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Research Article

A Meta-Analysis of American Black Duck Winter Habitat Use Along the Atlantic Coast

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ABSTRACT American black duck (*Anas rubripes*) populations declined by more than 50% between the 1950s and 1990s, and the species serves as a flagship for conserving salt marsh habitats along the Atlantic Coast. Black ducks have generally been well studied throughout the annual cycle, but surprisingly, we lack a synthetic, quantitative understanding of their space use during the winter. This limits our ability to prioritize habitat acquisition and restoration efforts. We used >17,000 telemetry locations from 235 black ducks ranging from Connecticut to Virginia to study home range composition and space use during winter in relation to habitat quality, urbanization, and severe weather. Despite substantial environmental variation, home range sizes were similar among regions and years. Smaller home and core ranges contained a greater proportion of salt marsh habitat, and ducks experiencing more 4-day freeze events had larger home and core ranges. Ducks exposed to prolonged periods of cold weather had smaller core ranges when those areas comprised more energy-rich freshwater habitats. When we examined individual telemetry locations, we found that ducks used irregularly inundated high marsh more at night, presumably for foraging, and urban habitats more during the day and evening crepuscular periods. We found that black ducks used regularly inundated low marsh less on days where the temperature never rose above freezing, and instead used subtidal areas and forested wetlands more. Finally, we found ducks were marginally more likely to use freshwater habitats during high tides. Our study confirms that

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black ducks depend on salt marsh for wintering habitat, and points to an unexpectedly important role for forested wetlands during periods of cold weather. We found no evidence that black ducks avoided urban areas or roads, which supports the inclusion of all available habitats in carrying capacity modeling. We emphasize that new hypothesis-driven, local telemetry studies are needed to further elucidate the relationships between black duck movements and environmental variation, especially cold weather. Further, given that most remaining coastal wetlands are currently protected via state and federal lands, we suggest black duck habitat management should strive to acquire and restore brackish and forested wetlands in close proximity to coastal marshes.

KEY WORDS *Anas rubripes*, disturbance, salt marsh, satellite, telemetry, tide, waterfowl, weather.

The American black duck (*Anas rubripes*) is a species of conservation concern in eastern North America, and is a flagship species for protecting wetland habitats along the Atlantic Coast. Black duck populations have steadily declined since the 1950s (Rusch et al. 1989), and although populations have stabilized in some regions, black ducks have never recovered to historical levels (Conroy et al. 2002). Conroy et al. (2002) reviewed the literature and concluded that several compounding factors have likely contributed to this decline, including harvest, reductions in the quantity and quality of breeding and wintering habitat, and interactions with mallards (*A. platyrhynchos*; see also Mank et al. 2004, McAuley et al. 2004, Masonneuve et al. 2006, and Petrie et al. 2012 for recent studies on black duck-mallard interactions).

Over the past decade, the Black Duck Joint Venture—the interagency group tasked with population monitoring and research on black ducks—has prioritized research on the wintering ecology of Atlantic Flyway black ducks (Black Duck Joint Venture Management Board 2014). The conservation of Atlantic Coast black ducks during the nonbreeding period is of increasing concern, primarily because the salt marsh upon which these birds depend (Morton et al. 1989*b*) is being lost and degraded by sea level rise, severe storms, and habitat conversion (Stedman and Dahl 2008). To better understand how these salt marsh habitats are able to support black ducks throughout the winter, several coordinated studies have been conducted to quantify food abundance in Atlantic Coast salt marshes (Plattner et al. 2010, Cramer et al. 2012, M. DiBona, Delaware Department of Natural Resources and Environmental Control, personal communication; M. Goldstein, University of Delaware, personal communication; B. Lewis, Virginia Department of Game and Inland Fisheries, personal communication; M. Livolsi, University of Delaware, personal communication), concurrent with research on the energetic demands of wintering black ducks (Cramer 2009, Jones 2012). Armed with these estimates of food supply and energetic demand, managers are better able to estimate the carrying capacity of salt marsh habitats for black ducks and other wintering waterfowl.

Despite these recent advances in black duck ecology and management, we lack a synthetic understanding of black duck habitat use during the wintering period. This is important from a management perspective because although we can quantify the amount of habitat available on the landscape, some habitats may not be used by black ducks, leading to an overestimate of carrying capacity. This seems especially likely given intensive urban development along the Atlantic Coast and the fact that black ducks are notoriously wary of human disturbance (Longcore et al. 2000). Furthermore, it is critical to understand black duck habitat use in relation to environmental variables such as tides and weather; for example, salt marshes may be a particularly important foraging resource during cold periods when freshwater habitats are frozen (Longcore and Gibbs 1988, Morton et al. 1989*c*), and black duck behavior varies with the tidal cycle (Jones 2012). There have been few rigorous efforts to generalize black duck habitat use across their range; instead, efforts have been typically restricted to a single study area and were published a generation ago (Ringelman and Longcore 1982, Costanzo 1988, Morton et al. 1989*c*). Thus, a better understanding of space use of wintering black ducks in relation to food availability, urbanization, and environmental variables is needed for deriving better estimates of black duck carrying capacities.

To address this, several radio- and satellite-telemetry studies on black ducks were conducted over the past decade, though none were ever published in refereed journals (Costanzo 1988, Cramer 2009, Anderson 2013, G. Costanzo, Virginia Department of Game and Inland Fisheries, personal communication; M. Huang, Connecticut Department of Energy and Environmental Protection, personal communication; B. Lewis, Virginia Department of Game and Inland Fisheries, personal communication; D. Plattner, Minnesota Department of Natural Resources, personal communication; metadata available in Supporting Information Table S1, available online at www.wildlifejournals.org). We attempted to synthesize these data ($n = 235$ birds, 17,425 total locations) on how black ducks are using salt marsh habitats throughout their wintering range on the Atlantic Coast. This is an exceptionally large and wide-ranging telemetry dataset, and afforded us a unique opportunity to generalize black duck behavior across a suite of locations and habitats, albeit at the cost of answering detailed questions at local scales. Our analysis proceeded in an exploratory fashion but was driven by the underlying hypothesis that wintering black duck populations are limited by energetic carrying capacity, and that home ranges and movements would be influenced by conditions that affect the ability of ducks to acquire food. Specifically, our goal was to provide a broadly applicable description of black duck habitat use, and determine how food abundance, weather, tidal regimes, and anthropogenic disturbance from urbanization affect this use.

STUDY AREA

We collected telemetry data between December 2004 and January 2011 from black ducks wintering along the Atlantic Coast, ranging from southern Connecticut to the Chesapeake Bay. We grouped these data into geographic regions that loosely corresponded with US states (CT, NY, NJ, DE, VA/MD; Table 1, Fig. 1). There were a range of foraging habitats classically associated with the feeding activities of black ducks, including natural and managed freshwater marsh, salt marsh that is regularly (low marsh) or irregularly flooded (high marsh) by the tide, mudflats, and subtidal habitats.

METHODS

Habitat Maps

To ensure state-to-state consistency, we used the United States Fish and Wildlife Service National Wetland Inventory (NWI) geographic information system (GIS) layer to identify these different types of foraging habitats; we slightly modified this cover map to parse (primarily at managed wildlife refuges) general salt marsh habitats into high marsh, low marsh, and mudflat based on ground-truthing in the field. The NWI often characterizes large areas of deep water as subtidal; however, we considered only subtidal waters <1 m deep to be accessible by foraging black ducks (Longcore et al. 2000). Therefore, we used National Oceanic and Atmospheric Administration (NOAA) bathymetry data to reclassify NWI subtidal habitats >1 m as open water, a non-forageable habitat type. We used waterfowl food energy values derived by Ringelman et al. (2015) from core sampling studies on the Atlantic Coast to estimate the average energy landscape available to black ducks.

There are a variety of other habitat types along the Atlantic Coast that are best classified as non-forageable (e.g., urban areas, deciduous forest) in terms of historical carrying capacity modeling for wintering waterfowl (Black Duck Joint Venture, personal communication). We used the Northeast Terrestrial Habitat Map developed by The Nature Conservancy (TNC) to identify upland habitat types not previously described by the NWI. We grouped habitat designations given by the NWI and TNC layers based on expert opinion to produce a consolidated, contiguous map of all available habitat types along the Atlantic Coast (Supporting Information Table S2, available online at www.wildlifejournals.org). We associated each telemetry location with a habitat type in a GIS. We also calculated the absolute area (in hectares) of each habitat type in each duck's home range and core range, the proportional habitat composition of the home and core range, and the total energy (in kcal) contained in the ranges.

Finally, we used 2010 county-level Topologically Integrated Geographic Encoding and Referencing (TIGER) data provided by the United States Census Bureau to identify all primary and secondary roads ($n = 28$ counties) as a measure of urbanization and human disturbance. We qualitatively classified primary roads as thoroughfares where cars travel rapidly and do not stop (e.g., highways), and secondary roads as thoroughfares where cars travel slowly and often stop (e.g., neighborhood roads; Supporting Information Table S3, available online at www.wildlifejournals.org). We then calculated the distance from each telemetry location to the nearest primary and secondary road in a GIS. For each duck, we also calculated the average distance to both primary and secondary roads.

Environmental Data

Because black duck habitat use can vary with the time of day (Jones 2012), we classified each location as diurnal, nocturnal, or as occurring during a 1-hour morning or evening crepuscular period (30 min before and after sunrise or sunset). For each location, we also included the daily maximum temperature using historical NOAA weather data from 17 different stations along the Atlantic Coast. We were particularly interested in cold days when the maximum daily temperature was $<0°$ C because black duck behavior and energetics are known to change when freshwater habitats begin to freeze (Albright et al. 1983, Morton et al. 1989*c*). To understand how prolonged periods of cold weather affect home ranges, we added up the number of consecutive frozen periods a duck experienced lasting at least n days, where n ranged from 1 to 5 days. Although our dataset contained some longer cold periods, they were too infrequent to include in the statistical analysis. Finally, we also included time (nearest hour) when the duck location occurred, and tide level (m) at the nearest NOAA tide station ($n = 14$ stations).

Table 1. Sample sizes of American black ducks (*Anas rubripes*) fitted with transmitters on each of 5 study areas along the Atlantic Coast, USA. Home ranges are 80% isopleths and core ranges are 50% isopleths, reported in hectares. Note that birds with <30 locations ($n = 59$) do not appear in this table (see Methods Section). Also shown are estimates of the average food energy contained in home and core ranges. Values presented are mean ± standard error.

State	Birds (n)	Date range	Points (N)	Home area (ha)	Home energy (million kcal)	Core area (ha)	Core energy (million kcal)
CT	32	17 Nov 2007 to 5 Apr 2010	1,572	808 ± 222	13.5 ± 2.8	574 ± 102	5.0 ± 1.1
DE	12	3 Feb 2009 to 3 Jan 2011	2,422	798 ± 201	25.7 ± 11.6	407 ± 117	9.9 ± 3.5
NJ	50	3 Dec 2006 to 16 May 2009	5,310	1,073 ± 218	43.3 ± 7.1	571 ± 81	16.7 ± 2.8
NY	43	2 Dec 2004 to 8 Apr 2009	3,241	1,150 ± 320	30.1 ± 8.1	863 ± 132	13.2 ± 4.0
VA	44	21 Dec 2006 to 22 Apr 2009	3,789	1,301 ± 237	48.8 ± 10.6	592 ± 89	20.7 ± 4.7
Total	181	2 Dec 2004 to 3 Jan 2011	16,334	1,082 ± 120	35.3 ± 4.0	647 ± 48	14.3 ± 1.7

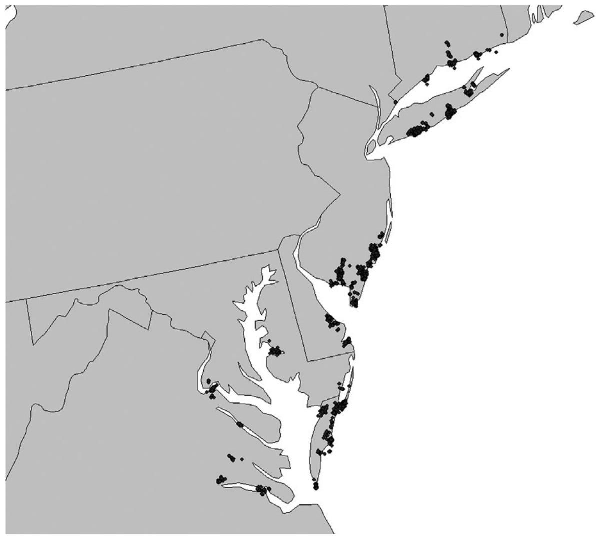

Figure 1. Map showing all telemetry locations in winter of American black ducks (*Anas rubripes*) along the Atlantic Coast, USA, 2004–2011.

In our analyses, we used mean-centered tide heights (standardized at each location) to reflect shifts between high and low tides.

Telemetry Data

Between December 2004 and January 2011, we collected 17,425 locations from 235 black ducks (177 very high frequency [VHF] radio backpacks and 58 global positioning system [GPS]/Argos transmitters; Southern Illinois University IACUC #04-022, 07-023; University of Delaware IACUC #1154; banding permit #05986). All black ducks marked were female, and included both first-year and adult birds. Using estimated error ellipses for VHF-tracked birds and ARGOS GPS accuracy codes, we eliminated locations with error >1,000 m (corresponding ARGOS codes: 0, A, B, Z). We acknowledge that imprecision in black duck locations could lead to misclassification of the habitat type in which the location occurred; our hope is that by considering >17,000 locations, we were nevertheless able to capture broad patterns of habitat use. We eliminated fixes within 24 hours of initial handling for satellite birds; radio birds were not relocated until ≥1 day after handling. Locations were taken ≥4 hours apart for satellite birds, and typically ≥1 day apart for radio birds and we considered consecutive locations to be independent. We acknowledge that radio-marking birds can have effects on behavior and survival (reviewed in Kesler et al. 2014), and as with all telemetry studies, we urge caution in interpreting our results as perfectly representative of free-flying black ducks.

Home Range Estimation

We built home ranges using fixed, bivariate-normal kernel methods with least-squares cross-validation in the Geospatial Modeling Environment (V. 0.7.2.1; Beyer 2012). Kernel methods for estimating home ranges are well established in the literature (Worton 1989, Seaman and Powell 1996), and are still preferred over newer methods (e.g., LoCoH methods; Getz et al. 2007) for waterfowl telemetry data (Cumming and Cornélis 2012). The sizes of kernel home ranges are sensitive to the number of points used to create them. A home range built with fewer points tends to be larger and oversmoothed, and the number of points required to build a precise home range varies between systems (Börger et al. 2006), though 30–50 are often necessary (Seaman et al. 1999, Millspaugh and Marzluff 2001). We used a Monte Carlo simulation approach to determine how many points were needed to build reliable home ranges (see Supporting Information for further details, available online at www.wildlifejournals.org). Following the results of this preliminary analysis, we included all birds with >30 locations in home range analysis ($n = 181$) and used all birds with >10 locations ($n = 240$) in locations-only analysis. We used 80% isopleths (to reduce kernel spillage) as our estimate of home ranges, and 50% isopleths as our estimate of core ranges (Seaman et al. 1999, Table 1).

Analyses

We conducted 3 analyses, examining both home and core ranges of birds, as well as individual telemetry locations. In the first 2 analyses, our goal was to determine which factors affected home and core range size. We used the individual animal as our sampling unit and calculated the habitat composition of home and core ranges. We also lumped habitats into salt marsh, fresh marsh, and non-forageable habitat categories, which follow important delineations in the energetic landscape for foraging black ducks (Ringelman et al. 2015). For each bird, we calculated the average distance to primary and secondary roads and how many cold periods of varying duration the duck had experienced during the tracking period. We also included duck age, the date of the first location (to account for seasonal variation), state, region, and year in our models of home and core range size (Table 2).

Because this analysis was exploratory, we first built a global model (without interactions) containing all variables that could potentially affect the size of home and core ranges. Following Crawley (2002), we examined the model fits using log-likelihoods and Akaike's Information Criterion (AIC) scores to determine which variables could be excluded, and sequentially reduced our model using the drop1 function in R. Some terms we judged a priori to be inherently highly correlated (e.g., the number of 3-day freeze events and 4-day freeze events), and we retained only the best-supported model as measured by ΔAIC. When we arrived at our best reduced model, we also evaluated possible interactions with state and year (reevaluating the main effects of those terms as well). Finally, we built a model set that included all possible combinations of the most informative parameters, ranked these by AIC scores, and calculated model-averaged coefficients for this reduced set (Burnham and Anderson 2002).

In our final analysis, we used individual telemetry locations to diagnose which variables were important in predicting use of a particular habitat. Each location was associated with a specific habitat, period of day, and hourly tide stage, and was designated as frozen or non-frozen. We excluded approximately 3,000 points for which the time of the telemetry

Table 2. Complete list of parameters used in analysis of home and core range size of American black ducks (*Anas rubripes*) wintering along the Atlantic Coast, USA, 2004–2011.

Parameter	Description
Age	Binary; either first-year or adult
First date	Date (days since 1 Jul of the previous year) of first telemetry location
State	US state in which the bird was located
Region	Rough approximation of latitude: North (NY and CT), Middle (DE and NJ), South (VA)
Year	Autumn year in which the points were collected
Primary dist	Average distance to primary roads
Second dist	Average distance to secondary roads
Frozen(N)	Total number of periods of cold weather lasting N days, where N ranged from 1 to 5 (e.g., Frozen4)
Salt marsh	Proportion of home range comprised high marsh + low marsh + mudflat + subtidal + general wetlands
Reduced salt marsh	Proportion of home range comprised high marsh + low marsh + mudflat + general wetlands
Fresh marsh	Proportion of home range comprised freshwater + forested wetlands

location was not recorded. Given the number of habitats and explanatory variables, a multinomial mixed-effect regression was intractable; instead, we used dummy variables for each habitat of interest and used generalized logistic mixed models to determine which environmental factors were important for determining its use. For example, a location in freshwater was coded as 1 in the freshwater habitat column and 0 for all other habitat types; we then modeled which environmental variables (day, tide, weather; see above) were associated with freshwater locations. We ran all possible combinations of age and environmental variables (age, period, tide, frozen). We used individual duck as a random effect to account for intrinsic differences among birds. We ranked models by AIC and calculated model-averaged coefficients as above; we discuss only variables that strongly influenced the use of each habitat (reported as coefficient estimates $\pm$ SE). We conducted all GIS analyses in ArcMap 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA). We conducted all statistical analyses in R 3.0.2 (R Core Team 2014), and we used the lme4 (v. 1.0-5; Bates et al. 2013), MuMIn (v. 1.9.13; Barton 2013), and adehabitat (v. 1.8.12; Calenge 2006) packages for our analyses.

RESULTS

Home and Core Range Analysis

Across all birds, average home range size was $1{,}082 \pm 120$ ha, and there was no difference between the home range sizes of birds located in different states (analysis of variance [ANOVA]: $F = 0.503$, $P = 0.73$; Table 1, Fig. 2). Core range size was substantially smaller, encompassing 381 ± 48 ha on average (Table 1), and there also were no differences among birds located in different states (ANOVA: $F = 0.505$, $P = 0.73$). Only 1 bird in our analysis shifted its range (i.e., moved from New Jersey across the Delaware Bay to Delaware and established a new territory for unknown reasons); nevertheless, we cannot rule out the possibility that some birds dispersed from the area and were never detected again.

In general, home and core ranges were composed of similar types of habitat, and there was dramatic variation between individuals: some home ranges were composed of 80% high marsh, whereas others had home ranges containing substantial amounts of urban habitat (Fig. 3). That said, when we examined which habitats were actually used by ducks (Fig. 3), many fewer points were located in urban areas and in other non-forageable habitats. One notable exception was an individual for which >40% of points were located in urban areas (Fig. 3). This duck spent most of the day near Smithville, New Jersey in a small lake where humans consistently fed ducks, and only occasionally made late-night forays into nearby salt marsh habitat.

Home range size was not affected by state, year, age, the distance to secondary roads, or the number of short-duration cold snaps. Preliminary step-wise analysis led to a reduced model that included the number of 4-day frozen periods, the average distance to primary roads, and the proportion of the range comprised of salt marsh. The addition of interactions between salt marsh (and fresh marsh [proportion comprised of freshwater + forested wetlands]) with the number of 4-day frozen periods did not improve model fit and were not considered further. Finally, salt marsh comprises several similar but distinct habitats (see Methods Section and Table 2); we sequentially replaced the aggregate variable salt marsh with each constituent habitat type and examined AIC

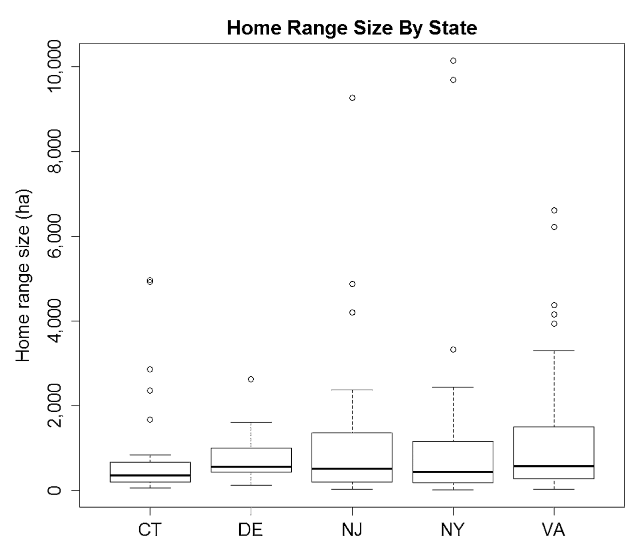

Figure 2. Boxplots of American black duck (*Anas rubripes*) wintering home range size by state, 2004–2011.

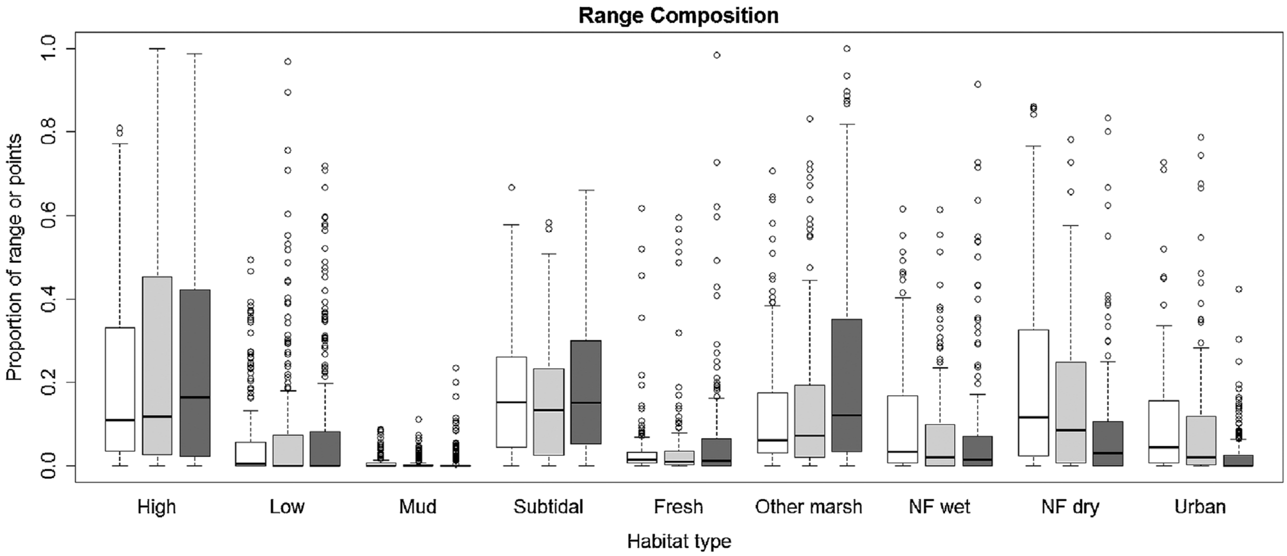

Figure 3. Habitat composition of American black duck (*Anas rubripes*) winter home ranges (open boxplots), core ranges (light gray boxplots), and the proportion of actual locations occuring in each habitat type (dark gray boxplots) along the Atlantic Coast, USA during 2004–2011. Forageable habitat categories are high marsh (high), low marsh (low), mudflat (mud), subtidal, freshwater marsh (fresh), and other marsh. Nonforageable (NF) habitats were grouped into wet habitats (e.g., open water) and dry habitats (e.g., deciduous forest), with urban areas broken out.

scores and parameter coefficients to determine the relative contribution of each habitat. All salt marsh habitats were associated with a larger home range, except subtidal habitats, which were associated with a smaller home range. Thus, we removed subtidal habitats from our lumped salt marsh classification; replacing salt marsh with the new parameter, reduced salt marsh, improved model fit by >5 AIC points. We elected to keep a modified lumped classification scheme for 2 reasons: 1) the general wetlands category already included high marsh, low marsh, and mudflat; 2) these habitats provided similar foraging access, whereas subtidal habitats could be qualitatively different because ducks may not forage at depths approaching 1 m. Inclusion of subtidal habitats as a separate variable from reduced salt marsh was not supported (increased AIC by 1.1).

Our best-fitting model for home range size included the average distance to primary roads, the number of 4-day frozen periods, and reduced salt marsh, and was 4.7 times more likely than our second-ranked model (Table 3). Home range sizes were larger for birds experiencing more 4-day cold snaps, and smaller for birds with more salt marsh in their home range (Table 4). There was a weak tendency for birds to have larger home ranges the farther they were from primary roads (Table 4).

Our analysis for core range size paralleled that of home range size, and we found similar support for excluding subtidal habitats from our lumped salt marsh parameter. Our candidate set of models for core range size was identical to that for home range size, except it also included the proportion of fresh marsh in the core range and an interaction between fresh marsh and number of 4-day freeze events. In diagnosing the constituent habitats of fresh marsh (Table 2), we did not find any support for splitting out freshwater and forested wetland habitats.

The best model predicting core range size included all parameters in the reduced set, and was 3.7 times more likely than the next best model (Table 5). Core range size increased with the number of 4-day cold snaps and distance to primary roads, and decreased with the proportion of salt marsh in the range (Table 4). Core range size depended strongly on the interaction between the proportion of freshwater habitat contained in the core range and the number of 4-day frozen periods the duck experienced: individuals with primarily freshwater core ranges tended to have smaller core ranges if they experienced more cold snaps than did birds with core ranges dominated by salt marsh.

Table 3. Candidate models describing home range size of American black ducks (*Anas rubripes*) wintering along the Atlantic Coast, USA, 2004–2011. Frozen4 refers to the number of 4-day spans with a maximum daily temperature <0° C experienced by a duck. Reduced salt marsh is the proportion of the home range comprising salt marsh habitats (excluding subtidal habitats). Primary dist is the average distance to primary roads. Only models comprising 0.99 of cumulative model weight are shown.

Parameters	AIC[a]	ΔAIC	Weight	Cumulative weight
Frozen4 + reduced salt marsh + primary dist	3,170.7	0.0	0.811	0.811
Frozen4 + reduced salt marsh	3,173.8	3.1	0.172	0.983
Reduced salt marsh + primary dist	3,180.4	9.8	0.006	0.989

[a] Akaike's Information Criterion.

Table 4. Model-averaged parameter estimates (±SE) for variables affecting home and core range size of American black ducks (*Anas rubripes*) wintering along the Atlantic Coast, USA, 2004–2011. Frozen4 refers to the number of 4-day spans with a maximum daily temperature <0° C experienced by a duck. Reduced salt marsh is the proportion of the home range comprising salt marsh habitat (excluding subtidal habitats). Primary dist is the average distance to primary roads. Fresh marsh is the proportion of home range comprising freshwater and forested wetlands.

Parameter	Home range coefficient	Core range coefficient
Frozen4	673.52 ± 195.20	365.67 ± 120.51
Reduced salt marsh	−1,817.26 ± 531.43	−657.00 ± 193.64
Primary dist	0.13 ± 0.06	0.06 ± 0.02
Fresh marsh		−303.27 ± 311.10
Frozen4 × fresh marsh		−1,813.58 ± 866.94

Analysis of Individual Telemetry Locations

Because there were several competing models that predicted the use of each habitat type (Supporting Information Tables S4–S21, available online at www.wildlifejournals.org), we discuss only model-averaged coefficients that had a strong effect on habitat use (parameter estimate $\pm 2 \times$ SE did not bound 0), and report those coefficient estimates (±SE). We found that black ducks used more high marsh habitat (0.63 ± 0.21) and less general wetland habitat (-1.21 ± 0.40) at night, and more urban habitats during the day (1.61 ± 0.74) and evening crepuscular periods (1.70 ± 0.77). Tides had only a weak influence on habitat use, but ducks appeared to use more freshwater habitats at high tide (0.20 ± 0.10). We expected ducks might use more saline habitats on days when it was frozen, and indeed, use of subtidal habitats was slightly higher (0.20 ± 0.09), but use of low marsh was actually lower (-0.43 ± 0.16); in addition, ducks appeared to use more forested wetland habitats (0.31 ± 0.13), and forests (0.30 ± 0.14) during cold weather.

DISCUSSION

In general, home and core range sizes were similar among states and years, which was surprising given the range of variation in climate (e.g., CT vs. VA in Jan) and urbanization (e.g., Long Island, NY vs. rural VA) along the Atlantic Coast. We had expected to detect consistent large-scale differences in range size across geography that correlated with general patterns of climate and food availability; instead, our analysis revealed substantial among-individual variation in home and core range size, driven by spatially and temporally refined habitat and environmental variables. Home and core range sizes were larger for black ducks experiencing more 4-day cold snaps during the winter. Interestingly, models which included 1-, 2-, and 3-day cold snaps were not supported, and 4-day cold snaps were better supported than 5-day cold snaps (likely because 5-day cold snaps were uncommon in the data). Several related insights can be gained from this: 1) unlike mallards, the black ducks we observed do not appear to undertake wholesale within-season shifts in wintering ranges in response to increasingly severe winter weather (sensu Schummer et al. 2010, but see also Morton et al. 1989*b*); 2) if the black duck strategy then is to hunker down and wait out the cold snap, the fact that we saw changes in home ranges after 4 days of frozen temperatures supports the hypothesis that black ducks can survive approximately 4 days on energy reserves before seeking new, but local, food sources (Albright et al. 1983, Cramer 2009); 3) black ducks may use habitats outside or on the periphery of their range in response to cold weather.

Interestingly, we found that ducks whose home ranges contained a greater proportion of fresh marsh tended to have smaller core ranges when they experienced more 4-day cold snaps. And although our analysis of individual telemetry locations indicated that ducks used more forested wetlands on cold days, when we broke out forested wetland habitats in our model of core range size, we found that the effect of fresh marsh × number of 4-day freeze events was not solely being driven by forested wetlands. Why do ducks have a smaller core range in situations where that area is more likely to freeze over? First, these areas may not freeze over even during prolonged periods of cold weather because many of the freshwater habitats included in this analysis are spring-fed pools or running streams, and can provide small patches of open water during freeze events. Second, some freshwater habitats have much higher levels of energy than salt marsh (Ringelman et al. 2015). This could mean that birds in using these habitats extensively may be in better condition, allowing them to wait out cold snaps without expanding their core range. However, if food energy were a primary driver of core range size, fresh marsh should have a negative main effect on core range size (i.e., regardless of weather), which was not supported by the data (Table 4). Unfortu-

Table 5. Candidate models describing core range size of American black ducks (*Anas rubripes*) wintering along the Atlantic Coast, USA, 2004–2011. Primary dist is the average distance to primary roads. Frozen4 refers to the number of 4-day spans with a maximum daily temperature <0° C experienced by a duck. Reduced salt marsh is the proportion of the core range comprising salt marsh habitats (excluding subtidal habitats), and fresh marsh is the proportion of the core range comprising freshwater and forested wetlands. Primary dist is the average distance to primary roads. Only models comprising 0.99 of cumulative model weight are shown.

Parameters	AIC[a]	ΔAIC	Weight	Cumulative weight
Primary dist + frozen4 + reduced salt marsh + fresh marsh + frozen4 × fresh marsh	2,836.4	0.00	0.544	0.544
Primary dist + frozen4 + reduced salt marsh	2,839.0	2.59	0.149	0.693
Primary dist + frozen4 + reduced salt marsh + fresh marsh	2,839.1	2.69	0.142	0.835
Frozen4 + reduced salt marsh	2,840.8	4.42	0.060	0.895
Frozen4 + reduced salt marsh + fresh marsh + frozen4 × fresh marsh	2,841.1	4.67	0.053	0.948
Frozen4 + reduced salt marsh + fresh marsh	2,841.5	5.05	0.044	0.992

[a] Akaike's Information Criterion.

nately, we lack ground-truthed information on which habitats were frozen on particular days, and indeed, many ducks were not able to be located on frozen days; this highlights the need for additional local-scale telemetry studies to address the effect of cold weather on black duck space use.

We also found that home and core range sizes were smaller for ducks with a greater proportion of salt marsh in their ranges (Table 4). This supports the idea that salt marshes are fundamental habitats that can provide for the majority of the needs of wintering black ducks, although they contain a lower density of food energy than some freshwater managed impoundments (Ringelman et al. 2015). Salt marshes may provide a greater diversity of foods that are replenished by tidal action, but this remains an area of active research (Ringelman et al. 2015). Black duck use of salt marsh may represent inherent niche separation from closely related species such as mallards (sensu Barnes and Nudds 1991), and birds with more salt marsh in their range may enjoy reduced competition for resources, and so can maintain a smaller range.

Over the course of refining the models for home and core ranges, we found that including subtidal habitats (those areas of open water <1 m deep) in our lumped salt marsh parameter reduced model fit. Although difficult to fully diagnose with this dataset, black ducks may respond differently to subtidal habitats than other types of salt marsh—possibly because our 1-m depth cutoff (the best resolution available for this analysis) is too deep for foraging black ducks. We urge caution in delineating subtidal habitats for carrying capacity modeling but argue they should be included because of their value during periods of cold weather (see also Morton et al. 1989*c*).

Finally, we found that ducks that were farther from primary roads (highways) had larger core ranges. On average, duck locations were approximately 2.2 km away from primary roads, so direct disturbance effects (i.e., flushing birds from the water) seem unlikely. Rather, the ducks closer to roads may have smaller home ranges because they have adopted a more localized, urban lifestyle, relying on human food subsidies instead of large expanses of native salt marsh. Indeed, this view is supported by Morton (2002), who suggested that persistent human disturbance at the landscape level would select for habituation. In our study, the birds close to roads with small home ranges tended to be found on Long Island and in coastal Connecticut and had ranges comprising 19% urban habitat, whereas individuals farthest from roads with large ranges tended to be from rural Virginia (ranges comprising 7% urban habitat). Given that only small patches of salt marsh remain in New York and Connecticut, black ducks may habituate out of necessity. The effect of distance to primary roads on home range size may be best interpreted as a behavioral-ecological gradient between urban-adapted and urban-avoiding individuals, rather than a direct, acute effect of anthropogenic disturbance.

Our goal in analyzing individual telemetry locations was to understand which habitats birds were using in relation to time of day, tides, and weather. Given the variation inherent in this large dataset, we expect our analysis captured only the broadest and strongest effects, or in some cases, perhaps only pieces of the puzzle. Here, we discuss the biology and ecology that may underlie our results; nevertheless, new GPS telemetry research and behavioral studies are needed to fully understand these effects. For example, our telemetry data were not suited for addressing black duck responses to spatially and temporally ephemeral influences, such as boat traffic and hunting, despite the fact that these are known to influence habitat use and energy expenditure (Morton et al. 1989*c*, Jones 2012).

We found evidence that black ducks were using high marsh more during nocturnal periods. Jones (2012) found that black ducks actively forage at night; our results may suggest that high marsh provides valuable nocturnal foraging resources. Also, given that many ranges contain a large proportion of high marsh, and that black ducks move less at night (Jones 2012), it may be that black ducks are simply more likely to select a nocturnal location in high marsh, and stay there. Morton et al. (1989*a*) and Jones (2012) and found that black ducks tended to feed less in (tidally influenced) salt marsh at high tide, and indeed, our results show that ducks were marginally more likely to be found in freshwater habitats during these periods. We were surprised to not identify stronger tidal influences; although we calculated location- and hour-specific tide stages, NOAA tide stations may have been too dispersed to accurately capture tidal swings at the sites black ducks were using. Tidal stage can vary dramatically even over a few dozen miles, depending on wind conditions, bathymetry, and local topography and so fully understanding these effects will require detailed, highly localized measurements of tides.

Concordant with our analyses of home and core ranges, we found that weather influenced space use. We found mixed support for the increased use of saline habitats during periods of cold weather: ducks used more subtidal habitat but less low marsh, likely because constant water circulation in subtidal habitats prevents freezing, whereas the surface of low marsh can ice over at low tide. This corroborates the findings of Morton et al. (1989*c*) who found increased use of subtidal habitats during cold weather. We suggest that direct observations of black ducks (or satellite telemetry) and concurrent ground-truthing of low marsh habitats are needed to determine whether these habitats are truly available during extended periods of frozen weather. Interestingly, we found strong support for increased use of forested wetlands on days when the temperature never rose above freezing. Black ducks in Tennessee may increase their use of forested wetlands in late winter (Chipley 1995, Clark 1996) and a brief survey of the historical hunting literature reveals that hunters often sought out black ducks in flooded woodlands during inclement weather (e.g., Van Campen 1939). Nevertheless, forested wetlands have generally not been considered important wintering habitats for black ducks, and so we are lacking information on what food resources and thermal refuges these habitats may provide. Forested wetlands are valuable habitats for breeding and brood-rearing black ducks in more northern areas (Ringelman and Longcore 1982, Diefenbach and Owen 1989), and our results suggest that these habitats deserve more attention as potentially important wintering resources.

We found that black ducks were using urban areas more during the daytime and evening crepuscular periods. In general, relatively few telemetry locations occurred in urban areas, and so these results may be driven by a subset of ducks that are adapted to urban environments. We speculate that these birds may have learned to take advantage of human subsidies in urban areas—for example, being fed in city parks—which are more likely to be available during daylight hours. Population surveys and behavioral studies conducted in areas with different levels of urbanization are important to substantiate these findings.

MANAGEMENT IMPLICATIONS

The goal of this study was to quantify black duck use of wintering habitats across the Atlantic Coast in relation to environmental stressors and anthropogenic influences. By identifying which habitats were used by black ducks, the Atlantic Coast Joint Venture (ACJV) and waterfowl managers can 1) determine which habitats should be included in carrying capacity modeling, and 2) target future conservation and restoration efforts in habitats that are critical for wintering black ducks. Currently, the ACJV estimates habitat delivery goals for black ducks assuming all wetlands are available. However, this assumption has been questioned based on anecdotal observations that black ducks are more likely to avoid areas with human disturbance than other waterfowl species. If true, current estimates of available habitat are biased high and habitat delivery goals are biased low. Our results show black ducks do not strongly avoid wetlands in urban areas, so we believe current estimates of available habitat are accurate and sufficient for habitat planning.

Our study confirms that salt marsh is heavily used by black ducks and that subtidal habitats may be particularly important during prolonged cold events. Our results provide some support for the assumption that salt marshes do not freeze as quickly as freshwater wetlands and provide important food resources during prolonged cold events. However, we also recommend that forested wetlands be included in carrying capacity models and habitat delivery plans. For example, the recently published Chesapeake Bay Program black duck management strategy (Chesapeake Bay Program 2015) is focused on acquiring and protecting areas with high food availability (i.e., salt marsh) that are at high risk of urban development. However, this strategy is based on the current ACJV bioenergetics model which does not incorporate forested wetlands because the ACJV lacks empirical estimates of the energetic capacity of forested wetlands along the Atlantic coast. More research is needed to determine the relative value of forested wetlands for foraging and refuge. Black duck use of forested wetlands increased after prolonged periods of cold weather, and so management for these types of habitats may become more pressing as winter storms increase in frequency and severity with climate change (Intergovernmental Panel on Climate Change 2014). Furthermore, as accelerating sea-level rise eliminates and alters coastal marsh habitat, coastal forested wetlands may become an increasingly valuable resource for wintering black ducks and also provide space for salt marsh migration. Finally, we recommend the ACJV and habitat managers strive to identify and protect areas comprised of a mosaic of salt marsh and forested wetlands in close proximity to maximize the overall carrying capacity for black ducks. The interspersion of these wetlands types should help maximize energetic availability and minimize energetic expenditures by minimizing travel distances between high-value habitats.

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