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Seasonal Patterns in Daily Flight Distance and Space Use by Great Egrets (*Ardea alba*)

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Abstract.—In an effort to quantify the value of wetland habitats, GPS technology was used to document the movement patterns of 16 Great Egrets (*Ardea alba*) in North America. Patterns in daily flight distances and utilization distributions (UD; estimates of area occupied on the ground) were documented throughout the annual cycle. Maximum Daily Displacement (MDD), the farthest distance occupied by a bird from colony/roost (central place) in 24 hr was greatest (4.3 ± 0.1 km) during breeding season and lowest (3.3 ± 0.1) during post-breeding season. As birds visited multiple foraging sites and made multiple round trips to central places, this Total Daily Distance (TDD) was also measured. It increased from a mean of about 12 km during the incubation phase to about 35 km at the time of fledging. Average TDD was greatest during breeding season (14.2 ± 0.3 km) and lowest during winter (11.0 ± 0.2 km). The utilization distribution increased from 128 (± 21.3) ha during breeding season to 179 (± 32.6) ha during winter. Birds that foraged at tidal sites used 183.3 (± 22.2) ha, twice as much area as birds that foraged strictly in freshwater sites (89.6 ± 21.3 ha). *Received 12 December 2020, accepted 17 August 2021.*

Key words.—*Ardea alba*, central place, daily flight distances, GPS telemetry, Great Egret, home range, wading bird, wetlands, utilization distribution.

Despite decades of conservation efforts, wetland habitats of all types continue to decline both in abundance and quality worldwide (Dahl 2011; Hu *et al.* 2017). While the rate of wetland loss has slowed in Europe and North America, net losses continue to occur even in developed countries such as the United States (2004 to 2009; Dahl 2011), and heavy losses are still occurring in Asia and Africa (Davidson 2014). Estimates of global wetland loss since 1900 range from 64-71% (Davidson 2014). Exacerbating the loss of wetlands from land-use changes are the consequences of climate change, which include the loss of coastal wetlands due to sea-level rise. The loss of such critical habitat presents a challenge both to conserva-tion biologists and to wetland-dependent fauna. Thus, there is a need to quantify the value of wetlands to prioritize conservation and restoration efforts. This paper describes patterns of area-use of a globally-distributed wetland species, the Great Egret (*Ardea alba*), and quantifies the use of wetland and shallow aquatic habitats by this species.

To meet caloric needs of nesting parents and young, central-place foraging birds must travel to a feeding site and then return to the colony to provision young (Orians and Pearson 1979). The duration, distance and energetics of such foraging trips have been relatively well-studied in colonial-nesting seabirds, which typically alternate long and short foraging trips, self-provisioning on

long trips and chick-provisioning on short trips (*e.g.*, Weimerskirch 1998; Weimerskirch *et al.* 2003). Seabird foraging trips also tend to increase in distance as the season progresses, as prey near the colony become depleted and the caloric demands of the growing young increase (Ashmole 1963; Gaston *et al.* 2007). However less attention has been given to central-place foraging dynamics of colonial nesting wading birds (Knight *et al.* 2016).

We believe that a better understanding of wading bird foraging patterns would clarify the role of wetland habitats for this guild of aquatic birds. Many long-legged wading birds (Family Ardeidae) rely heavily on the productivity of different types of wetlands for survival and reproduction. Great Egrets are mobile, generalist wetland predators known to adjust foraging location based on short-term changes in prey availability (Gawlik 2002; Beerens *et al.* 2015). For example, in tidal ecosystems, foraging decisions are strongly influenced by tide level and therefore water depth (Maccarone and Brzorad 2005; Calle *et al.* 2018). Great Egrets are gregarious and often breed in mixed-species colonies, roost in groups, and often forage with other guild members. Some theoretical work that has modeled the placement of colonies or roosts (central places) within the foraging territory suggests that birds weigh the benefits of occupying safer central places against the risks of flying greater distances to reach foraging areas (Orians and Pearson 1979; Guisan and Zimmerman 2000; Fagan *et al.* 2007; Olsson and Bolin 2014). Empirical studies of Great Egrets during the breeding season indicate that the average distance traveled to foraging locations ranges from 3-13.5 km from the colony (Kelly *et al.* 2008; McCrimmon *et al.* 2020).

The partitioning of space is an essential component of the realized niche and thus is important to quantitative ecology (Hutchinson 1957; Cunha and Vieira 2004). The amount of space used will be dependent on the energy required by the individual and its growing young during the breeding season, and the productivity of the habitat. The utilization distribution (UD) is a metric for quantifying the amount of space used by animals (Fieberg and Kochanny 2005), and better quantifies the long-established concept of home range (Burt 1943). UD is the amount of space used by the birds while on the ground. Such computational advances, when combined with innovative GPS telemetry, make it possible to merge the disparate fields of ecosystem science, avian foraging behavior and physiology, and remote telemetry into an integrated framework of energy flow and use of space by wetland-dependent species. Such efforts have the potential to act as crucial tools to support the scientific basis of wetland habitat protection and the importance of ecosystem services (Daily 1997).

Here we build upon previous studies of Great Egret foraging flight distances determined by VHF telemetry (Maccarone *et al.* 2008; Brzorad *et al.* 2015), by leveraging recent advances in GPS tracking technology. We measure seasonal patterns in daily flight distances by Great Egrets and hypothesize that Great Egrets use foraging flight in ways to minimize energy expenditure and maximize energy intake. Thus, we predict that birds will commute the shortest distances when energy demand is the lowest, such as in the post-breeding and wintering periods, and that greater energy demand during the breeding season will increase flight distances. We evaluate both Total Daily Distance (TDD), or the cumulative distance flown by a bird in 24 hr, and Maximum Daily Displacement (MDD), or the farthest distance occupied by a bird from its central place in 24 hr. We also examine two seasonal variables, the Utilization Distribution (UD95), or the amount of area that has a 95% probability of being occupied by a bird on the ground, and the Minimum Convex Polygon (MCP), or the smallest convex region that contains all points. We pose several questions about flight distances and the use of space: 1) Do TDD, MDD, UD95 or MCP differ among the breeding, post-breeding, and wintering periods? 2) Within the breeding season, do TDD and/or MDD increase as chick caloric demand increases? 3) Do TDD and/or MDD

differ by geographic location, breeding status, sex or type of foraging habitat?

METHODS

Capture and Processing of Birds

Between May 2013 and June 2018, we captured Great Egrets at foraging sites by using egret decoys and 1-m x 0.5-m x 20-cm black plastic bins stocked with live fish. Modified leg-hold traps set in and around the bins were used to capture birds (Brzorad and Maccarone 2014). We used a hanging scale to weigh each bird to the nearest gram, and measured culmen and tarsus lengths to the nearest mm. A blood sample was drawn from a vein in the tarsus to determine sex (HealthGene, Toronto, Ontario, Canada). Individuals too light (< 1,040 g) to support the weight of a 52-g (< 5% body mass) transmitter and harness were then released. A total of 17 birds were outfitted with a GPS transmitter (e-obs, Germany, 48-g Bird Solar): 5 in Wichita, Kansas,USA; 8 at sites along the East Coast of the United States, and 4 in central coastal California, USA. We classified birds into one of four life phases based on appearance and behavior following the time of capture: newly-fledged (one individual captured on its natal colony), first-year (one individual captured before the breeding season that lacked breeding plumes and did not visit a breeding colony), breeders (12 birds with breeding plumes at the time of capture that visited breeding colonies during the breeding season), or non-breeders (3 individuals with breeding plumes, but that did not visit breeding colonies regularly).

Treatment of Location Data

Whenever a transmitting bird passed near a cell-phone tower, its locations were uploaded as GPS coordinates to Movebank (Kranstauber et al. 2011). Ninety-three percent of the time-intervals of the approximately 1.3 million GPS points were 5 min. Six percent of all time-intervals were between 6 and 20 min, and 0.5% were greater than 20 min. For each record the bird was either flying, foraging, roosting or at a nest. To calculate travel distances between individual points on the ground or in trees we eliminate points where the bird was flying. Since foraging Great Egrets do not move faster than 1 m/s (Brzorad et al. 2004), points that exceeded this value (estimated by GPS tags) were excluded from the analysis. Because Great Egrets generally have habitual movement patterns (e.g., central-place foragers, repeated use of the same foraging area, etc.), we uniquely named each area that a bird used. Sites that were used repeatedly appeared as clouds of points with a very dense centroid. The more a particular area was used, the wider the overall scatter of the cloud. For a stationary tag, such as when a bird was incubating, 87% of the points in this cloud were within 25 m, and 96% of the points were within 40 m of the actual tag location (Brzorad, unpubl. data). All GPS locations within this cloud were given the same name. Flight distances were estimated by calculating distances between the centroids of differently named locations. This method overcame the inaccuracy of the tags which is 3.4 m (Brzorad and Maccarone, unpubl. data). Outliers were single points outside of these regions that could not have been reached by the normal flight speed of Great Egrets (Maccarone et al. 2008). These points were also excluded from the analysis. The algebraic distance formula $\sqrt{(x_2-x_1)^2+(y_2-y_1)^2}$, where x_1 and y_1 are the longitude and latitude, respectively, in Universal Transverse Mercator (UTM), was used to calculate the distances between successive, differently named locations (x_1, y_1) and (x_2, y_2). Distances traveled between named locations were summed for each day to calculate Total Daily Distance (TDD). Maximum Daily Displacement (MDD) was the most distant point occupied from the central place for each day.

All points were then classified into one of four main phases of the year: Breeding, Post-Breeding, Winter and Migration. A short pre-breeding period was also identified prior to oviposition but after Spring arrival to the breeding colony. The breeding phase, which represented the time between a bird's first and last visits to a breeding colony, was further subdivided into sub-phases determined by nest contents. Based on their day of first arrival and day of departure from a breeding colony, 12 birds appeared to be tending nests. Within the breeding phase, nest contents were either observed directly, or interpolated using phenology information from McCrimmon et al. (2011). Birds were classified as either non-breeding, courtship/brooding eggs, or tending chicks. We assumed incubation began 8.5 d after a male and 7 d after a female arrived at the colony (McCrimmon et al. 2011). The egg phase began with incubation and was recorded as Day 1. The period during which progeny were present were categorized sequentially as eggs/incubation (Days 1-34) during which incubation occurs, small chicks (Days 35-40), medium chicks (Days 41-50), and large chicks (Days 51-114), according to reported growth rates (McCrimmon et al. 2011). Thus, TDD and MDD could be tracked by the relative day within the breeding season (BDAY). TDD and MDD were averaged for each day.

Post-breeding phase was defined as the days after the last visit to the breeding colony until the time the bird migrated. Migration was classified as southward or northward, long-distance, nocturnal flight. Shorter regional flights were also identified, but neither they nor migration, were included in the study. Winter encompassed the time after the southward migration until the next northward migration. Three birds in California (GREGs 2, 3 and 5) and one bird in North Carolina (Newbern) made the distinction between Post-breeding and Winter more difficult to determine because these birds did not migrate. A shorter regional flight made to a different area was used to make this distinction.

Foraging habitat was classified as freshwater, tidal, or mixed. Some birds that foraged at sites with variable depths associated with the tides also used nearby non-tidal ponds, often during high tide. Birds that used freshwater habitats never experienced any tidal varia-

tion. Mixed use represented use by birds that spent seasons or weeks in either freshwater or tidal areas and that often shuttled between these areas in regional flights. Sites within seasons (breeding or winter) were classified as either temperate or tropical based on biogeographic region.

Index of Chick Food Demand and Flight Distances

In 2018 and 2019, the nests of four tagged birds (2 each in Kansas and California) were monitored during the breeding season, with nest status recorded every two or three days. To estimate the level of food requirement, a chick demand index (CDI) was created for these nests by multiplying the size categories of chicks described earlier (small, medium, large) by the number of chicks in the nest. As chicks increase in size, we hypothesize so does their demand for food. If true, we predict that adults will travel greater distances (TDD) each day as the CDI increases. They will not necessarily fly further (MDD) from the colony. For this group of four birds, MDD and TDD were examined from the basis of CDI.

Use of Space

Utilization Distributions (UD) for all non-migration phases were derived from GPS locations. The UD is defined as a probabilistic map of the area used by an egret during some set period of time (Worton 1989). Maps were generated for areas representing 95% usage. This means that there is a 95% chance that the bird will be found within the area delimited by the 95% contour. Each UD95 was computed separately for each of the annual phases described above. The UD95s were generated by using local convex hull analysis in the R package, T-LoCoH, and followed recommendations in Lyons *et al.* (2013). This analysis computed UDs through a process that involves generating and combining multiple polygons created from sets of neighboring points. One advantage of this technique over others such as kernel density is its ability to accommodate UDs that follow linear or angular features such as waterways and coastlines. Exploratory analysis found that the "A-method" (with A

= 1000 m for all analyses) resulted in the clearest designations of habitat and minimized the appearance of spurious triangular areas in the UDs in regions of sparser points (Lyons *et al.* 2013). All analyses were carried out using the Universal Transverse Mercator UTM coordinate systems and sizes of the resulting UDs were computed in hectares. The A-value removes outliers by constraining the analysis so that it stops "looking" for new neighbors to include once it hits a threshold (the A-value) of cumulative distance. For consistency, the same value (A = 1000) was used for each of the birds. To supplement this analysis, we also determined the area of a minimum convex polygon (MCP) of space use for each individual and annual phase. This area was defined as the smallest convex region that contained all points.

Statistical Analysis of Daily Flight Distances, UD's and MCP's

We first tested for differences in mean flight distances among the 17 birds and between sexes. The other independent variables used to examine patterns in daily flight distances, UD's, and MCP's are shown in Table 1. All response variables were found to be distributed normally and so parametric two-tailed ANOVA and t-tests were used to examine the effects of independent variables on MDD and TDD (Zar 1974). Means and standard errors, except where noted, are reported throughout. Separate linear regressions were performed between TDD and MDD and BDAY for the egg sub-phase and for the combined chick (small, medium, and large) sub-phases. An overall regression was also performed for the entire breeding phase (Proc. Reg. SAS 9.4) to assess the combined effects of independent variables on flight distances. We used multiple linear regression to examine overall variation in TDD and MDD for 16 birds (excluding Meadows), as well as for the 4 birds tending nests of known contents (number of chicks & size of chicks). In both cases statistical tests were not run when significant correlations were detected between independent variables. Independent variables were not included if probabilities exceeded 0.05.

Table 1. A listing and description of the independent variables used in understanding Maximum Daily Displacement (MDD; farthest distance from roost or colony each day), Total Daily Distance (TDD; cumulative daily flight distance), Utilization Distribution (UD95) and Minimum Convex Polygon (MCP) of Great Egret *(Ardea alba)*.

Variable	Description
BIRD	Identifier for birds 1-17
SEX	Male or Female
LIFE PHASE	Newly fledged/First year, Breeding adult, Non-Breeding adult
ANNUAL PHASE	Breeding, Post-Breeding, Winter
PROGENY	Bird attending a nest, Bird not attending a nest
NUMBER of CHICKS	Observed in four study nests. Range: 1-4
CHICK SIZE	Eggs, Small, Medium, and Large
YEAR	2013-2019
WATER	Freshwater sites used, Tidal sites used, Both freshwater and tidal
GEOGRAPHIC TEMP	Temperate or Tropical
REGION	Southern Plains, East Coast of N. America, California, and Mexico
BDAY	Relative day of the breeding season

We used the same independent variables to examine patterns of area use. Pearson's correlation was used to determine whether there was an association between the two measures of flight distances (TDD and MDD) and the UD. A two-tailed t-test was performed comparing the size of UD95 in freshwater (n = 16 bird-season combinations) and tidal (n = 13) foraging areas across all seasons. Birds were represented by one to three seasons, with some birds representing multiples of some seasons.

RESULTS

Seventeen birds in this study were monitored for periods ranging from 82 to 1095 days (Table 2). Meadows, a young-of-the-year bird, was excluded from further analysis because its transmitter stopped sending locations (either the bird expired or the transmitter stopped working) before the bird settled into an area. All other birds had established daily patterns and areas of use. There were significant differences among individuals both in mean MDD ($F_{15, 4125}$ = 24.2, P < 0.0001; range: 1.5 ± 0.4 km to 5.7 ± 0.2 km) and mean TDD ($F_{15, 4125}$ = 45.8, P < 0.0001; range: 5.3 ± 0.7 km to 19.0 ± 0.9 km) (Table 3). Both measures of flight distance also differed by sex: mean MDD for male birds (5.5 ± 0.1 km; n = 14 birds) was signifi-

cantly greater than for females (4.3 ± 0.3 km; n = 3 birds) ($F_{1, 5317}$ = 12.7, P < 0.0001), and mean TDD for male birds (14.2 ± 0.2 km) was greater than for females (13.0 ± 0.4 km) ($F_{1, 5317}$ = 6.5, P < 0.01).

Both measures of flight distances also differed by phase of the annual cycle. Mean MDD differed across the four phases ($F_{3, 4137}$ = 15.2, P < 0.0001) and was highest during the breeding phase (4.3 ± 0.1 km) and lowest during the post-breeding phase (3.3 ± 0.1 km). Mean TDD also differed across phases of the annual cycle ($F_{3, 4137}$ = 33.8, P < 0.0001), but showed a different pattern. The highest mean TDD occurred during the breeding season (14.2 ± 0.3 km) and the lowest during winter (11.0 ± 0.2 km; Fig. 1). Mean MDD differed significantly by the type of water (t_{3656} =16.6, P = 0.0001). The 13 birds that used tidal areas flew greater distances (5.6 ± 0.1 km) than the 8 birds that used freshwater sites (3.2 ± 0.1 km). Five birds foraged at times in freshwater, and at other times in tidal water. Likewise, mean TDD differed by type of water (t_{3656} = 12.3, P < 0.0001) such that birds that foraged in tidal areas flew significantly further each day (17.4 ± 0.4 km) than birds that foraged exclusively at freshwater sites (11.7 ± 0.3km). All the birds oc-

Table 2. Names, sexes, capture dates, days active, and capture locations (in the USA) for 17 Great Egrets (*Ardea alba*) used to study Maximum Daily Displacement (MDD; farthest distance from roost or colony each day), Total Daily Distance (TDD; cumulative daily flight distance), Utilization Distribution (UD95) and Minimum Convex Polygon (MCP). Birds were active for 5,693 total days at the time this paper was prepared (some birds were named after principals or teachers at schools who adopted them for class projects).

Bird	Sex	Capture Date	Days	Capture Location
Heller	F	3 March 2013	326	Beaufort, North Carolina
Kelly	M	29 March 2013	226	Englehard, North Carolina
Palma	M	30 March 2013	250	Englehard, North Carolina
Bisbing	M	21 April 2013	190	Corolla, North Carolina
Newbern	M	28 April 2013	192	Elizabeth City, North Carolina
2691	M	20 May 2013	88	Wichita, Kansas
Meadows	M	24 June 2013	82	Kure Beach, North Carolina
Waldo	M	20 May 2015	420	Wichita, Kansas
Nelson	M	24 May 2015	1095	Wichita, Kansas
Clarence	M	24 June 2015	226	Staten Island, New York
Edward	M	25 June 2015	802	Staten Island, New York
GREG1	M	8 June 2017	439	Tomales, California
GREG2	F	9 June 2017	378	Tomales, California
GREG3	F	10 June 2017	375	Tomales, California
Carl	M	1 June 2018	227	Wichita, Kansas
V's Bird	M	30 May 2018	115	Wichita, Kansas
GREG5	M	8 June 2018	262	Tomales, California

Table 3. Mean (± SE) Total daily distance (TDD) and mean (± SE) maximum daily displacement (MDD) (both in km) from a central place (roost or colony) for 16 Great Egrets (*Ardea alba*) monitored between May 2013 and June 2018. Birds are represented by one or more annual phases and habitat types. Regions include the southern plains of the United States (with Nelson migrating to winter in Mexico), the Eastern USA (north and mid-Atlantic, the Carolinas), and Western USA (Central and Southern California). Foraging refers to the type of habitat used for foraging (Fresh = exclusively freshwater; Tidal = tidal with freshwater used at high tide; Mixed = mixed use of freshwater and tidal sites; N = number of days used to calculate TDD and MDD).

Bird	Region	Foraging Habitat	TDD (km)	SE	MDD (km)	SE	N
2691	S. Plains	Fresh	6.6	2.6	2.9	1.3	88
Bisbing	E. USA	Tidal	13.0	0.8	5.2	0.4	172
Heller	E. USA	Tidal	12.1	0.4	4.9	0.2	310
Kelly	E. USA	Fresh	5.3	0.7	1.6	0.4	201
Newbern	E. USA	Fresh	7.3	0.7	3.0	0.4	183
Palma	E. USA	Tidal	10.5	0.6	3.7	0.3	244
Clarence	E. USA	Tidal	9.5	0.5	2.9	0.3	224
Edward	E. USA	Tidal	12.8	0.3	3.9	0.2	755
Nelson	S. Plains	Fresh	7.2	0.3	2.2	0.1	986
Waldo	S. Plains	Fresh	10.7	0.4	4.0	0.2	413
Carl	S. Plains	Fresh	12.5	0.5	4.1	0.3	221
V's Bird	S. Plains	Fresh	19.0	0.9	3.4	0.4	111
GREG 1	W. USA	Mixed	14.6	0.4	5.7	0.2	424
GREG 2	W. USA	Mixed	14.4	0.4	4.6	0.2	378
GREG 3	W. USA	Mixed	12.7	0.4	3.6	0.2	368
GREG 5	W. USA	Mixed	16.4	0.5	4.1	0.2	257

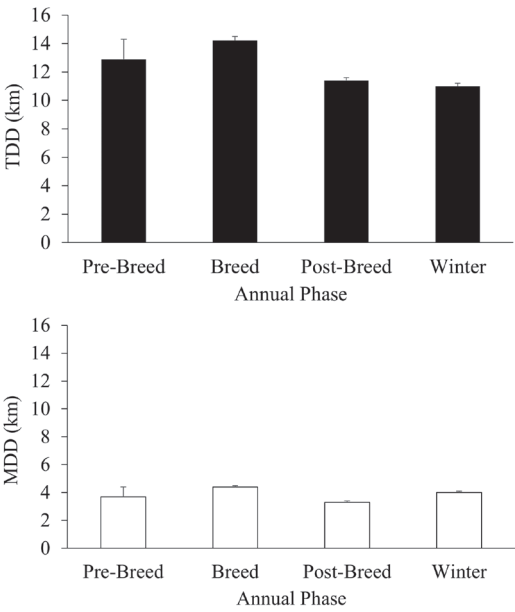cupied temperate locations, with just 4 of these spending winter periods in the tropics.

Figure 1. Mean (± SE) total daily distance (TDD; top) flown and average daily maximum displacement (MDD; bottom) (both in km) from a central place (roost or colony) by seasonal phase (excluding migration) for 17 Great Egrets (*Ardea alba*) monitored between May 2013 and June 2018.

Mean MDD did not differ between birds in temperate and tropical locations (t_{5466} = -1.1, P < 0.27); however, mean TDD for birds in temperate areas (16.4 ± 0.4 km) was significantly greater than for birds in tropical areas (10.1 ± 1.3 km) (t_{5466} = -5.4, P < 0.0001).

Breeding status, determined by whether or not a bird visited a breeding colony regularly while being tracked did not affect mean MDD, which averaged 5.3 ± 0.1 km for breeding birds and 4.7 ± 0.5 km for non-breeding birds ($F_{1, 5528}$ = 1.7, P = 0.3); however, mean TDD for breeding birds (14.1 ± 0.2 km) was significantly greater than for non-breeding birds (11.4 ± 0.7 km) ($F_{1, 5351}$ = 14.2, P < 0.0002).

In the full multivariate analysis of maximum daily distances, only annual phase and progeny were important predictor variables ($F_{2, 5467}$ = 5.0, P = 0.007). However, these two variables accounted for almost none of the total variation in MDD (MDD = 3.7 + 0.6PHASE + 1.9PROGENY; R^2 = 0.002). For TDD, only breeding status and type of water were important predictor variables ($F_{2, 5467}$ = 78.8, P < 0.0001). Similarly, these variables accounted for very little of the variation in

TDD (TDD = 10.4 + 10.2PROGENY + 1.8 WATER; R^2 = 0.03).

For the four birds whose nests were monitored during the breeding season, there was a strong relationship between mean TDD and chick food demand ($F_{1, 222}$ = 156.0, $P <$ 0.0001; R^2 = 0.41). This relationship is modeled by the regression equation TDD = 15.57 + 2.065 CDI; Fig. 2). A significant yet weaker relationship existed between mean MDD and chick food demand ($F_{1, 222}$ = 23.3, $P <$ 0.0001; R^2 = 0.09), modeled by the equation MDD = 4.032 + 0.162 CDI. During the egg/incubation period there was no statistical relationship between day of the breeding phase and either TDD (r_{62} = 0.10, P = 0.42) or MDD (r_{62} = 0.05, P = 0.7; Fig. 3). Over the course of the entire breeding season, however, mean TDD increased steadily ($F_{1, 1236}$ = 167.0, $P <$ 0.0001; R^2 = 0.12; Fig. 3), and is modeled as TDD = 9.39 + 0.24BDAY. Mean MDD also rose gradually over the course of the breeding period ($F_{1, 1236}$ = 76.6, $P <$ 0.0001; R^2 = 0.06): MDD = 3.03 + 0.05BDAY. In the multivariate analysis, the index of food demand and Julian date accounted for significant variation in MDD: MDD = 8.01 + 0.20DEMAND - 0.02JDATE ($F_{2, 202}$ = 12.3, $P <$ 0.0001; R^2 = 0.11). Two different independent variables (number of chicks, size of chicks) accounted for significant variation in TDD: TDD = 11.9 + 4.1NCHICKS + 3.5CHICKSIZE ($F_{2, 202}$ = 77.4, $P <$ 0.0001; R^2 = 0.44).

UD95 showed a wide range among individual birds and varied from 6.0 to 552.0 ($\pm$ 14.6) ha (Fig. 4, Table 4). Mean Minimum Convex Polygons (MCP) did not differ among birds ($F_{15, 9}$ = 1.5, P = 0.30), but did differ significantly by season ($F_{2, 60}$ = 4.3, $P <$ 0.02) where it was larger during the winter season than during both the breeding and post-breeding seasons (Table 4; for an example of change from breeding to post-breeding see Fig. 5). UD95 was not associated with MDD (r_{61} = 0.11, P>0.05). However, mean TDD was associated strongly with UD95 (r_{61} = 0.36, $P <$ 0.005), such that birds which flew further in a day also visited a larger area as opposed to repeatedly using the same foraging area. The relative variability in MCP (coefficient of variation ranged from 124.4 to 237.4) was greater than that of UD95 (ranged from 64.7 to 77.5) (Table 4). Birds that foraged in exclusively tidal sites used areas about twice as large (UD95=183.3 $\pm$ 22.2 ha) as birds that used only freshwater areas (UD95=89.6 $\pm$ 21.3 ha) (t_{25} = 3.0, P = 0.006).

The birds that were followed for multiple years (Nelson, Edward, and Carl; Table 2) showed strong breeding site fidelity. Edward and Carl used the same breeding colony over the course of the study. Nelson bred in Wichita each year but relocated his nest when the original colony was destroyed by homeowners (Fig. 5). Site fidelity was lower in the winter and birds occupied similar regions, but not necessarily the same roosts or foraging areas. During the breeding and post-breeding phases, birds exhibited the greatest fidelity in foraging, colony and roost sites. In many cases (California birds, Nelson, and Waldo) winter was associated with the lowest site fidelity for both foraging and roosting sites. Birds would frequent a roost for days or weeks and then relocate to a new roost and new foraging locations. Movement
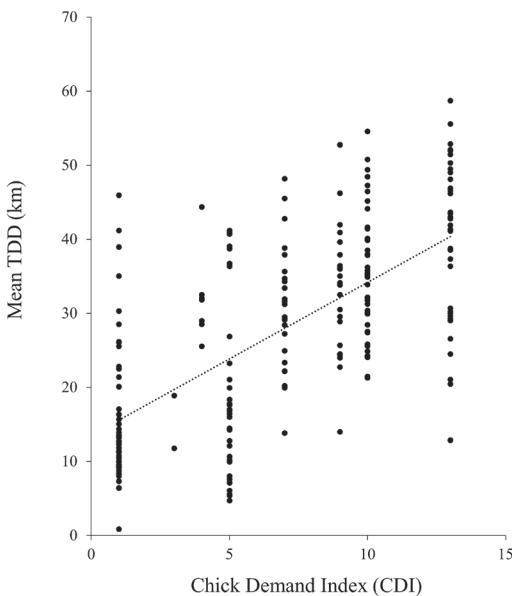

Figure 2. Regression of mean TDD (total daily distance) moved by 4 breeding adult Great Egrets (*Ardea alba*) against an index of chick food demand derived by multiplying chick size by the number of dependent chicks ($F_{1, 222}$=156.02, $P <$ 0.0001; R^2 = 0.413; each dot represents a daily mean).
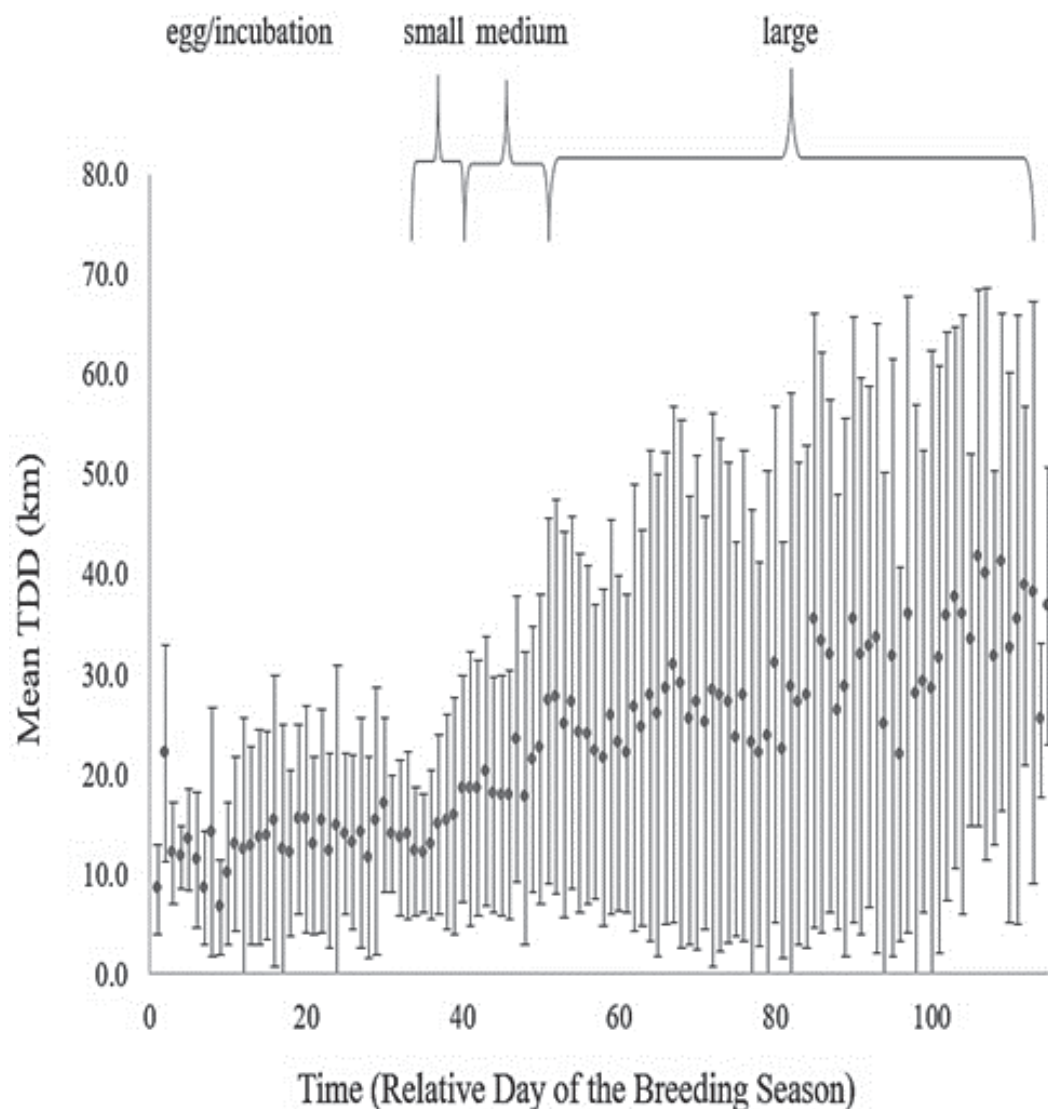
Figure 3. Mean (± SD) TDD (total daily distance) for 4 breeding adult Great Egrets (*Ardea alba*) monitored from incubation to large chick stages derived from McCrimmon *et al.* 2011: Incubation = days 1-34; Small Chicks = days 35-40; Medium Chicks = days 41-50; Large Chicks = days 51-114 ($F_{1, 1236}$ = 167.0, P < 0.0001; R^2 = 0.12, based on 1231 days).

patterns were most complex at this time and contributed to the large UD95 and MCP areas (Table 4).

DISCUSSION

An animal that ingests another organism to obtain energy for survival and reproduction occupies some finite space and performs a critical ecosystem function. By using state-of-the-art GPS technology, we have measured the amount of aquatic/wetland area needed to provide the energy to maintain 16 adult Great Egrets during the entire annual cycle. These areas averaged between 128 and 179 ha and represent the size of the aperture through which energy flows from one trophic level to the next. That aperture area represents the quantitative balance between 1) the productivity of prey in the ecosystem, 2) the energetic demand from the predator, and 3) the availability of the foraging habitat, often influenced by tidal
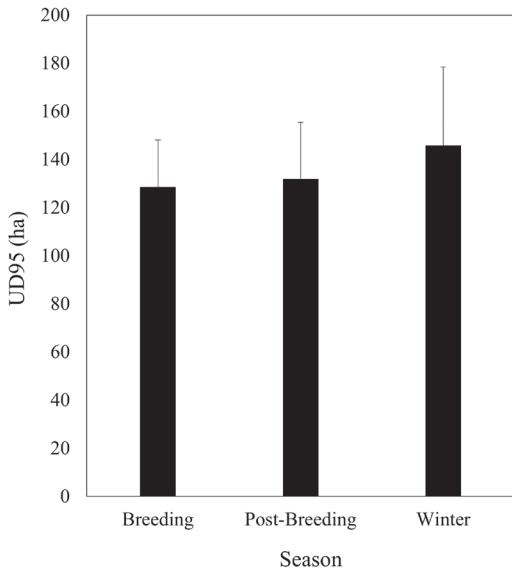
Figure 4. Seasonal means and standard deviations of the 95th percentile of the Utilization Distribution (UD95) in ha, for 16 Great Egrets (*Ardea alba*) monitored between May 2013 and June 2018. Data provided by individual birds ranged from 2 to 8 seasons (breeding, post-breeding, and winter; pre-breeding was excluded because of low sample size).

variation. As the total daily distance flown increases, UD95 increases as well, perhaps to fuel the expensive demand of flight. Thus, an energetic give-and-take determines the amount of wetland used. By contrast, MDD and MCP appear to be driven by geographic-landscape features (Kelly *et al.* 2008). The distances between safe central places and productive foraging sites depend on the vagaries of regional landscapes. For example, the meander of a river or shape of a coastline may expand or contract the distance between central places and foraging sites. Thus, in both absolute and relative terms, variation in MCP size is much greater than for UD95. Because both ecosystem productivity and animal demand have limits, some threshold must exist where even rich foraging sites would not warrant trips from a distant central place. It is not clear if that limit has been observed in the present study.

We also documented the flight distances required by individual Great Egrets to reach different foraging habitats. The variation in these flight distances is manifested in the size of the MCP. UD95 increased in size as birds increased the total distance they flew each day, since they presumably visited more sites. This same relationship was not true for increases in MDD, such that greater distances from the central place were not associated with larger areas used. The specific UD size is independent from its distance from the central place.

We hypothesized that Great Egrets are sensitive to landscape features where safe central places are within range of foraging sites of sufficient productivity (prey availability). Further, we predicted that egrets will only settle in areas where the distance between central places and foraging areas is below the MDD. In this study, the greatest such distance observed was 14 km recorded for Edward during the breeding season. But overall means ranged only from 3.3 km in the post-breeding season to 4.3 km during the breeding season. Mean distances for individual birds showed a greater range (1.6 to 5.7 km), and even more variation when individual averages were examined by season. For example, Newbern nested in a wooded swamp and was within only 1 km of much of his foraging sites. As a result, his mean MDD was only 0.9 km. Thus, during the breeding season, when MDD varies the most, we can expect most foraging Great Egrets in our study areas to be within 14 km of their breeding colony; however, this distance may be up to 28.5 km under certain circumstances (McCrimmon *et al.* 2020). This information can aid in the localization of unknown colonies by documenting the locations of highly-visible foraging birds. It can also guide or prioritize wetland protection around known colonies. The most distant point to which Great Egrets are willing to fly to from their central place sets the parameters for ecologically important factors such as TDD and MCP. Together, these habitat usage metrics may provide important information regarding energy use and habitat quality (*e.g.,* prey availability) at landscape scales.

Previously it was shown that 12 breeding Great Egrets equipped with VHS transmitters made an average of four foraging

Table 4. Utilizations Distributions (UD95, in ha) and home range (Minimum Convex Polygons, in km²) for 16 Great Egrets (*Ardea alba*) monitored during the breeding, post-breeding and winter seasons in the USA, 2013 - 2018. Most birds have single estimates for specific seasons, but some birds have multiple estimates (years) for a season, in which case standard deviation is given (number of years in parentheses if > 1). Average, SE, and coefficient of variation (CV) was calculated for all birds each season.

| Bird	UD95 (ha)						MCP (ha)					
	Breed	SD (yrs)	Post	SD (yrs)	Winter	SD (yrs)	Breed	SD (yrs)	Post	SD (yrs)	Winter	SD (yrs)
2691	32	—	6	—	—	—	23	—	4	—	—	—
Bisbing	61	—	75	—	—	—	255	—	86	—	—	—
Heller	142	—	189	—	164	86 (2)	56	—	45	—	31	16 (2)
Kelly	124	—	42	—	30	30 (2)	374	—	986	—	1,378	1,456 (2)
Newbern	21	—	51	—	192	—	3	—	412	—	1,378	—
Palma	113	—	226	—	121	24 (2)	2,000	—	28	—	13,714	19,218 (2)
Clarence	107	—	247	—	166	—	152	—	1,518	—	71	—
Edward	344	72 (2)	167	17 (3)	260	129 (3)	123	36 (2)	383	98 (3)	7,701	10,412 (3)
Nelson	28	8 (4)	27	—	243	226 (3)	177	230 (4)	9	—	3,666	3,029 (3)
Waldo	189	108 (3)	282	185 (2)	—	—	4,849	3,465 (3)	799	338 (2)	—	—
Carl	84	—	—	—	26	—	45	—	489	—	—	—
V's Bird	137	—	54	—	—	—	34	—	125	—	—	—
GREG1	90	25 (2)	84	—	552	—	34	9 (2)	188	—	15,689	—
GREG2	137	55 (2)	157	—	103	—	88	3 (2)	135	—	183	—
GREG3	154	33 (2)	78	—	128	26 (2)	130	71 (2)	91	—	123	107 (2)
GREG5	265	—	75	—	145	—	74	—	178	—	301	—
Average	128		132		179		761		364		4,135	
SE	21.3		23.5		32.6		40,993		9,956		171,011	
CV	67.4		74.3		77.5		237.4		124.4		143.5	
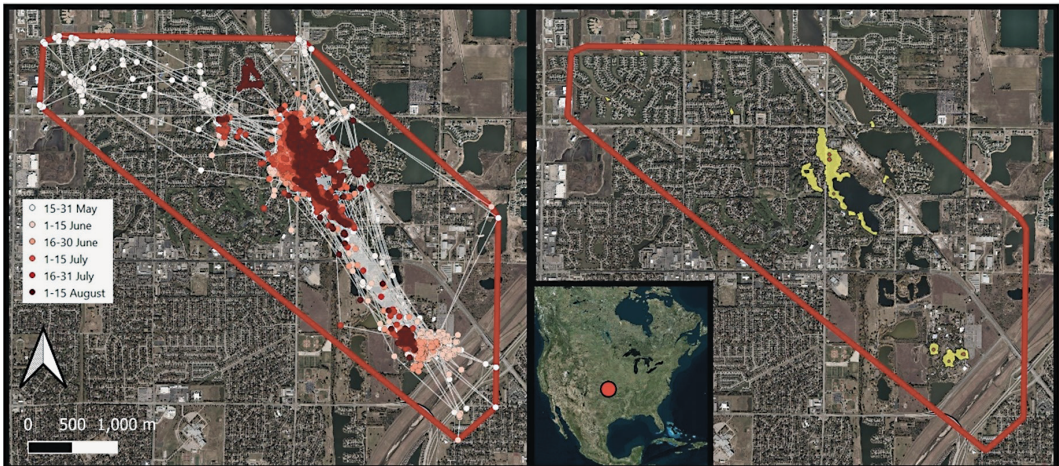
Figure 5. Left panel: Transit routes and minimum convex polygon (MCP) for Nelson during the 2016 breeding and early post-breeding periods in Wichita, Kansas; changes in the colors of points (2-week intervals) show how the amount of space used contracts after the breeding season. Right panel: Utilization Distribution (95% in yellow; 50% in red) for this same time period and location.

flights per day and spent a median 180 min per foraging trip. Significant individual variation existed in that these birds traveled mean one-way distances to reach their foraging sites that ranged from 2.8 km to 19.6 km (Brzorad *et al.* 2015). A later analysis of free-living Great Egrets showed that male birds are significantly heavier than females and have larger culmens and tarsi (Maccarone and Brzorad 2016). It is possible that males have different foraging capability than females (Kolts and McCrae 2017) since they can presumably carry a heavier payload back to the colony. Males and females may also spend different amounts of time attending nests. In addition, because egrets show frequent aggression at contested feeding sites (Brzorad *et al.* 2015), larger males may have an advantage. Since 81% of the birds in this study were males, we are cautious to make definitive conclusions about females.

Recent advances in remote sensing technology (Hulbert and French 2001; Cooke *et al.* 2004; Bograd *et al.* 2010) have uncovered some of the detail hidden in these earlier studies and have made possible a broader and deeper examination of avian flight. For example, like the earlier 12 birds that carried VHS transmitters (Brzorad *et al.* 2015), the birds in the present study also showed

significant variation in both MDD and TDD. However, unlike the first group, which nested in a single colony and were tracked only short distances during the breeding period, the birds described here lived in widely separated locations and could be tracked throughout the year and for unlimited distances. In addition, we documented significantly longer total daily flight distances for male birds.

In several ways, this study demonstrated the demands of reproduction on breeding adults. First, aside from migration, total daily flight distances were highest during the breeding season, such that parents flew further when they were feeding chicks than at other times. The pattern of longer flights during breeding was independent of geographic location and thus applied to birds that nested in widely separated locations. However, the type of wetland ecosystem within which a bird foraged appeared to affect how far it flew to get there. In general, birds flew farther to reach tidal areas than freshwater sites. During the breeding season, Edward had the longest MDD and foraged in a tidal estuary. We are uncertain whether the relationship between flight distance and wetland type reflected the spatial distribution of different wetlands relative to a colony or roost location, whether differ-

ent ecosystems vary in productivity or prey availability (Maccarone and Brzorad 2005; McKinney and Raposa 2013; Brzorad *et al.* 2015), or some other factor. In tidal areas, salt marsh or mangroves occupy the upper part of the intertidal zone, so a rising tide decreases the amount area available where a foraging bird can freely move without being encumbered by vegetation. Birds foraging in tidal areas could be forced to move to new areas on rising tides, and to which they could return on falling tides (Maccarone and Parsons 1994). This may add to their TDD and UD95, a situation that does not exist in non-tidal areas.

Second, both MDD and TDD increased linearly with the number of chicks in the nest. MDD increased only slightly, which suggests that breeding birds respond to increased demand by increasing their flight distance they travel within their foraging radius, rather than extending their radius appreciably. However, TDD more than doubled as chicks grew from hatching to nearly fledged, which means that birds visited more sites each day, and/or made more foraging trips. Total daily distance then decreased slightly just before chicks fledged. Perhaps adults begin to wean their chicks at this stage to encourage them to start flying and foraging on their own. An earlier nesting study (Maccarone *et al.* 2010) showed that when chicks reach adult size, both parents spend more than half the day away from the nest, presumably foraging. This study showed that parents then scale back on their daily flight distances. Finally, we believe our ability to overlay descriptions of nest contents with MDD and TDD measurements from breeding adults was particularly valuable. The four birds whose nests were monitored during the breeding season showed that TDD is closely tied to the level of food demand by chicks. In fact, the value of the index of food demand accounted for 41 % of the variation in daily flight distances. This study has generated values that the conservation community can use to inform and advocate for protection of specific wetland areas and their supporting ecosystems.

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