Hierarchical spatial analysis of Amur tiger relationships to habitat and prey

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Introduction

The tiger is a habitat generalist. Having successfully radiated throughout Asia, eight subspecies inhabited a wide range of habitats, including the tropical rainforests of the Sunda Shelf Islands (Seidensticker 1986), the tall grasslands and riverine forests of North India and Nepal (Schaller 1967; Sunquist 1981), the mixed deciduous, dry evergreen, and dry dipterocarp forests of Thailand (Rabinowitz 1989, 1993), the mangrove swamps of the Sunderbans (Hendrichs 1975), the temperate and boreal forests of the Russian Far East (Matyushkin et al. 1996) and, until recently, the 'reed jungles', riparian thickets and montane forests extending into the Middle East (Heptner & Sludskii 1972). Despite an apparent lack of specificity in habitat requirements, some authors have suggested that there are key components of habitat structure that are critical to survival (Sunquist 1981; Sunquist & Sunquist 1989; Karanth 1991; Rabinowitz 1989, 1993). In contrast, others have argued that, aside from some gross structural features, habitat parameters are relatively unimportant for tigers (Miquelle et al. 1996b) and that a specific complex of prey species is the key component of habitat for all tiger subspecies (Seidensticker 1986; Miquelle et al. 1996b). In either case, because habitat loss is a critical factor threatening the tiger with extinction, it is not a moot point to consider habitat requirements. Some minimum set of habitat components is obviously essential for the survival of this species.

Habitat selection can occur at a number of spatial and temporal scales (Orians & Wittenberger 1991; Pedlar et al. 1997). Johnson (1980) recommended a four-tiered approach to considering habitat selection at different levels of resolution (Fig. 6.1). First order selection describes the geographic range of a particular species; second order selection describes the range of habitats that are incorporated into home ranges of individuals; and third order resolution describes the selection of habitats within an individual's home range. Finally, fourth order represents selection of individual food items. Collectively, analyses at these various spatial scales describe not simply changes in resolution, but different sets of constraints that act on populations and individuals at different scales.

We believe that this construct is a valuable means of considering tiger habitat requirements, but argue that prey should be considered as one component of the habitat, and should be included as a parameter in analyses at the other three spatial scales. Fourth order selection (i.e. prey selection) has been examined extensively for the Amur tiger (Abramov 1962; Abramov et al. 1978; Zhivotchenko 1981; Yudakov & Nikolaev 1987; Matyushkin 1992; Miquelle et al. 1996b). Here we provide an examination of habitat use at the other three levels of selection.

Specifically, for tigers, we argue that prey density and distribution, not habitat parameters, are the key factors driving first and second order site selection, but that other factors are important at the third order. In the absence of human-induced mortality and disturbance, the geographical distribution of all tiger subspecies as well as the distribution and relative density of tigers within a subspecies range are driven primarily by prey distribution and density; but within an individual's home range,

First-order selection:
Geographic distribution of species

Second-order selection:
Selection of home ranges
by individuals

Third-order selection:
Selection of sites within home
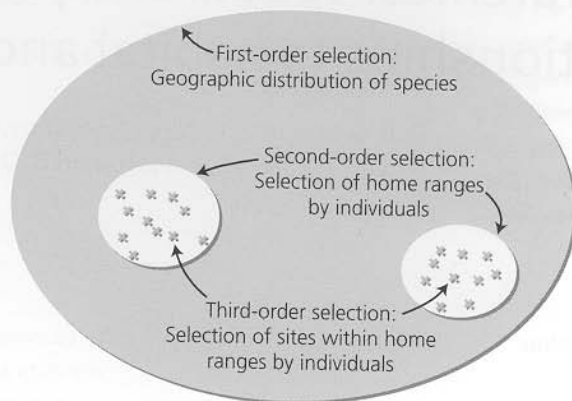ranges by individuals

FIGURE 6.1
Schematic view of 3 spatial scales for
assessing habitat selection (after
Johnson 1980).

other proximate factors temper the strength of this relationship. We assess this general concept with a series of testable hypotheses and an analysis of habitat relationships of the Amur tiger at each spatial scale.

The northern limits of the geographical range of tigers in Russia have historically occurred below 50° latitude in the Amur Basin (Heptner & Sludskii 1972; Kucherenko 1985). Yet forests extend far to the north, without obvious physical barriers, expanses of water, or tall mountains. What limits Amur tiger distribution to the north? Consideration of first order selection by the Amur tiger is particularly illuminating because it provides, on a gross scale, an assessment of habitat requirements at the limits of the range of this species. We address three general questions that relate to tiger distribution (i.e. first order selection): (1) can tiger distribution be predicted accurately by assuming tigers select directly for specific habitat types? (2) can tiger distribution be accurately predicted by mapping actual distributions of prey species? and (3) can tiger distribution be predicted accurately by mapping distribution of preferred habitat of key prey species within their known range? These questions have relevance when considering country and range-wide assessments of tiger distribution (e.g. Dinerstein

et al. 1997), and in understanding what limits tiger distributions. We assess habitat selection of the Amur tiger at the first order level (geographical distribution) with four testable hypotheses and an analysis based on data from a recent range-wide survey (Matyushkin et al. 1996), and large-scale habitat mapping.

At the second order spatial scale, tigers select location and size of home ranges from a range of available habitats and habitat parameters available within the landscape. In the Sikhote-Alin Mountains of the Russian Far East, where the majority of Amur tigers remain (Matyushkin et al. 1996), home ranges tend to occur within a single or associated set of basins (Yudakov & Nikolaev 1987; Miquelle et al. in prep.). We analysed habitat selection with radio locations of tigers and composition of home range habitat parameters in comparison to all existing potential habitats within a series of major drainages along the eastern slopes (or eastern 'macroslope', as it is referred to in Russian literature, e.g. Matyushkin 1992) of the Sikhote-Alin Mountain Range. Five hypotheses and an analysis of site selection at this level of resolution provide an indication of primary parameters driving home range selection.

At the third order of selection each individual

selects an array of habitats within its home range. Analysis of third order selection represents a fine-grained assessment of what components of a home range are most preferred. Selection of home range site within existing habitats (second order selection) and selection of habitats within a home range (third order selection) should reflect critical needs of the individual. For any carnivore, it has been hypothesised that habitat selection should be related primarily to distribution and density of prey (Sunquist & Sunquist 1989), but does this selection occur at the second or third level of resolution? Prey distribution should vary by season, especially in a northern ecosystem. Therefore, several questions arise: (1) do Amur tigers select habitats by mimicking habitat preferences of prey? (2) do tiger home ranges shift seasonally in response to shifting prey distributions? (3) do parameters that define prey habitat preferences also define tiger habitat preferences? and (4) how does home range size relate to habitat/prey parameters? Although these questions may appear merely academic, they relate directly to space requirements – and therefore conservation strategies – for viable tiger populations. We constructed eight testable hypotheses for an analysis of third order selection based on data collected from radio-collared tigers in Sikhote-Alin Zapovednik (nature reserve) in the northeastern portion of Amur tiger range. We assess seasonal fidelity to home range, preferences for specific habitat parameters, and habitat use in relation to habitat availability and prey distribution.

Study areas

Geographical range of the Amur tiger

The geographical range of Amur tigers in the Russian Far East stretches south to north for almost 1000 km throughout the length of Primorski Krai and into southern Khabarovski Krai east and south of the Amur River (Fig. 6.2). This region is represented mainly by the Sikhote-Alin Mountain Range, although tigers also occur within the Eastern Manchurian mountain system, which crosses into Russia from China at several places in southwest Primorye. In both regions, peaks are generally 500–800 m above sea level, with only a few reaching 1000 m or more. This region represents a merger zone of two bioregions: the East Asian coniferous-deciduous complex and the northern boreal (coniferous) complex, resulting in a mosaic of forest types that vary with elevation, topography and past history.

Over 72% of Primorye and southern Khabarovsk is forest covered. Typical tiger habitats are Korean pine/broadleaf forests with a complex composition and structure. This forest formation is considered by many to be key habitat for the Amur tiger (e.g. Kucherenko 1985). The large majority of these forests have been logged selectively at various times in the past, and human activities, in association with fire, have resulted in conversion of many low-elevation forests to secondary oak and birch forests. Above 700–800 m, spruce-fir forests prevail in central Sikhote-Alin. This elevational boundary for a predominantly coniferous forest type increases to the south, and decreases northward until, at 47°20' latitude, coniferous forests occur along the coastline (Fig. 6.2).

As with the plant communities, the faunal

Legend:
- Potential tiger habitat
- Boreal/high elevation forest types
- Agriculture/urban areas
- Wetlands/swamps
- Water bodies
- Tiger distribution
- Eastern macroslope study area boundary

Russia

Amur River

Khabarosk

China

Ussuri River
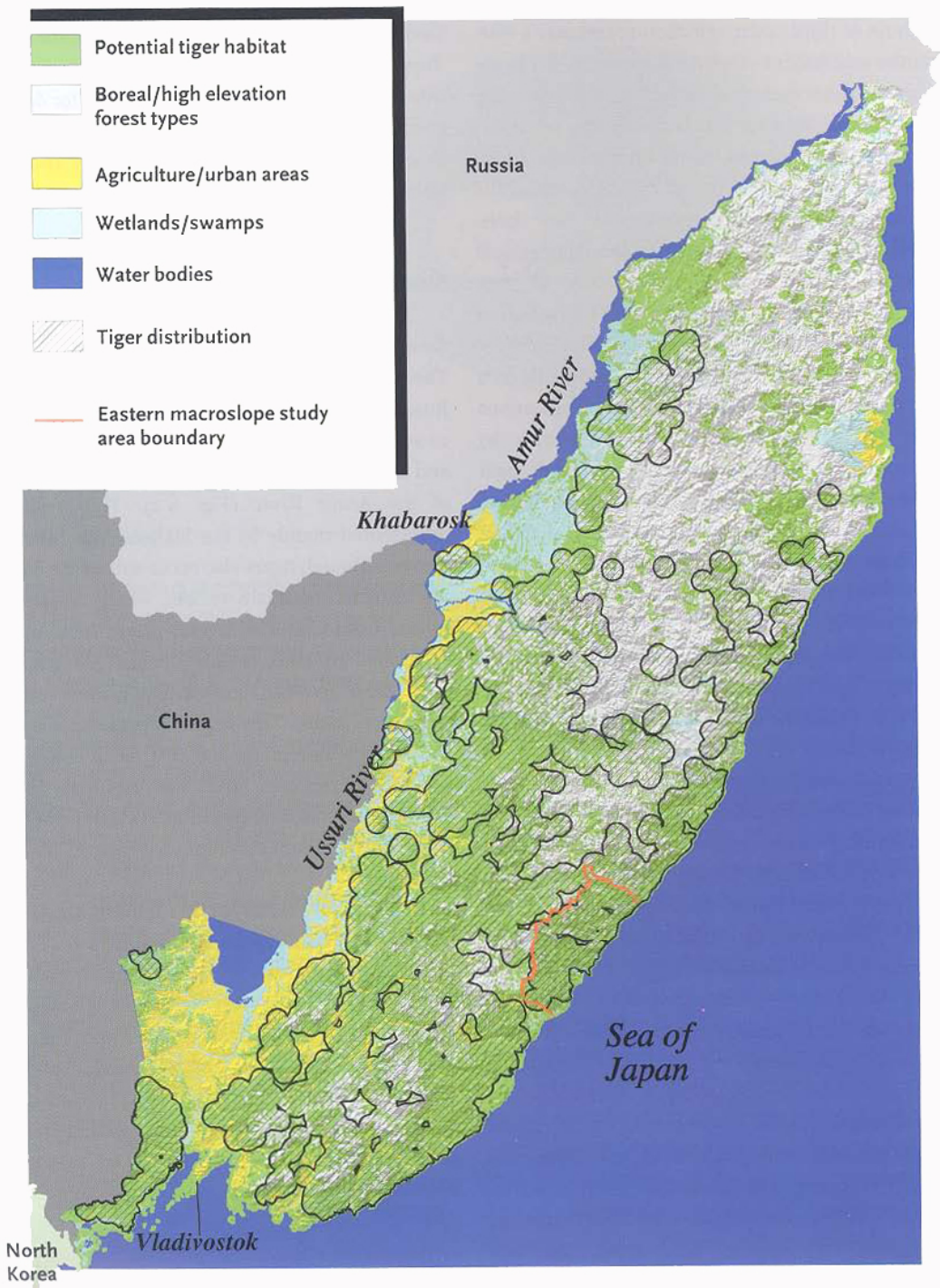
Sea of Japan

North Korea

Vladivostok

FIGURE 6.2

Distribution of major habitat types and distribution of Amur tigers in the Russian Far East. Tiger distribution was based on a 1996 range-wide survey (Matyushkin *et al.* 1996). The eastern macroslope study area is delineated in red. Scale: 1cm = 58km.

complex of the region is represented by a mixture of Asian and boreal life forms. The ungulate complex is represented by seven species: red deer, wild boar, sika deer, roe deer, Manchurian moose, musk deer and ghoral. Red deer and wild boar are the most common; both are found throughout the Sikhote-Alin and eastern Manchurian Mountains, but are rare in higher altitude spruce-fir forests. Manchurian moose are near the southern limits of their distribution in the central Sikhote-Alin Mountains, and are distributed sparsely in the inland boreal forests. Sika deer are near their northern limits at Sikhote-Alin Zapovednik. Musk deer are associated with the upper elevation conifer forests, and roe deer are confined to regions of limited snow depth. Ghoral, an endangered wild goat, are mostly restricted to coastal cliffs and some coastal mountains.

Sikhote-Alin Zapovednik and associated lands on the eastern 'macroslope' of the Sikhote-Alin Mountains

We confined the analysis of second order selection to those habitats within east-flowing drainages with some portion of their basins within Sikhote-Alin Zapovednik (Fig. 6.3). Although the crest of the Sikhote-Alin does not form a barrier to tiger movements, major ridges often form home range boundaries (Miquelle *et al.* in prep.), and the eastern 'macroslope' represents a discrete set of habitat parameters at a spatial scale within which tigers are likely to select home range location and associated habitat parameters. On the eastern coastal slopes of the Sikhote-Alin Mountains, temperatures and snow depth are moderated by the Sea of Japan, resulting in greater representation of southern forest types. Secondary Mongolian oak and white birch upland forests are most common nearer the coast. More inland, and at slightly higher elevations, Korean pine forest types are dominant and contain a mixture of deciduous and coniferous species, including birches, basswood, fir and larch. Spruce-fir and larch forests make up the remainder of the higher elevation, cooler forest types. Riverine forests are most often comprised of a variety of deciduous species, including willow, elm, chosenia,

cottonwood and ash, or a mixture of these deciduous species with Korean pine.

All radio-collared tigers included in this analysis had home ranges at least partially within the boundaries of Sikhote-Alin Zapovednik on the eastern side of the Sikhote-Alin Mountains. A total of 554 805 ha were included for second order analyses, representing 265 758 ha within the Zapovednik (approximately 66% of the Zapovednik) and 289 047 ha outside.

Methods

We defined two seasons for analyses: winter, from November to March (those months when snow was usually on the ground); and summer, extending from April to October (snow-free months). This division allows comparison of winter results to existing Russian studies, which have relied totally on traditional snow-tracking methods (Abramov 1962; Yudakov & Nikolaev 1987), and is relevant when considering tiger habitat selection in relation to ungulate distributions.

Radio-collaring and radio locations

Between January 1992 and November 1994, tigers were captured with modified Aldrich foothold snares, anaesthetised with a mixture of ketamine and Rompun and fitted with radio-collars. Of 11 animals captured and monitored, five (one male and four adult females) were monitored long enough (more than 15 months) to obtain sufficient sample sizes for analyses. Of the four females, one animal was followed from approximately 12 months old through her first litter; we include data starting 11 months after family break-up, when it was apparent that she had settled into her own home range. Two females appeared to be young animals establishing new territories at the time of capture (only one produced cubs during the study period), and one tigress was an adult already with cubs.

Locations from radio-collared tigers were obtained by three methods: aerial locations, triangulation and homing (White & Garrot 1990). Locations were plotted on 1:25 000 topographic
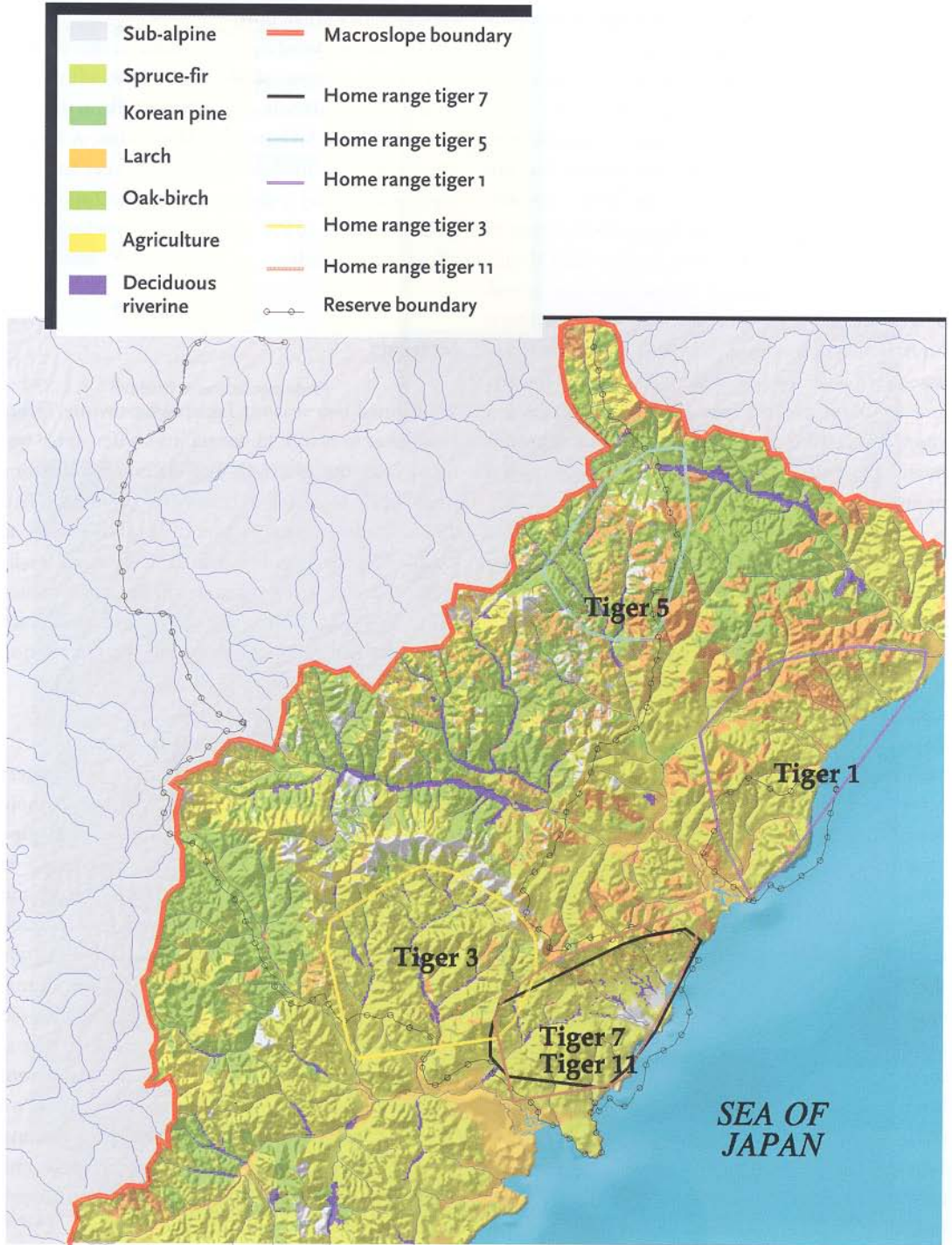
FIGURE 6.3
Study area on the eastern slopes of the Sikhote-Alin Mountain Range (eastern macroslope) used for second order habitat selection analysis, and home range boundaries (95% minimum convex polygons) of five tigers used for third order analyses (home range of male 11 overlaps that of female 7). Scale: 1cm = 8.26km.

maps. Many of our telemetry data were collected opportunistically and, except for aerial locations, a certain percentage of locations was biased by proximity of animals to roads, i.e. there was a greater probability of obtaining locations when tigers were close to roads. This bias affected methods used for home range analyses. For analyses of habitat selection, locations with a linear error estimated at less than 500 m were included.

To reduce the probability of serial dependence of locations, we used only one location per day for all analyses, unless subsequent same-day locations were separated by at least 5 km (Miquelle et al. unpubl. data). Sequential daily locations at den sites were eliminated, as were all locations within two days of capture. For third order analyses, boundaries of home ranges were defined by 95% minimum convex polygons of radio-collared tigers.

Spatial data

We developed a Geographic Information System (GIS) spatial data base at several levels of resolution for analyses. For first order analyses, landscape and forest-cover maps were developed at resolutions of 1:100 000 to 1:500 000, and generalised to a resolution of approximately 1:500 000. A forest-cover map was developed from the most recent Russian Forest Service inventory data (3–15 years old, depending on location) that categorised forest stands (averaging 30 ha) into an hierarchical classification scheme that could be resolved into 65 forest types (V. A. Rosenburg, unpubl. data). To ensure compatibility of the region-wide forest-cover map and the Sikhote-Alin forest-cover map, which were based on a different forest classification schemes, it was necessary to merge ('cross-walk') the 54 forest/habitat cover types of the Zapovednik into the 65 forest cover types of the region-wide map (S. M. Krasnepeev, unpubl. data). A landscape map for the entire region, developed from Russian satellite imagery (Murzin et al. unpubl. data) and existing 1:500 000 habitat maps, were used to define non-forest habitat. Sixty-five forest cover types from the forest-cover map and 42 landscape types were collapsed into 18 general habitat types used in first order analyses. For analysis of habitat selection at both the second and third order, these general habitat types were further collapsed into seven forest types: upland oak, upland birch/aspen, riverine, Korean pine, spruce-fir, larch, and 'other' (including rare forest types and human-influenced landscapes such as villages, agriculture and grazing lands).

Range-wide distribution of Amur tigers was based on the results of a 1995–1996 winter census (Matyushkin et al. 1996). Tracks of tigers were reported on 652 count units distributed throughout approximately 90% of potential tiger habitat. Field counters plotted out the location of each track on 1:100 000 maps. To develop a distribution map of tigers from this data set, each track was encompassed by a 10 km-radius circle that represents a potential radius of travel. Because each 10-km circle is less than the estimated home range size of adult female tigers (Miquelle et al. in prep.), and some tigers were likely missed during the survey, we believe the distribution map represents a conservative estimate of tiger distribution.

Distribution maps of large ungulate species, including red deer, wild boar, roe deer, sika deer, and moose and were developed in a two-stage process. First, general distribution and relative density maps were developed at a small scale of resolution (approximately 1:2 500 000) based on existing literature (e.g. Bromley & Kucherenko 1983) and unpublished information. Ungulate distributions were plotted at three relative densities (high, medium and low) that were species specific (e.g. high densities of moose were not equivalent, in absolute terms, to high densities of red deer). Secondly, predicted distributions of ungulates within this range, were then mapped 1:500 000 based on habitat preferences defined by local specialists (V. A. Nesterenko et al. unpubl. data) and the forest-cover map (based on 18 habitat types). Mapping predicted distributions based on habitat associations provides a much higher level of resolution than the original distribution maps (Scott et al. 1993; Csuti 1996). For our analyses comparing ungulate and tiger distribution, we excluded low-density contour distributions for each ungulate species, assuming that areas with low prey densities

Table 6.1. *Summary of hypotheses tested, methods of analysis, and results of analysis assessing the relationship of Amur tiger distribution to prey and habitat parameters at three spatial scales in the Russian Far East*

Order of selection	Scale		Hypothesis	Methods of analysis	Results
First	Geographical distribution	1	Tiger distribution associated with a single key prey species.	3 overlap measurements.	Closest association with red deer distribution.
		2	Tiger distribution associated with two prey species.	3 overlap measurements.	Closest distribution with red deer & any other prey.
		3	Tiger distribution associated with habitat of key prey species.	3 overlap measurements.	68% weighted mean overlap with wild boar and red deer habitat.
		4	Tiger distribution associated with Korean pine forests.	3 overlap measurements.	Weak association (36%).
Second	Eastern macroslope Sikhote-Alin Mountains	1	Tigers select for specific habitat types within eastern macroslope.	Friedman test Fisher's LSD.	Riverine most preferred, spruce-fir and Korean pine avoided.
		2	Habitat composition of home ranges differs from eastern macroslope.	Chi-square goodness-of-fit.	Significant differences ($P<0.001$) for 4 home ranges.
		3a	Tigers select for specific elevations.	ANOVA Tukey comparisons.	Home ranges lower than macroslope average for 4 of 5 tigers.
		3b	Tigers select for distance to water.	ANOVA.	No significant differences.
		3c	Tigers select for specific slopes.	1-sample t-test.	Steep slopes avoided by all 5 tigers.
		3d	Tigers select for specific aspects.	Chi-square.	1 of 5 tigers demonstrated a preference for aspect.
		4	Habitat selection of tigers mimics habitat selection of ungulates in winter.	Spearman's rank correlation.	$r = 0.712$, $P<0.05$.
		5	Home range of tigers seasonally shifts to track ungulate distribution.	Overlap of seasonal home ranges.	Overlap of seasonal home ranges <70% confounded by sample size.
Third	Within home range	1	Tigers select for specific habitat types within home ranges.	Friedman test Fisher's LSD.	Preferences exist ($P<0.05$) but tendency for neutral selection.
		2	Composition of habitat types within home ranges varies among tigers.	Friedman test Fisher's LSD.	Composition of tiger home ranges varies ($P<0.01$).
		3a	Tigers select for specific elevations.	ANOVA Tukey comparisons.	Only 1 tigress preferred lower elevations in winter.
		3b	Tigers select for distance to water.	ANOVA.	No significant differences.
		3c	Tigers select for specific slopes.	1-sample t-test.	Steep slopes avoided.
		3d	Tigers select for specific aspect.	Chi-square.	1 of 5 tigers demonstrated a preference for aspect.
		4	Habitat selection of tigers mimics habitat selection of ungulates in winter.	Median difference of ranks.	No signficant differences (weak test).
		5	Seasonal shift in central tendency within home range.	t-test for changes in mean x and y.	Significant shifts in 5 of 10 tests.
		6	Habitat preference varies between summer and winter.	Friedman test Fisher's LSD.	No differences found between summer and winter ($P>0.25$).

Table 6.1. (cont.)

Order of selection	Scale		Hypothesis	Methods of analysis	Results
		7	Tigers select lower elevations in summer than winter.	ANOVA.	No significant differences between summer and winter.
		8	Tigers select south slopes more in winter than summer.	Chi-square.	1 of 5 tigers preferred south and east slopes in winter.

are less likely to support tigers and would be poorer predictors of tiger distribution.

Values for habitat parameters within home ranges and the eastern macroslope (elevation, slope and aspect) were developed from a digital elevation model constructed by interpolating 100-m contour intervals from a 1:100 000-scale topographical map, supplemented with elevation points of major peaks and guided by flow direction of streams and rivers. Measurements of distance from water are based on a digital map of streams, rivers and lakes.

First order habitat selection (geographical distribution)

To assess parameters potentially related to distribution of Amur tigers, we tested the following hypotheses with first order spatial data (summarised in Table 6.1):

1   Amur tiger distribution in the Russian Far East is associated with the presence of red deer, wild boar, roe deer, sika deer, or moose (each species assessed separately).

2   Amur tiger distribution in the Russian Far East is associated with the aggregate presence of two key prey species.

3   Amur tiger distribution can be predicted by mapping the distribution of preferred habitat of key prey species.

4   Amur tiger distribution in the Russian Far East is associated with the presence of key habitat types (Korean pine forests).

Korean pine forests have been identified as key tiger habitat (Kucherenko 1985), primarily because they are considered key habitat for wild boar and, to

a lesser extent, for red deer. We therefore compared tiger distribution to this habitat type. Because large ungulates (red deer, roe deer, sika deer, moose and wild boar) comprise 96% of tiger prey (Miquelle et al. 1996b), we measured coincidence of tiger distribution to each of these species separately. However, it has also been suggested that two species (namely, red deer and wild boar) are the key combination of prey (Kucherenko 1985; Matyushkin 1992; Miquelle et al. 1996b). Therefore, we compared aggregate distributions of all combinations of two prey species with tiger distribution. Finally, we compared the predicted distribution of red deer and wild boar based on habitat preferences to tiger distribution.

We used three measurements to compare the relationship of tiger distribution to various prey and habitat distributions: (1) percentage overlap of prey species (or habitat type) distribution with tiger distribution; (2) percentage overlap of tiger distribution with prey/habitat distribution; and (3) percentage of the total area of tiger and prey/habitat combined that is shared by both. High percentage overlap of the first measure suggests that this parameter (specific prey or habitat distribution) occurs over much of the tiger range; high percentage overlap of the second indicates that tigers inhabit much of the area where prey/habitat occurs (but could occur over a much larger area), and a high percentage of total area shared (third measure) indicates a good association between tigers and prey/habitat. High percentage overlap of all three measures indicates a high degree of concordance between tiger distribution and prey (or habitat) distribution; however, high percentage overlap of prey/habitat distribution

with tigers (the second measure) was not as strong a measure because tigers could occur widely outside the range of any particular prey or habitat. Therefore, we used a weighted mean percentage for these three measures (weighting the second overlap measure by 0.5) as a general indicator of the level of association.

Moose distribution extends far to the north of our defined study area, thereby biasing our analyses because the full distribution of this species was not included. Despite this potential positive bias, we eliminated moose from the two-species comparisons because single species comparisons indicated a poor association with tigers.

Second order habitat selection (within the eastern macroslope)

We used some of the same hypotheses for tests of second order and third order relationships (Table 6.1). However, for clarity, we present them separately here. We tested the following hypotheses on second order (within the eastern macroslope) habitat selection:

1   Tigers demonstrate preference for specific habitat types (based on locations of radio-collared tigers) within the eastern macroslope study site.
2   Composition of habitat types within home ranges is different than composition of habitat types within the eastern macroslope.
3   Tigers select for some component of the following habitat parameters on a seasonal basis within the eastern macroslope:
    a.   elevation;
    b.   distance to water;
    c.   slope;
    d.   aspect.
4   Habitat selection by tigers should mimic habitat selection by ungulates within the eastern macroslope (tested for winter only).
5   Because ungulate distributions shift seasonally, the geographical location of tiger home ranges should shift to 'track' areas with high ungulate densities. Therefore, home range locations in summer and winter may

not overlap, i.e. low site fidelity (at the second order spatial scale) on a seasonal basis may occur.

Hypotheses 1–3 imply that tigers demonstrate preferences for habitat types, or features of the environment, at the second order of selection. Hypotheses 4 and 5 imply that habitat selection and location of home ranges is driven, at the second order of selection, by the distribution of ungulates on a seasonal basis.

Third order habitat selection (within home ranges)

We tested the following hypotheses on third order habitat selection (summarised in Table 6.1):

1   Tigers demonstrate preference for specific habitat types within their home ranges.
2   Composition of habitat types within home ranges varies among tigers.
3   Tigers select for some component of the following habitat parameters on a seasonal basis within home ranges:
    a.   elevation;
    b.   distance to water;
    c.   slope;
    d.   aspect.
4   Habitat selection of tigers should mimic habitat selection of ungulates within home ranges (tested for winter only).
5   As an alternative to hypothesis 5 in second order selection, if a single year-round home range provides an adequate prey base, there may still be seasonal shifts within a home range as tigers track localised shifts in prey distribution (i.e. a shift in central tendency of home range).
6   Habitat preference within the home ranges of tigers varies between summer and winter season, reflecting seasonal changes in prey distribution.
7   Because ungulates usually move to lower elevation habitats in winter (Myslenkov unpubl. data), average elevation selected by tigers within their home range (third order selection) should be lower in winter than summer.

Because ungulates tend to use south slopes more in winter (A. E. Myslenkov unpubl. data), tigers should select south slopes in winter more than summer, and more than the percentage available within the home range (third order selection) in winter.

Hypotheses 1–5 at the second and third order of selection examine the same variables, but at different spatial scales. Because it is likely that a variety of 'combinations' of habitat types can meet the needs of tigers, hypothesis 2 (third order spatial scale) suggests that the composition of habitat types within home ranges of tigers is likely to vary. Hypotheses 2 and 3 imply that tigers demonstrate preference for habitat types, or features of the environment on a seasonal basis within their home ranges. Hypotheses 4 (at second and third order spatial scales) both state that tigers should demonstrate the same preference for habitat types as their prey, but at different spatial scales. Hypotheses 5–8 test various ways in which tigers may 'track' distribution of prey seasonally, which may affect use of the home range. As in most seasonal environments, the distribution of ungulates in Sikhote-Alin Zapovednik shifts seasonally, reflecting the effect of snow depth, food availability and shelter from extreme weather conditions (A. E. Myslenkov unpubl. data). Without specifying the exact distributions within each tiger home range, hypotheses 5–8 test for evidence of tigers 'tracking' changes in assumed ungulate distribution through seasonal changes in preference for habitat parameters. Changes in either home range location (hypothesis 5, second order scale), or focal use areas within home ranges (hypothesis 5, third order) are expected due to changes in ungulate distribution.

Habitat selection was compared seasonally at both the second and third order spatial scale. The most commonly used test for habitat preference, the χ^2 goodness-of-fit test (Neu *et al.* 1974; Byers *et al.* 1984) was inappropriate because low expected cell frequencies violated basic assumptions of this statistic. We used the Friedman test, in which habitats represented 'treatments' and animals were 'blocks' (Conover 1980; Alldredge & Ratti 1986),

and ranked availability (determined from GIS spatial databases) and use of habitats by tigers (based on radio locations) to compare the following: differences in habitat availability and selection within the eastern macroslope (hypothesis 1, second order); the difference in habitat availability and selection within home ranges (hypothesis 1, third order); variation in the composition of habitat types among four home ranges (tigress 7 and tiger 11 had virtually identical home ranges, so one was deleted for these comparisons) (hypothesis 2, third order); and seasonal differences (winter and summer) in habitat preferences of all five tigers (hypothesis 6, third order). Where significant differences were found, Fisher's least significant difference (LSD) method was used to determine which habitats were different in terms of selection versus availability (Conover 1980; Alldredge & Ratti 1986). To compare composition of habitat types within home ranges to the eastern macroslope (hypothesis 2, second order selection), individual χ^2 goodness-of-fit tests were conducted for each home range, for which expected values were represented by composition of the eastern macroslope.

We assessed the importance of habitat parameters that may influence site selection by tigers at both the second and third order spatial scale, including elevation, distance to water, slope and aspect (hypotheses 3a–d at both scales). We assessed the relationship of tiger selection to availability of habitat parameters by comparing an equal number of tiger locations with randomly selected 200-m-wide grid cells across the eastern macroslope (second order selection), and within home ranges (third order selection); this level of resolution approximately equalling the average accuracy of radio locations. For two continuous variable parameters (elevation and distance to water), '*a posteriori*' Tukey pair-wise comparisons were made if an analysis of variance (ANOVA) test on each individual tiger determined significant differences among four categories of data: summer tiger locations, winter tiger locations, random locations within the eastern macroslope study area, and random locations within home ranges. This analysis of elevation also provided a test of hypothesis 7, third

order selection. Winter and summer mean slope selection by tigers were compared to each other with two-sample t-tests (hypothesis 8, third order selection), and to mean values within each home range and on the eastern macroslope (derived from a digital elevation model) using one-sample t-tests (hypotheses 3c second and third orders). Aspect was converted from a continuous variable of the digital elevation model into categorical data with four elements: 315–45°=north, 46–135°= east, 136–225°=south; 226–315°=west. Because the digital elevation model delineated few areas as truly flat, this category was deleted from analyses. Overall and seasonal use of aspect by each tiger was tested independently with χ^2 goodness-of-fit tests based on expected distributions for each home range and for the eastern macroslope (derived from the digital elevation model).

We used data developed by Matyushkin (1992) to assess the correlation between winter habitat selection by prey species (red deer, roe deer and wild boar) and tigers across the eastern macroslope (hypothesis 4, second order selection). These data were based on relative track densities of prey and tigers along prescribed transect routes that included 10 habitat types. We used a Spearman's rank correlation test to assess the relationship between tigers and each of the three main prey species. Definitions of habitat types and study site boundaries by Matyushkin (1992) are slightly different from those described above, although still focused on the eastern macroslope. Despite some differences, the data provide an opportunity to test this hypothesis within the same general study site at the appropriate level of resolution.

Because data on summer habitat selection of prey were unavailable, we compared a ranking of total winter prey density in habitat types within each home range to winter habitat preference of tigers (hypothesis 4, third order scale). Prey density in winter was based on 1994 aerial surveys within home ranges of four radio-collared tigers (A. E. Myslenkov & D. G. Miquelle unpubl. data) where conifer habitat types were rare and visibility was equal among the dominant habitat types. For the fifth home range, we used relative ungulate track density in habitat types. We believe that these two methods are comparable in our analysis because, in all cases, density counts were reduced to a ranking by habitat type. Confidence intervals for the median of the absolute difference in ranks of habitats selected by tigers and habitats selected by prey in winter were constructed to determine if selection varied between tigers and prey (i.e. median difference greater than 0 representing variation in selection).

We tested tiger home range fidelity at two spatial scales: (1) overlap of winter and summer home ranges, based on 95% minimum convex polygons (hypothesis 5 second order selection) estimated using the software programme 'CALHOME' (US Forest Service Pacific Southwest Research Station and California Department of Fish and Game); and (2) changes in mean x and y coordinates of tiger locations within a home range (hypothesis 5, third order selection). High overlap of summer and winter home ranges should be an indicator of high seasonal fidelity to home range location (second order selection). Insignificant changes of mean x and y coordinate values between seasons would suggest no change in central tendency of year-round home range location (third order selection).

Null hypotheses of statistical tests were rejected when significance levels exceeded 5%.

Results

First order habitat selection (geographical distribution)

Tiger distribution was more closely associated with distribution of red deer (61% overlap) than any other prey species (Table 6.2, column 1). Distributions of wild boar, red deer and roe deer overlapped more than 70% with tiger distribution (Table 6.2, column 2), indicating that tigers occurred over most of the region where these prey species occurred within the region defined by our study. The high overlap of tiger distribution to red deer in comparison to other single-species distributions (Table 6.2, column 1) and the percentage of total area shared (Table 6.2, column 3) suggest a strong correlation between tiger distribution and red deer (Fig. 6.4a). Although wild

Table 6.2. *Overlap of Amur tiger distribution over their entire range in Russia with prey and habitat distributions, overlap of prey and habitat distributions with tiger distribution, and percentage of total area of combined distributions shared by both tiger and prey or habitat. Distribution of prey based on moderate to high distribution contours (see text)*

Species/habitat	Overlap of tiger distribution with prey/ habitat distribution (%)	Overlap of prey/ habitat distribution with tiger distribution (%)	Percentage of total area shared with tiger (%)	Weighted mean[a] (%)
One species				
Red deer	61	73	50	59.0
Wild boar	37	84	34	45.0
Sika deer	9	67	9	21.0
Roe deer	31	72	27	38.0
Moose[b]	19	29	3	15.0
Two species				
Red deer and wild boar	74	73	58	67.0
Red deer and roe deer	71	78	59	68.0
Red deer and sika deer	72	67	53	63.0
Boar and roe deer	76	46	41	56.0
Boar and sika deer	80	41	37	55.0
Roe and sika deer	72	32	28	46.0
Habitat				
Korean pine forests	24	85	23	36.0
Red deer and boar habitat	93	52	50	68.0

[a] Weighted mean of 3 measures of percentage overlap, with overlap of prey/habitat distribution with tiger weighted by 0.5, and the other two weighted as 1.
[b] Moose were not included in two-way comparisons (see text).

boar have been considered key prey for tigers, their distribution was more patchy than that of red deer (Fig. 6.4b), and consequently, although tigers occurred almost everywhere boar were found at high and medium densities (84% overlap), boar distribution was overall not as strong a predictor of tiger distribution (Table 6.2, column 4). Although tigers prey on both roe deer and sika deer, overlap of these two species with tigers was low (Table 6.2; Figs. 6.4c, d). Distribution of moose was poorly associated with tiger distribution (Table 6.2; Fig. 6.4e).

The combination of two prey species improved the relationship between tiger and prey distribution (Table 6.2), but not dramatically. Red deer plus any other prey species provided consistently high measures of weighted mean overlap (63–68%) (e.g. Fig. 6.4f), while boar and other species (except red deer) provided slightly lower measures (Table 6.2). As expected based on the single-species analysis, the combination of roe deer and sika deer was relatively poorly correlated with tiger distribution.

The distribution of Korean pine forests did not relate well to tiger distribution (Table 6.2; Fig. 6.4g). Although tigers occurred throughout Korean pine forests (Table 6.2, column 2), tigers occurred in a variety of other habitats, and consequently the overall association was low. In contrast, the aggregate set of habitats preferred by red deer and wild boar (Fig. 6.4h) provided as strong a relationship to tiger distribution as the distributions of the species themselves. (Fig. 6.4f; Table 6.2).
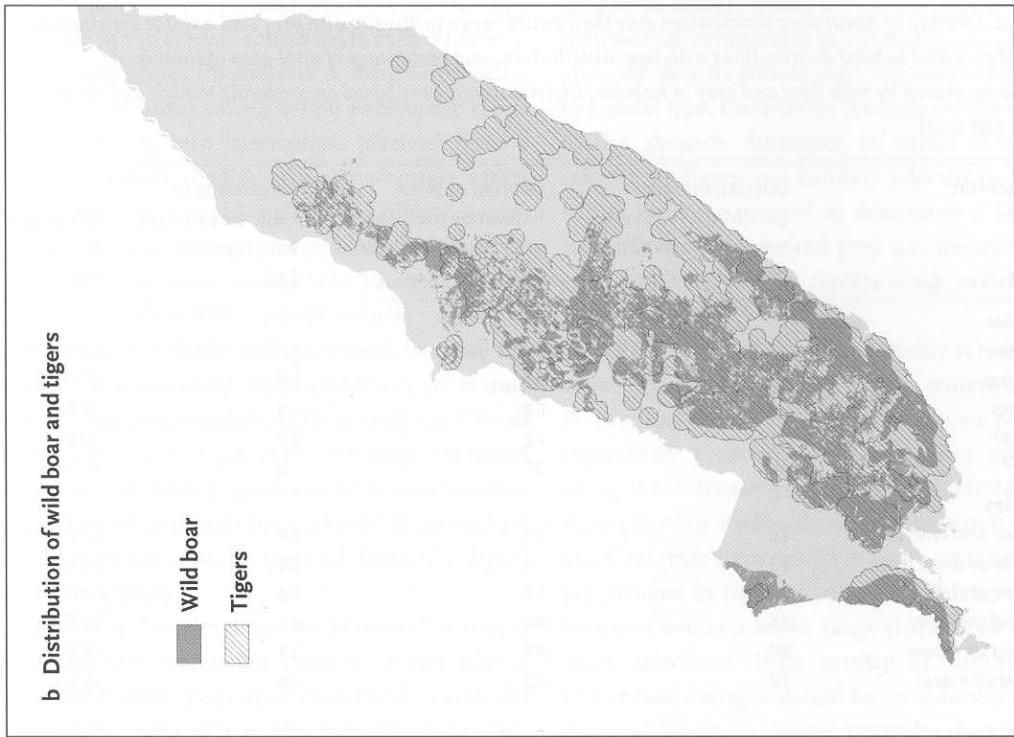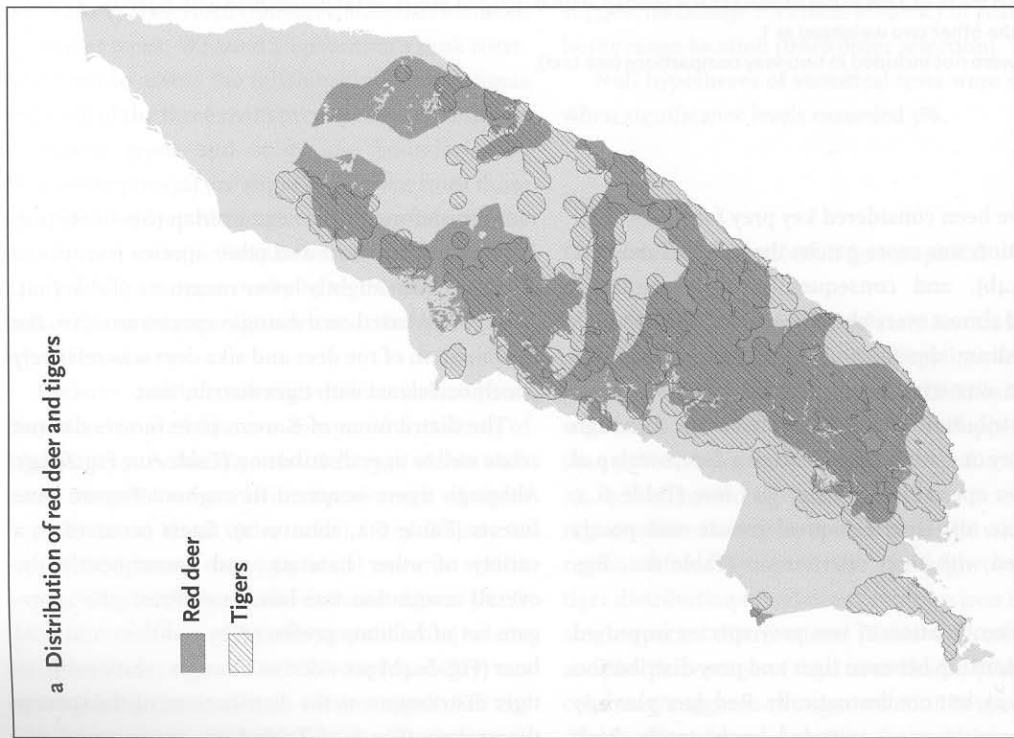
FIGURE 6.4

Overlap of tiger distribution with distribution of five prey species and two habitat complexes: **a.** red deer; **b.** wild boar; **c.** roe deer; **d.** sika deer; **e.** moose; **f.** red deer and wild boar distribution; **g.** Korean pine forests; **h.** habitats preferred by red deer and wild boar.

c Distribution of roe deer and tigers

Roe deer
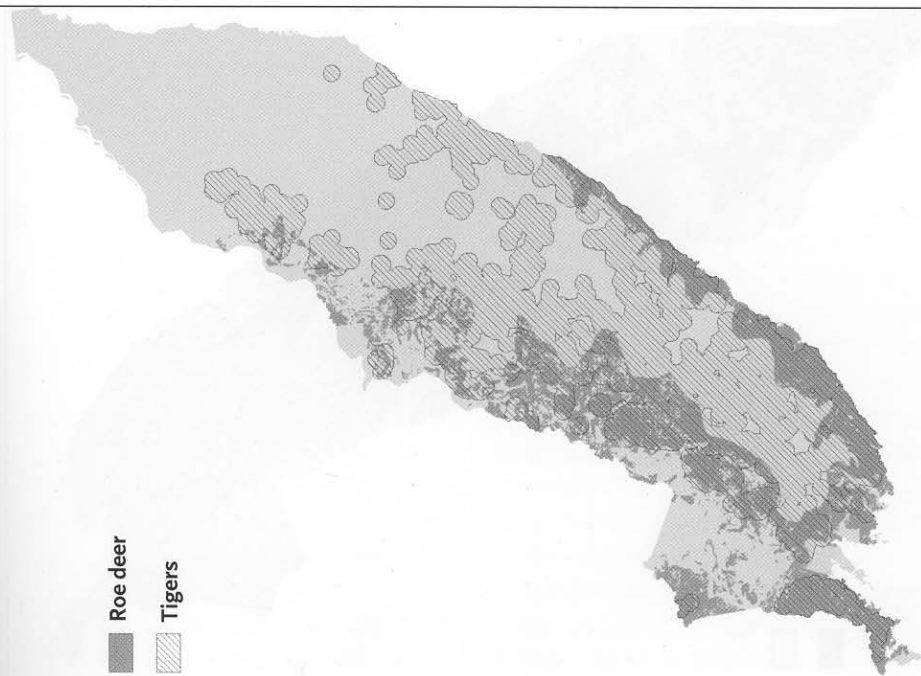
Tigers

d Distribution of sika deer and tigers

Sika deer

Tigers

f Distribution of wild boar, red deer and tigers

Wild boar or red deer

Wild boar and red deer
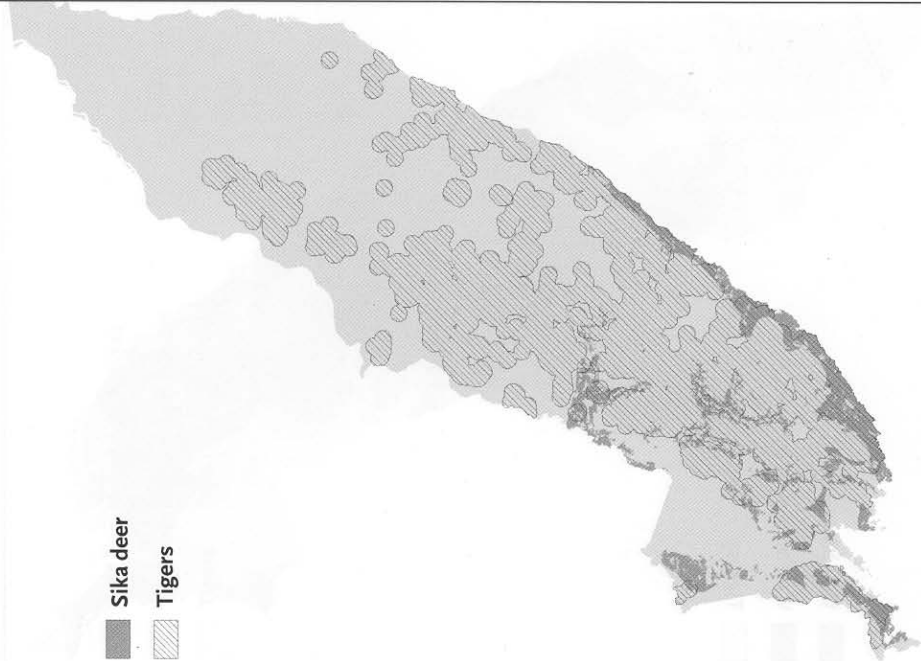
Tigers

e Distribution of moose and tigers

Moose
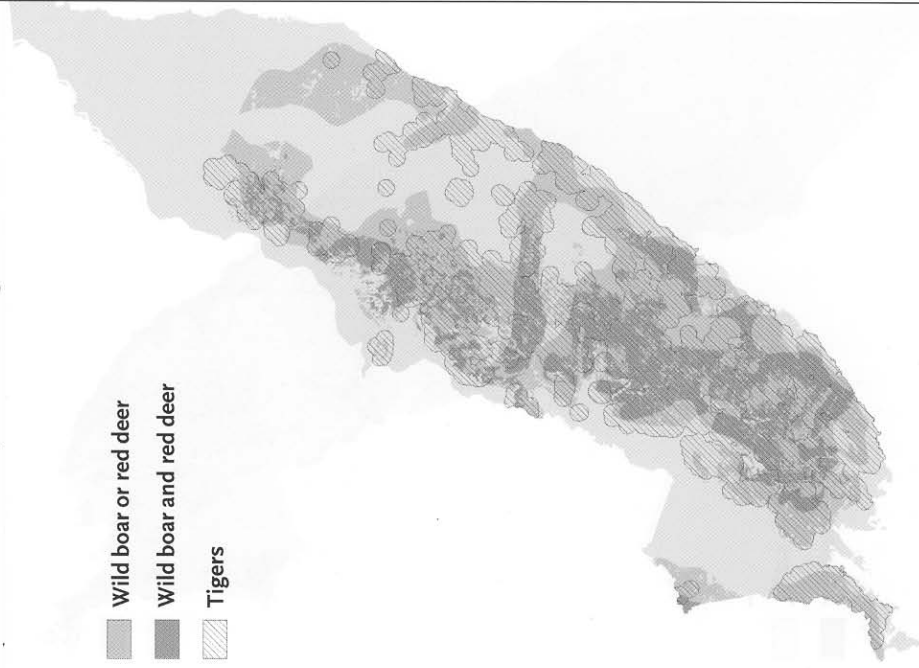
Tigers

g Distribution of Korean pine and tigers

Korean pine
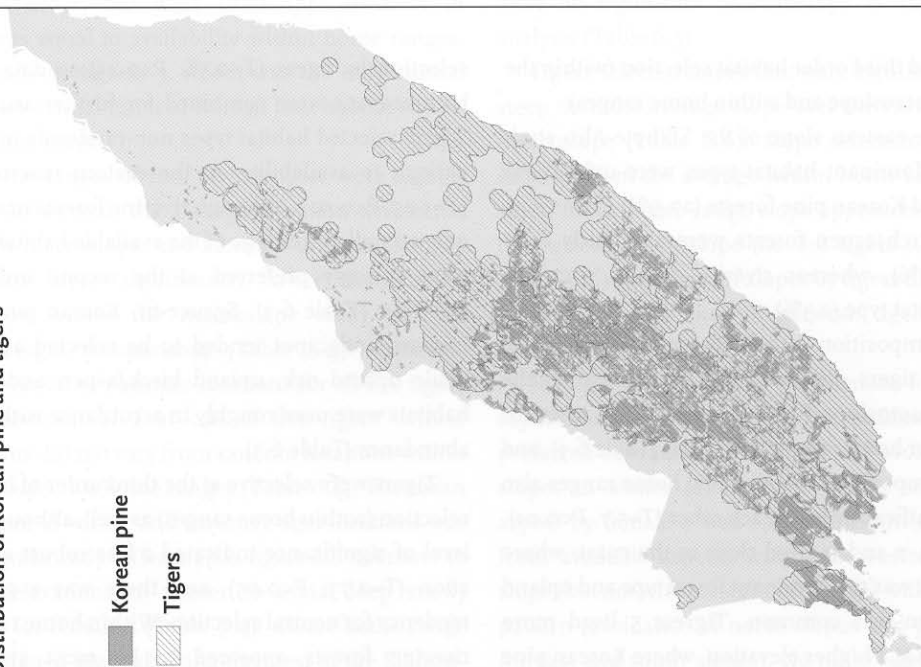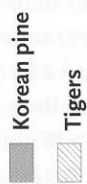
Tigers

h Distribution of wild boar and red deer habitat and tigers

Wild boar or red deer habitat

Wild boar and red deer habitat

Tigers

Table 6.3. *Habitat availability and use based on locations of radio-collared Amur tigers on the eastern slope of the Sikhote-Alin Mountains (second-order 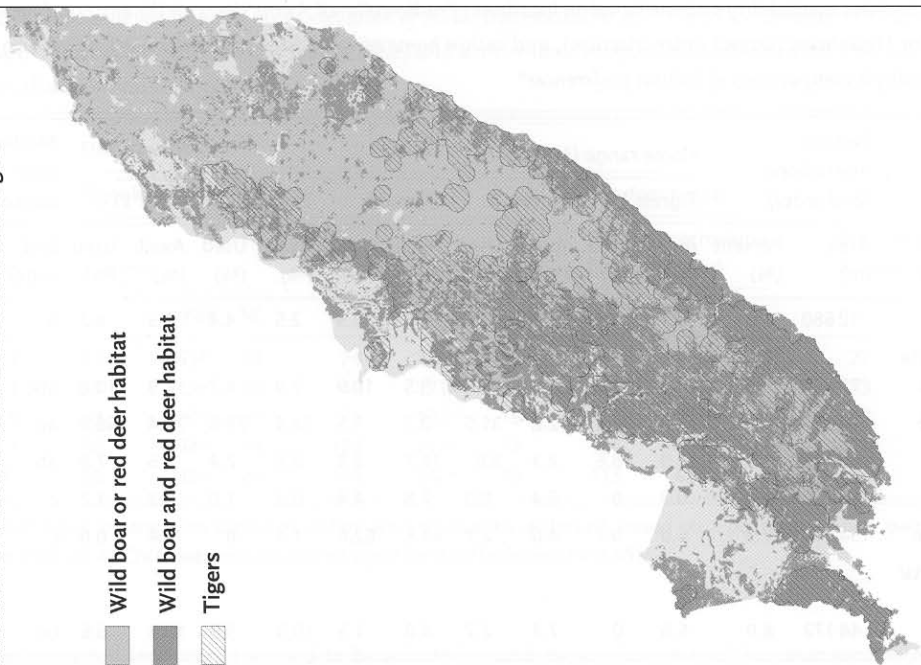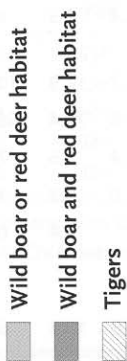selection), and within home ranges (third-order selection), 1992–1995, and results of multiple comparisons of habitat preferences*[a]

Forest type description	Eastern macroslope (2nd order) Area (m)	Percent (%)	Home range (3rd order) Tigress 1 Avail. (%)	Used (%)	Tigress 3 Avail. (%)	Used (%)	Tigress 5 Avail. (%)	Used (%)	Tigress 7 Avail. (%)	Used (%)	Tiger 11 Avail. (%)	Used (%)	Multiple comparisons[a] 2nd order	3rd order
Riverine	12 680	2.3	0.1	0	2.7	9.9	3.8	10.9	2.5	4.4	2.5	4.2	a	a
Upland white birch/aspen	73 168	13.2	15.3	10.3	35.0	48.7	5.5	10.9	7.9	8.7	7.9	10.8	abc	ab
Upland oak	174 632	31.5	51.8	70.4	42.2	31.5	0.7	1.5	74.4	79.6	74.4	68.8	ab	abc
Larch	48 813	8.8	19.9	18.6	2.3	3.6	16.7	8.8	2.6	2.4	2.6	7.8	ab	abc
Spruce-fir	46 729	8.4	0.3	0	6.4	0.9	7.8	4.4	0.3	1.0	0.3	1.2	c	abc
Korean pine	154 611	27.9	6.0	0.7	4.0	2.7	61.5	62.0	1.4	0	1.4	0.6	c	bc
Other forests/human landscapes	44 172	8.0	6.6	0	7.4	2.7	4.0	1.5	10.9	3.9	10.9	6.6	bc	c

[a] Tigers demonstrated significantly different ($P < 0.05$) preferences (a=most preferred) for habitat types with different letters based on Fisher's least significant difference multiple comparison test (after a Friedman's test demonstrated overall significance).

Second and third order habitat selection (within the eastern macroslope and within home ranges)

Within the eastern slope of the Sikhote-Alin study area, the dominant habitat types were upland oak (31.5%) and Korean pine forests (27.9%) (Table 6.3). Upland birch/aspen forests were also fairly common (13.2%), whereas riverine forests were the rarest habitat type (2.3%).

The composition of habitat types within home ranges of tigers differed from availability on the eastern macroslope (four goodness-of-fit tests for each of four home ranges, $P<0.001$) (Table 6.3), and habitat composition of individual home ranges also varied significantly from each other ($T=5.7$, $P<0.01$). Tigers 1, 3, 7 and 11 lived close to the coast, where upland oak was the dominant forest type and upland birch/aspen was common. Tigress 5 lived more inland and at a higher elevation, where Korean pine forests were dominant (Table 6.3).

We found no seasonal differences in habitat selection by tigers ($T=0.58$, $P>0.25$) so data from both seasons were combined for further analyses. Tigers selected habitat types non-randomly in comparison to availability on the eastern macroslope ($T=3.25$, $P<0.01$). Although riverine forests made up only a small percentage of the available habitat, they were strongly preferred at the second order of selection (Table 6.3). Spruce-fir, Korean pine and human landscapes tended to be selected against, while upland oak, upland birch/aspen and larch habitats were used roughly in accordance with their abundance (Table 6.3).

Tigers were selective at the third order of habitat selection (within home ranges) as well, although the level of significance indicated a less robust association ($T=2.73$, $P<0.05$), and there was a greater tendency for neutral selection. Within home ranges, riverine forests appeared to be most strongly preferred, although they comprised only a small percentage of the available habitat (Table 6.3).

Table 6.4. *Seasonal variation in mean elevation of Amur tiger locations in comparison to random locations within the eastern macroslope (second-order spatial scale) and within home ranges (third-order spatial scale) of the Sikhote-Alin Mountains, 1992–95*

	Elevation (m)											
	Tiger locations						Random points					
							Eastern macroslope (second-order)			Within home range (third-order)		
	Summer			Winter								
	n	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE
Female 1	77	255[a]	18	74	210[a]	17	77	456[b]	29	77	278[a]	22
Female 3	73	369[a]	20	40	371[ab]	26	73	451[b]	30	73	346[a]	14
Female 5	63	590[a]	23	76	433[ab]	15	76	451[b]	29	76	616[a]	17
Female 7	86	194[a]	14	124	212[a]	12	124	414[b]	21	124	219[a]	14
Male 11	58	248[a]	26	115	262[a]	16	115	416[b]	24	115	276[a]	25

[ab] For each tiger, means with different letters are significantly different, based on *a posteriori* Tukey pair-wise comparisons after an ANOVA determined overall significant differences ($P < 0.05$).

Human-impacted landscapes tended to be selected against (Table 6.3), whereas tigers used upland oak, upland birch/aspen, larch and spruce-fir roughly in accordance with their abundance. Korean pine and spruce-fir forests appeared to be avoided at the second order, but were used approximately in amounts equal to availability within home ranges, especially by tigress 5, which was the only animal with substantial tracts of Korean pine habitat within her home range.

Home ranges of four of five tigers were significantly lower than the average elevation within the eastern macroslope, and summer and winter tiger locations were significantly lower than mean elevation within the macroslope study area in six of eight comparisons (Table 6.4). However, the elevation of summer locations for all five tigers and elevation of four out of five tigers' winter locations did not vary from random locations within their respective home ranges (Table 6.4). The mean elevation of winter and summer tiger locations was not significantly different (i.e. tigers did not move to lower elevations in winter to avoid deep snow) except for female 5 (Table 6.4), whose home range was situated high, abutting the crest of the Sikhote-Alin. Mean elevation within her home range was greater than average along the eastern macroslope, and mean elevation of her summer locations was also greater. In winter, however, she selected lower elevations.

Distance from water appeared to be an unimportant parameter determining tiger locations; there were no significant relationships at any level of analysis (Table 6.5).

Tigers selected slopes that were significantly less steep than the average slope over the entire eastern macroslope (Table 6.6). Slope selection by tigers differed from the average within home ranges only when mean home range slope approached that for the eastern macroslope (i.e. for tigers 1, 3, and 5) (Table 6.6). Selection of slopes by tigers did not vary between seasons but, in general, tigers avoided steep slopes.

No tiger demonstrated preferences for specific aspects in summer or winter except female 7, who preferred east and south slopes and avoided north slopes in winter (Table 6.7). Winter selection of aspect by female 7 was also significantly different from available aspects within the eastern macroslope (but not within her home range) with the same pattern (avoidance of north slopes and preference for east and south slopes). No other tigers showed any such trend (Table 6.7).

Across the eastern macroslope, there was a

Table 6.5. *Seasonal variation in distance from water of Amur tigers in comparison to random locations within the eastern macroslope (second-order spatial scale) and home ranges (third-order spatial scale) of the Sikhote-Alin Mountains, 1992–95*

	Distance to water (m)											
	Tiger locations						Random points					
							Eastern macroslope (second-order)			Within home range (third-order)		
	Summer			Winter								
	n	mean	SE	n	mean	SE	n	mean	SE	n	mean	SE
Female 1	77	361	29	74	349	29	77	357	32	77	381	31
Female 3	73	351	36	40	258	44	73	358	33	73	334	32
Female 5	63	325	32	76	252	28	76	357	32	76	329	30
Female 7	86	373	31	124	363	24	124	369	25	124	366	24
Male 11	58	359	35	115	330	27	115	367	25	115	337	25

[a,b] For each tiger, means with different letters are significantly different, based on *a posteriori* Tukey pair-wise comparisons after an ANOVA determined overall significant differences ($P < 0.05$). Rows with no letters indicate no overall significant differences.

Table 6.6. *Seasonal selection of slope by Amur tigers in comparison to mean slope within the eastern macroslope (second-order spatial scale) and within home ranges (third-order spatial scale) of the Sikhote-Alin Mountains, 1992–95*

	Slope (degrees)									
	Tiger locations						Area (spatial scale)[c]			
							Eastern macroslope (second-order)		Within home range (third-order)	
	Summer			Winter						
	n	mean	SE	n	mean	SE	mean	SD	mean	SD
Female 1	77	10.6[ab]	0.9	74	10.0[ab]	0.9	15.0	10.0	13.6	9.4
Female 3	73	12.6[ab]	0.9	40	10.2[ab]	1.3	15.0	10.0	16.0	9.8
Female 5	63	11.7[ab]	1.0	76	12.3[ab]	1.0	15.0	10.0	15.5	10.0
Female 7	86	9.7[b]	0.9	124	10.4[b]	0.8	15.0	10.0	10.4	9.0
Male 11	58	11.3[b]	1.6	115	10.3[b]	0.9	15.0	10.0	10.4	9.0

[a] Tiger locations significantly differ from the average slope within the home range, based on one-sample *t*-tests.
[b] Tiger locations significantly differ from the average slope on the eastern macroslope, based on one-sample *t*-tests.
[c] Summary statistics from digital elevation model for home ranges and eastern macroslope.

significant correlation between habitat selection by tigers and red deer ($r=0.712$, $P<0.05$) and tigers and wild boar ($r=0.757$, $P<0.05$), but not between tigers and roe deer ($r=0.388$, $P>0.20$).

Estimates of ungulate use of many habitat types within tiger home ranges were not available because those habitats comprised such a small percentage of tiger home ranges that they were not sampled for ungulate density (Table 6.8). The confidence interval for the median difference in ranks of ungulate habitat use and tiger habitat preference included 0 (1±1) indicating no significant difference in habitat selection by tigers and ungulates. Missing values (i.e. habitats not sampled) precluded a more

Table 6.7. *Seasonal selection of aspect by 5 radio-collared Amur tigers in comparison to available aspects within home ranges and within the eastern slopes (macroslope) of the Sikhote-Alin Mountains, 1992–95*

Tiger home range/ eastern macroslope	Aspect	% used summer[c]	% used winter[c]	% available[c]
Female 1	(n)	(77)	(74)	(151)
	N	27.3	16.2	20.1
	E	28.6	25.7	33.5
	S	26.0	28.4	24.6
	W	18.2	29.7	21.8
Female 3	(n)	(73)	(40)	(113)
	N	16.4	15.0	17.6
	E	23.3	27.5	24.4
	S	31.5	27.5	31.1
	W	28.8	30.0	26.9
Female 5	(n)	(62)	(76)	(138)
	N	24.2	18.4	25.7
	E	22.6	35.5	22.3
	S	32.3	23.7	24.3
	W	21.0	22.4	27.7
Female 7	(n)	(86)	(124)	(210)
	N	26.7[a]	12.1[b]	16.7[a]
	E	26.7[a]	36.3[b]	31.5[ab]
	S	30.2	35.5	26.6
	W	16.3[ab]	16.1[a]	25.2[b]
Male 11	(n)	(58)	(115)	(173)
	N	19.0	18.3	16.9
	E	37.9	27.0	29.5
	S	29.3	28.7	33.9
	W	13.8	26.1	19.7
Eastern macroslope[d]	N	—	—	24.6
	E	—	—	28.8
	S	—	—	24.1
	W	—	—	22.5

[ab]For each tiger, values with different letters within a row indicate where largest cell chi-square values contributed to significant overall chi-square goodness-of-fit values.
[c]No sample size because values are based on the sum of values generated by the digital elevation model.

powerful test, but results suggest only moderate concordance in winter habitat use by tigers and prey within home ranges (Table 6.8).

Although tigers demonstrated strong year-round fidelity to home ranges, all tigers demonstrated some seasonal shift in home range boundaries, and shifts in mean locations. Although tigers remained within the same basic home range, overlap of summer and winter home ranges did not exceed 70% for any of the five tigers (Table 6.9). These relatively low measures of overlap are partially due to biases associated with small sample sizes. The minimum convex polygon method is sensitive to sample size, and our initial analyses suggest that greater sample sizes may be necessary before the size of minimum convex polygons begin to

Table 6.8. Ranks of prey abundance and tiger preference (use versus availability) in winter for 5 habitat types, and the difference in those two ranks within home ranges of 5 Amur tigers on the eastern slope of the Sikhote-Alin Mountains, 1992–95

Relative prey abundance and tiger habitat preferences within home ranges[a]

	Tigress 1			Tigress 3			Tigress 5			Tigress 7			Tiger 11		
	Prey[b] (rank)	Tiger[c] (rank)	Difference[d] (tiger–prey)	Prey (rank)	Tiger (rank)	Difference (tiger–prey)	Prey (rank)	Tiger (rank)	Difference (tiger–prey)	Prey (rank)	Tiger (rank)	Difference (tiger–prey)	Prey (rank)	Tiger (rank)	Difference (tiger–prey)
Riverine	2	2	0	1	2	1	3	1	-2	2	2	0	2	2	0
Birch/aspen	4.5	4	-0.5	3	1	-2	1	2	1						
Upland oak	1	1	0	2	3	1				1	1	0	1	3	2
Larch	4.5	3	-1.5							3	3	0	3	1	-2
Korean pine	3	5	2				2	3	1						

[a] Missing values indicate habitat was not present in home range or was inadequately sampled.
[b] Habitat with highest prey density = 1.
[c] Habitat most preferred by tiger = 1.
[d] Zero differences indicate concordance of habitat selection by tigers and relative prey density.

Table 6.9. *Seasonal home range size (95% minimum convex polygon estimates) and fidelity to location (% overlap of summer and winter home ranges) of five radio-collared Amur tigers in Sikhote-Alin Zapovednik, 1992–95*

Animal	Summer home range		Winter home range		Overlap[a]	
	n	(km²)	n	(km²)	(km²)	(%)
Female 1	103	353	76	302	225	53
Female 3	77	413	40	203	155	34
Female 5	65	224	81	172	128	48
Female 7	88	245	145	227	190	68
Male 11	59	235	129	288	208	66

[a] Total area (summer and winter home ranges combined) that includes both summer and winter home ranges.

Table 6.10. *Differences in mean coordinates of locations of five radio-collared tigers in summer and winter in Sikhote-Alin Zapovednik, 1992–95*

		Seasonal difference in mean coordinates			
		x coordinate		y coordinate	
Tiger	df	Test statistic F	Mean difference (km)	Test statistic F	Mean difference (km)
Female 1	177	33.19	6.2***	0.04	0.2
Female 3	116	1.27	1.4	7.67	3.0**
Female 5	145	30.62	3.5***	51.60	6.6***
Female 7	231	0.23	0.4	0.01	0.1
Male 11	187	14.14	3.3***	9.85	2.2**

* Significant difference in seasonal mean coordinates, based on t-tests ($P < 0.05$).
** ($P < 0.01$).
*** ($P < 0.001$).

asymptote (Miquelle *et al.* unpubl. data). Even with five animals, there was a strong correlation between total sample size and degree of seasonal overlap ($r^2 = 0.87$, $P < 0.02$). No doubt, with larger sample sizes, overlap of summer and winter home ranges would increase, reinforcing the argument of strong seasonal fidelity to a single home range.

There were significant shifts in the mean x and/or y coordinates for summer and winter locations for four of five tigers (Table 6.10). The largest differences (for tigresses 1 and 5) were largely artefacts of seasonal localisation during denning. The largest linear shift of mean locations (6.6 km) was still relatively small in comparison to total home

range dimensions. Nonetheless, tigers did show small but significant shifts in mean coordinates of locations between summer and winter.

Discussion

First order habitat selection (geographical distribution)

In assessing the four hypotheses associated with first order selection (Table 6.1), we found:

1   Amur tiger distribution was associated closely with red deer distribution, but there

was poor association between tigers and wild boar, another prey species considered 'key'.

2   A combination of two prey species, especially red deer and any other prey, did increase the strength of the relationship between prey and tiger distribution.

3   Distribution of preferred habitat for key prey species was an accurate predictor of tiger distribution.

4   Amur tiger distribution was poorly related to what has been considered a 'key' habitat type, namely Korean pine.

Amur tiger distribution is closely associated with prey distributions. There has been a long-standing debate on the relative importance of red deer versus wild boar in the diet of Amur tigers (Abramov 1962; Pikunov 1981; Kucherenko 1985; Yudakov & Nikolaev 1987). Our results concur with those of Matyushkin (1992) in that red deer distribution appears to be the strongest predictor of tiger distribution in Russia. However any combination of red deer and a second prey species improves the overall relationship (Table 6.2). In the case of roe deer and red deer, the strength of the relationship is likely to be an artefact of excluding low-density prey areas from the analysis. Density of roe deer is largely inversely related to that of red deer and wild boar; roe deer reach highest densities in fragmented landscapes that include agricultural production areas, whereas red deer and boar reach highest densities in predominately forested areas. The cumulative result, in terms of our analysis, is that roe deer 'fill in' the distribution map where tigers occur and red deer and boar are found at low density. The same is true, although to a lesser extent, for sika deer. Therefore, although the weighted means of red deer and boar versus red deer and roe deer are nearly equivalent (67 and 68%), we believe that the first value may be more meaningful biologically. Roe deer make up a relatively small percentage of the diet of tigers throughout their range in Russia (Miquelle et al. 1996b). Although the strength of the relationship between elk, boar and tiger distributions is likely to be greater if low density contours were included in the analysis, exclusion of low-

density areas provided a more powerful means of assessing the relative value of each prey species in predicting tiger distribution.

Moose distribution was a poor predictor of tiger distribution, even within our limited (for moose) study area. Moose distribution extends far to the north of our defined study area, and extension of the area of study to include all moose habitat would show a very low, and in fact inverse, correlation between tiger and moose distribution.

Our finding that habitat preferences of prey can be used with the same reliability as prey distributions themselves should be viewed with caution for two reasons. First, elimination of low-density contours in the analysis provided greater discriminative powers in discerning differences between prey species, but suggested weaker associations than actually existed. Because it is a multi-prey system, tigers will occur in regions even if one species is at a lower density. Secondly, because our definition of prey distribution is dependent on distribution of prey habitat, there is some redundancy in the comparison of prey distribution versus prey habitat distribution, and the results have an inherent bias towards stronger associations with habitats. Mapping preferred prey habitat can give a meaningful picture of 'potential' tiger habitat, but it may not be a good predictor of tiger presence because the presence of prey habitat does not always equate with presence of prey. Therefore, it is dangerous to make predictions on tiger distribution based solely on existence of prey habitat; some assessment of the habitat must be made to determine the status of prey populations and human disturbance in those regions.

Contrary to earlier assessments, Amur tigers do not appear to be closely tied to Korean pine forests per se. Distribution of Korean pine habitat has decreased dramatically due to repeated fires over the past century and intensive harvesting in the last half century (Budzan 1996; Kolosova & Kondrashov 1996; Petropavlovski 1996). Tiger distribution was probably more closely related to Korean pine forests prior to these disturbances, but the fact that tigers have thrived while Korean pine forests have decreased in distribution and quality is evidence

that tigers are not dependent on this forest type. Red deer and tigers thrive in a variety of forest types; wild boar may be more dependent on pine mast crops for winter survival (Bromley 1964).

The northernmost distribution of tigers is tied closely to the northern distribution of red deer and wild boar (Kucherenko 1985; this analysis). Red deer and wild boar are in turn linked clearly to temperate forest complexes in the Russian Far East: where spruce-fir and larch forests become dominant in the north and along the crest of the Sikhote-Alin Range (Fig. 6.2), these ungulates are rare or absent, especially in winter. Thus the distribution of this complex of parameters – temperate forests, red deer and wild boar – appear to define the northern limits of tiger distribution.

Second and third order selection (habitat selection within the eastern macroslope and within home ranges)

Our results demonstrate that the spatial scale of analysis has important consequences in interpreting habitat selection data. Spruce-fir and larch forests appeared to be selected in direct relation to abundance (neutral selection) within home ranges (third order spatial scale) (Table 6.3). Across the eastern macroslope landscape (second order spatial scale), larch still appeared to be used in relation to abundance, but spruce-fir forests were avoided. Finally, over the whole tiger range (first order spatial scale), distribution of both larch and spruce-fir forests is clearly inversely related to distribution of tigers and prey (Fig. 6.2). Although this pattern seems intuitively contradictory, it is not unlikely. Patches of larch or spruce-fir within a home range may represent unique habitats that provide parameters selected by a particular animal when they occur in limited amounts (e.g. tigress 1 gave birth to her first litter in a larch stand) but, at another scale, that forest type may be associated negatively with overall distribution. Relative abundance of habitats, at the landscape level and within home ranges, also no doubt affects use-availability analyses: Korean pine forests appeared to be avoided by radio-collared tigers when availability was low, but tigress 5 showed a slight preference for that forest type when it represented 61% of available habitat (Table 6.3).

Hypotheses pertaining to second and third order selection relate either to selection for habitat parameters *per se* (hypotheses 1–3 second and third order, hypothesis 6 third order), or selection for habitat parameters that relate to prey distribution (hypotheses 4–5 second and third order, hypotheses 7–8 third order) (Table 6.1). We review hypotheses within these two broad categories to compare the relative importance of factors driving selection at these two spatial scales.

At the second order spatial scale, an animal should attempt to include within its home range those parameters that increase the potential for reproduction success. Indeed, tigers selected home range locations with a composition of habitat types (hypothesis 2) and habitat parameters (hypothesis 3) different from that of random points within the eastern macroslope. Habitat type (hypothesis 1, second order), elevation (hypothesis 3a), and slope (hypothesis 3c) appeared to be important variables that were incorporated into the 'decision-making process' of home range selection.

Evidence for selection of habitat parameters within home ranges (at the third level of analysis) was not as strong as that for second order selection. For instance, habitat preferences were not as pronounced at the third order, i.e. there was a stronger tendency for habitat types to be used in amounts equal to their availability within home ranges. Where selection occurred at the third order, it was often manifested in winter, or when values of parameters within specific home ranges approached those across the eastern macroslope. For example, although tigers selected for lower than average elevations across the eastern macroslope (second order selection), only one tigress preferred lower than average elevations within her home range, in winter only. Tigers avoided steep slopes in comparison to the average slope within the eastern macroslope, but preference at the third order was demonstrated only when the average slope within home ranges approached that of the entire macroslope.

The strength of the relationship between habitat

selection by tigers and habitat selection by their prey varied with the scale of analysis. At the second order of selection, there was a significant correlation in habitat selection between tigers and red deer, and between tigers and wild boar, but no correlation between tigers and roe deer. This relationship is expected given the results of the first order analysis, and the knowledge that red deer and boar are the dominant prey species (Matyushkin 1992; Miquelle *et al.* 1996b). Tigers should select home range locations that correlate with presence of prey.

At the third order of selection, while there were no significant differences between tigers and prey, absence of data for many habitat types precluded a more powerful test. We consider this analysis only a preliminary assessment, and believe that what data exist suggest that the relationship between tiger and prey habitat selection within home ranges is not strong.

It is not known whether the observed shifts in location of seasonal home ranges (hypothesis 5, second order) are a true representation of tiger movements, or an artefact of inadequate sampling. A longer term data base in the study areas (J. M. Goodrich *et al.* unpubl. data) suggests the later, and that home ranges are in most cases stable over years and through seasons. Similarly, observed shifts in central tendency within home ranges (hypothesis 5, third order) may relate to factors other than prey distribution (e.g. birthing and associated localisations). Perhaps these hypotheses are ill-defined, because it is not known whether seasonal ungulate movements occurred within tiger home ranges, or whether ungulates migrate in and out of tiger home ranges, resulting in a seasonally fluctuating density of prey for an individual tiger. Available evidence suggests that wild boar can move far greater distances than the diameter of tiger home ranges in search of winter mast crops (Bromley 1964). Less is know about seasonal movements of red deer in this region. Despite the potential for fluctuating prey abundance, available evidence suggests that Amur tigers within the study area show high site fidelity.

With the exception of one animal, tigers did not move to lower elevations in winter (hypothesis 7, third order), and did not use south slopes more in winter (hypothesis 8), as would be expected if tigers were 'tracking' distribution of prey.

Some caution is required in interpreting some of our results, especially with second order analyses. In many cases, our analyses are hampered by inadequate sample size. The five tigers incorporated in this analysis are obviously not representative of all tigers within Amur tiger range, and are unlikely to be representative of all tigers within the eastern macroslope study area. Tigers are distributed over a broader range of habitats than indicated in our analysis. Nonetheless, given that larger sample sizes for such an analysis are unlikely to be available in the near future, we believe that the attempt to understand habitat selection criteria of tigers at several spatial scales has value and important conservation implications.

We propose that prey density and distribution, and habitat parameters associated with prey, are the key factors driving first and second order habitat selection, but have only an indirect influence on third order selection. That is, geographical distribution of tigers and the locations of tiger home ranges within the landscape are determined by a set of habitat types and habitat parameters that are linked closely to distribution of prey, but within a home range there is relatively little selection for specific parameters. We believe this generality may extend across much of tiger habitat. Exceptions will occur where there are extreme environmental challenges other than prey density. For Amur tigers, selectivity within the home range is likely to be more pronounced on the western macroslope of Sikhote-Alin Mountains, especially in the northern limits of Amur tiger distribution. In these places, deeper snow and colder weather may force tigers to seek habitat parameters that mitigate those factors (Kucherenko 1985). On the eastern macroslope, moderate temperatures and relatively low snow depths probably do not impose serious constraints on tigers. In the arid Panna region of India, tigers are apparently closely tied to water (R. Chundawat *et al.* this volume), a factor that likely affects home range location (second order selection) and selection of sites within home ranges (third order selection). Therefore, while third order selection of

habitat parameters within home ranges may be important in extreme conditions, we predict that under most conditions tigers will show little selection at this spatial scale. Selectivity will be reduced within home ranges by other mitigating factors.

In the absence of human-induced mortality and disturbance, the geographical distribution of all subspecies as well as the distribution and relative abundance of tigers within their range are driven by prey distribution and density; but within an individual's home range, habitat selection is driven, for females, by the need to maintain a home range that ensures cub production and survival, and, for males, by the need to obtain access to females. Neither of these constraints is necessarily related to structural components of the habitat, habitat types, or directly to prey density (see below).

Both female and male tigers in Nepal and the Russian Far East have demonstrated site fidelity and territoriality (McDougal 1977; Sunquist 1981; Smith *et al.* 1987a; this chapter, D. G. Miquelle *et al.* in prep. and J. M. Goodrich *et al.* unpubl. data). Maintenance of an exclusive home range (territory) appears to be an important component of tiger social structure (although it is unclear if territoriality is a characteristic of all tiger populations, e.g. N. Franklin *et al.* this volume), and may be a defining element of reproductive success. If this hypothesis is true (or for populations where this is true) we predict that selection of preferred habitats and habitat parameters within a home range will be tempered by the cost of maintaining the integrity of the territory. Scent-marking and 'patrolling' are costs associated with maintaining a territory (Yudakov & Nikolaev 1987; Smith *et al.* 1989; Matyushkin 1992) and may require use of areas that do not necessarily contain high prey density or include preferred habitat. We predict that this pattern should be most consistently demonstrated by females. Males may also attempt to maintain exclusive access to females by maintaining territories (e.g. Smith *et al.* 1987a), but male competition for access to mates could be expressed in a variety of ways.

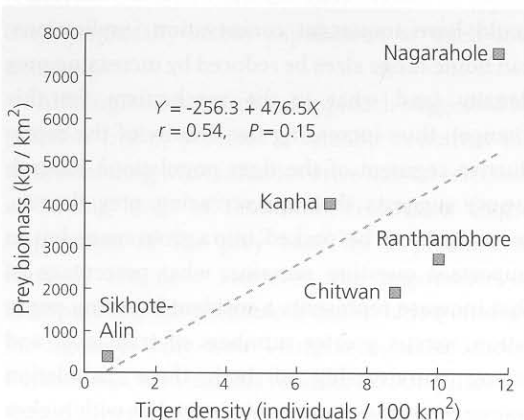If prey biomass is a key variable driving second order selection by tigers, then home range size

$Y = -256.3 + 476.5X$
$r = 0.54,$ $P = 0.15$

FIGURE 6.5
Relationship between prey biomass and tiger density across tiger range. Data from Karanth (1991), and Miquelle & Myslenkov (unpubl. data).

should be directly related to prey density. Across tiger range, there is insufficient information to assess this relationship. Only two 'data points' exist: in Chitwan National Park, Nepal, where ungulate biomass is nearly 2000 kg/km² (Tamang 1982), home ranges of female tigers average 20.7 km² (Smith *et al.* 1987a); and in Sikhote-Alin Zapovednik, Russia, where ungulate biomass is less than 400 kg/km², female home ranges are an order of magnitude larger (D. G. Miquelle *et al.* this volume, chapter 19). We predict that while prey density fluctuates greatly across tiger range, the total available prey biomass within the female home range size should be fairly consistent.

A related measurement does exist, indicating a clear relationship between prey biomass and tiger density across tiger subspecies (Fig. 6.5). Although this relationship is not statistically significant ($r=0.54$, $P=0.15$), given the small sample size, biases and methodological variations inherent in these datasets the relationship appears biologically meaningful.

The difference between these two relationships, tiger home range size versus prey biomass and tiger density versus prey biomass, is slight but important. An understanding of the response of a tiger population to long-term changes in prey biomass – in

terms of home range size and social structure – could have important conservation implications; can home range sizes be reduced by increasing prey density (and what is the mechanism for this change), thus increasing the density of the reproductive segment of the tiger population? Karanth (1991) suggests that by increasing prey density, more tigers can be 'packed' into a given space, but an important question remains; what percentage of that increase represents a resident breeding population, versus greater numbers of transients and young (survivorship of both these population segments would presumably be higher with higher prey density)? Changes in home range size and the number of resident animals within a 'tiger conservation unit' (Dinerstein *et al.* 1997) relate directly to changes in effective population size, while a change in density has an unknown relationship with changes in effective population size.

Management implications

What are the conservation implications of this spatial hierarchical analysis? First, distribution of tigers across their geographical range appears tied to a complex of ungulate species, as has been suggested by Seidensticker (1986). But the key prey species, i.e. where management efforts should focus, may be limited; our results are in agreement with Matyushkin (1992), suggesting that red deer are the key component in the Russian Far East, contrary to earlier assessments (Abramov *et al.* 1978; Kucherenko 1985). Secondly, 'micro-management' of habitat parameters within a tiger's home range to increase suitability is probably unnecessary. While tigers may select some components of a home range over others, the important selection process occurs at the landscape level (second order spatial scale). The one exception is where there exist extreme environmental challenges which management

The formula for the future of wild Amur tigers is straightforward: protect large blocks of habitat so that tiger populations are demographically and genetically viable; give local people a reason not to poach tigers; and give local people an incentive to support higher populations of key prey species.
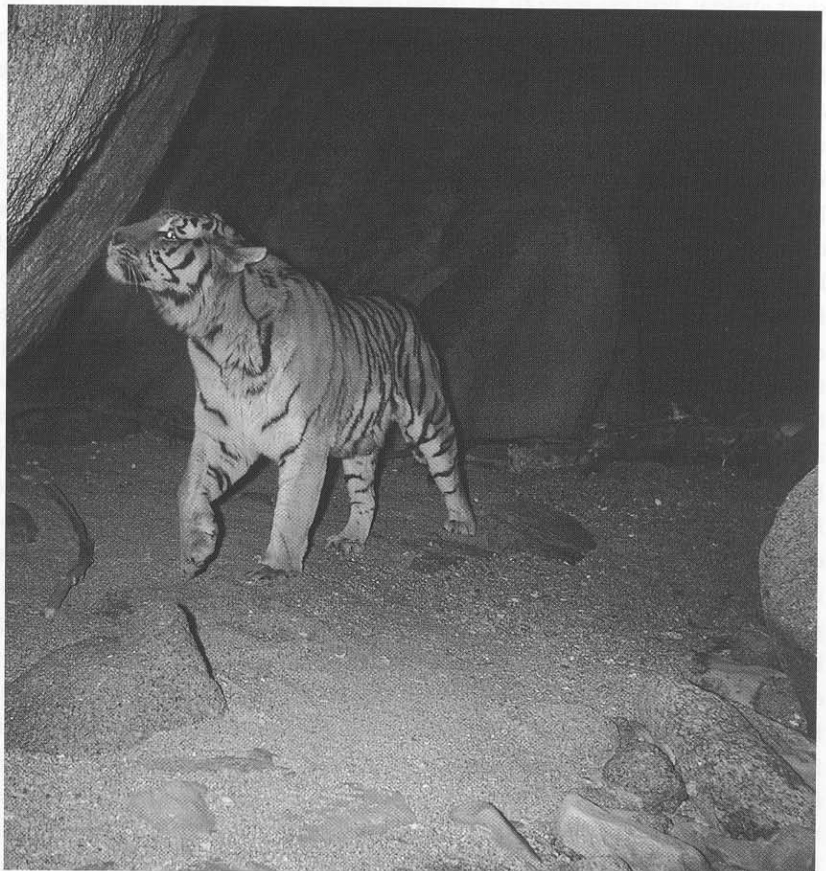
actions could mitigate, e.g. development of water sources in arid environments (Karanth 1991).

Riverine forests appeared to be highly preferred by Amur tigers at both the second and third order spatial scales. While riverine forests make up only a small proportion of the available habitat, their importance to tiger conservation is high; prey densities are often high in these habitats, especially in winter (Matyushkin 1992), and tigers use river valleys as travel corridors (Matyushkin 1977). Just as importantly, because riverine habitats are the first disturbed by human intrusion, they act as potential fragmentation points. Trails and roads are built along river bottoms, and forests are cleared for agricultural production and human settlements. Most of the large riverine forest complexes are gone in the Russian Far East. Continued clearing of riverine complexes may result in fragmentation of the Sikhote-Alin tiger population.

In addition to riverine forests, Korean pine and oak forests appear to be important for Amur tigers. Although not always 'preferred', these habitats are common (in conjunction with riverine forests they total over 50% of tiger habitat in Primorski Krai), they provide winter mast for prey species (pine nuts and acorns), and prey species can be maintained at relatively high densities in these habitats.

Although many of the details are still lacking, in general the conservation implications are clear – the higher the prey biomass, the more tigers can fit into a unit area (Fig. 6.5), and the less land is required for a given population size. Land requirements of Amur tigers – for individuals and populations – are vast because prey densities are low. Other subspecies of tigers could theoretically live at the same low densities as Amur tigers, but in most range countries the land base does not exist to support demographically stable populations at such low densities.

Although the hierarchical approach suggested by Johnson (1980) provides a valuable construct for understanding what variables drive habitat selection at varying levels of resolution, realisation of the importance of the prey base for a predator is certainly not new. However, the importance of incorporating the prey into a conservation strategy for tigers is only now being recognised (K. U. Karanth & B. M. Stith this volume; M. Sunquist et al. this volume). Ungulate management is an integral component of tiger conservation. Prey density is one of the critical issues in the Russian Far East today due to intensive legal and illegal harvest by humans. Similar situations exist elsewhere (Rabinowitz 1989; K. U. Karanth & B. M. Stith this volume). Biologists, conservation organisations, funding organisations, and policy makers need to focus on this issue. We need to protect habitat at the local level for ungulates as much as for tigers; we need to manage habitat for ungulates, not tigers; and we need to make responsible ungulate management worthwhile to local hunters and the local communities. It is not essential to define tiger habitat except in terms of defining it for the key prey species. The formula is straightforward: (1) protect large blocks of habitat so that tiger populations are demographically stable and genetically viable; (2) give local people a reason not to poach tigers; and (3) give the local people an incentive to support higher populations of key prey species. If the prey species are there, and poaching is minimised, the land will support tigers.