THE BIOLOGICAL FOUNDATION OF CRITICAL HABITAT FOR SPECIES AT RISK: A LITERATURE REVIEW

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This draft document represents a synthesis of scientific literature on issues related to the biological foundation of critical habitat and was drafted for discussion purposes within the Critical Habitat Working Group.

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I. Abstract

The identification of critical habitat for species at risk should be based on a strong biological foundation if it is to be effective in their protection and recovery. This review of the primary literature lays the groundwork for that foundation by synthesizing the scientific community's current understanding of habitat requirements for species at risk, and outlining the biological and ecological characteristics of critical habitat. This review is expected to help inform development of science policy relating to the identification of critical habitat and the implementation of the Federal Species at Risk Act.

The review covers three distinct, complimentary perspectives that are thought important to consider as part of the critical habitat identification process. The first perspective encompasses requirements of individuals. In this respect, critical habitat should comprise the mosaic of habitat types individuals need to complete their respective life cycles, including how habitat requirements may differ through the year, among age/sex classes and across geographic localities. Some thought should also be directed to species habitat requirements that stem from vital relationships with other species (e.g., obligate pollinators & seed dispersers) and disturbance processes (e.g., floods, fire).

The second perspective that should be considered in the identification of critical habitat are population-level requirements. Ideally, critical habitat should contain sufficient habitat to provide for a high likelihood of long-term population persistence, or viability. Narrowing habitat requirements down to a minimum amount is complicated by the fact that needs may vary according to matrix quality, fragmentation, reproductive rate, dispersal ability, etc. Further confounding minimum habitat-amount determinations include the existence of habitat extinction thresholds and time lags in species' response to habitat loss. Area-sensitivity is another feature of critical habitat that should be viewed from a population perspective. While area-sensitivity is an individual-level phenomenon, the net effect of multiple individual responses may be population-level consequences (e.g., population sinks).

The final perspective that warrants attention in the identification of critical habitat is that afforded through the lens of landscape ecology. It is well recognised that population viability may be effected not only according to within-patch characteristics, but also to conditions of the surrounding landscape. For instance, the quality of the matrix, or non-habitat portion of the landscape, can have a large effect on the amount of habitat required for long-term population persistence. This potentially has important management implications, since for many species increasing the quality of the matrix may be a more practical option than increasing the overall amount of critical habitat. Similarly, for species that persist in fragmented landscapes in which habitat patches are occupied by way of dispersal movements, the surrounding matrix can impact the ability of individuals to effectively move between habitat patches. Such inter-patch movements may be key to the survival of populations that exist as meta-populations, and elements of the landscape that allow species to maintain these inter-connections should be identified and included as critical habitat. In addition, both habitat configuration and landscape complementation may have important effects on population persistence and thus, should be evaluated in the identification of critical habitat. The importance of habitat configuration, or the spatial arrangement of habitat patches, may increase when the amount of habitat in the landscape is

low, as is the case for many species at risk. Habitat configuration may be especially important for species that that rely on landscape complementation, or more than one type of habitat, to complete their life history requirements.

II. Introduction

Biologists disagree about many things, but one thing they agree on is the importance of habitat to species' conservation. Organisms cannot exist in isolation; species-specific habitats, for all stages of their life cycle, are essential to their survival. The importance of these species-specific habitat requirements, in addition to the negative effect of habitat loss and degradation due to anthropogenic activities, is recognized in the federal Species at Risk Act (SARA; Species at Risk Act 2003). SARA calls for the identification and protection of a species' critical habitat. Within the Act, critical habitat is defined as:

> *the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species* [s. 2(1)].

SARA requires the identification of critical habitat during the recovery planning process for listed endangered, threatened and extirpated species. Most often, critical habitat should include the habitat required for full recovery and eventual de-listing of a species at risk. However it should be recognised that for some species, such as those that have always had a very limited range (e.g., Banff Springs Snail), full recovery and de-listing may never be possible. Further, for some species it may be determined that recovery is not technically and biologically feasible (see SARA, s. 40). For these species, critical habitat may provide for mere survival.

SARA's provisions for the protection of a species' critical habitat recognise the importance of species-specific habitat for conservation and recovery. Understanding these habitat requirements is especially important for species at risk, as loss and modification of their habitat is often one of the main reasons species are designated as being at risk in the first place (Ehrlich and Ehrlich 1981, Groombridge 1992, Wilson 1992, Noss et al. 1997, Lande 1998). Thus, to facilitate the recovery of listed species it is imperative to have an understanding of the specific physical and biological habitat attributes on which to focus protection efforts. Identification and protection of species' critical habitat, in combination with identification and mitigation of the threats to species' survival, will form the backbone of recovery for species at risk under SARA.

The purpose of this literature review is to survey and synthesise the scientific community's current understanding of habitat requirements for species at risk, including the ecological and biological characteristics of critical habitat. This synthesis will inform the development of science policy relating to the identification of critical habitat and the implementation of SARA. Admittedly, this review draws from literature focused on terrestrial organisms, though many concepts discussed herein also apply to species in aquatic environments. Fisheries and Oceans Canada is undergoing similar exercises for identifying critical habitat in the aquatic realm, and as a starting point please refer to a paper by Phelps (2001).

This review is based on a survey of the primary literature. With the exception of a few key books and articles, the majority of papers included in this analysis were published between the years 1990 and 2003. Therefore, concepts and principles discussed herein represent the current understanding of the scientific community, and are based on results from both empirical and theoretical research. Several fields of study were investigated, ranging from habitat biology to population biology and landscape ecology, and the papers included in this analysis cover a wide variety of topics related to the biological meaning of critical habitat. Review papers that summarise the current state of knowledge in a particular subject area were included whenever possible. Also included, are articles related to the implementation of the Endangered Species Act (ESA) by the U. S. Fish and Wildlife Service (USFWS), especially papers that pertain to critical habitat (Endangered Species Act 1988).

This paper is divided into five main sections. In the first section the term *habitat* is discussed, including an examination of the various definitions of habitat found throughout the literature and the importance of using standard terminology. In addition, the legal definition of habitat under SARA is presented as well as an operational definition of habitat from the literature, recognising that a clear understanding of what is meant by a species' habitat is essential to identifying and protecting critical habitat.

Section two begins to examine the biological meaning of critical habitat by proposing species' life histories as a framework for defining the criteria that could be considered for individual organisms. This section explores these life history requirements, and the need for critical habitat to encompass the different habitats that a species requires for fulfilling its life history functions. Demographic and temporal differences in habitat use are discussed, as well as the value of incorporating essential ecological processes and important life history relationships into a species' critical habitat. In addition, spatio-temporal shifts in habitat are discussed, along with their implications for identifying critical habitat.

The third section moves from the individual-level to the population-level, and examines biological considerations of critical habitat that are specific to populations. This section focuses on area-sensitivity, as well as species-specific minimum habitat requirements and factors that are thought to influence these quantitative requirements. A distinction is made between individual-level area requirements and population-level area requirements, as critical habitat is identified as a population-level requirement. Other population-level phenomena are discussed, including the need to incorporate flexibility and redundancy into a species' critical habitat.

Landscape-scale issues are discussed in section four, which begins with a brief overview of what a landscape is, and why landscape-scale issues are important to consider when identifying critical habitat. Several topics are discussed including matrix quality, landscape connectivity, habitat configuration and landscape complementation.

The fifth and concluding section synthesises the biological considerations outlined in this review, and discusses their implications for the development of guidelines for identifying critical habitat under SARA.

In addition to the five main sections that explore the biological considerations of critical habitat, there are two additional topics discussed in this review paper. While these topics are not directly related to the biological meaning of critical habitat, they are nonetheless significant as they lead to important insights about critical habitat and its identification. First, the application of population viability analysis (PVA) to the identification of critical habitat for species at risk is discussed in Box 1. In this segment, a brief introduction to PVA is followed by an exploration of how PVA may be useful for the identification of critical habitat, and recovery planning in general. In addition, the criticisms and potential limiting factors of PVA are discussed.

Box 2 briefly examines the use of broad-scale recovery strategies for species at risk. SARA's provision for the development of multi-species and ecosystem-based recovery strategies (s. 41(3)) is discussed, along with the critical habitat requirements for individual species.

III. What is habitat?

The importance of habitat to species' conservation is well supported by the scientific community. However, the term *habitat* has been used loosely in the literature; definitions of habitat have ranged from a general association with a particular type of vegetation, to a detailed description of a species' immediate surroundings (Hall et al. 1997). This inconsistency has led to a call for a consistent and clear operational definition of the term *habitat* (Murphy and Noon 1991, Hall et al. 1997). As such, Hall et al. (1997) offer the following operational definition of habitat:

> *The resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism.*

Under this definition, habitat includes both the biological and physical characteristics of an area that provide an organism with the resources it needs to survive. In other words, habitat is the sum of the biotic and abiotic environment, as well as their interactions, which allow an organism to fulfil its life history functions.

The definition proposed by Hall et al. (1997) is similar in meaning to the definition of habitat found in SARA, although SARA defines habitat slightly more broadly (see below):

> *(a) in respect of aquatic species, spawning grounds and nursery, rearing, food supply, migration and any other areas on which aquatic species depend directly or indirectly in order to carry out their life processes, or areas where aquatic species formerly occurred and have the potential to be reintroduced; and (b) in respect of other wildlife species, the area or type of site where an individual or wildlife species naturally occurs or depends on directly or indirectly in order to carry out its life processes or formerly occurred and has the potential to be reintroduced* [s. 2(1)].

The definition of habitat found in SARA includes not only the areas that a species depends on directly to carry out its life processes, but also the areas that a species depends on indirectly and the areas in which the species has the potential to be reintroduced. This broader definition of habitat has implications for the identification of critical habitat; a clear understanding of what is meant by habitat is crucial to understanding what constitutes critical habitat, as critical habitat is the *habitat* that is necessary for the survival or recovery of a listed wildlife species. With this clarification of terms, an exploration of the biological considerations of critical habitat for species at risk is possible. The following section begins to outline some of these biological considerations, by summarising what critical habitat means to individual organisms.

IV. Criteria for characterising critical habitat

Life history requirements

Primary biological needs

An individual's ability to complete its life history functions, and thus contribute to population persistence, is at least partly dependent on the availability of the appropriate habitat. The primary biological needs (i.e., key life history stages and activities) that may be considered when attempting to identify critical habitat for a particular species include, but are not necessarily limited to: (1) reproduction (e.g., rutting, courtship, mating, pollination, spawning, nest/den/burrow/cavity construction, egg-laying, gestation/incubation, germination, brood rearing/fledging); (2) cover/shelter/refugia; (3) feeding/foraging; (4) basking/roosting/loafing; (5) dispersal (e.g., seed dispersal, larval dispersal, natal dispersal, breeding dispersal); (6) moulting/pupation/metamorphosis; (7) hibernation/estivation/diapause; and (8) migration. When specific habitats, or habitat elements, are required to successfully perform one or more of these primary biological needs, that habitat should form a component of the species' critical habitat.

In addition to identifying specific habitat features or elements associated with a species' life history, it may also be useful to identify sensitive stages in the life cycle that may require special attention. For the threatened Eastern Spiny Softshell Turtle (*Apalone spinifera*), nesting is an example of a life cycle stage that may require specific consideration. This species reaches sexual maturity at a late age (12 years), and produces only one clutch per year (Campbell and Donaldson 1991). During nesting, females often congregate on the same areas of shoreline, and these areas are threatened by a variety of factors such as pollution, recreation, predation, and construction (Campbell and Donaldson 1991). For this species, these traditional nesting sites may be a particularly important component of its critical habitat because their destruction could have significant negative impacts on the population. Critical habitat for the Spiny Softshell Turtle should take into account the habitat requirements for this vulnerable nesting stage.

Variability

The habitat that an organism requires for completing its life history functions may vary both temporally, and between different demographic groups. The following examples illustrate the importance of considering demographic (age/stage, sex) and temporal (daily, seasonal) differences in habitat requirements when identifying critical habitat for species at risk. These differences should be considered when characterising the habitat required by a species to complete its life history.

The need for a reasonable understanding of a species' life history is apparent for species whose habitat requirements vary temporally. For example, seasonal differences in habitat use occur in the Northern Leopard Frog (*Rana pipiens*) which is designated as endangered in the Southern Mountain population and special concern in the Western Boreal / Prairie populations. The Northern Leopard Frog requires three different habitats to complete its life cycle, including: (1) temporary ponds for reproduction and tadpole development in the spring; (2) grassy fields used by juveniles and adults for foraging throughout the summer; and (3) ponds or streams that do not freeze solid for overwintering (Pope et al. 2000). Loss or degradation of any one of these habitats may result in local extinction if alternative habitat is not available within the dispersal distance capabilities of the Leopard Frog.

As well as seasonal variation in habitat use, some species may use different types of habitat on a daily basis. The threatened Pallid Bat (*Antrozous pallidus*) of British Columbia for example undergoes daily movement between its daytime roosting habitat in crevices along steep cliffs and rock faces, to its night time feeding habitat in open grasslands and sagebrush (Willis and Bast 1999). The loss of either of these habitats (or an inability to move between them) may have negative effects on population persistence, especially if fidelity to roosting sites is high. Temporal differences in habitat requirements should be considered when identifying critical habitat for a species at risk.

In addition to temporal differences in habitat requirements, there may also be differences between different demographic groups of the same species; habitat requirements may vary between males and females, as well as between individuals in different age or stage classes. For example, gravid (i.e., pregnant) females of the Massasauga (*Sistrurus catenatus catenatus*), which is designated as threatened in Canada, have very different habitat requirements than males and non-gravid females. Gravid females congregate on rocky outcrops during gestation, whereas males and non-gravid females use more structurally diverse habitats such as mixed forests, grassy shrublands, and beaver meadows (Prior et al. 2002). The threatened Jefferson Salamander (*Ambystoma jeffersonianum*) is a species for which habitat requirements differ between stage classes. The Jefferson Salamander breeds in ephemeral ponds during early spring and the larval salamanders remain in these ponds, feeding on microcrustaceans, until metamorphosis occurs. The adults on the other hand, leave the breeding ponds and move into deciduous forests where they feed on terrestrial invertebrates (Rye and Weller 2002). Failure to recognise these differences in life history habitat requirements may result in the omission of one or more required habitat features or components in a species critical habitat. Understanding the life history requirements of a species at risk, including the link to required habitat elements, is fundamental to the comprehensive identification of its critical habitat.

Community and ecosystem considerations

Species interactions and ecological processes

While SARA focuses on the survival or recovery of individual species at risk, species ultimately exist as part of functioning communities and ecosystems. Therefore, it is important to look at the larger context by understanding the biotic (e.g., food webs, mutualisms, keystone species) and abiotic (e.g., disturbance regimes) environment in which the species lives; to achieve survival or recovery of species at risk, consideration should be paid to both species interactions and ecosystem context. While it is virtually impossible to incorporate all species interactions and abiotic processes into a species' critical habitat, it is important to identify, and make provisions for, the essential and potentially limiting factors. Listed below are several examples of the types of species interactions and ecological processes that should be considered when identifying critical habitat for a species at risk.

Co-evolved obligate relationships

The identification of critical habitat for some plants may require special consideration, because many plant species are dependent on other species for reproduction and dispersal. An endangered or threatened plant will be unable to reproduce and recover if their critical pollinators or seed dispersers are limiting. The threatened Soapweed (*Yucca glauca*), which occurs at the northern edge of its range in southern Alberta, is an example of a plant species whose geographical range in Canada may be limited by its obligate pollinator, the endangered Yucca Moth (*Tegeticula yuccasella*) (Csotonyi and Hurlburt 2000). When identifying critical habitat for plants that are dependent on pollinators and seed dispersers for survival, the habitat requirements of these pollinating and dispersing organisms should also be considered (Allen-Wardell et al. 1998). This is especially important if pollination or dispersal is found to be a limiting factor in the species' recovery, as is the case for Soapweed. The obligate mutualistic relationship between the Yucca Moth and Soapweed is unique; not only is Soapweed dependent on the Yucca Moth for pollination, but the Yucca Moth is also dependent on Soapweed as it is the only known host for the developing Yucca Caterpillar (Csotonyi and Hurlburt 2000). Therefore, because Soapweed cannot survive without the Yucca Moth and vice versa, critical habitat should consider the habitat requirements of both species. Preliminary studies may be required to determine the important pollinators and seed dispersers of some of the plant species at risk, as knowledge about dispersal and pollination is limited for many species (Kearns and Inouye 1997, Allen-Wardell et al. 1998).

Like plants, many species of freshwater mussels are dependent on other organisms to complete their life cycle. Young mussel larvae (i.e., glochidia) attach to the gills or fins of specific host fish, where they live as parasites for a few weeks of their life cycle (McMahon 1991, Haag and Warren 1999). The endangered Mudpuppy Mussel (*Simpsonais ambigua*) is unique in that its larvae attach to an amphibian host, the Mudpuppy Salamander (*Necturus maculosus*) (Watson et al. 2001). For species such as the Mudpuppy Mussel, which are dependent on specific hosts for larval dispersal, the habitat requirements of the host species should be considered as a potential component of the mussel's critical habitat, especially if host availability is found to be a limiting factor in the mussel's recovery. Because this is an obligate, parasitic relationship for the mussel, their conservation is intimately linked with the host's survival. As with many plants, further research is required to determine the specific hosts for many freshwater mussels (McMahon 1991).

Disturbance dynamics

Critical habitat is dynamic for species that depend on natural disturbance regimes to maintain their preferred habitat. The northern Great Plains breeding population of the Piping Plover (*Charadrius melodus*), which is listed as threatened in the U.S., is dependent upon alkali lakes, ephemeral prairie wetlands, and rivers for breeding (U.S. Fish and Wildlife Service 2001). Annual fluctuation in precipitation and river flow cause water levels in the Piping Plover nesting grounds to vary considerably between years. Due to the dynamic nature of these hydrological systems, the locations of appropriate breeding sites change from year to year (U.S. Fish and Wildlife Service 2001). The endangered Eastern Loggerhead Shrike (*Lanius ludovicianus migrans*) is another example of a species whose habitat shifts in space over time. This species depends on periodic disturbance to maintain its preferred habitat, which consists of pastureland/open areas with a few trees and shrubs dispersed in the landscape (Cadman 1991). Similarly many grassland plants, such as the endangered Small White Lady's Slipper (*Cypripedium candidum*), are dependent on fire to prevent the encroachment of woody species into their preferred open grassland habitat (Brownell 1981). This dependence on disturbance-maintained habitat results in habitat patches that are not fixed in space and time. When identifying critical habitat for these species, allowances should be made to accommodate this shifting of habitat patches to the extent possible. As a result, not all areas that are identified as critical habitat may contain the required key habitat attributes in every year. Rather, critical habitat may comprise a mosaic of landscape patches, such that sufficient habitat patches occur at any point in time.

The most ecologically meaningful way to accommodate geographically shifting habitat patches is to incorporate, to the extent possible, the natural processes (e.g., fire, flood) in which the species evolved into the critical habitat. Ideally, identifying critical habitat in this way should allow for natural disturbance processes to continue, even if these processes sometimes originate from outside of occupied areas. SARA allows for the inclusion of these processes in a species' critical habitat by including in the definition of habitat, "…the area or type of site where an individual or wildlife species naturally occurs or *depends on directly or indirectly* in order to carry out its life processes." Even though a species may not occur in a particular area, it may still be considered critical habitat if the species directly or indirectly depends on that area in order to carry out its life processes (e.g., external processes such as periodic flooding maintaining a species' habitat). Therefore, it is important to look at an appropriate spatial and temporal scale in order to capture enough critical habitat to accommodate the species through time. The above examples illustrate the importance of understanding the life history of a species at risk, and the natural processes of its habitat, when identifying critical habitat.

In some areas, natural disturbance regimes no longer occur because the landscapes have been dramatically altered. Therefore, while historically the habitat for some species naturally shifted in space over time, today many of these species are dependent on active management to maintain their required habitats (Allen and Hoekstra 1992, Noss and Cooperrider 1994). In reality, therefore, their habitat may be more spatially fixed over time. For these species, critical habitat should be identified in places that fall and, if required for survival or recovery, could potentially fall (with restoration) under these active management areas. The Garry Oak and associated ecosystems in southern British Columbia is an example of an ecosystem that requires active management. The extent of the Garry Oak ecosystem has been severely reduced over the past few decades, mainly as a result of conversion to urban and agricultural land uses (Fuchs et al. 2002). This reduction in area has resulted in a disruption of the natural fire regime that historically maintained the Garry Oak ecosystem, by preventing the encroachment of Douglas-Fir forests. The Garry Oak ecosystems recovery team is currently investigating the impacts of different management actions (e.g., fire, manual removal of exotics and woody species) on plant community structure, including the distribution of species at risk, and stand dynamics (Fuchs et al. 2002).

Future shifts in species' habitat?

Climate change

Climate change is another phenomenon that is likely to cause shifts in species' habitats and distributions over time. The current global warming trend is predicted to result in species distributions shifting both to higher elevations, and to higher latitudes (i.e., toward the poles), a response due in part to shifts in habitat (Hughes 2000). Several studies have already documented these geographical range shifts. For example, Parmesan et al. (1999) investigated range shifts in 35 non-migratory European butterfly species. They found that the geographical range of 22 species shifted northwards by 35-240 km during this century. In contrast, only two species were found to have a southward range shift, and 10 species had no significant shift in geographical distribution.

In general, most documented range shifts have occurred in species that either have a very mobile phase in their life cycle, or species whose distributions are clearly restricted by climate (Hughes 2000). Unfortunately predicting these shifts is very difficult, as it depends on various interacting factors such as a species' dispersal ability, its capacity to adapt to new conditions, changes in the timing of life cycle events, and interactions with other organisms (Hughes 2000). Additionally, it is unlikely that all aspects of a species' habitat will respond uniformly to climate change. While some species may benefit from global warming, others will certainly be harmed by it (Pimm 2001, Warren et al. 2001). Species with smaller geographical ranges, such as many species at risk, are more likely to be negatively affected by climate change as they have far fewer populations to try to adapt to, or track, the changing climatic conditions (Pimm 2001).

In the future, climate change is expected to amplify the dynamic nature of ecosystems and habitat. If geographical range shifts continue to occur, critical habitat will need to be revised over time as species' ranges push northwards and/or toward higher elevations. A further result of these northward range shifts is that many species that do not currently occur in Canada may do so in the future. Additionally, for many species at risk whose northern geographical range limits cross into Canada, what may be considered marginal habitat today could be considered core habitat in the future. Thus, protecting habitat at the edge of a species' geographical range may be important, even if the habitat is currently considered to be of marginal quality. In Canada, the habitat at the northern edge of the range may also be important for species that have experienced severe habitat loss, due to high levels of human settlement in the United States, in the core of their range. The Massasauga (*Sistrurus catenatus catenatus*), which is designated as threatened, is an example of a sub-species for which populations at the northern edge of its range are extremely important for its recovery and conservation (Prior et al. 2002). The populations in the Bruce Peninsula and Georgian Bay areas of southern Ontario are amongst the largest and healthiest populations throughout the sub-species' geographical range, while many of the U.S. populations, in the core of its range, are small and isolated (Prior et al. 2002). The northernmost populations of the Massasauga, therefore, could play a major role in the sub-species conservation.

V. From individual to population needs

Population-level requirements

In addition to understanding how particular habitat attributes affect the suitability of an area for a species, consideration should also be paid to how area requirements affect suitability. The simple presence of essential habitat features is not sufficient, since they must also be adequate in number or amount to support a population. Too few or small an area and the population will decline.

It is important to distinguish between individual-level area requirements, and population-level area requirements. An individual-level area requirement is the amount of habitat required for an individual, or a breeding pair. A population-level area requirement is the amount of habitat that is able to support a population that is large enough to have long-term viability. Calculations of area requirements for the purpose of identifying critical habitat should be based on the amount of habitat required for long-term population persistence, and not just on the amount required for individual occurrences or individual reproductive events (Hayden et al. 1985, Soulé 1987, Wenny et al. 1993).

Minimum habitat-amount requirements

The proportion of suitable habitat in a landscape necessary to maintain viable populations is not constant across species or across regions (Kareiva and Wennergren 1995, Bascompte and Solé 1996, Doncaster et al. 1996, Gibbs 1998, With and King 1999, Fahrig 2001). Modelling studies suggest that these minimum habitat-amount requirements depend on landscape factors such as the quality of the matrix or non-habitat portion of the landscape (Fahrig 2001), and the pattern (i.e., fragmentation) of habitat destruction (Dytham 1995, With and King 1999, Fahrig 2001). Minimum habitat requirements are predicted to increase with decreasing matrix quality, such that more habitat is required for population persistence when the matrix quality is low (Fahrig 2001). Increasing the quality of the matrix, therefore, may have a positive effect on population persistence. Similarly, minimum habitat requirements are predicted to increase with an increase in habitat fragmentation. Populations in highly fragmented landscapes, therefore, may require more habitat for long-term population persistence than populations in less fragmented landscapes (Dytham 1995, With and King 1999, Fahrig 2001).

In addition to landscape factors, modelling studies also predict that minimum habitat-amount requirements depend on species characteristics such as reproductive rate (Lande 1987**,** With and King 1999, Fahrig 2001), dispersal ability (Lande 1987, Dytham 1995, Hanski et al. 1996, With and King 1999), and the rate of emigration from habitat patches (Fahrig 2001). Minimum habitat requirements are predicted to increase with a decreasing reproductive rate, such that species with lower reproductive rates require more habitat for population persistence than species with higher reproductive rates. This is because species with higher reproductive rates can recover more quickly from low population numbers caused by environmental disturbance, disease, or predation, and thus they are less likely to go extinct due to demographic stochasticity (Goodman 1987, Pimm et al. 1988). Minimum habitat requirements are also predicted to increase with decreasing dispersal ability, such that species that are less able to move through the landscape and colonise new habitat patches require more habitat for population persistence than species that have a greater ability to colonise new habitat patches. Finally, minimum habitat requirements are predicted to increase for species with a higher tendency to leave habitat patches and enter the matrix (i.e., high rate of emigration). While historically this may have had a positive effect on population persistence through recolonisation of empty habitat patches, in today's altered landscapes mortality rates are often high in the matrix, and therefore higher emigration rates may actually be detrimental to the population. Carr and Fahrig (2001), for example, found a negative relationship between population abundance and traffic density (a surrogate for traffic mortality) for the more vagile leopard frog (*Rana pipiens*), but found no such relationship for the less vagile green frog (*Rana clamitans*). These results suggest that higher mortality in the matrix may have a negative effect on population dynamics and that species with higher vagility may be more susceptible to these negative influences. Gibbs (1998) also supports the model prediction with his comparative analysis of the distribution of five woodland amphibians along a forest cover gradient. He found that species with a high level of mobility were more sensitive to forest loss, and thus disappeared from the landscape earlier, than species with a low level of mobility. In contrast, Holland's (2003) study on Cerambycid beetles showed species that emigrate from forest habitat patches required less habitat for population persistence (i.e., a lower extinction threshold; see below) than non-emigrating species. Interestingly however, the matrix in this study is not very hostile to the study species and thus does not likely represent a large source of mortality. In landscapes undergoing habitat loss and fragmentation, the advantage of high versus low levels of vagility for population persistence is dependent on the levels of mortality in the intervening matrix.

Modelling studies, like the ones discussed above, are valuable for investigating the relative effects of both species and landscape characteristics on population persistence, but they are unable to provide actual minimum habitat-amount requirements. A prediction of minimum habitat-amount requirements for real species requires models that are specifically tailored to the species in question.

Extinction Threshold

Modelling studies also predict the existence of species-specific habitat extinction thresholds for population persistence, whereby a small reduction in habitat at the threshold results in a sharp drop in the probability of persistence (Lande 1987, Bascompte and Solé 1996, Pagel and Payne 1996, Bevers and Flather 1999, With and King 1999, Fahrig 2001). Empirically the detection of extinction thresholds is much more difficult, because while modelling studies are closed to immigration, in reality landscapes are open to immigration. Immigration causes the thresholds to dampen, therefore making them more difficult to detect empirically (Vance 2002, Flather et al. in prep.). In addition, immigration into the landscape results in an underestimation of the amount of habitat required for population persistence (Pagel and Payne 1996, Flather et al. in prep.). The identification of habitat extinction thresholds is further complicated by the existence of time lags in species extinction (Tilman et al. 1994, Eriksson and Kiviniemi 1999). The current presence of a species or a population does not necessarily mean there is enough habitat for long-term persistence.

A term that is closely related to minimum habitat requirements is population viability. Population viability refers to the probability that a population of a particular species will survive over some (subjective) time period, given the population size and characteristics, and the threats to its survival (Gilpin and Soulé 1986, Soulé 1987). The amount of habitat required for a population's long-term viability is then called the minimum habitat requirement.

A species' viability can be measured using one of a diverse set of methods known collectively as viability assessments (see Andelman et al. 2001). Viability assessments are extremely useful recovery management tools, and can potentially be used to determine if the amount and configuration of critical habitat is adequate for species' survival or recovery. Population viability analysis (PVA) is one form of viability assessment that may be used to give insight into the question of how much habitat is required for population persistence. PVA, and its application for the identification of critical habitat for species at risk, is explored in Box 1.

Area sensitivity

Area-sensitive species are those species that have varying levels of tolerance to habitat fragmentation and its resultant decrease in patch size. Area-sensitivity is an individual-level phenomenon. However, in combination these individual responses to area can result in population-level effects. It is well know that many species of forest birds (Whitcomb et al. 1981, Hayden et al. 1985, Robbins et al. 1989, Porneluzi et al. 1993, Wenny et al. 1993) and grassland birds (Walk and Warner 1999, Winter and Faaborg 1999, Johnson and Igl 2001) are area-sensitive. However, area-sensitivity has also been observed in other organisms including the dormouse (*Muscardinus avellanarius*) (Bright et al. 1994) and the American marten (*Martes americana*) (Chapin et al. 1998).

Winter and Faaborg (1999) identified three different types of area sensitivity in their study of grassland-nesting birds in south-western Missouri. The most area-sensitive species was the Greater Prairie Chicken (*Tympanuchus cupido*) which was absent from all grassland fragments less than 77 ha. The Henslow's Sparrow (*Ammodramus henslowii*) displayed an intermediate type of area-sensitivity, occurring at lower densities in smaller fragments and higher densities in larger fragments. In addition to these two types of distributional area-sensitivity they also identified a demographic-level area-sensitivity, where nesting success was found to be lower in smaller grassland fragments (Winter and Faaborg 1999). Similar demographic-level area-sensitivity has also been reported for forest birds (Porneluzi et al. 1993, Villard et al. 1993, Donovan et al. 1995, Robinson et al. 1995).

Box 1. Population viability analysis

Population viability analysis (PVA) is a computer-based, quantitative modelling tool that is used to explore either a population's extinction probability over some specified time period, or its projected population growth under proposed management scenarios (Boyce 1992, Beissinger and Westphal 1998, Reed et al. 2002). There are no set rules about what comprises a PVA; each PVA is unique. This is because a PVA's structure depends on several factors such as: the essential components of a species' ecology that affect its extinction probability, the availability of data, the question(s) being addressed, and the experience of the modellers (Boyce 1992). In general, PVA uses demographic data and other life history and environmental information to parameterise a model that is then used to predict the size and structure of the population, or risk of extinction, at some point in the future. While PVA is closely linked to the idea of a minimum viable population (MVP), it does not attempt to estimate the 'true' minimum number of individuals required for long-term population persistence (Soulé 1987). Determining the MVP is unrealistic for most species because of the enormous amount of data that are required to accurately estimate the necessary parameters (Boyce 1992, Beissinger and Westphal 1998, Reed et al. 2002).

Use of PVA

The use of PVA is becoming more prevalent in the management of species at risk, as it offers a very powerful way to integrate various types of data, and explore potential management options. Beissinger and Westphal (1998), and Coulson et al. (2001) list several ways in which PVA is used in wildlife management: (1) to predict the future size of a population; (2) to estimate the probability of a population going extinct over a given time; (3) to develop the criteria for recovery; (4) to classify a species' risk category; (5) to assess which of a suite of management or conservation strategies is likely to maximise the probability of a population persisting; (6) to evaluate research priorities; and (7) to explore the consequences of different assumptions on population dynamics for small populations.

Using PVA for identifying critical habitat

Option number five represents the most appropriate way that PVA can be used with respect to identifying critical habitat. PVA can be used to model the effects of changes to a species' habitat, and to evaluate various approaches to managing this habitat (Boyce 1992). For critical habitat, a PVA can be used to investigate how different amounts of habitat, or their spatial configuration in the landscape, affect a population's viability. The goal of PVA should not be to predict the actual probability of population extinction or the actual population growth rate (Boyce 1992, Beissinger and Westphal 1998, Reed et al. 2002). There is always a potential for error in measuring the model parameters, and therefore any predictions from a PVA is likely to have a large degree of uncertainty associated with it (Ellner et al. 2002). A more valuable output of a PVA that models different amounts and configurations of critical habitat is the ranking of different options to see which produces the most favourable population trajectory, or extinction probability (Boyce 1992, Beissinger and Westphal 1998, Reed et al. 2002).

Sensitivity analysis

Sensitivity analysis is an important component of any PVA. A sensitivity analysis is conducted by varying certain model parameters, and then studying the model's response, to determine which parameters have the largest effect on model predictions (Boyce 1992, Beissinger and Westphal 1998, Reed et al. 2002). If a particular parameter is found to have a large effect on model predictions, and there is a simultaneous large natural variation in that parameter, then this would help identify potential management strategies or suggest possible recovery action options that could be carried out to try and improve population trajectories for the species in question (Reed et al. 1998). For example, Lande (1988) used sensitivity analysis to determine that annual adult survivorship has the largest effect on the annual growth rate of the Northern Spotted Owl (*Strix occidentalis caurina*). This information was then used to help guide management efforts to focus on improving adult survival for the Northern Spotted Owl. Identifying which parameters have the largest effect on model predictions will also help direct research to the parameters for which we need to obtain accurate, habitat-specific measurements, and the parameters for which more accurate measurements are not as important because of their lesser effect on population viability (Lande 1988, Beissinger and Westphal 1998, Reed et al. 1998).

Box 1 continued…

Criticisms and/or limitations of population viability analysis

While PVA is an extremely powerful conservation tool, biologists and resource managers need to fully understand its limitations in order to avoid misinterpreting the results (Boyce 1992, Brook et al. 2002, Reed et al. 2002). There are many papers that examine the use of PVA in conservation biology, and discuss its limitations. Some of the criticisms and shortcomings of PVA include:

- Predictive accuracy of PVA is generally low (Beissinger and Westphal 1998, Reed et al. 1998, Ludwig 1999, Coulson et al. 2001, Ellner et al. 2002)

    → Many types of PVA have large species-specific data requirements that often aren't available, especially for species at risk, or are difficult to measure (e.g., dispersal processes) (Boyce 1992, Beissinger and Westphal 1998, Menges 2000, Coulson et al. 2001, Reed et al. 2002).

    → Quality of data used to estimate species' vital rates for use in a PVA is often poor because it is not based on adequate field studies. This can cause large errors in these vital rate estimates, which in turn creates model prediction errors (Beissinger and Westphal 1998, Ludwig 1999, Menges 2000, Coulson et al. 2001).

- Catastrophic events have a large effect on population numbers, but little is known about the scale or frequency of catastrophes for particular species, and thus they aren't often included in PVA (Beissinger and Westphal 1998, Ludwig 1999, Coulson et al. 2001, Reed et al. 2002).

- For species at risk it is difficult to validate the model when all of the existing data is used to parameterise the model, as is often the case (Beissinger and Westphal 1998, Coulson et al. 2001).

- PVA is usually limited to a single-species focus, because for most species we don't understand multi-species processes well enough to incorporate them into a PVA. For most species, this results in an unrealistic depiction of what is regulating population growth (Boyce 1992).

- Mechanisms regulating population size are often looked at separately, thus ignoring possible interactions/synergisms between the mechanisms (Gilpin and Soulé 1986, Boyce 1992).

While there is a possibility that the predictions of a PVA may be misinterpreted, or may not produce the desired level of accuracy, this does not mean they should be dispensed with entirely. PVA is best thought of as a comparative, adaptive management tool. All available information about a species is used to parameterise the model, and the model is run to compare the predictions under various management scenarios (Beissinger and Westphal 1998, Brook et al. 2002). The chosen management action(s) should then be monitored so that the data can be used to improve and update the PVA in an adaptive fashion (Menges 2000). As a general rule, demographic PVA models and alternative management strategies should be linked by performing field tests of the model's assumptions (e.g., carrying capacity, density dependence), and validating the model's secondary predictions (e.g., distribution of individuals) through field work (Beissinger and Westphal 1998).

This has been a fairly brief exploration of the use of PVA. Even though PVA is a relatively recent tool, there is a wealth of literature available on the subject. If you are interested in learning more about PVA, the following list of books and review papers explore its use in species management: Boyce 1992, Burgman et al. 1993, Beissinger and Westphal 1998, Menges 2000, Beissinger and McCullough 2002.

The above studies illustrate how relying solely on census data (e.g., presence/absence and/or abundance) as a measure of habitat quality, or to determine a species' area-sensitivity, may be misleading. Species that do not exhibit area-sensitivity with respect to density may do so on a demographic level (Winter and Faaborg 1999, Donovan and Lamberson 2001). Similarly, areas of high density do not necessarily have correspondingly high nesting success, and thus may not represent high-quality habitat (Van Horne 1983, Pulliam 1988, Vickery et al. 1992, Purcell and Verner 1998). Habitats where local reproduction is not able to compensate for local mortality are known as sink habitats and, conversely, habitats where local reproduction is equal to or greater than local mortality are known as source habitats (Pulliam 1988). To prevent local extinction, sink habitats are therefore dependent on immigration from source habitats (Brown and Kodric-Brown 1977, Pulliam 1988). When identifying critical habitat for species at risk it is important to consider potential source and sink habitats, and it is vital that the more productive source areas be included as critical habitat (Carroll et al. 1996, Gaston et al. 2002). However, sink habitats aren't necessarily unimportant as they may serve as valuable connections between disjunct source areas (Noss 2002), and may increase the overall size and persistence probability of a metapopulation (Gaston et al. 2002).

Identifying potential source and sink habitats will require not only a measure of density in that habitat, but also a measure of reproductive success (e.g., number of young produced); a positive relationship between habitat quality and density should not automatically be assumed (Van Horne 1983). There are several documented cases where density was found to be higher in lower quality habitats. For example, discrepancy between density and habitat quality has been shown for species that display intraspecific social dominance, whereby the adults force juveniles out of the higher quality habitats where reproductive success is high, into the lower quality habitats where reproductive success is low. These dominance interactions can result in the uncoupling of density and habitat quality, and this uncoupling has been documented for several small mammal and bird species (Van Horne 1983).

Margin for error and flexibility

Due to the dynamic nature of ecosystems and populations, chance plays an important role in the survival of species at risk. While stochastic events tend to balance out in large and healthy populations, they play a prevalent role in population persistence when population numbers are low, as is the case for many species at risk. Thus, because of the stochastic nature of both environmental and demographic events, it is important to use precaution in identifying critical habitat, in order to safeguard against extinction. Incorporating flexibility and redundancy into critical habitat is essential for the recovery of species at risk.

Bigger habitat patches are better than smaller ones

All things being equal, bigger habitat patches are able to support larger populations than smaller patches, and thus they are less likely to go extinct due to stochastic events (MacArthur and Wilson 1967, Goodman 1987, Pimm et al. 1988, Murphy and Noon 1991, Boyce 1992). In addition, larger habitat patches generally have a smaller perimeter to area ratio, and therefore are less susceptible to the negative influence of edge effects such as predation and nest parasitism (Murcia 1995, Kremsater and Bunnell 1999).

Emergency habitat

Under conditions of severe environmental stress, some species may utilise habitat that is not normally used, or that would be considered marginal habitat. The Florida Snail Kite (*Rostrhamus sociabilis*) is an endangered raptor whose range is restricted to a handful of large wetlands in the Everglades of southern Florida (Sykes 1983). However, during years of severe drought when their preferred wetlands dry out, the Florida Snail Kite moves to permanent lakes and wetlands that otherwise are considered suboptimal habitat (Takekawa and Beissinger 1989). When critical habitat was designated for the Florida Snail Kite in 1977, the importance of these emergency habitats during years of severe drought was unknown, and therefore these refuge areas were not included in the critical habitat designation (Takekawa and Beissinger 1989). In this example, the importance of considering habitat use over time is apparent; investigating habitat use over an adequate time-scale is important for identifying such things as changes in habitat use during times of severe environmental stress. While there is always a level of uncertainty when identifying habitat that is critical to a species survival or recovery, it is valuable to explore the environmental history of an area so that the possibility of changes in habitat use can be examined. In addition, it is important to use precaution when identifying critical habitat. Incorporating flexibility into critical habitat, by providing some slack in the critical habitat network, may help to accommodate an uncertain future. Finally, because ecosystems and habitats are dynamic in both space and time, and because the identification of critical habitat was based on the best available current information, it is important to remember that critical habitat is not set in stone; critical habitat may be modified, as new data becomes available.

Buffers

For some species it may be necessary to include a buffer of unoccupied areas when identifying critical habitat (Carroll et al. 1996). Inclusion of a buffer zone may be particularly important for species that are highly sensitive to external influences such as predation, environmental disturbances, and human activities (Wiens 1996). Buffers are also important when habitat quality is highly dependent on the surrounding landscape (Carroll et al. 1996). Habitat quality for aquatic species, for example, is directly affected by the quality of the upland habitat, particularly upstream from the area in question. Thus, while most species are likely to benefit from incorporating buffers into critical habitat, for both aquatic species and species that are highly sensitive to external influences, it is essential to look at a larger scale (e.g., watersheds) when identifying critical habitat (Carroll et al. 1996).

Redundancy of habitat patches is essential

A certain level of redundancy of habitat patches is required for critical habitat in order to protect the species from extinction due to stochastic environmental events and catastrophes (Gaston et al. 2002, Shaffer et al. 2002). Thus, not only are bigger patches better than smaller patches, but more patches are better than fewer patches. Species will be less susceptible to extinction when critical habitat is distributed over the species' entire geographical range (Noss and Cooperrider 1994, Shaffer et al. 2002). Well-distributed critical habitat will also maximise the probability of capturing intraspecific genetic variation.

VI. Importance of landscape-scale conservation

Recently it has been recognised that species respond not only to within-patch characteristics, but also to habitat at a landscape scale (Turner 1989, Freemark and Collins 1992, Andrén 1994, Freemark et al. 1995, Wiens 1995). Thus, instead of considering only patch size and quality, it is important to consider the amount and quality of habitat in landscapes at larger scales (see Box 2) (Flather and Sauer 1996, Findlay and Houlahan 1997, Jansson and Angelstam 1999, Trzcinski et al. 1999, Villard et al. 1999). The appropriate scale (extent) to consider for the identification of critical habitat depends on the species, as different species respond to the landscape at different scales (Turner 1989, Wiens et al. 1993).

Box 2. Ecosystem and multi-species approaches

Researchers advocate the use of broad-scale, ecosystem or multi-species approaches to biodiversity conservation (Rohlf 1991, Franklin 1993, Orians 1993, Tear et al. 1995, Carroll et al. 1996, Noss et al. 1997, White et al. 1997, Freemark et al. 2002). As the number of endangered and threatened species grows there is an increased realisation that dealing them all on a species-by-species basis is impractical, if not impossible. The Species at Risk Act, in recognising the value of these broad-scale approaches to the conservation of species at risk, states:

> *The competent minister may adopt a multi-species or an ecosystem approach when preparing the recovery strategy if he or she considers it appropriate to do so* [s. 41(3)].

There are several multi-species recovery strategies that currently exist across Canada, including the Sydenham River watershed in Ontario, and the Garry Oak and associated ecosystems in British Columbia. However, despite SARA's explicit statement that multi-species and ecosystem approaches for recovery plans are acceptable, the Act still specifies that critical habitat be identified on a species-by-species basis. Critical habitat must be identified for every endangered, threatened, and extirpated species regardless of whether it is part of a multi-species or ecosystem recovery strategy. Therefore, the habitat needs of each species at risk have to be considered separately. Pursuing these broad-scale recovery strategies, however, is still encouraged as it highlights the importance of considering broader issues of habitat quality and quantity (Carroll et al. 1996). The best way to protect the critical habitat of a species at risk is to protect the entire ecological community of which it is a part (Miller and Douglas 1999). This is especially relevant for rare communities (e.g., Garry Oak ecosystem).

The Critical Habitat Working Group (CHWG) is planning to undertake a literature review that investigates the use of broad-scale recovery strategies for species at risk. The purpose of this literature review is to build the scientific perspective on why broad-scale approaches to species' recovery are appropriate, and to explore the circumstances under which single-species, multi-species, and/or ecosystem recovery strategies should be employed. The results of this literature review will be used to inform the development of policy guidelines for the use of multi-species and ecosystem-based recovery planning.

Landscape-scale issues

Matrix quality

In addition to considering the amount and quality of habitat in a landscape, it is also important to consider the matrix or non-habitat portion of the landscape (Wiens 1996, Ricketts 2001). Habitat does not exist in isolation; it is imbedded in the surrounding matrix.

Modelling studies have indicated that the quality of the matrix may have a large effect on the location of the habitat extinction threshold along the habitat amount axis (Fahrig 2001). This effect of matrix quality on population persistence has important management implications. Improving the quality of the matrix (e.g., reducing pesticide use, increasing heterogeneity, reducing risk of traverse) may reduce the inputs of potentially harmful substances into habitat patches, decrease individual mortality during dispersal (Fahrig 2001), and decrease the resistance of the inter-patch matrix to species' movement (Ricketts 2001), all of which would increase population persistence. For species at risk in which habitat is very limiting (e.g., species at the northern limits of their range, rare species), increasing the quality of the matrix may be a more feasible management option than increasing the amount of habitat available to the species. Increasing the quality of the matrix may decrease the amount of habitat that is required for species' survival or recovery (i.e., critical habitat).

Studying the effects of a heterogeneous matrix is relatively new to landscape ecology, and thus there are few empirical studies that directly test the effect of matrix quality on the distribution and/or abundance of organisms. Dunford (2001) tested the effect of matrix quality, independent of habitat, on forest bird species richness and abundance by selecting landscapes with different amounts of urban areas, and high- and low-intensity agriculture in the matrix. The species richness and abundance of Neotropical migrant, forest interior, and interior-edge birds was found to be greater in forest fragments surrounded by larger proportions of less intensive agriculture in comparison to fragments surrounded by larger proportions of high intensity agriculture or urban areas (Dunford 2001). Similarly, Joly et al. (2001) compared the abundance of three newt species in ponds surrounded by varying amounts of cultivated fields and pastureland. The life cycle of newts requires regular migration between ponds, which are used for breeding and foraging, and forest, which are used for estivation and overwintering. They found that the amount of cultivated field in the surrounding matrix had a negative impact on newt abundance, probably due to an increased mortality in the matrix as individuals move between their aquatic and terrestrial habitats (see landscape connectivity below). These represent two of the first field studies to explicitly test the effects of matrix quality and they show that increasing the quality of the entire landscape mosaic, and not just the habitat patches, can have a positive effect on species' distribution and abundance (and therefore on population persistence).

Landscape connectivity

Landscape connectivity is a measure of landscape structure that has significant implications for species' conservation and management (Wiens 1996). It is a species-specific measure of the extent to which the landscape enhances or inhibits inter-patch movement by individuals (Taylor et al. 1993, Freemark et al. 2002), and is dependent on matrix quality, elements in the landscape such as corridors that are used for dispersal, and species' behaviour and dispersal ability. This measure of landscape connectivity is sometimes called functional connectivity in order to distinguish it from structural connectivity, which is a measure of habitat contiguity with no consideration given to the species' behavioural response to the landscape (Tischendorf and Fahrig 2000).

In today's fragmented environment, many species exist in habitat patches scattered throughout the landscape. The result of these fragmented landscapes is that many species are dependent on dispersal for population survival (Levins 1969, Taylor et al. 1993, Wiens 1996). Dispersers serve both to re-colonise patches that have gone extinct (Hanski 1999), and to increases the population size of existing habitat patches, thus reducing the chance of local extinction (Brown and Kodric-Brown 1977, Hanski et al. 1996). In addition to its critical role in population dynamics, dispersal is also necessary for maintaining genetic diversity through gene flow, and avoiding the deleterious effects of inbreeding (Pusey and Wolf 1996). When species exist in fragmented landscapes, with habitat patches that are connected via dispersal, critical habitat should include elements of the landscape that are necessary to allow dispersal between these habitat patches to continue.

When identifying critical habitat, habitat patches should be within the dispersal range of the species in question if demographic connections between the patches are to be maintained (Ruggiero et al. 1994). In addition, in order to determine what landscape connectivity means to a particular species it is valuable to have an understanding of the small- and large-scale dispersal behaviour and movement ability of that species through various landscape elements (Tischendorf and Fahrig 2000). Therefore, examining the species' response to such things as corridors, stepping stones, various land-cover types, barriers and patch boundaries may be a useful research area.

Habitat configuration

Modelling studies that have tested the relative effects of habitat loss and habitat configuration (i.e., spatial arrangement of habitat patches) have found that habitat amount has a much larger effect on population persistence than does configuration (Fahrig 1997, 1998, Flather and Bevers 2002). Most empirical studies have corroborated these findings (McGarigal and McComb 1995, Flather and Sauer 1996, Trzcinski et al. 1999). However, the arrangement of the habitat patches in the landscape can be important under certain circumstances (Andrén 1994, Fahrig 1997, 1998, Flather and Bevers 2002). Fahrig (1998) found that when the amount of habitat in the landscape was ≤20%, the importance of habitat configuration on population persistence increased. Similarly, Flather and Bevers (2002) found that when the amount of habitat in the landscape fell below the extinction threshold (~ 30%-50% in their study), habitat configuration played an important role in explaining population size. With less habitat in the landscape, population persistence is uncertain because dispersal mortality in the matrix is increased (Fahrig 2001, Flather et al. 2002). Under these circumstances, landscape configurations that result in aggregated habitat patches may help to ameliorate the negative effects of habitat loss by decreasing dispersal mortality in the matrix (Flather and Bevers 2002). If different configuration options are available for critical habitat, or for habitat restoration, population viability analysis may be a useful tool for exploring/ranking the different options (see Box 1).

Landscape complementation

For species that require more than one type of habitat to complete their life cycle, the configuration of habitat patches can be very important (Dunning et al. 1992). For these species it is necessary to travel between different habitat patches in order to obtain the required resources. This need for different types of habitat patches to be linked through movement is known as landscape complementation (Dunning et al. 1992). When identifying critical habitat for species that rely on landscape complementation, consideration should be given to not only the amount of the different habitat types, but also their spatial arrangement. Generally, landscapes in which the required habitats occur in close proximity will be able to support larger populations than landscapes in which the habitats are farther apart (Dunning et al. 1992). Pope et al. (2000) found that the relative abundance of the Northern Leopard Frog (*Rana pipiens*) was higher in breeding ponds that contained more summer foraging habitat (i.e., higher degree of landscape complementation) within the frog's potential dispersal distance (1 km). Thus, consideration of critical habitat configurations for landscape complementation requires an understanding of the species' dispersal ability.

VII. Summary

Implications for identifying critical habitat under SARA

Best scientific information

When a species is listed under SARA, and recovery strategies and action plans are being developed, the data that are available for most species may not be adequate to allow a clear-cut identification of critical habitat. Thus, for many species at risk, the first step on the road to identifying critical habitat may be the development of research and monitoring programmes geared toward obtaining species-specific information for such things as key habitat attributes, area requirements, demographic parameters such as survival and fecundity, the threats facing the species, and the movement and dispersal ability of the organism. It should be understood from the onset, however, that the information available to identify critical habitat will never be perfect. Nonetheless, the identification of critical habitat should be based on the best scientific information available for a species.

Guiding principles for critical habitat identification

Individual-level needs

The preceding synthesis identifies three fundamental issues that should be considered when identifying critical habitat for species at risk. The first issue to consider is the requirements of individual organisms. In order to identify critical habitat for a species at risk, there should be a solid understanding of what an individual requires to complete its life history. Critical habitat should encompass the mosaic of habitats that a species needs to complete its life cycle, and it is important that both temporal and demographic differences in habitat requirements are identified. For example, some species use different types of habitat on a daily basis, while others have different habitat requirements for various parts of their life cycle. In addition, habitat requirements may also differ between adults and juveniles and/or between males and females. These contrasting habitat requirements should be recognised, and included as critical habitat.

In addition to considering demographic and temporal differences in habitat requirements when identifying critical habitat, consideration should also be paid to the habitat requirements of species that are dependent on obligate inter-species relationships and/or ecological processes for survival. For example, many plants are dependent on other species for pollination and seed dispersal. The habitat requirements of these pollination and dispersal agents should therefore be considered for inclusion in the critical habitat of the species that depend on them, especially if dispersal or pollination is found to be a limiting factor in the species' recovery. Other species are dependent on habitat that is dynamic, and thus shifts in space over time. For these species, it is important to incorporate, to the extent possible, the natural processes (e.g., fire, flood) in which the species evolved into their critical habitat. The result will be that not all areas identified as critical will contain the required habitat features in every year, but rather critical habitat will consist of a mosaic of habitat patches such that some patches contain the appropriate habitat features at any point in time. These examples highlight the importance of understanding the life history of a species at risk, the community in which it lives, and the natural processes of its habitat.

Population-level needs

Once the habitat requirements of a species at risk are identified at the individual-level, consideration should be paid to the second major issue identified in this literature review: population-level requirements. This jump from the individual-level to the population-level is a crucial one. Critical habitat should be identified at the population-level, and should contain enough habitat (i.e., an area or areas of ample size) for long-term population persistence. Viability assessments (e.g., PVA) can be extremely useful for investigating how different amounts of habitat, and/or their spatial pattern in the landscape, affect a population's viability.

Modelling studies predict that several landscape and species characteristics affect the amount of habitat required for long-term population persistence. Minimum habitat requirements are predicted to increase with decreasing matrix quality, increasing habitat fragmentation, decreasing reproductive rate, decreasing dispersal ability, and increasing rate of emigration. Thus, minimum habitat requirements differ both between species and between regions. Modelling studies however fall short of providing actual minimum habitat-amount requirements. A prediction of minimum habitat-amount requirements for real species requires models that are tailored to particular species. The existence of habitat extinction thresholds, and time lags in species response to habitat loss, makes the determination of minimum habitat-amount requirements more complicated. The current presence of a species or a population does not necessarily mean there is enough habitat for long-term persistence.

Area-sensitivity is another biological consideration of critical habitat that is specific to populations. While area-sensitivity is an individual-level phenomenon, in combination these individual responses to area have population-level effects. At the population-level, demographic (e.g., reproductive success) and distributional (e.g., density) responses to area can create source and sink habitats. It is essential that the more productive source habitats are identified and incorporated into a species' critical habitat.

Another population-level biological consideration for critical habitat identification is the need to incorporate flexibility and redundancy into a species' critical habitat. Because ecosystems and populations are dynamic by nature, chance plays an important role in the survival of species at risk. Thus, to safeguard populations from extinction there is a need to incorporate some slack in the critical habitat network.

Landscape-scale considerations

The importance of landscape-scale considerations to critical habitat identification is the third fundamental issue identified in this literature review. Research has shown that species respond not only to within-patch characteristics, but also to the surrounding landscape. Thus, it is important to look beyond the patch-scale when identifying critical habitat.
The quality of the matrix, or non-habitat portion of the landscape, can have a large effect on the amount of habitat required for long-term population persistence. This has important management implications, because for many species at risk increasing the quality of the matrix may be a more feasible management option than increasing the amount of habitat. In addition, for species that exist in fragmented landscapes, with habitat patches connected via dispersal, the matrix has a significant impact on the ability of dispersers to move between habitat patches. These inter-patch movements are critical to the survival of populations that exist as metapopulations, and elements of the landscape that allow the species to maintain these inter-connections should be identified and included as critical habitat. In order to incorporate the landscape elements necessary to maintain connectivity, it is valuable to have knowledge of the small- and large-scale dispersal ability of species through various landscape elements.

Two additional biological considerations for critical habitat identification at the landscape-scale are habitat configuration and landscape complementation. While habitat amount has been shown to have a much larger effect on population persistence than habitat configuration, the importance of the spatial arrangement of habitat patches may increase when the amount of habitat in the landscape is low, as is the case for many species at risk. PVA is a useful tool for investigating the effect of different habitat configurations on population persistence or population size.

The configuration of habitat patches in the landscape is also important for species that require more than one type of habitat to complete their life cycle. For species that rely on landscape complementation, the spatial arrangement of habitat patches in the landscape is important for population persistence. Landscapes with the required habitats in close proximity will, in general, support larger populations than landscapes with the required habitat patches spaced farther apart. Consideration of critical habitat configurations for landscape complementation will therefore require an understanding of the species’ dispersal ability.

In conclusion, the identification of a species' critical habitat is not set in stone; critical habitat should be seen as a work in progress. SARA states that the identification of critical habitat should be based on the best available information and therefore, as more and better information becomes available for a species at risk, its critical habitat should be modified accordingly. Critical habitat will best function in the recovery of species at risk, if its identification is thought of as an ongoing, adaptable process.

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