



Exploring the influences of multiscale environmental factors on the American dipper *Cinclus mexicanus*

S. Mažeika P. Sullivan and Kerri T. Vierling

S. M. P. Sullivan (sullivan.191@osu.edu) and K. T. Vierling, Dept of Fish and Wildlife Resources, Univ. of Idaho, Moscow, ID 83844-1136, USA. Present address of SMPS: School of Environment and Natural Resources, The Ohio State Univ., 2021 Coffey Rd., Columbus, OH 43210, USA.

Aquatic organisms respond to the physical environment across a range of spatial scales, but the precise nature of these relationships is often unclear. In order to forecast ecosystem responses to environmental alterations in watersheds, understanding how processes at different spatial scales affect the ecology of organisms is critical. We used the semi-aquatic American dipper *Cinclus mexicanus* to evaluate how large-scale, regional variables (e.g. climate); landscape-scale, watershed variables (e.g. land use/cover); and local, reach-level variables (e.g. stream geomorphology) influenced various descriptors of American dipper ecology, including productivity, stable nitrogen isotopes ($\delta^{15}\text{N}$), and individual condition. From 2005 to 2008, we collected data at 26 American dipper territories distributed throughout a 25 000 km² region within Idaho, USA. We then used structural equation modeling to consider potential direct and indirect relationships among scalar factors on measures of American dipper ecology. We found that complex interactions among factors at all three spatial scales influenced dipper productivity, but that $\delta^{15}\text{N}$ and individual condition were explained by characteristics at the regional and landscape scales only. In particular, model results demonstrate that precipitation was associated with notable variation in multiple dipper responses. Local factors, influencing only dipper productivity, were dominated by hydrogeomorphic characteristics. Our study underscores the simultaneous independent and synergistic roles of environmental factors across spatial scales on American dippers, and offers evidence that pathways influencing aquatic biota may not always conform to hierarchical spatial relationships in watersheds.

Watersheds are increasingly understood as unique landscape units whose characteristics have pervasive effects on stream ecosystems (Hynes 1975, Allan and Johnson 1997, Allan 2004). Conceptually, watersheds are often presented as a hierarchical suite of filters that constrain biotic and abiotic processes (Imhof et al. 1996, Poff 1997, Burcher et al. 2007). Characteristics operate across a range of spatial scales ranging from basin- to microhabitat-levels (Frissell et al. 1986, Wright and Li 2002), and characteristics at one scale may profoundly affect those at another (Allan et al. 1997, Poff 1997). For instance, factors at the regional scale including climate (Guegan et al. 1998, Sipkay et al. 2009, Camilleri et al. 2010) and geology (Brown 1995, Hubbel 2001, Townsend et al. 2003) exert fundamental influences on watershed processes and aquatic biota.

Superimposed on complex watershed ecosystems are past and present land-use patterns, which represent one of the primary threats to stream ecosystems (Harding et al. 1998, Foster et al. 2003, Allan 2004). Although landscapes in the American West are thought to be comparatively less affected by human activities than many other regions, the effects of agriculture, increasing human populations (including rapid rates of urban and exurban development), and secondary road networks are serious concerns (Leu et al. 2008). While

landscape changes are more prevalent in valleys and other topographically-accessible areas, timber, grazing land, and other high-commodity natural resources can lead to high-intensity human activity in mountainous regions (Leu et al. 2008). Headwater streams draining these areas provide critical source waters, nutrients, and energy inputs for large river systems and may represent areas of low ecological resiliency, making them highly susceptible to landscape alterations.

Although it has become clear that the influence of land use on stream ecosystems is scale-dependent (Allan et al. 1997, Townsend et al. 2003), research relating to the influences of terrestrial ecosystems on stream characteristics at different scales has yielded mixed results (Allan 2004). For example, some investigators have found that watershed-scale properties better predict in-stream conditions (Roth et al. 1996, Johnson et al. 1997). Others have found riparian and local, reach-level factors to be most influential (Richards et al. 1997, Sponseller et al. 2001). Furthermore, identifying cause-response relationships can be challenging when evaluating multiple factors that operate simultaneously across spatial scales (Allen and Hoekstra 1992, Lowe et al. 2006).

As our understanding of terrestrial-aquatic linkages continues to grow (Nakano and Murakami 2001, Fausch et al. 2002, Baxter et al. 2005), birds that forage on stream biota

are increasingly recognized as critical components of stream-riparian ecosystems (Steinmetz et al. 2003). Indeed, many species of aquatic-obligate birds occupy high trophic levels and reflect functional impairments at lower trophic levels (Steinmetz et al. 2003, Sullivan et al. 2006a). Birds and other mobile organisms redistribute stream-derived nutrients both longitudinally (e.g. upstream and downstream) and laterally (e.g. into riparian and upland zones; Ben-David et al. 1998, Baxter et al. 2005). Birds that use multiple habitat components of riverine landscapes might be expected to be integrators of the linkages between the stream and the watershed (Sullivan et al. 2007, Vaughan et al. 2007).

The American dipper *Cinclus mexicanus* may provide unique insight into understanding how factors at different spatial scales affect species-ecosystem relationships in watersheds. The American dipper (hereafter 'dipper') is found year-round in mountainous watersheds across much of the western United States. Dippers are intimately connected to their stream habitats, foraging on aquatic macroinvertebrate larvae and small fish (Ealey 1977, Ormerod 1985). Structural characteristics of stream channels (e.g. boulders, fallen trees, overhanging ledges and crevices) are critical for nesting sites, refuge areas, and perches for foraging and roosting (Kingery 1996). Clear, unpolluted water is essential for in-stream habitat and food requirements (Ormerod 1985, Ormerod and Tyler 1987).

The substantial supporting evidence for the use of *Cinclus* species as environmental monitors for both in-stream and riparian conditions suggests that dippers are an appropriate choice in representing the effects of physical processes as mediated through biological processes, such as the aquatic invertebrates that dippers consume (Ormerod et al. 1991, Logie et al. 1996, Sorace et al. 2002, Morrissey et al. 2004). Moreover, during the reproductive season, breeding pairs and their offspring are directly reliant on the resources of a constrained length of stream as determined by territory size (Ealey 1977). During this period, their potential to reflect ecosystem condition for a defined spatial extent is heightened. Whereas the distribution of dippers is restricted to the narrow spatial extent of the stream corridor, processes operating both within and beyond this extent may influence their distribution, demographics, and body condition.

In this paper, we consider the relative influences of physical environmental factors on dipper ecology at the regional, landscape, and local scales. We collected abiotic and biotic data at dipper reproductive territories in streams in a 25 000-km² region of Idaho, USA, where the varied geographies, topographies, and local climates provided a wide range of environmental conditions. We posed the following guiding questions: 1) do dippers respond more strongly to environmental characteristics at the local, landscape, or regional scales? 2) Do multiscale environmental characteristics influence descriptors of dipper ecology [e.g. reproductive success, stable nitrogen isotopes ($\delta^{15}\text{N}$), body condition] in different ways? We subsequently use these data to consider hierarchical spatial relationships in watersheds.

Methods

From 2005 to 2008, we conducted research at 26 stream reaches distributed across 20 different watersheds in Idaho,

USA (Fig. 1). We first used the known literature to focus our search efforts on watersheds likely to support dippers. From field reconnaissance of these watersheds conducted in 2005 and 2006, we primarily selected study reaches based on the presence of breeding dipper pairs. However, we also strove to select streams that represented dipper-bearing drainages of the region at large. Each study reach represented the breeding territory of a dipper pair, which typically ranged from 0.2 to 1.0 km (Sullivan unpubl.). We collected a suite of data related to stream and riparian habitat (and by proxy, aquatic macroinvertebrates), dipper reproductive measures, nitrogen stable isotopes in blood, and adult condition at a subset of the 26 reaches each year (2006–2008). During the reproductive season, we monitored breeding pairs at least twice weekly (on average) from nest initiation to fledging of the final brood. Additionally, for each reach, we gathered and/or generated data relating to landscape and regional factors.

American dippers

We located nests either by searching likely rock overhangs, bridges, boulders, and other prime nesting locations or by following birds while they were constructing nests, incubating, or feeding nestlings. We identified dates of clutch initiation, incubation, and hatching to within 1–2 d. If we did not find nests at the nest initiation stage, we back-calculated using estimates of 1 egg laid per day, a 16 d incubation period, and a 25 d nestling period (Price and Bock 1983, Kingery 1996, Gillis et al. 2008). We were successful in accessing all nests, using a ladder or rock-climbing techniques where necessary. We recorded clutch size, number fledged, and fledgling weights (g) based on daily visits to the nest once the nestlings were 23 d old.

We banded all nestlings in the nest with US Fish and Wildlife Service (USFWS) aluminum bands and weighed them 3–4 times during the nestling period. We used 6-m and 12-m passerine mist nets placed across the streams to capture adults. On average, we captured adults 3–4 times during the breeding season (March through August). We banded them on the first capture, and weighed (g) them on each capture to generate an average body mass, commonly used as a measure of individual condition (Hatch and Smith 2010). Using a syringe and needle, we drew approximately 0.7–0.8 ml of blood from the jugular vein (Ardia 2005) to use for nitrogen stable isotope analysis. We immediately stored blood in centrifuge tubes and 70% ethanol (Herrera et al. 2005). All sample collections were performed in compliance with Animal Care and Use Committee protocols; a valid Idaho Wildlife Collecting/Banding Permit; and a US Dept of the Interior (USDI), US Geological Survey (USGS) Federal Banding Permit. Handling of birds caused no observed mortality, no observed failure to hatch, and no nest abandonment. To account for potential variability in basal stable nitrogen isotope signatures among study reaches, at a subset of eight reaches (representing a range of watershed characteristics), we also collected stream periphyton from cobbles along the longitudinal length of the reach using a nylon brush.

Stream-riparian habitat surveys

At each dipper territory, we collected both stream and riparian habitat data. Given that reaches had fairly uniform riparian

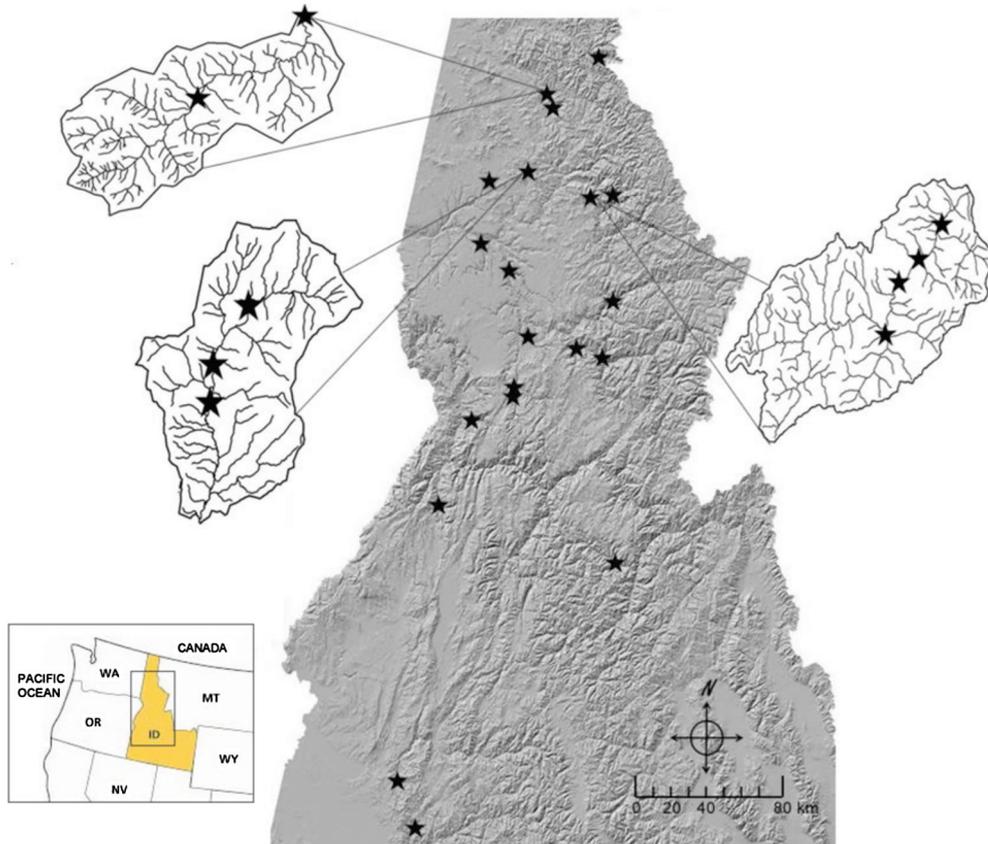


Figure 1. Map of American dipper *Cinclus mexicanus* study reaches ($n = 26$) used in this study and their distribution across Idaho, USA. For watersheds with multiple study reaches, drainages are enlarged (as call-outs) and show the distribution of study reaches within the watersheds.

zones, we conducted assessments of canopy coverage (%) and riparian width (m) and completed a proper functioning condition (PFC) assessment (Barrett et al. 1998) along 250 m centered around the nest. We estimated the percentage of canopy cover by walking the reach, using a spherical densiometer to estimate the degree of canopy extending over the stream at three representative locations. To measure the width of the riparian zone, we used a measuring tape to record the distance along three equidistantly spaced transects on each side of the stream, running perpendicular to the stream channel to the farthest extent of the riparian zone as determined by distinct changes in vegetation (Jackson and Sullivan 2009). The PFC is used to evaluate the ecological status and potential of a riparian area to dissipate stream energy associated with high flows. Each of seventeen conditions in the PFC representing vegetation, landform/soils, and hydrology are checked as yes, no, or N/A based on field observations. Typically, these responses guide selection of a functional rating of the riparian zone. To use the PFC in a more quantitative manner, we scored each riparian zone by calculating the percentage of 'yes' responses. Those riparian zones with the greatest percentage of 'yes' answers represented riparian areas in highest condition.

We developed a hybrid assessment of in-stream habitat quality based on both the Idaho small stream ecological assessment framework (Grafe 2002) and the Vermont rapid habitat assessment (RHA) protocols (VTDEC 2003). Essentially, this hybrid, hereafter referred to as the Idaho

rapid habitat assessment (IRHA), integrated the non-biotic Idaho evaluation criteria into the Vermont assessment framework to provide a more quantitative protocol aimed at capturing simplification of habitat diversity across the entire reach (Barbour et al. 1999). We scored ten categories (for each category, 0 represents worst condition and 20, optimal condition) representing flow conditions, sedimentation, habitat structure and complexity, bank condition, and riparian vegetation and structure. When aggregated, these individual scores yield an overall habitat evaluation ranging from 0 to 200.

We conducted stream geomorphic assessments focusing on both morphological characteristics and condition. Because dipper reaches in our study were typically homogenous in respect to channel morphology (Montgomery and Buffington 1997), we conducted geomorphic assessments along a 100 m reach around the nest site. We established two lateral, representative transects (e.g. across the stream) and one longitudinal transect (e.g. bisecting the stream, running down its length). We then measured slope, bankfull width, and mean depth using a stadia rod, laser level, and measuring tape (Cianfrani et al. 2004). At each transect, we assessed percent embeddedness (degree to which fine sediment surrounded cobbles) of 15 cobbles, and calculated the mean percentage for an estimate of reach embeddedness. Following Sullivan et al. (2006b), we evaluated the geomorphic condition of each reach using rapid geomorphic assessment (RGA) protocols (VTDEC 2003). We assigned a score

from 0 (worst condition) to 20 (optimal condition) for each of four geomorphic adjustment processes: channel degradation (incision), channel aggradation, over-widened channel, and change in planform (VTDEC 2003). We summed the scores of the four categories to form the composite RGA score.

We used ArcGIS 9.2 to derive drainage area (based on 1:100 000 National Hydrography Dataset; USGS 1997) and Strahler's (1952) stream order (based on 10-m digital elevation data, INSIDE Idaho; UI 2009).

Water quality and food abundance

Because our primary goal was to assess influences of the physical environment on dippers, we did not explicitly address water quality or food abundance in this study. However, given the potential influences of water quality and food abundance on dipper feeding, reproduction, and condition, we did address these factors through pre-study site screening and preliminary data. Although stream water quality across Idaho varies greatly, water quality concerns in mountainous regions where our sites were located are largely related to erosion and sedimentation (Mahler and Van Steeter 2002, Gravelle et al. 2009), which we captured through the RGA, RHA, PFC, and measurements of embeddedness. We screened all dipper reaches to ensure that no contaminant point-sources were present either within the reach or immediately upstream.

Given the associations between stream acidity and Eurasian dipper *C. cinclus* abundance and reproductive success (Ormerod et al. 1991, Tyler and Ormerod 1992), we surveyed pH at a random selection of half our dipper streams. Twelve of the 13 territories had a pH of 7.5–8.3 (circumneutral), while only one stream had a pH of 4.4 (acidic). Findings by other investigators gave us confidence that additional variability in water chemistry among our sites would not be confounding factors in our analysis. For example, Henny et al. (2005) reported high dipper reproductive success in spite of elevated MeHg concentrations in Ephemeroptera, Plecoptera, and Trichoptera (EPT) larvae, dipper eggs, and nestling feathers in tributaries of the Willamette River, Oregon.

The high correlation between measures of aquatic macroinvertebrates in the EPT orders and the in-stream habitat assessments (EPT density and RHA score: $r = 0.686$, $p = 0.0048$; %EPT of total macroinvertebrate community and RHA score: $r = 0.572$, $p = 0.0258$) at a subset of 15 of the dipper territories (Sullivan unpubl.) enabled us to use the RHA as a coarse surrogate for food abundance and quality. EPT larvae/nymphs are dominant in dipper diet during the breeding season (Ealey 1977, Loegering and Anthony 1999).

Landscape characteristics

We used the multi-resolution land characteristics consortium (MRLC) land-cover data layer based on 2001 national land cover data (NLCD; Vogelmann et al. 1998a, b) within a geographic information system (GIS) to calculate land-cover area percentages for each watershed (USGS 2009).

Detailed land-cover categories were summed to produce major land-use/cover classes: sparse (26–50% canopy cover), moderate (51–75% canopy cover), dense (76–100% canopy cover), developed, evergreen forest, grassland-herbaceous, mixed + deciduous forest, pasture/hay and cultivated crops, scrub/shrub, wetlands, and impervious surfaces > 10%. Although we considered combining canopy coverage classes into one category, we decided against this option due to the potential ecological importance of threshold vegetation coverage (Radford et al. 2005). For our roads layer, we accessed the United States Geological Survey (USGS) National Map Seamless Server (USGS 2010).

Regional characteristics

Regional characteristics focused on broad patterns related to climate and geography. We designated the ecoregions of each reach based on common ecosystem factors (e.g. geology, soils, vegetation, physiography, etc.) following the US Environmental Protection Agency's Level III and IV classifications (USEPA 2007). We used Garmin Rino 120 GPS units to record the elevation of each study reach at its center (i.e. at the nest); we confirmed these readings using DEMs generated using a GIS. We obtained temperature and precipitation data from the Western Regional Climate Center (WRCC 2010) and from the National Climatic Data Center (NESDIS 2010). For each study reach, we selected the closest weather station, which was usually within the watershed. For some very remote locations, the nearest station was located in a neighboring watershed. We used daily precipitation records to generate the amount of precipitation for each year of the study (2005–2008) and for the breeding season months (March–August) of each year. We averaged these values to calculate the breeding season mean precipitation (mm) and 2005–2008 mean precipitation (mm). Likewise, we used mean daily temperature readings to calculate the mean breeding season temperature (°C) for 2005–2008.

Stable isotope analysis

Applications of stable isotopes allow for increased investigation of trophic levels and diet studies and, therefore, are of particular use in describing food webs in aquatic ecosystems (Collier et al. 2002, Hicks et al. 2005). Conventionally expressed as $\delta^{15}\text{N}$ (‰) (see below), the ratio of ^{15}N to ^{14}N typically exhibits a 3–4‰ enrichment with each trophic step, and is commonly used to describe relative trophic position (Kelly 2000). In our study, we used dipper blood to yield information related to the short term diet/assimilated foods: in the case of ^{15}N , reflecting diet within 9–15 d (Hobson and Clark 1992, Bearhop et al. 2002). We interpreted dipper $\delta^{15}\text{N}$ signatures relative to baseline $\delta^{15}\text{N}$ values of stream periphyton (i.e. the difference between dipper $\delta^{15}\text{N}$ and periphyton $\delta^{15}\text{N}$) to compare dipper trophic position across our study reaches (Cabana and Rasmussen 1996).

In the laboratory, we filtered and dried periphyton (60°C, 48 h), followed by grinding in a ball mill and packing in tin capsules. Several samples per reach were combined to create composite periphyton samples for each reach. We dried all blood samples in a 60°C oven, and subsequently freeze

dried (using a Labconco lyophilizer) and pulverized (using a ceramic mortar and pestle) all samples to ensure sample homogeneity. We packed and weighed (0.5–0.7 mg) samples in 4 × 6 mm tin capsules. Periphyton and replicate blood samples were then analyzed at the Univ. of Washington Stable Isotope Core (Pullman, WA, USA). Values for ^{15}N were calculated and reported using the standard delta (δ) notation in parts per thousand (‰):

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where X is ^{15}N and R is the corresponding ratio $^{15}\text{N}:^{14}\text{N}$. Typical analytical precision was $\pm 0.1\text{‰}$ for $\delta^{15}\text{N}$ determination.

Statistical analysis

To guide our analysis and inferences, we developed a conceptual model that represented the general theoretical linkages without specifying statistical details (Grace 2006). This model is presented in Supplementary material Appendix 1, Fig. A1. We then screened for potential spatial autocorrelation among predictor and response variables using the Durbin–Watson d statistic (Connell et al. 1997). Subsequently, we analyzed our data using a sequential approach based on 1) exploratory regression analysis and 2) structural equation modeling (SEM; Mitchell 1992, Grace and Pugsek 1998, Riginos and Grace 2008).

For our exploratory analysis, we used principal component analysis (PCA) and multivariate regression to explore relationships between environmental features and dipper characteristics. Using environmental data gathered for each spatial scale, we used PCA to generate axes that represented our spatial scales of interest: regional, landscape, and local. We then used the retained axes (eigenvalues > 1 ; Rencher 1995) as predictor variables in mixed stepwise regressions. Dependent variables included dipper characteristics related to productivity (total no. eggs, total no. fledged, mean fledgling weight), $\delta^{15}\text{N}$, and condition (mean female weight, mean male weight). Given that multiple tests were performed for each spatial scale, we ran a sequential Bonferroni procedure to reduce type I errors (Holm 1979, Rice 1989). Where necessary, data were transformed to meet assumptions of multivariate normality. All analyses were performed using JMP 8.0 (SAS Inst.). For reference, results and additional details from this exploratory analysis are presented in Supplementary material Appendix 2, Table A2.1–3 and Appendix 3, Table A3.1.

SEM is a powerful tool in examining potential causal pathways among intercorrelated variables and exploring the associations among variables while statistically controlling for other model variables. SEM also generates estimates of measurement error and suggests model improvements in evaluating alternative models (Bollen 1989). In conjunction with available published dipper–environmental relationships, we used results from our exploratory analysis to select the most promising explanatory variables to represent our conceptual parameters of interest in our SE models, represented by measures of 1) dipper productivity (total no. fledged), 2) $\delta^{15}\text{N}$, and 3) condition (mean male weight). In this way, our exploratory analysis enabled us to produce

a priori models and sufficiently constrain the number of variables in each model (Riginos and Grace 2008, Paquette and Messier 2011).

Structural models were carried out using the SEM software Amos 17.0 (SPSS). Maximum likelihood procedures were used for estimation and to evaluate model goodness of fit. Sequential application of χ^2 tests was used to determine which pathways to retain in the models. Amos also generates a full-model χ^2 value, which measures the degree of discrepancy between the overall model and the data; when $p > 0.05$, the overall fit between the data and the final SE model is considered acceptable. Once we had arrived at the model (or models) that we viewed to represent the most likely relationships among the variables, we also generated Bayesian estimates on the retained paths for confirmatory purposes, as these estimates do not rely on large-sample theory (Lee 2007). A model whose retained path coefficients have Bayesian 95% credible intervals that do not include zero is considered supportive of a model derived from maximum likelihood procedures.

The use of SEM to analyze spatially-explicit datasets is becoming increasingly common (Anderson et al. 2010, Paquette and Messier 2011) and may be advantageous in identifying both unique and synergistic contributions of predictor variables. Graham (2003) offered SEM as an alternative approach to multiple regression, in which the functional nature of collinearities is considered. In the context of this study, indirect paths (those connecting one or more predictor variables between spatial scales) indicate a hierarchical and potentially synergistic influence on dipper responses. Conversely, direct paths between predictor variables at regional, landscape, and/or local scales indicate independent influences on dipper responses. However, because it is unlikely that SEM is fully robust against multicollinearity, we did not include any highly correlated variables ($r > 0.8$, Grewal et al. 2004) representing the same spatial scale in the same model; correlations of all variables between spatial scales were < 0.6 .

Results

Dipper weight and reproduction varied across the study reaches ($n = 26$), which represented a broad range of environmental conditions (Table 1). On average, male dippers weighed approximately 4–5 g more than females during the breeding months. The total number of eggs produced ranged from two to nine, with a mean of five. Eighteen of the 26 pairs only produced one clutch, and in 35% of nests the number of young successfully fledged was lower than the initial clutch size.

Across all reaches, dipper $\delta^{15}\text{N}$ signatures ranged from 5.0 to 10.2‰. Periphyton $\delta^{15}\text{N}$ values exhibited a narrow range (0.3–1.5‰) across the subset of study reaches from where it was collected. Dipper $\delta^{15}\text{N}$ signatures at these same reaches ranged from 5.0 to 8.7‰. Correcting for baseline periphyton $\delta^{15}\text{N}$ signatures yielded dipper $\delta^{15}\text{N}$ signatures ranging from 4.4 to 7.5‰, resulting in a shift of only 0.5‰ in the range of original dipper $\delta^{15}\text{N}$ values (3.7‰, uncorrected; 3.2‰, corrected). Based on these results, we considered it reasonable to use uncorrected dipper $\delta^{15}\text{N}$ values as surrogates for relative trophic position in an exploratory analysis.

Table 1. Summary statistics of measures of regional, landscape, and local environmental characteristics, as well as measures of dipper ecology from the 26 study reaches.

	Minimum	Median	Maximum	Mean	SD
Regional variables					
Elevation (m)	330.0	789.0	1176.0	758.4	217.6
Latitude (DD)	43.7	46.6	47.5	46.3	1.0
Precipitation (mm) – breeding season mean	0.8	1.1	2.7	1.5	0.3
Precipitation (mm) 2005–2008 mean	10.2	24.2	39.9	24.6	10.2
Temperature °C – breeding season mean	11.7	11.7	17.4	12.8	2.0
Level III ecoregion*					
Level IV ecoregion*					
Landscape variables					
Sparse canopy cover (%)	2.9	8.9	24.9	10.3	5.6
Moderate canopy cover (%)	5.3	20.7	36.0	20.2	5.8
Dense canopy cover (%)	2.0	47.9	48.9	48.0	48.0
Developed (%)	0.0	0.0	2.8	0.3	0.7
Evergreen forest (%)	8.5	80.9	95.2	72.7	22.3
Grassland-herbaceous (%)	0.0	0.4	21.2	3.1	6.3
Imperviousness surfaces > 10% (%)	0.0	0.2	13.2	0.8	2.6
Mixed + deciduous forest (%)	0.0	0.0	0.6	0.1	0.1
No. stream crossings (by roads) per stream length (no. 100 km ⁻¹)	0.0	36.5	61.8	35.0	17.9
Pasture/hay and cultivated crops (%)	0.0	0.0	60.7	2.5	11.9
Road density (km 100 km ⁻²)	0.0	108.4	271.9	108.4	60.6
Shrub/scrub (%)	1.1	14.2	38.9	18.1	12.3
Wetlands (%)	0.0	0.1	1.3	0.2	0.3
Local variables					
Bankfull depth(m)	0.5	1.0	2.3	1.1	0.4
Bankfull width (m)	5.7	13.7	31.5	14.8	6.9
Canopy (%)	0.0	16.3	50.0	17.9	11.8
Drainage area (km ²)	21.8	124.6	1178.2	239.8	280.0
Embeddedness (%)	5.0	40.0	60.0	37.1	12.4
PFC (% yes)	12.5	62.5	100.0	56.9	26.4
RGA score	47.0	58.5	79.0	58.9	6.9
RHA score	102.0	128.5	194.0	131.5	22.2
Riparian width (m)	4.8	12.4	50.0	16.2	11.3
Slope (m m ⁻¹)	0.004	0.015	0.122	0.024	0.023
Stream order	2.0	4.0	5.0	3.7	0.7
Dipper variables					
Mean female weight (g)	45.9	58.6	67.0	56.5	5.9
Mean fledgling weight (g)	41.6	49.9	62.5	50.2	5.2
Mean male weight (g)	51.7	60.4	71.0	60.9	4.5
Total no. eggs	2.0	4.0	9.0	4.9	2.0
Total no. fledged	0.0	4.0	9.0	4.2	2.5
δ ¹⁵ N	5.0	6.6	10.2	6.4	1.3

*Level III and IV ecoregions were coded into the analysis as nominal variables.

Durbin–Watson tests indicated we were largely successful in avoiding spatial autocorrelation among our variables, with $d > 2$ in the majority of cases (Durbin–Watson $d > 2.0$ indicates no pattern in variables across space, < 1 indicates clustering of variables in space) and with $p > 0.05$ in all cases except for grassland/herbaceous land cover ($d = 1.17$, $p = 0.013$). Given the low degree of autocorrelation of this variable and that it was incorporated into our exploratory analysis as part of landscape principal components (LandscapePCs, none of which were spatially autocorrelated), we felt it was appropriate to leave this variable in the analysis.

Structural equation models

The final structural equation models provided evidence that the influences of environmental factors at differ-

ent spatial scales were unique for each aspect of dipper ecology (Fig. 2). Productivity model 1 ($\chi^2 = 4.31$, $R^2 = 0.58$, $p = 0.89$; Fig. 2a) was the most spatially integrative of all our models, depicting a multifaceted suite of interactions across all spatial scales in predicting the total no. fledged. Precipitation 2005–2008 ($r = 0.65$) had the strongest direct influence on the total no. fledged. Dense canopy, in turn, was positively related to embeddedness, which was negatively related to total no. fledged. Bankfull width ($r = 0.29$) also had a direct, positive effect on the total no. fledged. Productivity model 2 ($\chi^2 = 5.13$, $R^2 = 0.45$, $p = 0.40$; Fig. 2b) was also a valid model in our analysis, but not as strong as productivity model 1 in predicting the total no. fledged ($R^2 = 0.58$). Productivity model 2 had no regional component, but both landscape variables (dense canopy cover and shrub/scrub) directly influenced the total no. fledged ($r = -0.34, 0.39$;

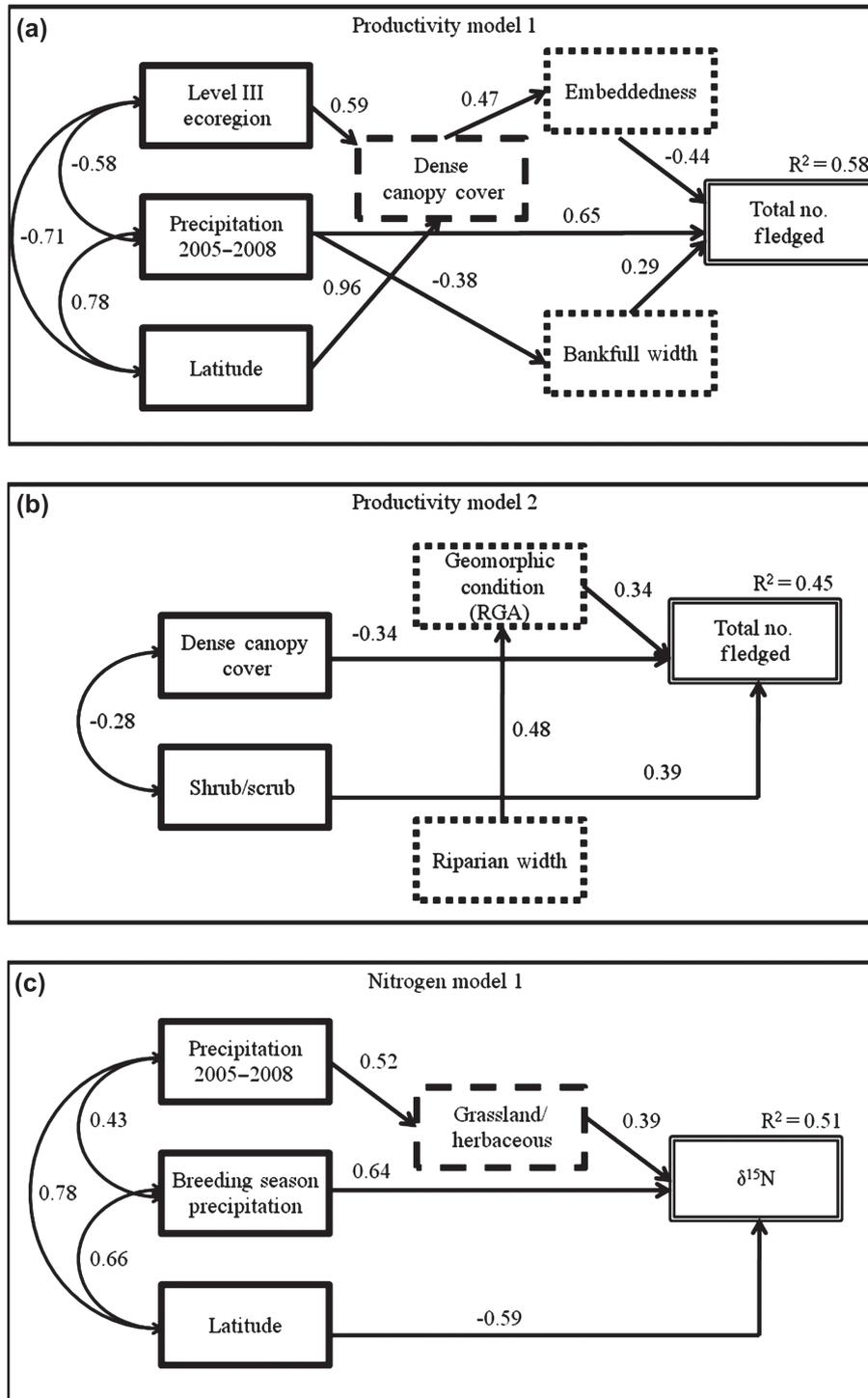


Figure 2. Structural equation modeling (SEM) analysis results for multiscale characteristics influencing dipper productivity (a, b), $\delta^{15}\text{N}$ (c, d), and condition (e). Arrows represent direct and indirect influences ($p < 0.05$). Numbers next to arrows are standardized regression coefficients, representing the relative strength of the given effect. The R^2 values above the dipper response variable boxes represent the total variance explained by the model. Spatial scales are represented as follows: \square regional, \square landscape; \square and local. $n = 26$ for models 1–4 and $n = 22$ for model 5.

respectively). Riparian width shared an important association with geomorphic condition ($r = 0.48$), which in turn positively influenced total no. fledged ($r = 0.34$).

Dipper $\delta^{15}\text{N}$ signatures, in contrast to number fledged, did not respond to variation in local characteristics (nitrogen model 1; $\chi^2 = 0.61$, $R^2 = 0.51$, $p = 0.89$; Fig.

2c). Regional characteristics, represented by measures of precipitation and latitude, were the most influential variables, accounting for the bulk of the variation observed in $\delta^{15}\text{N}$. The correlation between latitude and precipitation 2005–2008 showed that these two regional metrics were linked. Breeding season precipitation exerted a direct,

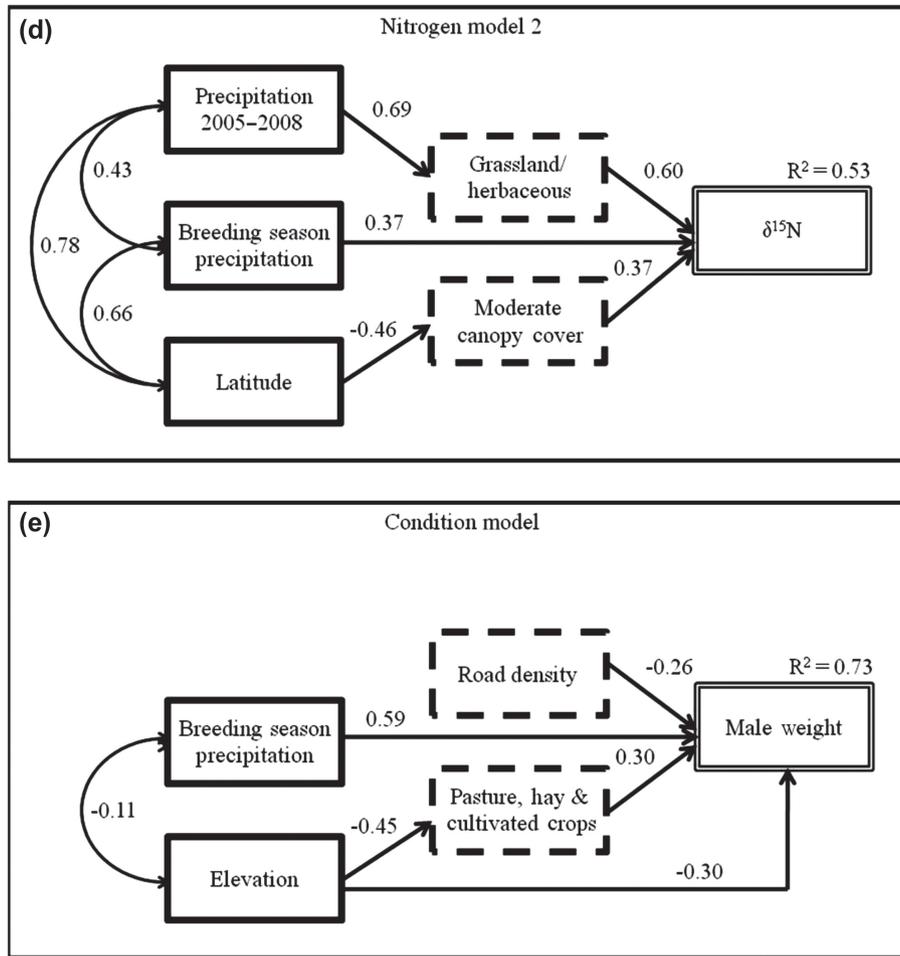


Figure 2. Continued.

positive influence on $\delta^{15}\text{N}$ in nitrogen model 2 ($\chi^2 = 9.29$, $R^2 = 0.53$, $p = 0.23$; Fig. 2d). Grassland/herbaceous was an important intermediary in both nitrogen models 1 and 2, positively influencing $\delta^{15}\text{N}$ in both cases. Nitrogen model 2 illustrated that moderate canopy cover may also represent a mechanistic link between latitude ($r = -0.46$) and $\delta^{15}\text{N}$ ($r = 0.37$).

Our condition model, represented by male weight ($\chi^2 = 2.79$, $R^2 = 0.73$, $p = 0.59$; Fig. 2e), included breeding season precipitation and elevation as regional influences on male weight. Breeding season precipitation exerted a direct, positive influence on male weight ($r = 0.59$), whereas elevation was linked indirectly with male weight via pasture, hay, and cultivated crops ($r = -0.45$). Pasture, hay, and cultivated crops, in turn, positively influenced male weight ($r = 0.30$). Road density appeared to act independently on male weight ($r = -0.26$).

Bayesian estimation procedures, used for small sample sizes, confirmed that all paths retained in productivity model 1, productivity model 2, and nitrogen model 2 had coefficients with 95% credible intervals that did not include zero. Nitrogen model 1 and the condition model had very slight deviations from zero but given the strength of the other measures of model fit and their ecological relevance, we felt they represented valid models.

Discussion

In this study, we have examined several dipper ecological responses to environmental characteristics at regional, landscape, and local scales. Many have illustrated the hierarchical influence of watershed characteristics on stream biota (Poff 1997); few have considered organisms that spatially integrate riverine landscapes across their multiple dimensions (Fausch et al. 2002, Sullivan et al. 2007). Our results show that among the physical environmental variables considered in this study, regional and landscape characteristics combined to exert the greatest influence, explaining patterns in dipper productivity, $\delta^{15}\text{N}$, and individual condition. Local characteristics of influence appear to be dominated by hydrogeomorphic characteristics. Overall, we found that multiple facets of dipper ecology were influenced by factors that operated simultaneously at different spatial scales. This information increases our understanding of dipper-ecosystem linkages and of hierarchical relationships in watersheds.

We considered multiple SE models for each dipper response variable, and have presented the strongest models for each of the three dipper measures representing our focal branches of dipper ecology—productivity, $\delta^{15}\text{N}$, and individual condition. It is not our intention that these models represent the only possible environment–dipper trajectories,

but rather that they present scenarios for which our data lend the greatest support among the models considered. Overall, in spite of detailed data representing many environmental features, direct regional-to-dipper and landscape-to-dipper pathways dominated SE models (Fig. 2). Across all models, there were only three local-to-dipper pathways (productivity models 1 and 2, Fig. 2a, b). Among these, only productivity model 1 (Fig. 2a) exhibited the full complement of interactions and influences across the three spatial scales.

Productivity

Productivity, expressed by total no. fledged, was heavily influenced by average precipitation over the study period, both directly ($r=0.65$) as well as indirectly via bankfull width ($r=-0.38$) (productivity model 1, Fig. 2a). Although our results indicate that greater amounts of precipitation may be favorable for dipper productivity, extreme precipitation events may reduce productivity due to higher flows, increased suspended sediment, and lower food availability, as observed by Price and Bock (1983) in Colorado, USA. Conversely, drought conditions might also be expected to adversely affect dipper productivity through changes in water quality and macroinvertebrate communities (Finn et al. 2009, Whitehead et al. 2009). During our study, variability in precipitation, ranging only from 10.2 to 39.9 mm yr⁻¹, was unlikely to capture potential dipper responses to extreme precipitation shifts.

Differences in latitude, representing an approximate 450-km span between the northernmost and southernmost study reaches, may play at least some role in governing productivity (Fig. 2a), notably through indirect effects of dense canopy coverage, and in turn, stream embeddedness. Although there is scant literature related to relationships between land use and aquatic bird reproductive success in watersheds (Ormerod and Watkinson 2000, Mattson and Cooper 2006), evidence suggests that catchment forest cover may explain significant variation in productivity of other aquatic taxa including algae, invertebrates, and fish (Stephenson and Morin 2009). Dense canopy cover in our study was heavily influenced by latitude, with greater coverage of dense canopy at higher latitudes. Higher latitudes also correlated with greater precipitation (Fig. 2a), which we speculate may lead to greater embeddedness in these streams due to surface runoff. Catchment forest cover might be hypothesized to also influence nest predator abundance and activity (Chalfoun et al. 2002, Mattson and Cooper 2006), but predation rates on dipper nests in this and other studies (Morrissey 2004) are relatively low compared to nest predation rates for many passerine species.

In our study, factors of influence at the local scale (Fig. 2a, b) were largely related to hydrogeomorphic variables (e.g. geomorphic condition, embeddedness, bankfull width). Study streams with low geomorphic conditions exhibited significant sediment accumulation, eroding banks, widened channels with reduced heterogeneity in flow patterns, and other characteristics suggestive of channel adjustment and homogenization of habitat. Other investigators have also documented associations between stream geomorphic adjustment, habitat quality, and multiple aquatic taxa (Walters et al. 2003, Sullivan

et al. 2004, 2006b, Sullivan and Watzin 2008). In a study in Vermont, USA, Sullivan et al. (2006a) showed that stream channels undergoing geomorphic adjustment were negatively associated with belted kingfisher *Ceryle alcyon* reproductive measures. Vaughan et al. (2007) found that *C. cinclus* occupancy was associated with multiple hydromorphological measures (e.g. cobble substrate, rocky channel, riffles) recorded by the United Kingdom's Environmental Agency's River Habitat Survey (RHS). Price and Bock (1983) observed that heavy siltation reduced dipper productivity, a result consistent with our findings that increased embeddedness negatively influenced dipper productivity.

Productivity model 2 (Fig. 2b) also included riparian width, an important predictor of in-stream condition (Allan et al. 1997, Naiman and Décamps 1997, Frimpong et al. 2005) and of considerable importance to both migrant and resident birds (Saab 1999, Donovan et al. 2002). Currently, the importance of riparian forests to dippers is uncertain. Loegering and Anthony (2006) observed that 91% of dipper nest locations in their study area were located where trees dominated both sides of the stream. Tyler and Ormerod (1994) observed a link between bank tree cover and *C. cinclus* distribution, whereas Vaughan et al. (2007) found no strong association with riparian tree coverage. Our results provide evidence that riparian characteristics may be indirectly important to dippers by improving stream geomorphic condition (Fig. 2b).

Nitrogen

Many investigations have greatly contributed to our knowledge of stream food webs at the local scale (Schmid-Araya et al. 2002, England and Rosemond 2004, Coat et al. 2009), yet there exists a current knowledge gap relating to the spatial scales of trophic dynamics in streams (Finlay et al. 2002). Nitrogen models 1 and 2 (Fig. 2c, d) highlight the importance of regional characteristics on dipper $\delta^{15}\text{N}$ signatures. $\delta^{15}\text{N}$ signatures may reflect differences in the relative trophic position of consumers, given comparable signals among stream autotrophs (Post 2002), as in our study. The 5.7‰ range in dipper $\delta^{15}\text{N}$ values across our study reaches represents ~1.5 to 2 trophic steps among sites (Kelly 2000). The positive influence of grassland-herbaceous and moderate canopy cover on $\delta^{15}\text{N}$ signatures is consistent with the concept that trophic links may increase in streams flowing through more open environments (Vannote et al. 1980). For instance, Gothe et al. (2009) observed that both basal resources and aquatic invertebrate consumers were ¹⁵N-enriched in clear-cut compared to old-growth streams. However, recent findings by Sabo et al. (2010) suggest that increases in food chain length may be governed by increases in drainage area, with hydrologic variability acting as the underlying mechanism. Although this pattern was represented by a trend in our raw data, the relationship was not sufficiently strong to emerge in our SE models, likely because breeding dippers are constrained to high-gradient, smaller stream systems. Given that dippers represent top predators in these systems, our results contribute to the current understanding of drivers of food chain length, and support the potentially important role of spatial effects (Sabo et al. 2009).

Condition

Body mass of birds has often been used as a measure of habitat quality (Johnson et al. 2006, Smith et al. 2010) and can be influenced by a number of factors, including latitude, food availability, habitat type, species-specific traits, and gender-specific roles during breeding (Moreno 1989). The condition model (Fig. 2e) explained the majority of the variation observed in male weight, indicating that by and large, male condition during the breeding season is controlled by factors operating beyond the local scale. Breeding season precipitation again emerged as an influential factor, signifying that climatic variability is expressed at the individual as well as population levels (Saether et al. 2004).

At the landscape scale, human activities in the form of agricultural and transportation infrastructure influenced male weight. Whereas elevation was negatively associated with the percentage of agriculture, road density emerged as a factor independent from regional characteristics. Our results support existing literature related to the detrimental ecological impacts of roads (Angermeier et al. 2004, Wheeler et al. 2005). For dippers, local populations can be limited by the lack of suitable nesting sites (Loefering and Anthony 2006), and breeding pairs frequently nest under bridges, where localized changes in channel geomorphology and streams sedimentation may exacerbate the effects of roads. In our study, road density appeared to negatively influence male weight, but not female weight, emphasizing that males and females may respond differently to factors during the breeding season. For instance, Morrissey et al. (2010) observed that egg-laying females fed at a higher trophic level than males by consuming more fish in streams in British Columbia, Canada. Because female dippers are solely responsible for incubating eggs and are primarily responsible for feeding of nestlings in the early stages of hatchling development (Kingery 1996), it is likely that females remain closer to the nest. Conversely, male condition, reflecting activity across the full length of the breeding territory, might be expected to integrate landscape-level habitat characteristics.

Conclusions

Increased understanding of spatial patterns in stream ecosystems (Fausch et al. 2002, Vaughn 2010) highlights the need for empirical research that addresses species-ecosystem linkages across spatial scales (Lowe et al. 2006). In the present study, we have shown that both direct and indirect effects related to multiscale environmental characteristics influenced multiple aspects of dipper ecology. Our SE models (Fig. 2) highlighted the prevalence of regional-to-dipper and landscape-to-dipper relationships, with local factors often by-passed. Precipitation, for instance, drove patterns in dipper productivity, $\delta^{15}\text{N}$, and individual condition. Our results offer evidence that although stream-watershed habitats may be spatially-nested, the pathways influencing American dippers may not always conform to hierarchical spatial relationships (Burcher et al. 2007). Investigating if these patterns are unique to dippers or are shared by other aquatic biota offers an intriguing line of future research.

Regional variables are not commonly considered in watershed studies, but as human activities continue to expand their reach, it will be increasingly important to incorporate broad-scale attributes. For example, our understanding of the impacts of climate change on aquatic organisms is hobbled by the difficulty in gathering data at and assessing large spatial scales. Changes in temperature and precipitation, however, may alter the distribution (Peterson et al. 2002, McKenney et al. 2007) and abundance (McLaughlin et al. 2002) of many species. For instance, rainfall extremes influenced reproduction of the Louisiana waterthrush *Seiurus motacilla*, a riparian obligate species (Mattsson and Cooper 2009), and these authors suggest that rainfall patterns are likely to have variable species-specific effects on riparian breeding birds. In our study, dippers responded to precipitation measured at two temporal scales, indicating that both immediate and longer-term precipitation patterns may drive the demographics of dipper populations. Likewise, Chiu et al. (2008) found strong associations between flood magnitude and brown dippers *Cinclus pallasi* and proposed that influences of flooding be considered when using dippers as bioindicators.

There are some important caveats regarding this study. Firstly, the covariation of anthropogenic and natural landscape attributes can often lead to an overestimation of the influence of land use (Allan 2004). Although we have identified land-use attributes of potential influence on dipper ecology, our primary goal was to use these attributes to represent the impact of factors at the landscape spatial scale. Secondly, our study focused on physical environmental characteristics. Additional factors that would account for unexplained variance include more detailed data relating to food resources (Morrissey et al. 2010), water quality (Ormerod and Tyler 1993, Brewin et al. 1998), and competition for territory and nesting sites (Loefering and Anthony 2006, Gillis et al. 2008).

Our study provides a perspective on species-ecosystem relationships based on multiple facets of dipper ecology, a broad array of environmental characteristics, and multiple spatial scales. The potential of dippers as bioindicators of stream condition and water quality (Price and Bock 1983, Strom et al. 2002, Morrissey et al. 2004) suggests that our results may extend beyond American dipper ecology and, to an extent, represent broader stream-watershed associations. In particular, the influences of environmental characteristics at multiple spatial scales indicate that dippers may spatially integrate watershed landscapes through their productivity, feeding, and individual condition (Sullivan et al. 2007, Sullivan and Vierling 2009). As we continue to consider stream-riparian ecosystems from a landscape perspective, we propose it will be beneficial to consider organisms with potential to represent both the riverscape (Fausch et al. 2002, Sullivan et al. 2007) and spatial components of watersheds in ways that other, more traditional aquatic biota, may not. Given the heavy influence of regional and landscape characteristics on dippers, our results also advocate for increased incorporation of large-scale features in both the development and application of stream-riparian habitat assessment and conservation protocols.

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Supplementary material Appendix E7071 at <www.oikosoffice.lu.se/appendix>. Appendix 1–3.