Landscape factors and hydrology influence mercury concentrations in wading birds breeding in the Florida Everglades, USA

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HIGHLIGHTS

- Hydrologic variables may influence Hg exposure in wading birds.
- Hg in adult great egrets was most influenced by region.
- Adult white ibis Hg was most influenced the number of days a site was dry.
- Hg in egret chicks was most influenced by date.
- Hg in ibis chicks was most influenced by chick age, region, and water recession rate.

ARTICLE INFO

ABSTRACT

The hydrology of wetland ecosystems is a key driver of both mercury (Hg) methylation and waterbird foraging ecology, and hence may play a fundamental role in waterbird exposure and risk to Hg contamination. However, few studies have investigated hydrological factors that influence waterbird Hg exposure. We examined how several landscape-level hydrological variables influenced Hg concentrations in great egret and white ibis adults and chicks in the Florida Everglades. The great egret is a visual "exploiter" species that tolerates lower prey densities and is less sensitive to hydrological conditions than is the white ibis, which is a tactile "searcher" species that pursues higher prey densities in shallow water. Mercury concentrations in adult great egrets were most influenced by the spatial region that they occupied in the Everglades (higher in the southern region); whereas the number of days a site was dry during the previous dry season was the most important factor influencing Hg concentrations in adult ibis (Hg concentrations increased with the number of days dry). In contrast, Hg concentrations in egret chicks were most influenced by calendar date (increasing with date), whereas Hg concentrations in ibis chicks were most influenced by chick age, region, and water recession rate (Hg concentrations decreased with age, were higher in the southern regions, and increased with positive water recession rates). Our results indicate that both recent (preceding two weeks) hydrological conditions, and those of the prior year, influence Hg concentrations in wading birds. Further, these results suggest that Hg exposure in wading birds is driven by complex relationships between wading bird behavior and life stage, landscape hydrologic patterns, and biogeochemical processes.

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1. Introduction

A greater understanding of the global distribution and atmospheric deposition of mercury (Hg) has led to heightened concern for wildlife exposure, because as impairment thresholds become refined and better quantified, there is increasing evidence that environmentally relevant Hg exposure can result in impaired reproduction and other toxicological endpoints such as endocrine disruption (Frederick and Jayasena, 2010; Jayasena et al., 2011). Waterbirds are particularly prone to elevated Hg exposure and associated toxicity in wetland ecosystems (Frederick et al.,

2002; Eagles-Smith et al., 2009; Ackerman et al., 2011) where they often are top predators, and biogeochemical conditions facilitate the conversion of inorganic Hg to methylmercury (MeHg; Marvin-DiPasquale et al., 2003; Hall et al., 2008), the most toxic and bioavailable form. Wetlands with substantial hydrologic fluctuations can potentially enhance both the methylation and availability of MeHg (Cleckner et al., 1998; Gustin et al., 2006). Consequently, waterbirds that rely on ephemeral hydrology for enhanced foraging opportunities can be exposed to elevated MeHg through food web biomagnification (Sundlof et al., 1994; Frederick et al., 2002; Custer et al., 2008).

Shallow wetland ecosystems with regularly fluctuating hydrologic conditions and elevated loading of reactive inorganic Hg also present an ideal situation to study landscape hydrologic factors that may

promote the exposure and uptake of MeHg by upper trophic level waterbirds. The Florida Everglades is particularly well suited for this type of study because it is a very large (8713 km²) pulsed hydrologic system (wet and dry seasons; Obeysekera et al., 1999), and over 60% of the landscape dries out each year (USGS, 2006). The Everglades has a well-documented history of elevated atmospheric Hg deposition and conversion of inorganic Hg to MeHg on a landscape scale (Osborne et al., 2011), and supports extensive populations of breeding wading birds which have previously been shown to have elevated Hg concentrations (Sundlof et al., 1994; Rumbold et al., 2001; Frederick et al., 2002; Herring et al., 2009). Importantly, large areas of the Everglades contain elevated dissolved sulfate concentrations (20–50 mg/l) that exceed background levels (<1 mg/l) (Orem et al. 2011). Sulfate in the Everglades originates from the Everglades Agricultural Area and is associated with both agricultural practices and from the sulfur released by oxidation of organic soils (Orem et al. 2011). Sulfate plays a critical role in the production of MeHg, via microbial sulfate reduction, resulting in increased bioavailability and biomagnification of MeHg (Gilmour et al., 2007; Orem et al., 2011). Further, periphyton which serves as the base of the Everglades food web (Cleckner et al. 1998), has relatively high MeHg concentrations (Liu et al. 2008), and enhances the bioavailability of Hg in Everglades species (Cleckner et al., 1998; Molina et al., 2010). Thus, the hydrological pulsed nature of the Everglades, elevated atmospheric wet deposition of Hg (Mercury Deposition Network, 2012), periphyton based food web, and high concentrations of sulfate result in considerable MeHg production and subsequent availability within Everglades food chains.

Wading bird reproduction in the freshwater region of the Everglades occurs during the dry season (Dec–June), when water levels recede across the landscape, increasing aquatic prey density in shallow depressions (Kushlan, 1981; Gawlik, 2002). As such, hydrologic patterns are the dominant driver of wading bird foraging locations (Bancroft et al., 2002; Russell et al., 2002; Beerens et al., 2011), reproductive success (Kushlan, 1987; Frederick and Collopy, 1989; Herring et al., 2010), and health (Herring et al., 2011; Herring and Gawlik, 2012). Importantly, hydrologic factors associated with wading bird foraging patterns also may be associated with Hg methylation. The influence of hydrologic factors on waterbird MeHg exposure is poorly understood, but has important ramifications for water management activities in wetland ecosystems.

We evaluated MeHg exposure in two species of wading birds in relation to landscape-level hydrologic factors that are known to influence either MeHg production or wading bird foraging ecology. The great egret (*Ardea alba*; hereafter egret) and white ibis (*Eudocimus albus*; hereafter ibis) breed extensively throughout the Everglades and serve as long-term indicator species for Hg risk to the Everglades ecosystem (see Sundlof et al., 1994; Rumbold et al., 2001; Frederick et al., 2002; Heath and Frederick, 2005; Herring et al., 2009). Accordingly, they serve as important indicator species for the Everglades ecosystem. Although egrets and ibises nest and breed and feed sympatrically (that is coexist), they differ both in their foraging strategies (Gawlik, 2002; Beerens et al., 2011) and diets (Smith, 1997; Dorn et al., 2011). Ibises are "searchers" who target ephemeral high-quality patches of biomass, then abandon them once prey biomass declines, whereas egrets are "exploiters" that continue foraging at sites even when prey densities are low (Gawlik, 2002). Suitable foraging conditions for ibises also span a much narrower range of water depths than egrets (Beerens et al., 2011). Further, ibises usually consume crayfish (*Procambarus* spp.) but can switch to consuming fish when water recession rates and depths produce high fish densities (Kushlan, 1979; Dorn et al., 2011). In contrast, egrets select larger prey items than ibis (generally fish) regardless of habitat conditions (Smith, 1997). We hypothesized that differences in prey resources and habitat conditions (e.g., depths) would result in differential Hg exposure between these two species. Further, there may be differences in prey delivery to chicks of both species associated with chick size and semi-altricial (down covered at birth, nest bound, and fed by parents) life history of both species (Heath et al., 2009; McCrimmon et al., 2011), as well as associated differences in diets delivered to chicks

under varying hydrological conditions and landscape level prey densities (Dorn et al., 2011). Our objectives in this study were to assess the relative importance of factors associated with foraging habitat conditions, the production of MeHg, and large scale regional MeHg patterns on Hg concentrations in great egrets and white ibises, and to determine whether the drivers of Hg exposure are similar across adult and chick life stages.

2. Materials and methods

2.1. Study area

The Florida Everglades is a large, subtropical and oligotrophic wetland in southern Florida with pronounced annual wet and dry seasons (Obeysekera et al., 1999). The dry season, when most wading birds breed, typically spans from November through May. The Everglades ecosystem has been highly altered over the past 60 years, with more than half of its spatial extent lost to agriculture and urban development (Ogden et al., 2003). As a result, the hydrologic patterns of remnant areas are greatly altered, with changes to the timing, magnitude and predictability of both the hydrology and seasonal prey availability events that are critical to wading bird reproduction (Ogden, 1994). Although Hg concentrations in the Everglades wildlife have generally declined over the past decade, some areas still pose reproductive risks to piscivorous birds (Rumbold et al., 2008).

2.2. Bird capture and sample collection

2.2.1. Adult sampling

Adult egrets and ibises were captured during the pre-breeding season (Jan 10 to Mar 23 in 2006 and 2007) using either a netgun or modified flip trap (Herring et al., 2008a) and decoys (Crozier and Gawlik, 2003; Heath and Frederick, 2003). Birds were captured at 21 sites in the northern Everglades, within Water Conservation Areas (WCA) 2A, 3A, and the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox; Fig. 1). We attached radio transmitters (16 g) using a figure-8 harness to all birds to quantify foraging movement patterns throughout the breeding season and to estimate hydrologic conditions at foraging sites and within foraging ranges of breeding colonies.

We used blood as our matrix to measure Hg because it reflects recent exposure (Bearhop et al., 2000), whereas feather Hg concentrations are reflective of an equilibrium of both Hg exposure and body burden depuration only during the period of feather growth. Therefore, we could not accurately link feather Hg concentrations with recent foraging. From each bird, we collected up to 2 ml of blood from the brachial vein using a 27.5-gauge needle. Blood samples were stored in heparinized cryovials and placed on ice until transported to the lab. The blood volume available for collection while following American Veterinary Medical Association guidelines was limited due to the need to measure other physiological parameters (see Herring and Gawlik, 2012), therefore we measured the red blood cell (RBC) fraction for total Hg concentrations because most of the Hg in blood is in the RBC fraction, and RBC THg concentrations are correlated with the more commonly measured whole blood matrix (Chen et al., 2011; Lieske et al., 2011). Plasma and red blood cells were separated in the lab via centrifugation (15 min, 5000 rpm), and each fraction was frozen at −20 °C for later analysis. All adult birds were later sexed using DNA analysis (Zoogen Services Inc., Davis, CA; Herring et al., 2008b).

2.2.2. Chick sampling

We monitored nests within egret and ibis colonies that were associated both with our radio-tagged adults and easily accessible (Herring et al., 2010; Beerens et al., 2011; Fig. 1). Those nests (egrets = 59, ibises = 70) were revisited approximately every 7 days, and the order of chicks was determined by the hatching sequence noted during visits. Upon arrival at each monitored nest, we immediately removed the nestlings by hand and held them in either a cloth bag or large plastic container to keep
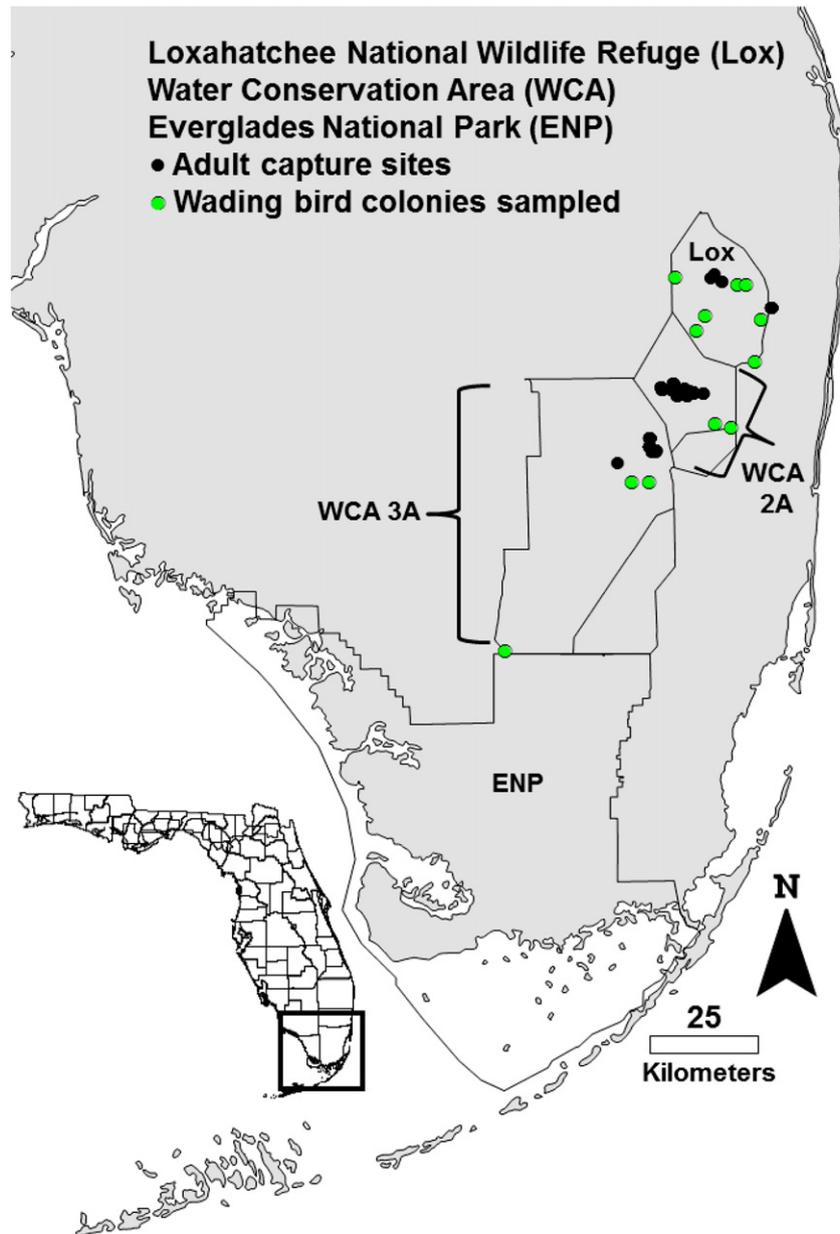
Fig. 1. Location of study area indicating adult wading bird capture sites and wading bird nesting colonies sampled during 2006 and 2007. The primary Water Management Areas (WCAs), Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox), and Everglades National Park (ENP) are indicated.

them calm and minimize movement during subsequent sampling and measurements. Blood collection and storage followed those methods described for adults above.

2.3. Hydrological conditions

We used the Everglades Depth Estimation Network (EDEN; USGS, 2006) to estimate water depths, water level recession rates, and the number of days sites were dry during the previous dry season (days dry) at both foraging sites where adults were captured and their associated breeding colonies where chicks were sampled. The EDEN uses a network of water level gauges to produce a water surface model that, when combined with a ground elevation model, provides an estimate of water depth for the entire freshwater portion of the Greater Everglades (Liu et al., 2009). EDEN calculates water level depths in 400 m × 400 m grid cells at daily time steps accounting for evapotranspiration, rainfall, and sheet flow. The estimated water depths are accurate to within 5 cm (Liu et al., 2009).

We estimated water recession rates, water depths, and days dry at foraging sites by first delineating the EDEN grid cells located within a 3-km radius of each bird capture site using ArcGIS 9.1 (ESRI, Redlands, CA). The 3-km radius was used because, in a prior study, radio-tagged egrets and ibises primarily foraged within 3 km of the capture site for up to 2 weeks prior to capture (Herring and Gawlik, 2012). We then extracted daily water depth values for the 14 days preceding each bird's capture for all cells within the foraging area, and used the mean depth and change-in-depth over each period as the measures of water depth and recession rate, respectively. Positive recession rates indicate decreasing water levels. We estimated days dry by counting the total number of days within the previous dry season that a site remained dry (i.e., depth < 0 cm). Surface water could still be present when estimated cell depth <0 cm; however, the 5-cm error in EDEN depths suggests that a majority of the ground surface would be exposed in a given 400 m × 400 m grid cell.

To estimate recession rates, water depths, and days dry associated with chicks sampled later in the breeding season we first used ArcGIS

9.1 (ESRI, Redlands, CA) to establish fixed radius buffers (hereafter foraging range) around colonies based on mean distances flown + 1 SE by the radio tagged adult egrets and ibises described above. We defined foraging range as the average distance that radio tagged individuals flew from breeding colonies to a foraging site throughout the breeding season. Egrets and ibises are central place foragers, and the use of foraging ranges was supported by our telemetry data. Estimates of foraging distances from colonies were obtained by locating the adult radio-tagged egrets (n = 76) and ibises (n = 125) via aerial surveys during 2006–2007 using a left–right control box and two side view directional yagi antennas. A random subset (20–30) of all radio-tagged adult egrets and ibises were aerially tracked each day during the morning 3–4 days per week throughout the breeding season to foraging sites. After each flight all located birds were removed from the tracking list, and after two successive aerial surveys all birds were added back into the tracking list. This approach resulted in individual birds being located no more than two times per week, with a minimum of three days between locations to ensure independence. Locations of foraging birds derived from radios were verified visually. The mean distance that adults flew from their nesting colony in 2006 and 2007, respectively, was 12.5 km ± 0.4 SE (n = 227) and 7.4 ± 0.5 SE (n = 178) for ibises, and 8.1 km ± 0.7 SE (n = 60) and 4.6 ± 0.3 SE (n = 163) for egrets (Beerens, 2008). We extracted the water depth from each EDEN grid cell within the foraging ranges for specific colonies by year and species. For each day that we sampled nestling blood, we calculated water recession rate and water depth as the mean value for the preceding 2-week period.

2.4. Mercury determination

We analyzed red blood cells for total mercury (THg) because the majority of Hg in blood is in the red blood cell fraction (Myers and Davidson, 1998; Day et al., 2007), and almost all (>95%) of the mercury in avian blood is in the methylmercury form (Thompson and Furness, 1989; Fournier et al., 2002). To minimize any potential variability in THg concentrations associated with differential moisture loss during long-term storage of samples, red blood cell fractions were dried (48 h at 50 °C) to a constant weight before THg analysis. We measured up to 0.05 g of dried blood into a quartz sample vessel (weighed to the nearest 0.00001 g; Mettler Toledo model XS105, Mettler Toledo, Columbus, Ohio, USA). Following U.S. Environmental Protection Agency method 7473 (US EPA, 2000), we determined THg concentrations in each red blood cell sample at the USGS Contaminants Ecology Lab in Corvallis, Oregon on a Milestone DMA-80 direct mercury analyzer (Milestone, Monroe, Connecticut, USA). Analytical equipment was calibrated using certified standard solutions prior to analysis, and accuracy and precision were evaluated within each analytical batch through the inclusion of certified reference materials (either dogfish muscle tissue [DORM-3] or dogfish liver [DOLT-4] by the National Research Council of Canada, Ottawa, Canada), calibration verifications (liquid standards), duplicates, and blanks. Batches consisted of 30 total samples, two of those with duplicates for a total of 32 samples per batch. The remaining 8 places in the DMA sample tray were used for quality assurance and quality control. Recoveries averaged 102.3 ± 0.07% (n = 30) and 96.4 ± 0.01% (n = 44) for certified reference materials and calibration checks, respectively. Absolute relative percent difference for all duplicates averaged 3.1% ± 0.12% (n = 27).

2.5. Statistical analyses

We used an information-theoretic approach (Burnham and Anderson, 2002) and linear mixed models in R (LME4; R Development Core Team, 2011) to determine the variables that most influenced THg concentrations in adults and chicks of both egrets and ibises. We specified the maximum likelihood estimation method in our linear models. We built and ranked separate competing candidate models for each species and life stage (adult and chick), in order to understand how their individual Hg concentrations responded to differing habitat conditions (i.e., hydrology and date within years). We also included an intercept only (null) model and global model for each species and life stage. Mercury concentrations were natural log transformed to improve normality of residuals. Where appropriate we included linear, quadratic, and cubic forms of variables (e.g., age). Mercury values are presented as red blood cell THg (µg/g dw ± standard error [SE]).

We assessed the influence of variables potentially affecting Hg concentrations in two stages; first we assessed those variables associated with just adults, and in the second stage we examined variables potentially associated with Hg concentrations in chicks. Variables were included that could result in egrets and ibises being exposed to differing levels of Hg through their foraging habitat preferences and habitat conditions (date, water recession rate, water depth; Gawlik, 2002; Beerens et al., 2011), prey selection behavior (year, sex, age of chicks; Smith, 1997; Loftus, 2000; Dorn et al., 2011), landscape factor related to the production of MeHg (days dry, region; Krabbenhoft and Fink, 2001; Axelrad et al., 2007; Gilmour et al., 2007), factors related to the dilution of Hg associated with chick growth (age; Ackerman et al., 2011), and large scale regional MeHg patterns (region; Herring et al., 2009). Prior to the model selection analyses we examined correlations between all variables to detect any autocorrelation issues. For adults there were no autocorrelation issues (all $r^2 \leq 0.30$). However, for chicks we observed a positive correlation between age and date ($r^2 = 0.40$–0.69) because nesting was moderately synchronous during our study. To determine which variable to include in our candidate models we ran a preliminary model sets for each species that included all variables but did not allow age and date to be in the same model, we compared the most parsimonious model (included date for egrets and age for ibises) with the first model where age or date was replaced by the reciprocal. For both egrets ($\Delta AIC_c = 12.76$) and ibises ($\Delta AIC_c = 18.03$), there was strong support for retaining either date or age respectively, but not both variables in their respective model sets. For subsequent egret models we included only the date variables, whereas for ibis chicks we included the age variable only. For adults we included seven model variables: year, region, water recession rate, water depth, date, days dry, and sex. In the case of chicks we included seven model variables: year, region, water recession rate, water depth, days dry, hatch order and either date (egrets) or age (ibises). We included the following random effects; colony location (colony) to account for sampling different numbers of nests within colonies, chick identification number to account for the repeated sampling of chicks, and nest identification to account for the non-independence of sampling multiple chicks within a nest.

We used Akaike's information criterion adjusted for small samples sizes (AIC_c) and considered the model with the lowest AIC_c value to be the most parsimonious (Burnham and Anderson, 2002). We determined the relative ranking of each model by subtracting each candidate model's AIC_c value from the best model (ΔAIC_c). We ran all possible models and considered candidate models with $\Delta AIC_c \leq 2.0$ to be equally plausible and models with $\Delta AIC_c > 4.0$ to have less support. We present all candidate models with $\Delta AIC_c \leq 4.0$ and the null model in tables. We calculated Akaike weights (w_i) to assess the weight of evidence for candidate models (Burnham and Anderson, 2002). We also calculated cumulative variable weights by summing Akaike weights across all models that included the variable to assess the relative importance of each variable. Where multiple forms of a variable (age) were included (linear, quadratic, and cubic) we present only the variable with the highest relative variable weight. In this case the only way for the cubic effect of age to be included is with both the linear and quadratic effects. We calculated model-averaged beta coefficient estimates from all candidate models (Burnham and Anderson, 2002) and present them with 95% confidence intervals.

3. Results

During the 2006 and 2007 pre-breeding seasons we captured and collected blood from 187 adults (68 egrets; 2006 = 22, 2007 = 46, and 119

ibises; 2006 = 54, 2007 = 65). The geometric mean red blood cell THg concentration (µg/g dw) averaged across dates, regions, sex, and years was 4.46 ± 0.40 (SE) in egret adults and 2.44 ± 0.12 in ibis adults. During the 2006 and 2007 nesting seasons we collected blood samples from 254 chicks (169 egret; 2006 = 28, 2007 = 147, and 85 ibis; 2006 = 30, 2007 = 55). The geometric mean red blood cell THg concentration (µg/g dw) averaged across age, dates, hatch order, regions, and years was 4.14 ± 0.16 in egret chicks, and 0.58 ± 0.07 in ibis chicks.

3.1. Adult mercury

3.1.1. Great egret

The most parsimonious model explaining adult egret THg contained the variables for region and recession rate with an Akaike weight (w_i) of 0.14 (Table 1). Two additional models containing region, recession rate, and water depth, and region, recession rate, and sex also had reasonable although the log-likelihood values for these competing models did not improve substantially (<2 ΔAIC_c units, Table 1). Using cumulative variable weights to assess variable importance, we found that models containing region had a high level of support with a combined AIC_c weight of 0.91, followed by moderate support for recession rate (0.76), with little evidence for effects of sex (0.31), water depth (0.30), year (0.27), date (0.26), or days dry (0.24). The model-averaged estimate for adult egret THg concentrations by region was 416% higher at WCA 3A than Lox, 61% higher at WCA 3A than WCA 2A, and 221% higher in WCA 2A than Lox (Fig. 2). Although recession rate had a moderately strong variable weight, the model averaged beta coefficient estimate

had 95% confidence intervals that overlapped zero, indicating recession rate ($\beta = 0.410 \pm 0.421$) had a smaller effect on adult egret Hg concentrations than did region ($\beta = 1.733 \pm 1.131$).

3.1.2. White ibis

The most parsimonious model explaining adult ibis Hg concentrations contained the variables for days dry, date, and water depth with an Akaike weight of 0.15 (Table 1). Two additional models containing days dry, date, water depth, and year and days dry, date, water depth, and sex also had reasonable support although the log-likelihood values for these competing models did not improve substantially (<2 ΔAIC_c units, Table 1). Using cumulative variable weights to assess variable importance, we found that models containing days dry had a high level of support with a combined AIC_c weight of 0.95, followed by date (0.73), and water depth (0.64), with little evidence for effects of year (0.40), sex (0.28), recession rate (0.26), or region (0.20). Model-averaged estimates for the effect of days dry on adult ibis Hg concentrations indicated an increase in Hg concentrations of 119% across an increasing numbers of days a site was dry prior to the proceeding rainy season (range = 4–109 days, $\beta = 0.007 \pm 0.005$; Fig. 3).

Although date and water depth had moderate variable weights, the model averaged beta coefficient estimates for these variables had 95% confidence intervals that overlapped zero indicating that both date ($\beta = -0.007 \pm 0.008$) and water depth ($\beta = 0.010 \pm 0.013$) had a much smaller effect on adult white ibis Hg concentrations than did days dry ($\beta = 0.007 \pm 0.005$).

Table 1
Ranking of candidate models describing variables influencing Hg concentrations in adult great egrets and white ibises in the Florida Everglades.[a] Models are ranked by differences in Akaike's information criterion. Only candidate models within ΔAIC_cd ≤ 4.0 and the null model are presented.

Model structure	K[b]	-2LogL	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Evidence ratio[f]
Great egrets (n = 62)						
Region + recession rate	5	119.45	130.52	0.00	0.14	1.00
Region + recession rate + water depth	6	118.32	131.84	1.32	0.07	1.94
Region + recession rate + sex	6	118.69	132.22	1.69	0.06	2.33
Region + recession rate + days dry	6	119.17	132.70	2.18	0.05	2.97
Region + recession rate + date	6	119.26	132.79	2.26	0.05	3.10
Region + recession rate + year	6	119.27	132.80	2.27	0.05	3.12
Region	4	124.61	133.31	2.79	0.04	4.03
Region + recession rate + water depth + sex	7	117.53	133.61	3.09	0.03	4.68
Region + sex	5	122.95	134.02	3.50	0.02	5.76
Region + recession rate + water depth + year	7	118.25	134.33	3.80	0.02	6.70
Region + recession rate + water depth + days dry	7	118.30	134.37	3.85	0.02	6.85
Region + recession rate + water depth + date	7	118.32	134.39	3.87	0.02	6.92
Intercept	2	135.24	139.44	9.84	0.00	136.89
White ibises (n = 105)						
Days dry + date + water depth	5	170.75	181.36	0.00	0.15	1.00
Days dry + date + water depth + year	6	169.88	182.74	1.38	0.07	1.99
Days dry + date + water depth + sex	6	170.08	182.94	1.58	0.07	2.21
Days dry + date + water depth + recession rate	6	170.70	183.56	2.20	0.05	3.01
Days dry + date + year	5	173.09	183.70	2.34	0.05	3.23
Days dry + date	4	175.37	183.77	2.42	0.04	3.35
Days dry	3	177.61	183.85	2.50	0.04	3.49
Days dry + water depth + year + region	7	169.27	184.43	3.07	0.03	4.65
Days dry + date + year + sex	7	169.49	184.65	3.29	0.03	5.18
Days dry + date + water depth + year + recession rate	7	169.86	185.01	3.66	0.02	6.23
Days dry + year	4	176.63	185.03	3.67	0.02	6.28
Days dry + water depth	4	176.81	185.21	3.85	0.02	6.87
Days dry + date + water depth + sex + recession rate	7	170.06	185.21	3.86	0.02	6.89
Days dry + date + water depth + region	7	170.20	185.36	4.00	0.02	7.39
Intercept	2	196.13	200.25	18.89	0.00	7.82E±06

[a] Adults were sampled during the pre-breeding stage across Water Conservation Areas 1–3 during 2006–2007. Variables considered included: region, date captured, number of days a site was dry the previous dry season (days dry), water depth, recession rate, year, and sex.
[b] Number of estimated parameters in the model including the intercept and variance.
[c] Second-order Akaike's information criterion (AICc).
[d] The difference in the value between AICc of the current model and the value of the most parsimonious model.
[e] Likelihood of the model given the data, relative to candidate models.
[f] The weight of the evidence that the top model is better than the selected model, given the candidate model set.
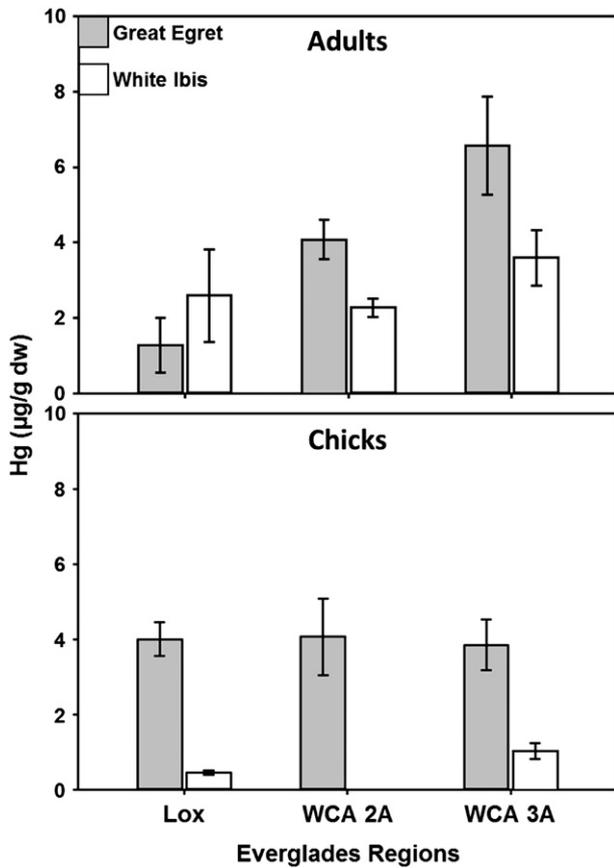
Fig. 2. Model averaged least square mean red blood cell Hg (μg/g dw) ± SE concentrations in great egret and white ibis adults and chicks in the Arthur R. Marshall Loxahatchee National Wildlife Refuge (Lox), and Water Conservations Areas 2A and 3A (WCA 2A, WCA 3A) during 2006 and 2007. No ibis chicks were sampled in WCA 2A during the study.

3.2. Chick mercury

3.2.1. Great egrets

The most parsimonious model explaining egret chick Hg concentrations contained the variables for date, days dry, and year with an Akaike weight of 0.09 (Table 1). A number of other models provided a reasonably good fit to the data although the log-likelihood values for these competing
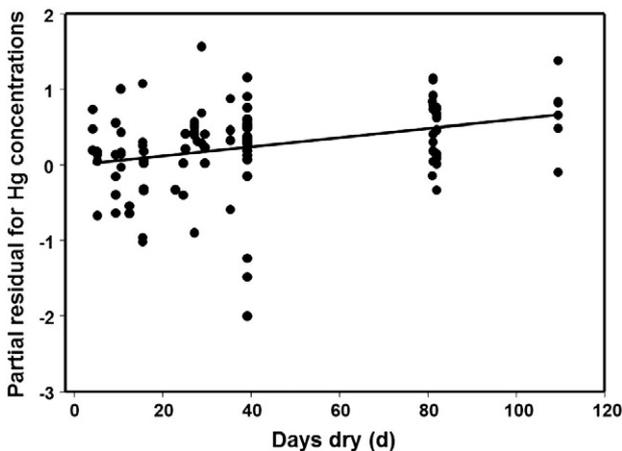
models did not improve substantially (<2 ΔAIC$_c$ units, Table 1). Using cumulative variable weights to assess variable importance, we found that models containing date had a high level of support with a combined AIC$_c$ weight of 1.0, with moderate support for days dry (0.53), and little support for year (0.43), recession rate (0.33), water depth (0.30), hatch order (0.19), or region (0.10). The model averaged beta coefficient estimate for date on egret chick Hg concentrations ($\beta = 0.026 \pm 0.005$) indicated an increase in Hg concentrations of 326% across the observed range of dates (range = April 14–June 8; Fig. 4). Although days dry had a moderate variable weight the model averaged beta coefficient estimate for this variable had 95% confidence intervals that slightly overlapped zero, indicating that days dry ($\beta = 0.003 \pm 0.005$) had much smaller effect on egret chick Hg concentrations than did date.

3.2.2. White ibises

The most parsimonious model explaining ibis chick Hg contained the variables for age, age^2, age^3, region, and recession rate with an Akaike weight of 0.36 (Table 2). One other candidate model provided a reasonably good fit to the data although the log-likelihood values for these competing models did not improve substantially (<2 ΔAIC$_c$ units, Table 2). Using cumulative variable weights to assess variable importance, we found a high degree of support for models containing age^3 (AIC$_c$ weight of 0.99), followed by region (0.91), recession rate (0.84), and little support for water depth (0.37), days dry (0.19), hatch order (0.05), or year (0.01). Model-averaged estimates for the effect of age on white ibis chick Hg concentrations indicated a two-fold decrease in Hg concentrations across the observed range of ages (range = 3–30 days, $\beta = -0.001 \pm 0.000$; Fig. 5A). Ibis chick Hg concentrations were 126% higher in WCA 3A than Lox (Fig. 2), and increased by 162% as water recession rates increased (range = −2.29–1.58 cm/d, $\beta = 0.248 \pm 0.201$; Fig. 5B).

4. Discussion

4.1. Factors influencing adult egret and ibis mercury concentrations

These results highlight the complexities of Hg cycling through food webs and the interaction between biogeochemical processes, landscape processes, and foraging responses (Fig. 6). Although there was substantial overlap in the sampling sites for each species, the factors influencing their Hg concentrations were different and depended on both foraging strategies and factors likely associated with landscape production of MeHg. In the case of egrets, region was found to be the most important variable influencing their Hg concentrations. Similar to previous studies of wading bird Hg exposure in the Everglades (see Herring et al., 2009), we found that THg concentrations were higher in WCA 3A than WCA
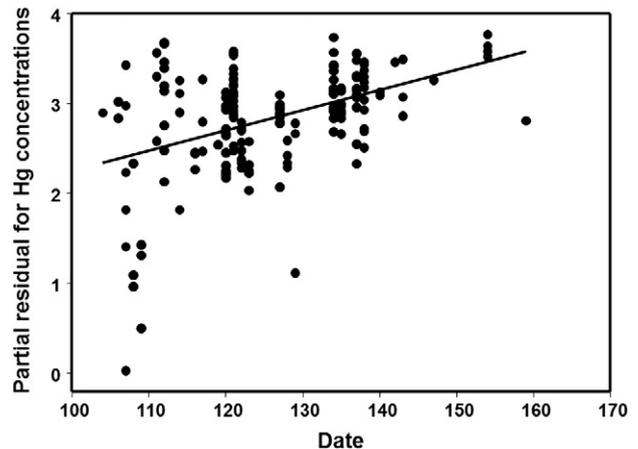

Fig. 3. Relationship between partial residuals of red blood cell Hg value (μg/g dw) and days dry (number of days a site was dry during the previous dry season) for adult white ibises in the Florida Everglades, after accounting for the other predictor variables in the best models (see Table 1). THg concentrations increased by 119% across the range of day sites were dry (cumulative parameter weight = 0.95, $\beta = 0.007 \pm 0.005$).

Fig. 4. Relationship between partial residuals of red blood cell Hg value (μg/g dw) and the date great egret chicks were sampled in the Florida Everglades, after accounting for the other predictor variables in the best models (see Table 2). THg concentrations increased by 326% across the range of dates (cumulative parameter weight = 1.0, $\beta = 0.026 \pm 0.005$).

Table 2

Ranking of candidate models describing variables influencing Hg concentrations in great egret and white ibis chicks in the Florida Everglades.[a] Models are ranked by differences in Akaike's information criterion. Only candidate models within $\Delta AIC_C d \leq 4.0$ and the null model are presented.

Model structure	K[b]	-2LogL	AIC_C[c]	ΔAIC_C[d]	w_i[e]	Evidence ratio[f]
Great egrets (n = 169)						
Date + days dry + year	7	229.01	243.71	0.00	0.09	1.00
Date	5	233.57	243.94	0.23	0.08	1.12
Date + days dry	6	231.55	244.07	0.37	0.08	1.20
Date + year	6	232.04	244.56	0.86	0.06	1.53
Date + recession rate	6	232.24	244.76	1.06	0.05	1.70
Date + days dry + year + recession rate	8	228.02	244.92	1.21	0.05	1.83
Date + days dry + water depth	7	230.41	245.11	1.40	0.05	2.02
Date + days dry + recession rate	7	230.54	245.24	1.53	0.04	2.15
Date + year + recession rate	7	230.67	245.36	1.66	0.04	2.29
Date + water depth	6	232.96	245.48	1.78	0.04	2.43
Date + days dry + year + water depth	8	228.95	245.85	2.15	0.03	2.93
Date + recession rate + water depth	7	231.57	246.27	2.56	0.03	3.60
Date + days dry + recession rate + water depth	8	229.42	246.32	2.61	0.03	3.69
Date + hatch order	7	231.75	246.45	2.74	0.02	3.94
Date + days dry + hatch order	8	229.65	246.55	2.84	0.02	4.14
Date + year + water depth	7	232.03	246.73	3.02	0.02	4.53
Date + days dry + year + hatch order	9	227.88	247.02	3.31	0.02	5.23
Date + days dry + year + recession rate + water depth	9	227.97	247.10	3.40	0.02	5.47
Date + recession rate + hatch order	8	230.40	247.30	3.60	0.02	6.03
Date + year + recession rate + water depth	8	230.65	247.55	3.85	0.01	6.84
Date + year + hatch order	8	230.80	247.70	3.99	0.01	7.36
Intercept	4	279.94	288.18	44.48	0.00	4.55E + 09
White ibises (n = 85)						
Age + age^2 + age^3 + region + recession rate	9	202.19	222.59	0.00	0.36	1.00
Age + age^2 + age^3 + region + recession rate + depth	10	200.37	223.35	0.75	0.25	1.46
Age + age^2 + age^3 + region + recession rate + days dry	10	202.10	225.07	2.48	0.10	3.45
Age + age^2 + age^3 + region	8	208.42	226.32	3.72	0.06	6.43
Intercept	4	249.96	258.46	35.87	0.00	5.85E ± 09

[a] Chicks were sampled 12 breeding colonies across Water Conservation Areas 1–3 during 2006–2007. Variables considered included: region, date sampled, number of days a site was dry the previous dry season (days dry), water depth, recession rate, year, and hatch order.

[b] Number of estimated parameters in the model including the intercept and variance.

[c] Second-order Akaike's information criterium (AICc).

[d] The difference in the value between AICc of the current model and the value of the most parsimonious model.

[e] Likelihood of the model given the data, relative to models in the candidate set.

[f] The weight of the evidence that the top model is better than the selected model, given the candidate model set.

2A or Lox in adult egrets. Egrets have the flexibility to exploit sites with deeper water (Gawlik, 2002), and a wider range of prey densities (Herring et al., 2010, Herring and Gawlik, 2012), and subsequently can spend more time in regions of the Everglades whereas ibises cannot. Thus, regional differences in adult egret THg appear to be less influenced by the specific hydrological variables we included in our models than the long-term overarching factor of region (Lox, WCA 2A, WCA 3A). Specifically, MeHg concentrations in soils and biota tend to be lower in areas of decreased wetland disturbance (e.g., Lox) and higher in more eutrophic areas of WCA 2A and WCA 3A (Axelrad et al., 2007). These results may also be exacerbated by sulfate concentrations that are higher in WCA 2A and WCA 3A than Lox (Axelrad et al., 2007), because sulfate has been shown to be a limiting factor in the cycling of mercury in the Everglades (Gilmour et al., 2004; Gilmour et al., 2007; Orem et al., 2011).

Conversely, regardless of region, THg concentrations in adult ibis increased in individuals foraging in sites with greater number of days dry, suggesting that this relationship may be driven by the complex Hg methylation process. Everglades soils that become dry for longer periods of time may have more oxidation of sulfides to sulfate. Moreover, Hg in drier soils is more likely oxidize to reactive Hg(II) forms (Krabbenhoft and Fink, 2001). Together, these processes will facilitate the production of MeHg once soils reflood during the wet season, providing anaerobic microbial communities the requisite electron acceptors and bioavailable inorganic Hg needed for elevated MeHg production (Gilmour et al., 2007; Orem et al., 2011). Aquatic prey species with limited movement during the dry season (e.g., crayfish, small fishes) would then be exposed to spikes in MeHg at these sites when they flood, resulting in very specific Hg exposure patterns in wading birds that target wetland areas with these specific hydrology conditions (i.e., short hydroperiod wetlands

that regularly dry out each year). We hypothesize that Hg continues to increase with the number of days sites are dry for some period of time (up to 110 days in our study) because when the average depth of a 400 m × 400 m EDEN cell is 0 cm, the higher elevation portions of that cell have likely been dry several weeks (oxidation of sulfides may have already begun), and the lower elevations will continue to dry out for several more weeks. Subsequently shallow landscape depressions where tactile foragers like ibis target prey species (crayfishes and small fishes), will have the longest periods of drying and potentially the highest THg concentrations.

### 4.2. Factors influencing egret and ibis chick mercury concentrations

Similar to adults, egret and ibis chicks differed considerably in the variables that influenced their Hg concentrations. Egret chick Hg blood levels were most influenced by date, whereas ibis chick Hg levels were most influenced by chick age, region, and water recession rate. The influence of date on egret Hg blood levels may be a factor of the age of chicks; as wading bird chicks get older they are often fed larger prey items (Ogden et al., 1976) that contain higher concentrations of Hg (Loftus 2000). Egret nests were highly synchronous across regions during our study; subsequently egret chick age and date were highly correlated. Date may not have been as important to ibis chick THg concentrations because ibis nesting was not as synchronous as that observed for egret chicks.

Variables that influenced ibis chick THg concentrations differed from factors that affected egret chicks. Whereas egret THg levels were only influenced by date, ibis THg levels were influenced by age, region, and water recession rates. Total Hg concentrations decreased with ibis
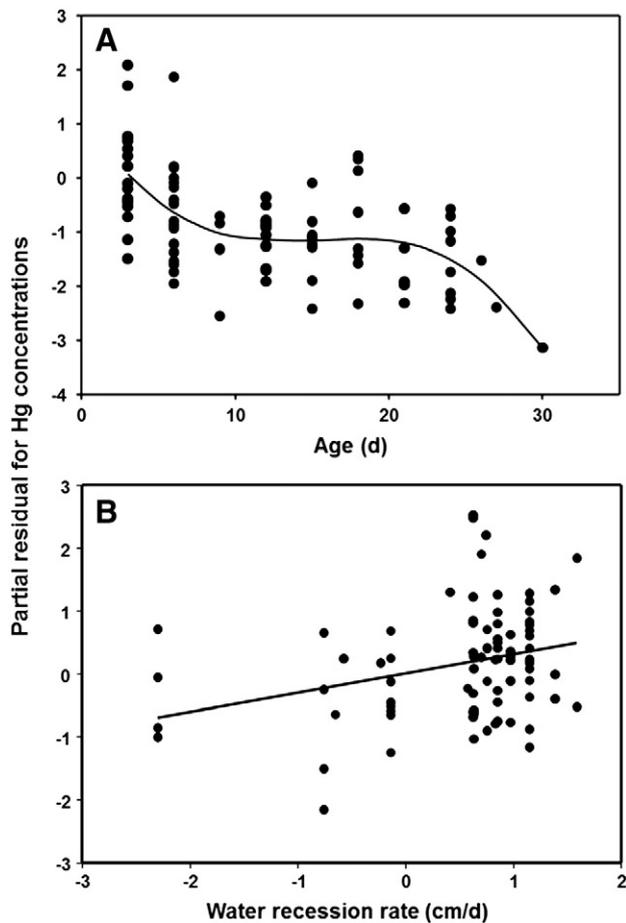
Fig. 5. Relationship between partial residuals of red blood cell Hg value (μg/g dw) and (A) age (d) of chicks at sampling and (B) water recession rate (cm/d) during the previous two weeks before sampling at adult foraging sites associated with colonies where white ibis chicks were sampled in the Florida Everglades, after accounting for the other predictor variables in the best models see Table 2). THg concentrations decreased by two-fold and increased by 162% across the range of ages and water recession rates, respectively (cumulative weights = 0.99 and 0.84, $\beta = -0.001 \pm 0.000$, $\beta = 0.248 \pm 0.201$, respectively).

chick age, suggesting that chicks likely depurated Hg into growing feathers or minimized their Hg burdens through mass dilution as they aged (Ackerman et al., 2011). Recent research on Forster's terns (*Sterna forsteri*), America avocets (*Recurvirostra americana*), and black-necked
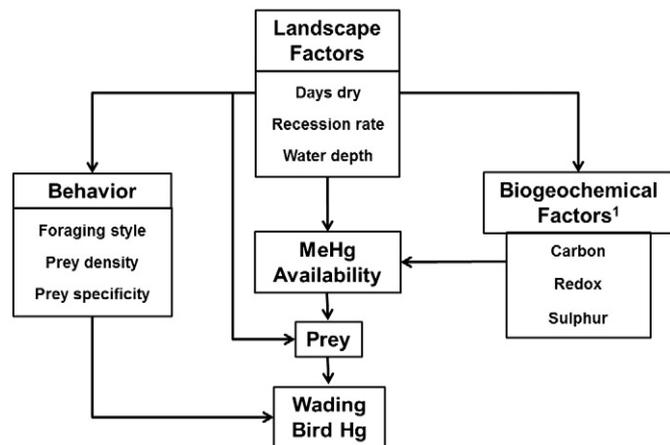
Fig. 6. Conceptual model of the relationships between representative landscape environmental factors, foraging behavior, and related biogeochemical factors that may influence MeHg exposure in wading birds. Biogeochemical factors[1] were not assessed in modeling efforts.

stilts (*Himantopus mexicanus*) demonstrated that blood Hg concentrations followed a U-shaped pattern, Hg was highest just after chicks first hatched, decreased when they began to increase in size and depurate Hg into growing feathers, and then increased as both body growth and feather growth slowed (Ackerman et al., 2011). Previous research on Hg in ibis and egret chick feathers found a positive linear pattern in Hg concentrations (increasing with culmen length; a surrogate for age) in egrets but a negative linear pattern in ibises during the same two years of study in the Everglades (Herring et al., 2009). Similar to Ackerman et al. (2011), we found that ibis chick THg concentrations were elevated at a young age and then decreased considerably as they got older (3–12 days of age), were relatively stable in medium aged chicks (13–22 days of age), and actually decreased in older chicks (23–30 days of age). These differences in age-related Hg patterns may be associated with lower overall Hg exposure levels in Everglades' ibises relative to the avocets, stilts, and terns that were exposed to considerable higher levels of Hg in the San Francisco Bay (Ackerman et al., 2011). There is some evidence that ibis chick diet changes as chicks get older (switching to a diet with more crayfish). Dorn et al. (2011) found that at least during one year of our study (2007) in the Everglades, ibis chicks ate more fish earlier in the nestling period than at later stages of nesting, when crayfish were consumed more often than in the early nestling period. Lower Hg levels in crayfish relative to fish in the Everglades (Loftus, 2000) would then result in a decrease in Hg concentrations in old chicks prior to when their diet included more fish.

Similar to adult egrets, but not adult ibises, ibis chick THg concentrations were lower in Lox colonies than in WCA 3A colonies. These results are consistent with previous findings on feather Hg concentrations in ibis chicks in the Everglades during 2006 and 2007 (Herring et al., 2009). Further, as was the case in this study, Herring et al. (2009) found no differences in feather Hg concentrations in egret chicks between northern and southern regions. During the pre-breeding stage, adult ibises move around the landscape while searching for high quality sites (Beerens, 2008) and subsequently are not tied to specific regions as strongly as after they initiate nesting. Once they initiate nesting and begin provisioning chicks, the costs of foraging may restrict their movements to the localized region (e.g., Lox, WCA 3A) among which there are preexisting differences in Hg levels (Axelrad et al., 2007). It is unclear why egret chicks did not follow this pattern but overall egret chick THg patterns were consistent with egret chick feather Hg concentrations in Everglades in the same years (Herring et al., 2009).

Ibis chick THg concentrations were also influenced by water recession rates, increasing with positive recession rates (when water levels decrease). Positive water recession rates can result in decreased water depths over time, however in our study recession rates and water depths were not strongly correlated. Thus any effect recession rate had on ibis chicks is likely independent of the effect of decreased water depths resulting in prey becoming more abundant in shallow pools of water, and foraging adults consuming and subsequently feeding chicks potentially larger prey with higher Hg burdens. Previous research has shown that both recession rates and water depths determine when and where wading birds forage, however that relationship can change depending on levels of prey availability in the landscape (Beerens et al., 2011). We suspect that the relationship between ibis chick THg concentrations and recession rates is likely being driven by species-specific foraging patterns and foraging habitat selection processes (Beerens et al., 2011).

4.3. Egret and ibis Hg toxicity

To facilitate an understanding of egret and ibis adult and chick toxicity risk, we back-calculated whole blood THg values using linear model equation functions derived from a separate study and dataset on blood fraction THg concentrations in egret and ibis chicks ($R^2 = 0.63–0.85$; Herring, unpub data). The back-calculated geometric mean whole blood THg concentration (μg/g wet weight [ww]) was 0.33 in egret adults, 0.32 in egret chicks, 0.06 in ibis adults, and 0.03 in ibis

chicks. We assessed the potential for reproductive impairment in adults using toxicity values established in a recent experimental dosing study on ibis (Frederick and Jayasena, 2010). Based on our back-calculated values, both adult egrets and ibises on average were at low to no risk of impairment. Although toxicological threshold has not been developed for chicks, blood THg concentrations in egret and ibis chicks were lower than those of egret chicks in a dosing study where no effects were observed on plasma biomarkers (Hoffman et al., 2005). Further, at least in the case of egrets, chick blood THg concentrations at these sites have declined by over 60% since the mid 1990's (Sepulveda et al., 1999), suggesting that any risk for impairment of chicks has declined significantly during the last two decades. These findings are consistent with a reduction of external loading of Hg to the Everglades, however portions of the Everglades still have elevated Hg concentrations in fish, and wading birds may still be at risk of elevated Hg exposure (Rumbold et al., 2008).

5. Conclusions

Different landscape variables influenced THg concentrations across species and life stages in our study. Further, our results suggest differences among variables that influenced adults versus chicks, although we suggest caution when interpreting these results because the spatial and temporal differences in how the data were collected. For instance data in adults and chicks were collected from two separate time periods, resulting in potential differences in the hydrology and prey resources to which they were exposed to. Regardless, these results demonstrate for the first time that the hydrological conditions over temporal scales (in both the previous year and more recent [two weeks]) can play an important role in the subsequent Hg exposure of wading birds. The mechanisms associated with these two time scales may be different and are likely driven by the complex relationship associated with foraging ecology, landscape factors, and biogeochemical processes (Fig. 6).

Sites that regularly dry out provide an opportunity for methylation and mobilization of Hg from the surrounding landscape (Krabbenhoft and Fink, 2001; Osborne et al., 2011; Orem et al., 2011). Although drying of wetland sites in the Everglades is associated with the natural annual hydrologic cycle (Obeysekera et al., 1999), the elevated atmospheric deposition of Hg onto the landscape (Osborne et al., 2011) has resulted in situations where wading birds may be continually exposed to Hg in this ecosystem dependent on the local hydrology and their foraging strategy. Further, in large portions of the Everglades, the numbers of days that sites are dry annually has increased due to the changes in hydrology associated with human alteration of the ecosystem (Davis et al., 1994; Bancroft et al., 2002; Lockwood et al., 2003). Although the exact relationship between the number of days a site was dry and the associated Hg in adult ibises is not clear, our results at least suggest that minimizing soil dry-out could aid in lowering MeHg production and wading bird Hg exposure (Krabbenhoft and Fink, 2001; Axelrad et al., 2007). Additionally, an improved understanding of how prey selection and associated Hg exposure may change with hydrologic conditions and across additional "searcher" and "exploiter" species may provide some clarity for this relationship.

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