Chapter 16

Contribution of Source-Sink Theory to Protected Area Science

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Summary

The concept of source-sink population dynamics may be especially relevant to protected areas. Places set aside as nature reserves often have steep gradients in climate, topography, and other abiotic factors that result in spatially explicit population dynamics occurring within in them. Protected areas are also frequently placed in relatively extreme parts of the landscape with regards to climate, soils, elevation, and water. Consequently, spatially explicit population dynamics may occur between protected areas and the more moderate surrounding landscape. The goal of this chapter is to evaluate the contribution source-sink theory has made to understanding population viability in and around protected areas. A review of the literature for the past 20 years indicated that the source-sink concept has been applied to protected areas primarily in three ways. (1) Protected areas may be sinks for some species due to the more extreme biophysical conditions within them. These sink populations may be vulnerable to loss of source areas in unprotected surrounding lands. Land use intensification around reserves may drive the degradation of these sources and reduce viability of the species in the protected area. (2) The areas surrounding protected areas may become "attractive" sinks due to human activities and lead to loss of viability of the source population. Large carnivores appear to be especially vulnerable to this dynamic. (3) Protected areas may serve as population source areas that supplement hunted or fished populations in surrounding areas. Many marine protected areas have been designated as means of allowing more sustainable fisheries in surrounding waters. I summarize the conceptual basis of each of these scenarios, provide examples and draw implications for conservation and management.

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Introduction

In the 20 years since the publication of Pulliam (1988) on source-sink population dynamics, the theory has been the basis for advances in ecological theory (e.g., chapters in this book). It has also contributed to strategies for conservation of species. One type of conservation application has involved the viability of species in and around protected areas. Protected areas are places where human activities are minimized to provide for the maintenance of natural ecological processes and native species (Possingham, 2006). They serve as places for the protection of nature, research sites into the functioning of intact ecosystems, benchmarks for understanding change in human-altered systems, and areas for human enjoyment and renewal (Arcese and Sinclair, 1997). It is increasingly apparent, however, that many protected areas are not functioning as envisioned. Ecological processes such as disturbance regimes have been altered and native species have been lost in many protected areas (Newmark 1987, 1995, 1996; Rivard et al., 2000; Parks and Harcourt, 2002). Source-sink theory offers a basis for understanding some of the factors that influence the function of protected areas.

The spatially explicit population dynamics that are the basis of source sink theory may be particularly likely in and around protected areas. Protected areas may be subject to source sink dynamics more than areas at random for three reasons. First, protected areas are often portions of larger ecosystems and native species move out of the protected area and across the larger ecosystem to obtain needed resources over the annual cycle (Wright and Thompson, 1935; Craighead,1979; Newmark, 1985; Hansen and DeFries, 2007). Second, protected areas are often surrounded by areas of more intense land use (Wittemyer et al., 2008). The resulting gradient in land use intensity and human interaction with native species can influence birth and death rates and create source sink dynamics (McKinney, 2002; Hansen et al., 2005). Hence, protected areas may be sources that maintain subpopulations in sinks in the surrounding more intensively used lands. Third, protected areas tend to be located in landscapes with strong gradients in topography, climate, soils, and other biophysical factors (Pressey, 1994) that can lead to differential habitat quality and spatially explicit population dynamics. In fact, protected areas are typically in the harsher portions of these biophysical gradients (e.g., high mountains, deserts, low productivity soils) (Scott et al., 2001) and may have relatively low habitat quality, resulting in populations moving outside of protected areas to better habitats seasonally or for some life-history phases. The lower quality habitats in some protected areas may result in them being population sinks for some species (Hansen and DeFries, 2007).

Over the past twenty years of theoretical development, two refinements have been added to the source sink model that are highly relevant to protected areas. “Refuge” habitats are places where survival of a population is relatively high but reproduction is relatively low, so the subpopulation is a weak source (Naves et al., 2003). This typically occurs in “suboptimal refuge areas with scarce nutritional resources but a lower risk of human-induced mortality that may allow for population persistence”, Naves et al. (2003: 1277). Such populations are often endangered species that have been displaced to the edges of their former ranges. “Attractive Sinks” are places where habitat quality is good allowing potentially high reproduction and high survival, but where either reproduction or survival is reduced by forces that are not detected by the organism (Delibes et al., 2001a). Hence, the organism selects habitat based on perceived quality, but suffers either high mortality or low reproduction there due to hazards that are not detected such as hunting or the presence of pesticides (Gunderson et al., 2001).

A key issue for protected areas is how the presence of source sink dynamics influences the viability of the metapopulation (Figure 1). The original source sink theory focused on how a subpopulation in a sink could be sustained by dispersal from a source and maintain a viable metapopulation. Loss of viability from the source due to loss of individuals to the sink was not expected because of the assumption that intraspecific density-dependent competition for the good habitat would lead to the fittest individuals occupying the source and force subdominant individuals into the sinks (Pulliam, 1988; Delibes et al., 2001a). This is highly relevant to protected areas because populations in protected areas in harsh biophysical settings may be sinks that are maintained by sources outside of the protected area (Figure 1a). However, populations in protected areas are vulnerable if land use change or other factors causes the external source to become a sink.

The assumption of density dependent habitat selection does not hold, however, in the case of attractive sinks. Because of the inability of the organism to perceive the threats in the attractive sink, even the fittest individuals may move from sources to attractive sinks, reducing population size in the source and reducing the viability of the metapopulation (Gunderson et al., 2001; Delibes et al., 2001a, 2001b). Thus, sources or refuges in protected areas could become inviable if too many individual from the source are lost to attractive sinks (Figure 1b).

A third scenario may allow sustained harvest of individuals in sink habitats. Under the density dependent model, protected areas can be created or maintained as sources which supply surplus individuals to surrounding areas that are attractive sinks through fishing or hunting pressure (McCullough, 1996). This scenario is being used as the basis for creating marine reserves to sustain fisheries in surrounding areas (Lubchenco et al., 2003).

This chapter explores and illustrates each of these three source sink dynamics with examples from various protected areas around the world. The examples were derived from a literature review of studies of source sink dynamics to protected areas for the period 1988-2008. These scenarios are graphically illustrates by depicting gradients in biophysical conditions and thus habitat conditions and land use intensity relative to protected areas. Following these examples, implications for management are drawn.

Protected Area as a Sink

Because protected areas were often established in places not productive for agriculture or other natural resource extraction, they are often in harsher biophysical conditions than surrounding areas (Scott et al., 2001). These conditions may constrain organisms directly or reduce primary productivity and food availability for consumers, resulting in lower habitat quality in protected areas. If habitat quality is sufficiently low, the protected area may be a population sink for a species that is maintained by dispersal from sources in the surrounding areas that have higher habitat quality (Figure 2). In this case, the presence of the species in the protected area is dependent upon the maintenance of the source areas in the unprotected portion of the landscape (Dias, 1996; Delibes et al., 2001a). If land use intensification leads to conversion of the source areas to sinks, the metapopulation is at risk of local extinction.

The implications for protected areas of source sink dynamics where density dependent habitat selection in the source regulates movement from sources to sinks were summarized by Delibes et al. (2001: 283), “The results of the scenario corresponding to an “avoided” sink [one occupied by overflow individuals from the preferred source] are well known (Pulliam, 1988).

The source is extinction resistant but the sink is not. Thus, reserves must be established in sources since preserving only sink habitats will probably lead to population extinction."

Example: Song Bird Population Dynamics in Greater Yellowstone

Yellowstone and Grand Teton National Parks in the Northern Rocky Mountains in the western United States are centered on the Yellowstone Plateau and surrounding mountains (Figure 3a). Climate is harsh at these higher elevations with a snow-free growing season as short as two months. The volcanically-derived soils are also poor in nutrients and water-holding capacity. Consequently, net primary productivity is relatively low in the protected areas (Figure 3b). In contrast, the valley bottoms along rivers flowing from the Yellowstone Plateau have substantially longer growing seasons, more fertile soils, and relatively higher primary productivity (Hansen et al., 2000).

Hansen et al. (1999) found that bird species were not distributed randomly relative to these abiotic gradients. Rather, they were associated with landscape settings that were warmer in June temperature, lower in elevation, on alluvial parent materials, and/or with higher primary productivity. These sites were dominated by the deciduous forest cover types and were relatively rare in the study area. "Hot spots" where bird species were numerous and abundant covered less than 3% of the study area and were mostly on or near private lands (Figure 3c). Only about 7% of the hot spots were within protected areas. Within the private lands, land use was more intense near hot spots (Hansen et al., 2002). Rural homes were placed closer than expected at random to biodiversity hot spots.

The primary means by which rural home development influenced birds in hot spots was by favoring avian brood parasites and predators (Hansen and Rotella, 2002). These species were especially abundant near rural residences. Consequently, those bird species susceptible to nest parasitism and predation suffered very low rates of reproduction. In the case of the yellow warbler (*Dendroica petechia*), for example, nearly half of nests in hot spots near homes suffered cowbird parasitism and only about 20% of the nests successfully fledged young. The American robin (*Turdus migratorius*), in contrast, is able to better defend its nests against cowbirds and predators. Nest success in hot spots near homes for this species was nearly 50% higher than that for yellow warbler. An important measure of the consequences of these differences in reproduction is the net population growth. Estimated population growth of the American robins was positive in these hot spots. The yellow warbler population, in contrast, was projected to be declining in these hot spots, likely due to the increased nest parasitism and predation associated with rural homes.

Projections of the population dynamics of yellow warblers across the northwest portion of the Greater Yellowstone Ecosystem revealed that rural home development near hot spots in the lowlands has likely increased the probability of extinction of these species even in protected areas such as Yellowstone National Park (YNP) (Hansen and Rotella 2002). Due to the harsh climate at higher elevations, yellow warblers in the hot spots in YNP have relatively low reproduction and these habitats are likely population sinks (Table 1). In pre-settlement times, populations in these high-elevation sinks were likely maintained by immigration from the low-elevation hot spots that were population source areas. Expansion of rural home development and other intense land uses in the lowlands has likely converted biodiversity hot spots that were source areas for species like yellow warbler to population sinks, thereby reducing the viability of subpopulations in the nature reserves. When the viability of yellow warbler populations in the nature reserves in the study area were modeled assuming no immigrants from outside the reserves, the probability of extinction was projected to be high. Nearly half of the simulated populations went extinct within 50 years. This example illustrates that changes in biotic interactions in small portions of the private lands can theoretically lead to increased risk of extinction tens of kilometers away in nature reserves.

Other Examples

Sinclair (1995) suggested that lion (P*anthera leo*) subpopulations in woodland habitats outside of Serengeti National Park in East Africa are sources for subpopulations occupying plains habitats within the park. Both subpopulations are regulated by resident prey. Resident prey are relatively stable in the woodland habitats allowing this habitat to be a net exporter of lions. The plains habitats are subject to the vagaries of weather and migratory prey movements, and lions cannot maintain themselves on the low resident prey numbers. Hence, they are sink habitats. The metapopulation may not be viable, however, because hunting and poaching in the source habitats has lead to increased lion mortality. Careful management of mortality in the source areas is likely needed to maintain the sink population in the protected area.

While the two examples cited indicate that protected areas may be sinks dependent upon surrounding sources, it is unclear how commonly this scenario occurs. These examples may stimulate additional research in protected areas that have the characteristics that could lead to this scenario.

Protected Area as Source at Risk from an Attractive Sink

The first scenario represents a conservation concern because the protected area is a sink for the species and persistence in the protected area is dependent upon the fate of the source areas in the unprotected portion of the landscape. In the second scenario described here, in contrast, the protected area represents a source habitat. Under the assumption of density dependent habitat selection in the source, the subpopulation in the protected area is predicted to remain viable regardless of the fate of the subpopulation in the adjacent unprotected lands. With the typical pattern of habitat quality increasing outside the protected area due to more favorable biophysical conditions (Figure 4), these surrounding areas are also expected to be sources. Recent conceptual developments identifying “attractive sinks”, however, lead to concern that human impacts on the unprotected lands may put at risk the subpopulation in the source habitats in the protected area.

Gundersen et al. (2001) demonstrated experimentally that high rates of mortality in a dispersal habitat patch (sink) could lead to reduced population growth in a source habitat. Delibes et al. (2001a) used a simulation modeling approach to show that high enough rates of mortality in sink habitats can lead to extinction of subpopulations in source areas, depending upon several factors including demography in sources and sinks, rates of dispersal, proportion of habitat that is a sink, etc. Delibes et al. (2001b) provide an explanation for these results that deals with the ability of organisms to perceive habitat quality. Most source-sink models assume that animals dispersing actively are able to recognize and, if possible, avoid substandard (sink) habitats. Thus, they should first select the source and only poorer competitors would occupy sinks. However, if individuals fail to select habitat properly the metapopulation may be at risk. The subpopulation in the source may become too small to remain viable if too many individuals disperse to the sink where demographic performance is poor.

Attractive sinks are thought to typically arise in association with human activity. "…the actual anthropogenically caused poor-habitat conditions may be difficult to detect by individual animals, as the causes of mortality or reduced breeding would be different from those in their evolutionary history. Hence maladaptive behaviors may be expected because most of these attractive sinks probably will be perceived by animals as sources.", Delibes et al. (2001a, Pg 278). These human activities include hunting and poaching which increase mortality rates and application of pesticides, which can reduce reproductive rates (Delibes et al., 2001b).

Example: Yellowstone Grizzly Bears

When the grizzly bear (*Ursus Arctos*) was declared an endangered species in the United States in 1973, the population in the contiguous 48 states was approximately 250 individuals with most located in Yellowstone National Park (YNP) (Craighead, 1979). Recovery efforts lead to a population expansion to the approximately 400-600 individuals today and a range expansion to the public and private lands surrounding YNP (Schwartz et al. 2006).

Extensive demographic analysis has been conducted on this population by Schwartz et al. (2007) for the period 1983-2002. Based on reproduction levels, they suggest that habitat quality is higher outside of YNP, due to higher primary productivity and the factors that drive it. They found that the reproductive rate across the population was 0.32 cubs/female/yr, an adequate level to support population growth. This reproductive rate was found to correlate with population density and measures of habitat quality (winter severity and whitebark (*Pinus albicaulis*) pinecone production). With regards to mortality, they found that 85% of mortality was caused by humans. Adult survival rates varied across land allocations. Survival was highest inside YNP, slightly lower on the federal lands within the grizzly bear recovery zone surrounding YNP (which has been managed to minimize bear mortality), and lowest on public and private lands surrounding the recovery zone (Figure 5). The primary correlates with survival rates were the density of developments, roads, and homes, found within a bears home range, plus the amount of time a bear spent in areas open to ungulate hunting during autumn (Schwartz et al. in review). Using these demographic estimates to model population growth across the Greater Yellowstone Ecosystem, Schwartz et al. (2010) found that YNP and the surrounding federal lands were population source areas. However, the surrounding private lands were population sinks (Figure 6). The strength and size of the source areas are currently sufficient to more than compensate for the sinks and the population has grown over the study period.

A key question is whether future human development outside of YNP could lead to mortality rates that result in a loss of viability of the population in YNP. Simulation models indicate an increased chance of population decline of the entire population if average female survival drops below 0.91 (Schwartz et al., 2007). Currently estimates of female survival (0.95) exceed this level. However, the human population size, rural home density, and backcountry recreation are growing rapidly in GYE (Gude et al., 2007). Regulatory agencies have concluded that future risks are unlikely to be sufficient to cause population extinction and the species was delisted in the U.S. in April 2007. The potential for loss of habitat quality under climate change (e.g., loss of the key food species, whitebark pine) and increasing human-caused mortality associated with human population expansion has lead conservation organizations to challenge this delisting of the species.

In sum, these studies suggest that the private lands surrounding YNP represent an attractive sink for Yellowstone grizzly bears. This sink currently does not appear to put the metapopulation at risk. However, careful monitoring of human development and bear demography across the system is clearly warranted to anticipate and prevent loss of viability of the bear source areas in Yellowstone National Park. As part of the delisting process, the Conservation Strategy (USFWS 2007) restricts all forms of development within Yellowstone National Park and the Recovery Zone to 1998 levels, requires state and federal agencies to monitor grizzly bear demographics, and document changes developments to ensure continued viability of the bear source areas within Yellowstone National Park and the Recovery Zone

Other Examples

Brown bears (*Ursus arctos*) in the Cantabrian Mountains of Spain are an endangered relict from a distribution that once covered the entire Iberian Peninsula. Human induced mortality is thought to be the primary driver of the range constriction. Naves et al. (2003) introduced the concept of population refuges to describe weak source areas for brown bears where reproduction is low due to poor habitat and mortality is low due to little human influence. They found that the brown bear population in the eastern portion of the study area mainly occupies areas of suboptimal natural habitat and relatively low human impact. Bear demographic data suggest that 38% of this area may function as a source and 41% as a refuge due to low habitat quality but also low human influence. The western population was located mainly in areas with high human impact but otherwise good natural quality. Some 41% was considered attractive sink and 16% as sink. Both reproduction and mortality rates were higher in the western population and it experienced a mean annual decrease of 4-5% during 1982-1995.

Although this example does not involve protected areas, it does illustrate how habitat quality and human activity often are correlated with humans being concentrated in the highest quality habitats and that this can have large effects on population viability. The authors concluded that the main management goal in the western population should be the reduction of human-induced mortality and, in the eastern population, extensive reforestation to increase habitat quality.

The pattern of elevated mortality for large carnivores outside of protected areas was found for several mammals in subsaharan Africa (Woodroffe and Ginsberg, 1998), lynx (*Lynx pardinus*) in Spain (Gaona et al., 1998), grizzly bears in the US and Canadian Rockies (Carroll et al., 2004, Neilsen et al., 2006), and wolves (*Canis lupus*) in the midwest US (Haight et al., 1998). Lynx in the Iberian Peninsula show a similar demography across habitat quality and land use gradients to brown bears studied by Naves et al., 2003). there. Gaona et al. (1998) concluded that Donana National Park was a likely population source and surrounding areas a likely sink due to human-induced mortality. The estimated probability of extinction of the population within 100 years is 22-34% depending on assumptions. In the Rocky Mountains of the US and Canada, Carroll et al.(2004) simulated spatially-explicit demography of grizzly bears and concluded that increasing the sizes and connectivity of protected areas increased population persistence.

The examples above suggest that it is not uncommon for some wildlife species to roam to what appear to be high quality habitats outside of protected areas and suffer high levels of human-induced mortality. Species with particular life history strategies are likely most susceptible to this situation. Specifically, those more likely to come into contact with humans, such as species with large home ranges that extend outside protected areas (Woodroffe and Ginsberg, 1998) or large predators that are dangerous to livestock that are less likely to be tolerated by people surrounding protected areas. Also, species likely to have strong demographic response to human induced mortality, such as those that are long-lived, have high survival rates, and exhibit population growth primarily set by female mortality (Naves et al., 2003).

I am unaware, however, of any documented cases of mortality in attractive sinks outside of protected areas being sufficient to cause the extinction of a source population in the protected area. The high rates of extinction of large carnivores in many African protected areas (Woodroofe and Ginsberg, 1988) are consistent with this hypothesis. Perhaps, development of the concept of attractive sinks will spur additional research for potential vulnerable species in protected areas.

Protected Area as Source Allowing Sustainable Harvest in Surrounding Areas

The third scenario is a case where population sources in protected areas are used to support human harvesting in the surroundings. Under this model, habitat quality is sufficiently high in the protected area for it to be a population source area (Figure 7). No assumptions need be made about habitat quality outside the protected area. Individuals dispersing outside of the protected area are harvested, creating a sink. However, the level of harvest is controlled to maintain the protected area as a source. This approach has been advocated to support hunting systems surrounding terrestrial protected areas and for the creation of marine protected areas to allow a more sustainable fishery than traditional methods. Detailed examples of the results of this approach are few and many questions remain.

Terrestrial Applications

The concept that the productivity of game in hunted areas can be supplemented by movement from source areas has received widespread attention only in recent decades. McCullough (1996) examined harvest theory in the context of spatially-structured populations. He described a harvest system where the landscape is divided into patches with a minimum patch size large enough to contain a viable subpopulation of the target species. A subset of these patches is withdrawn from harvest in order to ensure a viable population and to act as source areas. Harvest on the remaining patches may remove all or some of the population within them. Future harvest will then be dependent upon either dispersal from the protected patches or additional production within the hunted patches. The proportion of the landscape open to harvest may be increased up to the point where total harvest is maximized, which will be the maximum sustainable yield. By strictly enforcing no hunting in an adequate proportion of source areas, this system is protected from the accelerating overharvest that is characteristic of quota-harvest systems (McCullough (1996). A similar approach was presented by Joshi and Gadgil (1991).

Novaro et al. (2000) examined application of spatial control of harvest in the Neotropics. The previous nonspatial approaches for sustainable hunting that had been applied in the Neotropics had largely ignored the potential for dispersal into hunting areas and assumed that animal production was derived from within the hunted patch. Novaro et al. (2000) suggested that dispersal into hunted areas from surrounding areas can be significant. They reviewed the literature on subsistence hunting in the Neotropics and found that hunting is often conducted in areas adjacent to relatively undisturbed habitat that may act as sources of animals for the hunted sites. They also identified species that may show such dispersal dynamics. Many of the potential sources for game populations they identified occur in protected areas. They conclude that recognition of protected areas as vital sources of game is important in that it would help change the negative regard which many local people have for these areas.

Strong empirical tests of the role of protected areas in supporting source-sink hunting systems have apparently not yet been done in terrestrial systems. Navaro et al. (2005) used empirical data and simulation models of culpeo foxes (*Pseudalopex culpaeus)* in a study area in Argentina and concluded that they exhibit source sink dynamics between cattle ranches (no hunting) and sheep ranches (hunted). Circumstantial evidence was provided by Naranjo and Bodmer (2007) indicating the Lacandon Forest reserve in Mexico act as a source for ungulates hunted on surrounding lands. Source-sink theory was used as the basis for a management plan for sustainable harvest of puma (*Puma concolor*) in the western US based on protecting animals in source areas. Laundre and Clarke (2003) concluded that closing 63% of puma habitat to hunting would ensure long-term puma population viability while permitting traditional hunting levels in other areas.

Marine Applications

Source-sink theory also stimulated considerable thinking on the benefits of marine protected areas (MPA) for sustainable fisheries. Crowder et al. (2000) explained that the use of MPA is attractive because they can provide insurance against management uncertainty and can simplify the management of fisheries. The latter is true because an area completely closed to fishing is easier to police than one in which multiple gear regulations must be enforced. Like terrestrial protected areas, emigration of fish from sources to attractive sinks is expected to be driven by density-dependent habitat selection. An additional mechanism of dispersal in marine systems is water-borne larval export. Eggs and larvae produced in larger numbers by the greater spawning-stock biomass within reserves are transported to habitat outside of the protected area by water currents, leading to an increased recruitment in the fished areas. However, these mechanisms lead to substantial challenges in developing source-sink fisheries. Defining habitat quality and positioning MPA in population source areas are difficult in oceanic ecosystems (Crowder et al. 2000). The extreme complexity and unpredictability of marine currents makes it very difficult to backtrack dispersed larvae to their physical sources. Thus, designing the spatial distribution of MPA and harvest areas is very challenging.

The most widely cited study demonstrating a sustained yield fishery using MPA is Russ et al. (2004). From 1983-2001, they monitored changes in biomass of surgeonfish (*Acanthuridae*) and jacks (*Carangidae*) in a no-take reserve occupying 10% of the coral- reef fishing area at Apo Island, Philippines, and at a site open to fishing. Underwater visual censuses were used to assess fish densities in and outside of the MPA. They found that: fish biomass in the MPA increased three-fold during the study period; fish biomass did not change significantly across the entire harvest areas, however density did increase in proximity to the MPA; and fishery catch in the harvest zone was higher during 1985-2001 than before the MPA was established. The authors concluded, “The benefits of the reserve to local fisheries at the island were higher catch, increased catch rate, and a reduction in fishing effort. The fishery and tourism benefits generated by the reserve have enhanced the living standard of the fishing community.” (Pg 597).

In reviewing the state of MPA as a basis for sustainable fisheries, Sale et al. (2005) concluded that the approach is widely advocated. However, rigorous empirical tests of the effect of MPA designation on fish density within the reserves are few, and well studied effects outside of reserve borders are even rarer. The current network of MPA is small and often not placed on population source areas due to socioeconomic factors and lack of knowledge. Gaps in knowledge include:

- Distance and direction of dispersal, especially of marine larvae, but also juvenile and adult phases, which are needed to determine MPA size and location;
- Water movements near coastlines, and their effects on dispersal, and on siting of MPA;
- Spatial patterns of habitat quality and population performance;
- The effects of release from fishing on ecosystem processes such as trophic cascades which may inhibit recovery of target species density in MPA;
- Well studied cases of MPA establishment leading to a sustained yield fishery.

Acknowledging and remedying these gaps in knowledge should lay the basis for more effective application of no-take fishery reserves.

In sum, the use of terrestrial and marine protected areas as sources for sustainable harvest in the surrounding lands is supported by theory and has widespread appeal. Successful application of the approach will require greater knowledge on spatial patterns of habitat quality, target species demography and movement, ecosystem processes, and landscape design to achieve sustainable harvests. This use of protected areas provides additional justification for the creation and maintenance of protected areas.

Conclusions and Management Implications

During the two decades since the publication of Pulliam (1988), source-sink theory has strongly influenced theory and practice involving conservation in and around protected areas. The available studies on this topic largely depict three categories of applications: protected areas as sinks dependent upon outside sources, protected areas as sources vulnerable to extinction due to human activity creating attractive sinks in the surroundings, and protected areas as sources supporting sustainable harvest in surrounding areas. Current knowledge on these relationships points to various management strategies to increase species viability within protected areas and to increase their contribution to sustainable harvest in surrounding areas.

Defining greater ecosystems. Connectivity of subpopulations within protected areas with those outside is one example of the ecological processes and flows that often link protected areas to some larger surrounding ecosystem (Hansen and DeFries, 2007). Defining such “greater ecosystems” (Grumbine, 1990) is essential for developing a management approach that places the protected area in the context of the surrounding area that influences its functioning. Criteria for defining such greater ecosystems are presented in Jones et al. (2009) and DeFries et al. (2009). Among these criteria are population source and sink areas.

Create or expand protected areas. Existing protected areas were often established without the benefit of knowledge of source-sink relationships or other spatially-explicit processes. Identifying and maintaining source areas that are outside protected area boundaries may be necessary to ensure population viability within protected areas. Innovative approaches for functionally expanding the sizes of protected areas such as use of conservation easements are being widely employed in many places globally (Theobald et al., 2005). Newly created reserves can be placed and designed based on source-sink and other current theory to better maintain natural ecosystem and possibly support sustainable harvest in surrounding landscapes or seascapes (Margules and Pressey, 2000).

Modify human behavior in attractive sinks. In many cases, the negative effects of human activities on the demographics of at risk species are unintended and/or avoidable. Examples of unintended impacts include road kill, death or displacement of wildlife by pets, and spread of disease by livestock or by feeding stations. Intended but avoidable impacts include killing of dangerous animals to protect human lives or property. Both unintended and avoidable impacts can often be greatly reduced through education of local residents. Effective strategies are often low in cost and effort and may be widely embraced and supported by local citizens who appreciate the benefits of living more sustainably (Rosenzweig, 2003: Hansen et al., 2005).

Monitor population demography. The functioning of source-sink systems may be very sensitive to the proportions of source and sink habitats, population vital rates, lags in population response, and many other factors (Doak, 1995; Delibes et al., 2001b; Gunderson et al., 2007). Incomplete demographic information may be misleading on the status of populations in sources and sinks. For example, animal censuses in places that function as attractive sinks could lead to misinterpretation as the apparently stable or growing sink population could be misidentified as a source (Delibes et al., 2001a). Furthermore, harvest or other human induced mortality in the sink could be temporarily sustained by the sources, before resulting in a rapid collapse of the whole system. Careful demographic monitoring is essential to generate knowledge of management strategies that will maintain the function of source-sink systems. Progress is being made on diagnostic tools in this regard. Jonzen et al. (2005) offer a statistical method for estimating monitoring efforts in source or sink habitats needed to detect declining reproductive success in source habitats.

This review leads to the conclusion that much research, monitoring, and creative management is yet required to sustain source-sink populations in and around protected areas. However, the source-sink concept has thus far greatly enriched conservation biology and has considerable promise for future contributions.

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Figure Legends

Figure 1. Types of source and sink populations based on levels of survival and reproduction. Subpopulations in protected areas are denoted by the blue shading and those outside of protected areas in gray shading. Interactions between sources or sinks in protected areas and those outside of protected areas are indicated by the red lines. (a) A sink subpopulation in the protected area is maintained by a viable source subpopulation outside the protected area. (b) A source or refuge subpopulation in a protected area loses viability due to emigration to an attractive sink. (c) A source subpopulation in a protected area provides for a sustainable harvest in attractive sinks in surrounding areas.

Figure 2. Model depicting subpopulations in a protected area being a sink maintained by an external source under natural conditions (top). This results from the protected area being placed at the harsher end of the habitat quality gradient across the landscape (in the absence of human impacts). Human presence in the landscape leads to conversion of the unprotected source to a sink, reducing the viability of the subpopulation in the protected area (bottom).

Figure 3. (a) Shaded relief map of the Greater Yellowstone Ecosystem (GYE) in the Northwestern United States. Black polygons enclose public lands with Yellowstone National Park in the center (rectangle [this needs to be labeled]). (b) Distribution of primary productivity across GYE as derived from the MODIS satellite product. (c) Locations within GYE of native ungulate migration routes (arrows), high bird species richness (red), and rural residential home development (blue).

Figure 4. Model depicting subpopulations in a protected area being sources that are vulnerable to loss to attractive sinks. Under natural conditions, habitat quality is sufficiently high over the landscape such that the entire population is a source (top). Human induced mortality reduces reproduction in unprotected parts of the landscape creating an attractive sink, and loss of individuals to this sink puts at risk the source in the protected area (bottom).

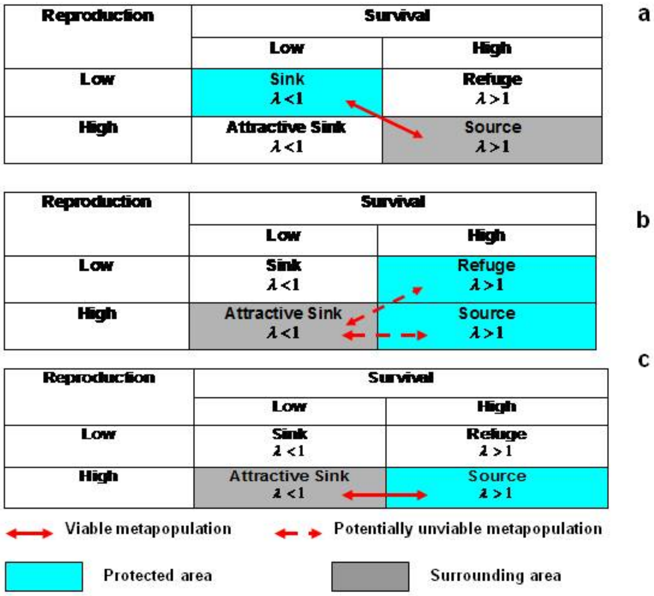
Figure 5. Effect of location on estimates and 95% confidence intervals of annual survival for female (F) and male (M) study sample grizzly bears in the Greater Yellowstone Ecosystem, 1983–2001. Locations were inside Yellowstone National Park (InYNP), inside the Grizzly Bear Recovery Zone (RZ) but outside YNP (OutYNP), and outside the RZ (OutRZ). From Schwartz et al., 2007.

Figure 6. Modeled sources (white) and sinks (blue - due to low reproduction and high mortality; and orange – due to low birth rates of grizzly bears in the Greater Yellowstone Ecosystem based on a female survival cutoff of 0.9. From Schwartz et al. 2010).

Figure 7. Model depicting the protected area as a source that contributes emigrants to surrounding areas sustainable harvest creates an attractive sink.

Table 1. Simulated net population growth of Yellow Warblers across the Greater Yellowstone Ecosystem across land allocations with and without the effect of land use. Modified from Hansen and Rotella (2002).

Land Type	Area (ha)	Current Population size	Net population change w/o homes	Net Population change with homes
Private	808	2942	309	-85
National Forest	4251	2003	41	6
National Park	984	804	-28	-35
			$\lambda = 1.06$	$\lambda = 0.98$



Reproduction	Survival	
	Low	High
Low	Sink $\lambda<1$	Refuge $\lambda>1$
High	Attractive Sink $\lambda<1$	Source $\lambda>1$

Reproduction	Survival	
	Low	High
Low	Sink $\lambda<1$	Refuge $\lambda>1$
High	Attractive Sink $\lambda<1$	Source $\lambda>1$

Reproduction	Survival	
	Low	High
Low	Sink $\lambda<1$	Refuge $\lambda>1$
High	Attractive Sink $\lambda<1$	Source $\lambda>1$

↔ Viable metapopulation

⇠ ⇢ Potentially unviable metapopulation

🟦 Protected area

⬛ Surrounding area

Figure 1

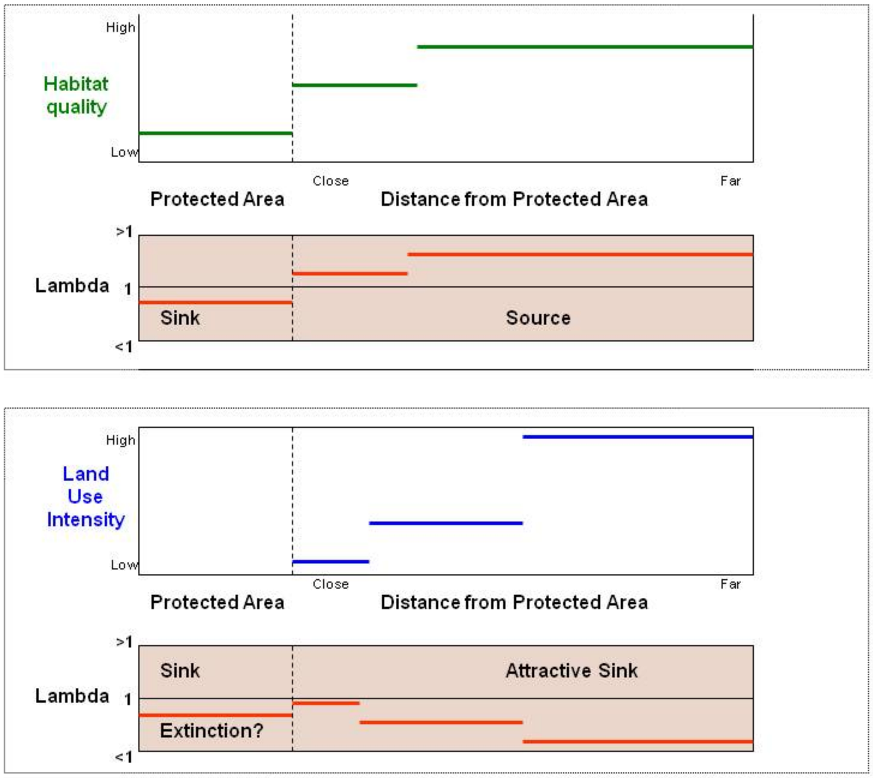

Natural Condition
High
Habitat quality
Low
Close
Far
Protected Area
Distance from Protected Area
>1
Lambda
1
<1
Sink
Source
Land Use Effect
High
Land Use Intensity
Low
Close
Far
Protected Area
Distance from Protected Area
>1
Lambda
1
<1
Sink
Attractive Sink
Extinction?

Figure 2

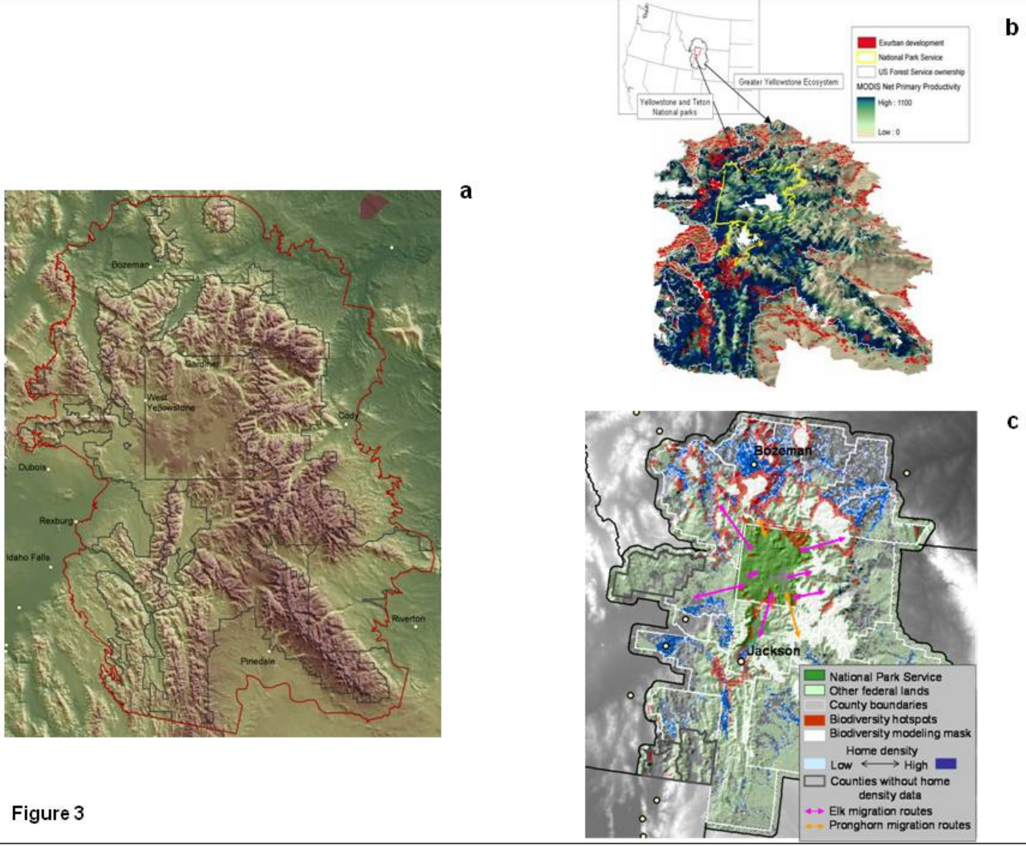
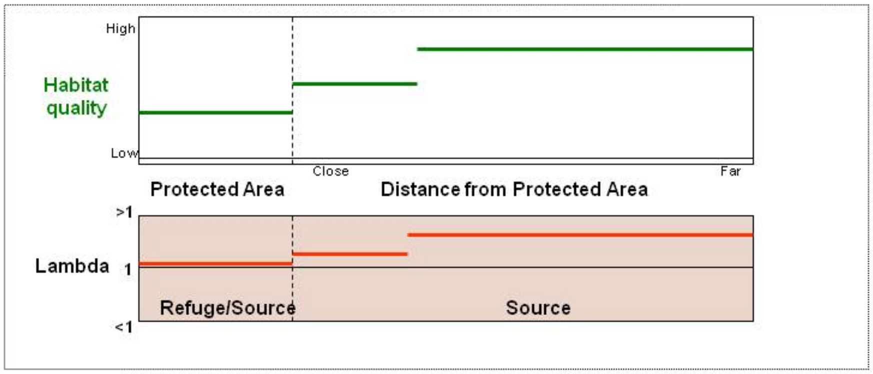

a
Bozeman
Gardiner
West Yellowstone
Cody
Dubois
Rexburg
Idaho Falls
Riverton
Pinedale
b
Exurban development
National Park Service
US Forest Service ownership
MODIS Net Primary Productivity
High : 1100
Low : 0
Greater Yellowstone Ecosystem
Yellowstone and Teton National parks
c
Bozeman
Jackson
National Park Service
Other federal lands
County boundaries
Biodiversity hotspots
Biodiversity modeling mask
Home density
Low
High
Counties without home density data
Elk migration routes
Pronghorn migration routes

Figure 3

Protected Areas as Sources Vulnerable to Attractive Sinks

Natural Condition



Land Use Effect

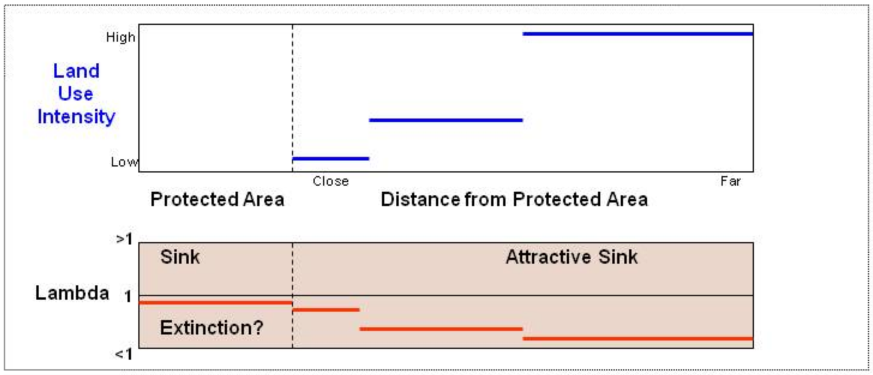


Figure 4

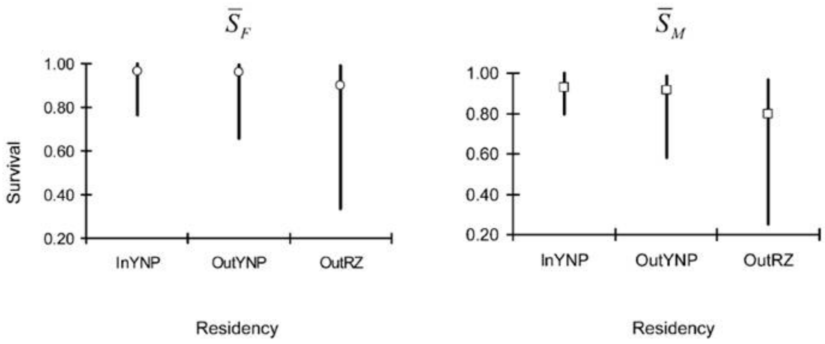
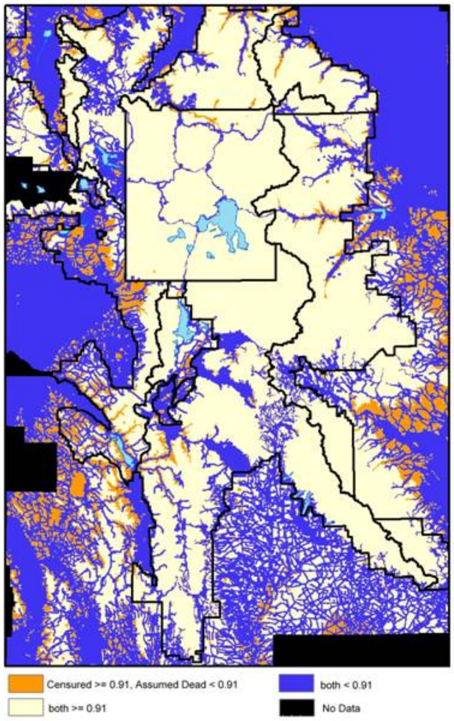

$\bar{S}_F$
1.00
0.80
0.60
0.40
0.20
Survival
InYNP
OutYNP
OutRZ
Residency
$\bar{S}_M$
1.00
0.80
0.60
0.40
0.20
InYNP
OutYNP
OutRZ
Residency

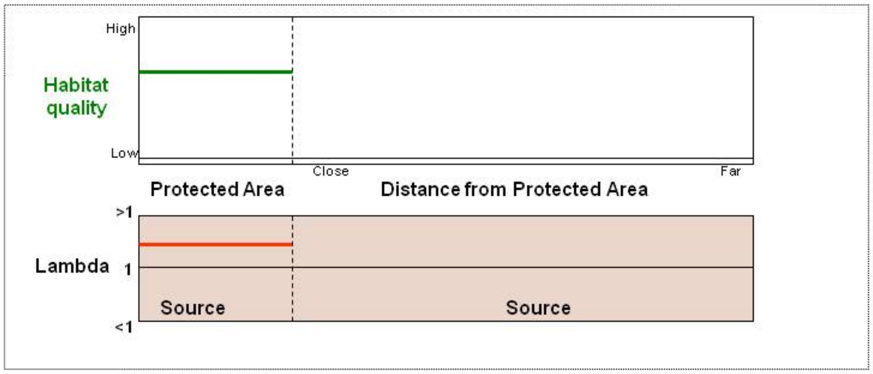
Figure 5.

Figure 6



Protected Areas as Sources for Harvest

Natural Condition



Land Use Effect

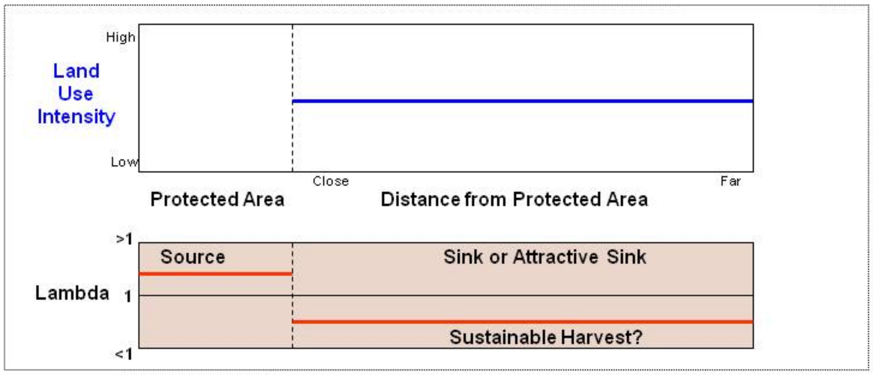


Figure 7