Mitigation of Habitat "Take": Application to Habitat Conservation Planning

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Abstract: *One of the most important provisions of the U.S Endangered Species Act precludes the "taking" of listed species on both public and private land. In past Endangered Species Act litigation, take has been broadly interpreted to include the destruction or modification of habitats as well as the direct killing of animals. This requirement created an extensive burden on private landowners to provide habitats for listed species. This burden was substantially lessened when the ESA was modified in 1982 to allow incidental takings conditioned on preparation of a satisfactory "habitat conservation plan." Because the majority of listed species are imperiled due to habitat modification, most habitat conservation plans must demonstrate defensible methods to mitigate ugainst incidental habitat loss. A review of HCPs for the Northern Spotted Owl* (Strix occidentalis), *and otber species, indicates that mitigation solutions are often arbitrary, lacking an empirical foundation in the species' life history requirements. Based on data from the Spotted Owl, we illustrate a biologically based method for estimating the areal requirements neccessary to mitigate against the take of essential habitats. Toward this goal we adopt the concept of "core area," that portion of an animal's borne range that receives disproportionate use. We estimated core areas by means of the adaptive kernel density function and tested against a null distribution of animal use that assumes a bivariate, uniform distribution of locations within the home range. The method we illustrate, which is defensible, repeatable, and empirical, is a clear improvement over the ad hoc methods used in many habitat conservation plans. Further, the methods we propose should be applicable to a large number of terrestrial species for which home range is a meaningful concept.*

Aplicación de la Mitigación de la "Toma" de Hábitat en la Planeación de Conservación de Hábitat

Resumen: *Una de las provisiones más importantes de1 Acta de Especies en Peligro de U.E.A. prohibe la "toma" de especies enlistadus tantcl en terrenos públicos como privados. En litigios de pasado, se ha interpretado ampliamente que la toma incluye la destrucción o modificación de1 hábitat así como la muerte directa de los animales. Este requerimiento creó una extensa carga para propietarios ya qu e debían proporcionar hábitats para las especies enlistadas. Esta carga se redujo substancialmente cuando el Acta fue modificada, en 1982, para permitir tomas incidentales condicionadas a la preparación de un "plan de conservación de hábitat" satisfactorio. Debido a que la mayoría de las especies enlistadas se encuentran en peligro a causa de modificaciones del hábitat, la mayoría de los planes de conservación de hábitat deben demonstrar que incluyen métodos adequados para la mitigación de pérdidas incidentules de hábitat. Una revisión de los planes de conservación de hábitat elaborados para el búho manchado de1 norte* (Strix occidentalis) y *otras especies indica que la soluciones de mitigación a menudo son arbitrarias, carecen de fundamento empírico de los requerimientos de la especie. Con base en datos para el búho manchado de1 norte, ilustramos un método basado en biología para estimar los requerimientos de área necesarios para mitigar la toma de hábitats esenciales. Para ello adoptamos el concepto del "área núcleo", aquella porción de1 rango de hogar de un animal que recibe un uso desproporcionado. Estimamos áreas por medio de la función adaptativa de densidud y la probamos contra una distribución nula de utilización que asume una distribución de localidades bivariada y uniforme dentro de1 rango de hogar. El método que presentamos, que es defendible, repetible y empírico, es una clara mejoría de los métodos* ad *hoc utilizados en muchos planes de conservación de hábitat. Más aun, los métodos que proponemos debieran aplicarse a numerosas especies terrestres para las que el concepto de rango de hogar es significativo.*

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Introduction

The Endangered Species Act (ESA) of 1973 invokes two primary restrictions on land use. Section 7 of the act prohibits federal agencies from "jeopardizing" the continued existence of threatened or endangered species. Section 9 prohibits any person, public official or private citizen, from "taking" a threatened or endangered species. Take "means to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or attempt to engage in any such conduct" (Endangered Species Act 1973). The terms "harass" and "harm" are not defined in the ESA, but are defined in U.S. Fish and Wildlife Service (FWS) (1981) regulations. Of particular relevance to the topic of this paper, the regulatory definition of *Ibann ex*tends take to include the effects of habitat loss and modification. As a consequence, private landowners may be prevented from engaging in otherwise legal activities, such as clearing land or harvesting trees, if the activity adversely modifies the habitat of a listed species.

To relieve the potential burden to private individuals of compliance to Section 9 requirements, the ESA was amended in 1982 to allow the incidental taking of listed species, conditioned on an approved habitat conservation plan (HCP). Section 10(a) authorized the U.S. Department of Interior to permit activities resulting in take of listed species "if such taking is incidental to, and not the purpose of, carrying out an otherwise lawful activity." To qualify for an incidental take permit, an acceptable HCP must (1) specify the impact of the taking; (2) outline the steps to be taken to minimize and mitigate the impacts; and (3) specify the alternative actions considered and why they were not selected (Thornton 1993). Before issuing the permit the Secretary of the Interior (Secretary of Commerce for marine species) must find, among other things, that the applicant will minimize and mitigate, to the extent possible, the adverse impacts of the taking.

The application of the taking prohibition to private property has been very contentious (Quarles et al. 1993). Nevertheless, Section 10(a) has provided an opportunity for those with varying opinions to work collaboratively with conservation advocates to find compromise solutions. The HCP vehicle has also provided the opportunity for conservation biologists to work directly with developers, city planners, loggers, miners, etc. to find scientifically defensible solutions to the dictates of acceptable mitigation. Section 10(a) has stimulated a number of HCP attempts-200 HCPs have been prepared or are in preparation and at least 179 incidental take permits have been issued (USFWS & NMFS 1996). Although most of the HCP attempts were for relatively small planning areas of less than 400 ha, at least 68 were for areas greater than 4000 ha of which 18 exceeded 200,000 ha (USFWS & NMFS 1996).

We contributed to the development of a draft HCP for the Northern Spotted Owl (*Strix occidentalis caurina*) in California (California Board of Forestry 1992). The process, apparently like that for most other HCPs, was prolonged, contentious, and adversarial. As with most listed species, one consistent source of debate has focused on the necessary area and the attributes and types of habitats within that area required for effective mitigation against the take of habitat. The participants in this debate tend to be highly polarized in their views, with some arguing for minimal and others maximal areas for mitigation. The final solutions to these debates are seldom based on ecological arguments or empirical analyses. They are often motivated by short-term economic considerations and the immediate interests of the stakeholders. Consequently, the mitigation guidelines that arise from the process are often arbitrary, with little or no empirical foundation in the specie's ecology or life history and area requirements (Tear et al. 1995).

The example of the Northern Spotted Owl demonstrates the sometimes arbitrary nature of mitigation guidelines. A recently approved HCP for private timber lands in northwestern California proposes the following mitigation measure: "If a nest is found, the nest tree will be marked and no timber falling or yarding will be allowed within a 0.25-mile radius of it until it has been determined that the young have fledged or that the nest has failed. After the young have fledged, the radius of protection will be 500 feet from the nest tree and connectivity to continuous habitat will be maintained. When the young have dispersed, or it has been determined that the nest has failed, falling and yarding will be allowed within the 500-foot radius" (Simpson Timber Company 1991). No data, analyses, or logic are presented in defense of the sufficiency of the 0.25-mile radius or 500-foot radius circles to mitigate take or to preclude "jeopardy" to the population. The arbitrary nature of these area1 mitigation measures is not unique to this species, and is found in many other HCPs (examples in Beatley 1994).

To address this common deficiency of HCPs, we propose a biologically-based, defensible method to estimate areal requirements for species of concern. The methods can be used to develop guidelines to mitigate against the take of essential habitats and to demonstrate compliance to the intent of the Section 9 and 10(a) requirements of the ESA. The methods we outline are mostly applicable to terrestrial species that occupy a home range (at least seasonally) or defend territories; however, the logic of the approach should have much wider application. The methods are illustrated with an example drawn from our studies of space use by Spotted Owls. The biological foundation for our proposal is the concept of core areas-areas within the home range receiving concentrated seasonal use by territorial animals (Ford 1983; Samuel et al. 1985).

Biological Rationale

Animal home ranges can seldom be characterized as homogeneous areas of vegetational attributes or uniform utilization. Typically, they are a mosaic of vegetation patches, differing in structure and composition, context, and presumably in quality to the animal. Thus, animals commonly exhibit selective behavior by utilizing certain areas within their home range more intensively than others. Both the size and habitat composition of these areas reflect life history requirements and are therefore relevant to effective conservation strategies. These areas of concentrated use by resident animals, loosely termed core areas, commonly include nest sites, daytime roost sites, refuges, and regions with the most dependable food sources (Burt 1943; Kaufmann 1962; Ford 1983).

Numerous approaches have been devised to identify core areas (Kaufmann 1962; Siniff & Tester 1965; Ables 1969; Murie & Harris 1978; Springer 1982; Clutton-Brock et al. 1982; Ford 1983; Samuel et al. 1985; Samuel & Green 1988; Seaman & Powell 1990). The earliest methods were based on visual assessment of aggregations of observations. More recent approaches employ radiotelemetry technology to estimate an animal's utilization distribution. In practice, the distribution is estimated by dividing the home range into discrete cells and fitting the observed distribution of locations within the cells to parametric distributions, such as the bivariate normal (Koeppl et al. 1975), or with nonparametric methods such as the harmonic mean (Dixon & Chapman 1980). Recently, Wray et al. (1992*b*) applied the harmonic mean, kernel (Worton 1989) and Dirichlet tesselation (Wray et al. 1992*a*) methods for estimating core areas within home ranges. These methods were all used to estimate core areas based on the cumulative proportion of an animal's locations and the related increase in area within the total home range.

There are continuing and unresolved debates over which home range estimator is most appropriate for bivariate data with various distributional patterns (Harris et al. 1990; White & Garrott 1990; Boulanger & White 1992). The recent works of Worton (1995) in combination with previous work by Boulanger and White (1992), however, point out many advantages to the use of kernel-based estimators. It is not our intent to debate the relative merits of various estimators nor to argue over their assumptions and data requirements. Rather, we simply assert that the arbitrary and ad hoc methods currently used to develop area1 mitigation guidelines should be replaced with methods based on biologically meaningful patterns of space use. In fact, there is probably no "best" estimator of utilization distributions as the most appropriate measure of space-use is likely to vary across species and study designs.

We believe the protection of core areas may be a key action to mitigate against the otherwise adverse impacts of regional habitat loss. We describe a method to empirically estimate the size of breeding-season core areas for territorial animals whose patterns of space-use can be represented by a set of locational data (x, y coordinates). The logic of our approach parallels that of Samuel et al. (1985) and Seaman and Powell (1990); however, we estimate core areas differently and use a different density estimator. Most novel, however, is our application of the core area concept to the mitigation of habitat take for threatened and endangered species, specifically its application to private lands and the HCP process.

We illustrate the method with locational data collected from individual Spotted Owls tracked during the breeding season. Collectively, this sample of owls demonstrates diverse patterns of space-use, assessed in terms of variation in the size and shape of the areas used. In our analyses we assume an animal's location during the breeding season can be described by a bivariate probability distribution. The likelihood of an animal being in a particular region of its home range is proportional to the volume below the surface of the bivariate probability distribution, directly above that region (Worton 1995). We employ individual owl telemetry relocations and the adaptive kernel algorithm (Worton 1989; 1995) to approximate the size, shape, position and habitat composition of core areas within their respective home range boundaries. We plan to apply these methods to conservation planning for Spotted Owls, address geographic variation in the size, shape and habitat composition of core areas, and demonstrate how these analyses can strengthen the scientific foundation of HCPs.

Study Areas

Locational data were collected by radio-tracking Spotted Owls within three study areas in northern California (Fig. 1): Mad River, Ukonom, and Lassen, all located primarily on U.S. Forest Service lands. Each study area represented a different physiographic region characterized by a distinct set of geologic, climatic, and floristic conditions (Irwin 1960; Hickman 1993). Descriptions of the study areas can be found in Paton et al. (1991), Verner et al. (1992), and Zabel et al. (1995). The Mad River and Ukonom study areas were occupied by Northern Spotted Owls. The Lassen site was inhabited by California Spotted Owls (*S. o. occidentalis*) and was located near the northern extent of that subspecies' distribution.

Methods

Radio Tracking

Following methods outlined by Forsman (1983), owls greater than 1 year old were captured, fit with radio

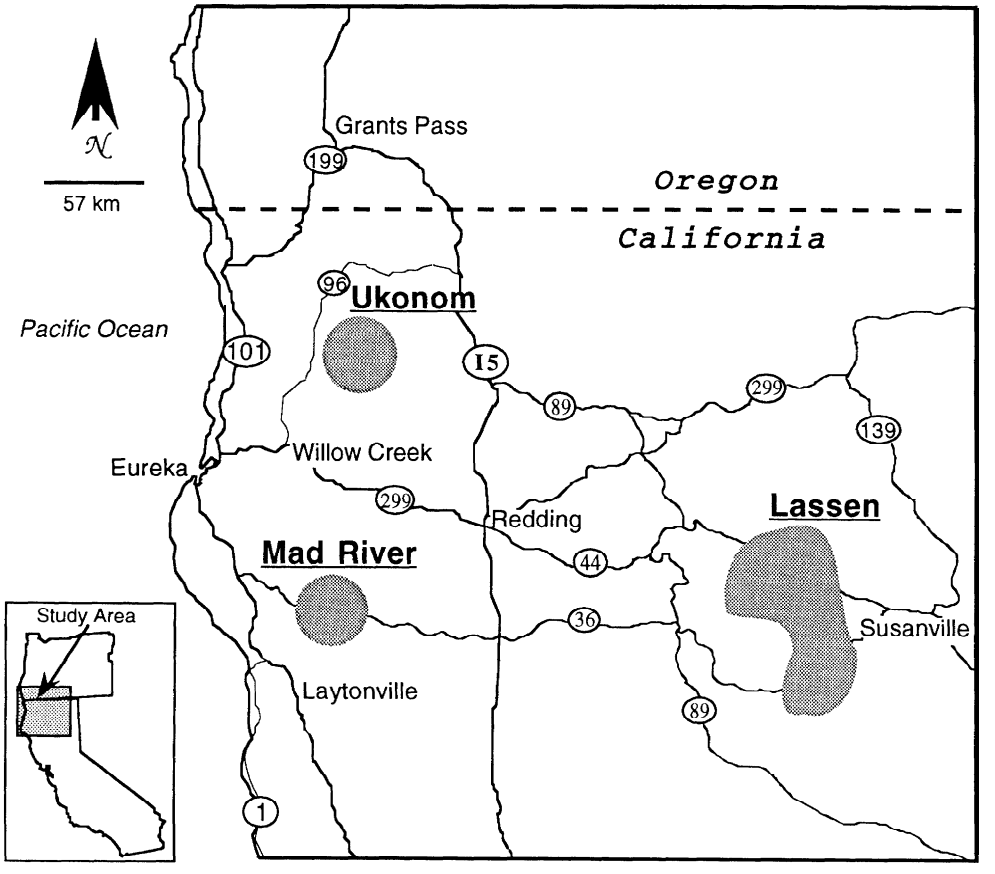

Figure 1. Geographic locations of the Spotted Owl study areas.

transmitters, and tracked for l-2 years at each study site. Fifty-five owls were fitted with transmitters--18 at Mad River, 19 at Ukonom, and 18 at Lassen-and sampled between April 1987 and September 1990. At least one entire breeding season was sampled for all owls at all sites. Further details on the methods of radio-tracking are in Paton et al. (1991), Verner et al. (1992), and Zabel et al. (1995).

Home Range and Core Area Estimation

The concept of home-range assumes the nonrandom use of an area. Because of limits to mobility, all animals will show spatial constraint in their movements over a finite time interval. The area used, however, should not be equated with a home range unless it can be demonstrated that sequential locations of the animal exhibit some degree of spatial autocorrelation. That is, if birds move nonrandomly and demonstrate significant site fidelity during some fixed time interval, then the area used is properly equated with a home range. For this reason we first determined whether individual owls exhibited site fidelity prior to their inclusion in any home-range size calculations. Following methods in Spencer et al. (1990), we concluded site fidelity to exist if the observed area used by an owl was significantly smaller than the area used if the owl's movement had been random. Sixteen of the owls in our sample failed the site fidelity test and were excluded from subsequent analyses.

Home-range and core area estimates for each bird were based on the distribution and density of relocations collected during the breeding season. To increase the likelihood that the estimates represented the area needed to meet the energetic requirements of individual birds, home ranges and core areas were calculated using both foraging (nighttime) and roosting (daytime) locations. Further, to assure biological independence, all estimates were generated using no more than one foraging location per night and no more than one roosting location per week.

Home-range size was estimated for each bird independently using the 95% adaptive kernel algorithm (AK; Worton 1989, 1995) and these estimates were used for all subsequent comparisons and statistical tests. The decision to omit the outlying 5% of observations is arbitrary. Nevertheless, the use of the 95% contour to define the home range is objective, repeatable, and consistent with home range studies for many species (White & Garrott 1990). Home-range size for breeding pairs was defined as the union (total area) of the home-range esti-

mates for the individual members of the pair (Thomas et al. 1990).

Our choice of the AK algorithm was based on its precision in accurately portraying the utilization distribution of an animal and its direct interpretation as a probability density function (Worton 1995). The AK method differs from the fixed kernel methods in that it varies the smoothing parameter over the plane of utilization so that areas with low concentrations of locations are smoothed more than areas with high concentrations of locations (Silverman 1986). There are a number of important decisions that must be made when using this algorithm, including selection of a grid-cell size and the smoothing parameter appropriate to the animal's home range (Wray et al. 1992*b*; Worton 1995). In making these decisions we used the analytical methods suggested by Worton (1995).

Based on our observations and previously published studies of the breeding chronology of Spotted Owls (e.g., Carey et al. 1990; Solis & Gutierrez 1990; Thomas et al. 1990), the telemetry data were initially partitioned into breeding (1 March through 31 August) and nonbreeding seasons (1 September through 28 February). An examination of the effect of sample size and time interval on breeding season home-range size estimates indicated that most owls showed an asymptote at sample sizes greater than 30 relocations, based on relocations collected prior to 1 August. We thus based our estimates of breeding season home range on locational data collected between 1 March and 31 July. Any birds with home range estimates failing to reach an asymptote during this period were omitted from subsequent analyses. Also excluded from further analyses were birds that had less than 100 radio-days (one radio-day = one 24-hour period with a functioning transmitter) and birds that had less than 50 breeding season locations.

To estimate the core area for each bird, we first estimated home range size by computing the 95% AK polygon. Second, we computed the sizes of 9 AK isopleths containing from 10-90% of the observations in increments of 10%. In subsequent regression analyses the nine AK isopleths represented the value of the independent variable, *x;* the area included within each AK isopleth, expressed as a percentage of the total home range (95% AK), represented the dependent variable, *y*. The unit of replication for these analyses was the individual bird, with each bird represented by a set of coordinate locations.

If the distribution of locations within the 95% AK isopleth were perfectly uniform, then the regression of *x* on *y* would be a straight line through the origin with a slope of 1.0. To the extent that locations are concentrated in certain parts of the home range, the regression of *x* on *y* will fall below the line $y = x$; that is, *b* will be less than 1.0. In this case the best fit regression curve will be concaved downward because area is accumulated less rapidly than expected under a uniform distribution of locations.

Based on the method of least squares (Neter et al. 1983), the overall best fit model for all owls was an exponential regression function ($y = e^{bx}$) forced through the origin (based on the transformation: $\ln(y + 1) = bx$). Based on the AK value at which the slope of this regression function = 1.0, (i.e., solving $x = (\ln(1/b))/b$ for each bird), we computed the percent AK (% AK) at which utilization was distributed as expected under a uniform distribution. Percent AKs less than this value included locations under-dispersed relative to a uniform distribution. Beyond this point, larger AKs began to accumulate locations over-dispersed relative to a uniform distribution. This point, slope of the tangent line = 1.0, determined the percentage of AK used to compute the size of the core area-that area of the home range in which use exceeds that expected under a null model of a uniform distribution of locations.

Each core area was examined for eventual independence from sample size in the same manner as described above for home range estimates (Harris et al. 1990; Wray et al. 1992b). Any core area estimate failing to reach an asymptote was rejected. Core area estimates for breeding pairs of birds were derived from the union and intersection of the core areas for individual members of the pair.

There are two sources of among-bird variability in core area estimates. First, the percent AK at which the density of the utilization distribution equals that expected under a uniform distribution (slope of the exponential regression function = 1.0). Second, the size of the core area associated with this break point. It is possible for animals to show greater among individual variations in one factor than the other, and these sources of variation may be important to proposed mitigation guidelines.

The Null Model for Core Area Estimation

Our null model assumed a bivariate, uniform distribution of animal locations. When *x* (% AK) and *y* (proportion of the home range at *x*) variables are estimated from random samples of the null distribution, core areas may appear simply as a result of small sample bias. Nevertheless, we were most concerned about the possibility of "false" core areas arising as a statistical artifact of the exponential model. When y-values are fit to an exponential regression model ($y = \exp[bx]$) and back-transformed to an arithmetic scale, the estimated *y*-values tend to be less than *x*-values, suggesting a clumped pattern of space-use. To test the magnitude of this artifact, we selected random samples of sizes equal to 50, 300, and 2000 locations from a uniform distribution. For each sample we calculated the 95% AK isopleth, the nine AK percent

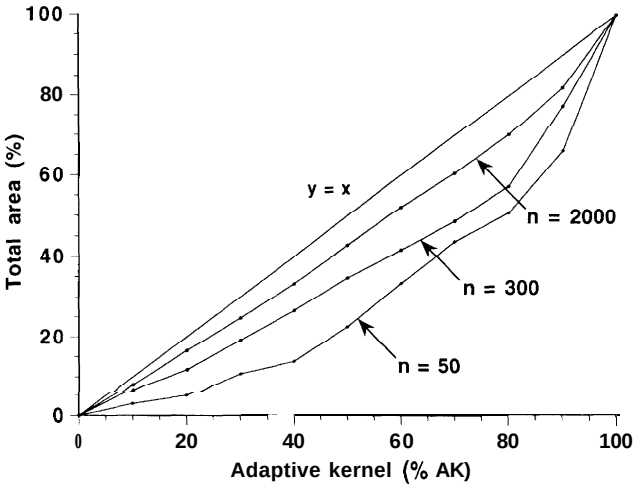

Figure 2. Regression of the percent adaptive kernel value (% AK) on the percent of home range area (area of the 95% AK isopleth represented by a given %AK. The line y = x is the expectation if all points within the home range were uniformly distributed and fit to a linear equation. The thee curves represent the average regression of x on y based on random samples and fit to the model y = e^{bx}. The curves were estimuted from random samples of' size 50, 300, and 2000 selected from a uniform distribution.

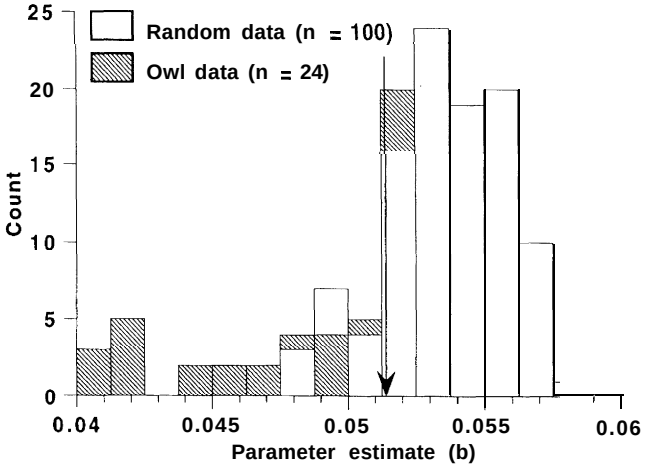

Figure 3. Frequency distributions of the estimated slope parameters (b) from regression analysis of two data sets: locational data from 24 Spotted Owl home ranges and 100 random samples of locational data from a uniform distribution. The data were fit to an exponential regression function (y = e^{bx}), where y = percentage of the home range area represented by a given percent adaptive kernel (% AK) isopletb, and x = the %AK at which y is computed. The arrow indicates the lower 10% limit of the 100 slope parameters (b) estimuted from the random samples.

isopleths (l0-90%), and estimated the regression of *x* on *y*. Only the largest sample (n = 2000) produced a relationship between *x* and *y*, after back-transformation, nearly indistinguishable from the expected relationship (*y* = *x*; Fig. 2). The function generated from the smallest sample (n = 50) fell substantially below the line *y* = *x* (Fig. 2).

These results suggest that fitting the exponential model to AK estimates of *x* and *y* for data sets characteristic of most wildlife telemetry studies (i.e., less than 300 locations / individual) could falsely suggest the existence of core areas. Therefore, it was necessary to examine the likelihood that our estimated regressions from the owl data differed significantly from the expected value of *b* based on repeated samples drawn from the null distribution. To address this concern we generated 100 random data sets, each of size 50 (the size of our smallest owl sample), by sampling from a uniform distribution. We then fit each data set separately to the same exponential regression function ($y = e^{bx}$) as fit to the owl data. The distribution of parameter estimates *(b)* from the 100 regressions on uniform-random data were compared to the parameter estimates obtained from the owl location data, separately for each bird. A clumped distribution of owl locations would have a *b* significantly < *b* estimated from the null distribution. The distribution of the two sets of estimates were distinct with 21 of 24 observed *b* estimates falling below the left, 10% tail of the null distribution (Fig. 3). These results indicate that our sample of owls were utilizing their home ranges in a concentrated, non-uniform fashion.

Results

Twenty-four birds met our criteria for site fidelity, number of radio-days and relocations, and stability in home range size and core area estimates. Our analyses included 11 birds from the Mad River (1988 breeding season), 9 from the Ukonom (1988 breeding season), and 4 from the Lassen (1990 breeding season) study areas. Our analyses included seven pairs of owls from two study areas; four from Mad River and three from Ukonom. Sample size (number of relocations) ranged from 50-86 relocations (mean = 65.9, SEM = 2.2).

Home Ranges

Home range size estimates for individual Northern Spotted Owls were smaller at Mad River than at Ukonom (Table 1). In contrast, home range (union) estimates for breeding pairs were slightly larger at Mad River than Ukonom (Table 1). Although more variable at Mad River, the size of the area shared (intersection) by members of

Table 1. Breeding season home range estimates for Northern Spotted Owls and owl pairs (Mad River and Ukonom) and California Spotted Owls (Lassen) in northern California.

	Mad River	*Ukonom*	*Lassen*	*All*
Individual owls	11	9	4	24
Home range (ha)[a]				
mean (±SE)	522.7 (72.7)	676.9 (108.6)	4263.3 (1954.2)	1199.5 (407.5)
Range	148.0–891.6	405.3–1374.0	1236.0–9982.0	148.0–9982.0
CV (%)	46.1	48.1	92.3	166.4
Owl pairs	4	3	n/a[e]	7
Home range (ha)[b]				
mean (±SE)	771.5 (90.1)	704.3 (121.5)		742.7 (67.9)
Range	511.6–897.6	545.3–942.8		511.6–942.8
CV (%)	23.4	29.8		24.2
Area shared (ha)[c]				
mean (±SE)	322.2 (73.5)	320.1 (31.4)		327.0 (41.1)
Range	188.3–494.2	272.5–379.3		188.3–494.2
CV (%)	44.3	17.0		33.3
Area shared (%)[d]				
mean (±SE)	42.7 (7.1)	47.8 (8.2)		44.9 (5.0)
Range	25.5–55.6	32.7–60.7		25.5–60.7
CV (%)	33.2	29.6		29.4

[a] *Individual owl home ranges were calculated using the 95% adaptive kernel, estimated from one foraging location per night and one roosting location per week, collected during the 1988 breeding seasons (1 March–31 July) at Mad River and Ukonom and the 1990 breeding season at Lassen.*
[b] *Owl pair home ranges were based on the union (total area) of home ranges for the male and female members of each breeding pair.*
[c] *Area shared is based on the intersection (overlap) of home ranges for the male and female members of each breeding pair.*
[d] *Area shared (%) is the intersection as a proportion of the pair home range.*
[e] *Data for breeding pairs not available.*

each owl pair, was similar at these two study areas. Home range sizes for individual California Spotted Owls at Lassen averaged 6–8 times larger than estimates for Northern Spotted Owls. The differences in home range size estimates between Northern and California subspecies is believed to reflect differences in habitat composition and prey availability rather than subspecific differences.

Core Areas

The exponential model fit the data well for all individual owls—the 24 adjusted R^2 values ranged from 0.72–0.99 (mean = 0.92). Variation in the 24 slope estimates (***b***) was low ranging from 0.0401–0.0524 (mean ***b*** = 0.0462) and the average model was markedly consistent among the three study areas (Fig. 4).

The majority of our core areas were defined by a single isopleth that included all areas of repeated use, or other areas of concentric isopleths (Fig. 5; cf. Wray et al. 1992*b*). A few birds had their core areas defined by two distinct polygons not encircled by a single larger isopleth (i.e., Fig. 6a). Examination of telemetry relocations and nest tree coordinates for these birds showed that utilization was concentrated in two disjunct areas sometimes separated by considerable distances. One core area isopleth contained the nest tree coordinates while the other core area isopleth was used consistently for nighttime foraging.

The variation in the percent AK defining the core area, or the core area AK, was quite low within and among the three study areas (AK at slope = 1; Table 2). The core areas for more than half of the birds were resolved between the 60% and 75% AK isopleths. Core area, as a proportion of the home range, also showed little variability, typically accounting for 21–22% of the total area of the home range (Table 2). Variation in core area size among study areas was more pronounced (Table 2) and paralleled the pattern of variation in total home range size within and among regions (Table 1). Variation in home range and core area size among and within study areas most likely reflects geographic variation in vegetational patterns (Carey et al. 1990, 1992; Thomas et al. 1990; Verner et al. 1992) and variation in the identity and abundance of the primary prey species (Carey et al. 1992; Zabel et al. 1995).

We computed core areas for breeding pairs in two ways—based on the union and based on the intersection of the male and female core areas (e.g., Fig. 6). The union (total area) averaged two to three times the size of the intersection (area shared) (Table 2). This difference between the union and the intersection reflects the differential use of area by the sexes. Pair core areas based on the union tended to be similar in size, but slightly less variable than the core area estimates for individual birds. In comparison to the home range estimates for pairs, the core area intersection, as a proportion of the total area shared by both sexes, was more variable (cf. Table 1 and Table 2, CV). The area (ha) of the intersection showed

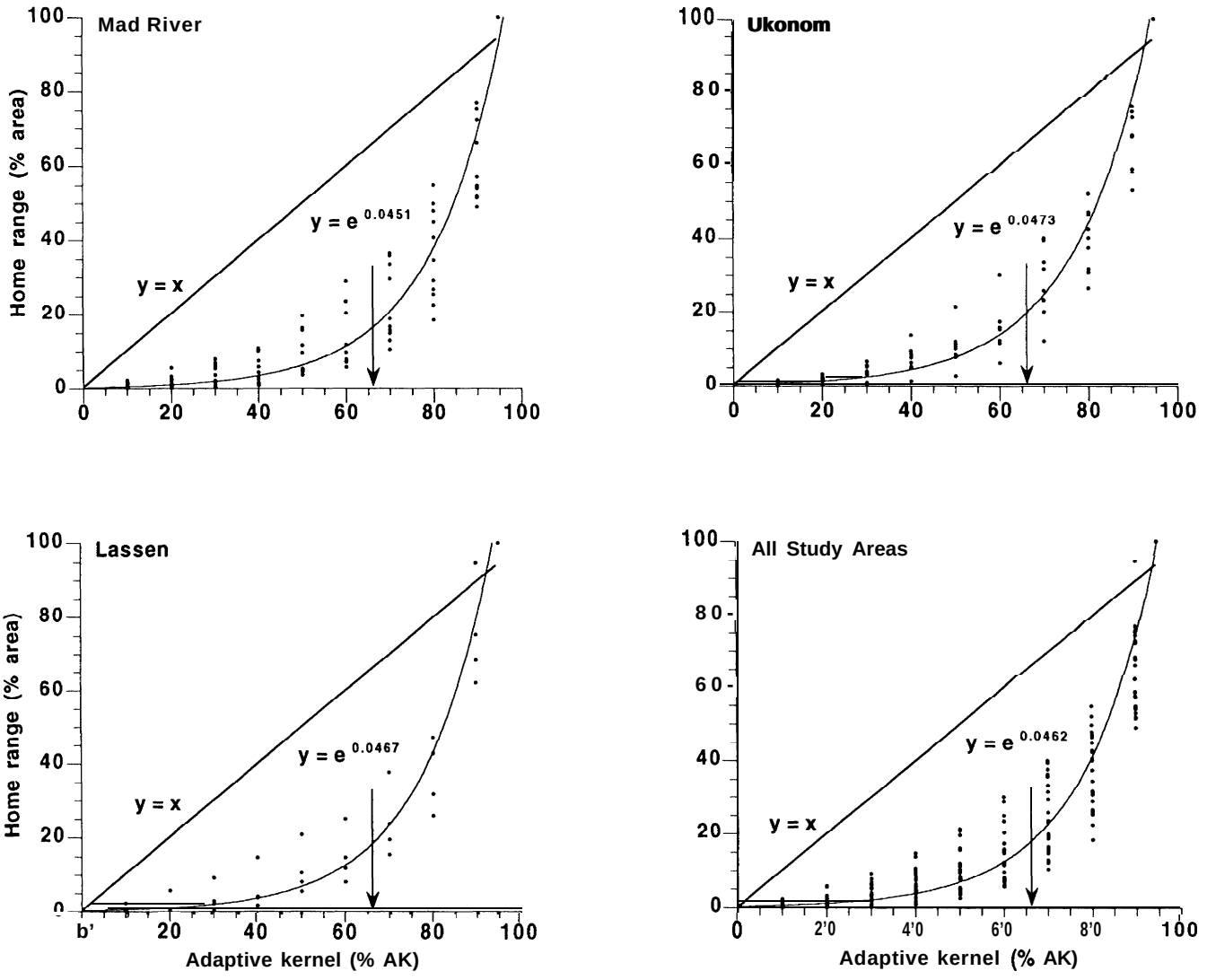

Figure 4. *Scattergram of the percentage of the 95% adaptive kernel home range area (y) against the corresponding percent adaptive kernel (x; %AK), with separate data points shown for each owl. Also shown is the combined exponential regression function* ($y = e^{bx}$) *based on the regression of* x *on y fit independently for each owl. The line y =* x *is the expectation if all points within the home range were uniformly distributed and fit to a linear equation. The arrows indicate the %AK at which the slope of the average fitted function = 1.0. This point (slope = 1.0) was estimated separately for each owl and the corresponding %AK was used to estimate core area size.*

patterns of variation that paralleled the intersection for pair home-range estimates (cf. Table 1 and Table 2, CV). Based on the union estimates, variation in core area size for breeding pairs was greater than that observed in home range size (cf. Table 1 and Table 2, CV). Assuming that the male and female members of a pair minimize spatial overlap to increase overall pair fitness, we believe union estimates are preferable as breeding pair core areas.

Core areas showed no consistent pattern in shape, although some did exhibit shapes similar to their respective home ranges (Fig. 5). Only a few core areas were circular, but non-circular home ranges are common in birds and mammals (Ford 1983). Most core areas were elongate or lacked distinct form, but all included more than one area of concentrated activity (i.e., the nest tree location and one or more other areas of repeated foraging or roosting) suggesting a heterogeneous or coarse-grained distribution of resources.

Discussion

Motivated by the ad hoc fashion in which habitat mitigation formulas were being developed for the Northern Spotted Owl on private lands, we sought more empirical and defensible methods for estimating an animal's minimal area requirements. We adopted the concept of "core area," the area within an animal's home range that

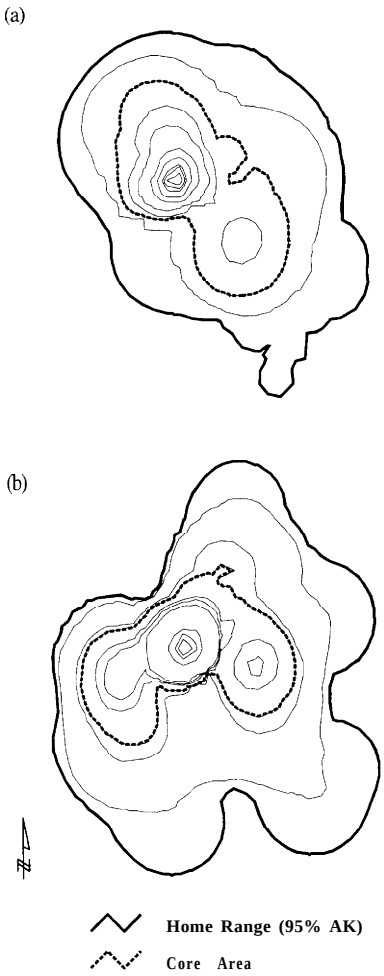

Figure 5. Successive adaptive kernel isopleths illustrating the relationship of the core area (broken line) to the 95% adaptive kernel home range estimate (outermost, heavy line). The relationships are shown for the female (a) and male (b) members of a breeding pair of Northern Spotted Owls. The female's 137-ha core area (a) was defined by the 80% isopleth. The males 131-ha core area (b) was defined by the 69% isopleth. Both core areas contain two series of concentric isopleths indicating that home range use was concentrated in more than one area.

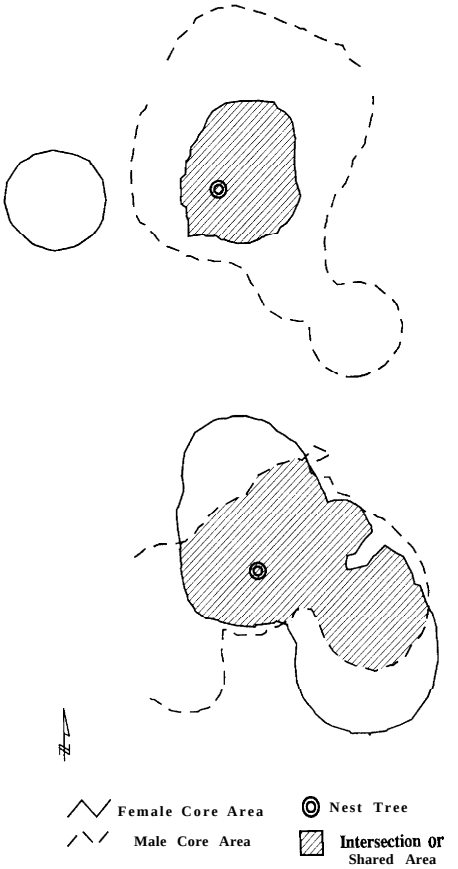

Figure 6. Core area isopleths shown separately for the male and female members of two pairs of owls (a and b). Hatched area indicates the intersection of the core areas. Male and female isopleths combined represent the union of the two core areas or the pair core area. Also shown are the locations of the nest trees for pairs (a) and (b).

is most intensely used, which has a long history of use in the practice of wildlife management (e.g., Kaufmann 1962; Siniff & Tester 1965; Ables 1969).

Core Areas

Similar to Samuel et al. (1985) and Seaman and Powell (1990), we defined an animal's core area as the overused (relative to a uniform distribution) portion of its breeding season home range. Wray et al. (1992*b*), in contrast, proposed different guidelines for identifying core areas. They first plotted the home range and then, starting with the most dense cluster of points, measured the areas enclosed by successively larger isopleths. The core area was resolved between those isopleths separated by the greatest increase in area. We used their method on our data and found that the maximal increase in area typically occurred between the 80 and 90% AK isopleths. In contrast, our method yielded smaller area estimates-all 24 core areas were defined by an adaptive kernel isopleth less than or equal to 80% (Fig. 4). Although different methods may yield different estimates of core area, our intent was not to argue for the advantage of one method over another. Rather, our goals were to argue for the biological significance of core areas, to propose an objective method for their estimation, and to encourage their use as a means of mitigating against the loss of habitat.

The grounds for estimating an animal's (or pair's) core area rests on the assumption that this area provides critical habitat elements (i-e., nest sites, roost sites, access to

Table 2. Breeding season core area estimates for Northern Spotted Owls and owl pairs (Mad River and Ukonom) and California Spotted Owls (Lassen) in northern California.

	Mad River	*Ukonom*	*Lassen*	*All*
Individual owls	11	9	4	24
AK (%) at slope = 1				
mean (±SE)	69.5 (2.8)	64.9 (2.3)	66.3 (4.2)	67.2 (1.7)
Range	57-80	57-80	56-76	56-80
CV (%)	13.3	6.9	12.7	12.2
Home range (%)				
mean (±SE)	21.6 (1.8)	21.7 (1.8)	21.4 (1.6)	21.6 (1.0)
Range	13.3-34.9	16.0-30.8	16.9-24.0	13.3-34.9
CV (%)	27.3	24.6	15.3	23.8
Core area (ha)"				
mean (± SE)	111.8 (18.5)	146.5 (25.4)	813.4 (301.1)	241.8 (70.5)
Range	33.2-209.7	73.0-275.7	296.2-1684.0	33.2-1684.0
CV (%)	54.8	51.9	74.0	142.9
Owl pairs	4	3	n/a[e]	7
Core area (ha)[b]				
mean (±SE)	183.6 (41.4)	141.9 (30.8)		165.7 (26.4)
Range	67.9-257.9	81.9-184.0		67.9- 184.0
CV (%)	45.1	37.6		42.1
Area shared (ha)[c]				
mean (± SE)	61.0 (12.4)	68.2 (8.0)		64.1 (7.4)
Range	37.2-86.8	56.4--83.3		37.2-86.8
CV (%)	40.7	20.2		30.7
Area shared (%)[d]				
mean (± SE)	37.8 (9.0)	53.2 (13.3)		44.4 (7.6)
Range	20.2-62.4	35.3-79.1		20.2-79.1
CV (%)	47.7	43.2		45.4

[a] *Individual owl core areas were based on the percentage adaptive kernel isopleth at which utilization was distributed as expected under a uniform distribution (AK % at slope = 1) and represents the over-utilized area(s) of each animal's home range. Individual owl home ranges were calculated using the 95% adaptive kernel, estimated from one foraging location per night and one roosting location per week and collected during the 1988 breeding seasons (1 March-31 July) at Mad River and Ukonom and the 1990 breeding season at Lassen.*
[b] *Owl pair core areas were based on the union (total area) of core areas for the male and female members of each breedng pair.*
[c] *Area shared is based on the intersection (overlap) of core areas for the male and female members of each breeding pair.*
[d] *Area shared (%) is the intersection as a proportion of the owl pair core area.*
[e] *Data for breeding pairs not available.*

prey) for survival and reproduction. Therefore, its protection will mitigate, in part, for the take of habitat external to the core area. The extent to which this is generally true is unknown. Nevertheless, all of our estimated core areas for Spotted Owls included the nest site and the primary breeding season roosting and foraging locations. Thus, core areas, at least for the Spotted Owl, provided meaningful habitat components contributing to their survival and reproductive success.

Owls in our sample typically used 20-21% of their home range as core area habitat, which generally included 60-70% of their breeding season activity. Core area size showed greater variation, although in a manner consistent with the geographic variation in home range size. The core area estimates for breeding pairs in the coastal and Klamath regions tended to be slightly larger than estimates for individual birds from the same locations. This is a reflection of variation in male-female overlap, or the area shared, and may arise from variation in reproductive outcomes (success or failure when in the nesting cycle failure occurred).

Estimates of the variation in core area size are important because effective conservation strategies for wide-ranging species must account for geographical variation in the behavior and ecology of local populations. Our analyses detected variation both within and among local populations of owls (Fig. 7). The among-population variation suggests that HCPs should be regionally specific in their area and habitat prescriptions. The within-population variability suggests that area guidelines should have a high likelihood of meeting the area requirements of the majority of individuals in the population (e.g., mean area + 1 SE). This, however, is more of a policy than a scientific decision.

We found considerable variation in core area shape with no consistent spatial relationship to a primary activity center, such as the nest tree. Nest trees did however tend to occur within the 10% AK isopleths for female owls. While the nest tree location may define an origin, core area shape is more strongly related to the variation in the distribution of foraging and roosting locations, and therefore may reflect a heterogeneous distribution

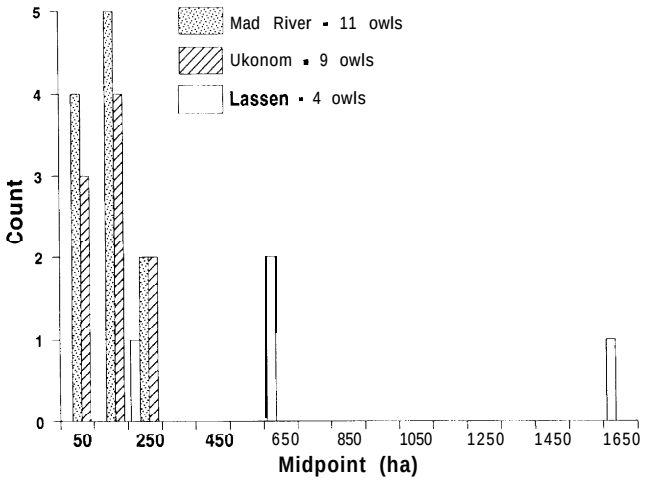

Figure 7. Frequency distribution of estimated core area sizes for individual Spotted Owls sampled from three different study areas. Mad River and Ukonom were Northern Spotted Owl sites and Lassen was a California Spotted Owl site.

of critical Spotted Owl resources (large trees and prey species).

Information on both the size and composition of core areas are required to mitigate against the take of habitat. We focused on the logic and methods of estimating core area size. This information by itself is insufficient unless there are guidelines for the habitat type composition and elements to be included within the core areas to meet a specie's life history requirements. The method described here, in combination with mapped information on habitat attributes (e.g., vegetation structure and composition), can directly link the spatial distribution of individual animals to attributes of their physical and biological environment. This is readily accomplished by intersecting the estimated coordinates of the core areas with existing habitat maps through a geographic information system (GIS) interface.

When this process is completed for a sample of animals, the task is then to examine the distribution of habitat types and elements for those components that are present in the majority of core areas. The logic is that these are the consistent aspects of the environment that trigger the habitat selection response of this species and are related to its survival and reproduction.

Application of the Core Area Method

The methods we propose for the estimation of core area size and composition are data intensive. To realize a core area's full potential requires spatially explicit information on the distribution of animals and the distribution of habitat and its key elements. This information will be available for only a handful of species. Further, for most species the relevant relationships among habitat area, habitat composition, and population biology is unknown. Thus, the degree to which the protection of core areas assures a population's viability is unknown-to attain such assurance will require years of concentrated field work.

Despite these limitations, the methods we describe make the process of mitigating against the loss of habitat considerably less ad hoc than in many approved HCPs. The relevant data are directly based on the animal's behavior and include biological factors relevant to a species' persistence. We believe the methods discussed have wide application; however, other species may require different analytical methods and study designs. Nonetheless, what is unarguable is that effective mitigation against habitat loss for a threatened species often entails the estimation of the size and habitat composition of an area relevant to the fitness of the individual animal. For Spotted Owls and many other species, we assume that one good biological measure is the area within the breeding season home range that receives the most intense use. The most appropriate unit for assessing spatial patterns of utilization may vary across species. We believe, however, that the breeding unit, the pair in the case of Spotted Owls, is often the most appropriate biological unit for the analysis of space-use.

In the context of the ESA, current FWS regulations define harm as "an act which actually kills or injures wildlife. Such acts may include significant habitat modification or degradation where it actually kills or injures wildlife by significantly impairing essential behavior patterns, including breeding, feeding, or sheltering" (1981: 54,748). Thus, methods that provide information on how to mitigate against the take of habitat are of immediate importance to listed species. The concept of a core area is relevant to species in decline because of habitat limitation, and relevant to the issue of take as addressed in HCPs or recovery plans. Such plans address several policy questions (Beatley 1994) including (1) the extent of habitat loss or degradation that is allowable; (2) the level of habitat protection and management required; and (3) the equitable distribution of costs of habitat protection. The first two of these are essentially scientific questions. The challenge for the conservation biologist is to estimate, in a scientifically defensible manner, the size and composition of an area that meets critical life history requirements. The necessity that the method of estimation be scientifically credible, as well as biologically sound, is of obvious importance given the current, heated debate over the appropriateness of the ESA, particularly its application to private property. The biologists can do no more, nor no less, than to propose scientifically based methods of mitigation that increase the likelihood of a species' persistence and address the intent of environmental laws.

The most effective way to protect biological diversity

is to protect areas that are large enough to allow the existence of mosaics of habitats and the dynamic processes of change within these areas (National Research Council 1995). For most species, however, detailed information on their patterns of space-use will not be available. So how does one apply the data-intensive methods discussed in this paper to the problem of multi-species planning? One way to accomplish this goal is to focus field work on species with large area requirements (so-called umbrella species). Managing habitat in a manner consistent with their persistence may indirectly assure the persistence of numerous other species with overlapping habitat needs and smaller area requirements. The combination of estimates of core area size (and habitat composition) for such umbrella species, with estimates of their viable population size, could provide the intial estimate for the necessary size of a conservation reserve.

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