THE IMPACT OF HUMAN DISTURBANCE ON THE FORAGING ECOLOGY OF GREEN HERONS *(BUTORIDES VIRESCENS)*

by

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ABSTRACT

As the trend towards urbanization continues, natural areas can become highly urbanized and recreational use of these natural areas might also increase. Waterbirds use areas that are generally subject to elevated levels of human disturbance and consequently are often considered highly susceptible to disturbance. In 2013 and 2014, I assessed the effects of human recreational disturbance on Green Herons (*Butorides virescens*) through the use of focal observations. I collected behavioral data during 154 observations along the headwaters of the San Marcos River located in Central Texas; the river varies in its degree of human recreational activity and thereby disturbance varied across sites. I built 15 linear regression models to assess the potential influence of human disturbance as well as potential influence of habitat differences between study sites on each of the response variables (4 foraging behaviors and foraging efficiency).

Using Akaike's Information Criterion (AIC) model selection, I found that differences in habitat provided the best explanation for the observed variation in 4 of the 5 response variables measured. These results suggest that Green Heron foraging behavior is not significantly affected by human recreational disturbance but influenced more by differences in habitat. It is possible that the birds have become habituated to disturbance and tolerant of humans and perhaps now only modify their foraging technique in order to maximize their foraging efficiency to suit a specific location. These findings are noteworthy because it is important to distinguish cases where human disturbance impacts a species from cases where it does not. The findings may assist in an ongoing effort to strike a balance between the needs of waterbird species for aquatic resources, and those of humans for recreational use of the same aquatic systems.

I. INTRODUCTION

The human population continues to grow, with trends towards an increasingly urbanized population. The U.S. population (currently estimated at approximately 319 million (U.S. Census Bureau 2010)) is expected to increase by up to 142 million by 2050 (U.S. Census Bureau 2008). As the trend towards urbanization continues, many natural areas near urban centers will likely become highly modified with a concomitant increase in recreational use of these natural areas. In 2012, the level of participation in outdoor recreation reached 141.9 million Americans, the highest level recorded, and in 2013 nearly 50 percent of all Americans over the age of 5 participated in outdoor recreational activities (2013 and 2014 Outdoor Recreation Participation Topline Report, Outdoor Foundation). Providing access and recreational opportunities in natural areas is a key element in educating and influencing the public to support conservation efforts for these areas. As the number of people participating in outdoor recreation rises every year, it becomes increasingly important to monitor the potential impacts human recreational activities can have on wildlife, and to be able to quantify these impacts in relation to the benefits of recreation.

Human recreational activities in aquatic systems can cause disturbances that can directly or indirectly impact avian species associated with these habitats (hereafter 'waterbirds'). Human recreational disturbance can be defined as anthropogenic activities or stimuli that directly or indirectly alter an animal's normal activity patterns, behavior and/or distribution (Fox and Madsen 1997). There are various forms of human recreation that can cause disturbances, including swimming, boating (Batten 1977), automobiles (Stolen 2003), and ecotourism (Klein et al. 1995). Since waterbirds use areas that many ecotourists and outdoor recreationists find attractive (e.g., shorelines, rivers, and lakes), they are often subject to elevated levels of human disturbance (Rodgers and Schwikert 2003). Human disturbances can influence waterbird occurrence, spatial distribution, behavior, abundance, and habitat use (Carney and Sydeman 1999; Gyimesi et al. 2012; Klein 1993; Klein et al.1995; Peters and Otis 2006; Rodgers and Smith 1995; Stolen 2003).

In many cases the impacts of human disturbance on waterbirds can be unclear and not easily observable since they might act through reduced access to resources such as feeding, nesting and breeding sites (Gill et al. 1996, Gyimesi et al. 2012). However, there are also many cases where there is a direct connection between human disturbance and negative impacts on waterbirds, include disruption during breeding season (Safina and Burger 1983), increased energetic demands (Burger 1991; Ydenberg and Dill 1986), increased vulnerability to predators (Safina and Burger 1983), as well as the reduction of nesting success, foraging efficiency, foraging rates and thus food consumption (Burger 1994; Stolen 2003). For instance, studies have shown the amount of time Piping Plovers (*Charadrius melodus*) devote to running and crouching increases and time devoted to feeding decreases as the number of people near foraging plovers increase, perhaps accounting for overall decreased reproductive success (Burger 1991; Burger 1994). Another study done by Burger and Gochfield (1998) looked at the effects of ecotourism on 5 species of waterbirds in the Florida Everglades. For all species, time devoted to feeding and number of strikes or pecks at prey decreased while people were present. Also, the percentage of time spent foraging and the number of strikes decreased as anthropogenic noise increased. By contrast, some studies found that human disturbances had no effect on birds, or that they developed a tolerance or become habituated to a source of disturbance (Lord et al. 2001; Nisbet 2000; Webb and Blumstein 2005; Weller 1999).

Waterbirds benefit from maximizing their foraging rate for a variety of reasons. Foraging success is an important factor affecting critical life history stages as well as reproductive success of waterbirds (Frederick and Spalding 1994; Powell 1983). For example, juvenile waterbirds are generally less successful at foraging than adults. Bildstein (1983) found that foraging efficiency increased with age among White Ibis (*Eudocimus albus*), and Rodgers (1983) found that adults of six species of ardeids demonstrated greater foraging success than did immature birds. To maximize foraging efficiency and compensate for lack of foraging skills, it is likely that young waterbirds require excellent foraging conditions. Additionally, energetic requirements greatly increase for adults during nesting due to physiological demands of clutch production and provisioning of nestlings (Ashkenazi and Yom-Tov 1996; Frederick and Powell 1994). Outside of the breeding season, foraging efforts of adults are focused on energy gain for migration and over-wintering. Human disturbance during these particularly stressful periods might cause changes in foraging behavior and decreased foraging efficiency, leading to detrimental effects.

The Green Heron (*Butorides virescens*) is a relatively small waterbird that forages along the banks or from the emergent vegetation in rivers, lakes and wetlands throughout much of North America. Despite its widespread distribution in the U.S., the North American Breeding Bird Survey (BBS) annual abundance indices for Green Herons in both Texas and the United States indicate that the species is in decline. The BBS Green

Heron abundance trends across all 2,262 monitored BBS routes during the most recent 10-year period available (2002 – 2012) were -1.16% per year (95% Credible Interval [-1.84, -0.48]) (Sauer et al. 2014).

As a fairly abundant species that might be in decline, the Green Heron is an ideal species with which to examine the potential effects of human recreational disturbance. Kaiser and Fritzell (1984) found that on three of four rivers surveyed, the number of Green Herons seen on the main river channel was negatively related to the number of recreationist groups. The study also found that increased human activity resulted in decreased foraging effort, and reduced length of foraging bouts. San Marcos, Texas, is the fastest growing city in the U.S. (cities over 50,000 people; U.S. Census Bureau Report, 2013). Polak (Texas State University, unpublished data) looked at the influence of human recreational activities on waterbird abundance at Spring Lake and along the San Marcos River, Texas. The study found that the highest abundance of waterbirds, including Green Herons, occurred in areas with the greatest amount of human disturbance. In the wake of increasing urbanization and recreational use in this freshwater aquatic system, it is important to examine critical factors for effective waterbird conservation and ecosystem function in this disturbance-prone habitat. The objectives of this study were to examine the foraging ecology of Green Herons in relation to the level of disturbance from human recreation, and provide insights into balancing human recreational needs and the basic requirements of the species inhabiting this ecosystem.

Study Species

The Green Heron is a small (241 g), stocky waterbird (41–46 cm long) in the family Ardeidae (Niethammer and Kaiser 1983). Male and female adults are morphologically very similar, but females tend to be smaller than males and have duller and lighter plumage. Foraging habitat includes marshes, riparian zones along streams and creeks, as well as human-made ditches, canals, lakes and ponds. Green Herons will feed any time of day or at night. Main prey items taken are fish and invertebrates; however, they will opportunistically take reptiles, amphibians and rodents (Davis and Kushlan 1994). Feeding behaviors include Standing, Walking Slowly, Walking Quickly, Baiting, Standing Fly-Catching, Head Swaying, Neck Swaying, Scanning, Feet-First Diving, Foot Stirring, Foot Raking, Diving, Jumping, Plunging, and Swimming (Kushlan 1976, Davis and Kushlan 1994).

Green Herons have been reported as solitary, colonial, and semi-colonial nesters, but most commonly they are found in loose aggregations (Kaiser and Reid 1987). The degree of colonial nesting exhibited by Green Herons might depend upon the distribution of food resources as seen in Galápagos herons (*Butorides sundevalli*), which nest solitarily, and feed in and defend the same territory (Kaiser and Reid 1987). Both adult and juvenile Green Herons disperse at the end of nesting, presumably to find more favorable foraging habitat (Kushlan 1981). For northern birds, including non-coastal populations of Green Herons in Texas, this dispersal merges with fall migration beginning in late August or early September. Migration northward to breeding grounds begins in late winter and early spring, with birds arriving in the U.S. in March and April.

II. METHODS

Study Sites

The study was conducted at three sites in San Marcos, Texas: one on the San Marcos River and two at the impounded headsprings known as Spring Lake (Fig. 1). I selected these three sites *a priori* based on variation in levels of human recreational disturbance (i.e. high, medium, and low), which result from variations in level of public access. The San Marcos River (below Spring Lake Dam) flows 6.4 km through the city of San Marcos, Texas. Since the river is a popular spot for recreational activities such as tubing, swimming, and paddling, it represented the high disturbance site. Data from flotation device ("tubes") rentals on the river reveals approximately 500-600 tubes are rented daily on weekends during Green Heron nesting season, and recreationists frequently float along and pass within a few meters of waterbirds foraging in the river (Polak, unpublished data). Spring Lake, arising from the San Marcos Springs, lies on Texas State University property where recreation is greatly restricted; in 2013, the only potential disturbance to birds on the lake came from occasional use of a wetland boardwalk. This boardwalk runs 0.16 km through an area of the lake referred to as the Basin and is used heavily by Green Herons for foraging. In 2014, an additional mode of potential human disturbance was introduced in the form of glass-bottom kayak tours. The wetland boardwalk area was selected as the medium disturbance site. An area of Spring Lake referred to as the Cove that lies towards the south side of the lake also contains foraging habitat used by the birds and does not sustain any noticeable human disturbance so this area was chosen as the low disturbance study site.

Focal Observations

I assessed the effects of human recreational disturbance on Green Herons through the use of focal observations. Observations were made from April 2013 to September 2013 and April 2014 to August 2014 at each of the three study sites. These dates were chosen to coincide with the Green Heron breeding season in central Texas.

During 20-minute observational periods, I collected behavioral data partitioned into nine discrete categories: Standing, Stalking, Walking Quickly, Walking Slowly, Peering, Alert Posture, Flight, Preening, Prey Handling. Feeding behavior terminology follows Kushlan (2011), with the exception of Stalking, which denotes locomotion of <1 step/sec (categories are capitalized in the text for clarity). I also recorded weather data; foraging efficiency (number of captures/number of total strikes); average flight distance (flights during foraging bouts); and conspecific, human, and predator interactions. I documented human activity by counting the number of people that passed the focal observation points and also noting the nature (e.g. swimmers, canoe/kayakers, etc.) of their disturbance. Observations were made at random times throughout the day to ascertain periodicity of human activity and account for differences in Green Heron foraging activity due to time of day. Observations were made only once on any individual bird at a given location and day and from a starting distance of at least 20 m (some birds would walk/fly closer to, or further from the observation point during an observation). Only actively foraging birds (as opposed to perching far away from foraging areas or only preening) were studied.

Statistical Analysis

For each 20-minute observational period, I determined the proportion of time that the bird spent in each activity. I calculated foraging efficiency (total number of captures/total number of strikes) for each observation and then arcsine transformed these data to normalize the distribution prior to analysis, although for convenience untransformed data are presented in the tables. To evaluate differences in foraging behavior between the three study sites, I used dummy variable regression analyses and Tukey's honestly significant difference (HSD) method when differences were significant. I established the cut-off for statistical significance ($\alpha = 0.022$) using false discovery rate (FDR) to correct for multiple comparisons (Benjamini and Hochberg 1995). To further assess if differences in behavior were a result of human disturbance or due to habitat differences between the three study sites, I used linear regression models. Fifteen models were built to assess the potential influence of study site variation and human disturbance (coded as yes or no) on each of the response variables. For all analyses, the response variables considered were: Standing, Stalking, Walk Slowly, Walk Quickly, and foraging efficiency. Study site and disturbance were modeled as categorical variables. I also tested a null model that assumed no effect of disturbance or study site.

The behaviors Peering and Alert Posture were not examined, as these behaviors were difficult to separate and therefore seen as too subjective. The amount of time spent flying during foraging bouts was not examined since it was confounded by territorial interactions, nor was the amount of time spent handling prey since it is a function of the type of prey caught. I used an information theoretic approach based on Akaike Information Criterion (AIC) to select the best model for each foraging behavior. I computed delta (Δ), Akaike weights (w_i), and adjusted r^2 values to determine the strength of evidence for each model. All analyses were performed in the program R (R Version 2.15.1, www.r-project.org, accessed 9 Sept 2012).

III. RESULTS

Foraging behavior was recorded for a total of 2,695 minutes during 154 observations. An incident of potential human disturbance occurred during 89% of the observations at the high disturbance site (n = 46), 50% of the observations at the medium disturbance site (n = 60) and 0% at the low disturbance site (n = 48). Green Herons spent the majority of each observation standing still (78 ± 1%, Table 1) which did not differ among sites in mean proportion of time spent ($F_{2, 151}$ = 0.903, p = 0.41, Table 2).

The dummy variable regression analyses comparing variation in foraging behavior between the three sites (low, medium, and high disturbance) yielded significant variation among the activity categories Stalking ($F_{2, 149}$ = 8.094, $p < 0.001$) and Walking Slowly ($F_{2, 151}$ = 4.938, $p < 0.01$). Green Herons spent significantly more time Stalking at the medium ($p < 0.001$) and high ($p < 0.01$) disturbance sites than at the low disturbance site, with no significant difference in Stalking between medium and high disturbance sites. Walking Slowly was significantly more frequent at the medium disturbance site than the low ($p < 0.01$), with no significant difference between high and low or high and medium disturbance sites.

Linear regression analysis with AIC model selection showed that differences in habitat provided the best explanation for the observed variation in four of the five response variables (Stalking, Walking Slowly, Walking Quickly, and foraging efficiency). Standing behavior was best suited to the disturbance model according to its Akaike weight; however, I selected the null model as the best fit for Standing since the r^2 value was so poor (r^2 = 0.019, Table 3).

IV. DISCUSSION

Kaiser and Fritzell (1984) showed that use of rivers by Green Herons was affected by recreational activities in terms of decline of use, however no data were collected on the effects of human disturbance on foraging behavior. In my study, I found very few significant differences in Green Heron foraging behaviors between the three study sites. Variation that was significant seems likely due to differences in habitat. For this study, I looked specifically at disturbance so I chose the study sites based on level of disturbance and the inclusion of appropriate foraging habitat for Green Herons. I chose the high disturbance study site located at the river because it had the greatest amount of potential human disturbance, however I recognize that there were habitat differences between this location and the other two study sites that might have confounded the results.

It is inherently difficult to study adverse effects of human disturbance on waterbirds because there are a variety of other factors that can influence behavior. A possible explanation for the detected variation in Green Heron foraging behavior is that that the birds responded to abiotic, temporal (Burger 1991) and environmental variables not directly evaluated in this study *i.e.*, light intensity, water flow, prey type and density, time of day, vegetation, etc. Green Herons might modify their foraging technique to maximize their foraging efficiency to suit their location. Studies of heron foraging success indicate that differences in vegetative density affect striking efficiency (Campos and Lekuona 2001; Kent 1987). Kent (1987) found a significant association between certain foraging behaviors and specific habitats in Snowy Egrets (*Egretta thula*) and Tricolored Herons (*Egretta tricolor*); for instance the behavior “disturb-and-chase” was associated with open water habitat for both species. Maurer and Whitmore (1981) examined the influence of habitat structure on foraging behavior of five species of passerine birds. The study found that each bird species modified their foraging behavior due to differences in vegetative structure that altered the distribution of resources.

Other factors such as competitor or intraspecific interactions, or locations of territories or nest sites in relation to foraging areas might have been confounding factors. The foraging behavior of solitary White Ibises was found to differ from that of ibises foraging in large flocks; birds in flocks spent less time vigilant and more time foraging (Petit and Bildstein 1987). During my study, there were between 1 and 9 conspecifics foraging during 78% of the observations recorded at the boardwalk site, 58% of the lake site observations, and 39% of the river site observations. Furthermore, there were 14 observed (plus numerous more incidental) instances of intraspecific interactions that caused a Green Heron to flush from a foraging bout, whereas there were 11 instances of human disturbance flushing a bird. These incidental observations show that intraspecific interactions between Green Herons might be considerably influential on foraging behavior.

A possible explanation for lack of observable effect of human disturbance on Green Heron foraging behavior in my study might be that birds habituated to the level of disturbance at each locale and became more tolerant in disturbed areas. In areas where people commonly visit or are continually present, some species of birds appear to habituate to certain types of disturbance (Lord et al. 2001; Weller 1999). Habituation and tolerance to human disturbance has frequently been reported in colonial waterbirds

(Nisbet 2000; Stolen 2003; Vos et al. 1985). Gill et al. (2001) found no evidence that human presence reduced the number of Black-tailed Godwits (*Limosa limosa*) supported in estuaries found to have some of the highest levels of recreational use in Britain. In addition, levels of human activity did not influence distribution or habitat use in their study. Webb and Blumstein (2005) found that Western Gulls (*Larus occidentalis*) on the Santa Monica Pier (a heavily visited tourist attraction in California, USA) showed a gradient of behavioral change and tolerance that reflected a gradient of human disturbance. In my study, Green Herons might have learned to tolerate human disturbance where it commonly occurs (i.e. headwaters of San Marcos River), suggesting habituation.

The risk of mortality associated with human presence is a major factor likely to influence whether or not species tolerate, or avoid, humans (Gill et al. 2001). For example, species that are hunted as game might avoid humans more than species not hunted. One reason for Green Herons' lack of detectable response to human disturbances could be because this species is not hunted anywhere within their range. The response to disturbance can be seen as a trade-off between food intake and the perceived risk of predation by human presence (Gill et al. 1996).

However, it is still possible that disturbance effects actually do occur but were obscured by other factors mentioned above. Indirect effects like reduction in access to nesting and foraging sites were not identified in this study. There were occasions when observations were not possible for days at time because Green Herons were not present at the river site. Presumably this could have been due to the number or distribution of people recreating on the river. Furthermore, under abnormal circumstances, human disturbance at these sites could present a significant conservation problem. For example, if severe environmental conditions cause birds to experience great stress (e.g. severe weather), any additional effects of human disturbance could exacerbate their situation. It should be noted, however, that the extent to which a bird is tolerant might depend on the availability of alternative resources and the physical state of the individual bird. Some birds under stress, for example, during cold weather when there is an increased risk of starvation, might be less easily disturbed by humans (Stillman and Goss-Custard 2002) as well as by predators (McGowan et al. 2002) than at other times. Nonetheless, it is important to point out that alteration of behavior is not necessarily negative if birds are still able to readily acquire adequate amounts of food.

My results demonstrate that the examined effects of human disturbance on Green Herons in San Marcos, Texas, are minimal. Waterbirds are important resources for scientific research because they can function as biological indicators that can help understand and predict human impacts on an ecosystem level (Kushlan 1993). Identifying a waterbird that is fairly tolerant to human disturbance might lessen the effects that investigator intrusions or activities might have on quality and reliability of data collected, as well as stress on the birds. Furthermore, it is important to distinguish between situations where human disturbance impacts a species and where it does not, to ensure the most appropriate and cost-effective management techniques are put in place. My results offer cautionary but encouraging results for ensuring a balance between aquatic systems supporting the life history requirements of Green Herons and providing recreational activities for human users.

The reported decline in Green Heron numbers (Sauer et al. 2014) may not be due to direct human disturbance of birds. Green Heron numbers along the San Marcos River seem not to have declined much over the last 40 years (D. G. Huffman, Texas State University, personal communication), while the local population has increased dramatically. Perhaps the loss of habitat is more highly correlated with the decline rate than is human recreational use of existing habitats.

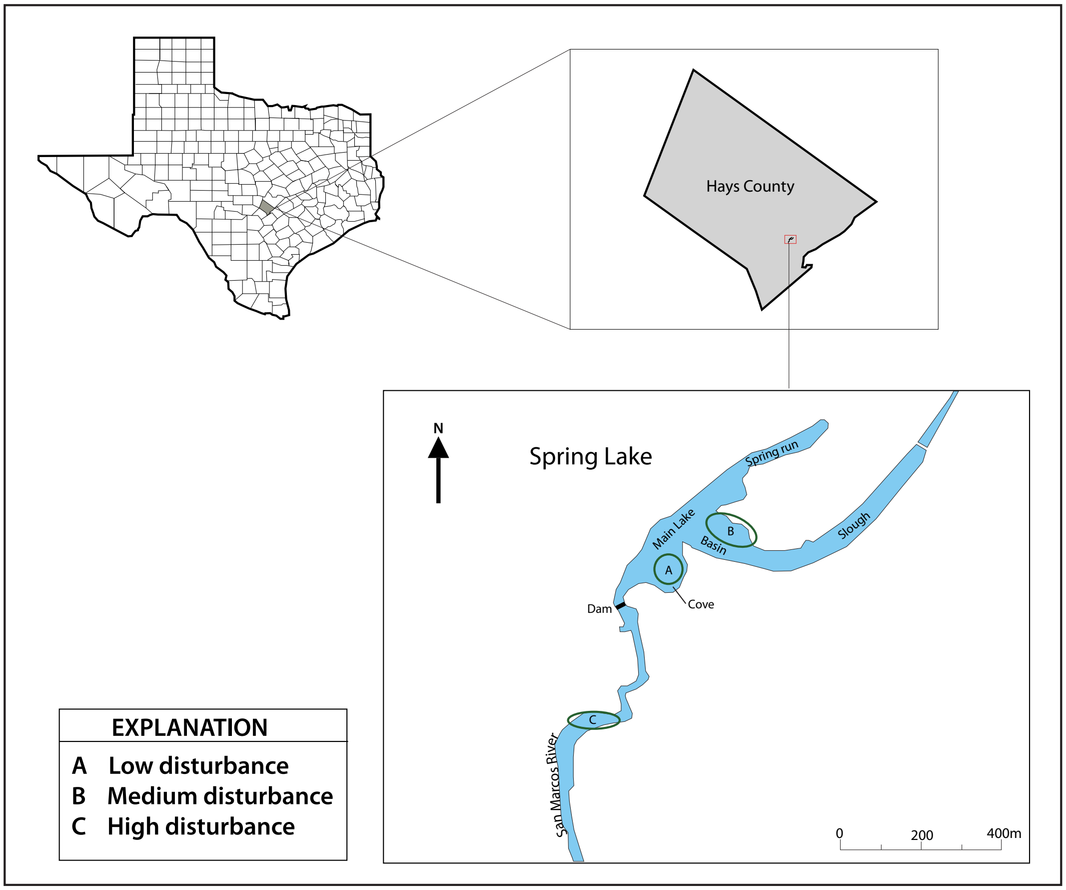

Figure 1. Location of study sites surveyed during April – September 2013 and April – August 2014 on Spring Lake and the San Marcos River in Hays County, Texas.

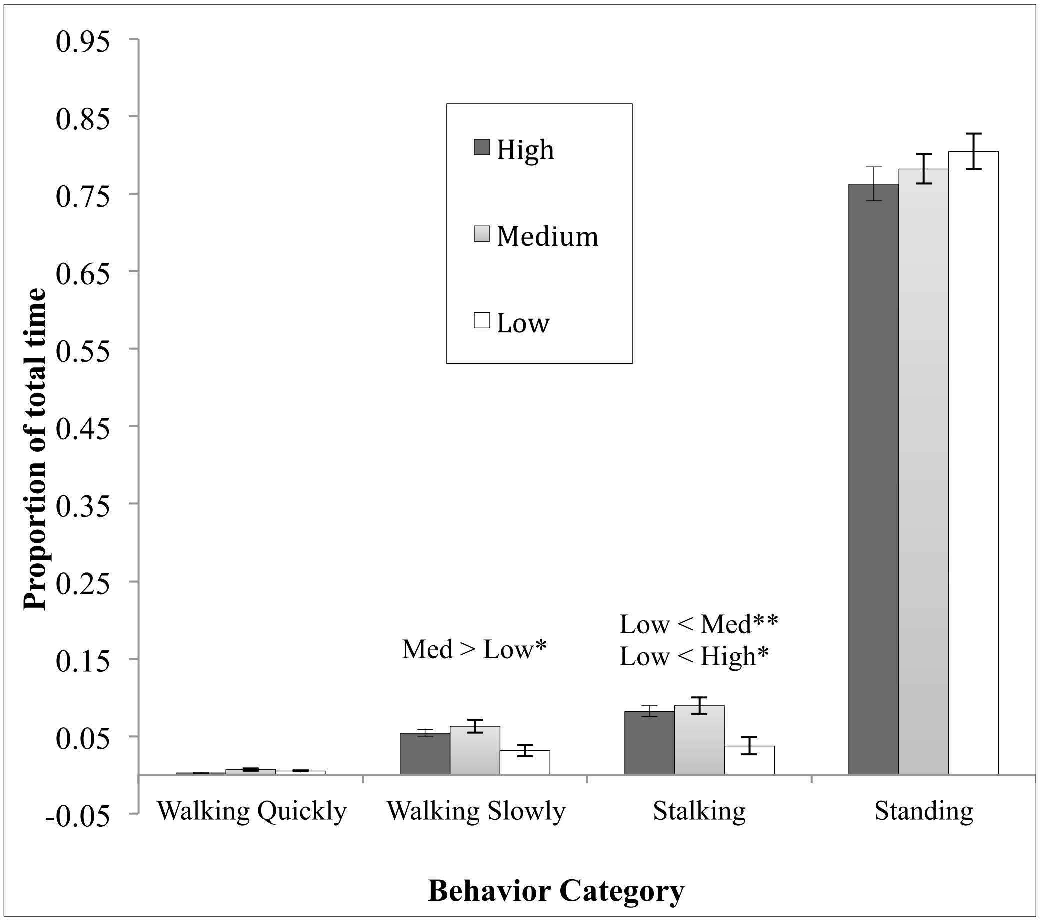

Figure 2. Mean proportion of time (±SE) Green Herons spent exhibiting specific behavior at high-, medium-, and low-disturbance study sites in San Marcos, Texas, 2013 and 2014. Significant differences between sites were determined by Tukey's HSD: * = $p < 0.01$, ** = $p < 0.001$.

Table 1. Mean proportion of time (±SE) Green Herons spent exhibiting each documented behavior and efficiency rates for all observations and at each study site, San Marcos, Texas, 2013 and 2014.

	All birds			Low disturbance site			Medium disturbance site			High disturbance site		
	n	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Standing	154	0.784	± 0.012	48	0.805	± 0.022	60	0.782	± 0.019	46	0.763	± 0.023
Stalking	152	0.071	± 0.006	48	0.038	± 0.007	58	0.089	± 0.010	46	0.082	± 0.011
Walking Slowly	154	0.050	± 0.004	48	0.031	± 0.005	60	0.063	± 0.009	46	0.054	± 0.007
Peering	154	0.041	± 0.007	48	0.056	± 0.016	60	0.032	± 0.009	46	0.038	± 0.014
Prey Handling	154	0.024	± 0.005	48	0.042	± 0.015	60	0.016	± 0.005	46	0.014	± 0.006
Preening	154	0.013	± 0.005	48	0.012	± 0.005	60	0.002	± 0.001	46	0.028	± 0.015
Flight	154	0.008	± 0.001	48	0.010	± 0.001	60	0.007	± 0.002	46	0.008	± 0.001
Walking Quickly	154	0.005	± 0.001	48	0.005	± 0.001	60	0.007	± 0.001	46	0.003	± 0.001
Alert Posture	154	0.005	± 0.002	48	0.001	± 0.000	60	0.005	± 0.002	46	0.009	± 0.006
Efficiency	138	0.756	± 0.022	40	0.841	± 0.029	54	0.699	± 0.040	42	0.762	± 0.040

Table 2. Efficiency rates and mean proportion of time (±SE) Green Herons spent exhibiting specified behavior at each study site in San Marcos, Texas, 2013 and 2014. Cut-off for statistical significance determined by FDR as a = 0.022.

	Behavior[a]									
Study Site	*n*	Walking Quickly	*n*	Walking Slowly	*n*	Stalking	*n*	Standing	*n*	Efficiency
Low	48	0.005 ± 0.001 A	48	0.031 ± 0.005 B	48	0.038 ± 0.007 D	48	0.805 ± 0.022 F	40	0.841 ± 0.029 G
Medium	60	0.007 ± 0.001 A	60	0.063 ± 0.009 C	58	0.089 ± 0.010 E	60	0.782 ± 0.019 F	56	0.692 ± 0.039 G
High	46	0.003 ± 0.001 A	46	0.054 ± 0.007 BC	46	0.082 ± 0.010 E	46	0.763 ± 0.023 F	42	0.762 ± 0.040 G
P		0.042		0.008		< 0.001		0.408		0.033

[a]Behavior at sites that share a common letter was not significantly different by Tukey's HSD test.

Table 3. Candidate models examining the relationship between habitat and disturbance on the foraging behaviors of Green Herons in San Marcos, Texas, 2013 and 2014.

Model	*K*	AIC	Δ	Log-likelihood	w_i	r^2
Standing						
null	**2**	**-142.35**	**1.95**	**0.38**	**0.25**	-
disturbance	3	-144.30	0.00	1.00	0.67	0.019
habitat	4	-140.18	4.12	0.13	0.08	0.001
Stalking						
null	2	-361.90	11.68	0.00	0.00	-
disturbance	3	-370.13	3.44	0.18	0.15	0.059
habitat	**4**	**-373.58**	**0.00**	**1.00**	**0.85**	**0.086**
Walking Slowly						
null	2	-459.28	5.76	0.06	0.04	-
disturbance	3	-462.71	2.33	0.31	0.23	0.028
habitat	**4**	**-465.04**	**0.00**	**1.00**	**0.73**	**0.049**
Walking Quickly						
null	2	-1037.30	2.49	0.29	0.21	-
disturbance	3	-1035.38	4.40	0.11	0.08	.006
habitat	**4**	**-1039.78**	**0.00**	**1.00**	**0.71**	**0.029**
Efficiency						
null	2	145.788	3.29	0.19	0.15	-
disturbance	3	147.225	4.73	0.09	0.07	0.003
habitat	**4**	**142.495**	**0.00**	**1.00**	**0.78**	**0.037**

The model selection procedure is summarized by the number of parameters estimated in the model (*K*), Akaike's Information Criterion (AIC), the difference between the AIC of a model and the model with the smallest AIC (Δ), the Akaike weight indicating relative support for the model (w_i), and r^2 values. The bold-faced values indicate the model selected for that response variable.

Table 4. Model parameter estimate, standard errors (SE), and confidence intervals of specified foraging behaviors and efficiency rates of Green Herons in San Marcos, Texas, 2013 and 2014.

	Stalking				Standing				Walking Slowly				Walking Quickly				Efficiency[a]			
Coefficient	SE	lb*	Coef. Est.	ub*	SE	lb*	Coef. Est.	ub*	SE	lb*	Coef. Est.	ub*	SE	lb*	Coef. Est.	ub*	SE	lb*	Coef. Est.	ub*
Study site model																				
River (intercept)	**0.010**	**0.062**	**0.082**	**0.102**	**0.022**	**0.719**	**0.763**	**0.807**	**0.008**	**0.039**	**0.054**	**0.069**	**0.001**	**0.000**	**0.003**	**0.005**	**0.039**	**0.684**	**0.762**	**0.840**
Boardwalk	**0.014**	**-0.073**	**-0.044**	**-0.016**	0.031	-0.020	0.042	0.103	**0.011**	**-0.044**	**-0.023**	**-0.001**	0.002	-0.001	0.003	0.006	0.056	-0.033	0.079	0.190
Lake	0.014	-0.020	0.007	0.035	0.030	-0.039	0.019	0.078	0.010	-0.012	0.009	0.029	**0.002**	**0.001**	**0.004**	**0.007**	0.052	-0.173	-0.071	0.032
Disturbance model																				
Undisturbed (intercept)	**0.008**	**0.038**	**0.053**	**0.069**	**0.016**	**0.773**	**0.806**	**0.838**	**0.006**	**0.029**	**0.041**	**0.053**	**0.001**	**0.003**	**0.005**	**0.007**	**0.031**	**0.708**	**0.769**	**0.831**
Disturbed	**0.011**	**0.014**	**0.037**	**0.060**	0.024	-0.096	-0.048	0.000	**0.009**	**0.003**	**0.020**	**0.037**	0.001	-0.002	0.000	0.003	0.044	-0.114	-0.026	0.061

Note: Estimates in boldface type represent the statistically significant covariates for each response variable.

* Coefficient estimates are given with lower (lb) and upper (ub) bounds of 95% confidence intervals. Covariates are statistically significant if confidence intervals exclude 0.

[a] Statistical analyses were performed with arcsine-transformed data, but untransformed data are presented here.

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