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RESEARCH ARTICLE

Ecosystem service flows from a migratory species: Spatial subsidies of the northern pintail

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Abstract Migratory species provide important benefits to society, but their cross-border conservation poses serious challenges. By quantifying the economic value of ecosystem services (ESs) provided across a species' range and ecological data on a species' habitat dependence, we estimate *spatial subsidies*—how different regions support ESs provided by a species across its range. We illustrate this method for migratory northern pintail ducks in North America. Pintails support over $101 million USD annually in recreational hunting and viewing and subsistence hunting in the U.S. and Canada. Pintail breeding regions provide nearly $30 million in subsidies to wintering regions, with the "Prairie Pothole" region supplying over $24 million in annual benefits to other regions. This information can be used to inform conservation funding allocation among migratory regions and nations on which the pintail depends. We thus illustrate a transferrable method to quantify migratory species-derived ESs and provide information to aid in their transboundary conservation.

Keywords Migration · Northern pintail duck · Spatial subsidies · Species conservation · Telecoupling · Transborder conservation

INTRODUCTION

In an increasingly interconnected world, global flows of ecosystem services (ESs) are recognized as vital to human well-being (López-Hoffman et al. 2010; Liu et al. 2016) but are often underrepresented in ES assessments (Schröter et al. in press). In particular, migratory species provide diverse and important provisioning, regulating, and cultural services (Kunz et al. 2011; Semmens et al. 2011; Wenny et al. 2011; Bauer and Hoye 2014; Green and Elmberg 2014) and function ecologically as "mobile links" across large landscapes (Lundberg and Moberg 2003; Runge et al. 2015). Conserving migratory populations is geographically challenging, as their habitats span multiple jurisdictions (Harris et al. 2009; López-Hoffman et al. 2017a). At the same time, stressors on migratory species have increased (Wilcove and Wikelski 2008), challenging managers' ability to target and fund needed conservation activities (Lee and Jetz 2008). Successful conservation of these populations requires not only coordination among diverse stakeholders and governments but also information about how conservation strategies will influence population dynamics and associated ESs at multiple scales (Martin et al. 2007; Mattsson et al. 2012; Runge et al. 2014). These challenges collectively motivate holistic approaches to conservation, which can integrate ecological and economic data to inform cross-border migratory species conservation (Semmens et al. 2011; López-Hoffman et al. 2013).

One such approach is the spatial subsidies framework, which integrates information about ESs provided by a migratory species and the species' dependence on discrete habitat areas to quantify ES flows and economic dependencies between regions in a species' migratory network (Semmens et al. 2011; López-Hoffman et al. 2013). Because migratory species commonly provide greater ES value to people in certain parts of their range, yet have greater dependence on habitat in other regions (which may have lower in situ ES value), people in areas receiving high ES value are effectively *subsidized* by habitat conservation in places on which the species is most dependent. Spatial

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subsidies provide a quantitative measure of these flows that can inform conservation across a migratory species' range, including allocation of conservation funding to secure migratory species-derived ESs. This method is thus one way to quantify the value to people of the transport and trophic effects of species that migrate across long distances (Bauer and Hoye 2014).

In North America, the northern pintail (*Anas acuta,* henceforth pintail) serves as an example to both demonstrate the spatial subsidies approach and suggest how it could enhance existing payment schemes for their conservation and management. Pintails are migratory dabbling ducks that require shallow wetlands for feeding. During summer they breed across parts of North America and Eurasia, and they winter in temperate, subtropical, and tropical grasslands and coastal areas of Africa, Eurasia, and the Americas almost entirely north of the equator (BirdLife International 2018). In North America, pintail winter range concentrations are greatest on the U.S. Gulf Coast and the Pacific Coast of Oregon and California; their primary summer breeding habitat includes the "Prairie Pothole" region of the north-central U.S. and central Canada, Alaska, and the Canadian Arctic (Clark et al. 2014). Pintails provide ESs to people throughout their migratory range, including subsistence hunting for indigenous communities in the Arctic (Goldstein et al. 2014) and recreational hunting and wildlife viewing, which are collectively valued at over $100 million per year (Mattsson et al. 2018). Pintails are one of the few dabbling duck species well below population goals and are of recognized conservation importance (Guyn et al. 2003; USFWS 2017a). Between 1955 and 1998, the total pintail population in North America declined by 74% to 2.5 million birds. By 2017, the population had grown to 2.9 million birds, but remained 28% below the goal of 4.0 million birds proposed by the North American Waterfowl Management Plan (NAWMP 2014). Just as some regions receive more pintail-derived ESs than others, certain areas also have disproportionately high importance in supporting pintail populations. For example, grasslands and shallow wetlands in the U.S. and Canadian Prairie Pothole Region have been shown to be highly important for supporting continental scale pintail population dynamics (Mattsson et al. 2012), as well as those of other migratory bird species.

Existing conservation payments between the U.S. and Canada informally and qualitatively acknowledge that pintails and other waterfowl species provide value to society across borders, and that areas receiving the greatest ES values are not co-located with those having the highest conservation importance (Rubio-Cisneros et al. 2014; López-Hoffman et al. 2017a). For example, since its inception in 1934, sales of the Migratory Bird Hunting and Conservation Stamp, or "Duck Stamp" have enabled investment of $800 million U.S. dollars to protect 2.3 million hectares of habitat in the U.S. (USFWS 2017b). A similar duck stamp in Canada generates revenue for habitat conservation in that country. In recent years, with the passage of the North American Wetlands Conservation Act, collaborations and mechanisms for sharing monies among the U.S., Canada, and Mexico have evolved through partnerships such as the North American Waterfowl Management Plan and the North American Bird Conservation Initiative. Since 1986, wildlife agencies from 30 U.S. states have annually contributed funding for waterfowl habitat conservation in the Canadian Prairie Pothole region. Some of these funds are derived from special fees for waterfowl hunters, for example, through a state duck stamp program (Association of Fish and Wildlife Agencies 2015). To our knowledge, this was the first example of international conservation payments by government entities (in this case, individual states) on behalf of domestic ES beneficiaries of a migratory species.

As an example of a nongovernmental organization heavily involved with trilateral waterfowl habitat conservation, Ducks Unlimited (DU) has affiliates in the U.S., Canada, and Mexico dedicated to waterfowl and wetland conservation. Since its inception in 1937, DU has supported transboundary conservation funding (Hatvany 2017), working with partners to conserve 5.6 million hectares of habitat throughout North America (Ducks Unlimited 2017). Given this history of international cooperation on North American waterfowl conservation, quantitative information about pintail-driven ES flows between regions can help to inform more rigorous decisions on pintail conservation, both within and between nations.

In this paper, we demonstrate the spatial subsidies approach for the northern pintail duck in North America. To operationalize the approach, we combine ecological and economic data on pintail habitat dependence and ES provision for five regions across their migratory range, and use this information to calculate ES flows between regions. We discuss the approach's potential to inform conservation payments for North American waterfowl, along with future research avenues to refine our estimates.

MATERIALS AND METHODS

Spatial subsidies approach

The spatial subsidy approach (Semmens et al. 2011; López-Hoffman et al. 2013) was designed to quantify the *net* flow of ES benefits between regions encompassing the full range of a migratory species. It is based on the concept that migratory species depend on all parts of their range, so benefits received in any individual region are sourced from the entire range (see "*Defining regions for northern pintail spatial subsidies*" below for details about the range we considered). Effectively, ES beneficiaries in all regions receive benefits from habitat in all regions, while habitat in a given region provides benefits to those in all other regions within their range.

The calculation depends on the estimation of two key parameters: V_i, the total annual value of ESs provided by the species at location i (which sums to $V.$ across the species' entire range), and D_i, the proportional dependence of a species or subpopulation on location i, defined as the extent to which a location contributes to the migratory population's overall viability. Gross benefit flows are composed of outgoing migration support provided by location i to other locations (M_{Oi}), incoming migration support received at location i from other locations (M_{Ii}), and locally received migration support from location i to location i (M_{Li}), defined as

$$M_{Oi} = (V. - V_i)D_i,$$

$$M_{Ii} = V_i(1 - D_i),$$

$$M_{Li} = V_i * D_i.$$

Values for D_i must satisfy two requirements across all m locations utilized by a species:

$$0 \le D_i \le 1,$$

$$\sum_{i=1}^{m} D_i = 1.$$

These requirements reflect the fact that migratory species, like all species, are 100% dependent on their environment. In the next section, we describe how the D and V parameters were estimated throughout the full North American migratory range of the pintail.

Gross flows into and out of each part of the migratory range (i.e., migration support) can be subtracted to calculate the net benefit flow to/from each location, which we define as the spatial subsidy, Y_i:

$$Y_i = M_{Oi} - M_{Ii} = V.\, D_i - V_i.$$

This is a measure of the difference between the benefits received and provided by any given location. Positive values indicate that the location is, on net, subsidizing other areas while negative values indicate that the location is being subsidized by other areas. When applied to all m locations throughout a species' range, this equation satisfies the requirement that all subsidies sum to zero:

$$\sum_{i=1}^{m} Y_i = 0.$$

Any number of regions can be used in this analysis and they can be defined in any way, so long as they encompass the migratory species' core breeding and non-breeding regions, are consistent throughout the analysis, and allow estimation of the needed D and V parameters.

In addition to net ES flows into or out of each region (Y_i), benefits are also received and supported locally (Semmens et al. in press). Net local flow (Y_{Li}) is the net benefit flow from ecosystems to people *within* each region, supported by the habitat within the region. When a region is providing a subsidy (i.e., $Y_i \ge 0$), the habitat in the region both supports all locally received benefits (V_i) and exports benefits to other regions. For receiving regions, the net local flow is equal to the locally received benefits less the total subsidy received by the region:

$$\left.\begin{array}{ll} Y_{Li} = V_i + Y_i & \text{if } Y_i < 0 \\ Y_{Li} = V_i & \text{if } Y_i \ge 0 \end{array}\right\}.$$

The sum of Y_i values greater than zero (i.e., the net ES flow from providing to receiving regions) plus all Y_{Li} values equals the total value provided by a species ($V.$), completing the view of how all ESs from a migratory species flow to beneficiaries throughout their range:

$$\sum_{i=1}^{m} \alpha_i Y_i + \sum_{i=1}^{m} Y_{Li} = V.,$$

where $\alpha_i = 1$ if $Y_i > 0$ and $p_i = 0$ if $Y_i \le 0$, so that the first summation is over regions providing a subsidy.

To quantify gross ES flows between any two regions, we rely on two important assumptions: (1) all regions both provide and receive migration support to/from all other regions within the species' range, and (2) the amount of migration support provided or received is a function of the magnitude of the flow and relative proportional dependence (for gross incoming migration support) or relative ES value (for gross outgoing migration support). Gross outgoing migration support from region a (M_{Oa}) can thus be distributed among the remaining regions according to their relative ES values. Similarly, the sources of gross incoming migration support (M_{Ia}) can be attributed to each of the remaining regions according to their relative proportional dependence values. For example, gross outgoing and incoming migrations support flows between regions a and b can be calculated as

$$M_{O\overrightarrow{ab}} = M_{Oa}\frac{V_b}{(V. - V_a)};\; M_{I\overleftarrow{ab}} = M_{Ia}\frac{D_b}{(1 - D_a)}$$

which simplifies to

$$M_{O\overrightarrow{ab}} = D_a V_b;\; M_{I\overleftarrow{ab}} = V_a D_b.$$

Net flows only occur from regions providing subsidies (i.e., $Y_i > 0$) to those receiving subsidies (i.e., $Y_i < 0$). We assume that each region providing a subsidy will do so in proportion to the magnitude of the subsidies in the receiving regions. For example, the net flow between region a ($Y_a > 0$) and b ($Y_b < 0$) can be calculated as

$$Y_{\overrightarrow{ab}} = Y_a \frac{Y_b}{\sum_{i=1}^{m} \beta_i Y_i},$$

where $\beta_i = 1$ if $Y_i < 0$ and $r_i = 0$ if $Y_i \geq 0$ so that the summation is only over regions receiving subsidies.

Defining regions for northern pintail spatial subsidies

The spatial subsidies method requires consistent definition of migratory regions for which proportional dependence and ES values, D and V, are calculated. The geographic range of pintails in North America is concentrated primarily in the western half of the U.S. and Canada, and the western and central portions of Mexico (Bellrose 1980). This range includes three primary breeding regions (Alaska, portions of the Yukon and the Northwest Territories and Nunavut in Canada, and the Prairie Pothole Region of the U.S. and Canada) and two primary wintering regions (the West Coast of the U.S. and the Texas Panhandle and Gulf Coast areas of Texas and Louisiana, Fig. 1). We used these five areas to assign the U.S. states and Canadian provinces and territories to the three breeding and two wintering regions (Mattsson et al. 2012, 2018). Pintail individuals using habitat outside these core regions do mix with those in the core regions during parts of the annual cycle (e.g., some birds wintering in Mexico breed in Prairie Pothole region, and some Japanese birds breed in Alaska). Including these outer-range populations could have a minor effect on the estimates, but would likely not change broad patterns in Y_i. We thus excluded from our analysis highly intermittent and/or low-concentration pintail use regions (e.g., stopover habitat in Nebraska, eastern

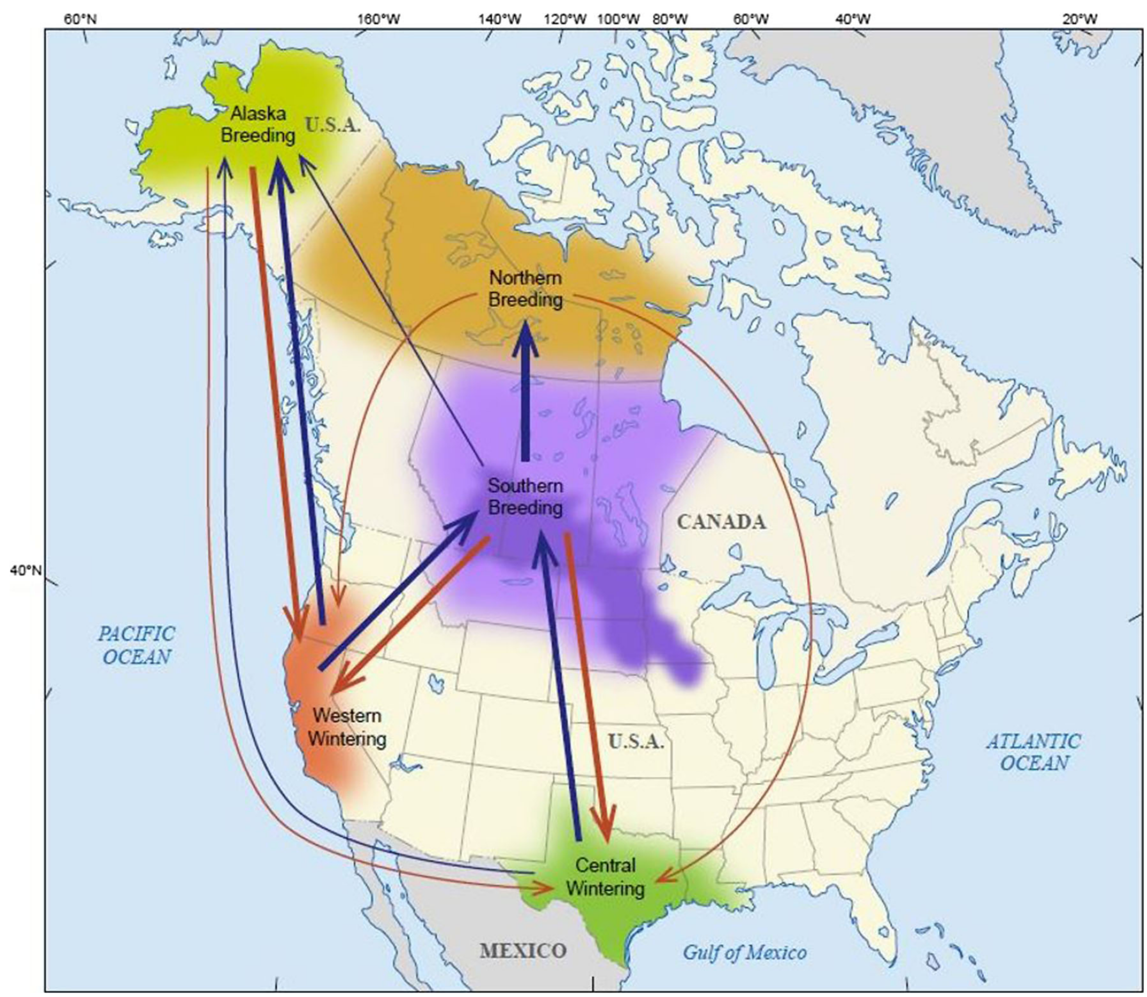

Fig. 1 Core breeding and wintering regions used by northern pintails in North America. Economic data from shaded geographies (states, provinces, and territories) were used for the analysis. The Prairie Pothole Region is shown in dark purple, and includes parts of Minnesota and Iowa that receive little use by pintails; we thus exclude these states from our analysis. Blue arrows indicate migration to breeding regions, and red arrows indicate migration to wintering regions. The arrows' thickness indicates the relative number of pintails migrating between regions

Prairie Potholes of Iowa and Minnesota and eastern North America, Mexico).

Ecosystem services from northern pintails (*V*)

We used existing studies to estimate monetary values associated with ESs provided by pintails, including economic values for recreational hunting and birdwatching (Mattsson et al. 2018) and subsistence harvest of northern pintail ducks by American Indian and First Nations people (Goldstein et al. 2014). We excluded non-use values and ESs that result from pintail habitat conservation (e.g., carbon storage or water quality, Gascoigne et al. 2011), which are not directly tied to pintails or their migration. All values are expressed in 2014 U.S. dollars, with results from Goldstein et al. (2014) adjusted to 2014 dollars using the Bureau of Labor Statistics' CPI Inflation Calculator (BLS 2015). We briefly summarize the data and methods used by these studies below.

Subsistence harvest

The monetary value of pintail subsistence harvest in the Northern and Alaskan Breeding regions was estimated using the replacement cost method, with store-bought chicken as the closest widely available commercial replacement for hunted duck meat (Goldstein et al. 2014). This estimate is a lower bound that does not address the cultural importance of pintail harvesting for indigenous communities. This study followed three steps. First, mean per-capita pintail harvest rates and consumption for each geographic region were obtained from a literature review. The literature review provided the average number of subsistence hunters per population in each region, allowing per-capita values to be scaled to the entire population. There was no evidence that harvest rates had changed systematically over time, so constant harvest and consumption rates were assumed. Second, the nutritional equivalent weight of edible meat for a store-bought whole raw chicken was estimated relative to that of a whole wild duck. Third, we estimated the price of store-bought whole raw chicken, adjusted to reflect higher retail prices in Arctic settlements. Multiplying the harvest-equivalent weight of chicken by the estimated cost of chicken yielded replacement cost values for each region.

Pintail viewing

Pintail viewing and hunting values in each region were derived from Mattsson et al. (2018), who estimated both expenditures and associated consumer surplus for hunting and viewing activities. Consumer surplus is the added economic value that hunters or birdwatchers obtain when their expenditures (e.g., on travel, equipment, ammunition, duck stamps) are less than the value of what they would be willing to pay for the experience.

Pintail viewing expenditures were calculated for each region following four general steps: (1) confirm that different data sources represent a similar population of birders by comparing days spent birding; (2) calculate expenditures on viewing all bird species; (3) determine proportion of birding activity directed toward pintails; and (4) calculate expenditures for viewing pintails. Three primary data sources were used, including recent surveys of birding and wildlife viewing for the U.S. (USFWS 2011; Carver 2013) and Canadian residents (DuWors et al. 1999; Leigh et al. 2000; Environment Canada 2016) and the eBird database (eBird 2016). eBird was used to estimate the fraction of all birdwatching activity in which pintails were observed in each geographic unit (i.e., state, province, or territory) from 2006 to 2015, which was used to apportion birdwatching expenditures to pintails (Mattsson et al. 2018).

Consumer surplus for pintail viewing was estimated using the Benefit Transfer Toolkit, which includes economic valuation studies for wildlife-based recreation in the U.S. between 1983 and 2006 (Loomis et al. 2008). The "Wildlife Viewing Value Table" (Colorado State University 2018) provided a database of values at the state level, which were averaged to yield state-specific consumer surplus estimates for wildlife viewing per viewer day. Values per viewer day were combined with estimates of the number of pintail viewing days in each geographic unit (described above). Canadian provinces were assigned consumer surplus per viewing day equivalent to the adjacent U.S. state.

Pintail hunting

Pintail sport hunting expenditures were calculated separately for the U.S. and Canada, owing to differences in the underlying data sources and the need to estimate pintail harvest, hunters, and expenditures equivalently. Key data sources included national harvest surveys (Raftovich and Wilkins 2013; Gendron and Smith 2016) and hunting economics surveys (Saskatchewan Environment 2006; USFWS 2008), combined with additional national surveys in Canada for outdoor recreation (DuWors et al. 1999; Leigh et al. 2000; Environment Canada 2016) and household economics (Statistics Canada 2014). To estimate consumer surplus associated with pintail hunting, we used the Benefit Transfer Toolkit's (Loomis et al. 2008) "Hunting Value Table" (Colorado State University 2018) to estimate consumer surplus per hunter day in each geographic unit.

Proportional dependence for northern pintails (*D*)

To inform spatial subsidy calculations, proportional dependence models must be able to generate information quantifying the relative contribution of different sites in terms of overall population growth or viability (Semmens et al. 2011). The modeling approach used represents a multi-year, multi-agency international effort to inform integrated pintail harvest and habitat management across North America. It is a relatively sophisticated model using metapopulation approaches familiar to ecologists and used for migratory species management with increasing frequency.

To estimate proportional dependence of the North American pintail population in each of the five core regions, we utilized an existing metapopulation model designed to inform integrated harvest and habitat management from regional to continental scales (Mattsson et al. 2012). This model represents pintail demographics and movements among five regions that match those used for this analysis (Fig. 1). We used the model to calculate C_r, a metric developed to estimate the per-capita contribution for each region over each season (i.e., wintering and breeding) within a migratory network (Wiederholt et al. in press; Erickson et al. 2018; Appendix S1). The per-capita contribution of a region is defined as the number of individuals in the entire population after one annual cycle that are generated from each individual that occupied the region, pathway, or transition at some stage of the year. If the contribution is > 1, the habitat contributes more individuals to the population than it loses through mortality and vice versa.

The contribution metric tracks migratory cohorts following a specific migratory route. For instance, after the breeding season, individuals migrate from a breeding habitat to a particular wintering habitat and, after the wintering season, migrate from a wintering habitat to a specific breeding habitat. In each migratory cohort, we estimate both the probability of adult survival and the per-capita recruitment of juveniles, for both males and females, by accounting for seasonal probabilities of survival, reproduction, migration survival, and the probability of migration between habitats. For each region, the sum of annual adult survival and number of young produced per female yields its per-capita contribution. To estimate C_r for each region, we assumed the annual calendar for a given habitat starts at the date of its initial occupancy. For breeding habitats, the anniversary date is the start of the breeding season after the completion of spring migration, for wintering habitats, the anniversary is the start of winter when individuals have completed their fall migration, and for stopover habitats, the anniversary is when the habitat is initially occupied during the spring migration.

We used the following calculation to estimate proportional dependence for each region i having one of $k = 3$ anniversary dates, t (i.e., start of breeding, winter, or spring migration stopover):

$$d_{t,i} = \frac{C^{♀}_{t,i} p^{♀}_{t,i} + C^{♂}_{t,i} p^{♂}_{t,i}}{\sum_{j=1}^{m} \left(C^{♀}_{t,j} p^{♀}_{t,j} + C^{♂}_{t,j} p^{♂}_{t,j} \right)}$$

Here, weighted contributions are calculated by the multiplying per-capita contribution for each region i and anniversary date t by $p_{t,i}$, the proportion of individuals in region I at the start of the anniversary date. Weighted contributions are computed separately for males (♂) and females (♀). The sum of these region-specific contributions is then divided by the weighted contributions across all m regions occupied at the start of the anniversary date.

To estimate the final proportional dependence for comparing all regions (i.e., breeding and wintering regions), we divided each season-specific proportional dependence value by the sum of season-specific values across all regions:

$$D_i = \frac{1}{k} \sum_{t=1}^{k} d_{t,i}.$$

Using this formulation, D_i values sum to one across all regions.

Table 1 Ecosystem service values and proportional dependence for northern pintail ducks throughout their range

Region	*V* subsistence	*V* viewing	*V* hunting	*V* total
Western Wintering	$0	$26 233 400	$20 182 400	$46 415 800
Central Wintering	$0	$9 775 200	$7 439 800	$17 215 000
Southern Breeding	$0	$6 020 400	$2 477 400	$8 497 800
Alaska Breeding	$45 200	$24 628 000	$933 300	$25 606 500
Northern Breeding	$22 900	$3 800 200	$47 100	$3 870 200
Total	$68 100	$70 457 200	$31 080 000	$101 605 300

Monetary values are in 2014 USD per year, rounded to the nearest $100

RESULTS

Ecosystem service values

Subsistence harvest values totaled $68 000—an approximate annual harvest of 15 000 birds that benefits small Arctic communities of about 50 000 people (Table 1; Goldstein et al. 2014). While this value is small relative to recreational hunting values, the subsistence harvest is 2% of the species' range-wide sport harvest, yet is currently unrecognized in harvest policy deliberations (Goldstein et al. 2014).

Viewing accounted for almost 70% of pintail ES value, totaling $70.5 million per year, with the largest values found in the Western Wintering and Alaska Breeding regions (Table 1). About 40% of this value is attributed to consumer surplus, with the rest as expenditures (Mattsson et al. 2018).

Pintail hunting was valued at $31.1 million per year, with the largest values in the two wintering regions, most notably the Western Wintering region (Table 1). About 42% of this value is attributed to consumer surplus; the rest is expenditures (Mattsson et al. 2018).

Proportional dependence

Our D_i estimates revealed the Southern Breeding region to be the most ecologically important, with more than four times the impact on overall pintail population dynamics than the least important region—the Northern Breeding region (Table 1).

Spatial subsidies

Total annual ESs (V_i) were greatest in the Western Wintering region, where many people engage in both viewing and hunting, and in Alaska, where bird viewing is both frequent and expensive (Table 2). The net pintail ES flow was greatest from the Southern Breeding region, which subsidized benefits in the receiving regions by more than $24 million annually (Table 2; Fig. 2). The Western Wintering region was the biggest receiver of ESs from provider regions; over half of the benefits received in the Western Wintering region were subsidized (i.e., flow from other regions). Locally supported benefits (M_{Li}) were greatest in the Alaska Breeding region and were dominated by expenditures and consumer surplus for wildlife viewing ($\sim$ 96%). As described in the methods and illustrated in Fig. 2, locally supported benefits M_{Li} (circular arrows) plus all subsidies (directional arrows) sum to the total value of ESs, $V_\cdot$.

DISCUSSION

We quantified ES flows generated by the northern pintail across its core North American migratory range. By far, the largest interregional subsidy is from the Southern Breeding to the Western Wintering region, with flows from the Southern Breeding to Southern Wintering and Northern Breeding to Western Wintering also in the multimillion-dollar range annually. This reflects past recognition of the Southern Breeding (or Prairie Pothole) region as "the duck

Table 2 Ecosystem service flows and spatial subsidies for the northern pintail duck migration in North America

Region	Proportional dependence (D_i)	Value of ecosystem services (V_i)	Gross outgoing migration support (M_{Oi})	Gross incoming migration support (M_{Ii})	Gross local migration support (M_{Li})	Net local flow (Y_{Li})	Net subsidy (Y_i)
Southern breeding	0.3225	$8 497 800	$30 027 200	$5 757 300	$2 740 600	$8 497 800	$24 269 900
Alaska Breeding	0.2654	$25 606 500	$20 170 100	$18 810 500	$6 796 000	$25 606 500	$1 359 500
Northern Breeding	0.0788	$3 870 200	$7 701 500	$3 565 200	$305 000	$3 870 200	$4 136 300
Western Wintering	0.2178	$46 415 800	$12 020 300	$36 306 500	$10 109 400	$22 129 600	($24 286 200)
Central Wintering	0.1155	$17 215 000	$9 747 100	$15 226 700	$1 988 300	$11 735 400	($5 479 600)
Total	1.0000	$101 605 300	$79 666 200	$79 666 200	$21 939 300	$71 839 500	$0

Locally supported benefits, M_{Li}, and the total (positive) outgoing subsidy, Y_i, sum to the total value of ecosystem services, V_i. All values are in 2014 USD per year, rounded to the nearest $100

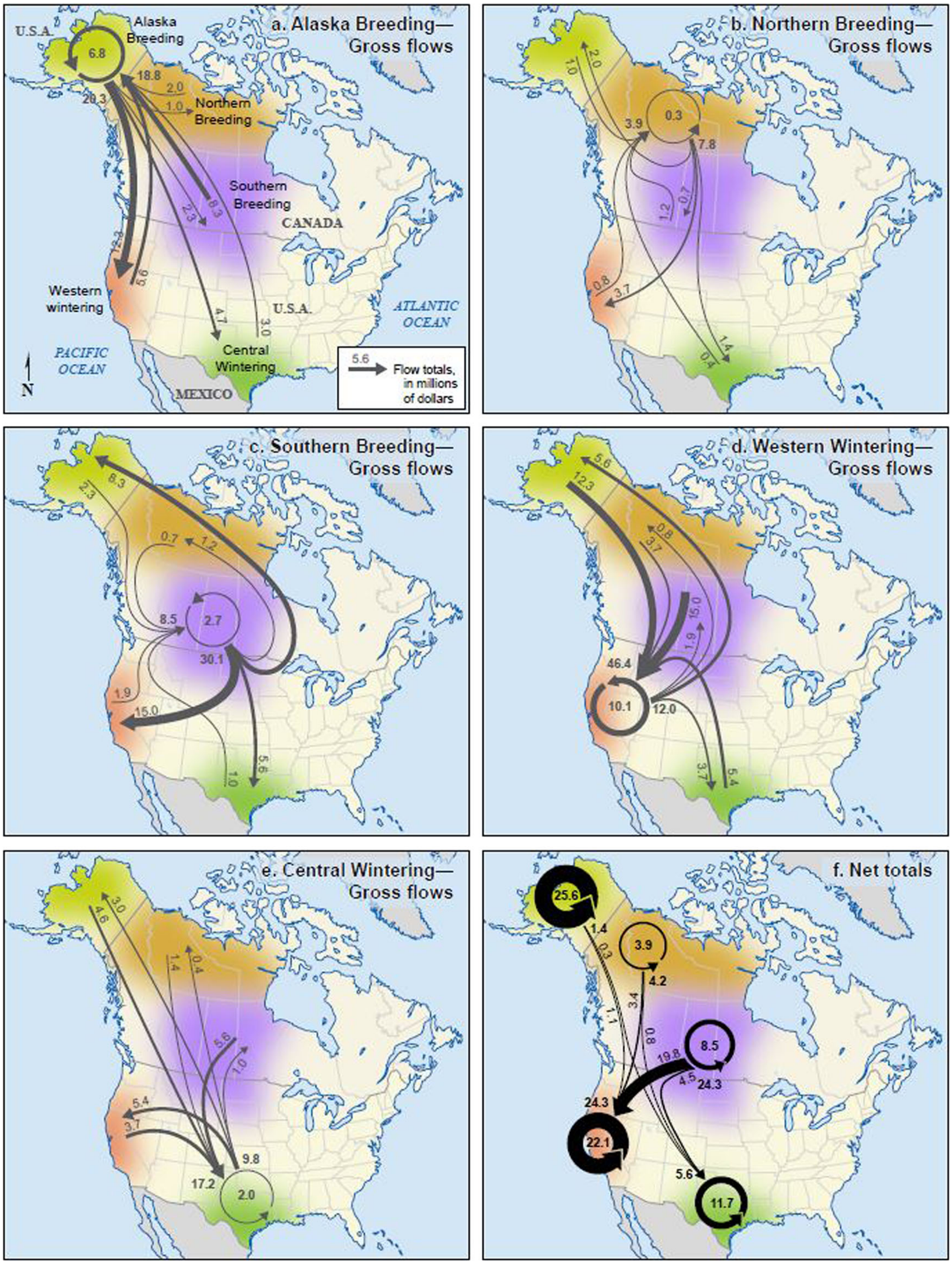

Fig. 2 Gross ES flows to, from, and within each of the five regions individually (**a**–**e**) and net ES flow (**f**) provided by pintails throughout North America. Arrows, and their width, represent the magnitude of ES flows in $ per year. Arced arrows represent ES flows from providing to receiving regions, and circular arrows indicate intraregional flows. In Fig. 2a–e, gross intraregional flows are equivalent to the local migration support M_{Li} value for each region; gross interregional flows are derived from outgoing (M_{Oi}) and incoming (M_{Ii}) migration support columns in Table 2. In Fig. 2f, intraregional flows are derived from the net local flow (Y_{Li}) column in Table 2; each interregional net flow ($Y_{\overrightarrow{ab}}$) is the proportion of the receiving-region subsidy (Y_b) relative to the sum of negative subsidies across all regions ($\sum_{i=1}^{m} Y_i < 0$), weighted by the providing-region subsidy (Y_a). The sum of all net ES flows is equal to V—the total annual value provided by pintails

factory of North America," because it is the most productive region for pintails (Mattsson et al. 2012) and other waterfowl species (Bellrose 1979; Batt et al. 1989).

Consumer surplus, the additional amount of money a hunter or birder would be willing to spend beyond his/her actual expenditures, reflects additional monies that could be available to pay a spatial subsidy. This is as opposed to recreation expenditures, the most commonly used economic indicator for wildlife-based recreation (USFWS 2008), which represent money already spent and no longer available to contribute to a conservation payment system. Consumer surplus related to hunting and wildlife viewing represents 40.7% of the economic value of pintails described in this system (Mattsson et al. 2018). While we recognize that it is unrealistic to expect that all consumer surplus could be captured for use in conservation payments (Rubio-Cisneros et al. 2014), it shows the scope of untapped potential for additional conservation dollars. The difficulty of converting consumer surplus into actual funding is likely to be a common challenge in operationalizing the spatial subsidies framework for conservation finance. For instance, we have also shown high levels of consumer surplus for monarch butterflies (*Danaus plexippus*) (Semmens et al. in press), yet mechanisms to translate that surplus into conservation activity are not always obvious.

Beyond estimating the magnitude of consumer surplus that could fuel additional conservation funding, the subsidy calculation demonstrates which regions could be targeted to receive funding (i.e., regions with positive net subsidies)—information that could improve efficiency and fairness in international conservation payments. Conservation payment schemes under consideration would ideally consider topics relevant to political ecology (Robbins 2011)—winners, losers, hidden costs of environmental decision making, and implications for economic equity. While political ecology recognizes that not all people experience value in the same way, leading to inherent challenges in monetizing nature, expressing pintail ES values in dollar terms provides a consistent means of adding up different types of values across a migratory species' range. While subsidy estimates can guide the direction of conservation payment schemes, as a first estimate of a single North American waterfowl species' subsidies, these estimates should not necessarily be interpreted as an absolute amount "owed to" or "owed by" any given region.

It is instructive to compare one of our subsidy calculations to interregional conservation payment data. For example, the Prairie Pothole region provides a subsidy of \$19.8 million/year to the Western Wintering region. In 2016, California sent Alberta an estimated \$102 000 for waterfowl habitat conservation (Mattsson et al. unpublished data). These funds were raised through sales of duck stamps to hunters and waterfowl enthusiasts and additional appropriations. In the same year, revenues from mandatory purchases of federal duck stamps by California residents contributed \$503 000 to U.S. portions of the Prairie Pothole region (Mattsson et al. unpublished data). Both of these payment vehicles recognize the importance of the Prairie Pothole region for waterfowl conservation (California Department of Fish and Wildlife 2017; Prairie Pothole Joint Venture 2017). This preliminary analysis raises several key conclusions. First, total actual payments from California in 2016 (\$605 000) were about 1/30 of the subsidy provided by the Prairie Pothole region for pintails alone (i.e., not considering other valued waterfowl species). Second, hunters are currently the only waterfowl user group required to contribute funding for interregional payments, with wildlife viewers providing funds only through voluntary duck stamp purchases. Third, while the subsidy for pintails is much greater than the amount of existing payments, funding and payment vehicles do exist for interregional conservation payments, offering the opportunity for subsidies information to better inform allocation of funding for waterfowl habitat conservation.

Our work sets the stage for additional research to more accurately quantify pintail spatial subsidies and provide relevant data for cross-border pintail conservation. First, the motivation for North American waterfowl conservation payments extends beyond just the pintail, and includes other waterfowl species migrating between the U.S., Canada, and Mexico. Our single-species analysis thus underestimates the ESs provided by North American migratory waterfowl that co-occur with the pintail, making it a partial and undoubtedly underestimated view of total interregional subsidy flows for the entire cohort of migratory waterfowl. If ES values and proportional dependence were estimated for additional migratory waterfowl species, North American waterfowl subsidies could be aggregated across multiple species to consider their combined effects. Such an analysis for a suite of waterfowl species with similar ranges and life histories would provide a more compatible metric that the North American waterfowl management community could use to inform international conservation payments schemes. Further, the grassland and shallow wetland habitat favored by pintails supports many other species, as well as ESs unrelated to migratory species (Gascoigne et al. 2011), so our analysis indicates just a portion of the economic value that these habitats provide to society.

Next, our estimates of consumer surplus, which are central to understanding beneficiaries' willingness to pay for conservation beyond current expenditures, rely on secondary data (Loomis et al. 2008). Replacing secondary data with primary data from surveys of the general public or key stakeholders (i.e., recreational waterfowl hunters and viewers) would strengthen our confidence in the accuracy of consumer surplus estimates.

Finer-scale modeling may be necessary to support more precise targeting of conservation funding, such as quantifying subsidies from the U.S. and Canadian portions of the Prairie Pothole region or to distinguish subsidies provided by wintering habitat in Mexico. Future work could also explore the model's sensitivity to inclusion of eastern U.S. and Canadian pintail populations in both proportional dependence calculations (and the effects on metapopulation dynamics of non-core range populations) and by quantifying the value of pintails to eastern hunters and wildlife viewers.

As suggested above by our preliminary analysis of conservation payments from California to the Prairie Pothole region, it would be beneficial to fully quantify current interregional and international conservation payments that support conservation of pintail habitat. Accurate interregional conservation payment estimates would help us understand how payments "offset" the spatial subsidy by providing revenue *back* to the regions providing the subsidy (i.e., in the reverse direction of the subsidy flow arrows, Fig. 2). Information about changes in payments over time can be used to inform scenarios regarding funding availability (Vrtiska et al. 2013) and resource allocation for habitat conservation in the critical Prairie Pothole Region. These scenarios can then be linked to existing demographic and population models to inform waterfowl management decisions.

Future analyses could also explore the effects of uncertainty on spatial subsidy calculations and changes in V and D over time, as this analysis did not account for uncertainty in either parameter. Uncertainty associated with both parameters could affect the relative flows of benefits between regions and therefore the estimated spatial subsidies. Some of this uncertainty is attributable to the stochastic nature of wildlife resources, but other aspects are uncertain because of the difficulties in properly observing elements contributing to D and V. Goldstein et al. (2014) and Mattsson et al. (2012, 2018) discuss major sources of uncertainty associated with their calculations. Future work could apply a range of values as informed by these and similar studies when calculating both V and D, generating confidence intervals and testing the system's sensitivity to changes in input parameters.

This study and other spatial subsidies studies (López-Hoffman et al. 2017b; Semmens et al. in press) have identified challenges in obtaining rigorous, range-wide estimates of V and D at appropriate scales. Relatively few studies comprehensively assess migratory species at the population level, or systematically address their functional interactions with people. As a result, data and modeling limitations may constrain the application of the spatial subsidies approach over the short term to the best-studied and monitored migratory species, which are often the most charismatic, imperiled, and/or economically important species. In the long term, the approach demands investment in, and coordination of, data collection, monitoring, and data management that can provide the information to support conservation finance for migratory species more broadly. Surveys that apply consistent methods to collect economic data across multiple countries would improve the accuracy of spatial subsidy estimates (Mattsson et al. 2018). The use of global databases and citizen science efforts like eBird (eBird 2016) and advanced sensor technology capable of monitoring animal abundance, movements, distributions, and demographics (Pimm et al. 2015; Christie et al. 2016) also offer promising data sources to improve the extent, replicability, and accuracy of spatial subsidies research.

CONCLUSION

Animal migration is found on every continent, across all major animal groups, and features prominently in cultural traditions around the world. ES values generated in one location depend on habitat and species movement across each migratory species' range. Migration processes for species from songbirds to saiga to monarch butterflies are at risk of being lost, with attendant consequences to the species' viability (Wilcove and Wikelski 2008; Semmens et al. 2016). Understanding the flow of species-related value is essential for determining who benefits and who can fairly shoulder the responsibilities of conservation, ensuring the survival of species and their migration processes. Spatial subsidies provide a tool for understanding imbalances between benefits received in a region and its overall contribution to the species' range-wide ES value. Along with pintails, the spatial subsidies method has also been used to quantify the value of migratory networks for monarch butterflies (Semmens et al. in press) and Mexican free-tailed bats (López-Hoffman et al. 2017b) in North America. Our work with these three species has illustrated both opportunities and challenges for estimating spatial subsidies for migratory species, and we believe the concept and methods are now mature enough to apply to migratory species conservation elsewhere on the globe. The insights generated using this method can help guide policy efforts and coordination between different jurisdictions for management and can provide structure for incentive-based programs such as payments for ESs.

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