Methods

Accounting for the ecosystem services of migratory species: Quantifying migration support and spatial subsidies

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ABSTRACT

Migratory species support ecosystem process and function in multiple areas, establishing ecological linkages between their different habitats. As they travel, migratory species also provide ecosystem services to people in many different locations. Previous research suggests there may be spatial mismatches between locations where humans use services and the ecosystems that produce them. This occurs with migratory species, between the areas that most support the species' population viability – and hence their long-term ability to provide services – and the locations where species provide the most ecosystem services. This paper presents a conceptual framework for estimating how much a particular location supports the provision of ecosystem services in other locations, and for estimating the extent to which local benefits are dependent upon other locations. We also describe a method for estimating the net payment, or subsidy, owed by or to a location that balances benefits received and support provided by locations throughout the migratory range of multiple species. The ability to quantify these spatial subsidies could provide a foundation for the establishment of markets that incentivize cross-jurisdictional cooperative management of migratory species. It could also provide a mechanism for resolving conflicts over the sustainable and equitable allocation of exploited migratory species.

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1. Introduction

A recent international effort to document the state of the world's ecosystems determined that drivers of global change – drought, land-use change, intensive water use, and climate change – are threatening the capacity of ecosystems to provide services (MEA, 2005). This has spawned intense interest in conserving the ecological processes and functions that support ecosystem services. Efforts are underway around the world to map locations where ecosystem services are provided in order to protect those areas deemed most critical to providing services (Egoh et al., 2008; Raymond et al., 2009).

Protecting areas where ecosystem services are provided may indeed conserve localized ecosystem services like recreation. Not all services are localized, however, leading some authors to note that there may be "spatial mismatches" between where humans use ecosystem services and the location of the ecosystems that produce them (Brauman et al., 2007; López-Hoffman et al., 2010). Other authors have noted the importance of understanding how services "flow" across the landscape for meeting management and policy

objectives (Fisher et al., 2009; Tallis et al., 2008). Spatial mismatches and flows may occur when species with complex movement dynamics provide ecosystem services; such services have been termed "mobile agent-based ecosystem services" (Kremen et al., 2007). Movement causes species to act as "mobile links," actively connecting ecological processes in different locations (Gilbert, 1980; Lundberg and Moberg, 2003). As they move throughout their ranges, species may provide critical ecosystem services. For example, migratory birds and bats provide ecosystem services as diverse as controlling crop pests to seed dispersal and pollination (Cleveland et al., 2006; Medellín, 2009; Sekercioglu, 2006; Wenny et al., 2011; Whelan et al., 2008). For migratory species in particular, spatial mismatches likely exist between those areas that most support population viability – and hence the species long-term ability to provide services – and the locations where the species provides the most ecosystem services.

Migration and the potential for spatial mismatches create a management and scientific challenge: to ensure the provision of ecosystem services by migratory species in one location, it may be necessary to protect habitat in other locations within the species annual migratory range. This will require methods for estimating the extent to which each location supports the provision of ecosystem services in other locations. This paper presents a conceptual framework, including new terminology and a mathematical

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formalization, to articulate spatial heterogeneity in the provision of ecosystem services by migratory species.

For this purpose, we utilize the following three terms. *Migratory services* is used to describe all ecosystem services provided by a migratory species throughout its range. *Migration support* is the degree to which one location supports the provision of ecosystem services in other locations by contributing to the viability of migratory populations. All locations utilized by a migratory species provide migration support; they also benefit from migration support in the form of migratory services that are locally provided by that species. *Spatial subsidy* is the net balance between migratory services received and migration support provided. It measures the degree to which the provision of migratory services in one location is subsidized by ecological conditions and processes in other locations. In effect, it is the amount a given location *owes* other locations for supporting migratory species and the services they provide locally. Based on the categories of ecosystem services defined by the Millennium Ecosystem Assessment (MEA, 2005), migration support should be considered a supporting service, while Fisher et al. (2008) would consider migration support an intermediate service.

How common is migration support and how frequently should spatial subsidies be included in assessments of ecosystem services? Based on the vast number of studies and theory in ecology related to spatial issues, we believe the majority of location-specific assessments of ecosystem services incorrectly estimate their value by not considering the ecosystem services provided by migratory species, or only considering those services mobile organisms provide locally. Ecologists have long recognized the critical role of space and movement in natural systems (Hansson et al., 1995; Huffaker, 1958; Polis and Hurd, 1996). Dispersal of individuals as eggs, seeds, juveniles, or adults, migration, and the occurrence of different life stages in different geographic locations are common phenomena (Clobert et al., 2001). The ubiquity of movement in natural systems has lead to the subfield of spatial ecology and the recognition that linkages across landscapes can affect ecosystem processes—now a major tenet of landscape ecology (Lovett et al., 2005; Turner, 1989). In this paper, we merge spatial ecology (Tilman and Karieva, 1997) with the developing field of ecosystem services assessment, valuation, and management.

To explore the issues of migration support and spatial subsidies, we first present three examples of how migratory species link ecosystems and ecosystem services across space. Second, we outline analytical methods for quantifying migration support and spatial subsidies. Next, we describe potential methods for estimating key parameters in our model and the types of data needed to estimate migration support and spatial subsidies. Finally, we consider how the estimates of migration support and spatial subsidies could be used to more effectively manage migratory species and sustain their ability to provide ecosystem services throughout their ranges.

2. Examples

2.1. Salmon

Diadromy has evolved in ~250 fish species around the world (McDowall, 2008) including salmon in the northern Pacific. In Alaska alone, the average annual commercial harvest from 1998 to 2002 was ~170 million fish, worth $260 million (Woodby et al., 2005). Salmon migrations move energy and nutrients between marine, freshwater, and terrestrial ecosystems. For example, a run of 20 million fish moves over 50 million kg of biomass and associated nutrients into freshwater and terrestrial ecosystems (Gende et al., 2002). In freshwater, decomposing salmon provide nutrients, which positively impact young salmon (Moore et al., 2007; Wipfli et al., 2003). In addition, a wide range of vertebrates and invertebrates consume salmon, resulting in higher densities near streams via both reproduction and

movement (Christie and Reimchen, 2008; Helfield and Naiman, 2006; Hilderbrand et al., 1999; Miller et al., 1997).

Successful management of Pacific Northwest salmon must include all of the diverse habitats supporting the species' entire life cycle and recognizing the spatial subsidies exchanged between different habitats. For example, because freshwater systems are spawning grounds and migratory habitat for young salmon, efforts to protect and manage terrestrial habitats near streams will benefit marine fisheries (Gende et al., 2002). Likewise, management decisions regarding commercial and recreational fishing will impact terrestrial ecosystems far inland. An example spatial subsidy calculation for Chinook salmon will be presented following our description of the model.

2.2. Bats

Bats provide critical regulating and supporting services via seed dispersal, pollination, and pest control. Several species of migratory neotropical bats summer in the US and winter in Mexico, including the lesser long-nosed bat *Leptonycteris curasoe*, the Mexican long-nosed bat *Leptonycteris nivalis*, and the hog-nosed bat *Choeronycteris mexicana*. Their collective range covers southern Mexico to southwestern Texas, southern New Mexico and Arizona. They disperse the seeds of several dozen plant species, including a variety of organ pipe cacti. People in central and northern Mexico harvest the cactus fruits, and in several areas this is an important cash crop (Pimienta-Barrios and Nobel, 1998). Bats also pollinate hundreds of plant species across the Americas, perhaps more than birds (Medellín, 2009), with the most famous example being agave, a main component of tequila. Small, artisanal producers who depend on bat pollination and use many genetic varieties and species of Agave are collaborating with conservation biologists to protect bats (R Medellín, personal communication). Bats also provide critical pest control services in both the US and Mexico. For example, roosts in Mexico support large amounts of 'free' pest control for farmers in the US. Every summer, maternity colonies of female Mexican free-tailed bats *Tadarida brasiliensis mexicana* consume large amounts of crop pests. Cleveland et al. calculated that in a 100 km^2 area of south-central Texas, the value of bat pest regulation is as much as $700,000 US dollars annually (Cleveland et al., 2006). These examples illustrate how ecosystem services provided by species can create cross-border incentives for conservation (López-Hoffman et al., 2010).

2.3. Rufous Hummingbird

Rufous hummingbirds (*Selasphorous rufus*) migrate from wintering grounds in central and western Mexico to breeding grounds throughout the Pacific Northwest, western Canada and southern Alaska (Schondube et al., 2004). When returning to their winter range Rufous hummingbirds follow high elevations along coastal ranges, the Sierra Nevada, and Rocky Mountains.

Hummingbirds provide pollination services throughout their migratory range. They serve as mobile links between plant populations in different landscapes, facilitating pollen and gene flow often over considerable distances (Nabhan, 2004) and the pollination may expedite secondary plant succession following disturbances (Calder, 2004). Rufous hummingbirds visit many of the plants in secondary succession vegetation (Calder, 2004) and likely facilitate the provision of berries for birds and bears and the retention of soil/sediment that protects salmon spawning habitat and maintains downstream water quality. Rufous hummingbirds are also a cherished visitor to residential feeders throughout western North America and thus provide an important cultural service.

While their importance to humans is easily recognized, ecosystem services associated with hummingbirds have not been quantified or valued. They do not directly or indirectly provide marketable

ecosystem goods, such as through the pollination of commercial crops, and they naturally distribute in space and time as they migrate. They share floral resources with other pollinators and the secondary services of the plants they pollinate have not been established. No primary economic research has revealed their cultural value as residential visitors throughout their range. As a result, the services associated with hummingbirds can only be inferred at this time.

3. Methods

In this section, we describe methods for estimating migration support and spatial subsidies. In our formalization, both migration support and the spatial subsidy are estimated for a specific geographic area, taking into account where a species provides services and on which habitat it depends throughout its full migratory range. Both calculations require estimates of two important parameters that are defined briefly below and discussed further in the following section. These parameters are the total value of services provided by species S at location A (V_{SA}), and the proportional dependence of species S on location A (D_{SA}).

The total value of the migratory services provided by a species at a location A, or V_{SA}, is the sum total of ecosystem service benefits derived from that species, either directly while it is physically present at that location or indirectly as a result of processes or functions it performed while it was there. V_{SA} represents a subset of V_S, the total value of a species' migratory services provided across its entire range.

The proportional dependence of a migratory species on a location A, or D_{SA}, is conceptualized as the degree to which the location contributes to the maintenance of the entire population of the migratory species. For example, if a location has a D_{SA} value of 0.1 for a particular species, the complete loss of its habitat at that location would result in a 10% overall population decline for the species assuming no less suitable alternative habitat exists.

3.1. Migration Support and Spatial Subsidies

We define migration support in terms of the gross benefits provided and received by a location. To estimate the gross migration support provided by location A *out* to all other locations, M_{Ao}, it is first necessary to estimate the total value of the services provided by migratory species that use the location (across the entire range of each species), subtract the value of services provided locally, and then multiply this amount by the species' proportional dependence on the location in question. This can be formalized for one species as follows:

$$M_{Ao} = (V_S - V_{SA})D_{SA} \tag{1}$$

where V_S is the total value of all (migratory) services provided by a species S throughout its range. Values for D_S must satisfy the following two requirements:

$$0 \le D_{SL} \le 1$$
$$\sum_{L=1}^{m} D_{SL} = 1$$

where D_{SL} represents the proportional dependence at any given location, and L encompasses all m locations utilized by a species. The latter requirement stems from the fact that migratory species are dependent upon the persistence of favorable conditions across their entire range; they cannot be more or less than 100% dependent upon their environment.

The gross migration support received *in* by a location from all other locations, M_{Ai}, is formulated in much the same way as the support provided. However, in this case the value of services provided locally (V_{SA}) is multiplied by the extent to which a species is dependent upon all other locations. Since the proportional dependence of a species

must sum to 1 across all locations within its range, the imported migration support can be expressed as follows:

$$M_{Ai} = V_{SA}(1 - D_{SA}) \tag{2}$$

The migration support values calculated in Eqs. (1) and (2) are based on the recurring, annual monetary value of services provided by all migratory species utilizing a location. All values must be consistent, sharing a common ratio scale. Nonmonetary values can be accommodated, provided this latter condition can be met.

The net difference between outgoing and incoming migration support is the spatial subsidy (Y_A):

$$Y_A = M_{Ao} - M_{Ai} = V_S D_{SA} - V_{SA} \tag{3}$$

which can be considered as the amount for each location that balances the support of and benefits from migratory services throughout a species range. Positive values indicate location A is subsidizing other areas and suggest that it is therefore owed a payment. Negative values indicate location A is being subsidized by other areas and suggest it owes a payment to those areas. When applied to all locations, L, throughout a species' range, Eq. (3) satisfies the requirement that the sum of all payments is 0, or

$$\sum_{L=1}^{m} Y_L = 0 \tag{4}$$

The net value of goods and services provided by a migratory species is therefore a function of the dynamics of services provided and environmental support received by the species throughout its range (Eq. (3)). Fig. 1 depicts a possible division of the migratory range of a hypothetical species into three distinct areas, or locations. While these areas could correspond with winter, migratory, and breeding range, the equations apply for any number of areas,
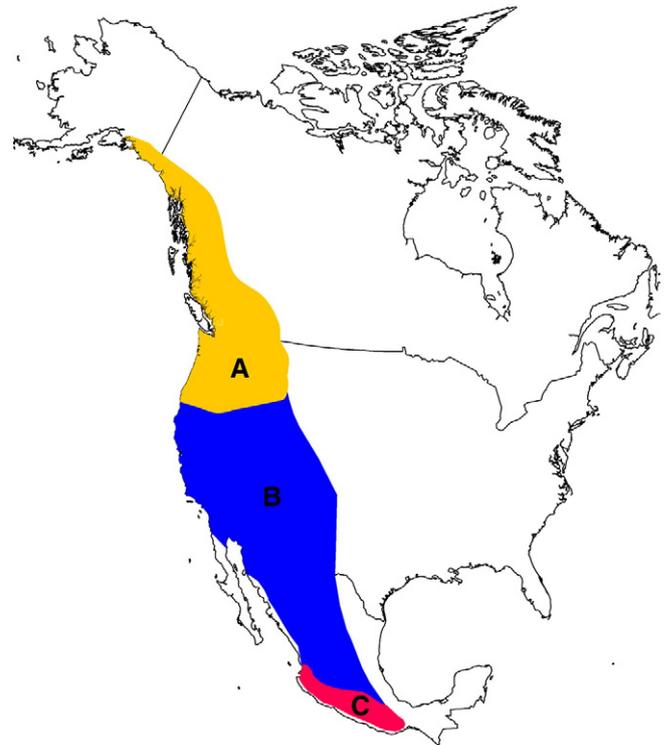

Fig. 1. Illustration of three locations utilized by a hypothetical migratory species S. The migratory range of a species may be divided into any number of locations with any size and is limited only by the availability of data for the species' proportional dependence and service provisioning within the selected units.

regardless of size or the manner in which they are defined. It is also important to note that while we have concentrated on migratory species, which often have substantial geographic ranges, the same approach could be applied at a much smaller scale for mobile organisms that have well defined foraging ranges such as pollinating insects.

A graphical depiction of how the spatial subsidy (Y) behaves for a range of V and D values is presented in Fig. 2. Fig. 2A and Eq. (3) indicate that as a local area (A) generates more migratory services (or when V_A gets closer to V_S, 10 in this example), it owes a larger and larger subsidy to other locations. This may seem counterintuitive until one recognizes that the species is equally dependent on all three locations in this example (Fig. 2A). Location A may provide a greater proportion of the total migratory services, but local production of services is dependent on support (population maintenance) from the other two locations. Conversely, as a species becomes more dependent on a location, that location is more likely to be owed payments for migration support (Fig. 2B).

The total annual value generated by a migratory species at a location, V_A, is the sum of the spatial subsidy and value of migratory services provided locally:

$$V_A = Y_A + V_{SA} \tag{5}$$

The value V_A would be useful for prioritizing sites for conservation or mitigation investment. It can also be incorporated into broader ecosystem service valuation exercises designed to map the distribu-

tion of value across the landscape, provided indirect values that might have been incorporated into V_S (i.e. enhanced production of other services) are not double counted. An analysis of tradeoffs associated with competing land uses, however, would require further analysis to establish the marginal value of the habitat that might be lost under alternative land-use scenarios.

Up to this point we have only considered one migratory species. However, Eqs. (3) and (5) can be rewritten to accommodate multiple species by simply summing across all n species of interest.

$$Y_A = \sum_{S=1}^{n} (V_S D_{SA} - V_{SA}) \tag{6}$$

$$V_A = Y_A + \sum_{S=1}^{n} V_{SA} \tag{7}$$

The migratory ranges of each species need not overlap completely. Eq. (6) still satisfies the requirement of Eq. (4), provided that the combined spatial extent of all ranges is considered.

3.2. Example Subsidy Calculation for Chinook Salmon

Returning to the salmon example, both economic and population data are readily available for Chinook salmon, though not from the same place. The economic value of Rogue River Chinook salmon in southern Oregon was estimated by Helvoight and Charlton (2009), with dollar value estimates derived for recreational and commercial fishing in both the river and ocean (Table 1).

A habitat-specific, density-dependent matrix population model for ocean-type Chinook was developed by Greene and Beechie (2004) for the Skagit and Duwamish Rivers in northern Washington. This model explicitly incorporated density dependence associated with the different life stages of Chinook salmon to explore the potential population-level implications of changes in the area of 5 different habitats associated with the salmon life cycle. Greene and Beechie (2004) performed sensitivity analyses for different types of density dependence and changes in habitat area. These analyses showed the overall change in population size caused by changes in the area of each habitat. We used these sensitivity analyses to estimate D_{SA} (Table 2). Because the economic data existed only for the entire river (Helvoight and Charlton, 2009), we combined sensitivity estimates from the redd, stream, and delta habitats into a single D_{SA} value for the river. If data on the locations of recreational fishing had existed, we could have partitioned the economic data into these river habitats. In the ocean, where the population is not limited by area, we use the sensitivity associated with adult survival, because it incorporates a
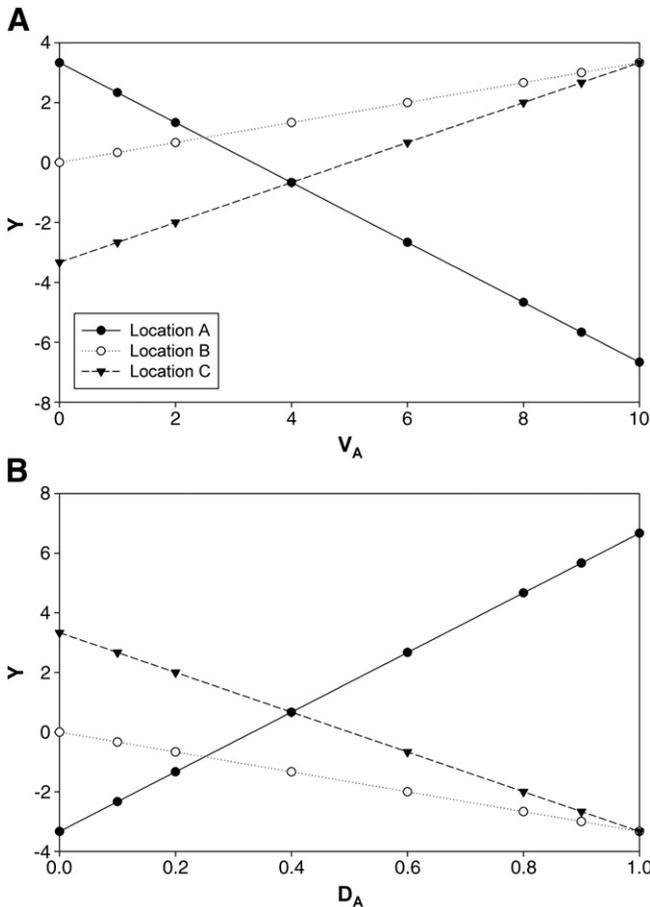

Fig. 2. Graphs depicting how the spatial subsidy Y varies with different values of V_A and D_A. A three-location, one-species example is used, with the constraint that the total value of migratory services (V_S) across all three locations is always equal to 10. Specific values are hypothetical; they are designed to most clearly represent how the model behaves. (A) Y as a function of V_A, when $D = 0.33$ at all three locations and $V_B = V_C/2$. (B) Y as a function of D_A, when $V = 3.33$ at all three locations and $D_B = D_C/2$.

Table 1
Annual economic value of Rogue River Chinook salmon fishing, from Helvoight and Charlton (2009).

	Sport	Commercial	Total
River	$3,711,003.00		$3,711,003.00
Ocean	$340,600.00	$1,271,379.00	$1,611,979.00
Total	$4,051,603.00	$1,271,379.00	$5,322,982.00

Table 2
Estimated proportional dependence (D) values associated with habitat used by Chinook salmon in the Skagit and Duwamish Rivers, from Greene and Beechie (2004).

Habitat	D
River (grouped)	(0.271)
Nearshore	0.510
Ocean	0.219
Sum	1

host of mortality variables in the ocean, as the estimate for proportional dependence. Finally, because commercial fishing for juvenile smolts (3–5 in long) does not take place in the near shore habitat, we used a value of 0 for economic benefits in this area.

The results (Table 3) indicate that commercial and recreational fisheries are subsidized approximately $2.7 million/year by near shore marine habitats such as beaches and eelgrass beds that are subject to freshwater influence, where juvenile Chinook remain for approximately 4 months (Greene and Beechie, 2004). The subsidy calculation reflects what the population model indicated—that conservation funding should be directed to nearshore habitat. This suggests that commercial and recreational fisheries might be well-served by providing the local municipalities and public agencies that manage nearshore habitat with payments for habitat protection. While the subsidy in this instance is large, it could decrease over time if conservation activities improved or increased the amount of habitat, thereby reducing the proportional dependence of species on this area. In the long term, subsidy payments would provide a steady source of income for communities that forego activities incompatible with maintaining the migratory population. We caution that this example is based on economic data and population models derived from different river basins with distinct Chinook populations. Though transferring ecosystem service values from one site to another is common (Brookshire and Neill, 1992; Wilson and Hoehn, 2006), in this case we are transferring population data and the forms of density dependence and the demographic estimates used by Greene and Beechie (2004) may not exist in the Rogue River.

4. Discussion

What types of information, research, and data are needed to advance the consideration of migratory services and migration support in conservation planning and decision-making? Though conceptually straightforward, estimating real values for V_S and D_S (respectively, the total value of migratory services and the proportional dependence of species on habitat) presents a substantial challenge. These are discussed further below in light of relevant previous research, along with the types of data that will be necessary to realize the full potential of the approach and implications for wildlife management if this information was more widely available.

4.1. Migratory Services Value and Proportional Dependence

In its most basic interpretation, V_{SA} represents the per capita generation of ecosystem services multiplied by the number of individuals at location A. Estimating V_{SA} is complex because different life stages or ecological roles occur in different locations. For example, bird watchers may flock to a particular location where interesting courtship behavior occurs, while nesting and overwintering occur in different locations with far fewer bird watchers. A species may play a particular ecological role (supporting predator populations, regulating a pest, pollination, seed dispersal, etc.) in one location, but not another. The calculation for V_{SA} must therefore be location specific, yet measured across all locations, thus creating considerable hurdles both

in the ecological understanding of a species and its valuation at each location. Wenny et al. (2011) detail the various ways in which bird species provide benefits to humans and describe the key research needs needed for their quantification. Similar approaches, including targeted studies of ecological functions and interactions, are necessary for non-avian species. In addition to challenges in quantifying services, new economic research is needed to value the services we derive, directly and indirectly, from individual species. By focusing on individual species, rather than ecosystems, caution is required to avoid counting intermediate goods, which can lead to double counting if species values are combined with other ecosystem service values (Boyd and Banzhaf, 2007).

Estimates of D_{SA} should allow comparisons of different sites in terms of their contribution to overall population growth or viability. Ecologists currently have a variety of tools to allow this estimation. For example, multisite demographic models (like the Salmon example) allow the estimation of demographic variables for individual subpopulations as well as probabilities of movement between subpopulations (Conroy et al., 1996; Mackenzie et al., 2009; Williams et al., 2001) and can be used to estimate D_{SA}. Metapopulation models that define unique areas migratory species use as subpopulations can be analyzed using sensitivity analyses to estimate the relative impact of each subpopulation on overall population dynamics (Touloumis and Stamou, 2009). In particular, pattern-oriented modeling (Grimm et al., 2005) could be structured to generate estimates of D_{SA} while reducing uncertainties caused by sparse data. Finally, integrodifference equations should allow robust estimates of D_{SA} (Dewhirst and Lutscher, 2009; Neubert and Caswell, 2000). Many different existing modeling methods thus currently exist for estimating D_{SA}.

As we discuss below, the most difficult aspect of estimating D_{SA} may be in developing demographic data across all sites. However, even when data are sparse, modeling techniques still may allow for estimates of D_{SA} and associated levels of uncertainty. For example, the literature on population viability analyses contains many examples where parameter values for an endangered species are not known, or based on sparse data. In these cases the modeling approach develops estimates of population viability that explicitly incorporate the uncertainty surrounding the parameter estimates (Beissenger and McCullough, 2002; Morris and Doak, 2002). Though this must be done with caution and awareness (Ellner et al., 2002), we suspect applications of our model will require a similar approach, where the uncertainty surrounding D_{SA} will influence the range of values estimated for spatial subsidies.

With our particular model a number of additional issues merit further investigation. For example, using Eq. (4) and placing empirically estimated bounds on V_S and D_S might allow the use of optimization algorithms, such as Linear Programming to estimate service provisioning under specific management scenarios, even when data are scarce. In addition, our framework should allow integration with a broad array of valuation methods, or even combinations of them (Kumar and Muradian, 2009). In general, investigating how different valuation methods can be utilized more or less suitably to estimate the variables in Eqs. (1) and (2) would greatly improve the applicability of our approach.

4.2. Data Requirements

Regardless of the specific methods utilized, estimation of V_S and D_S will require new data and data structures focused specifically on migratory species, their migratory behavior, their interactions with humans, and their ecological roles in the variety of ecosystems supporting their geographically diverse life histories. Spatially dynamic, citizen-based observation networks for the biological sciences (eBird, 2011; Pattengill-Semmens and Semmens, 2003) provide a tremendous resource for overcoming some of the difficulties associated with investigating migratory species, but lack the capacity to accommodate detailed information on observed species behavior and interactions.

Table 3
Annual spatial subsidy calculation for Chinook salmon. Negative values for the subsidy (Y) indicate the amount owed.

	River	Near shore	Ocean
V	$3,711,003.00	$0.00	$1,611,979.00
D	0.270555695	0.510635434	0.218808871
Mo	$436,130.10	$2,718,103.22	$812,000.38
Mi	$2,706,970.00	$0.00	$1,259,263.69
Y	−$2,270,839.91	$2,718,103.22	−$447,263.32

In the short term, data limitations will hamper the application of our approach and permit only analyses for those charismatic, endangered, and/or economically important species that are most well studied and monitored. In the long term, the approach demands substantial investment in and coordination of new data collection, monitoring, and database development to systematically address mobile organisms. It will be necessary to develop a standardized framework for collecting and organizing information on species distributions, populations, and the interactions between species, ecosystems, and human society. A centralized, web-based, publicly accessible, spatial interactions database is needed to house and serve this information and permit the queries required to both map and quantify migratory services. This is not a new idea—there is wide recognition of the need for more synthetic and integrative analyses in ecology (Jones et al., 2006; Kelling et al., 2009; Madin et al., 2007). The ontology for describing and synthesizing ecological observation data developed by Madin et al. (2007) could be extended with specialized domain vocabularies to accommodate interactions between species, ecosystems, and human society. It is therefore a real possibility that the type of information needed for estimating migratory services and spatial subsidies will be more readily available in the future. In addition to migratory service calculations, this information would have myriad potential applications related to understanding ecosystems, predicting ecosystem change, and, through the calculation of spatial subsidies, the establishment of markets for ecosystem services.

Finally, migration support is perhaps just one example in the broader issue of spatio-temporal dynamics in ecosystem services. Water, humans, and climate are all responsible for driving geographic movements (flows) and temporal fluctuations in ecosystem services. New tools are emerging that provide a spatial framework for quantifying the flow of benefits from ecosystems to people, and establishing a new means of estimating their economic benefits (Johnson et al., 2010). Migration, however, represents a very different type of flow from the unidirectional upstream or downstream fluxes that have been considered to date—migratory services in one location are dependent upon all other locations within the migratory range. New monitoring that is specifically designed to gather information on the pathways and timing of movement is of fundamental importance to understanding these flows, both in terms of elucidating species dependence on the landscape and the monetary and non-monetary value exchanged between different locations.

4.3. Management Implications

Conservation efforts will benefit from recognizing and accounting for the spatial mismatches between where ecosystem services are provided and where they are used. First, migratory species that link disparate regions should create additional incentives for cross-jurisdictional and even cross-border cooperative management. To date, the vast majority of arguments for cross-border management are largely driven by biodiversity concerns (Soule and Terborg, 1999). Placing them in the broader context of ecosystem services could result in a wider set of participants and more support for transboundary conservation efforts (López-Hoffman et al., 2009, 2010).

Second, though methods for establishing markets and payments for ecosystem services require large amounts of research and development (Antle and Stoorvogel, 2006; Fisher et al., 2008), a market based on geographically explicit valuation of services and migration support could improve funding levels for management of migratory species via payment transfers to locations with key migration support roles. Indeed, with the appropriate data, one could imagine maps of migration support 'hot spots' akin to the biodiversity maps used to prioritize or rank geographic regions for conservation planning (Myers, 1989; Myers et al., 2000). Overall, this could lead to greater support for conserving a larger proportion of the area within a migratory species' range.

In addition, including migration support into calculations of the ecosystem services provided by a local area should better reflect its true value and thus increase the overall accuracy of an assessment. In some cases, the migration support services could be large. For example, the United State Fish and Wildlife National Wildlife Refuge System includes ~150 million ac of land in over 500 refuges. In the system, 670,000 ac are Waterfowl Protection Areas, which provide migration support for a wide array of bird species. Including migration support and spatial subsidies into current assessments of the National Wildlife Refuge System (Carver and Caudill, 2007) could increase its estimated economic impact and thus increase the incentives for continued funding of the reserve system.

5. Conclusion

Countless authors have described corridors or stopover sites that are "critical" to the survival of migratory species, suggesting that these areas are disproportionately important and thus have high value. Although much current research is devoted to identifying and quantifying the importance of these areas in terms of species biology, a conceptual framework for assigning them value within an ecosystem services context has not been established. Owing to the transient nature of migratory species, the net value of goods and services they provide cannot be justifiably quantified at any one location without considering the dynamics of services they provide and environmental support they receive throughout their ranges. We present a simple model that distinguishes the value of ecosystem services an area supports from that which it receives, permitting estimation of the net value of an area resulting from one or more migratory species. As data and methods are established for estimating the ecological goods and services provided by migratory species and their dependence on ecosystems throughout migratory ranges, it will be possible to quantify the interdependency of ecosystems resulting from migration. It is anticipated that this can serve as a foundation for the establishment of markets that would facilitate cross-jurisdictional cooperative management and conservation of migratory species.

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