Scale-dependent habitat selection by reintroduced Eld's deer (*Cervus eldi*) in a human-dominated landscape

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Abstract

Context. Knowledge of the habitat selection of reintroduced species is crucial to successful re-establishment of viable populations and effective conservation decision-making.

Aims. The aim of our research was to examine habitat selection by reintroduced Eld's deer (*Cervus eldi*) in a human-dominated landscape.

Methods. The study was conducted during the period from July 2005 to November 2007 in the Chihao region, a human-dominated area located in western Hainan Island, China. Radio-telemetry was used to monitor 15 collared deer to gain their location information. Resource selection functions were used to quantify habitat selection of the study population at the landscape and home-range scales in both wet and dry seasons.

Key results. At the landscape scale, Eld's deer showed selection for habitats with scrubland, high elevation, gentle slope, close to water sources and roads. At the home-range scale, Eld's deer showed selection for habitats with dense forest, scrubland, grassland, low elevation and far away from roads, but they randomly used habitats without special consideration to the distance to water sources. At both landscape and home-range scales, Eld's deer showed strong avoidance of villages. In addition, Eld's deer showed increased selection of sparse forests and decreased use of grasslands in the dry season, as compared with the wet season at both spatial scales. Sexual differences in habitat selection existed in reintroduced Eld's deer. Males showed stronger avoidance to human disturbance, whereas females selected vegetation with higher forage availability but poor hiding cover, especially during the antler-growing period (i.e. wet season).

Conclusions. The habitat selection of reintroduced Eld's deer was scale-dependent. As a non-fatal anthropogenic factor, human disturbance had a strong influence on habitat selection of Eld's deer. They more strongly selected slope habitats at relatively high elevations. However, our results also indicated that the reintroduced Eld's deer had certain adaptive ability and tolerance to the disturbed environment.

Implications. This work provides insight into the habitat selection of reintroduced Eld's deer in a human-dominated landscape. If the essential food resources are available, the regions at a relatively high elevation with low human disturbance can be considered as potential sites of future Eld's deer reintroduction.

Additional keywords: *Cervus eldi*, Hainnan, human disturbance, reintroduction, resource selection function, scale.

Introduction

Reintroduction as a conservation tool can restore viable populations of endangered species within their historical ranges (Seddon *et al*. 2007). Because of effective reintroduction programs around the world, several reintroduced species have successfully established viable populations. A few good examples are the Arabian oryx (*Oryx leucoryx*) in United Arab Emirates (Kiwan *et al*. 2008), the sand gazelle (*Gazella leptoceros*) in Saudi Arabia

(Wacher and Robinson 2008) and the grey wolf (*Canis lupus*) in USA (Bangs and Smith 2008). However, most land surface of the Earth has been influenced by human activity (Sanderson *et al*. 2002). Human disturbance and limited suitable habitat are the biggest obstacles for successful reintroduction of endangered species in human-modified landscapes (Steury and Murray 2004). Regardless of the strategy used to establish viable populations, a reintroduction program would fail if the habitat at

the release location could not support the species (Seddon *et al.* 2007). The first key question is to understand what habitat conditions are needed for persistence of the reintroduced population (Armstrong and Seddon 2008). Therefore, in-depth investigation on the habitat selection of reintroduced species becomes crucial for making decisions about conservation and management planning (Seddon *et al.* 2007). The reintroductions of endangered species are assumed to be more successful when they are less affected by human disturbance and have more suitable habitat (Oakleaf *et al.* 2006; Kiwan *et al.* 2008).

Eld's deer (*Cervus eldi*) is an endangered cervid whose range formerly extended from the Manipur region of north-eastern India through much of Myanmar, Thailand, Laos, Cambodia and Vietnam to the Hainan Island of China (Timmin and Duckworth 2008). Over the past century, uncontrolled hunting and habitat loss have driven the deer population to collapse within most of its historic ranges (Zeng *et al.* 2005; Timmin and Duckworth 2008). For instance, the Hainan Eld's deer (*C. e. hainanus*) was once widely distributed in Hainan Island of China; however, by 1976, only 26 individuals remained in a 25-km^2 reserve, called the Datian Nature Reserve (Zeng *et al.* 2005). After 30 years of protection, the deer population in Datian Nature Reserve increased to over 1000 individuals (Zeng *et al.* 2005). The extremely high density of deer has led to starvation and habitat deterioration, and the news of saving the starved deer in the end of wet season have usually become headline news in the local media (Song and Li 1995). So as to preserve this endangered species and restore its wild populations, 131 deer from Datian Nature Reserve were released in 2005 into the Chihao region, a part of the historic range of the Eld's deer in Hainan Island. Unlike the reserves, this region is dominated by tropical dry forests, planted forests, farmlands, roads and interspersed villages, which represent a human-dominated landscape.

Disturbance by local people and limited suitable habitat are expected to be the biggest obstacles for successful reintroduction of Eld's deer, because the entire historic range of the Eld's deer in Hainan Island has been subjected to the rapid expansion of agriculture and an associated human population (Zeng *et al.* 2005). However, little information is available on habitat selection and behavioural response of Eld's deer in the human-dominated landscapes to guide restoration efforts because previous studies on Eld's deer were conducted in the reserves where little human disturbance existed (Song and Li 1994; Yuan *et al.* 1996; McShea *et al.* 2001). For example, in the Datian Nature Reserve, Eld's deer select for tropical dry forest and grassland habitats (Song and Li 1994; Yuan *et al.* 1996), whereas in South-east Asia, Eld's deer inhabit tropical dry forests with an open understorey and gently rolling terrain (McShea *et al.* 2001; Koy *et al.* 2005). A recent study showed that the translocated deer perceive human disturbance as a predation risk and become increasingly nocturnal from a normally crepuscular activity pattern (Pan *et al.* 2011). In the presence of humans, presumably it is unlikely for reintroduced Eld's deer to select open habitats (e.g. grasslands close to villages) because of perceived predation risk, and they are likely to select habitats far away from human disturbance. For successful reintroduction into human-dominated landscapes, it is necessary to better understand how Eld's deer may select habitat in human-dominated landscapes.

Habitat selection is scale dependent for many mammals (Anderson *et al.* 2005; Bowyer and Kie 2006; Ciarniello *et al.* 2007; Korte 2008; de Knegt *et al.* 2011). Some landscape attributes may be selected at one scale, whereas other characteristics of the environment may be selected at another (Bowyer and Kie 2006). Johnson (1980) first highlighted the hierarchical nature of habitat selection. Habitat selection is an inherently scale sensitive (Mayor *et al.* 2009). Scale influences the process of habitat selection, e.g. food resources are often selected at fine spatial scales, whereas landscape patterns at much larger scales typically influence the location of home ranges (Boyce 2006). Habitat-selection studies at different scales are conducive for understanding ecological processes of animal responses to the landscape. Resource-selection functions (RSFs) could explore the role of scale in determining patterns of habitat use (Boyce *et al.* 2003; Boyce 2006). We, thus, used RSFs to study and quantify the habitat selection of reintroduced Eld's deer at different scales.

Eld's deer is a medium-sized tropical deer with dimorphic body size; generally, adult males are >30% heavier than are adult females (Yu *et al.* 1984; Zeng *et al.* 2011). Historically, Eld's deer have inhabited the tropical plains and hills at altitudes lower than 200 m asl in Hainan Island, predominately vegetated with scrubland and grassland together with sparse trees on a gentle slope (Yu *et al.* 1984; Zeng *et al.* 2005). They consume primarily shrubs, forbs, grasses and agricultural crops (Song and Li 1992; Aung *et al.* 2001; McShea *et al.* 2001; Sun *et al.* 2009). The ratios of shrubs to grasses and forbs in their forages are 15.3% and 17.9% in the wet and dry seasons, respectively (Song 1997). In the Chihao region, natural vegetation is mostly distributed in the high-elevation areas, far from human disturbances, whereas vegetation at low elevations is modified by farmlands, roads and villages. Accordingly, we predicted that reintroduced Eld's deer would select the habitats at relatively high elevation and with low human disturbance.

Sexual habitat segregation occurs in most species of sexually dimorphic cervids (Barboza and Bowyer 2000; Apollonio *et al.* 2005; Loe *et al.* 2006; Long *et al.* 2009). Many hypotheses such as the predation-risk hypothesis and the gastrocentric hypothesis have been formulated to explain patterns of the sexual segregation (Barboza and Bowyer 2000; Loe *et al.* 2006). Because males are larger and presumably less vulnerable to predators, the predation-risk hypothesis postulates that males and females pursue different strategies of predator avoidance to maximise reproductive success, with females, particularly those with young, using relatively predator-safe habitats and males using habitats with a higher predation risk but better food quality (Bleich *et al.* 1997). Predator avoidance is a primary hypothesis for sexual segregation in cervids (Kie and Bowyer 1999; Apollonio *et al.* 2005; Oehlers *et al.* 2011). Female Eld's deer in central Myanmar are found more often in degraded forests and closer to crops than are males (McShea *et al.* 2001). However, sexual habitat segregation was not documented for the Eld's deer in Hainan, presumably because of the limited space in the Datian reserve. Being released to a larger area, the deer will be more likely to show their sexual differences in habitat selection. On the basis of the predator-risk hypothesis, we predicted that

females would select habitats with lower disturbance and denser cover, whereas males would use habitats with higher disturbance and higher forage availability.

We carried out the present field investigation to test for the above-mentioned two predictions, and to better understand the habitat selection of reintroduced Eld's deer. Our results could provide insight into the habitat conditions of reintroduced Eld's deer in a human-dominated landscape, and hence facilitate conservation-management decisions on future reintroduction programs of Eld's deer in Hainan Island and South-east Asia.

Materials and methods

Study area

The study area, Chihao region, was located in western Hainan Island, China (18°48′N–19°04′N, 108°47′E–109°01′E). The region covers an area of 383.2 km², with elevation ranging from 54 to 843 m (Fig. 1). The climate is hot and dry, with an annual mean temperature of 24.5°C. Monthly mean temperatures range from 18.2°C in January to 29.1°C in July. The area receives an annual mean rainfall of ~1000 mm, with a distinct wet season (July–November) and dry season (December–June).

The vegetation consists of tropical dry forests, planted forests, shrubs and grasslands, accounting for ~80% of total land in the Chihao region. The other land is occupied by villages, farmlands, reservoirs and roads. The tropical dry forests are dominated by *Albizzia procera*, *Lannea grandis*, *Phyllochlamys taxoides* and *Taxotrophis ilicifolius*. The planted forests consist of mangos and other economic trees (e.g. eucalypt and rubber trees). Some grasslands are used for cattle and sheep grazing. Farmlands consist generally of rice fields around the villages. Forest areas in flat or gentle slopes have been converted into croplands for growing bananas. Because of prevalent anthropogenic land uses, tropical dry forests with high canopy cover remain only in high-elevation areas that are far away from villages. In contrast, planted forests, shrubs and grasslands are mostly distributed in low-elevation areas. In the study area, dense forest (canopy >30%) is more likely found in tropical dry forests, and sparse forest (canopy <30%) is more likely found in planted forests. There are no predators for the reintroduced Eld's deer in this natural ecosystem, and >25 000 residents are scattered in 38 villages in the study area. People represent a threat to the deer because of long-term impacts of historical poaching on the deer population in Hainan Island (Zeng *et al.* 2005). The density of human population is 65 residents per km², and the road density is 1.16 km per km². Three small artificial reservoirs provide water resources here for the local people.

Animal data

We captured 131 adult Eld's deer by using nylon-cord net from March through July 2005 in Datian Nature Reserve, and released them into the Chihao region. Among these released individuals, we fitted 15 deer with radio-collars (two males and two females wore MOD-335, frequency 150–152 MHz, Telonics Inc., Mesa, AZ, USA; five males and six females wore SMRC-1, frequency 151–152 MHz, Lotek Wireless Inc., Newmarket, Ontario, Canada). We mostly monitored the collared deer from 0500 hours to 2000 hours each day, by using a three-element hand-held Yagi antenna and a portable receiver (Telonics Inc.), and obtained locations by the triangulation method (Loft and Kie 1988). The rate of deer activity (foraging or moving) was ~17% during the monitoring period (Pan *et al.* 2011). We took three strong signal bearings from different towers to form an error polygon and considered the centre of the polygon as the location of the animal. Only when the error polygon was smaller than 0.5 ha did we retain the data. With the same
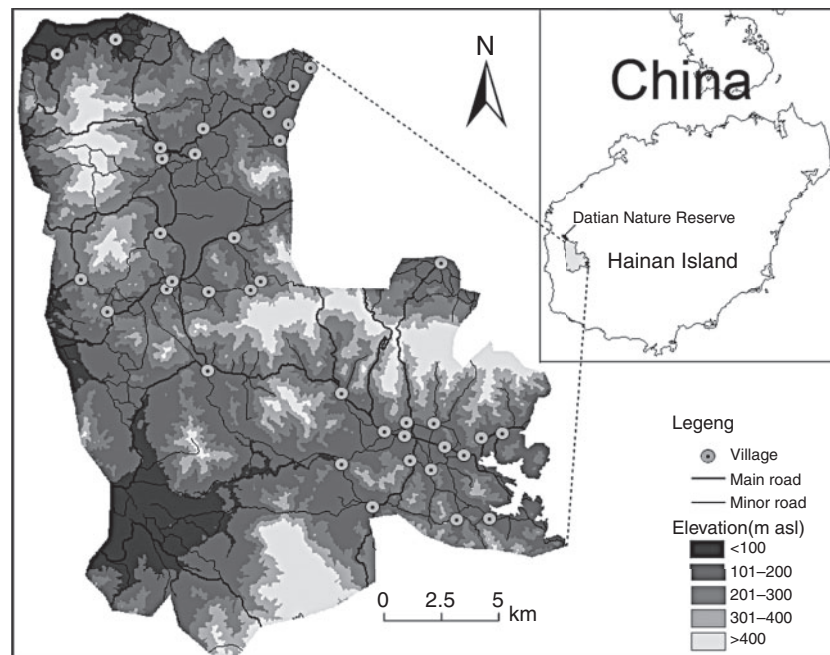

Fig. 1. Digital elevation model (DEM) and the location of the Chihao region in Hainan Island, China.

telemetry techniques, we located test collars to estimate telemetry error. We compared estimates of universal transverse mercator (UTM) coordinates from telemetry data with the actual UTM coordinates of test-collar locations to determine an error distribution. The mean error for telemetry location was 28 m (s.e. = 2, $n = 60$). We located each collared deer 1–3 times per week from July 2005 to November 2007. From 15 collared deer, we totally gathered 1619 telemetry locations, in which any two locations from one individual were at least 3 days apart. Among the 1619 locations, 818 locations ($n = 391$ in 2005, 349 in 2006, 78 in 2007) were in the wet season and 801 locations ($n = 95$ in 2005, 585 in 2006, 121 in 2007) were in the dry season. The monitored individuals did not show a clumped distribution in the study area. We used 100% minimum convex polygon (MCP) method to form and calculate individual's home ranges by its multi-year locations.

Habitat variables

Habitat variables consisted of three types, including land cover, terrain and human disturbance. We identified seven land-cover types in the study area, including dense forest (canopy >30%), sparse forest (canopy <30%), shrub (tree height <2 m), grassland, farmland, village and water body. According to the methods of Lay (2005), we used the supervised classification to develop land-cover layers from remote-sensing images, and first collected 40 ground-training samples for each land-cover type by using GPS during the study period from 2005 to 2007. We then developed the land-cover map by using the Landsat TM images ($30 \times 30 \text{ m}^2$ per pixel) acquired in August 2008 by the China Remote Sensing Satellite Ground Station. We performed CART decision tree classification algorithms with ENVI 4.7 to produce the seven classification categories (kappa coefficient of classification accuracy was 0.85). We calculated elevation and slope from a 30-m digital-elevation map (DEM) that was obtained from the State Bureau of Surveying and Mapping of China. We defined human disturbance as the distance to the edge of villages and roads from animal locations. We digitised roads from a 1 : 50 000 topographic map. We also distinguished the paved roads connecting towns and villages, and the unpaved roads being used by the local villagers for agricultural activities. The paved and unpaved roads were, respectively, considered as main and minor roads according to vehicle flow. We used random-point generator in ArcGIS (version 1.3, www.jennessent. com/arcview/random_points.htm, verified 9 November 2009) to generate random locations, and obtained the data on vegetation, elevation and slope of the telemetry or random locations by overlaying them on 30-m resolution raster grid maps in ArcGIS 9.3. We also calculated the nearest distances (m) to the village edges, the main roads, the minor roads and the water sources from the telemetry or random locations. We regarded the telemetric animal locations as the used habitat sites and the random locations as available habitat sites by Eld's deer.

Analysis of habitat selection

We developed RSFs to analyse habitat selection by Eld's deer at two extents in resource availability, namely landscape scale and home-range scale.

Landscape-scale design

The landscape was defined by the extent of the study area. We examined habitat variables predicting where reintroduced Eld's deer established their home range at the landscape scale. Individual animals were not identified at this scale. The intensity of random locations across the landscape was 100 locations per km². We pooled animal locations across individuals for the landscape analysis. We used standard logistic regression to construct RSF models at the landscape scale (Manly *et al.* 2002).

Home range-scale design

The home-range scale was defined for each individual animal from that animal's use of space. At this scale, we explored what reintroduced Eld's deer were selecting within their home ranges. Availability was drawn only from each deer individual's 100% MCP home range. The intensity of sampling random locations was also 100 locations per km², and the number of random locations varied with the size of the individual's home range. We used conditional logistic regression to construct RSF models at the home-range scale (Compton *et al.* 2002).

The habitat variables elevation, slope, and distance to villages were assumed to follow Gaussian distribution at the landscape scale. We thus used the following standard exponential equation for estimating a RSF, but included squared terms at the landscape scale and not the home-range scale:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_1^2 + \beta_3 x_2 \cdots \beta_i x_p),$$

where β_i is selection coefficient estimated using logistic regression analysis for each p variable, x_i, for $i = 1, 2, \ldots, p$ (Johnson *et al.* 2006). Telemetry locations of the Eld's deer were the used sites (1), and randomly generated locations were the available sites (0). When $\beta_i > 0$, use by Eld's deer was occurring more than would be expected if simply in proportion to availability, and when $\beta_i < 0$, use was occurring less than would be expected if simply in proportion to availability.

We used the following two procedures for evaluating the effects of scale on our RSF designs: (1) comparisons between the ranks of five candidate models and (2) comparisons within one candidate model. In the first procedure, we chose five *a priori* candidate models that we deemed biologically relevant to the habitat use of Eld's deer (Anderson *et al.* 2000; Burnham and Anderson 2002) (Table 1). Inclusion of variables in the candidate models was based on field knowledge and published literature on the habitat selection by Eld's deer (Song and Li 1994; Aung *et al.* 2001; McShea *et al.* 2001, 2005; Koy *et al.* 2005). We also screened habitat variables for collinearity, and did not adopt them in the same model if the correlation was ≥0.6. Within each scale of analysis, we ranked these five candidate models on the basis of Akaike's information criterion (AIC) to identify the most ecologically meaningful model (Burnham and Anderson 2002). We calculated AIC differences (Δ_i) and weights (w_i) for each candidate model. The low w_i value of the chosen model suggested that it might not be the best model. The smaller the Δ_i value was, the better the model would be (Burnham and Anderson 2002). We also accepted that models were considered comparable if Δ_i values were <2.0 (Burnham and Anderson 2002).

In the second procedure, we used the selected model to examine the effects of scale by comparing the coefficients

Table 1.   Five *a priori* candidate models for reintroduced Eld's deer habitat selection in the Chihao region, Hainan Island, China

Model	Variables in the model
I	Shrub + Dense forest + Sparse forest + Grassland
II	Shrub + Dense forest + Sparse forest + Grassland + Elevation + ^{A}Elevation^2 + Slope + ^{A}Slope^2
III	Shrub + Dense forest + Sparse forest + Grassland + Elevation + ^{A}Elevation^2 + Slope + ^{A}Slope^2 + Distance to water
IV	Shrub + Dense forest + Sparse forest + Grassland + Elevation + ^{A}Elevation^2 + Slope + ^{A}Slope^2 + Distance to village + ^{A}Distance to village^2 + Distance to main road + Distance to minor road
V	Shrub + Dense forest + Sparse forest + Grassland + Elevation + ^{A}Elevation^2 + Slope + ^{A}Slope^2 + Distance to water + Distance to village + ^{A}Distance to village^2 + Distance to main road + Distance to minor road

^{A}Adding squared terms to the candidate models accommodated Gaussian distribution of these variables (i.e. elevation, slope and distance to villages) at the landscape scale, but only linear terms at the home-range scale.

Table 2.   Akaike's information criterion (AIC) differences (Δ_i) and weights (w_i) for the candidate models of resource-selection functions analysing habitat selection of reintroduced Eld's deer in the Chihao region, Hainan Island, China

Model	Landscape						Home range					
	Wet season			Dry season			Wet season			Dry season		
	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i	AIC	Δ_i	w_i
V	5770.2	0.0	1.0	6012.1	0.0	1.0	11065.2	0.6	0.4	10878.6	1.4	0.3
IV	6185.8	415.6	0.0	6471.5	459.4	0.0	11064.6	0.0	0.6	10877.2	0.0	0.7
III	6018.7	248.5	0.0	6286.5	274.4	0.0	11129.5	64.9	0.0	10939.4	62.2	0.0
II	6423.6	653.4	0.0	6739.2	727.1	0.0	11130.3	65.7	0.0	10937.5	60.3	0.0
I	7057.8	1287.6	0.0	7298.7	1286.6	0.0	11148.5	83.9	0.0	10957.1	79.9	0.0

across scales. Because the number of random locations varied between designs, we could not use the AIC scores to rank models. Therefore, to account for difference in sampling intensity, we evaluated models using five-fold cross-validation (Boyce *et al.* 2002; Hastie *et al.* 2009). For each data fold, we estimated a model using 80% of the data, withholding 20% for evaluation. Then, we contrasted predictions of this model with the frequency of locations in the with-held test data distributed across 10 bins. To assess the prediction of the model, we calculated a Spearman's rank correlation (r_s) between the frequency of test-set locations and bin rank. We repeated this process five times, using each 20% at a test set. Then, we averaged the five rank correlations ($\bar{r}_s$) (Boyce *et al.* 2002).

Moreover, we used Student's *t*-tests for two independent samples to examine sexual differences of numeric habitat variables, including the distances (m) to villages, main roads and minor roads. Differences were considered significant at $\alpha < 0.05$

Results

Habitat-selection patterns of reintroduced Eld's deer were dependent on the scale examined (Table 2). At the landscape scale, the habitat selection by Eld's deer was best predicted by Model V that contained all variables (i.e. shrub, dense forest, sparse forest, grassland, elevation, elevation^2, slope, slope^2, distance to water, distance to village, distance to village^2, distance to main road, distance to minor road). At the home-range scale, Model IV, which did not include the water-source variable, ranked first, but the Δ_i value for Model V was also <2.0, suggesting that Model V was also comparable at this scale. Therefore, we chose Model V to compare across scales. On the basis of five-fold cross validation, we could discern that

Model V had high predictive capability at the landscape and home-range scales (Table 3).

For reintroduced Eld's deer, selection varied depending on the scale of available habitats (Table 3). Eld's deer selected shrub habitats at two scales, and showed stronger selection for shrubs at the landscape scale ($\beta = 1.569$ in the wet season, $P < 0.001$; $\beta = 1.534$ in the dry season, $P < 0.001$) than the home-range scale ($\beta = 0.802$ in the wet season, $P < 0.001$; $\beta = 0.616$ in the dry season, $P < 0.05$). Eld's deer did not select dense forest and grassland habitats at the landscape scale, but selected them when availability was restricted to the home-range scale (Table 3). They decreased the use of grasslands in the dry season, compared with the wet season at two scales. In addition, Eld's deer showed selection for sparse forest habitats at the landscape ($\beta = 0.350$, $P < 0.05$) and home-range ($\beta = 0.635$, $P < 0.05$) scales in the dry season.

Eld's deer selected habitats with high elevation at the landscape scale ($\beta = 0.092$ in the wet season, $P < 0.001$; $\beta = 0.072$ in the dry season, $P < 0.001$), whereas they showed selection for habitats at low elevation at the home-range scale ($\beta = -0.008$ in the wet season, $P < 0.001$; $\beta = -0.005$ in the dry season, $P < 0.001$; Table 3). The overall preferred elevations were, however, still <400 m, and the most selected elevation was ~200 m at the landscape scale (Fig. 2*a*).

Eld's deer selected slope habitats at two scales (Table 3). The most selected slope was ~10° (Fig. 2*b*). At the landscape scale, Eld's deer inhabited gentler slopes in the dry season than in the wet season; the overall preferred slopes were <25° in the wet season, but decreased to <20° in the dry season (Fig. 2*b*).

Eld's deer mostly selected habitats at a distance of 1.0–3.0 km to villages (Fig. 2*c*). The distance with the maximum RSF value was ~2.0 km at the landscape scale. The deer selected habitats far away from villages at the home-range scale (Table 3). In addition,

Table 3.   Resource-selection functions (RSFs) at two spatial scales in two seasons for reintroduced Eld's deer in the Chihao region, Hainan Island, China
The asterisk indicates that β (RSF coefficient) is significantly different from 0 on the basis of a Wald statistic: *$P < 0.05$, **$P < 0.001$

Variable	Landscape				Home range			
	Wet season		Dry season		Wet season		Dry season	
	β	s.e.	β	s.e.	β	s.e.	β	s.e.
Shrub	1.569**	0.157	1.534**	0.169	0.802**	0.155	0.616*	0.167
Dense forest	−0.138	0.166	0.328	0.173	0.623*	0.169	1.034**	0.176
Sparse forest	−0.096	0.172	0.350*	0.178	0.222	0.170	0.635*	0.174
Grassland	0.384	0.300	0.076	0.376	1.694**	0.301	1.046*	0.377
Distance to water	−1.181**	0.070	−1.202**	0.068	0.117	0.096	−0.075	0.096
Elevation	0.092**	0.008	0.072**	0.007	−0.008**	0.001	−0.005**	0.001
Elevation^2	-2.2×10^{-4}**	1.9×10^{-5}	-1.7×10^{-4}**	1.5×10^{-5}	A	A	A	A
Slope	0.068**	0.017	0.035*	0.015	0.021**	0.006	0.022*	0.006
Slope^2	−0.003**	0.001	−0.002*	0.001	A	A	A	A
Distance to village	2.321**	0.201	2.275**	0.189	0.579**	0.093	0.583**	0.091
Distance to village^2	−0.554**	0.064	−0.536**	0.057	A	A	A	A
Distance to main road	−0.422**	0.061	−0.434**	0.059	0.278*	0.102	0.223*	0.101
Distance to minor road	−0.450**	0.123	−0.433**	0.121	0.137	0.146	0.038	0.148
k-fold ($\bar{r}_s$)	0.964**		0.988**		0.976**		0.964**	
n	38 557		38 542		16 059		16 044	

^{A}Linear term only.

Eld's deer selected habitats close to the main and minor roads at the landscape scale, but avoided habitats close to these roads at the home-range scale (Table 3).

Eld's deer showed selection for habitats closer to water sources at the landscape scale in both wet and dry seasons (Table 3). However, at the home-range scale, the deer randomly used habitats without special consideration of the distance to water sources, although the data showed that Eld's deer were apt to use habitats closer to water in the dry season (Table 3).

Eld's deer showed sexual differences in habitat selection (Tables 4, 5). Males showed stronger avoidance of human disturbance than did females. In the wet season, males selected habitats closer to minor roads than did females at the landscape scale, but selected habitats farther from main roads at the home-range scale (Table 4). In the dry season, females selected habitats farther from minor roads than did males at the two scales, but males selected habitats farther from main roads than did females at the home-range scale (Table 5). The distances to villages ($t = 9.445$ in the wet season, $P < 0.001$; $t = 8.939$ in the dry season, $P < 0.001$) and to main roads ($t = 12.662$ in the wet season, $P < 0.001$; $t = 13.155$ in the dry season, $P < 0.001$) were significantly longer for males than for females, whereas the distance to minor roads for males was significantly shorter than that for females ($t = -9.103$ in the wet season, $P < 0.001$; $t = -10.531$ in the dry season, $P < 0.001$).

Sexual segregation existed in habitat selection for vegetation types. In the wet season, contrary to males, females selected grasslands ($\beta = 0.829$, $P < 0.001$) and avoided dense forest ($\beta = -0.916$, $P < 0.001$) and sparse forest ($\beta = -0.676$, $P < 0.001$) at the landscape scale; when restricted to the home-range scale, sexual differences in habitat selection were selection by females for grasslands ($\beta = 1.914$, $P < 0.001$) and shrubs ($\beta = 1.124$, $P < 0.001$) and by males for dense forests ($\beta = 0.479$, $P < 0.05$; Table 4). In the dry season, Eld's deer did not show sexual segregation in its selection of the vegetation type

at the landscape scale; however, at the home-range scale, males randomly used vegetation according to its availability, whereas females selected for shrubs, dense forests, sparse forests and grasslands (Table 5).

Discussion

Previous studies have demonstrated the role of scale in habitat selection by cervids as well as other mammals (Bowyer and Kie 2006; Mayor *et al.* 2009; de Knegt *et al.* 2011; Oehlers *et al.* 2011). Animals may select different habitat components at different scales (Mayor *et al.* 2009). Our study further indicated that the patterns of habitat selection of the reintroduced Eld's deer vary across spatial scales. As we expected, these animals selected habitats at a relatively high elevation and with low human disturbance. At the landscape scale, they selected areas at a relatively high elevation when establishing their home range, and at the home-range scale, they selected habitats at a low elevation and far from human disturbance. These results fill a knowledge gap on how Eld's deer select their habitats at different scales in human-disturbed environments.

Eld's deer in Datian Nature Reserve inhabit vegetation-covered areas with gentle slope and low elevation (30–80 m asl) (Song and Li 1994). In the study area, reintroduced Eld's deer had to face the situation that human disturbance was ubiquitous at low elevations, and their movement was blocked by anthropogenic factors such as villages and roads. Generally, ungulates avoid roads at the landscape scale (Rowland *et al.* 2000; McCorquodale 2003; Anderson *et al.* 2005). However, at a large scale, proximity to roads became unavoidable for the reintroduced deer. Therefore, these deer had to select habitats at a relatively high elevation and away from human settlements at the landscape scale, although roads were present at their present extent. In contrast, at the home-range scale, the reintroduced Eld's deer always kept a distance from habitats closer to villages and roads, so as to avoid human disturbances. In
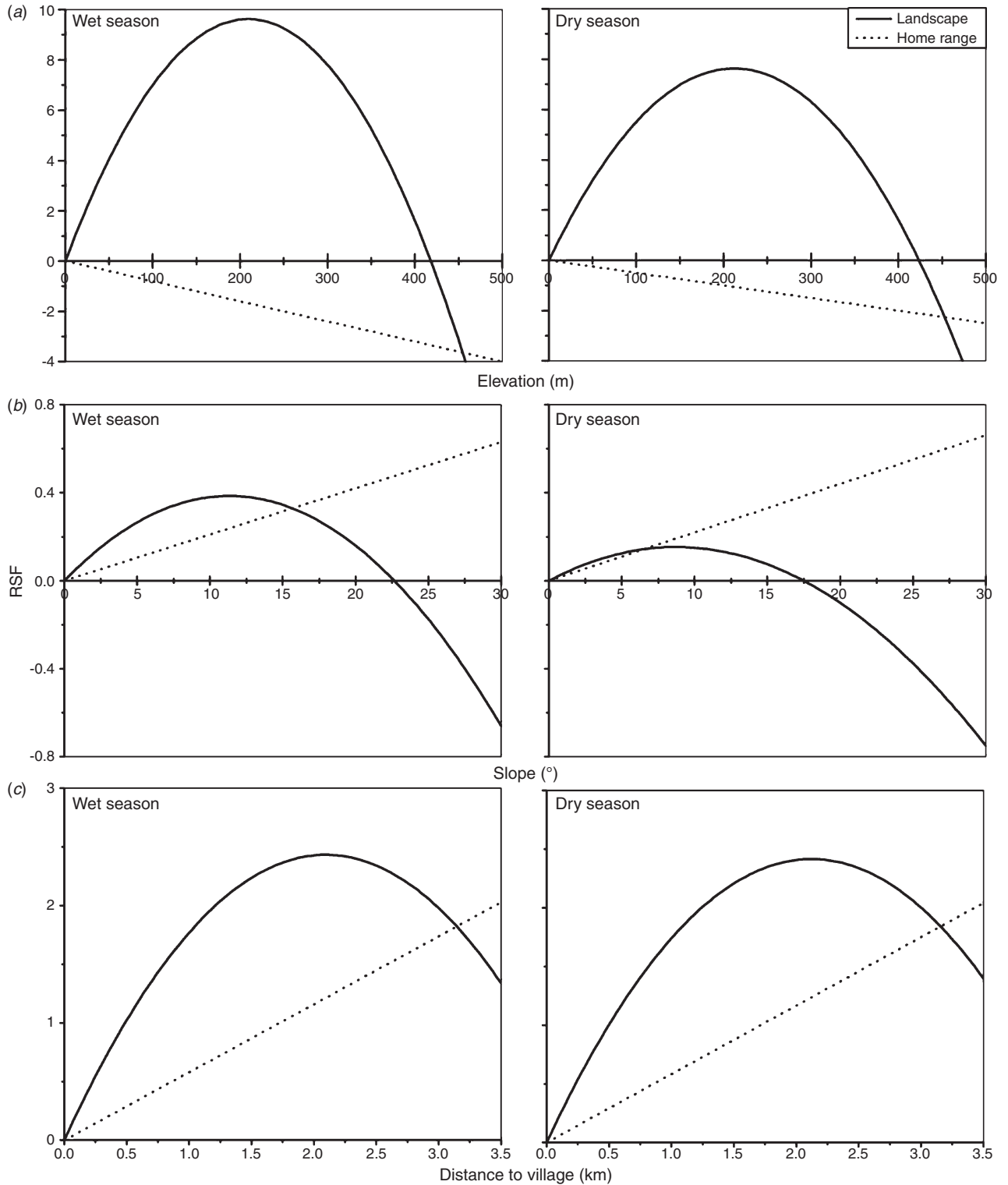
Fig. 2. The relative probability of occurrence for reintroduced Eld's deer as a function of (*a*) elevation, (*b*) slope and (*c*) distance to villages in the wet and dry seasons, while holding other variables in the model constant. Elevation, slope and the distance to villages were modelled with squared term at the landscape scale, thus yielding a quadratic relationship. Each function had a zero-intercept relative resource-selection function (RSF). The solid and dashed lines represent the probability at the landscape and home-range scales, respectively.

Table 4.   Resource-selection functions (RSFs) at two spatial scales in the wet season for habitat selection by reintroduced male and female Eld's deer in the Chihao region, Hainan Island, China

The asterisk indicates that β (RSF coefficient) is significantly different from 0 on the basis of a Wald statistic: *$P < 0.05$, **$P < 0.001$

Variable	Landscape				Home range			
	Male		Female		Male		Female	
	β	s.e.	β	s.e.	β	s.e.	β	s.e.
Shrub	1.617**	0.234	1.462**	0.206	0.346	0.229	1.124**	0.208
Dense forest	0.346	0.239	−0.916**	0.240	0.479*	0.241	0.376	0.248
Sparse forest	0.277	0.243	−0.676**	0.256	0.167	0.240	0.037	0.254
Grassland	−0.875	0.747	0.829**	0.344	0.819	0.759	1.914**	0.348
Distance to water	−1.136**	0.089	−1.186**	0.106	0.146	0.131	−0.039	0.147
Elevation	0.077**	0.009	0.117**	0.015	−0.006**	0.002	−0.008**	0.002
Elevation^2	-1.8×10^{-4}**	2.2×10^{-5}	-2.8×10^{-4}**	3.5×10^{-5}	A	A	A	A
Slope	0.054*	0.021	0.095**	0.026	0.016*	0.008	0.028**	0.009
Slope^2	−0.002*	0.001	−0.004**	0.001	A	A	A	A
Distance to village	3.135**	0.286	1.834**	0.344	0.562**	0.142	0.447**	0.133
Distance to village^2	−0.725**	0.086	−0.538**	0.129	A	A	A	A
Distance to main road	−0.169*	0.067	−1.016**	0.121	0.506**	0.141	−0.106	0.162
Distance to minor road	−1.231**	0.184	0.322	0.165	−0.024	0.229	0.246	0.191
k-fold ($\bar{r}_s$)	0.867*		0.964**		0.879*		0.939	
n	38 191		38 106		6060		9999	

^{A}Linear term only.

Table 5.   Resource-selection functions (RSFs) at two spatial scales in the dry season for habitat selection by reintroduced male and female Eld's deer in the Chihao region, Hainan Island, China

The asterisk indicates that β (RSF coefficient) is significantly different from 0 on the basis of a Wald statistic: *$P < 0.05$, **$P < 0.001$

Variable	Landscape				Home range			
	Male		Female		Male		Female	
	β	s.e.	β	s.e.	β	s.e.	β	s.e.
Shrub	1.664**	0.243	1.338*	0.229	0.327	0.237	0.742**	0.232
Dense forest	0.447	0.247	0.117	0.240	0.441	0.249	1.498*	0.247
Sparse forest	0.454	0.248	0.111	0.249	0.354	0.245	0.733*	0.250
Grassland	−1.369	1.030	0.637	0.422	0.279	1.040	1.217*	0.426
Distance to water	−1.177**	0.089	−1.197**	0.099	−0.054	0.130	−0.098	0.151
Elevation	0.071**	0.008	0.072**	0.010	−0.002	0.002	−0.008**	0.002
Elevation^2	-1.6×10^{-4}**	1.9×10^{-5}	-1.7×10^{-4}**	2.5×10^{-5}	A	A	A	A
Slope	0.028	0.020	0.055**	0.023	0.013	0.008	0.035**	0.009
Slope^2	−0.001*	0.001	−0.002**	0.001	A	A	A	A
Distance to village	3.364**	0.290	1.349**	0.278	0.715**	0.137	0.402*	0.133
Distance to village^2	−0.756**	0.084	−0.390**	0.094	A	A	A	#
Distance to main road	−0.198**	0.067	−1.044**	0.120	0.347*	0.138	0.165	0.1429
Distance to minor road	−1.488**	0.192	0.591**	0.160	−0.437	0.229	0.199*	6.3596
k-fold($\bar{r}_s$)	0.939**		0.976**		0.939**		0.903*	
n	38 196		38 086		6065		9979	

^{A}Linear term only.

Cambodia, the Eld's deer was also consistently present at locations away from human settlements and roads (McShea *et al.* 2005). Our results indicated that these deer had an ability to adjust their strategy of habitat selection at different scales and to tolerate human disturbance in the process of settling in a new environment. A similar result was reported in the case of reintroduction of elk (*Cervus elaphus nelsoni*) in Wisconsin, USA, where these animals showed tolerance to disturbances at a fine spatial scale (Anderson *et al.* 2005).

Habitat selection by the reintroduced Eld's deer in the dry season also showed their adaptation and tolerance to the disturbed environment. Compared with the wet season, the deer were increasingly selecting sparse forests and decreasingly using grasslands in the dry season. In contrast, Eld's deer are known to select forests, shrubs or grasslands in both seasons in Datian Nature Reserve (Song and Li 1994). This seasonal difference in habitat selection may be explained by a strategy of trade-off between avoiding human disturbances and seeking forages in human-dominated landscapes. In the dry season, variety and quantity of food for Eld's deer decreases, and foraging availability thus becomes a strong factor influencing habitat selection (Song and Li 1992; Song 1997). The sparse

forests mostly consisted of mango forests and other planted forests in the study area. The understorey, which was a source of grass forage for the reintroduced Eld's deer, underwent regular disturbances from human activities. Thus, the deer had to endure a certain degree of disturbance to obtain forages in the sparse forests in the dry season.

As a non-fatal anthropogenic factor, human disturbance produced a strong influence on the habitat selection by Eld's deer. First, the reintroduced Eld's deer changed their preferred habitats, presumably because of the human disturbance. Grasslands provide much higher biomass of forbs and grasses for Eld's deer (Song and Li 1992), and Eld's deer are known to select grasslands and shrubs in Datian Nature Reserve where there is no human disturbance (Song and Li 1994). By contrast, the reintroduced Eld's deer selected shrubs rather than grasslands at the landscape scale, because grasslands were available only in conditions of poor shelter and were mostly distributed in the disturbed regions in the Chihao region.

Second, the reintroduced Eld's deer explored slope habitats at relatively high elevations, so as to minimise human disturbance. They showed a similar selection towards vegetation types, but different selection in regard to terrain, compared with their counterparts in the Datian reserve and their historical ranges (Yu *et al*. 1984; Song and Li 1994; Zeng *et al*. 2005). Reintroduced Eld's deer inhabited higher elevations at the landscape scale, and accordingly, utilised habitats with steeper slopes at the home-range scale. This altered habitat use probably resulted from a trade-off between the need to avoid human disturbance and the need to seek out areas of suitable forage availability. Potential habitats on gentle slopes and at low elevation were encroached by farmlands and planted forests in the study area. Thus, the reintroduced species inhabited areas far away from villages and roads at the home-range scale, and had to utilise forage resources and slope habitats at high elevations.

Third, the presence of people kept the reintroduced deer away from areas close to water sources during daytime. Most animals need free-standing water to successfully occupy a location (Morrison *et al*. 2006). Water is an essential resource for the Eld's deer to survive in their nature habitat, especial in the dry season (Yuan *et al*. 1990). Local people have created three pools to hold water, delivering from a reservoir to solve the problem of water shortage in the dry season when the seasonal creek passing by dries up for Eld's deer in the Datian reserve (Yuan *et al*. 1990). After being released to the Chihao region, Eld's deer were closely dependent on water resource, as was another subspecies *C. e. thamin* in Myanmar (McShea *et al*. 2001). The reintroduced Eld's deer showed selection for areas close to water sources at the landscape scale, and their home range contained artificial reservoirs as water sources. However, the reservoirs were also important water sources for local residents. The radio-telemetry data during daytime showed that the presence of people led to the Eld's deer not selecting areas close to water sources at the home-range scale. We also observed some individual deer drinking water in the dark, and tracked the collared deer near the reservoirs at night.

The male and female deer did select habitats differently in the study area, but the sexual differences in habitat selection did not support the predator-risk hypothesis. Contrary to our prediction, females tended to select habitats with relatively higher disturbance but higher forage availability (i.e. grasslands and shrubs) in both wet and dry seasons at both landscape and home-range scales, whereas males selected habitats with lower disturbance and denser cover (i.e. dense forests) in the wet season and randomly used habitat types available in the dry season at the home-range scale. In Hainan Island, the wet season is the period of female giving birth and male growing velvet antlers, whereas the dry season is the rutting period for Eld's deer (Song and Zeng 2003; Zeng *et al*. 2011). Our results indicated that reintroduced males were more sensitive to human activities than were females, and females weighed forage availability over human activities. However, female Eld's deer in Myanmar are more responsive to both predator avoidance and forage quality than are males (McShea *et al*. 2001). This difference in behavioural response to predation risk might be caused by long-term poaching pressures on males at their historical distribution areas in Hainan Island. The local people believe that deer antlers, especially velvet antlers, are very valuable, so that male Eld's deer is the main objective of poaching, even in the reserve (Zeng *et al*. 2005). The sexual difference in selecting foraging habitat by Eld's deer may be explained by forage-based hypotheses, such as the gastrocentric hypothesis without invoking predation (Barboza and Bowyer 2000). On the basis of allometry, minimal food quality and digestive retention in dimorphic deer, this hypothesis predicts that large males consume large quantities of low-quality, highly fibrous forages, whereas smaller-bodied females are better adapted to post-ruminal digestion of smaller quantities of high-quality forage to accommodate energy and protein needs for reproduction (Barboza and Bowyer 2000). According to the gastrocentric hypothesis, the sexual difference in foraging-habitat selection by Eld's deer may be related to inherent differential nutritional requirements by the sexes. However, further studies are required to confirm this.

Currently, reintroducing Eld's deer into their historical distribution areas is an important conservation approach because of the space limitation in the Datian reserve. However, human disturbance is the largest problem for reintroduction of Eld's deer. Fortunately, the reintroduction of Eld's deer has a preliminary success in the Chihao region. The deer population in the study area increased to 156 individuals by May 2007 (Lin 2012). The findings of the present study have several important implications for future reintroduction programs of Eld's deer, especially when human-caused disturbances become a concern. First, regions at a higher elevation than the areas of historical distribution can be considered as potential sites of reintroduction for Eld's deer. The finding that the Eld's deer had an adaptive ability to inhabit slopes at relatively high elevations brings us positive information on the potential habitat availability. Second, under good vegetation conditions, regions with low human disturbance may also be selected as potential reintroduction sites. Reintroduced Eld's deer can tolerate human disturbance in their habitats by selecting vegetation with good concealment or taking food and water during the night. Thus, the behavioural response will reduce, to a certain extent, the negative influence of human presence. Third, an approach specified for habitat management, including creating a mosaic of habitat plots in a space to provide cover, forage and water for deer, may minimise

the influence of human presence. Overall, the results of the current study have introduced us the possibility of recovery of the Eld's deer population in its historical distribution region that is currently encroached by human beings.

Acknowledgements

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