

RESEARCH ARTICLE

Habitat selection of non-breeding American black ducks in an urban estuary

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Abstract

Shellfish aquaculture is a globally expanding industry, including in urban estuaries that support non-breeding waterfowl. The effects of shellfish aquaculture on the spatial distribution of non-breeding waterfowl, however, are poorly understood and depend on the ecology of waterfowl and cultivated shellfish species. We investigated how proximity to shellfish aquaculture influenced habitat selection and movement patterns of American black ducks (*Anas rubripes*) during the non-breeding season (~Oct–May) in 2020–2023 in Rhode Island, USA. The extent to which proximity to aquaculture influenced habitat selection of black ducks depended on factors specific to individuals' primary non-breeding sites, although proximity to aquaculture did not have biologically meaningful influences on black duck movement rates across all sites. Black ducks across sites consistently selected for areas better suited for aquaculture (i.e., areas of potential future development) relative to areas poorly suited for aquaculture (i.e., areas less likely to be developed). The continued expansion of aquaculture into preferred black duck habitats will increase black duck interactions with aquaculture and therefore should be considered in the decision-making process for siting future aquaculture leases. Future studies should quantify the extent to which continued expansion of aquaculture in those preferred coastal habitats directly influences black ducks.

KEYWORDS

Anas rubripes, GPS-GSM transmitter, integrated step selection, movement, oyster aquaculture, Southern New England

Habitat selection studies strive to quantify a species use of habitat components relative to their availability based on the assumption that animals should select elements that provide some benefit but avoid elements that pose risks or costs (MacArthur and Pianka 1966, Matthiopoulos et al. 2020). Understanding how animals select and avoid different habitat components can provide insight into population-level distribution patterns (Northrup et al. 2022). Habitat selection strategies can vary among individuals of the same species because of intrinsic characteristics (e.g., sex, age; Lesmerises and St-Laurent 2017, Muff et al. 2020), differences in habitat availability across individuals' locales (i.e., functional responses; van Beest et al. 2016, Holbrook et al. 2019), and the density of the study species, competitor species, or predators (Heithaus 2001, Avgar et al. 2020). Characterizing individual and site-specific habitat selection can therefore reveal important behavioral variation that might be overlooked by considering habitat selection at only the population level (Northrup et al. 2022). In addition, a focus on individual and site-specific habitat selection can provide insight for conservation agencies on how animals directly respond to anthropogenic development.

Quantifying how individual animals move through areas that they select or avoid may provide insights into how habitats are used for certain purposes (e.g., foraging, resting, movement corridors) and how animals respond to disturbance (Avgar et al. 2016, Dickie et al. 2020). Step selection functions (SSFs) take advantage of fine-scale animal tracking data by quantifying habitat selection along an animal's movement path rather than assuming habitat is uniformly available across space and time, as is the case in traditional selection analyses (Fieberg et al. 2021, Northrup et al. 2022). Integrated step selection functions (iSSFs) are an extension of SSFs that explicitly acknowledge that animal habitat selection and movement processes are inherently dependent on each other. The iSSF approach simultaneously estimates the effects of environmental variables on habitat selection and movement patterns and quantifies relationships between the 2 processes (Avgar et al. 2016). In particular, iSSFs can be used to explore animal habitat selection and movement patterns in response to anthropogenic features and are therefore useful for wildlife managers working in human-dominated landscapes. For example, iSSFs were used to understand the influence of energy infrastructure development on elk (*Cervus canadensis*) in southwest Alberta (Prokopenko et al. 2017), road and traffic intensity on wolverines (*Gulo gulo*) in northern Alberta (Scraftford et al. 2018), anthropogenic linear features on predator and prey mammals in Alberta and Saskatchewan, Canada (Dickie et al. 2020), and shellfish aquaculture gear on great egrets (*Ardea alba*) in California, USA (Jennings et al. 2021). Understanding animal movement and habitat selection behavior in environments with large anthropogenic influences is especially important for management strategies that mitigate human–animal conflicts.

Waterfowl that use coastal waters associated with urban centers can be particularly subject to direct and indirect effects of elevated anthropogenic activity (Zydelis and Dagys 1997; McKinney et al. 2006, 2015; Ethier et al. 2020; Musicz and Faragó 2021). For example, commercial fishing and shipping traffic, along with recreational activity including boating and kayaking, fishing, and shellfishing, can contribute to decreased waterfowl use of areas via habitat degradation and direct disturbance and displacement (Korschgen et al. 1985, Kahl 1991, Knaption et al. 2000, Pease et al. 2005). Another potential source of disturbance to waterfowl is shellfish and finfish aquaculture, which is a growing industry across the world (Food and Agriculture Organization Fisheries and Aquaculture 2021). Increased human presence associated with aquaculture has the potential to displace waterfowl from preferred habitats (Ross et al. 2001, Barrett et al. 2019). Alternatively, waterfowl could be positively associated with aquaculture if the infrastructure provides foraging or roosting opportunities (Kirk et al. 2007, Zydelis et al. 2009, Varennes et al. 2013, Barrett et al. 2019, Clements et al. 2021). Effects of shellfish aquaculture on the distribution of waterfowl are poorly understood, may vary among waterfowl species, and may differ by cultivated shellfish species and technique (Zydelis et al. 2006, 2009; Varennes et al. 2013; Callier et al. 2018). For example, common eiders (*Somateria mollissima*), long-tailed ducks (*Clangula hyemalis*), and goldeneyes (*Bucephala* spp.) forage on blue mussels (*Mytilus edulis*) cultivated via suspended longline systems in the North Atlantic Ocean (Ross et al. 2001, Roycroft et al. 2004, Varennes et al. 2013). In the North Pacific, scoter (*Melanitta* spp.) and Barrow's goldeneye (*Bucephala islandica*) distributions were negatively (Zydelis et al. 2006) and positively (Zydelis et al. 2009) associated with caged oyster (*Crassostrea virginica*) aquaculture operations. Thus, there is a need for

more species-specific studies that document habitat selection and movements of waterfowl in areas with increasing coastal shellfish aquaculture.

American black ducks (*Anas rubripes*; black ducks) are an omnivorous dabbling duck that winter in coastal brackish and freshwater systems of the Atlantic Flyway (Baldassarre 2014, Lawson et al. 2021, Monroe et al. 2021). Steady declines in the continental black duck population during the second half of the twentieth century were attributed to habitat loss and degradation, contaminants, over-harvest, and competition and hybridization with mallards (*Anas platyrhynchos*; Conroy et al. 1989, Devers and Collins 2011, Lawson et al. 2021). Black duck declines have continued since the turn of the century, with estimated breeding black duck populations reduced from approximately 828,500 in 1998 to 732,000 in 2023 in the eastern survey area of the Waterfowl Breeding Population and Habitat Survey (USFWS 2023). Moreover, the Atlantic coast is an important area for targeted habitat management and restoration to support black ducks (Robinson et al. 2016). The largest estuary in New England is in Rhode Island, USA, and provides habitat for numerous waterfowl species, including black ducks (McKinney et al. 2006, 2015). Estimated black duck numbers have declined from approximately 2,500 to 1,000 individuals during 2004–2020 based on a midwinter survey that covers all of Rhode Island's coastal and some inland waters (C. Cooper-Mullin, University of Rhode Island, unpublished data). Over a similar period (1996 to 2022), the number of active aquaculture leases in Rhode Island's coastal waters increased from 6 to 84 (Goetsch 2022). Increasing aquaculture infrastructure and associated human activity have the potential to influence Rhode Island's non-breeding black duck populations. Whereas several studies have investigated environmental and anthropogenic effects on southern New England's non-breeding waterfowl (McKinney et al. 2006, Loring et al. 2013, Kreakie et al. 2015, Beuth et al. 2017, Meattley et al. 2019), none have considered black ducks or the relative influence of shellfish aquaculture on habitat selection and movement patterns.

Our objectives were to estimate black duck habitat selection and movement rates relative to proximity to existing aquaculture leases and additional environmental and anthropogenic variables, and to estimate black duck habitat selection and movement rates in areas of coastal salt ponds that vary in suitability for shellfish aquaculture leasing. Regarding our first objective, we hypothesized that the influence of proximity to aquaculture leases on habitat selection and movement rates (faster reflecting foraging and slower reflecting roosting behavior) of black ducks would depend on site-specific characteristics (e.g., extent of aquaculture, site size) given the variable demonstrated relationships of other species with shellfish aquaculture (Ross et al. 2001; Roycroft et al. 2004; Zydulis et al. 2006, 2009; Varennes et al. 2013). Regarding our second objective, we hypothesized black ducks would select for areas in coastal salt ponds that are suitable for aquaculture, and that expected movement rates would reflect foraging (i.e., faster) in areas more suitable and roosting (i.e., slower) in areas less suitable for aquaculture.

STUDY AREA

Rhode Island's coastal waters include Narragansett Bay in the central-eastern portion of the state, Block Island and Rhode Island sounds along the southern border of the state, and several shallow, tidal, estuarine lagoons (i.e., coastal salt ponds) that are separated from the sounds by barrier beaches but connected to the sounds via breachways (Rhode Island Environmental Monitoring Collaborative 2023). Oysters are the primary cultivar of Rhode Island aquaculture farmers, accounting for approximately 99% of aquaculture production in the state, though a minority of farmers also cultivate blue mussels (*Mytilus edulis*), clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and sugar kelp (*Saccharina latissimi*; Goetsch 2022). In Rhode Island, oysters are grown in cages or mesh bags placed either directly on the bottom of a waterbody or floated in the water column (Goetsch 2022). The state of Rhode Island regulates aquaculture leases to $\leq 5\%$ of the surface area of any 1 coastal salt pond (Coastal Resources Management Council Working Group, unpublished report) but is considering increasing this limit to 10% (B. Goetsch, Coastal Resources Management Council and J. E. Osenkowski, Rhode

Island Department of Environmental Management, personal communication). There are currently no restrictions for the allotment of aquaculture leases in Narragansett Bay, making the bay the most likely area for continued aquaculture expansion in the state.

We captured non-breeding black ducks at 5 sites across Rhode Island and monitored black duck movements during the non-breeding seasons (~Oct–May) in 2020–2021, 2021–2022, and 2022–2023. We excluded data collected during migratory and breeding periods (~Apr–Sep) from our analyses. All sites have active aquaculture leases within 4.6 km (range = 0.4–4.6 km; Figure 1). Four of the 5 capture sites were within the Long Island Sound Coastal Lowland Level IV Ecoregion, characterized by low-elevation plains, tidal marshes, estuaries, dunes and beaches, and rocky shorelines, whereas the fifth site was in the Narragansett/Bristol Lowland Level IV Ecoregion, characterized by irregular coastal plains and elevations below 60 m (Griffith et al. 2009). All capture sites were on brackish saltmarshes dominated by smooth cordgrass (*Spartina alterniflora*) adjacent to larger coastal waterbodies. The Pawcatuck River and Wickford Harbor had no active aquaculture leases within their bounds. The other 3 capture sites were adjacent to coastal salt ponds in southern Rhode Island that contain active aquaculture (Winnapaug Pond, Ninigret Pond, Point Judith Pond; Table 1; Figure 1). Habitats were similar across these coastal salt ponds; however, these ponds differed in size, shape, and extent of active aquaculture (Table 1; Figure 1).

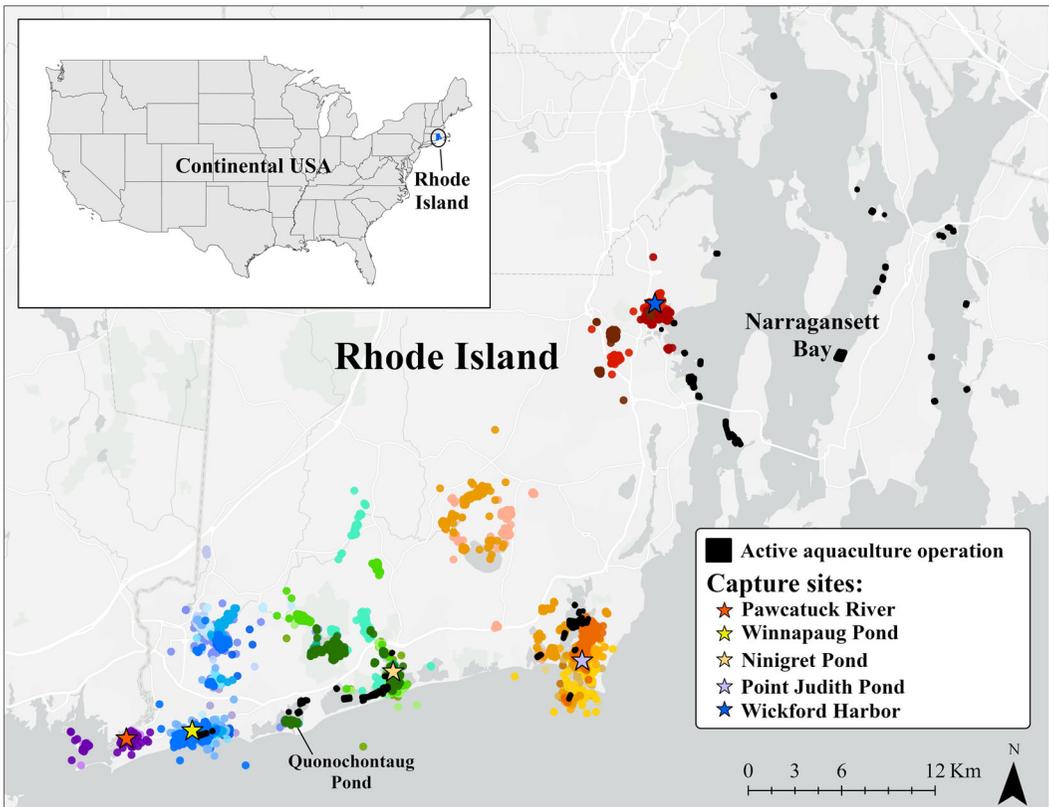


FIGURE 1 Study area where we tracked 26 American black ducks using Global Positioning System – Global System for Mobile Communications (GPS–GSM) transmitters in Rhode Island, USA, during winters 2020–2021, 2021–2022, and 2022–2023. Black duck relocations are indicated by circles with color representing individual birds. Capture sites are shown with stars and named according to the coastal waterbody to which they are adjacent, and which served as primary non-breeding season sites. Active aquaculture operations (as of winter 2022–2023) are depicted as black polygons.

TABLE 1 Characteristics of coastal waterbodies to which American black duck capture sites were adjacent, and which served as primary non-breeding season sites in Rhode Island, during winters 2020–2021, 2021–2022, and 2022–2023. Characteristics for the Pawcatuck River capture site are not described, as individuals from that site were not included in integrated step selection function analyses. Composition of aquaculture suitability categories for Wickford Harbor are not included (and shown as not applicable [n/a]), as individuals from that capture site were not included in that integrated step selection function analysis.

	Winnapaug Pond	Ninigret Pond	Point Judith Pond ^a	Wickford Harbor
Size (km ²)	1.93	8.54	7.88	1.76
Shape index ^b	4.65	6.10	8.16	4.69
Percentage composed of aquaculture (by area)	3.45%	3.47%	4.23%	0.00% ^c
Aquaculture suitability composition (percentage by area)				
Well suited	26.58%	29.23%	20.49%	n/a
Fairly well suited	12.96%	14.97%	15.47%	n/a
Poorly suited	60.45%	55.11%	63.78%	n/a
Not suited	0.00%	0.69%	0.26%	n/a

^aIncluding Potter Pond, which is connected to Point Judith Pond via a tidal channel.

^bUnitless, pond perimeter becomes increasingly complex as value increases.

^cWhile no aquaculture is present within the bounds of Wickford Harbor, there is an aquaculture operation 123 m east of the harbor.

In addition, Point Judith Pond was subjected to elevated anthropogenic activity relative to Winnapaug and Ninigret ponds, particularly at the southeastern extent of the pond, where an active commercial fisheries port and ferry terminal are located.

Rhode Island (including waterbodies) is approximately 4,000 km² and experiences a seasonal climate. In coastal Rhode Island, the mean minimum daily temperature during January and February (midwinter) is -4°C and a mean of 20–25 days/year have a maximum temperature of 0°C . Mean annual snowfall in coastal Rhode Island varies slightly along the southern shore and farther north along Narragansett Bay, ranging from 50–90 cm (Rhode Island Department of Environmental Management 2023b). Weather conditions during our study period were similar to the average climate of the area. Narragansett Bay supports an average of approximately 20,000 individual non-breeding waterfowl (McKinney et al. 2015), whereas the coastal salt ponds support an additional approximately 2,500 individuals (J. E. Kilburn, Rhode Island Department of Environmental Management, personal communication). The most abundant waterfowl species during the non-breeding season in Rhode Island from 2004–2020 included lesser (*Aythya affinis*) and greater (*A. marila*) scaup, brant (*Branta bernicla*), bufflehead (*Bucephala albeola*), Canada goose (*Branta canadensis*), common eider, and common goldeneye (*Bucephala clangula*; C. Cooper-Mullin, unpublished data).

METHODS

Collection of non-breeding season data

We used rocket nets at baited sites (Dill and Thornsberry 1950) to capture 30 black ducks during a single non-breeding season between 10 February to 3 March 2021. Upon capture we banded all individuals with a United

States Geological Survey federal leg band, weighed them, and determined sex and age (adult or juvenile) of individuals by examining plumage (Carney 1992). We then attached solar-powered 25-g Global Positioning System – Global System for Mobile Communications (GPS-GSM) transmitters (OrniTrack-25 4G; Ornitela, UAB, Vilnius, Lithuania) to adult birds using backpack-style harnesses (McDuie et al. 2019a, Casazza et al. 2020). Auxiliary markers (i.e., transmitter, harness, leg band) did not exceed 3% of an individual's body mass ($\bar{x} = 2.28 \pm 0.24\%$ [SD]).

We censored the first 4 days following deployment of external transmitters to allow sufficient time for individuals to recover from capture and handling (Cox and Afton 1998, Palumbo et al. 2019). Location collection interval varied based upon geographic location, annual phenology, and transmitter battery percentage. Primarily because of fluctuations over time in battery charge, GPS locations were collected every 1, 2, 12, or 36 hours during the non-breeding period (~Oct–May depending on individual's migratory phenology). Transmitter batteries were solar powered and could last multiple years. Therefore, it was possible for individuals to be monitored across multiple non-breeding seasons, and that individuals that provided more data might have narrower estimates of variance around reported coefficients than individuals that were only monitored during a single non-breeding season.

We completed all data formatting, manipulation, and analyses in R statistical software (R Core Team 2023). We first restricted potential non-breeding periods based on black duck movement phenology (Ringelman et al. 2015, Coluccy et al. 2020). Possible immigration periods to non-breeding areas were between 15 September and 1 February and emigration periods were between 1 March and 15 June. We then determined each individual's arrival and departure dates, using the periods defined above, by evaluating movement trajectories that we generated from individuals' GPS point data using the package *adehabitatLT* (Calenge 2006). We isolated individual-specific immigration and emigration dates within the periods using metrics of distance between consecutive locations and turn angle that distinguished between migratory and local-scale movements. For individuals that returned to Rhode Island multiple years, we identified the arrival location to non-breeding sites as those >3 km from the previous location, with a net-squared displacement within 15 km² of the individual's initial capture location, and with displacement in absolute turn angle <0, indicating a southward movement from the previous location. We then identified the first spring migration locations as those >3 km from the previous location, with a net-squared displacement >15 km² from the initial capture location, and with a displacement in absolute turn angle >0, indicating a northward movement from the previous location (Bunnefeld et al. 2011, Edelhoff et al. 2016, Johnstone et al. 2023). We identified final non-breeding season locations as those immediately preceding first spring migration locations. We retained all locations that occurred in the time between the individual's identified first and final non-breeding season locations.

Habitat covariates

We considered a suite of covariates that we expected *a priori* could influence the habitat selection and movement patterns of black ducks during the non-breeding season in Rhode Island (Devers and Collins 2011, Ringelman et al. 2015, Monroe et al. 2021). Covariates included proximity to aquaculture, human development (i.e., on-land areas comprised of ≥20% human-constructed materials), estuarine water (i.e., Narragansett Bay and the coastal salt ponds), fresh water (i.e., inland ponds and lakes with <25% cover of vegetation or soil), shoreline (i.e., nearest shoreline when on estuarine or fresh water), rivers (also includes streams, expected to provide more cover and seclusion for black ducks compared to the freshwater covariate), submerged aquatic vegetation (including patchily distributed widgeon grass [*Ruppia cirrhosa*] and eelgrass [*Zostera marina*] only present in estuarine waterbodies), and wetlands (emergent and forested waterbodies with >25% cover of vegetation or soil). We generated rasters of year-specific proximity to nearest active aquaculture lease from the aquaculture sites map maintained by the Rhode Island Department of Environmental Management Marine Fisheries (Rhode Island Department of Environmental Management 2023a). We generated proximity to aquaculture data for each non-breeding season to account for

lease activity patterns over the course of our study period. All other proximity data were the most available datasets retrieved from the Rhode Island Geographic Information System (RIGIS) and included forest cover (2020), submerged aquatic vegetation in coastal waters (2021), and integrated water quality monitoring assessment from 2010 and 2012 (RIGIS 2023). We generated all proximity rasters using Euclidean distance tools in ArcGIS Pro version 3.0.3 (Esri, Redlands, CA, USA). We projected all rasters at a 1-m resolution using the project raster tool in ArcMap to match the resolution of the finest-scale raster datasets in North American Datum of 1983 (High Accuracy Reference Network), Universal Transverse Mercator zone 19N (European Petroleum Survey Group code 3749). We incorporated a decay effect for all proximity covariates by taking the natural log of the proximity plus 1 (e.g., $\ln[\text{proximity} + 1]$; Timm et al. 2016, Prokopenko et al. 2017). The decay effect allowed us to account for the assumption that the farther a black duck was from a habitat feature, the less likely that feature was to influence selection and movement patterns. We ensured that no habitat covariates were correlated with a Pearson correlation coefficient $|r| > 0.7$. We additionally characterized the coastal waterbodies adjacent to each capture site by size, perimeter complexity (i.e., shape index), and percentage composed of aquaculture because we expected these characteristics to anecdotally influence black duck selection and movement patterns (Table 1).

To investigate black duck selection and movement patterns relative to an area's suitability for aquaculture leasing, we generated a 1-m resolution categorical raster using the Subaqueous Soils 2017 layer obtained from RIGIS (RIGIS 2023). This layer included an attribute that classified areas of the coastal salt ponds and some areas of Narragansett Bay along a spectrum of suitability for aquaculture depending on sedimentation and bottom substrate, water depth, slope, and navigation access. Specifically, this layer categorizes intertidal areas as not suited for aquaculture, deeper areas and those with fluid bottoms, obstructions, or navigation channels as poorly suited for aquaculture, areas of moderate depths and sandy or gravelly substrates with minimal sloping as fairly well suited for aquaculture, and areas with shallow water depth, minimal sloping, and sandy sedimentation outside of navigation channels as well-suited for aquaculture. We restricted this raster and analysis to the coastal salt ponds based on the limited spatial extent of the layer. Winnapaug, Ninigret, and Point Judith ponds were similar in composition of shellfish aquaculture suitability categories (Table 1).

Integrated step selection analyses

Because most GPS data were collected at either 1-hour (74.13%) or 2-hour (22.97%) intervals across the non-breeding season, we resampled individuals' movement tracks to regular 2-hour steps. We removed all locations with a recorded instantaneous speed ≥ 10 km/hour because we were interested in quantifying selection for only habitat features that black ducks were interacting with rather than flying over (McDuie et al. 2019a). We used the R package *amt* (Signer et al. 2019) to organize observed step data, generate random steps (assuming gamma distributions for step lengths and von Mises [a continuous probability distribution on a circle described by 2 parameters, mean and concentration] distribution for turn angles), fit iSSFs, and update movement parameters. We fit iSSFs to simultaneously estimate the parameters of habitat-dependent selection and movement processes (Avgar et al. 2016). This approach allowed us to make inference on the relative influence of proximity to aquaculture and the influence of suitability for aquaculture on black duck movement rates and habitat selection. We evaluated *P*-values to determine the strength of evidence for iSSF coefficient estimates (Muff et al. 2022).

Existing aquaculture iSSF

We first fit an iSSF separately to each individual that incorporated the additive effects of environmental and anthropogenic covariates we expected *a priori* to influence black duck habitat selection patterns and movement rates (i.e., existing aquaculture iSSF). We removed step lengths > 4 km ($\bar{x} = 2.76\%$ of steps/individual,

range = 0.00–15.09%) that reflected locale shifts between coastal and inland waterbodies, the latter of which includes no aquaculture leases. We fit each individual's model with increasingly large numbers of random steps (10, 100, 500) per observed step until coefficient estimates converged at consistent values across individuals (Northrup et al. 2013; Figure S1, available in Supporting Information). We calculated 95% confidence intervals for individual black duck estimates and population-level means and 95% reference ranges (i.e., range of values within which 95% of individual estimates fell) for each estimated coefficient. We considered the effect of the proximity to aquaculture on movement rates by estimating a coefficient for the interaction between the natural-log transformed step length and proximity to aquaculture at the beginning of a step. We calculated expected movement rates at differing proximities to aquaculture by multiplying the updated parameters of the step length distributions (Fieberg et al. 2021).

Aquaculture suitability iSSF

We then fit an iSSF to explore if and how black duck habitat selection and movements were related to suitability of an area within a coastal salt pond for aquaculture leasing (i.e., aquaculture suitability model). This approach allowed us to quantify how black ducks used areas likely to be leased for aquaculture in the future (i.e., areas classified as better suited for aquaculture) relative to those less likely to be leased for aquaculture (i.e., areas classified as less suited for aquaculture), and thereby explore the effects of potential aquaculture expansion on black duck space use. Because aquaculture leases cannot be in fresh water and suitability for aquaculture is only mapped across a small portion of Narragansett Bay, we restricted this analysis to only include steps that started and ended on the coastal salt ponds and immediately adjacent mapped waters. This inherently limited our inference to within-pond movements. Including only steps within the coastal salt ponds meant there were not enough steps per individual to fit this model separately to each individual as with the existing aquaculture iSSF. Instead, we randomly sampled steps across individuals to generate as balanced a sample across individuals and sites as possible. Areas unsuitable for aquaculture comprised <1% of each coastal salt pond considered in this portion of the analysis (Table 1), and too few steps ended in areas that were not suited for aquaculture, so we could not fit models incorporating that aquaculture suitability category. Thus, we modeled selection and movement rate in response to the categories: poorly suited for aquaculture, fairly well suited for aquaculture, and well suited for aquaculture leases. Our reference level suitability category was poorly suited for aquaculture leases. We fit the model separately to data from each site with increasingly large numbers of random steps (10, 100, 500, 1,000, 3,000, 5,000) per observed step until coefficient estimates converged at consistent values across sites (Northrup et al. 2013; Figure S2, available in Supporting Information). We calculated 95% confidence intervals for site-specific estimates and population-level means and 95% reference ranges (i.e., range of values within which 95% of pond-specific estimates fell) for each estimated coefficient. We considered the effect of aquaculture suitability category on movement rates by estimating a coefficient for the interaction between the natural-log transformed step length and aquaculture suitability category at the beginning of a step. We calculated expected movement rates in different aquaculture suitability categories by multiplying the updated parameters of the step length distributions (Fieberg et al. 2021).

RESULTS

Our initial marked sample included 30 adult black ducks (female $n = 14$, male $n = 16$). We removed 1 female that displayed irregular behavior (i.e., restricted motility and excessive preening for approximately 4 months after which the bird apparently died) following transmitter deployment leaving 29 individuals monitored during ≥ 1 non-breeding season. Seven black ducks returned to Rhode Island and provided data during the 2021–2022 non-breeding season (female $n = 5$, male $n = 2$), and 2 females returned again to provide data during the 2022–2023

non-breeding season. Waterbodies associated with our capture sites varied in size, perimeter complexity, and the amount of aquaculture present within their bounds (Table 1). Winnapaug Pond and Wickford Harbor were smaller (~2 km²) than Ninigret and Point Judith ponds (~8 km²). Winnapaug Pond and Wickford Harbor were also similar in perimeter complexity (i.e., relatively few coves), whereas Ninigret Pond was intermediately complex, and Point Judith Pond was the most complex (i.e., more coves). Winnapaug and Ninigret ponds contained similar amounts of aquaculture (~3.5% by area), whereas Point Judith Pond contains slightly more aquaculture (~4.2% by area), and Wickford Harbor contained no aquaculture directly within its bounds, although there was aquaculture east of this site.

Existing aquaculture iSSF

We removed 3 individuals from our sample that never came within 1 km of aquaculture. Therefore, 26 individuals across 4 sites (Winnapaug Pond $n = 10$, Ninigret Pond $n = 6$, Point Judith Pond $n = 8$, Wickford Harbor $n = 2$; Figure 1) provided sufficient data to quantify habitat selection and movement patterns relative to existing aquaculture infrastructure during the 2020–2021, 2021–2022, and 2022–2023 non-breeding seasons. Individuals took an average of 932 steps (range = 454–2,446) during the non-breeding period. Black ducks commonly moved between coastal and inland waterbodies throughout the non-breeding season but displayed great within- and across-year fidelity to the coastal waterbody on which they were captured (Figure 1; Table 1). No black ducks moved from the coastal waterbody on which they were captured to another capture site waterbody, and only 50 steps ended or started on a coastal waterbody on which no black ducks were captured (all 50 steps occurred on Quonochontaug Pond; Figure 1). Moreover, all black ducks that returned to Rhode Island for multiple non-breeding periods used the same coastal waterbody on which they were captured and demonstrated the same site fidelity described above during each non-breeding period. Therefore, we will hereafter refer to the coastal waterbody on which black ducks were captured as primary non-breeding sites.

At the population level (i.e., coefficients averaged across all individuals), black ducks selected areas closer to aquaculture (relative selection strength $\bar{x} = -0.18$, 95% reference range = -1.19 – 0.82), estuarine water (relative selection strength $\bar{x} = -1.29$, 95% reference range = -2.34 – -0.23), and to a lesser magnitude fresh water (relative selection strength $\bar{x} = -0.26$, 95% reference range = -1.08 – 0.56), shorelines (relative selection strength $\bar{x} = -0.60$, 95% reference range = -1.83 – 0.64), rivers (relative selection strength $\bar{x} = -0.26$, 95% reference range = -0.76 – 0.24), and wetlands (relative selection strength $\bar{x} = -0.60$, 95% reference range = -1.42 – 0.23). Black ducks at the population level selected areas farther from human development (relative selection strength $\bar{x} = 0.64$, 95% reference range = -0.55 – 1.83) and submerged aquatic vegetation (relative selection strength $\bar{x} = 0.21$, 95% reference range = -1.42 – 0.23 ; Figure 2). Individual black ducks showed relatively consistent within-site patterns of selection for proximity to aquaculture, which influenced the near-zero population-level relative selection strength for that covariate (Figure 2). All birds whose primary non-breeding site was Winnapaug Pond and 63% of birds using Point Judith Pond selected areas near aquaculture, whereas birds using Wickford Harbor and 50% of birds using Ninigret Pond selected areas farther from aquaculture ($P < 0.05$). The remaining 50% of individuals using Ninigret Pond did not demonstrate a relationship with proximity to aquaculture ($P > 0.05$). Most individuals across all sites selected areas far from development (85% of individuals; $P < 0.05$) and near estuarine water (96% of individuals; $P < 0.05$). Across-site selection patterns were less consistent for all other covariates (Figure 2).

Proximity to aquaculture at the beginning of the step influenced the movement rate of 10 of 26 (38%) black ducks ($P < 0.05$). Three of these individuals (1 from Winnapaug Pond, 1 from Ninigret Pond, and 1 from Point Judith Pond) moved faster as they got farther from aquaculture, whereas 7 individuals moved slower (5 from Winnapaug Pond, 2 from Point Judith Pond; Figure 3B, C). The average expected speed of individuals that moved faster as distance to aquaculture increased was 0.42 ± 0.23 km/hour (SD) when near aquaculture (2 SD less than the individual's average proximity to aquaculture), 0.43 ± 0.20 km/hour when an average distance from aquaculture,

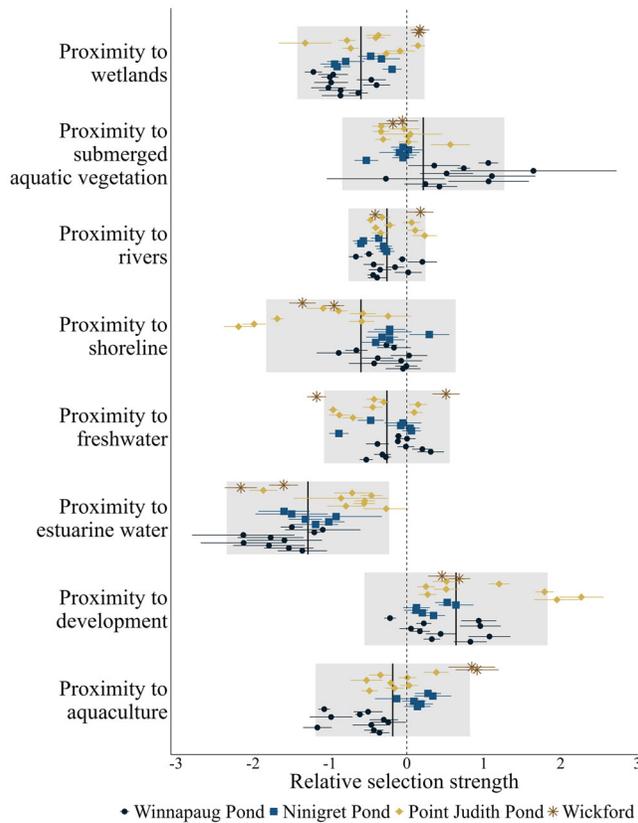


FIGURE 2 Coefficient estimates (relative selection strengths) for an integrated step selection function (iSSF) quantifying the relative influence of proximity to aquaculture on habitat selection and movements by 26 American black ducks in Rhode Island, USA, during non-breeding seasons 2020–2021, 2021–2022, and 2022–2023. Each point indicates an individual's coefficient estimate and 95% confidence interval. Shape and color represent primary non-breeding site. Solid vertical black lines indicate population averages for each coefficient and grey boxes represent 95% reference range across all individuals. Hatched vertical black line indicates a relative selection strength of zero. Relative selection strengths >0 indicate selection to be nearer to a habitat feature, relative selection strengths <0 indicate avoidance of (i.e., selection to be farther from) a habitat feature, and 95% confidence intervals overlapping zero indicate no statistically significant relative selection strength.

and 0.51 ± 0.34 km/hour when far from aquaculture (2 SD greater than the individual's average proximity to aquaculture). The average expected speed of individuals that moved slower as distance to aquaculture increased was 0.33 ± 0.12 km/hour when near aquaculture, 0.24 ± 0.12 km/hour when an average distance from aquaculture, and 0.20 ± 0.14 km/hour when far from aquaculture. Proximity to aquaculture at the beginning of the step did not influence the movement rate of either individual whose primary non-breeding site was Wickford Harbor ($P > 0.05$).

Aquaculture suitability iSSF

Our aquaculture suitability iSSF included the following primary non-breeding sites: Winnapaug Pond (n individuals = 10, n steps/individual = 30, n steps total = 300), Ninigret Pond (n individuals = 6, n steps/individual = 60, n steps total = 360), and Point Judith Pond (n individuals = 5, n steps/individual = 60, n steps total = 300). Primary non-breeding sites were relatively similar in aquaculture suitability composition (Table 1).

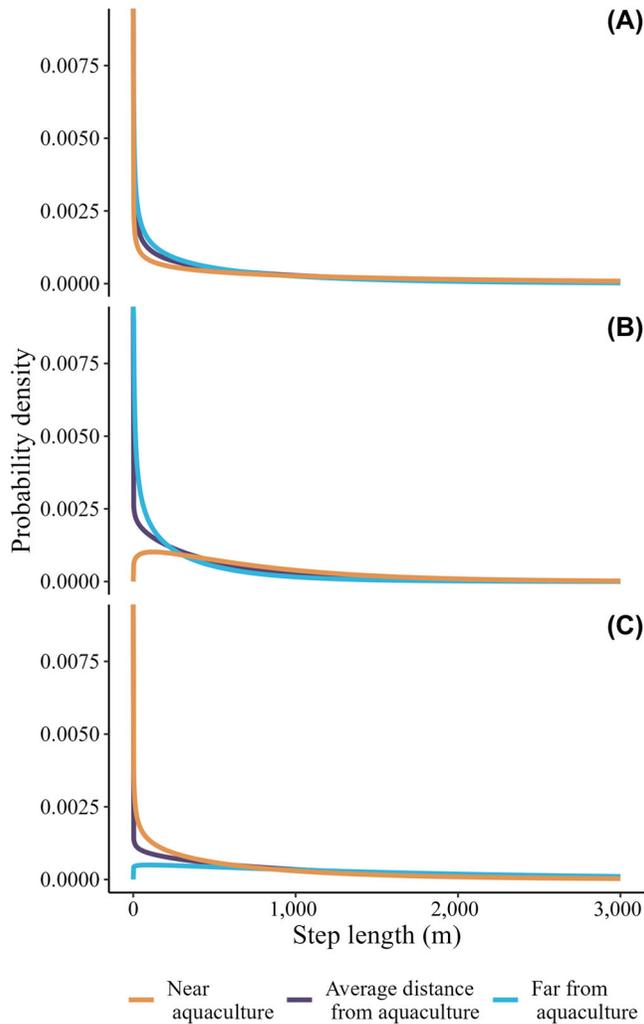


FIGURE 3 Step length distributions showing the relationship between proximity to aquaculture and movement rate for 26 American black ducks during the non-breeding season in Rhode Island, USA, during winters 2020–2021, 2021–2022, and 2022–2023. We present distributions for A) an individual that had no clear interaction between proximity to aquaculture and step length ($Z = -0.59$, $P = 0.55$), B) an individual that had a positive significant relationship between proximity to aquaculture and step length (i.e., movement rate increased farther from aquaculture; $Z = -3.23$, $P \leq 0.001$), and C) an individual that had a negative significant relationship between proximity to aquaculture and step length (i.e., movement rate decreased farther from aquaculture; $Z = 4.79$, $P \leq 0.001$). Line color indicates proximity to aquaculture, where near is 2 standard deviations closer than the individual's average proximity to aquaculture, average is the individual's average proximity to aquaculture, and far is 2 standard deviations farther than the individual's average proximity to aquaculture.

Black ducks whose primary non-breeding sites were Winnapaug or Ninigret Ponds had a greater relative probability of selection for areas that were fairly well suited for aquaculture relative to areas poorly suited for aquaculture (Winnapaug Pond: $P \leq 0.001$, Ninigret Pond: $P \leq 0.001$, Point Judith Pond: $P = 0.13$). For all 3 salt ponds, black ducks had a greater relative probability of selecting areas well suited for aquaculture relative to areas poorly suited for aquaculture ($P \leq 0.001$ for all ponds; Figure 4).

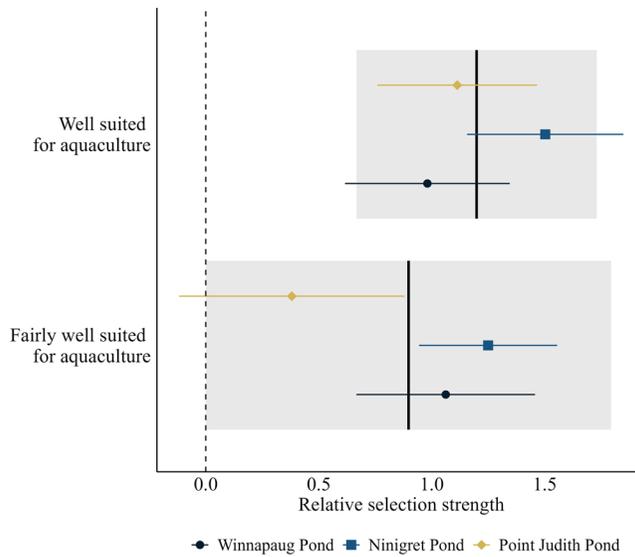


FIGURE 4 Coefficient estimates (relative selection strengths) for an integrated step selection function (ISSF) quantifying the influence of suitability for shellfish aquaculture on habitat selection and movements of 21 American black ducks across 3 primary non-breeding season sites in Rhode Island, USA, during the winters of 2020–2021, 2021–2022, and 2022–2023. Each point indicates the coefficient estimate and 95% confidence interval for each wintering area. Solid vertical black lines indicate population averages for each coefficient and gray boxes represent 95% reference range across wintering areas. Hatched horizontal black line indicates a relative selection strength of zero. Relative selection strengths >0 indicate selection to be nearer to a habitat feature, relative selection strengths <0 indicate avoidance of (i.e., selection to be farther from) a habitat feature, and 95% confidence intervals overlapping zero indicate no statistically significant relative selection strength. Relative selection strengths are relative to the reference level, poorly suited for aquaculture.

There were also relationships between black duck movement rate and aquaculture suitability across all primary non-breeding sites, as indicated by the estimated interaction of the natural log of step length and categorical aquaculture suitability. Black ducks whose primary non-breeding sites were Ninigret and Point Judith ponds moved faster in areas fairly well suited (Ninigret relative selection strength = 0.33, 95% CI = 0.08–0.58, $P = 0.01$; Point Judith relative selection strength = 0.77, 95% CI = 0.51–1.04, $P \leq 0.001$) and well suited (Ninigret relative selection strength = 0.38, 95% CI = 0.07–0.68, $P = 0.01$; Point Judith relative selection strength = 0.67, 95% CI = 0.32–1.01, $P \leq 0.001$) relative to areas poorly suited for aquaculture. Black ducks whose primary non-breeding site was Winnapaug Pond moved faster in areas fairly well suited (estimate = 0.43, 95% CI = 0.06–0.80, $P = 0.02$) but not areas well suited (estimate = 0.16, 95% CI = -0.12 – 0.44 , $P = 0.27$) relative to areas poorly suited for aquaculture. Step length distributions were right skewed for birds in areas fairly well (on all 3 primary non-breeding sites) and well suited (on Ninigret and Point Judith ponds) for aquaculture (i.e., individuals were expected to make longer steps in the same duration of time when in areas fairly well and well suited for aquaculture; Figure 5). Regardless, expected speeds were slow and had a narrow range (0.08–0.15 km/hr) across all primary non-breeding sites and aquaculture suitability categories.

DISCUSSION

We provide evidence that proximity to existing aquaculture leases had site-specific influences on black duck habitat selection but no biologically meaningful influence on movement rates. We also demonstrate that black ducks across primary non-breeding sites selected for areas better suited for aquaculture but suitability for aquaculture did not

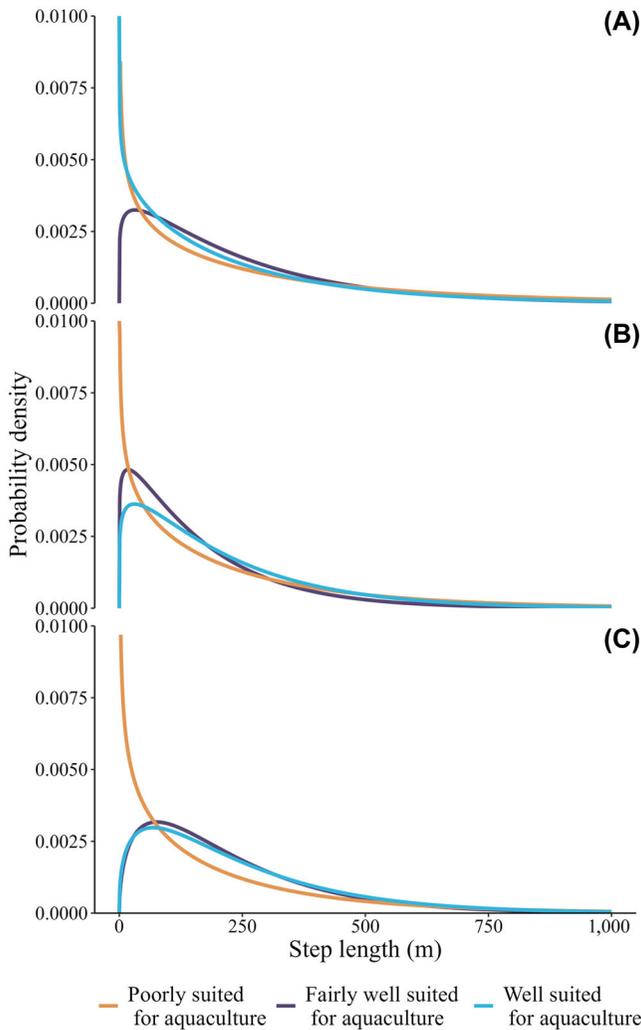


FIGURE 5 Step length distributions showing the influence of suitability of an area for shellfish aquaculture on movement rate for 21 American black ducks across 3 primary non-breeding season sites in Rhode Island, USA, during the winters of 2020–2021, 2021–2022, and 2022–2023. Panels indicate the primary coastal waterbody used during the non-breeding season: A) Winnapaug Pond, B) Ninigret Pond, and C) Point Judith Pond. Line color indicates suitability for aquaculture (poorly suited, fairly well suited, or well suited).

meaningfully influence black duck movement rates across sites. Thus, future siting of aquaculture leases in coastal Rhode Island, particularly the coastal salt ponds, should consider the habitat selection of non-breeding black ducks given that black ducks strongly selected areas most suitable for continued aquaculture development.

Existing aquaculture iSSF

The apparent fidelity of black ducks to primary coastal waterbodies during the non-breeding period resulted in differential habitat selection patterns based on the landscape of available habitat features individuals were exposed to (i.e., black ducks demonstrated functional responses in selection behavior; van Beest et al. 2016, Holbrook et al. 2019).

While 82% of black ducks demonstrated either selection or avoidance of existing aquaculture infrastructure, the magnitude and direction of this effect varied among sites (Figure 2). Black ducks whose primary non-breeding sites had a greater number of protected coves as indicated by shape index (Point Judith and Ninigret ponds) had greater relative probabilities of selecting to be farther from aquaculture than those whose primary non-breeding site was simpler in shape (Winnapaug Pond; Table 1; Figure 2). Whereas Wickford Harbor is less complex in shape compared to Point Judith and Ninigret ponds, all coves that do exist are on the western portion of the Harbor, with the nearest aquaculture leases beyond the mouth of the Harbor to the east (Figure 1). Individuals whose primary non-breeding site was Wickford Harbor selected for areas farther from existing aquaculture operations, and therefore farther into the coves (Figure 2). We offer that our observed patterns in black duck habitat selection behavior do not strictly reflect preferences for proximity to aquaculture but rather differential use of site-specific characteristics, specifically increased use of protected coves that are inherently farther from aquaculture than more open areas. Thus, siting future aquaculture leases in sheltered coves increases the chance of displacing black ducks from habitat that would otherwise provide shallow foraging habitat (Ringelman et al. 2015, Monroe et al. 2021) and refugia during strong wind and wave events (Stancill and Leslie 1973, Gebauer et al. 1992, McKinney et al. 2015) during the non-breeding season.

Further, in addition to all but 1 individual selecting to be near estuarine water, 54% of black ducks selected to be near fresh water (i.e., inland ponds and lakes with <25% cover of vegetation or soil) and 73% selected to be near rivers. This pattern was particularly evident for black ducks whose primary non-breeding site was Point Judith Pond, which could be related to elevated levels of human activity (e.g., commercial fisheries, ferry transit) on that pond relative to the other primary non-breeding sites. Most individuals in our sample demonstrated strong avoidance of human development (Figure 2), supporting the notion that black ducks are particularly sensitive to human disturbance (Conroy et al. 2002, Devers and Collins 2011, Macy and Straub 2015). Black ducks have also been shown to forage more in inland freshwater systems when estuarine areas are inundated by high tides and use running water that remains open during freeze events (Ringelman et al. 2015). Thus, whereas black duck use of inland freshwater systems during the non-breeding season is not abnormal (Morton et al. 1989, Devers and Collins 2011, Ringelman et al. 2015), the pattern demonstrated by our data suggests there is behavioral plasticity in habitat selection behavior that could benefit non-breeding black ducks in areas with limited coastal habitat. Such plasticity is particularly important given the extent of urbanization in coastal Rhode Island and that 85% of black ducks in our sample avoided human development.

Most black ducks (62%) did not demonstrate a relationship between movement rate and proximity to existing aquaculture infrastructure. Moreover, differences in mean estimated speeds for birds that did move at different rates as proximity to aquaculture changed were relatively small (minimum estimated speed $\bar{x} = 0.20$ km/hr, maximum estimated speed $\bar{x} = 0.51$ km/hr). These marginal differences in movement rates likely do not reflect behavioral differences (e.g., foraging versus roosting) given that the entire estimated range falls below reported duck walking and swimming speeds (1.8–2.52 km/hr; McDuie et al. 2019a). We suggest non-breeding season black ducks in coastal Rhode Island likely forage on and around aquaculture infrastructure, similar to other waterfowl species (Ross et al. 2001, Varennes et al. 2013). Moreover, researchers conducting ground surveys in our study area have directly observed black ducks loafing on aquaculture infrastructure (M. S. Müller, University of Rhode Island, unpublished data). We found no evidence that black ducks are actively disturbed from existing aquaculture operations, given that all estimated speeds (regardless of proximity to aquaculture) were well below reported dabbling duck non-migratory flight speeds (36.5–62.4 km/hr; McDuie et al. 2019b). This could be related to relatively minimal levels of human activity at aquaculture operations during the winter compared to other seasons.

Aquaculture suitability iSSF

Black ducks whose primary non-breeding sites were coastal salt ponds demonstrated selection for areas classified as fairly well suited (individuals using 2 of 3 coastal salt ponds) and well suited (individuals using all 3 coastal salt ponds) for aquaculture relative to areas poorly suited for aquaculture (Figure 4). Selection for areas better suited for aquaculture

likely reflects the benefits that relatively shallow water provides for foraging dabbling ducks (Morton et al. 1989, Guillemain et al. 2000, Behney 2020) and caged oyster aquaculture. The results of our existing aquaculture iSSF suggests that, at the population level, black ducks during the non-breeding season in Rhode Island are not displaced by current levels of aquaculture in the coastal salt ponds and may forage and rest close to aquaculture infrastructure (Figures 2 and 3). Nonetheless, continued increases in aquaculture infrastructure in preferred areas of coastal salt ponds (i.e., those classified as fairly well and well suited for aquaculture) will increase the frequency of black duck interactions with aquaculture infrastructure. Managers should monitor these interactions in both the coastal salt ponds and Narragansett Bay given our findings of strong avoidance of non-aquaculture human development (Figure 2) and evidence that black ducks have limited tolerance of human development (Conroy et al. 2002, Devers and Collins 2011).

We did not find strong evidence that black ducks moved differently in areas of coastal salt ponds that differ in suitability for aquaculture. The range of estimated speeds across ponds and suitability categories was very minimal (i.e., 0.07 km/hr difference between fastest and slowest expected speed), and all estimated speeds were well below reported duck walking and swimming speeds (1.8–2.52 km/hr; McDuie et al. 2019a). Whereas these results could indicate black duck preference for foraging in areas better suited for aquaculture and roosting or loafing in areas poorly suited for aquaculture, it is more likely that our reported differences in estimated movement rates have statistical but not biological implications.

MANAGEMENT IMPLICATIONS

The continued expansion of aquaculture into preferred black duck habitats will increase black duck interactions with aquaculture and therefore needs to be considered in the decision-making process for siting future aquaculture leases. We found evidence that non-breeding season black ducks on coastal waterbodies with greater perimeter complexities (i.e., more coves) selected to be farther from aquaculture. Therefore, managers should bear in mind not only the amount of aquaculture in a given coastal waterbody but other characteristics of the area including accessibility to protected coves, proximity to and extent of human development, and proximity to inland fresh water that remains open throughout the non-breeding season. Moreover, we stress that our findings are contingent on the current restriction on aquaculture leases in the coastal salt ponds that limits leases to 5% of the surface area of the pond. Black ducks across 3 coastal salt ponds consistently selected for areas that were classified as fairly well and well suited for aquaculture relative to areas poorly suited for aquaculture. Therefore, continued expansion of aquaculture into the most suitable areas of coastal salt ponds (i.e., areas strongly selected for by black ducks in our sample) will increase the frequency of black duck interactions with aquaculture. Further research into black ducks' fine-scale interactions with aquaculture as it expands in preferred coastal habitats will provide evidence for the extent to which continued aquaculture expansion will influence non-breeding black ducks.

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CONFLICT OF INTEREST STATEMENT

The authors report no conflicts of interest.

ETHICS STATEMENT

All methods were approved by the University of Rhode Island Institutional Animal Care and Use Committee (Protocol AN1920-027). Birds were banded under United States Geological Survey Federal Bird Banding Permit 06820.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. American black duck GPS data relevant to this study are available on Movebank (Movebank ID: 1442384859).

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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