way up a slope in valleys with a stream. The distances between neighboring nests of this solitary nesting species are usually 1–3 km (Li et al. 2001). Rice paddies serve as the main foraging sites for the crested ibis (Wang et al. 1985). Villages, with their nearby rice paddies, are situated near streams. Human density in the county is less than 60 people per km^2 (Yang County Agriculture Division Office 1986). All residents are farmers and farming is the major economic activity in the region.

Data collection and processing

Thirty-five nest sites were used by 25 different pairs of ibises from 1984 to 1999 (Fig. 1). All the nests were located using GPS with maximum horizontal error of 20 m (Hulbert and French 2001). Guided by the analysis of the survey data and our knowledge of the species we constructed a GIS database of four variables obtainable by remote sensing: wetland, vegetation, human impact, and elevation (Fig. 2). The fifth layer in the GIS database consisted of the 35 nest sites and 45 control sites spaced at 3 km intervals on a grid within the area having the most nest sites (Fig. 2). In the GIS database, wetland and vegetation were categorized and digitized from Landsat TM satellite images of Yang County obtained from the Institute of Geology (IOG), Chinese Academy of Sciences (Table 1). Wetland consisted of rice paddy, water body (lakes, reservoirs, and ponds), and dried areas adjacent to water bodies. We transformed the wetland layer from a polygon layer to a raster layer with resolution of 1 ha. The river data is a polyline layer, which was buffered by 50 m at each side to a polygon layer, then transformed to a raster layer with resolution of 1 ha. The pixels assigned to rivers in the raster layer were given the value one (present), the same as for water bodies (Table 1). Vegetation was identified to seven classes from Landsat imagery. The seven vegetation classes and bare area were assigned values from zero (no vegetation) to seven (dense forest) to form the vegetation index (Table 1). Human impact in the GIS database was estimated on the basis of the distance to the center of the nearest village. The villages are composed of scattered farmer houses with diameters of about 1 km. We defined four impact levels according to the distance to the center of village (Table 1). The layers of vegetation and human impact were also transformed from polygon to raster with resolution of 1 ha. Elevation data were obtained from a digital elevation model (DEM) database owned by IOG.

The three ordinal variables (i.e. wetland, vegetation, and human impact) were treated as continuous variables. This type of data manipulation is very common, yet inappropriate in most cases (Jakobsson 2004). However, in our multiscale analysis, we only need a general estimation of the habitat variables using these indices, so that it is acceptable. In the scale-up process, the values of each variable were averaged (the most common treatment for scaling

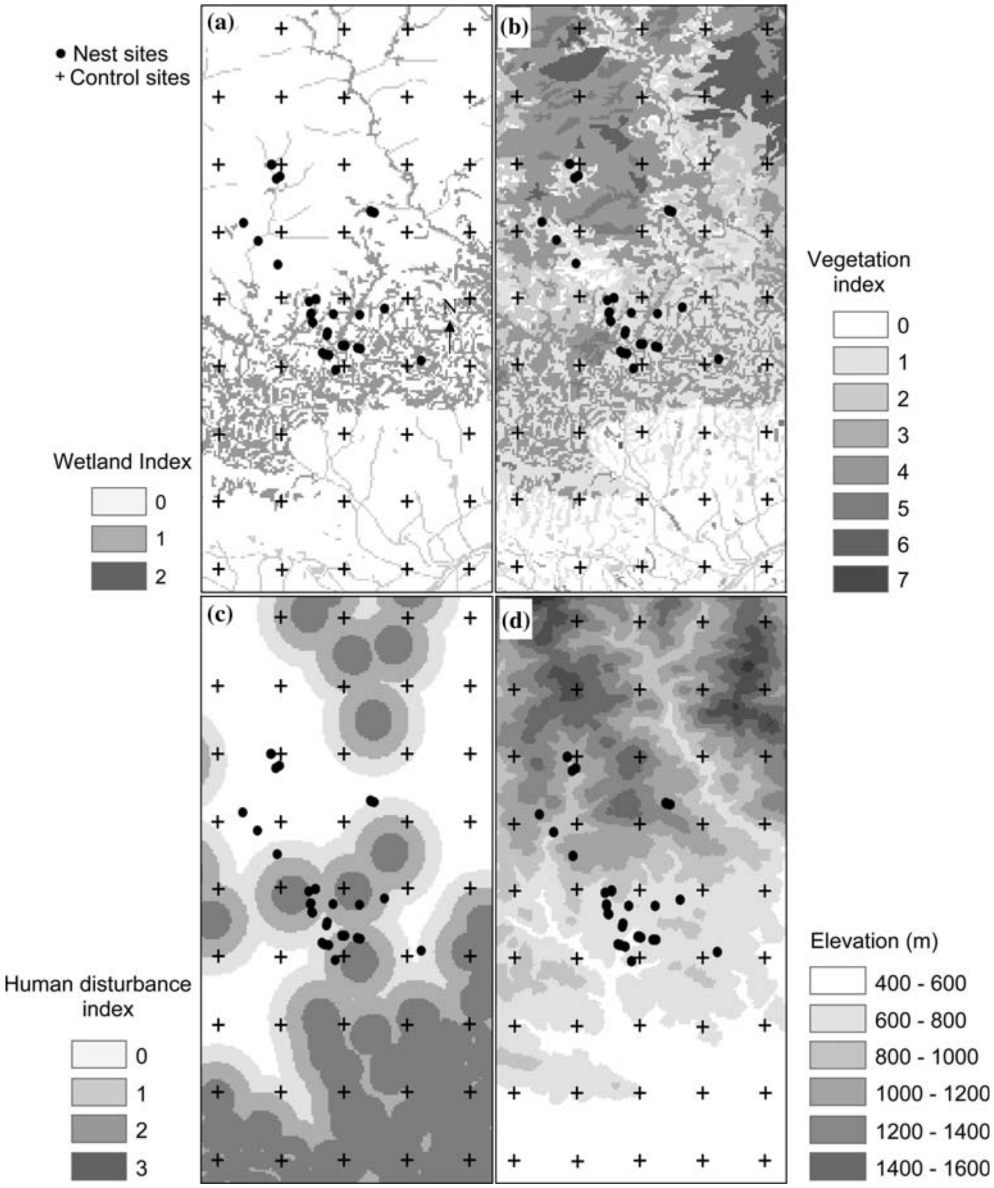

Fig. 2 The maps of nest sites and control sites, and four layers in the GIS database, i.e. (**a**) wetland index; (**b**) vegetation index; (**c**) human impact index; (**d**) elevation

(Jenkins et al. 2001; Ni 2003)) at contiguous quadrats to represent the variable values at larger grain sizes, so that all variables have continuous values at all scales.

Statistical and spatial analysis

We constructed a habitat suitability model by applying multiple logistic regression to the data from the 35 nest sites and 45 controls sites. The response variable was the odds of a site having a nest, where odds are calculated as $p/(1-p)$ and p is the proportion of sites having a nest. The statistical model was:

$$\text{Odds} = \exp(\beta_0 + \beta_1 \times X_1 + \beta_2 \times X_2 + \cdots + \beta_n \times X_n) + \text{error}$$

Table 1 The indices of habitat variables defined for regression analysis of crested ibis habitat use in the GIS database covering the area of Yang county, Shaanxi province, China

Habitat variables	Indices	Description
Wetland	0	Dried area
	1	Water body (lakes, reservoirs, and ponds) and river
	2	Rice paddy
Vegetation	0	Bare area
	1	Low grass land
	2	Middle grass land
	3	High grass land
	4	Forest such as orchard, tea garden, young growth forest, etc.
	5	Sparse forest (10% < coverage < 30%)
	6	Dense shrub (coverage > 40%)
	7	Dense forest (coverage > 30%)
Human impact	0	Distance to the center of village > 1500 m
	1	Distance to the center of village is from 1000 to 1500 m
	2	Distance to the center of village is from 500 to 1000 m
	3	Distance to the center of village is from 0 to 500 m

where n is the number of explanatory variables and error is consistent with a binomial distribution for p. The log of the odds is known as the logit transform of p.

To evaluate habitat suitability as a function of spatial scale we did multiple logistic regression at 13 grain sizes ranging from 1 to 6400 ha. At each grain size, the overall model fit was evaluated by the likelihood ratio test. The log transformation of the likelihood functions yields a chi-squared statistic, comparing the null hypothesis (no habitat variable included) with the full regression model. The overall model fit might change with scale, so that a characteristic scale of nest site selection could be identified. We further checked the significance of variable coefficient in the logistic regression model using a Wald chi-square test at each grain size, in order to detect the changes of contribution from each habitat variable in the scale-up process. Akaike information criteria (AIC) was used to remove insignificant variables from the multiple logistic regression model (SAS Institute Inc. 1999).

Mean values and variances of the habitat variables at the 35 nest sites and the 45 control sites were also computed at each grain size, in order to show the dynamics of variable statistics in the course of scale-up process. The difference in mean and variance between nest sites and control sites were checked using t-test and F-test, respectively (Sokal and Rohlf 1995).

To compare the spatial structure of nest sites with control sites we computed the semivariance of the four habitat variables as a function of lag (distance between every two samples). The semivariance is half the variance of the differences in variable values between all possible points spaced a distance apart, which can provide information of spatial autocorrelation and distribution pattern of a variable. The semivariogram is a plot of semivariance as a function of distance between the samples. We used the Geostatistical Analyst Extension in ArcGIS to plot the semivariograms. In this paper, semivariograms were produced individually for the four habitat variables at nest sites and control sites at two different grain sizes, 1 and 6400 ha.

Results

We investigated sensitivity to scale by comparing used to unused sites at resolutions ranging from 1 to 6400 ha based on four habitat variables. The goodness-of-fit of the four-factor habitat models decreased in the scale-up process (Fig. 3). Because of a complete separation of data points (i.e. independents completely predict the dependent, so that the error quadrants in the classification table will contain 0's, resulting in very large logit coefficients with very high standard errors) at grain size of 1 ha, the model fit statistics do not exist (SAS Institute Inc. 1999). In such circumstance, the model fit statistics reached the highest values at the grain size of 2 ha (Fig. 3).

Regarding to the effects of the four habitat variables, information explained by vegetation and elevation was substantially greater at the grain size of 2 ha than at

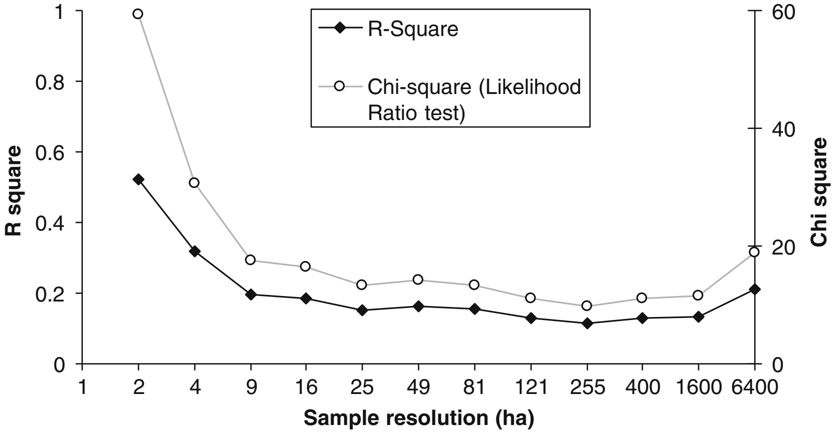

Fig. 3 The overall goodness-of-fit of logistic regression models for nest site selection of crested ibis regarding four habitat variables sampled at 13 grain sizes: the *R* square model fit statistics and the chi square of likelihood ratio test for the global null hypothesis. At grain size 1, there is a complete separation of data points, so that the maximum likelihood estimate does not exist (SAS Institute Inc. 1999)

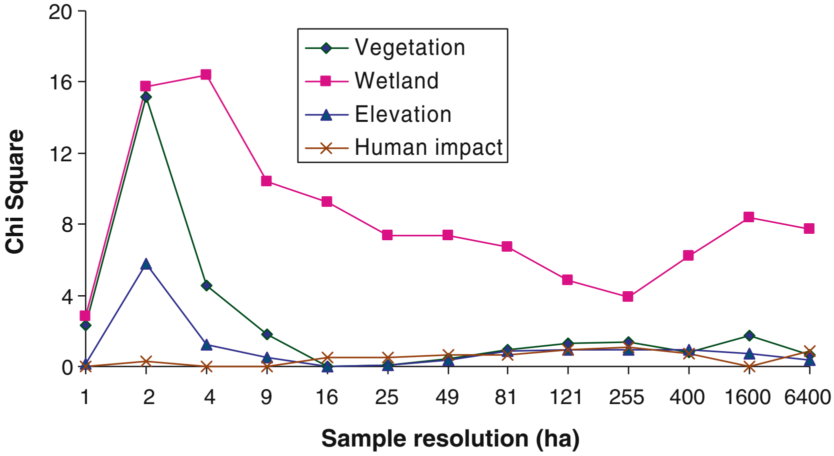

Fig. 4 The contribution (Wald chi square) of each of the four habitat variables to the logistic regression models for nest site selection of crested ibis when habitat variables were sampled at 13 grain sizes

1 ha or at larger grain sizes, and information explained by wetland peaked at grain size of 4 ha (Fig. 4). Wetland is the only variable that had significant effect on nest site use at all scales. Dependence on scale was very low for the index of human impact (Fig. 4). The best habitat suitability model was at grain size of 2 ha when the index of human impact was removed as judged from Akaike information criterion (AIC):

$$\begin{aligned}\text{Log(odds)} = & -1.5759 + 2.9383 \times \text{wetland index} \\ & + 1.4896 \times \text{vegetation index} - 0.0053 \\ & \times \text{elevation}\end{aligned}$$

Nest sites had significantly more wetland than control sites at all scales, and had significantly higher vegetation level at the grain size of 1 ha only (Fig. 5). Nest sites had less human impact and higher elevation than those of control sites without statistical significance (Fig. 5).

At a grain size of 1 ha the variances of the variables (except the human impact index) were significantly smaller at nest sites than at control sites (Fig. 5). The variance of wetland index at both nest sites and control sites decreased as grain size increased. The difference in variance between nest sites and control sites remained significant for vegetation

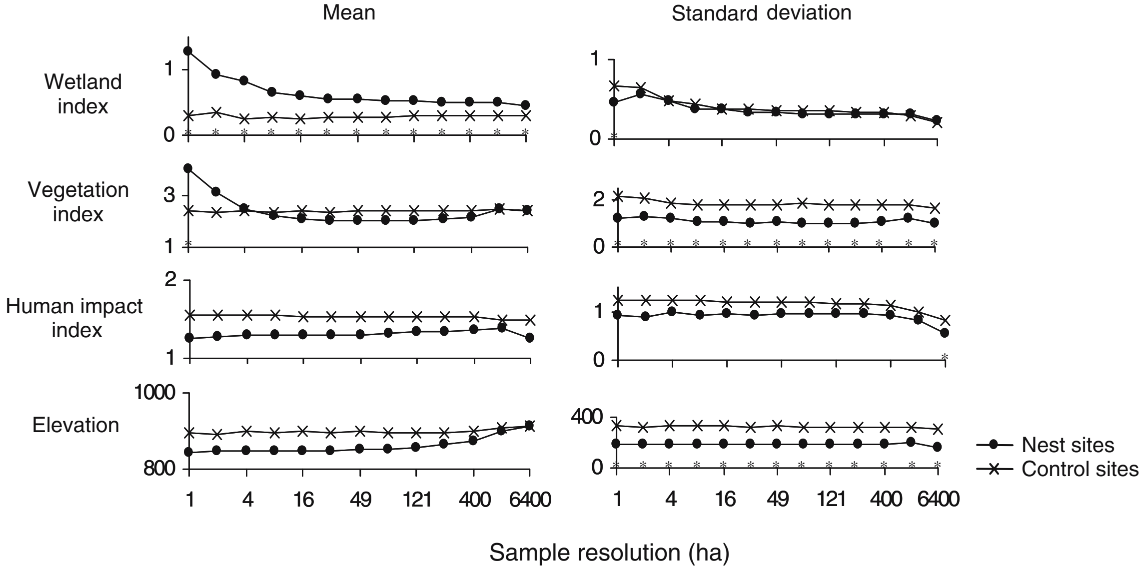

Fig. 5 The mean and standard deviation of wetland, vegetation, and human impact indices and elevation at 35 nest sites and 45 control sites at grain sizes from 1 to 6400 ha. The asterisks above abscissas indicate the differences between nest sites and control sites are significant at α level of 0.05 at the sample resolutions. *T*-test was used to test difference between means, and *F*-test was used to test difference between variance (Sokal and Rohlf 1995)

index and elevation at all scales, and it was just significant for human impact at grain size 6400 ha (Fig. 5).

Habitat spatial structure at control sites (3 km grid) did not follow the structure at nest sites. Spatial structure at control sites was stronger than that at nest sites as indicated by stronger patterns of change in semivariance with change in lag, especially for vegetation and elevation (Fig. 6). Spatial structure was more evident at larger than at smaller grain sizes. The semivariogram of the wetland index at control sites showed a bell-shaped distribution at grain size 6400 ha. The semivariance of vegetation and human impact indices at control sites increased with increasing lag at grain size 6400 ha. The semivariance of elevation at control sites increased with increasing lag at both scales (Fig. 6).

Discussion

Our multiscale analysis, as an effort to solve the MAUP of nest site selection of crested ibis, showed that the nest sites were associated with multiple habitat variables and this association was stronger at the scale of 2 ha (Figs. 3 and 4) than at a smaller scale (1 ha) or at larger scales (up to 6400 ha). This result stands in contrast to multiscale analysis of any one habitat variable, for which association increases monotonically with scale due to local decoupling (Schneider and Piatt 1986; Rose and Legget 1990; Veit et al. 1993; Schneider 1994). Studies of association with single variables are numerous (e.g. Schneider and Piatt 1986; Rose and Legget 1990; Veit et al. 1993; Schneider 1994) and have repeatedly shown that there is no characteristic scale of habitat selection, in the sense that association has no peak value at a particular scale. Our result for ibis, the first systematic analysis of multiple habitat variables as a function of scale, suggests that there may be a characteristic scale of habitat selection when multiple variables are considered. This may prove to be a general finding to the degree that organisms are forced to make tradeoffs in selecting habitat in relation to both large scale and local variables. The generality of our finding needs to be established with studies on other species.

We must note that the values of descriptive variables were averaged during the scale-up process, which means the increase of scale tends to move to the average of the region. When sum, variance, diversity, or maximum/minimum values of descriptive variables at different pixels of the landscape are used, the pattern of nest use might be different.

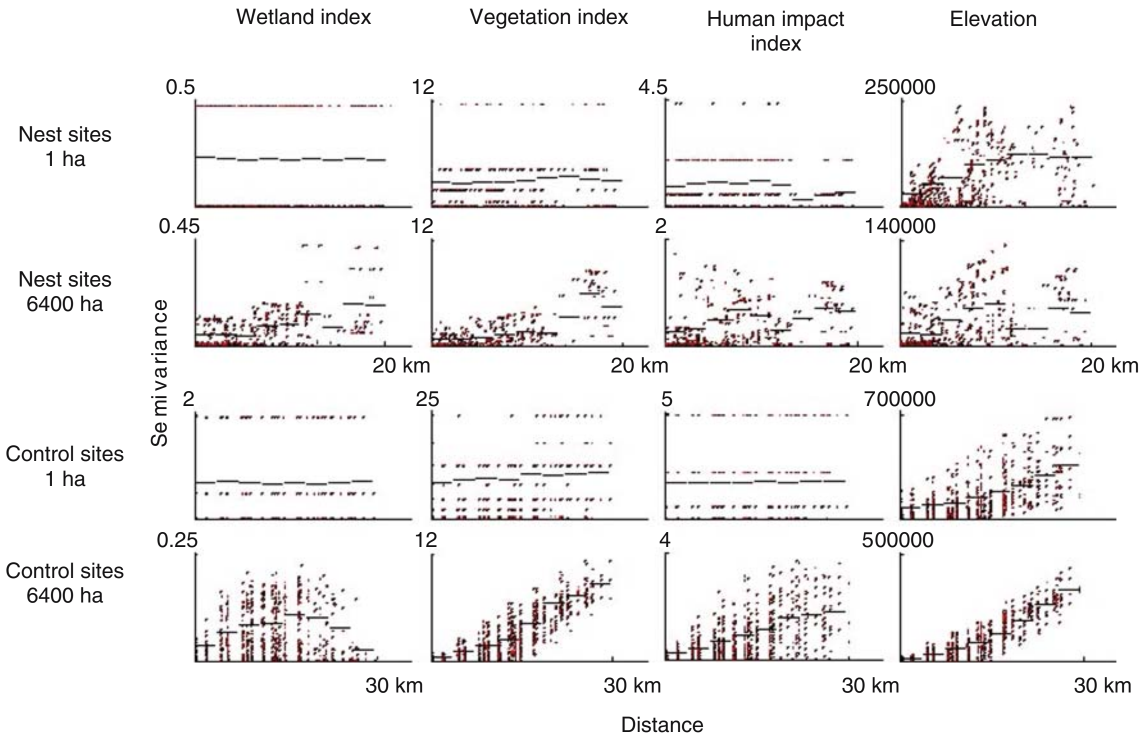

Fig. 6 Semivariogram of four habitat variables at nest sites and control sites at two grain sizes, 1 and 6400 ha. The bars indicate the average values of semivariance at certain extent of distance. The maximum distance between any two nests was 20 km, and any two control sites 30 km

Our results establish that multifactor models of habitat use depend on spatial scale. Consequently, an analysis carried out at a logistically convenient scale will likely not hold at other spatial scales. This dependence on scale together with variation in scale forced by logistics may explain much of the variation in model diversity found in the habitat literature. Dependence on spatial scale also means that important habitat variables can well go missing from a multifactor model constructed at a single scale. Increasing the spatial resolution of a survey does not guarantee a more informative habitat model, but our results are reassuring in that the most informative model was at a relatively fine scale.

Previous studies showed that ibis prefer habitat with high wetland availability and higher and denser trees (Wang et al. 1985; Zhai and Lu 1991; Shi et al. 1991b, 1991c; Wang 1993; Cao and Lu 1994; Li et al. 2001, 2002a; Ma et al. 2001). Our analysis extends this result, showing that wetland availability is important at a range of scales of analysis, whereas vegetation coverage/height loses its influence at scales other than 2 ha.

Elevation is considered an important variable in descriptive studies of crested ibis habitat (e.g. Wang et al. 1985; Zhai and Lu 1991; Shi et al. 1991c; Wang 1993; Li et al. 2001, 2002a; Ma et al. 2001). Crested ibis move north from elevations of 400–500 m to the breeding area at 680–1200 m above sea level in early spring, a seasonal pattern similar to migration of other species to breeding habitat at higher latitudes. However, in an analysis of nest site selection of the crested ibis using stepwise logistic regression, elevation did not appear to be significant in 11 habitat variables (Li et al. 2001), because of the correlation with other variables. In this paper, when a multiscale analysis was carried out on a multifactor model, elevation reappeared as important, consistent with descriptive studies and knowledge of seasonal migration.

The influence of human activity on nest site selection is complicated. Several studies have reported negative effects of human activity (e.g. Shi et al. 1991a; Cao and Lu 1994; Wang et al. 1995; Li and Li 1998), while other studies have reported positive effects (e.g. Li et al. 2001, 2002a, b; Ma et al. 2001). The relation of nest sites to human activity is tangled by the fact that crested ibis forage in rice paddies, which are located near villages. The previous study on nest site selection indicated that the odds of a site having a nest decreased with human activity (Li et al. 2001), whereas in this study the odds did not depend on human activity. This is due at least in part to the differences in how human activity was measured, either at the site (Li et al. 2001) or based on remotely sensed information (distance to the center of village) in this paper. This suggests that crested ibis select sites with moderate human activity at the landscape level (i.e. rice paddies), but low activity at the nest site level. Away from nesting sites crested ibis sometimes benefit from farmer's activities. We have often observed that crested ibis followed plowing cows to feed on worms exposed in overturned soil.

The importance of habitat structure for habitat use is well known (e.g. Cody 1981; Store and Jokimaki 2003). Our analysis showed that habitat structure and the relation of the crested ibis to that structure depends on scale of analysis. The dependence of semivariogram structure on grain size in our study is consistent with previous reports of the same phenomenon (Qi and Wu 1996; Fortin 1999; Anand and Li 2001). The patterns that emerged depended on the habitat variables. Variance in elevation increased with lag at small and large grain sizes. This likely reflects the presence of both gradients in elevation at all scales. The variance in vegetation index also increased with lag, but only at large grain sizes. This suggests that vegetation is tied to large scale patterns of elevation (as in Fig. 2). The variance in human activity increased with lag, but not as strongly as with vegetation; the human activity pattern was more evident at large than small scales. The growth in variance with lag may be due to larger scale structuring of human activity (villages clustered along rivers). Wetland showed a different pattern, that of an increase in variance only up to lags of 15 km. This reflects the absence of large scale structure or gradients in the map of wetland (primarily rice paddy), which is largely confined to a band in the middle of the study area (Fig. 2). We found that spatial structure was less defined for these habitat variables at the nest sites than at the control sites (Fig. 6). Our interpretation is that the crested ibis occupy narrow ranges of these habitat variables, relative to what is available in the region.

Our major finding was that the goodness-of-fit of a multifactor habitat use model depended strongly on grain size. In the case of the crested ibis, the goodness-of-fit peaked at a scale of 2 ha, less than the separation between nests. Consequently, multifactor models developed at one scale cannot be relied upon at other spatial scales when we evaluate the relative contribution of each variable to habitat use, estimate habitat suitability, or predict population density. Studies with other species will be needed to determine whether the goodness-of-fit of regression models peaks at a certain scale, as was the case in crested ibis.

For conservation of crested ibis, the contribution of our research was to reduce the uncertainty inherent in applying a habitat use model to new areas. Based on our results, the best habitat for reintroduction consists of a heterogeneous landscape with enough wetland, small stands of trees at preferred elevations, and acceptably low human impact near nests. Large area of forest is not necessary. The uncertainty in applying this model is least at the scale of 2 ha.

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