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Diel Feeding and Movement Activity of Northern Snakehead

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Abstract.—Understanding the diel activity of a species can shed light on potential interactions with other species and inform management practices. To understand the diel activity of Northern Snakehead *Channa argus*, feeding habits and movement patterns were observed. Two hundred seventy-three Northern Snakehead were captured by boat electrofishing during May and June of 2007 and 2008. Their gut contents were extracted and preserved. The level of digestion of each prey item was estimated from fresh (1) to >50% digested (4) or empty (5). Random forest models were used to predict feeding activity based on time of day, tide level, date, water temperature, fish total length, and sex. Diel movement patterns were assessed by implanting Northern Snakehead with radio transmitters and monitoring them every 1.5 h for 24 h in both March and July 2007. Movement rates were compared between March and July and among four daily time periods. Independent variables accounted for only 6% of the variation in feeding activity; however, temporal feeding patterns

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were apparent. No fresh items were observed in guts between 12:30 and 7:30 am, and the proportion of empty stomachs increased at the end of May coinciding with the onset of spawning. Overall, fish moved greater distances during the July tracking period compared to March. Fish showed a greater propensity to move during daylight hours than at night during the March tracking period. A similar but nonsignificant ($P > 0.05$) pattern was observed in July. Movement and feeding data both indicated greater activity during daylight hours than at night, suggesting that Northern Snakehead is a diurnal species. Based on our preliminary findings, we hypothesize that a) diurnal species are more susceptible than nocturnal species to predation by Northern Snakehead and b) Northern Snakehead are more likely to compete for food with diurnal than nocturnal predators.

Introduction

Diel activity patterns of fish determine many of their interactions with other species, governing which prey they are likely to consume and which predators they are vulnerable to (Helfman et al. 1997). Feeding activity increases susceptibility to predation compared to resting periods when fish may remain hidden or unnoticed. Understanding diel activity patterns is thus beneficial in identifying potential ecological interactions, particularly for species introduced to novel ecosystems.

Northern Snakehead *Channa argus*, introduced to North America in the 21st century, are a large, piscivorous freshwater fish. Much concern has been expressed about their potential invasiveness due to their tolerance for broad environmental conditions and potential effects on local fauna (Courtenay and Williams 2004). They feed on small-bodied organisms, primarily fishes (Saylor et al. 2012) and may compete with Largemouth Bass *Micropterus salmoides*, which support important recreational fisheries (Love and Newhard 2012). Northern Snakehead maintain restricted home ranges throughout much of the year, but a portion of the population disperses great distances (up to 40 km in the Potomac River) during the prespawn season (Lapointe et al. 2013). They select shallow (<2 m) habitats with dense macrophyte coverage (Lapointe et al. 2010). Nests are constructed in macrophyte beds and guarded by both parents (Gascho Landis and Lapointe 2010). Spawning may occur multiple times per year (Gascho-Landis et al. 2011). Considerable knowledge has been gained on the ecology and behavior of introduced Northern Snakehead since the species established in North America; however, diel activity patterns are not well understood. Knowledge of diel behavior can enable inferences about the likely relationships between Northern Snakehead and other species.

Northern Snakehead congeners are widely reported to exhibit nocturnal or crepuscular behavior (Courtenay and Williams 2004) with the exception of Giant Snakehead *C. micropeltes*, which are thought to feed diurnally (Lee and Ng 1994). Chevron Snakehead *C. striata* exhibit peak oxygen consumption at dusk suggesting crepuscular activity (Natarashan et al. 1983). Dwarf Snakehead *C. gachua* and Black Snakehead *C. melasoma* are reported to feed nocturnally, and Splendid Snakehead *C. lucius* are reported as crepuscular or nocturnal predators (Lee and Ng 1994). Similarly, Northern Snakehead are reported to spawn at dawn or in the early morning and to exhibit crepuscular feeding (Courtenay and Williams 2004). Beyond general reports and observations, empirical data on diel activity patterns of this species have not been published.

The goal of this study was to identify diel feeding and movement behavior of Northern Snakehead. This research was conducted in situ on a nonnative population in the Potomac River in Maryland and Virginia, USA. Feeding activity was characterized during the prespawn season by capturing fish throughout the 24-h cycle and examining their gut contents. Movement behavior was tracked over two 24-h periods—one during the winter, and one during the spawning season using radio telemetry. We tested the hypothesis that Northern Snakehead are crepuscular as indicated by feeding and movement patterns.

Methods

Feeding

We characterized diel feeding patterns of adult Northern Snakehead captured by boat electrofishing during the prespawn season in May and early June of 2007 and 2008. Sampling was conducted periodically throughout the 24-h time period and occurred whenever possible based on weather and other field activities (i.e., radio telemetry tracking). Fishes were collected from the lower Potomac River catchment in Virginia and Maryland (Figure 1). We targeted shallow bays and creeks near Fort Belvoir, Virginia, where Northern Snakehead were most abundant (Odenkirk and Owens 2007). All fish captured were dissected, and gut contents were removed. All gut contents were fixed with 10% formalin then transferred to 70% ethanol prior to identification. We identified the level of digestion of each prey item using a modification of Nilsson and Brönmark's (2000) procedure. The resulting levels of digestion were: 1) parts of skin and fins are digested but no more than 10% of original mass has been lost; 2) opercula, eyes, and ventral part of the head are partially digested, body cavity is just opened, major parts of skin and fins are digested, and digestion of muscle tissue has begun, with no more than 25% of the original mass digested; 3) opercula, eyes, fins, and skin are totally digested, head and muscle tissue are digested, digestion of viscera has started, and 25–50% of the original mass is digested; 4) the majority of the head and viscera are totally digested (resistant parts of viscera, detached from the trunk, may still remain), body cavity is almost completely digested, thicker areas of muscle on the body trunk remain intact, and more than 50% of the original mass is digested; and 5) the gut is empty. Overall, these ordinal scores roughly reflected time elapsed since feeding (hereafter "feeding activity"). Each fish was given a score based on the freshest item in its gut (i.e., if at least one diet item in a gut was fresh, that fish was given a score of 1 based on digestion levels described above).

Feeding activity was modeled as a function of time of day, tide level, date, water temperature, fish sex, and fish total length using random forests (RF) analysis (Breiman 2001). RF is a modification of classification and regression trees where predictions are generated by creating multiple trees, each based on a bootstrapped subsample of the data and a random subset of predictor variables at each node of each tree. Digestion level score was used as the response variable as a surrogate for feeding activity with low scores representing recent feeding activity. Tide levels were determined using historical data from www.saltwatertides.com. Tide data for Gunston Cove and Mount Vernon were used, relative to the capture location of each fish. The study area included freshwater habitats below the fall line that experienced

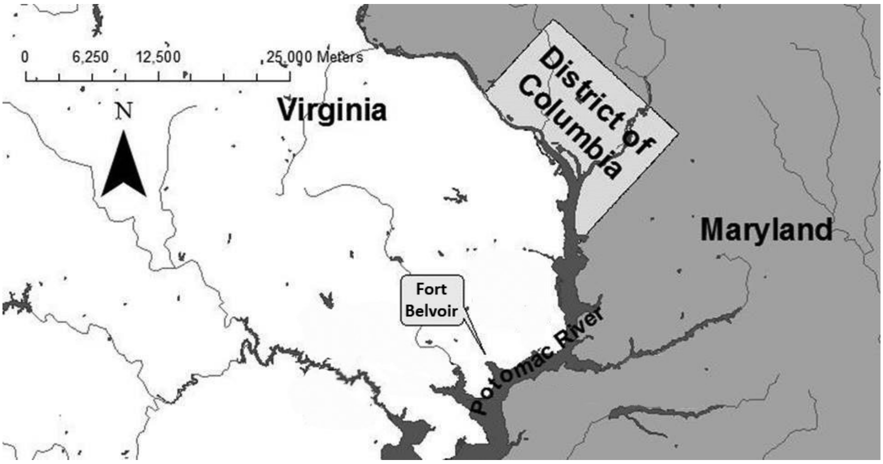

Figure 1. Map of the lower Potomac River catchment where Northern Snakehead were collected from embayments and creeks bordering Virginia and Maryland.

approximately 1-m tides. Tide level was characterized as a categorical variable with the following eight categories: high (>87.5% of tide remaining; *N* = 58 Northern Snakehead captured during this period); early outgoing (87.5–62.5% of tide remaining; *N* = 68), outgoing (62.5–37.5% remaining; *N* = 38), late outgoing (37.5–12.5% remaining; *N* = 33), out (<12.5% of tide remaining; *N* = 16), early incoming (12.5–37.5% of tide in; *N* = 15), incoming (37.5–62.5% of tide in; *N* = 14), and late incoming (62.5–87.5% of tide in; *N* = 31). Time was characterized using an ordinal value based on the hour of capture. RF analysis was implemented through the randomForest package in R (Liaw and Wiener 2002). The default setting was used for mtry, the number of predictor variables available for selection at each node (mtry = 2; the square root of the total number of predictor variables), and 1,000 trees were generated. Variable importance was estimated by the mean decrease in accuracy of the model when each variable was randomized. Partial dependence plots based on RF results were created to visually describe the relationship between the most important predictor variables and feeding activity independent of other predictor variables.

Movement

We captured 29 Northern Snakehead by boat electrofishing (438–722 mm TL, average = 594 mm, SD = 83; 790–3489 g, average = 2142 g, SD = 819) in the Dogue Creek embayment in Virginia, USA (38.697120, –77.120250) and implanted a radio transmitter in each fish. Transmitters (Advanced Telemetry Systems, Inc. Isanti, Minnesota, USA) weighed 15.5 g, had a pulse rate of 40 ppm, a pulse width of 20 ms, a warranty life of 327 d and an expected battery life of 654 d. Radio signals were transmitted at 150–151.999 MHz, and transmitters were equipped with a mortality sensor that signaled when the transmitter did not move for >8 h. Fish were anesthetized with MS-222 (200 mg/L), and radio transmitters were surgically implanted into peritoneal cavities. Incisions were sealed with single, interrupted sutures so that a whip antenna trailed from the incision's posterior edge. Northern Snakehead are obligate air breathers (Courtenay and Williams 2004), thus fish were observed for >15 min after surgery with their heads held above water to prevent drowning until fully recovered. All fish were captured, tagged and released 12–26 October 2006.

A subset of fish was tracked over a 24-h period on March 8–9, 2007 (*N* = 8) and July 15–16, 2007 (*N* = 10). We designated the March tracking dates as the winter period and the July dates as the spawning period. For both periods, fish were selected based on proximity to each other in the Dogue Creek embayment to reduce travel time. In winter, fish transmitting mortality signals at the start of the tracking period were excluded from 24-h monitoring.

Fish were located at intervals of approximately 1.5 h. During the spawning season tracking period, a thunderstorm prevented tracking at 2100 hours; thus movement was recorded over a three-hour interval. The apparent distance moved over each 1.5-h tracking interval was calculated for each individual. This is henceforth referred to as the minimum distance moved given that additional, or nonlinear movement, may have occurred (but was undetectable) during each 1.5-h interval.

The average minimum distance moved and time between subsequent locations was calculated for each fish location within each 24-h period. We examined whether this minimum distance moved differed between winter and spawning seasons for 24-h movement data. Additionally, we examined whether time between subsequent locations differed between winter and spawning seasons to control for the potential effect of time between subsequent locations on minimum distance moved. Neither minimum distance moved nor time was normally distributed after transformation ($P < 0.001$); thus, Wilcoxon Rank Sums tests were used to compare medians. Spearman's rank correlation was used to assess the relationship between minimum distance moved and time between subsequent locations.

We examined whether minimum distance moved differed among morning, afternoon, evening and night, separately for winter and spawning seasons. Each 1.5-h tracking interval was assigned to its respective 6-h daily time period. The starting times of each tracking interval differed between winter and spawning seasons based on the initial start time of each tracking period; thus, the start and end times for each time period differed slightly between seasons (Table 1). Given that thunderstorm-related outliers did not affect the significance of comparisons between seasons, these data were retained in analyses of spawning-season data. Minimum distance moved was log-transformed to improve normality; residuals were homogeneous in winter (Levene's $P = 0.860$) and nearly so during the spawning season (Levene's $P = 0.041$). One-way analysis of variance (ANOVA) tests were used to examine differences in minimum distance moved among time periods, and posthoc comparisons were tested with Tukey contrasts.

Results

Feeding

Two hundred seventy-three Northern Snakehead (average total length = 600 mm, SD = 125; average weight = 2452 g, SD = 1369) were captured, 55% of which had items in their gut, and 21% of which had fresh items in their gut (digestion level 1). At least 5 fish were captured during each 1-h period of the 24-h cycle. Northern Snakehead primarily consumed fish (97%), with Bluegill *Lepomis macrochirus* and Banded Killifish *Fundulus diaphanus* being the most common by weight and number, respectively (further details available in Saylor et al. 2012). The amount of variation in feeding activity explained by RF analysis was low (6.5%). Fish length was the most important variable in predicting feeding activity, with smaller fish (<600 mm) more likely to have fresh items in their gut compared to larger fish (Table 2; Figure 2). This was followed by date, with

Table 1. Mean minimum distances moved (with standard deviation, 'SD') between subsequent locations by time period and season (winter, spawning) for 24-hour tracking data. The number of pairs of locations (i.e., distances) is denoted by '*N*'. Different letters under "Post-hoc" indicate significant differences among time periods (tested separately for each season).

		Time Period	*N*	Average Minimum Distance (m)	SD	Post-hoc
Winter						
	Afternoon	1400–1900	24	29	35	A
	Evening	1900–0100	32	22	34	AB
	Night	0100–0700	32	11	17	B
	Morning	0700–1400	32	39	65	A
Spawn						
	Afternoon	1300–1840	30	70	124	A
	Evening	1840–0110	33	85	176	A
	Night	0110–0600	26	32	36	A
	Morning	0600–1300	38	135	208	A

Table 2. Variable importance results from random forests analysis to explain variation in feeding activity of Northern Snakehead. The % increase in mean square error is a measure of the importance of a predictor variable, calculated by randomizing each variable in turn and assessing how this affects the model.

Predictor Variable	% Increase in Mean Square Error
Fish length	19.06
Date	17.21
Hour	15.39
Tide level	11.91
Temperature	2.84
Sex	–6.60

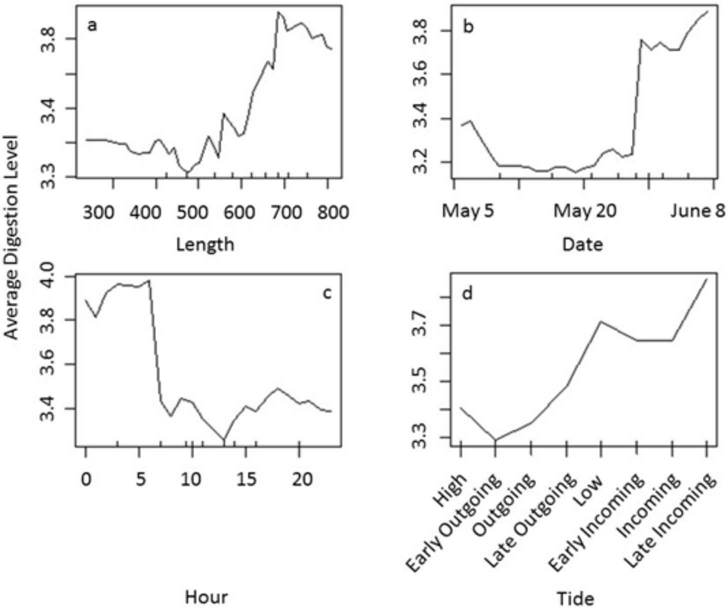

Figure 2. Partial dependence plots of important predictors from the random forests model of feeding activity based on environmental conditions and fish characteristics, including fish total length (a), date (b), hour (c), and tide level (d). Feeding activity is shown on the *y*-axis, with higher values representing highly digested items or empty guts. Deciles of distribution of the predictor variables are marked by dashes above the *x*-axes.

fish captured in early June being less likely to have fresh items in their gut compared to those in May. Time of day was also important (Figures 2 and 3). Fish did not appear to feed actively between midnight and 7:30. Fresh diet items were commonly found in fish captured between 8:00 and 16:00 with a secondary pulse occurring between 19:00 and 23:00. Tide level also influenced feeding activity with fresh diet items more frequently encountered during outgoing tides compared to incoming tides (Figures 2 and 4). Temperature and sex did not appear to affect feeding activity (Table 2).

Movement

A total of 266 fish locations was detected during the two 24-h tracking periods. In March, all fish were located during each tracking period resulting in 16 intervals with eight locations each (Figure 5a). The greatest observed distance moved was 315 m, from 7:25–9:01 (1 h, 36 min). Three fish began exhibiting mortality signals mid-way through the 24-h period and remained inactive through the remainder of the tracking event. One fish exhibited a mortality signal for at least 21.5 h but was later found alive (N. Lapointe, personal observation). In July, some fish could not be reached during low tides because of shallow waters. This resulted in a total of 14 tracking intervals with 8–10 locations each (Figure 5b). The greatest observed distance moved was 853 m, from 19:32–22:35 (3 h, 3 min).

Minimum distance moved was greater during the spawning period than in winter (spawning = 85. 6 m, winter = 24.8 m, $N = 247$, $P < 0.001$). Time between subsequent locations was also greater during the spawning season than in winter (spawning

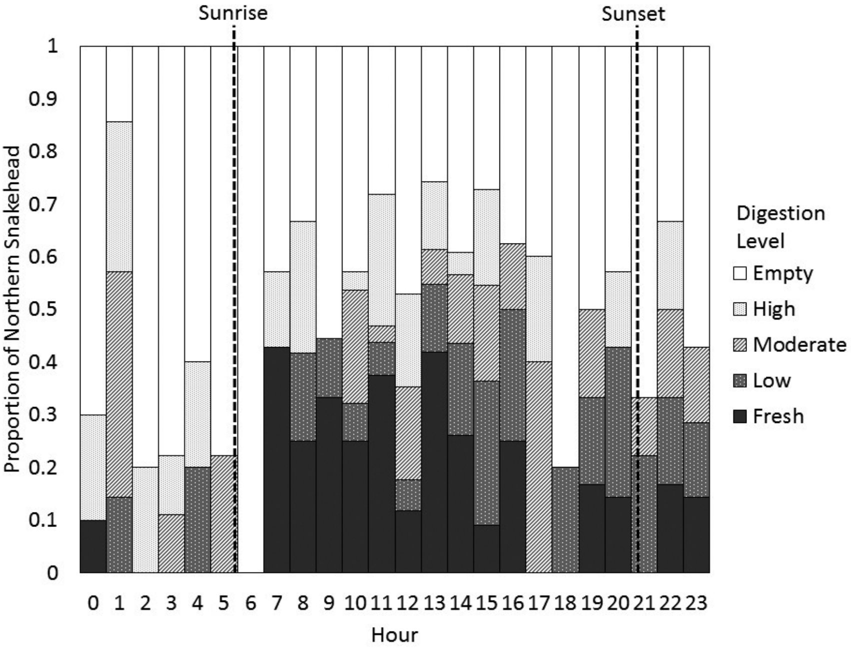

Figure 3. Diel feeding activity of Northern Snakehead captured in the Potomac River, Virginia in 2007 and 2008 (*N* = 273). Feeding activity was characterized by the freshest item among those found in the gut. The proportion of fish captured exhibiting each digestion category during each 1-hour period is shown.

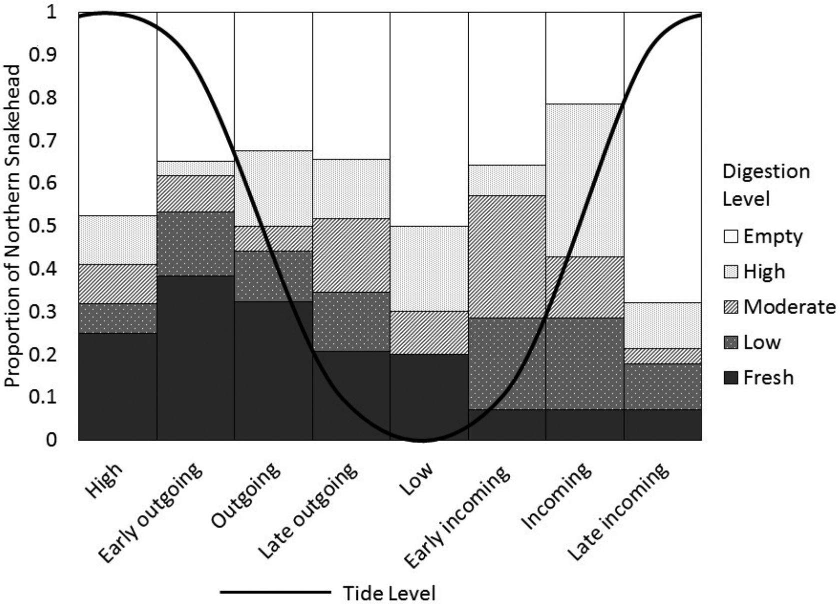

Figure 4. Feeding activity of Northern Snakehead captured in the Potomac River, Virginia in 2007 and 2008 (*N* = 273) according to tide level. Feeding activity was characterized by the freshest item among those found in the gut. The proportion of fish captured exhibiting each digestion category during each of eight tidal phases is shown.

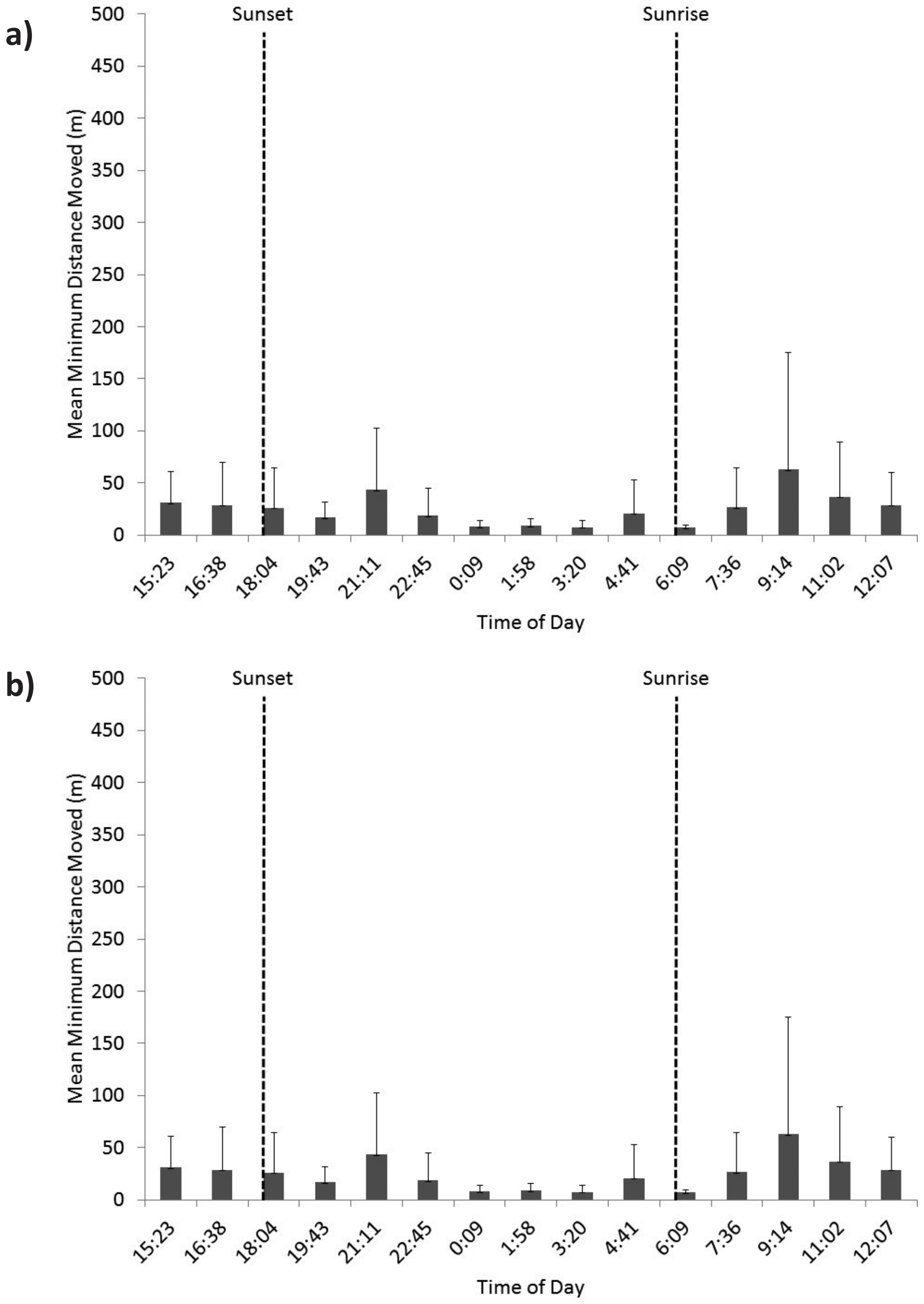

Figure 5. Mean minimum distance (+ standard deviation) moved by radio-tagged Northern Snakehead in the Potomac River, Virginia between paired tracking intervals over 24-hour periods during (a) winter (March 8–9, 2017) and (b) spawning (July 15–16, 2017) seasons. The time of day represents the start of each tracking interval. Thunderstorms increased the time between tracking intervals immediately after sunset (22:51) during the spawning season.

= 102.8 min, winter = 88.9 min, $N = 247$, $P < 0.001$). With outliers associated with the thunderstorm removed, time between subsequent locations remained higher in summer than in winter though significance decreased (Spawning = 95.6 min, Winter = 88.9 min, $N = 247$, $P = 0.002$). Most tracking intervals were approximately 1.5 h apart in each season, and time between subsequent locations was not significantly related to minimum distance moved with or without thunderstorm-related outliers ($P = 0.065$, $N = 247$; and $P = 0.243$, $N = 237$). There was a significant difference in minimum distance moved among time periods in winter ($N = 120$, DF = 3, F = 5.497, $P = 0.001$). Northern Snakehead moved greater distances in morning and afternoon compared to night (Table 2; Figure 5a); however, minimum distance moved did not differ significantly among time periods during the spawning season ($N = 120$, DF = 3, F = 1.426, $P = 0.238$). Movement rates appeared to be lowest at night and highest in the morning and evening during the spawning season; however, variance was high, and peaks in movement were often caused by one or two individuals moving a great distance rather than by increased activity for all fish (Table 1; Figure 5b).

Discussion

Northern Snakehead in the Potomac River exhibited diurnal characteristics based on feeding activity and movement behavior. This contradicts previous reports of Northern Snakehead as crepuscular or nocturnal (Guseva 1990; Courtenay and Williams 2004). Little indication was found of feeding activity at dawn, suggesting Northern Snakehead may wait for full daylight to become active; however, there was some indication of potential crepuscular activity and nocturnal activity shortly after dusk. Movement rates were nonsignificantly greater for several hours after sunset during the winter and spawning seasons (Figure 5), though this was partially explained by thunderstorm-related delays between subsequent locations at dusk during the spawning season. Fresh diet items continued to be observed in Northern Snakehead captured after dusk until approximately midnight, though not later (Figure 3). We frequently captured Northern Snakehead in shallow (<1 m) silty flats at night, and these individuals were often covered in silt indicating that they may have been resting or hiding in sediment (N. Lapointe, personal observation). We hypothesize that Northern Snakehead with empty stomachs may continue feeding after dark until they succeed in capturing prey then move to resting habitats for the remainder of the night.

Northern Snakehead appeared to differ in diel activity patterns from their congeners and other air-breathing fishes which are primarily crepuscular or nocturnal. Other (native) air-breathing fishes in the Potomac River are nocturnal (American Eel *Anguilla rostrata*; Eastern Mudminnow *Umbra pygmaea*) or nocturnal and crepuscular (Bowfin *Amia calva*; Jenkins and Burkhead 1994). Diel activity of Longnose Gar Lepisosteus osseus is unreported; however, Spotted Gar *Lepisosteus oculatus* is nocturnal (Snedden et al. 1999). Given that Northern Snakehead is an obligate air-breather (Courtenay and Williams 2004), diurnal activity would seem to increase the risk of avian predation. Predation on Northern Snakehead by wading birds such as Great Blue Heron *Ardea herodias* and birds of prey such as Osprey *Pandion haliaetus* has been observed in the Potomac River system (J. Odenkirk, Virginia Department of Game and Inland Fisheries, personal communication). We observed at least six Northern Snakehead (516–685 mm total length) with marks indicative of attempted avian predation, usually a beak-sized wound near the anterior portion of the head or in the dorsal musculature (R. Saylor, personal observation). The large average size of adult Northern Snakehead may reduce the risk of avian predation during diurnal activity. Fish eaten by Osprey in the Chesapeake Bay area weigh an average of 157 g (McLean and Byrd 1991), much smaller than the average size of Northern Snakehead in this study (>2,000 g). Future studies of Northern Snakehead might explore the adaptive tradeoffs between diurnal feeding and predation by birds as well as if diurnal feeding enhances the species' invasion potential.

Feeding

Feeding activity was highest during morning and on outgoing tides. We hypothesize that Northern Snakehead feed during all tides but are most successful at capturing prey such as Banded Killifish that inhabit Spatterdock *Nuphar lutea* beds and other intertidal freshwater habitats which contain prey only at higher tide levels. We frequently captured Northern Snakehead at the edge of such habitats (N. Lapointe, personal observation) where they may have been ambushing prey that moved with outgoing tides. Smaller Northern Snakehead were more likely to have fresh diet items than larger individuals which may be explained by ontogenetic shifts in feeding behavior. Smaller Northern Snakehead are more likely to feed on Banded Killifish and to consume multiple individuals; whereas larger individuals were more likely to prey on single individuals of larger prey species such as Yellow Perch *Perca flavescens* (Saylor et al. 2012). We also observed an increase in empty stomachs in June compared to May, which coincides with the onset of spawning. Lapointe et al. (2013) observed prespawning foray movements until June 7 2007, and Gascho-Landis et al. (2011) observed peak gonado-somatic index values on June 8 2007. The decrease in feeding activity reported here occurred approximately one week before these dates suggesting a portion of the population may have begun spawning at the end of May.

RF models explained a very small portion of the variance in feeding activity. This was likely due to the nature of the dependent and independent variables rather than a lack of strong drivers of feeding activity. By quantifying feeding activity based on the level of digestion of the freshest diet item, the early components of ongoing feeding activity were ignored. Additionally, time data and tide level were cyclic but were treated as continuous variables in our analysis. RF outputs are highly robust to nonnormal data and to combinations of continuous and categorical independent variables (Breiman 2001); however, they are not explicitly designed to handle cyclic data. To improve future analyses, validation of digestion rates are needed to back-calculate time of consumption for moderately and highly digested prey items. If available, such data would have enabled us to develop an index of feeding time that integrated ingestion times across all prey in the guts.

Movement

Movement rates were higher during the spawning season compared to winter and higher during the day than at night, though this difference was only significant during winter. The lack of significance during the spawning season may be driven by differences in spawning activity among individuals. Northern Snakehead can spawn multiple times each year and appear to spawn asynchronously based on variance in the gonado-somatic index (Gascho-Landis et al. 2011). During spawning, individuals guarding nests or young would be expected to move minimally compared to individuals foraging or searching for mates perhaps explaining the high variance in minimum distance moved (Table 1). Differences in foraging success may have also contributed to this variance given that fish with full stomachs may have moved less than those that continued to actively forage.

Conclusions

Our findings help fill important gaps in what is known about diel patterns of Northern Snakehead movement and feeding in North America. Our data indicate that Northern Snakehead are diurnal; however, these results should be interpreted as preliminary. Sample sizes in our movement study were small, and only a small amount of variation in feeding activity was explained by the variables we measured. Other unmeasured variables may influence feeding activity which may also be opportunistic and therefore stochastic. The high variance in movement rates we observed indicates that larger sample sizes (e.g., more fish) are needed to clearly characterize typical Northern Snakehead movement. We suggest measuring movement across multiple days per season and during the prespawn and postspawn seasons as well. Empirical data on temperature-, size-, and prey-species-specific digestion rates would allow back-calculation of ingestion time which could provide clearer insight into feeding activity patterns. We remain curious as to why, and in what situations, Northern Snakehead only begin to feed well after sunrise yet continue to feed after dusk.

The knowledge that Northern Snakehead feed most actively after sunrise and on outgoing tides can inform future sampling designs. Such activity may make them more susceptible to capture and demonstrates ideal conditions for capturing fish for future gut contents analysis. Diel behavior may differ during other seasons. For instance, Northern Snakehead movement rates may be higher during prespawn and postspawn periods when fish are feeding actively. It remains unknown precisely what time spawning occurs and whether parents actively guard nests and young at all hours or rest during night. Northern Snakehead may be more likely to prey on diurnal fish species such as sunfishes than on crepuscular or nocturnal prey species such as Mimic Shiner *Notropis volucellus* and Bluntnose Minnow *Pimephales notatus* (Johnson and Dropkin 1995) thereby informing risk assessments (e.g., identifying whether invading Northern Snakehead threaten at-risk species). The potential for competition between Northern Snakehead and co-occurring crepuscular and (especially) nocturnal predators appears limited.

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