An alternative approach to evaluating the energetic carrying capacity of the landscape for Mallard *Anas platyrhynchos* wintering in the Mississippi Alluvial Valley, USA

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Abstract

Habitat conservation planning for wintering waterfowl in North America uses estimates of waterfowl energy requirements to assess the ability of regional landscapes to support populations. However, because the spatial and temporal configuration of resources can influence an individual animal's use of the landscape, there may be benefits to considering the availability of energy from food within individual home ranges on developing conservation planning. This possibility was investigated for female Mallard *Anas platyrhynchos* wintering in the Mississippi Alluvial Valley using: (1) published energy values for different landcover types (quantified as duck energy days; DEDs/ha), (2) maps of landcover and water availability, and (3) winter home range estimates created using location data from 128 birds fitted with VHF radio transmitters. Following current methods used for regional assessments of food resources available for birds, landcover types were first transformed into their corresponding DED values, and the amount of energy considered potentially accessible to Mallard within their home ranges was then limited by accounting for water availability and DED decay rates. Relatively energy-rich landcover types, such as moist-soil wetlands and croplands, were less likely to be accessible given water coverage. Moreover, a large proportion of Mallard locations were in areas that provided no apparent energy value. Most (> 90%), but not all, Mallard home ranges surpassed the birds' minimum winter energy needs (*i.e.* 123 DEDs). We suggest that waterfowl habitat conservation planning should consider an individual bird, home-range approach for DED assessments, and use those assessments to: (1) begin examining potential gaps in landscape water coverage, (2) ensure that multiple resource patches are accessible to individual birds, and (3) provide the mixture of landcover types (including those used for other life history needs), required by focal waterfowl species.

Keywords: *Anas platyrhynchos*, animals' use of landscape, landscape energetic carrying capacity, Mississippi Alluvial Valley, waterfowl habitat management.

An animal's home range is the ultimate result of its movement given its life history needs, endogenous and exogenous influences, and constraints on the movements of the species (Börger *et al.* 2008; Webb *et al.* 2014; Van Moorter *et al.* 2016). Animal movement patterns can change in response to heterogeneity in resources across space and time, as individuals attempt to use space efficiently to optimise resource gains amid travel and other costs, such as maintenance, predator avoidance, competition and reproduction (Mitchell & Powell 2004; Nathan *et al.* 2008; Tamburello *et al.* 2015). Such alterations in animal movement, prompted by the spatiotemporal distribution of resources, can lead to changes in the structure and location of animal home ranges (*e.g.* Eide *et al.* 2004; Marable *et al.* 2012). Food resource requirements cannot however be considered in isolation; the animals' distribution across their home range requires complex habitats that fulfil a variety of needs, including thermal cover, refugia and areas for social interactions (van Beest *et al.* 2011; Pearse *et al.* 2012; Tufto *et al.* 2019). At large spatial (*e.g.* regional) scales, individuals within a population encounter variable environmental conditions, which result in variability among individuals' use of sites within the region. Knowledge of individual variability therefore is crucial for making ecological inferences and wildlife management decisions to ensure that resources needed by individuals to carry out life history needs are available and sufficient for maintaining the viability of their populations (*e.g.* Shields *et al.* 2012).

In North America, waterfowl habitat conservation planning and practices on non-breeding grounds (*i.e.* habitat used during the winter season from November–March inclusive; hereafter "wintering grounds") focuses on food availability and operates under the premise that food limitation during the non-breeding season can limit demography (Reinecke *et al.* 1989; Wilson & Esslinger 2002; Soulliere *et al.* 2007; Williams *et al.* 2014). As a result, conservation planners assess the capacity of landscapes to support waterfowl populations by determining the potential energetic carrying capacity of key regions (*i.e.* the Joint Venture Areas) of the North American Waterfowl Management Plan (NAWMP 2018). Potential energetic capacity of locales and regions are quantified as duck energy days (DEDs, Reinecke *et al.* 1989; Heitmeyer 2010; Williams *et al.* 2014). Estimates of DEDs are calculated using landcover-specific estimates of food density (assumed to be available and accessible), true metabolisable energy of known foods of waterfowl (*e.g.* agricultural and natural seeds and aquatic invertebrates, Miller & Reinecke 1984; Kaminski *et al.* 2003; Callicutt *et al.* 2011; Bauer *et al.* 2023), and the daily energy requirements for a species or sympatric species in a defined area (*e.g.* DEDs/ha, Reinecke *et al.* 1989; Bauer *et al.* 2023). The total energetic carrying capacity of a region is defined as the sum of DEDs across landcover types (Miller & Eadie 2006; Williams *et al.* 2014; Petrie *et al.* 2016).

Habitat conservation planning for waterfowl on their wintering grounds aims to achieve adequate DEDs for a specific regional population, such as *c.* 4 million ducks in the Mississippi Alluvial Valley (MAV, Lower Mississippi Valley Joint Venture (LMVJV) 2015). Despite the rigour involved in regional DED estimation, joint venture planning recognises that individuals within a population vary in their ability to move and acquire resources, and that this variation is important to consider in waterfowl habitat management (Miller *et al.* 2014). This individual variability has potential demographic ramifications if individuals within a population are resource-limited, as resource limitation can lead to decreased survival (*e.g.* Moon & Haukos 2006), altered or delayed mate selection (*e.g.* Heitmeyer 1995; Lercel *et al.* 1999), and reduced recruitment (*e.g.* Heitmeyer & Fredrickson 1981; Kaminski & Gluesing 1987; Sedinger & Alisauskas 2014; Osnas *et al.* 2016). It is therefore useful to explore DEDs in relation to the home ranges of individual birds, to assess potential resource limitations for a given population.

To date, the distribution and abundance of DEDs for wintering waterfowl have been examined in relation to bird movements (Beatty *et al.* 2015), and individual bioenergetic needs, evaluated through agent-based (Miller *et al.* 2014) and daily ration modelling (Williams *et al.* 2014; Bauer *et al.* 2023). However, there remains less progress in broadly incorporating the use of space by individual animals into habitat conservation planning. Here, our objective was to evaluate an alternative approach to the classic population-level DED assessments, by examining the potential availability of energy in food for individual female Mallard *Anas platyrhynchos* within their winter home ranges in the MAV using three sources of data: (1) estimated DED values for different landcover types, (2) maps of landcover and water availability and (3) winter location data from radio-tagged birds. Integration of DED and landcover information enabled identification of the energetic landscape, while water availability identified the portion of the energetic landscape potentially accessible to Mallard (Nichols *et al.* 1983; Delnicki & Reinecke 1986; Pearse *et al.* 2012). Placing home ranges on this landscape allowed us to investigate individual variability in space use and infer whether winter home ranges of individuals may have contained adequate DEDs to survive the winter.

Methods

Study area

Data were collected from radio-tracked female Mallard monitored over four winters (November to March 2010–2015; *i.e.* in winters 2010/11–2014/15) in the Mississippi Alluvial Valley, an important region in the southeast United States for wintering

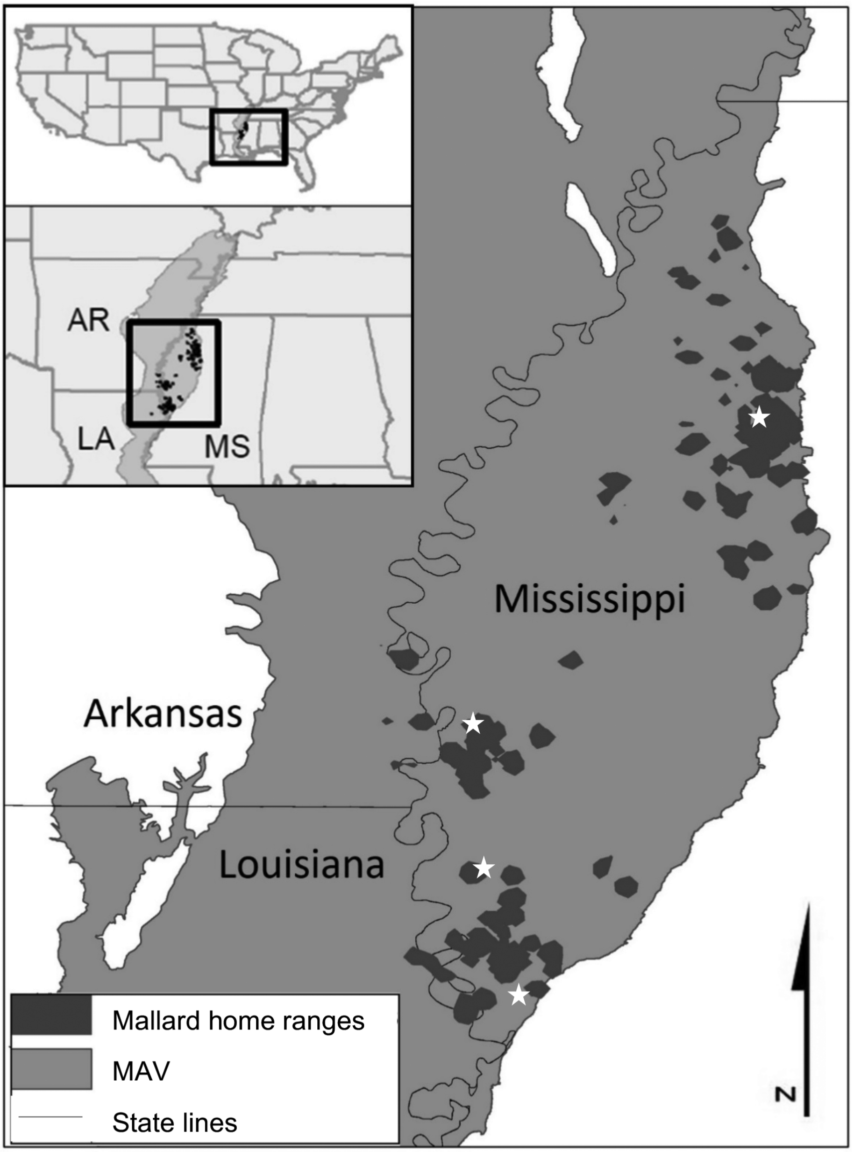

Figure 1. Home ranges of radio-tagged female Mallard (right panel), in winters 2010/11–2014/15 within the Mississippi Alluvial Valley (top left panel). Mallard were primarily in Mississippi (MS) with a few individuals occurring in portions of Arkansas (AR) and Louisiana (LA). Detailed views of the location data are provided in Supporting Materials Fig. S1, and individual home ranges appear in Fig. S2. Capture sites, indicated by stars, included the Howard Miller (32°49’48”N, 90°58’51”W), Mahannah (32°32’54” N, 90°52’14” W) and Muscadine Farms (33°13’29”N, 90°59’01”W) Wildlife Management Areas and the Coldwater River National Wildlife Refuge (34°6’1”N, 90°7’58”W).

waterfowl (Reinecke *et al.* 1989, 1992; Pearse *et al.* 2008). The Mallard were predominantly located in the Mississippi portion of the MAV (Fig. 1), a 20,000 km^2 floodplain which drains most of the Mississippi Alluvial Plain (Saucier 1994), situated in the Mississippi River Alluvial Plain, an ecoregion characterised by mild winters and hot summers where temperature and precipitation gradients increase from north to south, with mean annual precipitation of 115–165 cm, mean temperature of 14–21°C and a growing season of 210–250 days. During the winters of our study, the Mississippi portion of the MAV received an average of 71–117 cm of precipitation and average temperatures ranged from 5.8–9.6°C (NOAA 2020). Dominant landcover types included agricultural fields, bottomland hardwood and scrub-shrub wetlands, rivers, lakes, reservoirs, aquaculture ponds and seasonally-flooded herbaceous wetlands, all of which are used by Mallard (Reinecke *et al.* 1989; Heitmeyer 2010; Pearse *et al.* 2012; Tapp *et al.* 2018).

Telemetry data collection

Within the study region, female Mallard were captured using baited, swim-in traps at four sites on public land (Fig. 1), banded with a United States Geological Survey standard aluminium tarsus band, and fitted with a 23 g harness-type VHF transmitter with a "mortality switch", which intensified VHF pulse rates when the transmitter did not move for over 8 h (Advanced Telemetry Systems, Minnesota, USA; Dwyer 1972). Radio-tagged Mallard (n = 242) were released at their capture site, and then monitored daily, by tracking the birds in the field and using triangulation to determine their location, from three days post capture (to omit biases from capture and handling, Dugger *et al.* 1994; Davis *et al.* 2009) until the end of March each year. Two locations were obtained each day; one diurnally (*i.e.* 30 min before sunrise to 30 min after sunset) and one nocturnally (*i.e.* 30 min after sunset to 30 min before sunrise), each day for 93–118 days depending on the year (Cox & Afton 1998; Davis *et al.* 2009). Duck locations were recorded using vehicles with roof-mounted, 4-element, null-peak antenna systems (Advanced Telemetry Systems, Minnesota, USA), electronic compasses (calibrated ± 0.5° to known locations of beacon transmitters; Azimuth 1000R, KVH Industries, Rhode Island, USA), and LOAS software (Location Of A Signal 4.0.3.8, Ecological Software Solutions, Hegymagas, Hungary; Cox *et al.* 2002; Davis & Afton 2010). At least 3 compass bearings were obtained to estimate locations and 95% confidence ellipses in LOAS (each with a threshold tolerance of ≤ 3° standard deviation). Further details of capture and radiotracking methods are available in Lancaster (2018). All capture and handling protocols were approved by Mississippi State University Institutional Animal Care and Use Committee (protocols 10-070 and 13-073) and authorised under Federal Bird Banding and Auxiliary Markers Permit (06604).

Location data were used to estimate the total home range size for each Mallard using the 90% isopleth (Börger *et al.* 2006; Fleming & Calabrese 2017) of biased random bridge estimates (R package *adehabtatHR*; Calenge 2006) in R v. 4.0.5 (R Core Team 2021). This estimator accounted for clustered *vs.* long-distance movements of individuals (Benhamou 2011) and created home range sizes representative of those previously estimated for this species (Legagneux *et al.* 2009). A sensitivity analysis was performed on the number of locations required to create relatively stable home ranges and determined that home range size increased, on average, by < 9% (*i.e.* < 1–4 km^2) for ≥ 30 locations (Supporting Materials Fig. S3). Thus, all Mallard with ≥ 30 locations were retained for analysis. None of the Mallard had data spanning multiple winters, because the battery life of the transmitters was limited.

Defining the energetic landscape

Having estimated the home ranges for the individual Mallard, the energetic landscape was defined for each winter across the Mississippi portion of the MAV, using Cropland Data from the United States Department of Agriculture's National Agricultural Statistics Service repository. These data consisted of digital surfaces representing natural landcovers and crop types at a 30 m resolution (U.S. Department of Agriculture 2010–2014). A DED value was assigned to each landcover type for each year of study, according to Mallard DED information currently being used in habitat conservation planning in the region (*i.e.* the LMVJV, Edwards *et al.* 2012, Table 1). Only landcover types with potential foraging habitat which had a known energy value to Mallard and which were used by Mallard > 1% of the time during the study were included in analyses (Table 1, Supporting Materials Table S1). Of the landcover types which were included, fallow croplands were subsequently combined into the moist-soil wetland category as fallow croplands act like moist soil wetlands (Table 1). In accordance with regional habitat conservation plans, two assumptions were made when assigning DED values (Edwards *et al.* 2012; M. Mitchell, Ducks Unlimited Inc., pers. comm.). First, private croplands were assumed to have been harvested before winter because most were production agricultural fields, and there was no capacity to delineate fields which were not harvested and left intentionally for use by waterfowl (*e.g.* Wilkerson 2016). However, DEDs corresponding to publicly managed lands which were known to contain unharvested crops were delineated according to Lower Mississippi Valley Joint Venture boundary vector data (LMVJV 2021). Secondly, while the energy value for forested wetlands varies with Red Oak *Quercus* sp. canopy coverage and acorn masting (Straub *et al.* 2024), the DED value of 40% Red Oak canopy coverage reflects the average Red Oak canopy coverage estimated across the MAV for years overlapping this study (estimated at 41.7% in winters 2009/10 and 2010/11 by Straub 2012), and this value was applied to this landcover type. Energy values were then converted from DED/ha to DED per 900 m^2 (*i.e.* the resolution, 30 m pixels of the landcover dataset; Table 1) and pixels were assigned their associated DED value using ArcGIS (ESRI 2019).

Restricting the energetic landscape using water coverage and resource decay

Given that Mallard primarily use inundated areas in the Mississippi MAV and rarely

Table 1. Landcover type on private land derived from annual cropland data layers (with pixel values in parentheses), and on public land derived from Lower Mississippi Valley Joint Venture data. For each landcover type, the associated duck energy day (DED) values per ha and DEDs per pixel (900 m²) for Mallard are provided, along with resource decay rates and the DED value associated with decay rates for landcover types in the Mississippi Alluvial Valley (derived from 2010–2014 Cropland Data Layers, United States Department of Agriculture). Additional information for the "other" category is provided in Supporting Materials Table S1.

Landcover	**DED/ ha**[a]	**DED/ 900m²** [b]	**Decay (%/day)**	**Source**
Private land				
Corn (1)	1,248	112	0.00465	Reinecke *et al.* 1989; Krapu *et al.* 2004
Rice (3)	341	31	0.00213	Reinecke *et al.* 1989; Stafford *et al.* 2006
Sorghum (4)	1,186	107	0.00322	Sherfy *et al.* 2001
Soybean (5)	89	8	0.01083	Mayeaux *et al.* 1980; Reinecke *et al.* 1989
Fallow cropland (61)[c]	4,615	415	0.00299	Kross *et al.* 2008; Hagy & Kaminski 2012
Moist-soil wetland (87 & 195)	4,615	415	0.00299	Duffy & LaBar 1994; Penny 2003; Reinecke & Hartke 2005
Forested wetlands (190)[d]	385	35	0.00004	Kaminski *et al.* 2003; Batema *et al.* 2005
Other (all other values)	0	0	–	
Public land				
Unharvested Corn	70,647	6,358	0.00465	Reinecke *et al.* 1989
Unharvested Rice	58,891	5,300	0.00213	Reinecke *et al.* 1989
Unharvested Sorghum	44,591	4,013	0.00322	Sherfy *et al.* 2001
Unharvested Soybean	11,557	1,040	0.01083	Reinecke *et al.* 1989
Unharvested Millet	12,856	1,157	0.00478	Reinecke *et al.* 1989; Sherfy *et al.* 2001; Checkett *et al.* 2002

[a] Values were transformed from DED/acre to DED/ha by dividing by 0.4047 for easier conversion to m².

[b] Values were transformed from DED/ha to DED/900 m² (*i.e.* DED/pixel in the landcover layer) by multiplying by 0.09.

[c] Fallow croplands are surrogates of moist soil wetlands (following Kross *et al.* 2008; Hagy & Kaminski 2012).

[d] Forested wetlands in Mississippi are analogous in DED to the 40% Red Oak value (Edwards *et al.* 2012; Straub *et al.* 2024).

forage on dry land (Pearse *et al.* 2012), we determined the extent to which surface water was available across landcover types. There are three known publicly available datasets with surface water information: the National Land Cover dataset (Dewitz 2019), the Cropland dataset (as depicted above), and the Global Surface Water dataset (Pekel *et al.* 2016). The Land Cover and Cropland datasets are created using Landsat images from autumn of each year, a time when flooding is least prevalent across the MAV, so the water pixels within these two datasets do not truly reflect areas waterfowl may access in winter. In contrast, the Global Surface Water dataset is a compilation of information on surface water detected from Landsat satellite imagery (30 m resolution) across > 35 years (1984–2015) of information taken across seasons. As a result, water pixels in this product also reflect flooding that can happen while Mallard are wintering in the MAV and thus provides information on areas that Mallard may access. The creators of these data reported that < 1% of pixels were false water detections and that < 5% of surface water was missed (Pekel *et al.* 2016). We therefore used the water occurrence layer from the Global Water dataset to assess the ability of Mallard to access forage containing landcover types and thus determine potential DEDs. This data layer shows pixels as a probability of being flooded from 0–100%. Adjusting DED values using this percentage was assumed to provide a measure of the birds' potential access to each landcover type, given the proportion of time that a pixel would likely be inundated.

Next, standard decay rates for forage within each landcover type were used, as is typical for DED calculations in conservation planning (Edwards *et al.* 2012), to adjust total DED values and account for decay of the food resource during the winter for each landcover type (Table 1). In total, the number of DEDs within an individual's home range were calculated as:

$$\mathrm{DED}_{\mathrm{HR}} = \Sigma\,(\mathit{Inundation} \times \mathit{DecayRate}_l \times \mathit{DED}_l)$$

where $\mathrm{DED}_{\mathrm{HR}}$ is the calculated DEDs for each individual Mallard's home range (HR) in a given pixel, and l is the landcover type associated with that pixel.

For each Mallard, we calculated: (1) the total area of each landcover type where water occurred (*i.e.* any area that had ≥ 1% water occurrence) within their home range, (2) the proportional use of different landcover types by each Mallard (*i.e.* the number of locations in a landcover type divided by the total number of locations per bird) and (3) the total number of DEDs potentially available in each landcover type, given the estimated water occurrence and decay rates over winter. The LMVJV uses a 110-day wintering period and calculates a DED as the energetic equivalent of 294.35 kcal or the average daily energy demand across seven dabbling duck species including Mallard (*Anatini* sp.) and also the Wood Duck *Aix sponsa* (Edwards *et al.* 2012). However, the general daily energy demand for Mallard is greater because the Mallard's body mass is greater than that of the average dabbling duck in the MAV (*i.e.* *c.* 330 kcals/day; calculated as Mallard resting metabolic rate * 3, based on the average Mallard body mass reported by Miller & Eadie 2006). We accounted for this higher energy demand in Mallard, which was 1.12 times the joint venture DED value used for multiple species. As a result, a single Mallard was estimated to need *c.* 123 DEDs (*i.e.* 110 days × 1.12) to sustain itself through winter. Consequently, (4) the number of Mallard which did or did not have 123 total DEDs within their home ranges was tallied.

Results

We removed 114 individuals from analysis which had < 30 locations, leaving 7,120 locations from 128 females across winters for use in home range estimation (mean ± s.e. = 57 ± 2 locations; range = 31–116). Of these individuals, three Mallard died in late January from hunter harvest (n = 1) and unknown natural causes (n = 2) but were included in analyses as there was enough information to quantify their space use during winter (*i.e.* ≥ 38 locations). Mallard winter home range sizes averaged at 43.0 ± 2.9 km^2 (range = 7.2–169.9 km^2; Supporting Materials Fig. S2) and were similar in size among individuals and years (coefficient of variation (CV) = 0.07).

Across individual home ranges, some landcover types had a greater likelihood of inundation than others, with 50.4–99.3% of available moist-soil wetlands, unharvested rice, unharvested soybean, unharvested millet and unharvested sorghum being inundated (Table 2). These were followed by 40.4% for landcover types with little or no energy value (*i.e.* the "other" category; primarily open water and scrub-shrub; Supporting Materials Table S1), 21.4–34.8% for harvested crops, 18.9% for forested wetlands, and 10.6% for unharvested corn (Table 2). Given potential water coverage across home ranges, the most available landcover types for Mallard, on average, were areas with little to no energy value (26.4% of the total home range) and forested wetlands (23.7%), followed by harvested soybeans (21.0%), moist-soil wetlands (18.4%), harvested rice and corn (4.6 and 3.7%, respectively), and all other harvested and unharvested crops (< 1% each; Table 2).

Mallard detections followed trends in landcover availability with individuals occurring most frequently in forested wetlands (38.4% of 7,120 detections) and landcover types with little or no energy value (24.5%), harvested soybean (14.6%), moist-soil wetlands (14.0%), harvested rice and corn (3.2 and 2.5%, respectively), and harvested and unharvested crop types (< 1.5% each; Table 2). Mallard were not detected in unharvested corn or millet (Table 2). When accounting for water variability and forage decay rates, home ranges contained an average of 959 ± 106 DEDs (range = 38–11,300; CV = 0.11). Ten (7.8%) Mallard home ranges did not contain the calculated 123 DED threshold needed to survive winter (Fig. 2). These 10 individuals were, on average, 34% (range = 2–69%) below the 123 DED threshold (Fig. 2), and the three mortalities detected during winter were within this cohort.

Discussion

An estimated 1.1–1.8 million Mallard winter in the Mississippi Alluvial Valley (Reinecke *et al.* 1992), which is also an area used by large numbers of other migratory waterfowl (Reinecke *et al.* 1989, 1992; Pearse *et al.* 2008; NAWMP 2018). Conservation plans for waterfowl are often focused on meeting the energy requirements of waterfowl at a

Table 2. Average percentage of total home ranges described for radio-tagged Mallards that was cover by water, for each landcover type, together with the percentage (± s.d.) of each landcover type within the inundated portion of the home range (*i.e.* landcover availability), and proportional use of each landcover type by radio-tagged female Mallard in the Mississippi Alluvial Valley, in winters 2010/11–2014/15 inclusive.

Landcover	% Home range covered by water	Landcover availability (%)	Observed use by Mallard (%)
Corn	21.4	3.7 ± 0.4	2.5 ± 0.3
Rice	28.9	4.6 ± 0.4	3.2 ± 0.5
Sorghum	34.8	0.9 ± 0.2	1.0 ± 0.2
Soybean	33.8	21.0 ± 0.9	14.6 ± 1.1
Moist-soil wetlands[a]	50.4	18.4 ± 1.0	14.0 ± 1.0
Forested wetlands	18.9	23.7 ± 0.9	38.4 ± 1.0
All Others	40.4	26.4 ± 1.5	24.5 ± 1.0
Unharvested Corn	10.6	0.02 ± 0.01	0
Unharvested Rice	99.3	0.2	0.4
Unharvested Sorghum	68.0	0.9 ± 0.3	1.4 ± 0.5
Unharvested Soybean	73.4	0.1 ± 0.1	0.06 ± 0.05
Unharvested Millet	70.3	0.04 ± 0.03	0

[a] Moist-soil wetlands also include fallow croplands because this landcover type is analogous to moist soil wetlands.

regional level; however, not only the scale of the landscape but variation in the birds' use of the different landcover types can have substantial implications for management and conservation of the species (Johnson 1980; Williams *et al.* 2014). Although the primary objective of this study was to explore the implications of evaluating DEDs from an individual's perspective, our findings revealed that Mallard habitat use was disproportionate across landcover types relative to water availability. For example, moist-soil wetlands were amongst the most prevalent landcover types within home ranges, and contained the most potential energy for Mallard, but were not the most available, partly because fallow, non-flooded croplands comprised part of this category (8% on average) as fallow croplands can function like moist soil wetlands if flooded. Similarly, high energy crops such as corn were less accessible given that corn is not typically planted in naturally flood-prone areas and must be intentionally planted

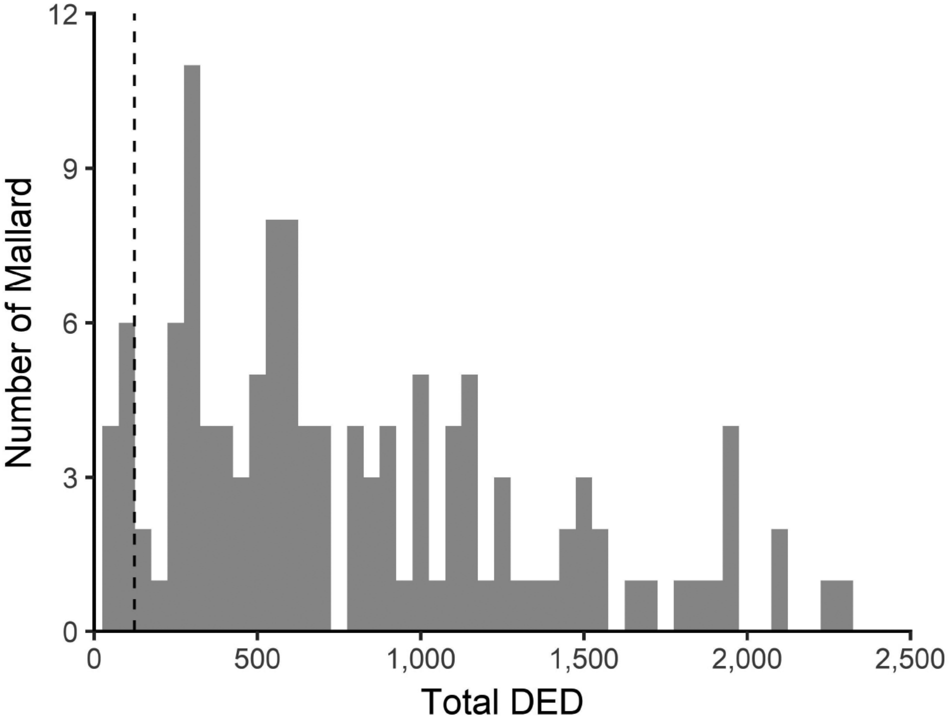

Figure 2. The number of radio-tagged female Mallard in relation to total DED amounts within each home range in the Mississippi Alluvial Valley, winters 2010/11–2014/15. Black dotted line indicates the minimum number of DED (*i.e.* 123 days) required for overwintering. For visualisation, Mallard with > 5,000 DED (*n* = 6) were not plotted.

within impoundments flooded for waterfowl use. Hence, the mere presence of high-energy resources on the landscape does not guarantee their accessibility to Mallard in the MAV, and regional habitat planning is aware of the critical need to create accurate maps of water coverage for these types of assessments. While the Global Surface Water dataset is a useful resource, there is still much work needed to capture flooding in forested systems where canopy coverage blocks satellite imaging and water cannot be delineated accurately in shallowly-flooded areas. Moreover, there is a lack of fine-scale temporal water data which leads to limited understanding of how water coverage changes throughout the winter season and thus affects Mallard access to resources. While these dynamics could not be incorporated here, an understanding of fine-scale water changes will greatly increase understanding of DED availability for individual birds.

While water inundation clearly impacts forage availability for Mallard, > 90% of the radio-tracked Mallard had home ranges that encompassed landcover types that met their minimum winter energy needs. However, 10 Mallard (8%) had home ranges apparently failed to provide sufficient DEDs to meet the 123 DED winter threshold. Seemingly this energetic limitation did not impair their short-term survival, given that seven of the 10 birds survived the winter. The analyses showed that landcover types with little or no food were also used by Mallard – mainly open water and scrub-shrub – both of which also had the greatest water availability. These open water habitat types are known to be used by Mallard and other ducks when shallow wetlands are frozen or for loafing away from disturbance, and scrub-shrub provides thermal cover, isolation for pair-bonding, and refuge from disturbance and predation (Reinecke *et al.* 1988; Heitmeyer 2006; Osborn *et al.* 2017; Palumbo *et al.* 2019; Davis *et al.* 2022). Mallard using areas with insufficient DED not only had large areas within their home ranges that were classed as being of no energy value, but these also lacked clusters of high energy foraging patches (Supporting Materials Fig. S4). Adjacency or proximity of foraging patches is a component lacking in waterfowl habitat planning that has been previously mentioned (Beatty *et al.* 2014; Weller *et al.* 2023) and could influence survival or other annual life cycle events. For example, creating a mixture of land types that are managed to provide forage and sanctuary in close proximity to each other can reduce travel distances and thus energy expenditure on moving between forage patches (Beatty *et al.* 2014; Weller *et al.* 2023). While Mallard have been shown to be resilient and survive in a deprived physiological state, as demonstrated experimentally in food-restricted wild-strain captive Mallard and Wood Ducks (Richardson & Kaminski 1992; Demarest *et al.* 1997), which could explain the short-term survival of resource-limited birds, increased travel costs associated with resource limitation can lead to decreased survival (*e.g.* Moon & Haukos 2006), and reduced recruitment on the breeding grounds (*e.g.* Heitmeyer & Fredrickson 1981; Kaminski & Gluesing 1987; Sedinger & Alisauskas 2014; Osnas *et al.* 2016); consequences we were not able to measure in this study. If this small cohort of birds occupied the landscape in a way that rendered them unable to obtain adequate resources, and that lack of resources has consequences at some point in the annual cycle, then how DEDs are assessed at regional scales may not be adequate in the management of waterfowl. We therefore suggest that waterfowl habitat planning should work on improving the assessment of inundation areas and the understanding of how mosaics of habitats (both extent and relative proximity) combine to provide Mallard needs at local scales.

There are several alternative explanations for birds being identified as having a lack of DEDs in their winter home ranges. First, as Mallard can lose body mass endogenously during winter (Loesch *et al.* 1992), perhaps the birds in the 8% cohort simply had adequate body reserves to sustain them and did not need to occupy areas where energetic patches were plentiful. Second, while DEDs are currently assessed using the best means possible, it is known that calculations currently cannot account for other factors that may limit or augment energy gain. For example, availability of energy to wintering waterfowl can also be affected by variation in the types of resources within landcover types. For instance, more energy is provided when herbaceous wetlands are dominated by moist-soil grasses and sedges *vs.* cattails (*Typha* sp.; Lishawa *et al.* 2020) or there is active over passive moist-soil management (Kross *et al.* 2008; Fleming *et al.* 2015). Additionally, fine-scale temporal variations in natural or artificial flooding (Nichols *et al.* 1983; Delnicki & Reinecke 1986; Fredrickson *et al.* 2005; Pearse *et al.* 2012), variation in water depth (Hagy & Kaminski 2012; Behney 2020), interspecific competition between avian species (Osborn *et al.* 2021) and human disturbance (*e.g.* St. James *et al.* 2013; Lancaster *et al.* 2015; Blake Bradshaw *et al.* 2023; Dittmer *et al.* 2023) can each have a major influence on the birds' ability to access food. Assessments can also be influenced by assumptions made about variables that spatiotemporally fluctuate in their availability, such as DEDs related to variation in the acorn masting of oak tree species and abundance of aquatic invertebrates (Straub *et al.* 2024). Moreover, they can be affected through the extent of crop harvest on private lands, and the relative forage available through crop waste left on the landscape post-harvest (Foster *et al.* 2010). While these types of limitations on DED assessments are well known to regional habitat planning, a greater effort to quantify these types of data would help greatly in elucidating the extent to which forage resources are available on the landscape for the birds.

The birds' use of the landscape is influenced by habitat characteristics that meet a variety of their needs, including the availability and location of water, food resources, thermal cover and refugia. These phenomena lead to great variability in individuals' home ranges given landscape heterogeneity at large spatial scales. Here, we aimed to provide an alternative to how DEDs are assessed (*i.e.* moving from the population to individual level), to help elucidate potential gaps in landscape management based on food resource availability, which is dependent on factors such as landcover type, inundation and variation in forage decay and harvest rates. Our study suggests that, as some tracked birds did not appear to have sufficient DEDs, current methods used to assess DEDs within a landscape do not necessarily translate to (or equate with) the DEDs needed for some individuals to survive, and that forage patch proximity influences DED assessments at the home range scale. Future work should examine how this DED limitation translates to performance across annual cycle events, for example, by using GPS tracking data to examine resource use and survival on both breeding and wintering grounds. Based on our current study, we suggest that waterfowl habitat conservation planners should consider our approach or a modification to assess landscape DEDs for focal waterfowl species in important conservation regions and compare DEDs using individual bird home ranges versus other traditional strategies to determine their comparative utility for conservation planning.

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Photograph: Female Mallard in the southeastern United States, by Duncan Fraser.