An Ecology-Based Method for Defining Priorities for Large Mammal Conservation: The Tiger as Case Study

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Abstract: *The disappearance of large vertebrates in the tropical belt may be the next biological insult of the global extinction crisis. Large predators and their prey are at particular risk in Asia, where they are threatened by poaching and habitat loss. To facilitate the best use of limited conservation resources, we created an objective, ecology-based method for identifying priority areas for conservation that incorporates both habitat representation and landscape-level features. Using tigers as an example, our method captures the range of ecological habitats where they occur, accounting for ecological, demographic, genetic, and behavioral differences. Our analysis is hierarchical. We divided the tiger range into distinct bioregions and identified tiger habitat types within each. We then delineated tiger conservation units throughout the bioregions and ranked the units based on habitat integrity, poaching pressure, and tiger population trends. To maintain representation of tiger populations and their ecology in the different tiger habitats, we made comparisons only among tiger conservation units from the same tiger habitat types nested within the same bioregion. We identified 159 tiger conservation units in three bioregions—the Indian subcontinent, Indochina, and Southeast Asia. We ranked the units in three categories that reflect the probability of long-term persistence of tiger populations (highest in level I units). Twenty-five tiger conservation units were classified as level I, 21 as level II, and 97 as level III. An additional 16 tiger conservation units for which little information is available were identified for immediate surveys. Levels I, II, and those identified for immediate surveys are the priority areas for immediate funding and for a regional tiger conservation strategy. One feature emerging from the study showed that protected areas cover only small areas of tiger conservation units. If the long-term prospects for tiger conservation are to improve, poaching must be stopped and protected areas increased in number, linked, and buffered by natural habitats. To enhance landscape integrity, the priority tiger conservation units that straddle international borders should be managed as transboundary reserves, giving tiger conservation a stronger regional structure. Like tigers, populations of other wide-ranging mammalian carnivores and large herbivores also are declining due to poaching and loss of habitat. The method we present for tigers can be adapted readily to improve conservation strategies for these species as well.*

Método con Bases Ecológicas para Definir Prioridades para la Conservación de Mamíferos Mayores: El Tigre como Caso de Estudio

Resumen: *La desaparición de vertebrados grandes en el cinturón tropical podría ser el siguiente insulto biológico de la crisis de exteinción global. Los depredadores grandes y sus presas se encuentran en un riesgo particular en Asia donde la caza furtiva y la pérdida de hábitats los amenaza. Para facilitar el mejor uso de*

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los limitados recursos de conservación, hemos creado un método objetivo con bases ecológicas que incorpora tanto la representación del hábitat, como las características a nivel de paisaje en la identificación de áreas prioritarias para conservación. Utilizando tigres como ejemplo, nuestro método captura el rango de hábitats ecológicos donde los tigres pueden estar presentes tomando en cuenta diferencias ecológicas, demográficas, genéticas y de conducta. Nuestro análisis es jerárquico. Dividimos el rango de los tigres en bioregiones distintas e identificamos tipos de hábitat para tigres dentro de estas regiones. Posteriormente delineamos unidades de conservación de tigres a lo largo de las bioregiones y organizamos por rangos las unidades en base a la integridad del hábitat, presión por caza furtiva y tendencias de las poblaciones de tigres. Para mantener la representación de las poblaciones de tigres y su ecología en los diferentes hábitats, únicamente hicimos comparaciones entre unidades de conservación de tigres del mismo tipo de hábitat para tigres, anidados dentro de una misma bioregión. Identificamos 159 unidades de conservación de tigres en tres bioregiones—el subcontinente Indú, Indochina y Sur de Asia. Organizamos por rangos las unidades en tres categorías que reflejan la probabilidad de persistencia a largo plazo de poblaciones de tigres (los mayores en unidades de nivel I). Veinticinco unidades de conservación de tigres fueron clasificadas como nivel I, 21 como nivel II y 97 como nivel III. Dieciséis unidades de conservación de tigres adicionales con poca información viable fueron identificadas para muestreo inmediato. Los niveles I y II y aquellos identificados como muestreos inmediatos son áreas prioritarias para financiamiento immediato y para una estrategia de conservación de tigres. Una característica emergente en el estudio muestra que áreas protegidas cubren únicamente áreas pequeñas de unidades de conservación de tigres. Si las perspectivas a largo plazo para la conservación de tigres van a mejorar, la caza ilegal debe ser detenida y las áreas protegidas incrementadas en número, ligadas y amortiguadas por hábitats naturales. Para mejorar la integridad del paisaje, las unidades prioritarias de conservación de tigres que presentan fronteras internacionales deberán ser manejadas como reservas transfronterizas otorgándole a la conservación de tigres una etsructura regional mas fuerte. Así como los tigres, poblaciones de otros carnívoros de amplio rango y herbívoros grandes estan en disminución debido a la caza furtiva y la pérdida del hábitat. El método que presentamos para tigres puede ser adaptado fácilmente para mejorar también las estrategias de conservación de estas especies.

Introduction

Large mammalian predators and large herbivores exert a strong influence on community structure within the diverse range of habitats they occupy (Owen-Smith 1988; Dinerstein 1992), so their extirpation from an ecosystem is of grave ecological concern. Protecting wide-ranging megafauna requires taking the "representation" approach designed for habitat conservation and adapting it to species conservation, so that we not only conserve individual populations but also the suite of adaptations and ecological interactions associated with them.

We offer a new method to rank areas with the greatest potential for conserving individual species. The goal is to conserve a representative sample of areas that captures the full range of ecological roles occupied by the species of interest. By conserving these representative priority areas, we can conserve populations of these species that are genetically, behaviorally, demographically, and ecologically distinct. We use the tiger to illustrate this ecologically representative approach to setting conservation priorities. The method, however, is easily adaptable for use with other widely distributed megafauna, such as such as cheetahs, pumas, lions, wolves, bears, elephants, and black rhinoceros, that occupy a range of different habitat types.

The tiger is one of the most threatened large carnivores in the world, and its numbers are decreasing rapidly in many areas. The rapidly increasing human populations and the loss and degradation of natural habitat across Asia (Dinerstein & Wikramanayake 1993) suggest a grim future for tigers. The past 5 years have witnessed an intensification of threats to tigers because of rampant poaching of tigers and their prey and intensive logging in valuable tiger habitat (Nowell & Jackson 1996). Although all areas containing tigers are worthy of conservation effort and support, available funds and personnel are insufficient to protect them adequately. Thus, it is essential that conservationists direct most resources toward conserving the tiger populations that have the highest probability of long-term persistence.

The traditional approach to conserving tiger populations strives to preserve subspecies (Seal et al. 1987; Seal 1991). But the phenotypic characteristics on which the subspecific taxonomy is based—body size, pelage color and pattern, and cranial morphometrics—may not be reliable enough to warrent a subspecific classification (Hemmer 1987; Herrington 1987; Kitchener 1998). Instead, we recognize that, in seeking to conserve representative populations of tigers, we must consider not only the genetic distinctiveness of tigers across their range but also behavioral, demographic, and ecological distinctiveness. This has the additional benefit of not only considering the tiger as an organism but also giving prominence to the ecological value of tigers as top predators in ecosystems and their role as "umbrella species" for conservation of other species and ecological processes.

We promote the use of long-term trends, rather than absolute numbers, to evaluate the conservation potential of tiger populations. Previous approaches have relied on mathematical models and computer simulations using population numbers to evaluate the viability of tiger populations (Seal 1990, 1991; Smith & McDougal 1991; Tilson 1993; Wiese et al. 1993). Felids are extremely difficult to census, and the results are often unreliable unless a great deal of time and effort is invested in the process (Karanth 1987; Nowell & Jackson 1996).The ability of population viability analyses (PVA) to simulate real-life situations is also limited (Ewens et al. 1987; Soulé 1987; Ralls et al. 1988; Boyce 1992; Caughley 1994). Therefore, we suggest that 10-year demographic trends of tiger populations are a convenient and biologically sound alternative for assessing population status. These general trend estimates are more easily obtained from field staff and people familiar with local conditions than absolute numbers of animals, and they likely reflect an equally precise status of tiger populations. Trends also reflect trajectories, which are important for conservation planning and management.

The historical demographies of many tiger populations severely depleted by poaching (e.g., India, Nepal, and the Russian Far East) have shown that if poaching is reduced or eliminated through protection, and if water and food are available, tiger populations can recover relatively rapidly (Mishra et al. 1987; Panwar 1987; Spitsin et al. 1987). Tigers, along with wolves, are two large predators that breed faster than their prey. Thus, we do not downgrade the importance of populations highly depleted through poaching.

Finally, many of Asia's protected areas are relatively small and isolated (Dinerstein & Wikramanayake 1993). The chances for long-term survival of megafauna in many of these protected areas are slim (Seidensticker 1987; Rabinowitz 1993) unless they are linked by natural habitat corridors to permit dispersal of tigers and their prey and are buffered to minimize impacts from other land uses. Therefore, a landscape-level approach accomodating corridors and buffer zones is essential to a long-term tiger conservation strategy (Karanth 1991; Karanth & Sunquist 1995; Nowell & Jackson 1996). Our method incorporates these landscape-scale features as variables in ranking conservation priorities.

Methods

Framework Approach

Our method has a hierarchical framework (Fig. 1), allowing us to maintain representation of tiger ecology and tiger habitat. We first divided the extant tiger range into five bioregions: Indian subcontinent, Indochina, South-

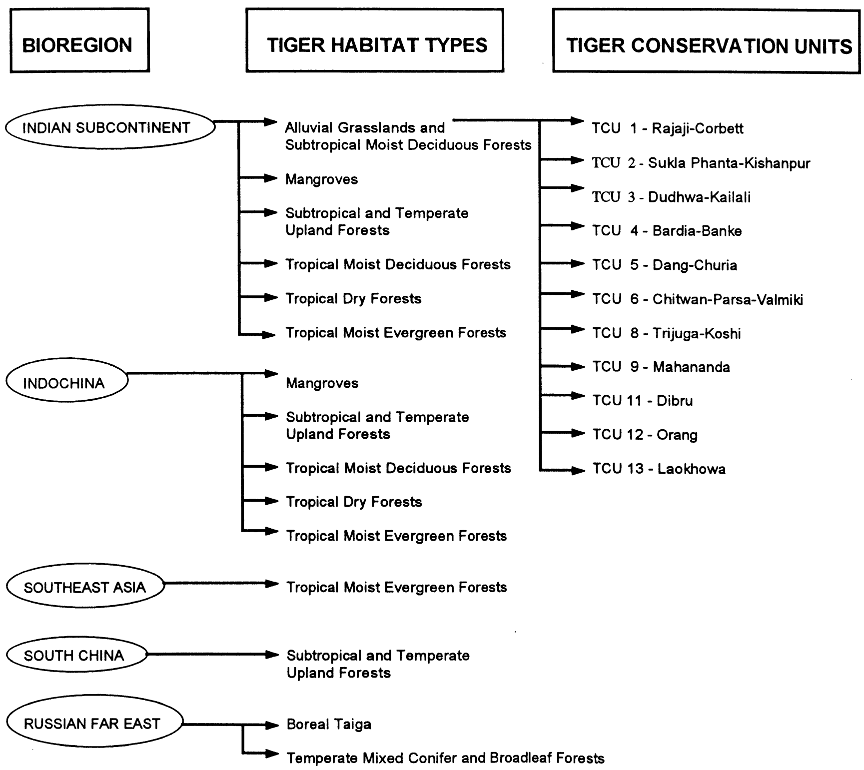


Figure 1. Framework structure showing hierarchical relationships between bioregions, tiger habitat types, and tiger conservation units (TCUs). The TCUs are shown only for the alluvial grasslands and subtropical moist deciduous forest tiger habitat type.

east Asia, south China, and the Russian Far East. Bioregions provide a first level of stratification so that tiger populations from different regions are not compared. We focus on three of the five bioregions because they best illustrate our method. We did not include the Russian Far East bioregion because there is evidence that, from the perspective of tiger dispersal, the entire region consists of a single connected landscape, or tiger conservation unit (Dinerstein et al. 1997). Our knowledge of the distribution of tigers in southern China is so marginal and the remaining population of tigers in south China is apparently limited to such a small area that priority setting is academic. The boundaries between the tropical Asian bioregions are explained by MacKinnon and MacKinnon (1986) and Dinerstein et al. (1997).

We then identified tiger habitat types within each of these bioregions (Fig.1) to ensure that tiger populations of differing habitats would not be compared. Thus, tiger habitat types, which provide the second layer of stratification, are those where tigers are considered to have different ecological roles and to have different behavioral, demographic, and genetic characteristics (Figs. 2 & 3, inset maps).

Delineating Tiger Conservation Units

Within each bioregion we identified Tiger Conservation Units (TCUs), defined as a block or a cluster of blocks of habitat that contains or has the potential to contain interacting populations of tigers. Thus, a TCU can consist of several adjacent blocks of habitat if the configuration or the intervening area permits tiger dispersal among these blocks.

Drawing on field experience and observations, we considered 5 km of cleared or open land to be the threshold for dispersal between blocks (Dinerstein et al. 1997). A matrix consisting of degraded scrub, tall crops, and plantations, (e.g., coffee or sugar cane), and stream and river courses was considered to permit dispersal. A TCU need not be restricted to or contain protected areas. Instead, it consists of the entire landscape of natural habitats in which tigers can live, disperse, or establish themselves. This reflects the premise that an effective tiger conservation strategy should move beyond protected area boundaries.

The TCUs were delineated on maps showing remaining forest cover and type by identifying contiguous and adjacent blocks of habitats meeting the above criteria. The forest cover data were obtained from the Asian Bureau for Conservation and the World Conservation Monitoring Centre. Human-made features such as roads, railroads, settlements, and villages, from the Digital Chart of the World (Environmental Systems Research Institute 1992) were also overlayed to identify potential dispersal barriers. If habitat blocks were separated by these barriers, the blocks were placed in separate TCUs. The actual delineation of TCUs was done by using maps with scales ranging from 1:1,000,000 to 1:50,000. To calculate TCU area, we summed the areas of the intact habitat blocks within the TCU polygons; thus, the TCU area is not the size of the entire TCU polygon. This geographic information system procedure was done with workstation ARC/INFO.

Scoring Tiger Conservation Units

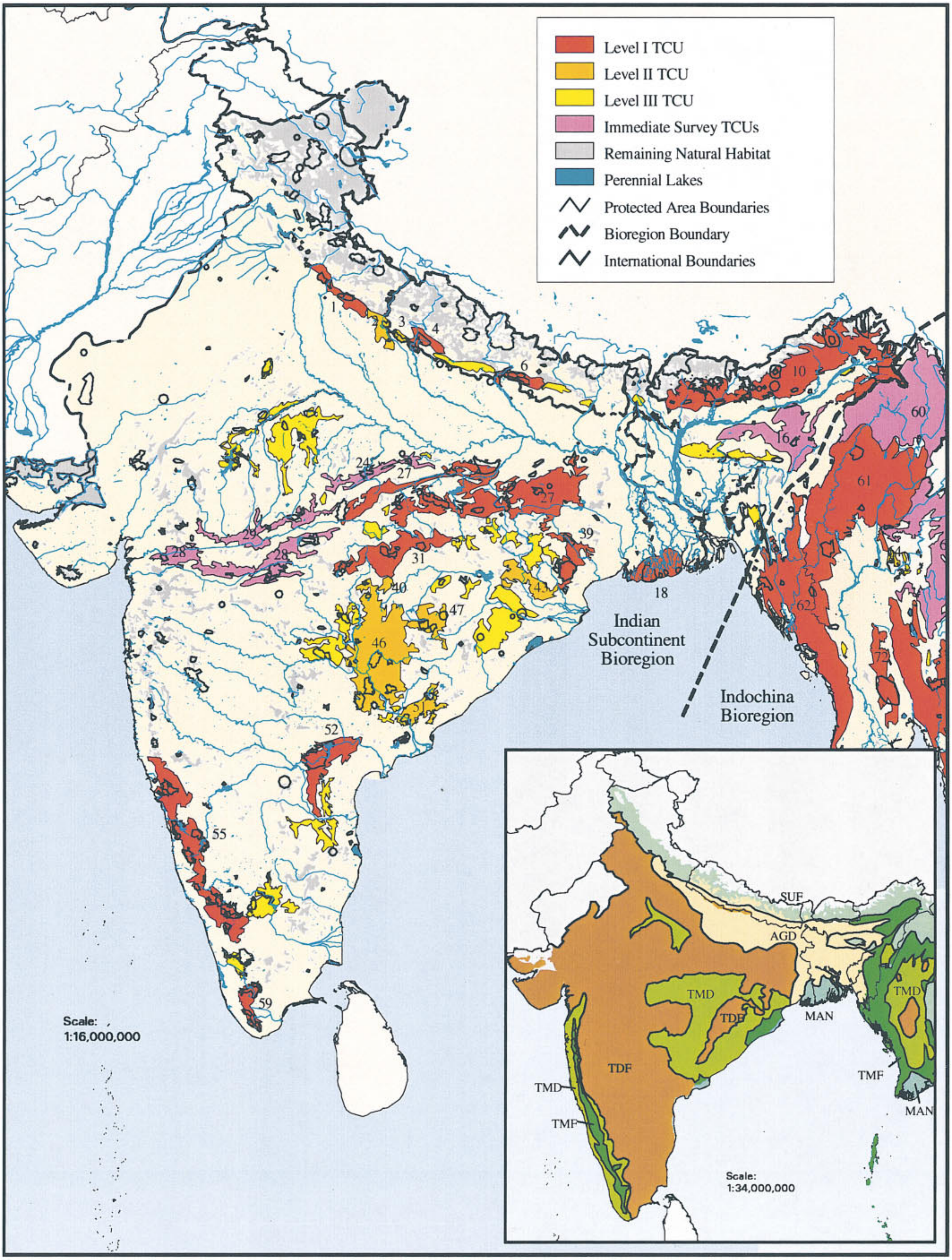
We created three variables to index the root sources of threats to tigers: (1) habitat integrity, which indexes the size, degree of degradation, fragmentation, and connectivity of tiger habitat blocks (Appendix 1); (2) poaching pressure, which indexes the intensity of illegal hunting of tigers and their prey and the potential for its control (Appendix 2); and (3) population status, which indexes tiger abundance and recent population trends within each tiger habitat type.

We assessed population status over 10 years because many park staff and scientists working in an area seldom remain longer than a decade. Knowledgeable local residents may provide valuable information in some areas. An intact population is one that is "minimally affected" and will represent the best possible situation. An intact population does not decline or increase, so only the stable trend is shown. A moderately depleted population can be evaluated as a population that is affected by habitat loss, loss of prey density, or poaching but which occurs where tigers or their signs are still encountered "rather frequently" for this habitat type. A severely depleted population is one that is highly affected by poaching, habitat loss, or lack of prey and which occurs where tigers or their signs are rarely encountered for this habitat type. In a stable population the numbers can fluctuate about the mean.

We assigned scores to the population trend as follows: an intact population is stable (10 points); a moderately depleted population is increasing (10 points), stable (8 points), declining (7), or its status is unknown (7); and a severely depleted population is increasing (7), stable (5), declining (1), or its status is unknown (3).

While many factors contribute to the decline of tigers, we suggest that habitat integrity, poaching pressure, and population status are the most powerful predictors of

Figure 2. Map of the Indian subcontinent bioregion showing tiger conservation units (TCUs). The level I, II, and "immediate survey area" TCUs are numbered, and the numbers correspond to those in Table 1. The names and numbers for level III TCUs (in yellow) are given in Dinerstein et al. (1997) and Wikramanayake et al. (1998). The inset map shows the original extent of tiger habitat types.


Level I TCU
Level II TCU
Level III TCU
Immediate Survey TCUs
Remaining Natural Habitat
Perennial Lakes
Protected Area Boundaries
Bioregion Boundary
International Boundaries
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4
6
10
16
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Indian
Subcontinent
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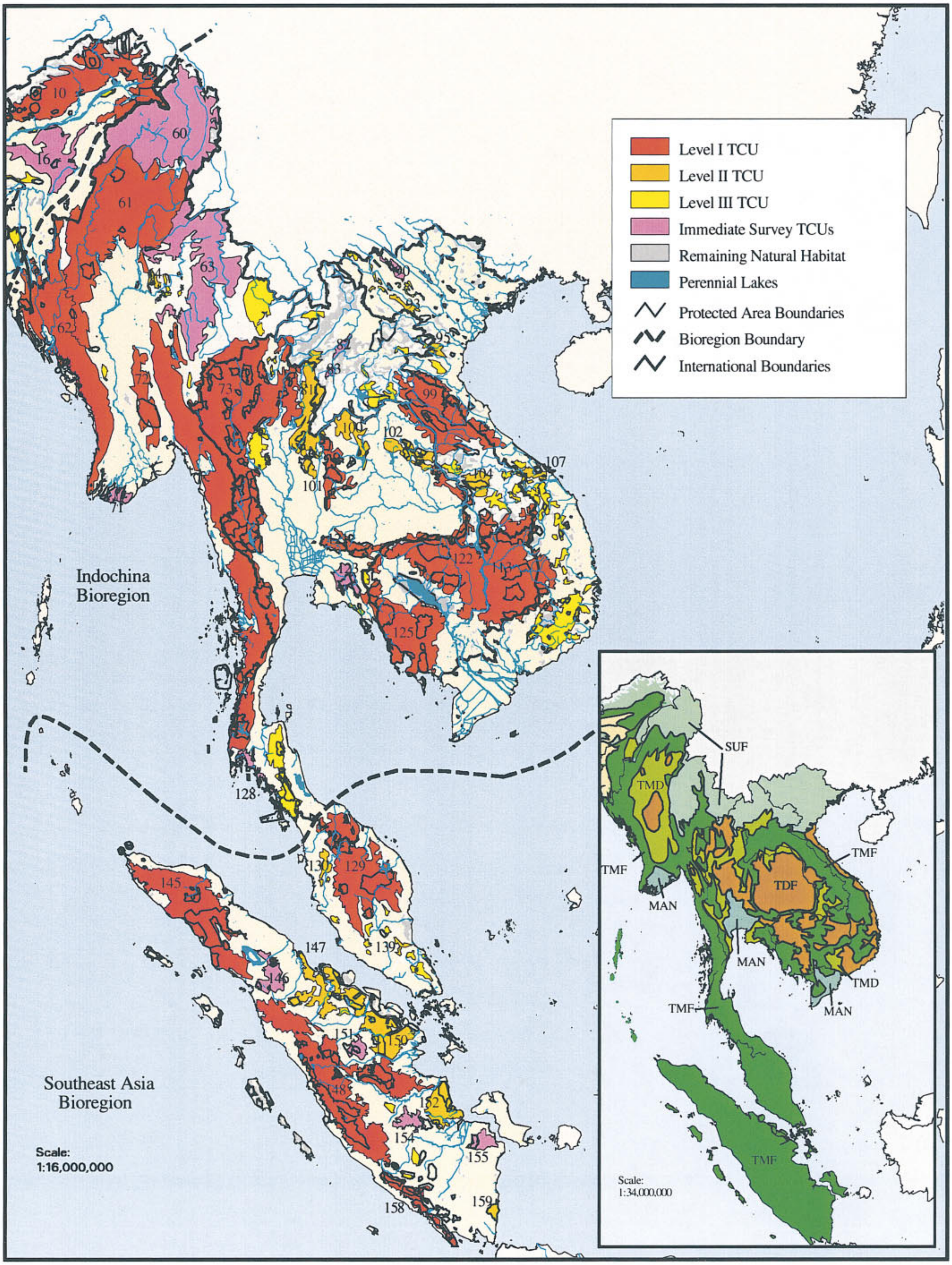
Level I TCU
Level II TCU
Level III TCU
Immediate Survey TCUs
Remaining Natural Habitat
Perennial Lakes
Protected Area Boundaries
Bioregion Boundary
International Boundaries
Indochina Bioregion
Southeast Asia Bioregion
Scale: 1:16,000,000
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101
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146
151
150
148
152
154
155
158
159
SUF
TMD
TMF
TDF
MAN
Scale: 1:34,000,000

the long-term persistence of tiger populations. Many of the other factors will be likely correlated with these three sources.

We weighted the variable scores as 4:2:1 for habitat integrity, poaching pressure, and population status, respectively, to reflect the reversibility of threats to tiger conservation. Loss of habitat integrity, which we considered the most difficult to reverse, was weighted twice as high as poaching pressure, which can be abated more quickly. Poaching pressure, in turn, was weighted twice as high as population status because tiger populations severely depleted by poaching can rebound quickly if they, their habitat, and their prey are protected over sufficiently large areas. Each TCU was assigned an index score for each variable.

The three variable scores for each TCU were summed to provide a single TCU score that reflected the probability of persistence of its resident tiger populations over the long term. The TCUs were then ranked and assigned to four categories: level I, II, III, or "immediate surveys," based on the rank score. Level I TCUs offer the highest probability of persistence of tiger populations over the long term. They are essential for a global tiger conservation strategy and share the following attributes: large blocks of habitat suitable for tigers and prey with adequate core areas; low to moderate poaching pressure on tigers and prey species either as a result of remoteness or vigilant protection. Level I scores ranged from 45 to 70 points. Level II TCUs offer medium probability of persistence of tiger populations over the long term. They contribute to bioregional tiger conservation strategies and share the following attributes: moderate- to large-sized blocks of habitat suitable for tigers with adequate core areas; moderate to high poaching pressure on tigers and prey species but with potential for effective anti-poaching measures in the near future. Level II scores ranged from 32 to 44 points. Level III TCUs offer low probability of persistence of tiger populations over the long term due to their small size, small or no core area, isolation from other habitat blocks containing tigers, fragmentation within its respective habitat type, and high poaching pressure on tigers and prey species. With intensive management and protection, level III TCUs can harbor small populations of tigers. They are most important to national tiger conservation strategies and typically scored less than 32 points. Immediate survey TCUs are any TCUs that potentially contain extensive blocks of appropriate tiger habitat with or without protected core areas, but for which data on habitat quality, poaching pressure, and population status for the most important habitats within the TCU are unavailable or unreliable.

Scores for each TCU were compared only with other TCUs that shared the same tiger habitat type within the same bioregion (Fig. 1). Thus, TCU scores from the Indian subcontinent bioregion were not compared with TCUs from the Southeast Asia bioregion, nor were TCUs from the alluvial grasslands compared with the tropical dry forest tiger habitat type in the Indian subcontinent bioregion.

Decision Rules for Scoring Tiger Conservation Units

Each TCU was assigned to the dominant tiger habitat type represented in that TCU. If a TCU spanned two or more tiger habitat types, the habitat that consisted of more than 50% of the TCU area was considered the primary tiger habitat type. Habitat representing 30–49% of the TCU were considered secondary tiger habitat types. TCUs were named after the largest or most significant protected areas within the TCU. If a TCU contained no protected areas, it was given a name to signify its regional location. TCUs that straddled international boundaries were listed first under the country that contained the largest or best-quality block of habitat within the TCU.

When scoring TCUs for habitat integrity, we considered habitat blocks with extensive roads, railroads, or settlements, to be degraded. Long, narrow TCUs not offering adequate protection within core areas were considered suboptimal and were scored lower than circular-shaped TCUs (Appendix 1). We solicited regional and local expertise to assess and score TCUs, and we corroborated these evaluations with published and unpublished literature (for sources see Dinerstein et al. 1997).

We considered three high-priority TCUs, (i.e., levels I, II) of each tiger habitat type in each bioregion to be the minimum number necessary to maintain representation. If less than three TCUs were level I or II for a particular habitat type, the appropriate number of level III TCUs with the highest scores for that tiger habitat type were elevated to level II. If reliable information was lacking to score a TCU, it was flagged for survey and information verification. We set the scores for unknown poaching pressure and population status trends at slightly above the mid-range of the scales for the respective variables (Appendices 2 & 3) to ensure that, until reliable data are available, the TCUs will remain potentially high-priority areas if the habitat is suitable.

Figure 3. Map of Indochina and Southeast Asia bioregions showing tiger conservation units (TCUs). The level I, II, and "immediate survey area" TCUs are numbered, and the numbers correspond to those in Table 2 and 3. The names and numbers for level III TCUs (in yellow) are given in Dinerstein et al. (1997) and Wikramanayake et al. (1998). The inset map shows the original extent of tiger habitat types.

Results

We identified 25 level I TCUs (16% of all TCUs), 21 level II TCUs (13%), and 97 level III TCUs (61%) across the tiger range in Asia. We also identified 16 TCUs (10%) for immediate survey. These TCUs, for which data are lacking, may be suitable for long-term tiger conservation and may be on par with some level I or II TCUs. Details of level III TCUs, including maps giving their locations and names, are provided by Dinerstein et al. (1997) and Wikramanayake et al. (1998).

Indian Subcontinent Bioregion

We identified 59 TCUs in the Indian subcontinent bioregion, of which 11 were level I, 7 level II, and 4 were identified for immediate survey (Table 1, Fig. 2). Three of the six tiger habitat types in this bioregion—alluvial grassland/moist deciduous forest, tropical moist deciduous forest, and tropical dry forest—have adequate replication as level I or II TCUs, as per our a priori decision rules. Because tropical moist forest TCUs were inadequately represented, we elevated a level III TCU (Parambikulam TCU 58) to level II. The Sunderbans was the only TCU in mangrove habitat in the bioregion, so increased representation of mangroves was not possible. The subtropical and temperate upland forest was also represented by one TCU (Manas-Namdapha, TCU 10), which extended across the eastern Himalaya in Bhutan and northeastern India (Fig. 2).

Of the 59 TCUs in the Indian subcontinent, 20 did not contain any protected areas (World Conservation Union categories I–IV). The mean size of protected areas for all TCUs having any was 1621 $\pm$ 2458 km^2, representing 17% of the TCU area. Only 2 of the 22 priority TCUs did not contain strict protected areas (Table 1). The mean

Table 1. Priority tiger conservation units (TCU) in the Indian subcontinent bioregion.

Level and TCU no.[a]	*TCU name*	*TCU area (km^2)*	*Area of TCU protected (km^2)*[b]	*Tiger habitat type*[c]
Level I[d]				
55	Dandeli-Bandipur (India)	23,881	7,013	TMF
59	Periyar-Kalakad (India)	5,440	1,493	TMF
31	Kanha-Pench (India)	13,223	2,138	TMD
39	Simlipal-Kotgarh (India)	7,709	2,980	TMD
27	Bagdara-Hazaribagh (India)	61,172	6,042	TDF
52	Nagarajunasargar (India)	13,127	3,862	TDF
10	Manas-Namdapha (India, Bhutan)	59,901	13,181	SUF
18	Sunderbans (Bangladesh, India)	6,624	873	MAN
6	Chitwan-Parsa-Valmiki (Nepal, India)	3,549	2,075	AGD
1	Rajaji-Corbett (India)	4,357	1,498	AGD
4	Bardia-Banke (Nepal)	2,231	1,437	AGD
Level II[e]				
58[f]	Parambikulam (India)	2,349	336	TMF
46	Indravati-Navegaon (India)	31,413	4,678	TMD
51	Papikonda (India)	7,293	770	TMD
43	Orrisa Dry Forests (India)	6,763	0	TDF
47	Sitapani-Udanti (India)	5,743	1,521	TDF
40	Kanha-Indravati Corridor (India)	1,377	0	TDF
2	Sukla Phanta-Kishanpur (Nepal, India)	1,897	439	AGD
3	Dudwa-Kailali (India, Nepal)	567	567	AGD
Immediate survey				
16	Kaziranga-Meghalaya (India)	18,984	488	TND
28	Melghat (India)	25,287	2,415	TDF
29	Ratapani-Singhori (India)	14,089	406	TDF
24	Panna-Son Gharial (India)	8,599	733	TDF

[a] *TCU numbers correspond to those in Fig. 2.*
[b] *Area of TCU protected is the sum of all strictly protected areas within the TCU.*
[c] *The tiger habitat type acronyms are TMF, tropical moist forests; TMD, tropical moist deciduous forests; TDF, tropical dry forests; SUF, subtropical and temperate upland forests; MAN, mangroves; AGD, alluvial grasslands and subtropical moist deciduous forests. Details of level III TCUs are given by Dinerstein et al. (1997) and Wikramanayake et al. (1998).*
[d] *Level I tiger conservation units offer the highest probability of persistence of tiger populations over the long term and are essential components of a global tiger conservation strategy. Level I TCUs share the following attributes: large blocks of habitat suitable for tigers and prey with adequate core areas and low to moderate poaching pressure on tigers and prey species as a result of either remoteness or vigilant protection.*
[e] *Level II TCUs offer medium probability of persistence of tiger populations over the long term. They share the attributes of moderate to large-sized blocks of habitat suitable for tigers with adequate core areas, moderate to high poaching pressure on tigers and prey but with potential for implementing effective anti-poaching efforts in the near future.*
[f] *Elevated to level II.*

area protected within the priority TCUs was 2482 ± 2984 km^2.

Indochina Bioregion

We identified 69 TCUs in the Indochina bioregion, of which 10 were level I and 8 level II (Table 2, Fig. 3). Another 8 were identified for immediate survey. Three of the five tiger habitat types in the bioregion—tropical dry forests, tropical moist deciduous forests, and tropical moist evergreen forests—had the minimum number of TCUs required to achieve representation. There were no level I or II mangrove TCUs, but we identified two level III mangrove TCUs for immediate survey to determine if they qualified for level II status (Table 2). The subtropical and temperate upland forest was represented by two level II TCUs, but three others were identified for immediate survey.

Thirty-six of the 69 TCUs in the Indochina bioregion did not contain any strictly protected areas. The mean size of protected areas in those TCUs with any protection was 3182 ± 6225 km^2, or 17% of the TCU area. Three of the 26 priority TCUs did not contain strictly protected areas (Table 2), and the mean area protected within the priority TCUs was 3884 ± 6892 km^2.

Southeast Asia Bioregion

We identified 31 TCUs in the Southeast Asia bioregion, of which 4 were level I, 6 level II, and 4 were identified for immediate survey (Table 3, Fig. 3). All TCUs consisted of tropical moist forests. Because other forest types such as mangroves, peat swamps, and other tropical forests are fragmented in this bioregion, they were included within the tropical moist forest tiger habitat type. Two level II TCUs (150 and 152) had large areas of peat swamp, which is considered poor tiger habitat (Seidensticker 1986), so these TCUs were given a score of 14 for habitat integrity (Appendix 1, 6a).

Fourteen of the 31 TCUs in this bioregion did not contain any strictly protected areas. The mean size of protected areas in those TCUs with strictly protected areas was 2908 ± 4544 km^2, or 36% of the TCU area. Two of the 14 priority TCUs did not contain strictly protected

Table 2. Priority tiger conservation units (TCU) in the Indochina bioregion.*

Level and TCU no.	*TCU name*	*TCU area (km^2)*	*Area of TCU protected (m^2)*	*Tiger habitat type*
Level I				
73	Huay Kha Khaeng-Thumg Yai Naresuan (Thailand)	155,829	32,459	TMF
62	Arakan Yomas (Burma)	52,353	446	TMF
125	Phnom Bokor-Aural (Cambodia)	31,715	10,833	TMF
99	Nam Theun Nakai-Vu Quang (Laos, Vietnam)	24,626	6,830	TMF
121	Khao Yai (Thailand)	1,945	1,852	TMF
61	Chin Hills (Burma)	82,464	3,078	TMD
72	Pegu Yomas (Burma)	12,600	4,600	TMD
122	Kulen Promtep-Thap Lan (Cambodia)	45,880	11,311	TDF
113	Virachay-Xe Piane-Yok Don (Cambodia, Laos, Vietnam)	52,643	13,897	TDF
101	Phu Khieo-Nam Nao (Thailand, Laos)	5,702	3,325	TDF
Level II				
104	Xe Bang Nouane (Laos)	2,196	1,260	TMF
107	Bach Ma-Nui Thanh (Vietnam)	2,081	188	TMF
93	Song Da Forest (Vietnam)	1,079	0	TMF
81	Thung Salaeng-Nam Poui (Thailand, Laos)	13,823	2,977	TMD
102	Phu Phan (Thailand)	4,384	716	TMD
100	Phu Kao-Phu Kham (Thailand)	3,579	299	TMD
95	Bu Huong-Nam Xam (Vietnam, Laos)	1,121	316	SUF
64	Maymo (Burma)	1,114	28	SUF
Immediate survey				
123	Khao Ang Ru Nai-Khao Soi Dao (Thailand)	4,751	1,798	TMF
82	Louangphrabang (Laos)	1,067	0	TMD
83	Muang Xaignabouri (Laos)	689	0	TMD
3	Shan Plateau (Burma)	41,075	153	SUF
60	Northern Triangle (Burma)	33,884	109	SUF
90	Nui Hoang Lien (Vietnam)	1,550	395	SUF
128	Hat Chao Mai (Thailand)	1,971	226	MAN
71	Irawaddy Delta (Burma)	1,733	122	MAN

** For explanation of column heads, see Table 1 footnotes.*

Table 3. Priority tiger conservation units (TCU) in the Southeast Asia bioregion.*

Level and TCU no.	*TCU name*	*TCU area (km^2)*	*Area of TCU protected (m^2)*	*Tiger habitat type*
Level I				
148	Kerinci Seblat-Seberida (Sumatra)	50,884	16,605	TMF
145	Gunung Leuser-Lingga Isaq (Sumatra)	36,530	11,423	TMF
129	Taman Negara-Belum-Halabala (Malaysia, Thailand)	27,469	7,135	TMF
158	Bukit Barisan Selatan-Bukit Hitam (Sumatra)	6,594	4,784	TMF
Level II				
150	Kerumutan-Istana Sultan Siak (Sumatra)	11,816	1,742	TMF
152	Berbak-Sembilang (Sumatra)	6,670	2,196	TMF
147	Siak Kecil-Padang Lawas (Sumatra)	2,235	1,995	TMF
130	Selama (Malaysia)	1,684	0	TMF
159	Way Kambas (Sumatra)	1,300	1,300	TMF
139	Endau (Malasia)	788	0	TMF
Immediate Survey				
146	Sibolga-Dolok Surungan (Sumatra)	4,685	594	TMF
154	Dangku (Sumatra)	3,431	106	TMF
155	Padang Sugihan (Sumatra)	2,505	652	TMF
151	Air Sawan (Sumatra)	2,444	605	TMF

* *For explanation of column heads, see Table 1 footnotes.*

areas (Table 3). The mean area protected within the priority TCUs was 3510 ± 4798 km^2.

Discussion

Where to Invest First

Ranking from among 159 potential tiger conservation units across Asia, we identified only 16% as level I and 13% as level II TCUs that represent all tiger habitats in the three bioregions (Tables 1–3). Sixteen other TCUs have been identified for immediate survey to confirm tiger presence and population trends, verify poaching pressure, and ground-truth habitat integrity. Even though this is a broad-scale, rapid assessment, we are confident of our ability to designate TCUs as level I and II and believe that even after extensive field surveys of the TCUs, few if any level III TCUs will be elevated to level I or II.

By identifying priority TCUs we do not imply that level III units are unimportant. Level I and level II TCUs are globally significant and are recommended as targets for international donors and for planning a regional conservation strategy in Asia. National and local-level tiger conservation planning may have different priorities that point to several level III TCUs (e.g., Ranthambore, TCU 20; Dinerstein et al. 1997). This analysis is not meant to supplant these national conservation plans, but we strongly urge that national and local-level planning be developed in the context of a regional strategy to achieve a more effective long-term tiger conservation plan.

Our results also indicate that many level I and II TCUs straddle or lie near international borders (Figs. 2 & 3). Over the past few years there have been several forums where transboundary conservation strategies have been discussed or are underway (Dinerstein et al. 1995; Ji & Rabinowitz 1995; Rabinowitz 1995). The tiger has been proposed as a "flagship" species to promote such strategies and as an umbrella species to plan these strategies (Rabinowitz 1995), and organizations such as the Global Tiger Forum should support these regional conservation strategies.

Many of the forested areas in the Indian subcontinent bioregion have been lost (Fig. 2), but several large blocks of tropical moist evergreen forest, tropical moist deciduous forests, tropical dry forests, and subtropical and temperate upland forests remain and are identified as level I and II TCUs (Table 1, Fig. 2), particularly in the Western Ghats (TCU numbers 59, 55) and the Deccan Plateau (TCU numbers 27, 31, 52, 39, 46, 51, 43).

In the Himalayan foothills, the Chitwan-Parsa-Valmiki (TCU 6), Bardia-Banke (TCU 4), and—to a lesser extent—the Rajaji-Corbett (TCU 1) are the best areas for conserving tigers in alluvial grassland/subtropical moist deciduous forest habitat (Fig. 2). Kaziranga-Meghalaya (TCU 16) consists mostly of tropical moist deciduous forest, but the alluvial grasslands in and around the Kaziranga area represent some of the best preserved examples of this habitat. Although relatively small compared with the TCUs in other tiger habitat types (Table 1), the alluvial grasslands of the Himalayan foothills support a larger number of tigers because the prey density is high; the size of the tiger's territory and its density tend to be positively correlated with prey density (Sunquist 1981; Karanth & Sunquist 1995).

The only high-priority TCU representing subtropical and temperate upland forest (TCU 10) extends from the Manas reserve complex in India and Bhutan to the temperate hardwood and conifer forests of central Bhutan and Arunachal Pradesh in northeastern India (Fig. 2). This large TCU provides the last opportunity in south Asia to conserve the ecological phenomenon of tigers living close to the timberline and preying on montane ungulates. The severe depletion of extensive mangrove swamps in Asia is such that the only prime example left in the world of tigers in mangroves is the Sunderbans (TCU 18), and this area is a global conservation target.

Several large forested areas remain in Indochina. For instance, the border areas of Burma, Thailand, Cambodia, Laos, and Vietnam still have large, contiguous tracts of tropical moist evergreen and tropical dry forests in which we identified several priority TCUs (Fig. 3). Even though Cambodia and Laos have declared several large protected areas in these forests, granting of large-scale logging concessions to outside interests (Dinerstein et al. 1995) and the lack of trained staff and infrastructure threaten and impair conservation activities (Burkmuller et al. 1995). In Vietnam much of the forests are fragmented, but tigers are present in TCUs along Vietnam's borders with Laos and Cambodia in areas now included under level I TCUs (99, 113; Table 2). Several large mammals have been described recently from these Indochinese forests (Do Tuoc et al. 1994; Peter & Feiler 1994; Dung et al. 1993), attesting to their conservation importance. Tigers can be used as umbrella species for developing management strategies for these transboundary TCUs.

Much of the best remaining habitat for tigers in the lowlands of Peninsular Malaysia and Sumatra has been lost or highly fragmented (Fig. 3). Tigers are now mostly restricted to upland tropical moist evergreen forests, which is not as suitable as the lowland forests for tigers (Santiapillai & Ramono 1987). Opportunities to improve landscape management for tigers in remaining lowland tracts should be a high priority.

The Landscape Approach to Tiger Conservation

Tigers are territorial, and the size of tiger home ranges can vary from about 20 to over 400 km^2, depending on the density and availability of prey (Smith et al. 1987; Seidensticker & McDougal 1993; Smith 1993; Miquelle et al. 1995). Therefore, protecting large populations will require managing extensive areas of habitat for conservation. But protected areas typically cover only a small fraction of TCUs (Tables 1, 2, 3), and several TCUs do not have any protected areas. Because protected areas provide essential refuge and core breeding areas for tigers (Karanth 1991, 1995), all high priority TCUs should have strict protected areas. Some of the level I and II TCUs we have identified are also very large, exceeding 50,000 km^2 in area, and will not likely receive complete protection. If there is tiger dispersal among adjacent blocks of habitats, these TCUs represent the last remaining places where there is still an opportunity to plan land-use based on landscape conservation principles (Noss & Cooperrider 1994) before these large forest tracts succumb to fragmentation.

The ecological requirements of tigers and their prey can be effectively used to design landscape-level land-use options that include conservation of core areas coupled with restoration of degraded lands, and sustainable natural resource use plans to meet the needs of the local people. Several initiatives through which conservation of tigers directly or indirectly benefits local people through integrated conservation and development programs are already underway in the region, especially in India, (Panwar 1987; World Bank 1996; MacKinnon et al. 1998) and Nepal (Dinerstein et al. 1998); they can be used as models to adapt to other areas.

Ecology-Based Methods for Conserving Wide-Ranging Megafauna

Recent studies show that genetic or morphological variation among wild tiger populations is insufficient to warrant any of the existing subspecific designations (Kitchener 1998; Wentzel et al. 1998). Nonetheless, it is imperative that we focus on conserving the suite of adaptations of tigers to the environmental conditions and prey assemblages in which they live. Tigers preying on moose in the Russian far east is as important a phenomenon to conserve as tigers preying on rhino calves in Nepal or on a wide variety of primates across Asia.

The same argument applies when conserving the phenomena associated with other wide-ranging mammals. For example, brown bear (*Ursus arctos*) adapted to life in the deserts of Turkmeinistan feed heavily on the nuts of pistachio (*Pistacia vera*) trees, the keystone species in this ecoregion, whereas brown bear in the north temperate coastal forests prey on anadromous fish. Brown bears occupy even more major habitat types than tigers and, like tigers, they vary in behavior and morphology across their range (but brown bears are all the same species).

Other examples of large mammals that occur in different habitat types across extensive spatial scales include wolves, Asian and African elephants, banteng, gorillas, black rhinoceros, and several large deer and antelope species. This framework can be easily adapted and applied to these species. Because of the large area requirements of large carnivores, landscape-scale planning in representative habitat types also contributes greatly to biodiversity conservation at regional and continental scales. Our method in particular reinforces the role of these mammals as umbrella species for conservation of diverse species assemblages associated with them. Ecology-based methods offer a new opportunity for conservation biologists and ecologists to join with museum taxonomists and geneticists in ranking the conservation value of wild populations of megafauna.

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Appendix 1

Habitat Integrity Index Used to Score Tiger Conservation Units

This index takes into consideration the size and spatial configuration of habitat blocks, the quality of the habitat within the forest blocks and intervening areas, and the extent to which a tiger conservation unit contains one or more protected areas that will provide effective refuge to tigers and prey.

1. TCU consists of small ($\leq$200 km^2), isolated fragment or fragments with low potential for tiger dispersal. *1 point*

2. TCU consists of isolated fragment or fragments, with at least one being larger than 200 but not over 500 km^2, with low potential for tiger dispersal among them. *2 points*

3. TCU consists of several isolated fragments larger than 200 but not over 500 km^2, with potential for tiger dispersal among them, and forms a network of tiger habitat which adds up to more than 1000 km^2. *5 points*

4. TCU consists of one or more isolated, mid-sized fragments ($>$500 and $\leq$1000 km^2) of tiger habitat with low potential for tiger dispersal among the larger habitat blocks. *10 points*

5. TCU consists one or more isolated mid-sized fragments ($>$500 and $\leq$1000 km^2) of tiger habitat with potential for natural tiger dispersal (existing or potential for restoration) among the larger habitat blocks. (For 5 and 6, degraded habitat is defined either as: forest in which the understory or the forest has been degraded by livestock grazing, firewood collection, swidden agriculture, or human-made fires or as grasslands or savannas in which the tall

grass cover has been degraded by livestock grazing, collection of fodder/thatch, or human-made fires.)

a. But with more than 50% of habitat known to be degraded (but not cleared) and/or not prime tiger habitat. *10 points*
b. But with habitat quality unknown across most of TCU. (Flag TCU for surveys.)
c. With more than 50% of TCU considered to be good quality habitat suitable for tigers. *16 points* (Both 5b and 6b will be flagged for surveys to determine the status of habitat quality. No scores will be assigned).

5.1 If more than 50% of the tiger habitat of TCU for category 5 consists of effectively protected areas. *2 points*

6. TCU consists of one or more habitat blocks larger than 1000 km^2 with potential for natural tiger dispersal among them (existing or potential for restoration).

a. But with more than 50% of habitat known to be degraded (but not cleared) and/or not prime tiger habitat. *14 points*
b. But with habitat quality unknown across most of TCU. (Flag TCU for surveys.)
c. With more than 50% of TCU considered to be good-quality habitat suitable for tigers. *24 points*

6.1 More than 25% of the tiger habitat of TCU for category 6 consists of effectively protected areas. *4 points*

7. TCU consists of contiguous habitat throughout and exceeds 5000 km^2; is relatively intact, and contains the full range of habitat types necessary for tigers that is expected to occur in the THT and/or Bioregion. *36 points*

7.1 More than 20% tiger habitat of TCU for category 7 consists of effectively protected areas. *4 points*

Appendix 2

Poaching Pressure Index Used to Score Tiger Conservation Units

1. Low poaching concentrated in only a few areas and/or sporadic; prey-base relatively intact; effective anti-poaching program and network in place. *20 points*

2. Low to medium poaching concentrated in a few areas and/or sporadic; poaching on prey relatively high but on tigers low; anti-poaching program relatively effective; potential for reversing poaching pressure. *19 points*

3. Medium poaching pressure of widespread but low intensity; tigers and/or prey poached; potential for anti-poaching measures. *17 points*

4. Medium poaching pressure of widespread but low intensity; tigers and/or prey poached; no potential for anti-poaching measures in near future but tigers not severely threatened. *14 points.*

5. Medium to high poaching pressure; poaching pressure on tigers and/or prey; potential for anti-poaching measures. *11 points*

6. High poaching pressure on tigers and/or prey; potential for effective anti-poaching measures. *8 points*

7. Medium to high poaching pressure on tigers and/or prey; no potential for anti-poaching measures. *4 points*

8. High poaching pressure on tigers and/or prey; no potential for effective anti-poaching measures. *1 point*

9. Extent of poaching pressure unknown. *13 points*