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Original Article

Smartphone Technologies and Bayesian Networks to Assess Shorebird Habitat Selection

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ABSTRACT

Understanding patterns of habitat selection across a species’ geographic distribution can be critical for adequately managing populations and planning for habitat loss and related threats. However, studies of habitat selection can be time consuming and expensive over broad spatial scales, and a lack of standardized monitoring targets or methods can impede the generalization of site-based studies. Our objective was to collaborate with natural resource managers to define available nesting habitat for piping plovers (Charadrius melodus) throughout their U.S. Atlantic coast distribution from Maine to North Carolina, with a goal of providing science that could inform habitat management in response to sea-level rise. We characterized a data collection and analysis approach as being effective if it provided low-cost collection of standardized habitat-selection data across the species’ breeding range within 1–2 nesting seasons and accurate nesting location predictions. In the method developed, >30 managers and conservation practitioners from government agencies and private organizations used a smartphone application, “iPlover,” to collect data on landcover characteristics at piping plover nest locations and random points on 83 beaches and barrier islands in 2014 and 2015. We analyzed these data with a Bayesian network that predicted the probability a specific combination of landcover variables would be associated with a nesting site. Although we focused on a shorebird, our approach can be modified for other taxa. Results showed that the Bayesian network performed well in predicting habitat availability and confirmed predicted habitat preferences across the Atlantic coast breeding range of the piping plover. We used the Bayesian network to map areas with a high probability of containing nesting habitat on the Rockaway Peninsula in New York, USA, as an example application. Our approach facilitated the collation of evidence-based information on habitat selection from many locations and sources, which can be used in management and decision-making applications. Published 2017. This article is a U.S. Government work and is in the public domain in the USA

KEY WORDS Atlantic coast, barrier islands, Bayesian network, Charadrius melodus, coastal geomorphology, habitat availability, iPlover, nesting habitat, piping plovers.

Knowledge gaps create challenges to optimizing the conservation of endangered species and ecosystems (Bottrill et al. 2011, Cardoso et al. 2011, Hou et al. 2013). Knowledge gaps relating to habitat selection can be of particular concern given that habitat loss, fragmentation, and degradation pose the largest threats to species worldwide (Wilcove et al. 1998, Lawler et al. 2002). To protect endangered species in the face of such threats, conservation managers must identify environmental and landscape characteristics that define a species’ habitat. Ideally, the definition of “habitat” is based on observed behaviors related to habitat selection, such as nest establishment or active foraging (Hall et al. 1997). Knowing which characteristics can be used to describe habitat throughout a species’ geographical range can also allow managers to identify habitat characteristics universally important across sites versus those used locally by specific populations (Holt and Keitt 2005, Flesch and Steidl 2010). Such information can also allow researchers and managers to identify environmental thresholds explaining a species’
distribution or abundance, which is relevant for protecting species where global climate change is expected to shift those thresholds (Travis 2003, Holt and Keitt 2005, Flesch and Steidl 2010). Selection studies encompassing all or a significant portion of a species’ geographic distribution are particularly valuable for species with broad geographic ranges, such as red-cockaded woodpeckers (Picoides borealis; McKellar et al. 2014), northern spotted owls (Strix occidentalis; Noon and McKelvey 1996), and sea turtles (Caretta spp.; Liles et al. 2015). However, collecting habitat-selection data across a species’ range can require tremendous resources, which explains the attractiveness of citizen-science-based efforts (Catlin-Groves 2012). Furthermore, assembling data in standardized formats across sites and management entities can be difficult (Pullin and Knight 2005, Cook et al. 2010). As a result, many managers rely on personal observations or within-organization reports when crafting conservation management plans (Pullin and Knight 2005, Cook et al. 2010). Although conservation based solely on local or experiential evidence can be successful, there are also examples where actions based on limited evidence are ineffective or detrimental to ecological systems (Sutherland et al. 2004). A framework that collates evidence from scientists and managers across sites can support managers in making conservation decisions (Sutherland et al. 2004), particularly for wide-ranging species (e.g., migratory shorebirds) that rely on geographically distributed habitats and are managed accordingly by multiple entities at broad regional scales that cross administrative boundaries.

To help coastal managers plan for threats posed by sea-level rise to piping plovers (Charadrius melodus) and other shorebirds along the U.S. Atlantic coast, we investigated the value that can be extracted from knowledge of broad-scale piping plover habitat-selection patterns from Maine to North Carolina, USA. In this study, we utilize substantially more habitat-use samples compared with previous studies that focused on local habitat selection in areas of Massachusetts, New York, and New Jersey, USA, at the core of the species’ Atlantic coast distribution (e.g., Burger 1987, Strauss 1990, Cohen et al. 2009, Maslo et al. 2011). We also investigate the value of data that could be derived quickly and on a limited budget.

Our objectives were to 1) develop a data collection and analysis method to meet our research needs and 2) test this method’s application to problems relevant to the broader coastal management community. We characterized a methodological approach as being effective if it allowed for collection of standardized habitat-selection data across the species’ U.S. Atlantic coast breeding range within 1–2 nesting seasons, data assemblage and distribution at a low cost, and development of models that accurately predict nesting locations or “habitat.” The approach we developed integrated existing monitoring efforts by managers and biologists from government agencies and private organizations (Table S1, available online in Supporting Information), who used a smartphone-based tool (“iPlover”) to collect standardized data on nesting habitat selection (Thieler et al. 2016). Data were automatically collated into a single database and used to establish prior probability distributions in a Bayesian network. Within the Bayesian network, we assumed that habitat was “selected” and “available” for nesting based on the presence of a piping plover nest. In this paper, we 1) further describe our data collection and analysis approach; 2) test the accuracy of a Bayesian network to predict habitat availability; and 3) provide an example case study that illustrates the potential value to coastal managers by identifying areas with a high probability of containing nesting habitat for piping plovers along a portion of Long Island, New York (Fig. 1).

**METHODS**

**Data Collection With iPlover**

We developed the smartphone application “iPlover” (Thieler et al. 2016) to collect data on piping plover nesting habitat-use patterns. This application provided field biologists with a streamlined, relatively inexpensive, and robust tool that could be used to record 1) information on the habitat characteristics at a given location; 2) images of the habitat; and 3) spatial coordinates. Under our collection protocol, each user, after finding a nest in the course of monitoring efforts, used the smartphone’s internal sensors within iPlover to record the nest’s geolocation coordinates and observation date and time. After using the phone’s camera to take a photograph of the nest from a 5-m distance, the user completed a simple habitat assessment by assigning categorical values to a fixed set of variables listed in iPlover. Users were instructed to base their habitat assessment on the area within a 5 × 5-m area containing the nest site at its center. Habitat variables considered in iPlover included Geomorphic setting, Substrate type, Vegetation type, and Vegetation density (Table 1). iPlover records were locally stored on smartphones while users were in the field and uploaded to a centralized database as soon as internet connectivity was available. Our data-collection partners followed guidelines for the use of wild birds in research and minimized disturbance as much as possible (Fair et al. 2010).

We repeated an identical protocol at the coordinates of random points (also referred to as “background points”; Keating and Cherry 2004, Phillips et al. 2009) generated by SLZ within the confines of a subsite’s boundaries in ArcGIS (Version 10.2; ESRI, Redlands, CA, USA; Figs. S2.1 and S2.2, available in online Supporting Information). We defined a “subsite” as an entire barrier island or, in the case of mainland beaches, as the area monitored by our collaborators to approximately 500 m inland from the beach. We used the nest points to delineate the characteristics of available nesting habitat, but we used random points to describe the characteristics of areas not used for nesting in that year. Such “absence” points can significantly reduce error in conservation applications (Hermoso et al. 2015). Random points could fall anywhere within a study area; therefore, these points allowed us to approximate levels of relative availability for the various habitat characteristics. We conducted a training seminar for all iPlover users before each breeding season and provided users with a recording of this webinar-based training and written protocols for later reference.
We collected iPlover data from 12 sites (34 subsites) during the breeding season (April–August) in 2014, with efforts extended to 20 sites (83 subsites) in 2015. Many sites contained several beaches and barrier islands, which we refer to as “subsites” (Table S1, available in online Supporting Information). For example, the Cape Lookout National Seashore site contained 3 barrier islands (or subsites): North Core Banks, South Core Banks, and Shackleford Banks. We therefore also report numbers by subsite. We made assessments at random points at only 5 of the 34 subsites (Table S1, available in online Supporting Information) in 2014, and collected all in the field with iPlover. In 2015, we recorded iPlover data at random points from all 83 subsites; however, we characterized some random points (511 total) using the most recently available orthoimagery (2013 or 2014) from the U.S. Department of Agriculture’s National Agricultural Imagery Program (USDA 2015a). We categorized these remotely classified random points, which fell within inaccessible areas or private property, in the same manner as points collected with iPlover; and we henceforth referred to them as “remote random points.” We validated the accuracy of classifications at remote random points for one of our sites and found an accuracy level of 86–90% (Tables S2.1–S2.4, available online in Supporting Information). Although these remotely classified random points added a small amount of uncertainly to our analysis, they allowed us to characterize locations that were inaccessible from the ground. We examined the iPlover data set for errors or inconsistencies before use in a Bayesian network (Table S3, available online in Supporting Information); the final “cleaned” data set included 1,244 nest points and 1,066 random points.

**Bayesian Network**

Our general description of Bayesian networks is derived from Korb and Nicholson (2004). A Bayesian network is a directed acyclic graph composed of nodes and edges intended to organize knowledge about a system. The nodes represent a set of variables describing the relevant system components; in our case, 1) biogeomorphic landcover variables (i.e., input...
Table 1. Variables and their definitions used to describe landscape characteristics associated with piping plover nests and random locations at sites from Maine to North Carolina, USA (part of the iPlover data set). These variables were also used as input nodes in the iPlover Habitat Bayesian network, used to predict the availability of piping plover habitat on the Rockaway Peninsula, New York, USA, in 2014.

<table>
<thead>
<tr>
<th>Habitat variable</th>
<th>Definition</th>
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<tbody>
<tr>
<td><strong>Geomorphic setting</strong></td>
<td></td>
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<tr>
<td>Beach</td>
<td>The relatively thick and temporary accumulation of loose, water-borne material (usually well-sorted sand and pebbles, accompanied by mud, cobbles, boulders, and smoothed rock and shell fragments) that is in active transit along, or deposited on, the shore zone between the limits of low water and high water (Neuendorf et al. 2011). In this study, the Beach geomorphic setting occurred between the ocean- or sound-side study area boundary and the mean high water line (approximated for by the upper-most wrack line in the field).</td>
</tr>
<tr>
<td>Backshore</td>
<td>The upper, usually dry, zone of the shore or beach, lying between the high-water line of mean spring tides and the upper limit of shore-zone processes; it is acted upon by waves or covered by water only during exceptionally severe storms or unusually high tides (Neuendorf et al. 2011). In this study, the Backshore geomorphic setting occurred between the mean high water line and either (i) the dune toe, (ii) the edge of developed areas, or (iii) the edge of dense vegetation (or forest).</td>
</tr>
<tr>
<td><strong>Vegetation density</strong></td>
<td></td>
</tr>
<tr>
<td>None</td>
<td>No vegetation observed in the 5 x 5-m area surrounding an iPlover data point or map cell.</td>
</tr>
<tr>
<td>Sparse</td>
<td>Vegetation was apparent and covered &lt;20% of the 5 x 5-m area surrounding an iPlover data point or map cell.</td>
</tr>
<tr>
<td>Moderate</td>
<td>Vegetation covered 20–90% of the 5 x 5-m area surrounding an iPlover data point or map cell.</td>
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</tr>
<tr>
<td><strong>Development</strong></td>
<td></td>
</tr>
<tr>
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</tr>
<tr>
<td>Sand</td>
<td>Rock or mineral grains with diameters between 0.074 and 4.76 mm (Neuendorf et al. 2011). In this study, a predominantly &quot;Sand&quot; substrate consisted of finer grains with no discernible shells fragments or large rock fragments.</td>
</tr>
<tr>
<td>Shell–Gravel–Cobble</td>
<td>In this study, Shell–Gravel–Cobble described substrate containing a mixture of sand, shell or rock fragments, or large rocks.</td>
</tr>
<tr>
<td>Mud–Peat</td>
<td>A sticky, fine-grained, predominantly clay- or silt-sized marine detrital sediment (Neuendorf et al. 2011).</td>
</tr>
<tr>
<td>Water</td>
<td>In this study, we selected Water as the substrate type for any iPlover data point or location that (i) is always submerged (e.g., points several meters into the ocean, bay, or inland water body) or (ii) was submerged at the time of iPlover point collection (i.e., intertidal regions of beaches).</td>
</tr>
<tr>
<td>Development</td>
<td>In this study, we selected Development as the substrate type for any iPlover data point or location that fell within areas obviously influenced by anthropogenic activities (e.g., housing developments, paved roads or parking lots, recreational sports fields, etc.).</td>
</tr>
<tr>
<td>Marsh</td>
<td>A relatively flat, low-lying, intermittently water-covered area with generally halophytic grasses existing landward of a barrier island (Neuendorf et al. 2011).</td>
</tr>
<tr>
<td><strong>Vegetation type</strong></td>
<td></td>
</tr>
<tr>
<td>None</td>
<td>Areas lacking vegetation of any type. Such areas were common on beaches, backshores, and washovers that frequently or recently experienced wave-action.</td>
</tr>
<tr>
<td>Herbaceous</td>
<td>Areas containing primarily herbaceous vegetation of the forb–herb growth habit (USDA 2015b) and lacking shrubs, trees, or any other vegetation with woody stems (Neuendorf et al. 2011). In this study, the Herbaceous vegetation type typically described the vegetation cover found in Godfrey’s (1976) ‘grassland’ ecological zone along the backshore and dunes, dominated by beach grasses (e.g., Ammophila breviligulata) or (ii) ‘interdune marsh’ ecological zone dominated by cordgrass (e.g., Spartina patens).</td>
</tr>
<tr>
<td>Shrub</td>
<td>Areas containing low (&lt;5 m), multistemmed woody plants of the shrubshrub or shrub growth habits (USDA 2015b). In this study, the Shrub vegetation type typically described vegetation cover found in Godfrey's (1976) heath-like ‘shrublands’ ecological zone in stable dune systems.</td>
</tr>
<tr>
<td>Forest</td>
<td>Areas containing trees and tall (&gt;5 m) shrubs of the tree growth habit (USDA 2015b). In this study, the Forest vegetation type typically described vegetation cover found in Godfrey's (1976) 'woodlands–forests' ecological zone found in barrier island interiors and dominated by deciduous (e.g., Quercus velutina), pine (e.g., Pinus rigida), and juniper (e.g., Juniperus virginiana) species.</td>
</tr>
<tr>
<td>Development</td>
<td>In this study, we selected Development as the vegetation type for any iPlover data point or location that fell within areas obviously influenced by anthropogenic activities (e.g., housing developments, paved roads or parking lots, recreational sports fields, etc.).</td>
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<tr>
<td><strong>Substrate type</strong></td>
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<td>Beach</td>
<td>The relatively thick and temporary accumulation of loose, water-borne material (usually well-sorted sand and pebbles, accompanied by mud, cobbles, boulders, and smoothed rock and shell fragments) that is in active transit along, or deposited on, the shore zone between the limits of low water and high water (Neuendorf et al. 2011). In this study, the Beach geomorphic setting occurred between the ocean- or sound-side study area boundary and the mean high water line (approximated for by the upper-most wrack line in the field).</td>
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</tr>
<tr>
<td>Washover</td>
<td>A fan of material deposited from the ocean landward on a mainland beach or barrier island, produced by storm waves breaking over low parts of the mainland beach or barrier and depositing sediment either landward (mainland beaches) or across a barrier island into the bay or sound (barrier islands). A washover typically displays a characteristic fan-like shape (Neuendorf et al. 2011).</td>
</tr>
<tr>
<td>Barrier Interior</td>
<td>In this study, the Barrier Interior geomorphic setting described all areas spanning the interior boundary of the dunes (or backshore in the absence of dunes) on the ocean-side to the interior boundary of the marsh, dunes, or backshore on the back-barrier side. This setting was typically used to describe areas that did not fall into any other geomorphic setting (e.g., washovers, ridge or swale complexes).</td>
</tr>
<tr>
<td>Ridge–Swale complex</td>
<td>Long subparallel ridges and swales aligned obliquely across the regional trend of the contours. Common on the &quot;hooks&quot; (i.e., a low peninsula or barrier ending in a recurved spit and formed at the end of a bay; e.g., the hook of Chincoteague Island) of barrier islands of the Mid-Atlantic, USA (Neuendorf et al. 2011).</td>
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nodes) and 2) the probability that a combination of those variables will identify nesting habitat (i.e., output node). Nodes are broken down into discrete characteristics or, for continuous variables, discretized into bins. Edges connect nodes to convey dependencies, correlations, or causal influences among nodes (Fig. 2).

After a network is structured, conditional probability distributions are calculated for each node based on data published by others in the scientific literature, expert opinion, or empirical data collected by the researcher. Calculations are made within the Bayesian network according to probability rules for marginalization and via Bayes Theorem:

\[
p(F_i | O_j) = \frac{p(O_j | F_i) p(F_i)}{p(O_j)}
\]

where \( p(F_i | O_j) \) is the updated posterior probability of a prediction \( F_i \) given a set of observations \( O_j \); \( p(O_j | F_i) \) is the probability that the observations would be seen if the predictions were perfectly known (likelihood function); \( p(F_i) \) is the probability of the prediction without knowledge added from updated observations (the prior); and \( p(O_j) \) is a normalizing constant. The set of all possible node–value combinations forms a conditional probability table that underlies a “trained” network (Fig. 2). Given an incomplete set of node values, the trained Bayesian network can be used to determine the probability of observing specific states for nodes in which the true state is unknown, with epistemic uncertainty represented in the evenness of predicted conditional probabilities.

We constructed a Bayesian network for habitat selection (“iPlover Habitat BN”) in Netica (Version 5.12, Norsys Software Corp., Vancouver, BC, Canada) after Gieder et al.’s (2014) model for Assateague Island National Seashore, Berlin, Maryland, USA. We connected 4 categorical input nodes for the landcover variables Geomorphic Setting, Substrate Type, and Vegetation Type, and Vegetation Density to an output node for Habitat Availability (Fig. 2). Network structure was based on biogeomorphic characteristics deemed important for predicting piping plover nest presence in the published literature (e.g., Burger 1987, Strauss 1990, Jones 1997, Cohen et al. 2009, Maslo et al. 2011), in Gieder et al.’s (2014) model, and as specified by the expert opinion of our iPlover partners. We were primarily interested in landcover characteristics that could be shaped by sea-level rise in the future, so we did not include additional ecological factors that often drive habitat selection patterns, such as predator density or human activity. However, these variables could easily be added if relevant to a management application. We also purposely simplified the network structure for this study (e.g., compared with Gieder et al. 2014) so that we could 1) evaluate network skill with limited data requirements, 2) reduce model complexity for use at a regional scale, and 3) inform prior probability distributions through ground-based measurements (without reliance on potentially expensive or unavailable remotely
sensed data sets such as Light Detection and Ranging (LIDAR). Prior probability distributions in the Bayesian network were derived from field data we collected as part of this study in iPlover.

The Bayesian network output node for Habitat Availability described the probability that a location was available for piping plover nesting, given that location’s specific combination of landcover characteristics. In the data used to train the network, we approximated for habitat with the presence (i.e., high probability of being available, probability = 1) or absence (i.e., low probability of being available, probability = 0) of a piping plover nest. We used nest presence as a proxy for habitat availability instead of, for example, egg fate or fledging rate; therefore, we cannot make conclusions regarding whether selected habitat was optimal for nesting or acted as an ecological trap (Battin 2004).

Skill and Sensitivity Testing
We assessed the predictive skill of the iPlover Habitat Bayesian network in 2 separate approaches. In the first, we randomly divided the 2014–2015 iPlover data set into halves. The first half of the data set (1,155 points) was used to establish prior probability distributions in the iPlover Habitat Bayesian network while the second half (1,155 points) was used to independently test the network’s ability to correctly predict nest presence (i.e., habitat). In MatLab (Version 8.5 2015a, MathWorks Natick, MA, USA), we generated a $2 \times 2$ confusion matrix showing the proportions of nest points in predicted habitat (true positives; $p_{11}$); random points located in predicted habitat (false positives; $p_{12}$); nest points predicted to be in nonhabitat (false negatives; $p_{21}$); and random points predicted to be in nonhabitat (true negatives; $p_{22}$).

We assumed a test point’s combination of input variables was associated with habitat if the model predicted a probability of $\geq 0.66$. We assumed input-variable combinations where the model predicted a probability of $\leq 0.33$ to be associated with nonhabitat. We assumed combinations where the probability was between 0.33 and 0.66 to be as likely as not habitat and excluded them from skill testing because the availability prediction was overly uncertain. We selected these criteria in accordance with the Intergovernmental Panel on Climate Change’s outcome likelihoods (Pachauri et al. 2014). The iPlover Habitat Bayesian network, trained on the training data set alone, made predictions for all points contained in the testing data set. Using this confusion matrix, we calculated Cohen’s kappa ($\kappa$):

$$\kappa = \frac{P_e - P_r}{1 - P_r}$$

where $P_e$ is the proportion of observations in agreement (from the confusion matrix, $p_{11} + p_{22}$), and $P_r$ is the proportion of observations in agreement due to chance ($\{p_{11} + p_{12}\}(p_{11} + p_{22}) + (p_{12} + p_{22})(p_{21} + p_{22})$). $\kappa$ measures the proportion of all possible cases of presence (habitat) or absence (nonhabitat) that were predicted correctly by the network after accounting for chance agreement (Manel et al. 2001). Landis and Koch (1977) suggest the following model performance thresholds: poor $\kappa = 0$; fair $0 < \kappa \leq 0.4$; moderate $0.4 < \kappa \leq 0.6$; substantial $0.6 < \kappa \leq 0.8$; and almost perfect $\kappa > 0.8$.

In the second testing approach, we employed the cross-validation method described in Fienen and Plant (2015). We used the Python module CVNetica to perform $k$-fold cross-validation, where the calibration data set was randomly divided into folds or partitions without replacement to create separate independent training and testing data sets. Once the data set was partitioned into $k$-folds, we reserved one fold for testing or validation and used the remaining folds to train the iPlover Habitat Bayesian network. We conducted a 3-fold and a 10-fold cross-validation routine. We assumed a correct prediction when a nest point was assigned a $>0.5$ probability of being habitat and when a random point was assigned a $<0.5$ probability of being habitat. We conducted calibration-validation multiple times for the 3-fold and 10-fold cross-validation, so we report the Bayesian network skill as the ensemble mean error rate of prediction over the $k$-folds.

During skill testing, we conducted sensitivity testing by evaluating model performance at predicting habitat availability (nest presence) for iPlover points in the test data set for models where habitat variables were iteratively removed. For example, we calculated model performance for a version of the iPlover Habitat Bayesian network where all nodes except for Geomorphic Setting were removed (“Only Geomorphic Setting”) as well as another version where all nodes were retained except for Geomorphic Setting (“Not Geomorphic Setting”). We repeated this testing with versions of the network where each variable was either removed or retained. We calculated the skill of each version of the Bayesian network using that Bayesian network’s $\kappa$-value according to the first skill-testing approach described above.

Rockaway Peninsula Application
We used the iPlover Habitat Bayesian network to determine likely areas of habitat availability on the Rockaway Peninsula, including the Breezy Point Unit of the Gateway National Recreation Area, in New York, USA (Fig. 1) to illustrate a practical application of this work. We used orthoimagery (2014; National Oceanic and Atmospheric Administration 2014), LIDAR (2013–2014; U.S. Geological Survey 2015), and landcover types delineated by U.S. National Park Service resource managers for the study area (H. Abouelezz, U.S. National Park Service, unpublished data; described online in Supporting Information) to create 4 Geographic Information System (GIS) layers in ArcGIS that represented each input node in the iPlover Habitat Bayesian network. We combined the 4 layers to form a single GIS layer, where every $5 \times 5$-m cell had an attribute for Geomorphic Setting, Substrate Type, and Vegetation Type and Density (Figs S4.1–4.4, available online in Supporting Information).

The attribute table associated with the combined landcover GIS layer showed every unique combination for the 4 habitat variables and was used as a case file. We trained the iPlover Habitat Bayesian network on all iPlover points collected in
2014 and 2015 and ran the case file through this trained network with the Process Cases function in Netica. This analysis generated a probability value for the Habitat Availability node for each combination of characteristics that we joined back to the original attribute file in ArcGIS for mapping purposes.

RESULTS

Our collaborative network of conservation practitioners collected 2,310 sampling points from 83 subsites from Maine to North Carolina in 2 years. These data showed piping plover habitat selection patterns across the species’ U.S. Atlantic coast breeding range—patterns that are reflected in the prior probability distributions used in the iPlover Habitat Bayesian network (Figs. 2 and 3). In 2014 and 2015, piping plovers primarily established nests on washovers and, to a lesser extent, within backshore areas and dune complexes (Fig. 3a). Piping plovers also nested in areas with substrates consisting of sand and shell fragments, gravel, or cobble as well as predominantly sandy substrates (Fig. 3b). Nests were established in areas either lacking vegetation or containing sparse herbaceous vegetation (Fig. 3c and d).

The iPlover Habitat Bayesian network, when trained on half of the 2014–2015 iPlover data set, had a high skill level ($\kappa = 0.8$) when tested with the remaining half of the data set, with 497 and 389 correctly predicted nest locations and random points, respectively. Of the 1,155 test points, 150 were considered as likely as not to be in predicted habitat (probability = 0.33–0.66) and were excluded from the calculation of $\kappa$. Under this skill-testing approach, most error in model predictions arose from false positives (98 points out of 119 with erroneous predictions), where high probability of being habitat (nest presence) was associated with a random point. Another 21 iPlover points were misclassified as false negatives, where a low probability of being habitat (nest absence) was associated with an observed nest.

Figure 3. Habitat characteristics pertaining to (a) Geomorphic setting, (b) Substrate type, (c) Vegetation type, and (d) Vegetation density for locations where piping plover nests were present versus randomly selected locations according to habitat evaluations made using the iPlover application at 1,244 nest points and 1,066 random points on 83 beaches or barrier islands from Maine to North Carolina, USA. iPlover data used in this study were collected from April to August in 2014 and 2015.
Cross-validation showed that the Bayesian network’s predictive capabilities were not sensitive to the amount of data used for training, with error rates ranging from 9.43% to 13.22% (Table 2). Validation error rates increased by only a few percentage points under 3-fold (training on 66% of data) compared with 10-fold (training on 90% of data) cross-validation, indicating a low level of overfitting in a model with nearly 3,000 free parameters (Table 2). Sensitivity testing demonstrated that no single node had a major effect on model predictions (Table 3).

When we used the iPlover Habitat Bayesian network to evaluate habitat availability for the Rockaway Peninsula study area, we found that 8.4% (2.1 km²) of the study area was composed of habitat (i.e., probability ≥0.66; Fig. 1b). Twenty-seven of the 40 piping plover nests observed in 2014 and 2015 were found in locations predicted to contain habitat by the Bayesian network; the remaining 9 and 5 nests were found in areas predicted to be as likely as not and unlikely to be habitat by our Bayesian network, respectively (Fig. 1b and c).

**DISCUSSION**

The iPlover smartphone application simplified collaboration among scientists and managers by standardizing data collection and allowing immediate collation into a single centralized database, where data free of transcription-related errors could be analyzed in near real-time. The iPlover data-collection protocol was designed to leverage existing monitoring efforts and resources, so this data set was generated with little extra effort on the part of managers and no additional disturbance to a sensitive species. Yet, the approach allowed us to develop a powerful model with accurate predictive capabilities. This simple model of piping plover habitat selection (e.g., compared with Gieder et al. 2014) had a $\kappa$ coefficient of 0.8 and a mean calibration-validation error rate ranging from 9% to 13%. Furthermore, the majority of observed errors were false positives (82% of all error), where the model predicted high probability of habitat availability (nest presence) when a nest was actually absent. Errors of this form are common and actually expected for species such as piping plovers (Fielding and Bell 1997); territorial behaviors and population sizes below carrying capacity can mean that available habitat remains unoccupied (Elliot-Smith and Haig 2004). The Bayesian network model also correctly identified one region of the study area as having a high probability of containing habitat despite a lack of iPlover data coverage for this region. Although piping plovers frequently nest in this area (7 nesting pairs were reported in both 2014 and 2015; K. Jennings, New York State Department of Environmental Conservation, personal communication), it is private property and was not monitored by collaborators in this study. Therefore, we conclude that the coupled smartphone application and Bayesian network approach successfully met our needs for quickly and inexpensively collecting habitat-selection data over broad spatial scales to produce accurate predictions of habitat availability for piping plovers.

The data set that resulted from our collaborative work described nesting site selection over much of the piping plover Atlantic coast breeding range that was consistent with previous site-based studies. For example, other studies in Massachusetts, New York, and New Jersey have shown that piping plovers most often establish nests in washovers, backshore areas, and dune complexes (Strauss 1990, Jones 1997, Cohen et al. 2009, Maslo et al. 2011) where substrate is predominantly sandy or a mixture of sand, shell, gravel, or cobble and where there is either no vegetation or sparse herbaceous vegetation (Burger 1987, Elias-Gerken 1994, Jones 1997, Cohen et al. 2008, Maslo et al. 2011). The consistency between interpretations from iPlover data and previous site-based studies increases our confidence in data used for model training. This collaborative data set also adds to existing knowledge by describing patterns of habitat selection over a large geographical area (>1,500 km). Previous studies have focused on smaller spatial scales at

<table>
<thead>
<tr>
<th>Error rate (%) by fold</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>Mean error rate (%)</th>
<th>$\kappa$</th>
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</thead>
<tbody>
<tr>
<td><strong>Calibration</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>10.15</td>
<td>0.79</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>12.80</td>
<td>0.79</td>
</tr>
<tr>
<td>Calibration$^a$</td>
<td>9.43</td>
<td>9.57</td>
<td>10.75</td>
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<td></td>
<td></td>
<td>9.92</td>
<td></td>
</tr>
<tr>
<td>Validation$^a$</td>
<td>12.80</td>
<td>12.40</td>
<td>9.60</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>11.60</td>
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</tr>
<tr>
<td>10-fold cross-validation</td>
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<td></td>
<td></td>
<td></td>
<td>10.00</td>
<td>11.29</td>
</tr>
<tr>
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<td>10.06</td>
<td>10.06</td>
<td>9.77</td>
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<td>9.67</td>
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<td>9.97</td>
<td>9.82</td>
<td>10.13</td>
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<td>Validation</td>
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<td>10.00</td>
<td>11.45</td>
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<td>11.89</td>
<td>9.96</td>
<td>11.29</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Landis and Koch (1977) suggest the following model performance thresholds: poor $\kappa = 0$; fair $0 < \kappa \leq 0.4$; moderate $0.4 < \kappa \leq 0.6$; substantial $0.6 < \kappa \leq 0.8$; and almost perfect $\kappa > 0.8$.

$^b$ Errors that occur when the testing and the training data sets are the same are referred to as “calibration errors.” Errors that occur when the testing data set is independent from the training data set are referred to as “validation errors.”
and all remaining data points were used for error testing. Data for training and testing purposes were collected at piping plover nests and random points at sites from Maine to North Carolina, USA, in 2014 and 2015 using the iPlover data collection application. For all testing scenarios, the Bayesian network was trained on half of the iPlover data set, which did not result in a loss of model skill. However, Thieler et al. (2016) showed that extensive “scrubbing” or “cleaning” of these data may not be necessary when data are analyzed in a Bayesian framework, which can be time-consuming and difficult.

Table 3. Sensitivity testing for the iPlover Habitat Bayesian network used to predict habitat availability for piping plovers on the Rockaway Peninsula, New York, USA, in 2014. Data for training and testing purposes were collected at piping plover nests and random points at sites from Maine to North Carolina, USA, in 2014 and 2015 using the iPlover data collection application. For all testing scenarios, the Bayesian network was trained on half of the iPlover data set, and all remaining data points were used for error testing.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Cohen’s k</th>
<th>False positives</th>
<th>False negatives</th>
<th>True positives</th>
<th>True negatives</th>
<th>Excluded points</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full network</td>
<td>0.8</td>
<td>106</td>
<td>16</td>
<td>590</td>
<td>430</td>
<td>17</td>
</tr>
<tr>
<td>Not geomorphic setting</td>
<td>0.8</td>
<td>104</td>
<td>16</td>
<td>590</td>
<td>430</td>
<td>19</td>
</tr>
<tr>
<td>Not substrate type</td>
<td>0.8</td>
<td>100</td>
<td>1</td>
<td>548</td>
<td>323</td>
<td>187</td>
</tr>
<tr>
<td>Not vegetation type</td>
<td>0.8</td>
<td>80</td>
<td>17</td>
<td>544</td>
<td>430</td>
<td>88</td>
</tr>
<tr>
<td>Not vegetation density</td>
<td>0.7</td>
<td>126</td>
<td>15</td>
<td>581</td>
<td>403</td>
<td>34</td>
</tr>
<tr>
<td>Only geomorphic setting</td>
<td>0.7</td>
<td>88</td>
<td>6</td>
<td>449</td>
<td>216</td>
<td>400</td>
</tr>
<tr>
<td>Only substrate type</td>
<td>0.8</td>
<td>64</td>
<td>1</td>
<td>478</td>
<td>326</td>
<td>290</td>
</tr>
<tr>
<td>Only vegetation type</td>
<td>0</td>
<td>0</td>
<td>11</td>
<td>11</td>
<td>104</td>
<td>1,044</td>
</tr>
<tr>
<td>Only vegetation density</td>
<td>0.9</td>
<td>29</td>
<td>1</td>
<td>243</td>
<td>251</td>
<td>635</td>
</tr>
</tbody>
</table>

- a False positives: no. of times that the model predicted the presence of a nest (high probability of being habitat) when a nest was actually absent (low probability of being habitat).
- b False negatives: no. of times that the model predicted the absence of a nest (low probability of being habitat) when a nest was actually present (high probability of being habitat).
- c True positives: no. of times that the model correctly predicted the presence of a nest (high probability of being habitat) when a nest was also observed at that location.
- d True negatives: no. of times that the model correctly predicted the absence of a nest (low probability of being habitat) when a nest was also not observed at that location.
- e According to the likelihood scales used by the Intergovernmental Panel on Climate Change (Pachauri et al. 2014), probability values between 33% and 66% are considered “about as likely as not.” In other words, iPlover test points that were assigned a probability of habitat availability of 33–66% were as likely as not to be a nest point in habitat. We therefore excluded these points from our skill calculations. However, an increasing number of points with uncertain predictive probabilities is indicative of lost model skill.
- f For all scenarios preceded by “Not,” we looked at the network’s ability to predict habitat availability using all nodes in the network except that node. For example, in “Not Geomorphic Setting,” the network only contained nodes for Substrate type, Vegetation type, and Vegetation density and was tasked with predicting habitat availability without being given knowledge of Geomorphic setting.
- g For all scenarios preceded by “Only,” we looked at the network’s ability to predict habitat availability using only that node. For example, in “Only Geomorphic Setting,” the network was tasked with predicting habitat availability using only information on Geomorphic Setting (and no information on Substrate type, Vegetation type, and Vegetation density).

Given that iPlover fields were identical to nodes used within the iPlover Habitat BN, data could be quickly incorporated into the network with minimal to no processing. As our work continues, the iPlover Habitat Bayesian network can be updated and extended to additional sites as new iPlover data are uploaded to the centralized server in subsequent years (Uusitalo 2007, Morrison et al. 2012). Therefore, our approach fulfills a need to organize and collate habitat-use patterns for this species across its Atlantic coast breeding range, which can be used by managers in making habitat conservation and restoration decisions. Furthermore, the Bayesian network, now adequately trained and operational, can be used in support of decision-making without requiring additional data collection. The methods described herein can be used with “current” spatial data sets (i.e., as exemplified by the Rockaway Peninsula case study) to quantify and locate quality available habitats throughout a management unit, or it can be used with historical data sets to examine habitat change through time. Finally, other modeling tools can be used to produce predictive spatial data sets (e.g., state–and-transition models such as ST-Sim, Daniel and Frid 2011; ArcGIS add-ons such as Land Change Modeler, Clark Labs 2016), which can then be used with the Bayesian network to make predictions of future habitat availability. To this point, we are developing tools to predict future coastal landcover
characteristics that can be linked to the iPlover Habitat Bayesian network to determine habitat availability and location given sea-level rise (Gutierrez et al. 2014, 2015). Managers can use information on historical, current, and future habitat availability to inform conservation decisions, including reserve design and the best placement of infrastructure for recreation.

Our approach also facilitates knowledge-transfer back to managers to support their applied efforts in species and landscape management. For example, research products, including habitat availability maps and iPlover data points, were disseminated to managers and other stakeholders. In addition, as reviewed in McCann et al. (2006), the graphical nature of Bayesian networks in programs such as Netica allows even individuals lacking a strong statistical background to understand the parameters considered, how they relate to final outputs, and the level of uncertainty associated with network predictions. The Bayesian network approach is also extensible. Additional nodes can be added to the iPlover Habitat Bayesian network to depict other important habitat characteristics (e.g., predator density, human disturbance) or effects of management decisions (e.g., artificial dune construction) on piping plover habitat availability. Thus, iPlover and its associated Bayesian network can guide adaptive management in this system. To our knowledge, this is the first approach of its kind to link scientists with the management community and provide a flexible mechanism for evaluating habitat over varying time horizons for decision-making applications. Following Nichols and Williams (2006), our approach facilitates the use of monitoring data in conservation decision-making, moving existing efforts beyond surveillance monitoring to “monitoring for active conservation.”

Methods described here can be modified for other species in other habitats. For instance, the iPlover application and Habitat Bayesian network could be used in its current form to understand and map habitat for other coastal species of conservation concern, such as tiger beetles (Cicindela dorsalis dolaitis), snowy plovers (Charadrius nivosus), American oystercatchers (Haematopus palliatus), sea turtles (Cheloniidae spp.), or seabeach amaranth (Amaranthus pumilis). This approach could also be used in other habitats by modifying the habitat characteristics of interest. Furthermore, although data collection for this disturbance-sensitive species leveraged an established network of professional monitors, other species may be amenable to data collection with our approach by citizen-scientists. Long-term use of this approach could enable scientists and managers to capture shifts in habitat selection as both climate and human-driven landcover change alter ecosystems. The applications of this approach are broad and, as we have described here, facilitate data collation across sites for supporting the conservation of endangered species.

MANAGEMENT IMPLICATIONS

The iPlover smartphone application facilitated standardized data collection and collaboration among a large network of scientists and managers from several government agencies and private organizations. With the iPlover data set and Bayesian network that comprise our approach, habitat availability patterns can be mapped to inform decisions regarding, for example, protection, restoration, or multiuse allowances of the landscape. Given the scale of the underlying habitat-use data, our approach can be used to support management at within-site, regional, or range-wide scales. Furthermore, use of a Bayesian network allows for the explicit consideration of uncertainty in modeling results that managers can take into account in decision-making. This approach is highly flexible and can be used with minimal modifications for understanding habitat-use patterns for other species.

ACKNOWLEDGMENTS

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LITERATURE CITED


Rusche, E. 1990. Reproductive success, life history patterns, and behavioral variation in a population of piping plovers subjected to human disturbance. Dissertation, Tufts University, Boston, Massachusetts, USA.


SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher’s website. This supplemental material includes 1) counts of iPlover nest and random points collected by site and collaborator; 2) methodology and results for generating, classifying, and validating remote random points; 3) alterations made to the raw iPlover data set during QA/QC processing; and 4) methodology for creating geographic information system layers of the Rockaway Peninsula for the mapping example.